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A revision of the genera *Salpa* Forskål, 1775, *Pegea* Savigny, 1816, and *Ritteriella* Metcalf, 1919 (Tunicata, Thaliacea)

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ABSTRACT

Based on material from all oceans the Salp genera *Salpa*, *Pegea* and *Ritteriella* are revised. Particularly the study of the number of muscle fibres has shown that *Salpa maxima* var. *tuberculata*, the subspecies *Pegea confoederata bicaudata* and the generally synonymized species *Ritteriella retracta* are valid taxa, which are given the status of species. The existence of two groups of individuals differing biometrically within the species *Salpa aspera* and *Ritteriella retracta* is reported.

INTRODUCTION

As part of a current study of the taxonomy of the Salpidae by the present author the genera *Salpa* Forskål, 1775, *Pegea* Savigny, 1816 and *Ritteriella* Metcalf, 1919 are revised in this paper. Recently, Foxtton (1961) dealt extensively with the genus *Salpa*, although his main source of material originated from Antarctic and Subantarctic waters; the species occurring in warmer waters were treated only provisionally with the exception of *Salpa fusiformis* Cuvier, 1804. Foxtton (*l.c.*) concluded that the genus consisted of five species: *Salpa maxima* Forskål, 1775, *Salpa fusiformis* Cuvier, 1804, *Salpa aspera* Chamisso, 1819, *Salpa thompsoni* Foxtton, 1961, and *Salpa gerlachei* Foxtton, 1961. Van Soest (1973b) described a sixth species, *Salpa younti*. A seventh taxon, *Salpa maxima* var. *tuberculata* Metcalf, 1918, has received little attention and is apparently quite rare. The species are distinguished on the basis of such characters as the absence or presence of test serrations, the arrangement of the body muscles and the number of muscle fibres.

Of the genus *Pegea* two taxa are known: *Pegea confoederata* (Forskål, 1775) and *Pegea confoederata* subsp. *bicaudata* Quoy & Gaimard, 1826. The

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validity of the subspecies *bicaudata* as a taxon separate from *P. confederata* has been a subject of discussion among previous authors.

The genus *Ritteriella* has received much attention recently. Berner (1954) newly described the unknown aggregate zooid of *R. picteti* (Apstein, 1904). Meurice (1970) published a detailed account of *R. amboinensis* (Apstein, 1904). Kashkina (1973) provided new information of both species. Next to these a third species was described by Ritter (1906): *Ritteriella retracta*, which is, however, generally considered synonymous with *R. picteti*. The species are reported to differ in the shape of the alimentary canal, the number of body muscles (a variable character in this genus), the number of muscle fibres of the aggregate zooid and the arrangement of the oral musculature.

MATERIAL

The studied material is listed below. It consists of samples collected by various oceanic expeditions and a number of incidental samples. Of the major expeditions (Dana Expeditions, Discovery Expeditions, Siboga Expedition, Galathea Expedition), only the station numbers are given; for detailed information of the stations one is referred to the station lists. The Ocean Acre material all originated from the immediate vicinity of Bermuda. The United States Mediterranean Cruises were all held in the vicinity of two geographic positions in the Mediterranean, viz. 37°N, 01°E and 40°N, 12°E. In addition, a chart showing the localities of the studied samples is given in fig. 1.

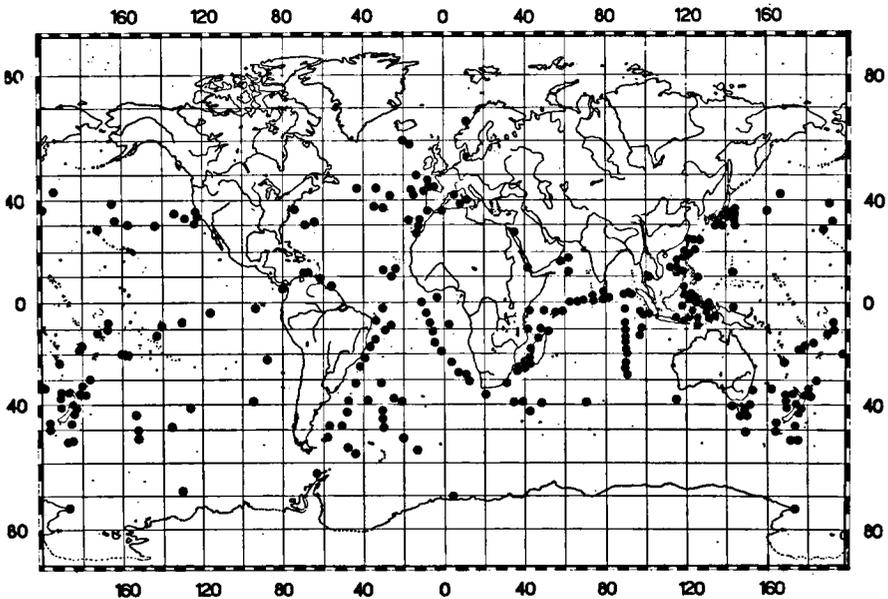


FIG. 1. Chart showing the localities of the studied samples.

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Atlantic Ocean (including the Mediterranean):

Dana Expeditions: Station 3978 IV, VII, VIII, IX, X; 3979 III, IV, V; 3980 IV, V; 3981 IV, V; 3996 V, VIII; 3997 III; 3998 IV, V, X, XI; 3999 I, II, III; 4000 IX, XI; 4010 IV; 4018 III; 4160 VIII+XII; 4201 XIX; 4762; Galathea Exp. st. 26; Naples, coll. Traustedt, 1888 (all ZMUC).

Ocean Acre Project st. 6—10C+D, 6—16A, 6—16D, 6—17C+D, 6—23, 10—5M, 10—8A, 10—10M, 10—11B, 10—17A, 10—17B, 10—23B, 10—23C, 10—38N, 11—1B, 11—1M, 11—2B, 11—2M 11—3A, 11—3C, 11—3M, 11—4C, 11—5M, 11—7A, 11—8C, 11—8M, 11—9M, 11—12B, 11—12M, 11—13A, 11—13B, 11—13C, 11—13M, 11—31B, 12—1A, 12—1B, 12—1C, 12—1M, 12—8B, 12—8M, 12—13B, 12—14M, 12—21M, 12—23M, 12—28C, 12—28M, 12—31M, 12—34C, 12—35M, 13—1C, 13—2M, 13—4M, 13—5M, 13—6M, 13—10C, 13—10M, 13—13M, 13—15B, 13—15C, 13—16M, 13—17M, 13—21M, 13—22C, 13—24M, 13—25M, 13—28B, 13—28C, 13—28M, 13—29C, 13—29M, 13—30C, 13—32B, 13—32C, 13—32M, 13—33M, 13—34M, 13—35C, 13—36M, 14—3B, 14—3P, 14—8M, 14—10C, 14—17M, 14—21A, 14—28C; US/SI-Med. Project st. 1—1M, 1—8M, 1—9C, 1—10M (USNM/ZMA); Walther Herwig Cruise 1970, st. 380—I (39°S, 21°W), 478 (01°04'N, 18°22'W), 482—III (04°38'N, 19°41'W); Albatross Exp., st. 2248 (South of Nantucket) (all USNM).

Discovery Expeditions st. 668, 669, 671, 677, 687, 691, 699, 701, 702, 706, 707, 709, 710, 711, 713, 715, 716, 717, 718, 2850, 2851, 2861, 2869 (all IOS). Cirrus/Cumulus Expedition st. K (45°N, 16°W, several samples), st. I (59°N, 19—20°W, several samples); Snellius Exp. st. Navado III (43°N, 25°W), st. Mike 4 (45°N, 43°W), st. India 1 (33°53'N, 12°55'W), st. India 2 (33°52'N, 19°20'W); Tridens Exp. st. 2 (47°31'N, 06°59'W), st. 4 (43°30'N, 09°44'W), st. 5 (42°23'N, 12°38'W), st. 7 (39°15'N, 21°25'W), st. 9 (39°40'N, 23°00'W), st. 12 (49°00'N, 11°27'W); Chazalie Exp. st. (37°48'N, 33°47'W),

(30°N, 70°W), (37°N, 36°W); CICAR Exp. cruise 12B/13/14/15 (12°N, 68°W), cruise 16/17 (6°N, 53°W); Curaçao, coll. P. J. Roos, 1961; Villefranche-sur-Mer, coll. Ihle, 1922, 1928; Villefranche-sur-Mer, coll. Stock & Kruseman, 1961; 42°N, 30°W, (no further data); Valdivia Exp. st. 50 (01°N, 06°W) (all ZMA).

Challenger Expedition st. 332 (37°29'S, 27°31'W); (36°N, 07°W), coll. Murray, ss "Dacia"; W-side of Pico (Açores), coll. Wolfenden; Bødø, Norway, coll. HMS "Vidal"; Falkland Isl., coll. W. Wright; Bay of Biscay, coll. HMS "Research" (all BMNH).

Indian Ocean (including the Red Sea):

Dana Expeditions st. 3815 III; 3843 I, II; 3847 III; 3856 IV; 3893 IX; 3903 III; 3904 II; 3907 III; 3912 III; 3914 III; 3915 I; 3917 VI, X; 3918 V; 3919 II; 3921 VII; 3922 V; 3932 II; 3934 II+VII+IX; 3935 II, V; 3946 I; 3948 II, III; 3950 III; 3955 IV; 3957 II; 3958 II; 3961 I; 3962 II, III, IV; 3964 II; 3969 IV; 3972 I; 4763; 4764; Galathea Exp., st. 237, 263, 266. (all ZMUC).
Discovery Expeditions st. 1611, 1612, 2684, 2689, 2690, 2691, 2887, 2889, 2890, 2891, 2892, 2893, 4030. (all IOS).

Kamaran (Red Sea), coll. J. H. Ziesel, 1937 (RMNHL).

Valdivia Exp. st. 215 (07°N, 85°E) (ZMA).

Sherm-al-Sheik (Gulf of Aqaba), coll. Manihine Exp.; John Murray Exp., st. 46 (18°34'N, 38°14'E), st. 95 (12°08'N, 63°04'E) (all BMNH).

Pacific Ocean (including the Indo-Malayan Archipelago):

Dana Expeditions st. 3550 V; 3553 I, II; 3561 I, II, IX, X; 3563 II, III, V; 3567 II; 3569 III; 3578 V; 3579 III, IV; 3584 VI, VII; 3585 VII, VIII; 3587 XI, XII; 3591 IV; 3593 X; 3598 X; 3601 V; 3620 II; 3627 IV, VI, X; 3629 I; 3630 III; 3640 VI, VIII; 3642 II; 3650 I; 3651 III; 3654 IV; 3658 II; 3676 II, IV; 3686 III; 3714 IV; 3716 I; 3720 I; 3722 III, IV; 3723 V; 3729 IV; 3731 V; 4760; 4761; 4765; 4768; 4771; 4772; 4773; 4775; 4776; 4777; 4778; 4779; 4783; 4789; 4790; 4791; 4793; 4797; 4798; 4802; 4806; 4808; 4809; 4812; 4813; 4815; 4818; 4820; Galathea Exp. st. 402, 412, 451, 552, 626, 641, 658, 669, 702, 727, 728; Step I Exp. (coll. J. Nielsen), st. 61 (23°41'S, 86°09'W), st. 80 (01°59'S, 94°55'W) (all ZMUC).

Discovery Expeditions st. 878, 896, 922, 923, 964, 968, 1257, 1295, 2736, 2738, 2739 (all IOS).

USARP-Eltanin Cruise 28, 36 (43°S, 148—150°E), 27 (51°S, 150°E), 38 (40°S, 152°E), 51 (54°S, 173°E) (all USNM).

Rede van Pamaroekan, coll. Buitendijk (RMNHL).

Siboga Expedition, st. 29, 96, 109, 110, 118, 128, 136, 143, 144, 146, 148, 152, 177, 189a, 201, 210a, 220, 225, 259, 262, 280; Albatross Exp., st. 5200 (Pamilcan Isl., W. Bohol, Philippines); Celebes Bay, N. coast of Flores, coll. Van der Sande (all ZMA).

Challenger Exp. st. 256 (30°N, 156°W), st. 295 (38°07'S, 94°04'W), st. North of New Guinea; MLR-Cruise st. 9790-5805 (coll. Berner); Misaki, Japan (coll. Insole, Owston); Cape Adare (Antarctica), coll. Borchgrevink Exp. (all BMNH).

Genus *Salpa* Forskål, 1775

Type species: *Salpa maxima* Forskål, 1775 (cf. Waal, 1966: 232).

Nomenclatorial note: The name *Salpa* Forskål, 1775 is a junior homonym of *Salpa* Edwards, 1771, as was pointed out by Waal (1966). This monotypical genus is currently considered synonymous with *Lutianus synagris* (Linnaeus, 1758) (Pisces). Therefore, Waal (*l.c.*) proposed to the International Commission on Zoological Nomenclature to suppress *Salpa* Edwards, 1771, in favour of *Salpa* Forskål, 1775, in order to conserve this well known Tunicate name, which is accepted by all recent specialists without reservation. It is assumed here that the Commission will eventually decide in favour of this proposal.

Diagnosis:

Solitary zooids: Animal cylindrical with the oral and atrial aperture both terminal. Test thick, firm, with blunt or sharp longitudinal test ridges. The surface of the test ridges may be smooth or echinated in various degrees. No protuberances, although in some species the test ridges may end sharply posteriorly giving the impression of short posterior projections. In one species the test bears some echinated cushions posteriorly. Body elongately cylindrical. Generally there are no projections. Nine body muscles (MI - M IX), of which the anterior two or three and the posterior two may or may not approach, touch or fuse in the mid dorsal region. M IV - M VII are always parallel. The body muscles only cover the dorsal and lateral parts of the body; the entire ventral side bears no muscles. The oral musculature consists of three dorsal and three ventral sphincters, a pair of oral retractors and the intermediate muscle. There may be slight differences in the arrangement of these muscles in the different species. The atrial musculature consists of a large but varying number of atrial sphincters and a pair of atrial retractors. The shape of the dorsal tubercle varies in the different species from a shallow C-shape to an elaborate L- or G-shape. Internal organs: intestine coiled into a tight round ball ("nucleus") lying posteriorly in front of the atrial aperture. In some species the nucleus causes a distinct ventral swelling of the test. Endostyl extending far anteriorly up to the oral musculature. The trabeculae of the gill bar may be slightly different in the different species (cf. Yount, 1954: fig. 16). Stolon: in young specimens simply coiled around the nucleus, in mature specimens showing a large forward loop (cf. Foxton, 1966: text fig. 14).

Aggregate zooids: Animal generally fusiform with a distinct anterior and posterior projection of considerable size, which tapers into a narrow point and contributes strongly to the fusiform appearance. Test thick, firm, with blunt or sharp ridges. The surface of the test may be smooth or echinated in various degrees. In one species the test bears some echinated cushions posteriorly. Body fusiform, extending into the anterior and posterior projection. Oral and atrial aperture dorsoterminal. The body is asymmetrical in that

the atrial aperture lies to the left or the right of the mid dorsal line in specimens originating from the right or the left side of the stolon. This asymmetry is also found in the position of the posterior projection, only it lies to the right side of the middorsal line in specimens with the atrial aperture on the right side. Six body muscles (M I - M VI) of which M I - M IV and M V - M VI fuse or touch in the mid dorsal region.

M IV and M V approach or fuse laterally. Oral musculature consists of three dorsal and three ventral sphincters, an intermediate muscle and a pair of oral retractors. There may be slight differences in the arrangement of these muscles in the different species. The atrial musculature consists of a high number (up to nine) of atrial sphincters and a pair of atrial retractors; a branch of M VI surrounds the atrial aperture. The shape of the dorsal tubercle differs in the different species from a simple small stick to a large C- or L-shape. Intestine coiled into a tight nucleus, which lies ventral to the atrial aperture. In some species the nucleus causes a distinct swelling of the test. The endostyl extends forward to the base of the anterior projection. Testis included in the nucleus. Ovary and embryo between M V and M VI on the right side.

Seven taxa are recognized:

***Salpa maxima* Forskål, 1775**

Synonymy:

Salpa maxima Forskål, 1775: 112, pl. 35 figs. A, A-1, pl. 36 fig. H; Bruguière, 1789: pl. 74 fig. 2 (after Traustedt, 1885); Gmelin in Linnaeus, 1791: 3129; Bosc, 1802: 178 (after Traustedt, 1885); Lamarck, 1816: 116; de Blainville, 1827: 117; Cuvier, 1828: 120, text-fig. 1, pl. 122 (after Traustedt, 1885); Quoy & Gaimard, 1833: pl. 73 fig. 3, 1834: 503; Costa, 1839: 195, pls. 1—2; Apstein, 1894: 15; Apstein, 1906a: 249; Apstein, 1906b: 164, figs. 11—12; Streiff, 1908: 21, figs. 11—14; Sigl, 1913: 234; Metcalf, 1918: 83, figs. 64—71; Stiasny, 1919: 8 (in part), fig. 1; Sewell, 1926: 83; Stiasny, 1927: 419, pl. 21 figs. 12—17, text-fig. C; Apstein, 1929: 8, figs. 9—10; Belloc, 1938: 319, figs. 7—8; Krüger, 1939: 132, fig. 77; Thompson, 1948: 154, pl. 68 figs. 1—2, pl. 69 figs. 1—6; Yount, 1954: 300 (in part), fig. 14a; Van Zijl, 1959: 15; Godeaux, 1962: 23; Godeaux & Goffinet, 1968: 70; Godeaux, 1969: 73; Meurice, 1970: 202, figs. 7—9; Kashkina, 1973: 197 (in part); Braconnot, 1973: 14, pl. 8 fig. c; Kashkina, 1974: 189 (Non: Meyen, 1832: 412 (= *S. fusiformis*); nec: Yount, 1954: 300 (in part), figs. 13a-m, 14b-e (= *S. younti* + *S. aspera*)).

Salpa africana Forskål, 1775: 116, pl. 36 fig. C; Bruguière, 1789: pl. 75 fig. 7 (after Traustedt, 1885); Bosc, 1802: 180 (after Traustedt, 1885); Lamarck, 1816: 117; Costa, 1839: 226.

Salpa birostrata de Blainville, 1827: 119.

Salpa forskalii Lesson, 1830: 272.

Salpa africana-maxima Krohn, 1846: 112; Vogt, 1854: 6; Traustedt, 1885: 374, pl. 2 figs. 32—34, 44—45; Herdman, 1888: 83; Traustedt, 1893: 6.

Type locality: Off the Tunisian coast.

Diagnosis (Fig. 14a):

Solitary zooids: Test entirely smooth with shallow longitudinal depressions; not very transparent because of its extreme thickness. Length:

up to 117 mm (n=38); according to Traustedt (1885) it may reach 137 mm. All nine body muscles run parallel across the dorsal side. In accordance with Foxton (1961) only the number of muscle fibres of M IV was counted. The range in 38 investigated specimens is 42—80, $m = 55.5$. There is some evidence that this number is subjected to clinal variation as described for *Salpa fusiformis* (cf. van Soest, 1972). The range and mean of this number in tropical waters (roughly between 30°N and 30°S) is 42—64 ($m = 50.8$, $n = 28$), in cold water specimens 64—80 ($m = 74.6$, $n = 7$). Dorsal tubercle: an elaborate and large G. Nucleus big, causing a distinct swelling of the test on the ventral side. A rudimentary elaioblast is visible in the largest specimens. **Aggregate zooids:** Animal cylindrical/fusiform with a relatively short anterior and posterior projection, both strongly abaxial. Length (excluding projections): up to 91 mm (n=36); according to Traustedt (1885) it may reach 150 mm. Test entirely smooth, bulging over the nucleus; it is not very transparent in big specimens. Body muscles M I - M II and M III - M IV are fused dorsally; M II and M III touch in the mid dorsal line. M IV and M V are widely separated laterally. M V and M VI approach or touch in the mid dorsal line. Muscle fibre number of M I to M VI is 100—205 ($m = 138.3$, $n = 53$). Divided into tropical and cold water specimens these data are: 100—137 ($m = 118.8$, $n = 31$) and 139—205 ($m = 165.9$, $n = 22$). According to Yount (1954: 304, fig. 15) the oral musculature of *S. maxima* differs slightly from that of *S. fusiformis*. A few specimens investigated during the present study seem to confirm this. The oral musculature of *S. maxima*, *S. aspera* and *S. younti* have been found to be identical; *S. fusiformis* shows a slight difference in the arrangement of the ventral sphincters. However, prior to attaching any taxonomic significance to this, an intensive study of the variation of the oral and atrial musculature of the Salpidae should be made. Dorsal tubercle: a deeply concave C-shape. Nucleus big, causing a distinct swelling of the test.

Distribution (fig. 2):

Salpa maxima seems to be a moderately abundant species distributed over all three oceans from 50°N to 45°S. Particularly in the Mediterranean and the North Atlantic it is not uncommon.

***Salpa tuberculata* Metcalf, 1918, nov. comb.**

Synonymy:

Salpa maxima var. *tuberculata* Metcalf, 1918: 87, fig. 72; Stiasny, 1919: 8 (in part), fig. 2; Stiasny, 1927: 422, pl. 21 fig. 18; Sewell, 1953: 8 (in part), fig. 1; Van Name, 1952: 219; Kashkina, 1973: 197.

Type locality: Pamilacan Island, vicinity Western Bohol, Philippine Islands.

Note: It is proposed here to treat this variety of *Salpa maxima* as a separate species, analogous to similar proposals made in the case of comparable forms,

varieties and subspecies in other salp genera (cf. van Soest, 1973a, 1973b, 1974). *Salpa maxima* and *Salpa tuberculata* are apparently sympatric, so the mechanism which would maintain the differences, if they were conspecific, must be of an as yet unknown nature.

Diagnosis: (fig. 14b)

Solitary zooids: The only solitary zooids of this form ever described are those of Van Name (Manihine Expedition). The present author has had the opportunity to re-examine these specimens in the British Museum (Natural History). The solitary zooid is in all but a few details similar to that of *S. maxima*. The most striking difference is the presence of four echinated oval cushions surrounding the atrial aperture of the test. The number of muscle fibres seems to be slightly less than in *S. maxima*: the four investigated specimens showed a range of 38—50 fibres in M IV ($m=41.8$).

Aggregate zooids: Animal more fusiform than *S. maxima* greg. because of the more pronounced and distinctly longer anterior and posterior projections. The test bears two echinated cushions of unequal size on the dorsal side, just anterior to the nucleus. The arrangement of the body muscles is exactly like that in *S. maxima*. The number of muscle fibres of M I to M VI is 82—102 ($m=89.2$, $n=13$), which is clearly lower than the number in *S. maxima* greg.

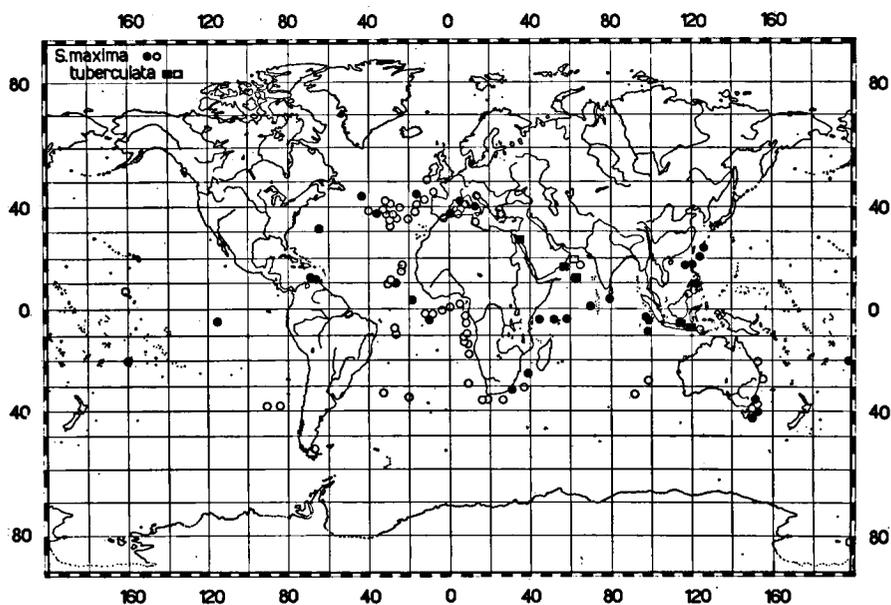


FIG. 2. Distribution of *Salpa maxima* (black dots and open circles) and *S. tuberculata* (black and open rectangles). Black symbols represent studied material, open symbols represent literature data.

Distribution (fig. 2)

The species has been reported from the Gulf of Aqaba (Van Name, 1952), the south coast of Arabia (Sewell, 1953), the Gulf of Bengal (Kashkina, 1973), the Philippine Islands (Metcalf, 1918) and from the Java Sea (Stiasny, 1919). Three aggregate specimens collected by van der Sande in the Celebes Bay on the north coast of Flores (Indonesian Archipelago) comprise a new record for this species. Although most records are from near-shore localities, some are definitely not, so the possibility that *S. tuberculata* is merely a neritic form (ecophenotype) of *S. maxima* seems small.

Salpa aspera Chamisso, 1819

Synonymy:

- Salpa aspera* Chamisso, 1819 (after Foxton, 1961); Foxton, 1961: 10, pl. 1 figs. A-C; Kashkina, 1973: 197; Kashkina, 1974: 187.
Salpa echinata Herdman, 1888: 66, pl. 5 figs. 1—4.
Salpa fusiformis var. *echinata*; Apstein, 1894: 14 (in part).
Salpa fusiformis-runcinata forma *echinata*; Ritter, 1905: 67, figs. 14—15; Ritter & Byxbee, 1905: 199.
Salpa fusiformis-runcinata; Ritter & Byxbee, 1905: 197.
Salpa fusiformis forma *echinata*; Apstein, 1906a: 250 (in part), fig. 4; Apstein, 1906b: 165 (in part), fig. 15; Ihle, 1910: 31 (in part).
Salpa fusiformis forma *aspera*; Ihle, 1911: 587; Metcalf, 1918: 92, fig. 81.
Salpa fusiformis; Yount, 1954: 297 (in part) figs. 11a-e, 12b, d-e.
Salpa maxima; Yount, 1954: 300 (in part), fig. 13i-m.

Type locality: Sandwich Islands.

Diagnosis (fig. 14c):

Solitary zooids: Length up to 90 mm (n=65); according to Foxton (1961) it may reach 95 mm. Longitudinal test ridges simply echinate (serrated, denticulated) (cf. Foxton, *l.c.*). Echinations stronger on posterior half of the test. Distinct posterior spinose processes, which are formed by the sharp endings of the test ridges. No distinct bulging of the test over the nucleus. M I - M III fuse or touch in the mid dorsal region; M VIII and M IX widely separated, although tending to approach each other. Muscle fibre number of M IV is 34—102 (m = 62.7, n = 152). Foxton (*l.c.*: fig. 3b) gives a variation of about 70—115 and a mean of 100.7 (n=9). He may have included one or more specimens of *S. younti* in his countings. A detailed analysis of the muscle fibre data of the present material is given below. It must be pointed out that the number of muscle fibres of M IV in *S. aspera* overlaps with that of *S. fusiformis* and *S. younti*; the arrangement of the body muscles and the serrations of the test, however, prevent the possibility of confusion of these species. Dorsal tubercle: L-shaped, more elaborate than in *S. fusiformis*, but lacking an anteriorly directed ventral stick as found in *S. younti*. Nucleus smaller than in *S. younti*, not causing a distinct swelling of the test. The rudimentary elaioblast disappears in a young stage.

Aggregate zooids: Test bearing several echinated ridges, the most prominent being the lateral ones. Mostly also a well echinated dorsoposterior ridge is present. A difference with *S. younti* is the presence of serrations on the anterior projection. The posterior projection almost invariably has a cut off, sometimes even bifid appearance, a feature which is never found in *S. younti*. Length (excluding projections): up to 46 mm (n=154); according to Foxton (*l.c.*) it may reach 60 mm. M I - M IV are fused in the mid dorsal region; M IV and M V are separated laterally, though not as widely as in *S. maxima*. M V - M VI are fused in the mid dorsal region. Muscle fibre number of M I - M VI is 58—212 (m = 116.1, n = 364). Foxton (*l.c.*: fig. 3a) gives a variation of 115—305. He may have included specimens of *S. younti* in his countings; it is also possible that the present data do not cover the range of variation in the number of muscle fibres. Judging from the presently studied material there is a clear clinal variation in the number of muscle fibres, at least in the Pacific Ocean. In tropical waters a maximum of 166 muscle fibres has been found. Oral musculature as in *S. maxima*. Dorsal tubercle: L-shaped, differing slightly from *S. younti*. Nucleus distinctly smaller than in *S. younti*, not causing a distinct swelling of the test.

Distribution (fig. 3):

Due to the great similarity with *S. younti* one has to be careful with literature data on *S. aspera*. From the present material it is clear that the latter species

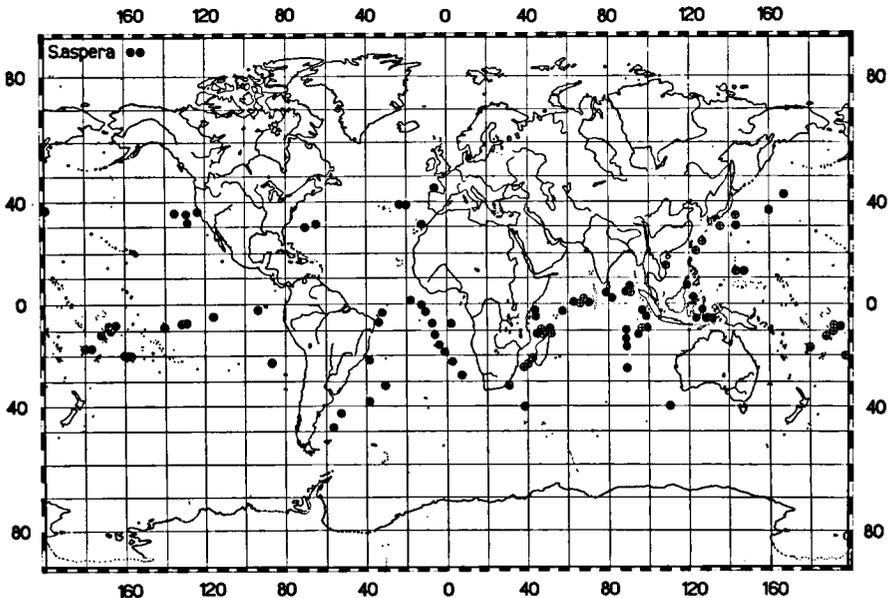


FIG. 3. Distribution of *Salpa aspera*. Black dots represent specimens with a high number of muscle fibres, circled crosses represent specimens with a low number of muscle fibres.

has a wide distribution from about 45°N to 45°S in all three oceans. It is absent from the Mediterranean, but has been observed in the Bay of Biscay.

Remark:

When studying Indo-Pacific samples of *S. aspera* the author got the distinct impression that the specimens could be divided into two groups on the basis of muscle fibre counts. A further analysis confirmed this impression. The data are represented in fig. 4. When all the specimens from all three oceans are considered indiscriminately (fig. 4c) a slight bimodality in the graph is found, which is not sufficient to suspect any subgroups. However, when only the specimens from the Indo-Pacific area are considered, a clear and undeniable bimodality is found (fig. 4a) in the aggregate as well as in the solitary specimens. This is not found in the Atlantic material (fig. 4b), which, no doubt, causes the diminished bimodality of the graph representing the specimens from all three oceans. Both groups of Indo-Pacific *S. aspera* specimens seem also to differ morphologically. It is striking that in solitary specimens with a low number of muscle fibres M I - M III touch barely or merely approach without actually touching in the mid dorsal line, while in specimens with a high number of muscle fibres M I - M III seem to be firmly fused in the mid dorsal region. In solitary specimens with a low number of muscle fibres the dorsal tubercle has a very small but distinct anteriorly directed tip on the ventrally pointing leg of the "L", while this is absent in specimens with a high number of muscle fibres. These differences are very subtle and the state of preservation of the material is not too good, so the author has refrained from giving taxonomic status to the observed groups of specimens, merely reporting their existence. It must be mentioned that the above described morphological differences occur within the variation pattern of specimens of the Bermuda area.

Salpa younti van Soest, 1973

Synonymy:

?*Salpa mollis* Herdman, 1888: 68, pl. 5 figs. 11—15.

Salpa fusiformis forma *echinata*; Ihle, 1910: 31 (in part).

Salpa maxima, echinated form; Yount, 1954: 300 (in part), figs. 13a-h, 14b-e.

?*Salpa aspera*; Foxton, 1961: 10 (in part).

Salpa younti van Soest, 1973: 10, figs. 1—3.

Type locality: Bermuda area.

Note: The appearance of many Pacific solitary specimens, which were not included in the material studied previously (van Soest, 1973b) necessitate a correction of the diagnosis of the species as compared to the original description. These solitary specimens appear to possess test ridges serrated exactly like those of *S. aspera* sol. in Pacific waters. Subsequent re-examination of the type material led to the conclusion that there is apparently a difference in the serration of the test in solitary specimens of the eastern Pacific as compared to those of the Atlantic (and the Indian Ocean).

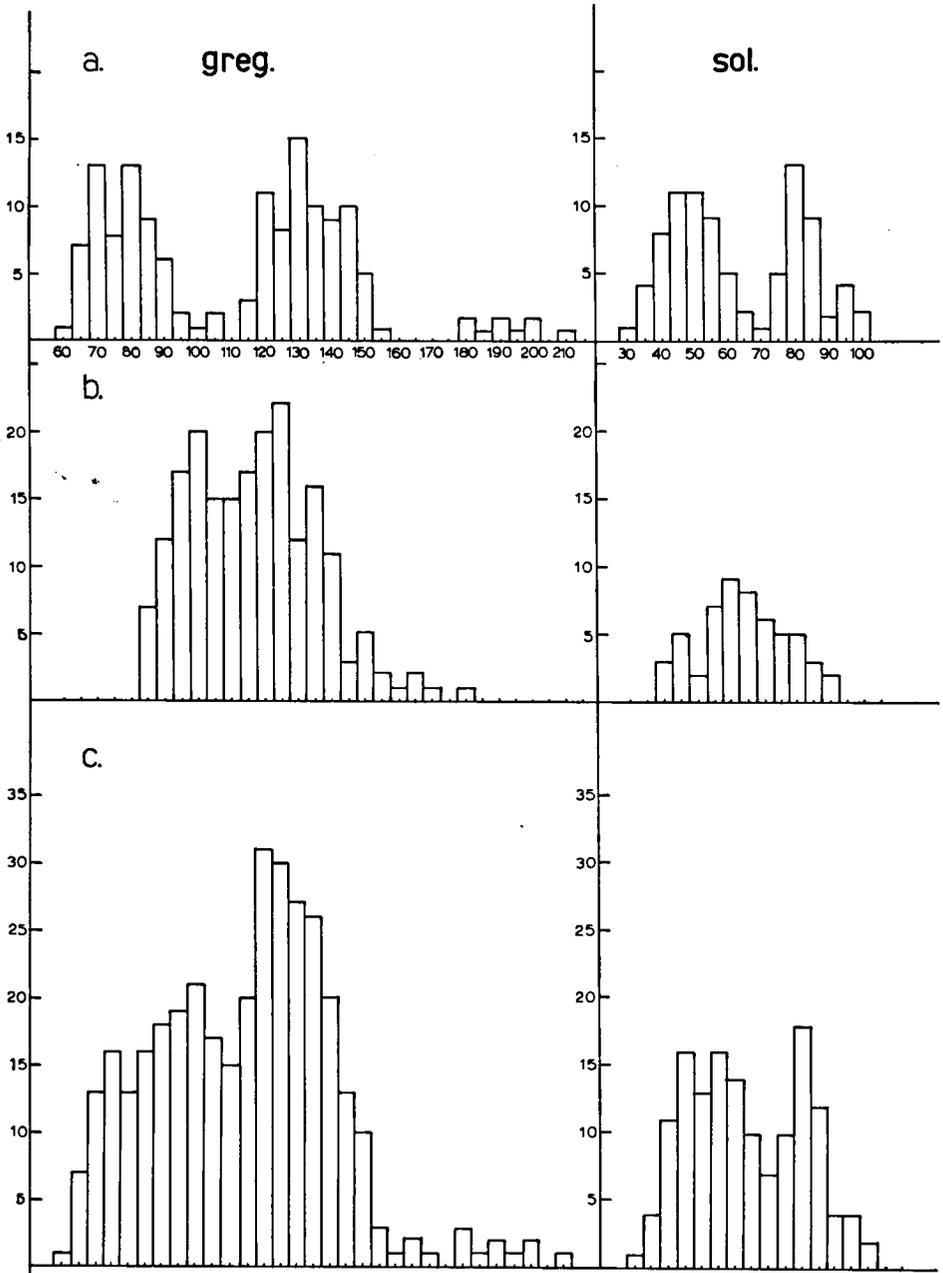


FIG. 4. Frequency diagrams of muscle fibre numbers in *Salpa aspera* specimens (left side: aggregate specimens, right side: solitary ones). a. Indo-Pacific material, b. Atlantic material, c. material from all oceans taken indiscriminately. Vertical axis: no. of specimens, horizontal axis: no. of muscle fibres.

Diagnosis (fig. 14d):

Solitary zooids: Test ridges bear serrations either in the posterior part only or over the whole length of the animal. No distinct posterior processes. Test bulging over nucleus. Length: up to 140 mm ($n=41$). M I approaching or touching M II; M III parallel to M II; M IX approaching M VIII. Muscle fibre number of M IV is 85—164 ($m = 117.7$, $n = 41$). There appears to be a clinal variation in the number of muscle fibres: in tropical waters this number varies from 85—110. Dorsal tubercle: G-shaped, slightly less elaborate than in *S. maxima*. Nucleus distinctly larger than in *S. aspera*, causing a swelling of the test. The rudimentary elaioblast is visible in the biggest specimens.

Aggregate zooids: Test bearing two echinated ridges posteriorly: a lateral one reaching to about halfway the length of the animal, and a dorsoposterior one extending from the tip of the posterior projection to the nucleus. Posterior projection not cut off or bifid, but tapering into a narrow tip. Test slightly constricted at the base of the anterior test projection. Length: (excluding projections) up to 75 mm ($n=62$). M I - M IV strongly fused in the mid dorsal region; M IV and M V approaching (but not touching) laterally; M V - M VI strongly fused. The body muscles are very broad. Muscle fibre number of M I to M VI is 176—282 ($m = 208.4$, $n = 73$). Clinal variation in the number of muscle fibres of aggregate specimens is not very distinct: the maximum number encountered in tropical water is 254. Oral musculature as in *S. maxima*. Dorsal tubercle: L-shaped, bigger and more elaborate than that of *S. aspera*, resembling that of *S. maxima*.

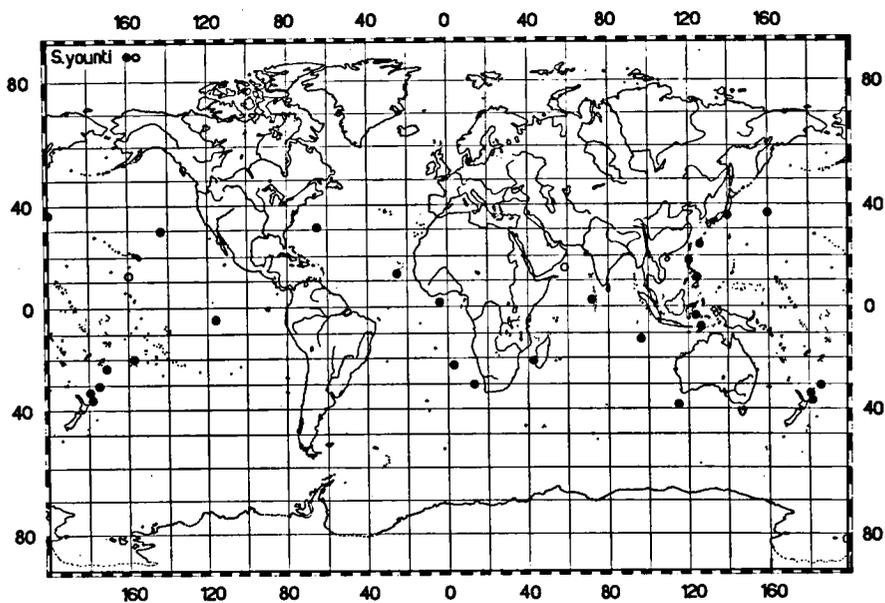


FIG. 5. Distribution of *Salpa younti*.

Distribution (fig. 5):

The records of this species from the tropical South Atlantic given in a previous paper (van Soest, 1973b) must be referred to *S. aspera*, as they are based on badly preserved aggregate zooids (without tests) with muscle fibre numbers up to 154. New records can be added from all over the Indo-Pacific area. Apparently *S. younti* has a distribution almost as wide as *S. aspera*; it is, however, less frequently taken.

Note: The identification of aggregate zooids of *S. aspera* and *S. younti* in colder waters may present some difficulties as the number of muscle fibres apparently overlaps broadly in these areas. In most cases the shape of the test (including the projections) and the shape of the dorsal tubercle will prevent confusion. Both species seem to be largely sympatric and have not infrequently been taken together in the same sample.

***Salpa fusiformis* Cuvier, 1804**

Synonymy:

Salpa maxima var. Forskål, 1775: 113, pl. 35 fig. Aa-1.

Salpa fusiformis Cuvier, 1804: 382, pl. 68 fig. 10; Lamarck, 1816: 119; Cuvier, 1817: 23, fig. 10; de Blainville, 1827: 117; Meyen, 1832: 413; Apstein, 1894: 14, fig. 7; Apstein, 1906a: 249; Apstein, 1906b: 164, figs. 13—14; Farran, 1906: 11; Streiff, 1908: 24, fig. 15; Ihle, 1910: 30; Sigl, 1913: 237; Bomford, 1913: 234; Metcalf, 1918: 89, figs. 73—79; Stiasny, 1927: 424, pl. 21 figs. 19—24, text-fig. D; Apstein, 1929: 4, figs. 1—2; Krüger, 1939: 127 (in part); Thompson, 1948: 156, pl. 70 figs. 1—2, pl. 71 figs. 1—3; Berrill, 1950: 293; Sewell, 1953: 10; Yount, 1954: 297 (in part), figs. 11f-h, 12a,c; Fagetti, 1959: 219, pl. 5 figs. 1—2; Foxtton, 1961: 8, fig. 1; Godeaux, 1962: 23; Amor, 1966: 331; Hunt, 1968: 228; Godeaux & Goffinet, 1968: 71; Godeaux, 1969: 73; Esnal, 1970: 247; van Soest, 1972: 59; Kashkina, 1973: 197; Braconnot, 1973: 10, pls. 3—4; Kashkina, 1974: 183 (Non: Stiasny, 1919: 11, fig. 3 (= *S. aspera* or *S. younti*); nec: Yount, 1954: 297 (in part), figs. 11a-e, 12b, d-e (= *S. aspera*)).

Salpa runcinata Chamisso, 1819: 16 (after Foxtton, 1961); Quoy & Gaimard, 1833: pl. 87 figs. 1—5, 1834: 573.

?*Salpa emarginata* Quoy & Gaimard, 1824: 511, pl. 74 figs. 11—12.

Biphora depressa Sars, 1829: 51 (after Traustedt, 1885).

Biphora tricuspidata Sars, 1829: 56 (after Traustedt, 1885).

Salpa coerulea Quoy & Gaimard, 1833: pl. 89 figs. 20—24, 1834: 589.

Salpa runcinata-fusiformis; Krohn 1846: 112; Traustedt, 1885: 370, pl. 2 figs. 29—31, 42; Herdman, 1888: 74, (in part) pl. 6 figs. 5—12; Traustedt, 1893: 5.

Salpa fusiformis-runcinata; Ritter, 1905: 64, figs. 12—13; Ritter & Byxbee, 1905: 197 (in part).

Type locality: unknown

Nomenclatorial note: Cuvier (1804) made a mistake in referring fig. 5 to *Salpa fusiformis* (which clearly is *Pegea confoederata* sol.) instead of to fig. 10. Furthermore in his description of *Salpa cylindrica* (= *Weelia cylindrica*) he refers to fig. 10 as representing this species. Fig. 10 is clearly in accordance with his description of *Salpa fusiformis* (greg.) and not with that of *S. cylindrica* (sol.). Metcalf (1918) thinks, this is, strictly taken, a confusing and thus invalid species designation, but proposes to let it go by. The present author takes the view, that Cuvier's mistake is clear and cannot be misunderstood.

Diagnosis (fig. 14e):

Foxton (1961) redescribed this species excellently.

Solitary zooids: Test entirely smooth, moderately thick to thin. Metcalf's (1918) "intermediates between *S. fusiformis* and *S. aspera*" must be referred to *S. fusiformis*, as the present author, having had the opportunity to study some of this material, could not find any *aspera*-like specimens. Length: up to 52 mm (n=150). M I - M III strongly fused over a wide area in the mid dorsal region; M VIII and M IX likewise strongly fused. Muscle fibre number of M IV is 14—40 (m = 22.0, n = 454); muscle fibre number of M I to M IX is 136—296 (m = 201.0, n = 140). Clinal variation in this character has been reported previously (cf. van Soest, 1972). Dorsal tubercle: a small and shallow C-shape. Nucleus relatively small, not causing a swelling of the test. Rudimentary elaioblast disappears in a young stage.

Aggregate zooids: The shape of the body is typically fusiform with long and narrow anterior and posterior projections. Test entirely smooth, moderately thick to thin. Length (excluding projections): up to 52 mm (n=247). M I - M IV strongly fused over a wide area in the mid-dorsal region; M IV - M V laterally fused; M V - M VI strongly fused in the mid-dorsal region. Muscle fibre number of M I to M VI is 25—68 (m = 42.7, n = 613). The existence of clinal variation in this character has already been reported upon. Oral musculature differing slightly from the preceding species (cf. Yount, 1954: fig. 15). Dorsal tubercle: a simple, slightly arched stick. Nucleus relatively small, not causing a swelling of the test.

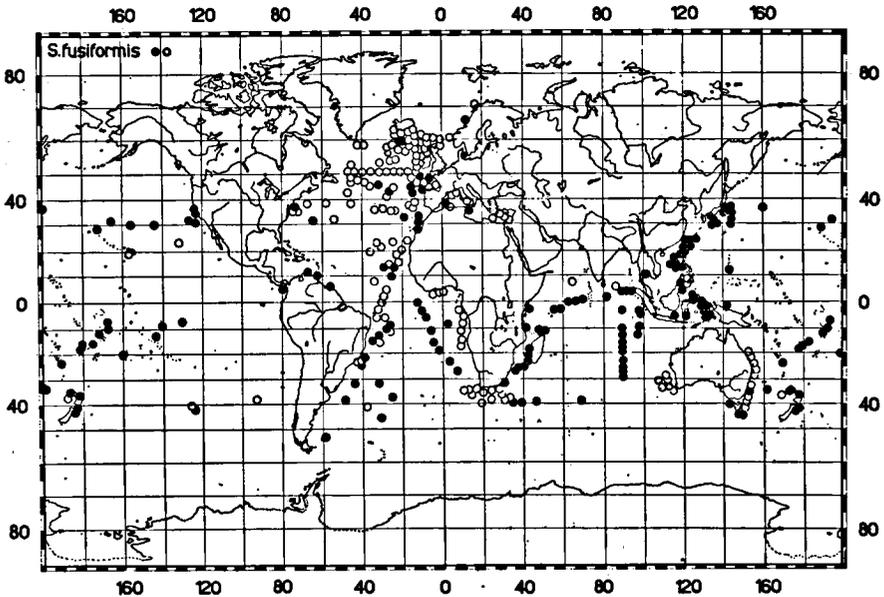


FIG. 6. Distribution of *Salpa fusiformis*.

Distribution (fig. 6):

Salpa fusiformis has the widest distribution of all salps, occurring from 70°N to 45°S in the Atlantic Ocean, to 45°S in the Indian Ocean and from at least 50°N to 45°S in the Pacific Ocean. Furthermore it is one of the most abundant salp species.

***Salpa thompsoni* Foxton, 1961**

Synonymy:

Salpa runcinata-fusififormis; Herdman, 1888: 79 (in part), pl. 5 figs. 5—12.

Salpa fusiformis var. *echinata*; Apstein, 1894: 14 (in part).

Salpa fusiformis forma *echinata*; Apstein, 1906a: 250 (in part), fig. 6; Apstein, 1906b: 165 (in part), fig. 16.

Salpa fusiformis forma *aspera*; Metcalf, 1918: 92 (in part), fig. 80; Mackintosh, 1934 (after Foxton, 1961); Hardy & Gunther, 1935: 227; Bary, 1960: 109, figs. 14—15.

Salpa fusiformis; Krüger, 1939: 217 (in part).

Salpa thompsoni Foxton, 1961: 11, pl. 2 figs. A-C; Caldwell, 1966: 4; Amor, 1966: 361; Esnal, 1970: 400; Kashkina, 1974: 189.

Type locality: Discovery Exp. st. 2144: 48°04'S, 101°07'E.

Diagnosis (fig. 14f):

As Foxton (1961) studied and measured over two hundred specimens for the description of this species, the present author has refrained from duplicating Foxton's study. Only 32 specimens have been examined, which were in complete accordance with the data of Foxton.

Solitary zooids: Test moderately thick, strongly serrated. Length: up to 60 mm (n=8); according to Foxton (*l.c.*) it may reach 120 mm. M I - M III strongly fused in the mid-dorsal region; M VIII - M IX likewise strongly fused. Muscle fibre number of M IV is 73—110 (m = 89,7, n = 7); Foxton gives 70—130 (m=93.2). Dorsal tubercle: a simple shallow C-shape. Nucleus not causing a distinct swelling of the test.

Aggregate zooids: Shape of the body less fusiform than in *S. fusiformis*. The anterior and posterior projections are more conical with a broad base, although there is considerable variation in this. Test thick, strongly serrated. Length (excluding projections): up to 30 mm (n=24); according to Foxton it may reach 60 mm. M I - M IV fused over a wide area in the mid-dorsal region; M IV - M V fused laterally; M V - M VI likewise strongly fused in the mid-dorsal region. Body muscles notably broader than in *Salpa gerlachei*. Muscle fibre number of M I to M VI is 137—228 (m=167,9, n = 24); Foxton gives 140—235 (m=177.7). Oral musculature as in *Salpa fusiformis*. Dorsal tubercle: a simple arched stick. Nucleus may cause a swelling of the test.

Distribution (fig. 7):

Foxton concluded that *S. thompsoni* is a circumpolar Antarctic species occurring from the subtropical convergence at about 40°S to the ice edge. It is absent only in the area between 60°W—170°E bordering the ice-edge, where it is replaced by *S. gerlachei*.

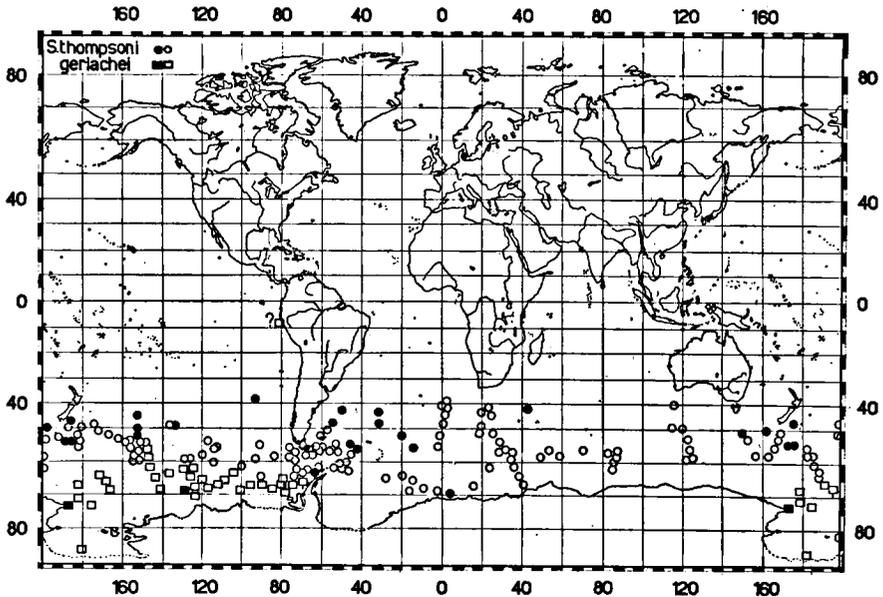


FIG. 7. Distribution of *Salpa thompsoni* (black dots and open circles) and *S. gerlachei* (black and open rectangles).

Salpa gerlachei Foxton, 1961

Synonymy:

Salpa runcinata-fusiformis var. *echinata*; Herdman, 1910 (in part?) (after Foxton, 1961).

Salpa fusiformis var. *gerlachei* van Beneden & de Selys Longchamps, 1913 (after Foxton, 1961).

Salpa gerlachei Foxton, 1961: 13, figs. 2a-b; Caldwell, 1966: 6; Esnal, 1970: 400.

Type locality: Discovery Exp., st. 1654: 75°43.6'S, 176°59.4'E.

Diagnosis (fig. 14g):

This species differs only biometrically from *S. thompsoni*.

Solitary zooids: Test ridges heavily serrated, identical to that of *S. thompsoni*. Length: up to 75 mm (Foxton, 1961). M I - M III are fused in the mid-dorsal region as are M VIII - M IX; the area of contact is less than in *S. thompsoni*. Muscle fibre number of M IV is 36—49 ($m = 43$, $n = 3$); Foxton gives 36—71 ($m = 48.8$). The body muscles are notably narrower than those of *S. thompsoni*.

Aggregate zooids: Test and shape of the body similar to that of *S. thompsoni* greg. Length (excluding projections): up to 33 mm (Foxton, *l.c.*). M I - M IV and M V - M VI fused strongly in the mid-dorsal region. M IV - M V fused laterally. Muscle fibre number of M I - M VI is 112—142 ($m = 126.7$, $n = 12$); Foxton gives 113—159 ($m = 128.8$). The body muscles are notably narrower than those of *S. thompsoni*.

Distribution (fig. 7):

According to Foxton (*l.c.*) *S. gerlachei* is to be found exclusively in the area along the ice-edge (south of 55°S) between 60°W (Drake Passage) and 170°E (Cape Adare). In addition to Foxton's observations, Caldwell (1966) reported the species from the Drake Passage area and from the Peru-Chile trench far north (08°S), in tropical waters but at great depths. This last record is surprising if it is correct. It seems very important to check this material carefully, as the number of muscle fibres of M IV given by Caldwell (*l.c.*), i.e. 48, in itself is not enough to identify the species. From the present study it can be concluded that *S. aspera* also has a range of muscle fibre numbers covering the number given by Caldwell.

The present material includes two samples collected by the Borchgrevink Expedition near the beach of Cape Adare (incorporated in the British Museum).

Remark: Caldwell (1966), Esnal (1970) and also Foxton (1961) himself point out that there is a broad overlap in the number of muscle fibres of the aggregate zooids between *S. gerlachei* and *S. thompsoni*. Caldwell (*l.c.*) and Esnal (*l.c.*) state that it is impossible to assign specimens within the overlap range to either species. It seems quite probable that *S. gerlachei* and *S. thompsoni* are clinal forms of the same species, the more so as the intermediate specimens are reported from the boundary region between the areas of distribution of both.

Genus *Pegea* Savigny, 1816

Type species: *Salpa confoederata* Forskål, 1775.

Diagnosis:

Solitary zooids: Animal barrel-shaped, without projections or protuberances. Test generally smooth, although in young specimens the area ventral to the nucleus may be finely granulated. Test thick, voluminous (particularly in the area around the nucleus), but not very firm. Oral and atrial apertures terminal. Four body muscles (M I - M IV), arranged in two groups: M I - M II approaching, touching or fusing in the mid-dorsal region, as do M III - M IV. Body muscles only cover the dorsal surface of the body. Oral musculature: two dorsal and three ventral sphincters and a pair of oral retractors. The intermediate muscle consists of two independent, partly parallel running muscles of which the anterior one (termed "dorsal horizontal muscle" by Metcalf, 1918: 130) turns forward to approach the second dorsal sphincter. The atrial musculature differs considerably in both species. Dorsal tubercle: a huge G-shaped structure. Internal organs: intestine coiled into a tight nucleus, which is situated at about two thirds the distance from oral to atrial aperture. Endostyl not reaching the oral aperture. Stolon: coiled flatly around the nucleus.

Aggregate zooids: Animal barrel-shaped. It may or may not have two short or long limp projections posteriorly, which are generally of unequal length. Test smooth, voluminous, not very firm, except for the spherical terminal part containing the nucleus. Oral aperture terminal, atrial aperture dorsal. Four body muscle arranged in two groups: M I - M II approaching, touching or fused in the mid-dorsal region, as do M III - M IV. Body muscles only cover the dorsal surface of the body. Oral musculature: almost identical to that of the solitary generation. Atrial musculature: there are three partly interrupted dorsal sphincters and three ventral ones. The third ventral sphincter joins the fourth body muscle. Parallel to this the fourth body muscle gives off a branch encircling on the ventral side the atrial aperture, but it is interrupted on the mid-ventral line. Dorsal tubercle G-shaped, slightly simpler than that of the solitary generation. Internal organs: intestine coiled into a tight nucleus, which is positioned posterior-terminal. Endostyl not reaching the oral aperture. Embryo situated between M III and M IV on the right side; together with the placenta it has a very characteristic club-shaped appearance. Aggregate zooids are attached in their chains by four big, disc-like attachment organs, two at each side: one pair anteriorly at the level of M I, one pair posteriorly between M III and M IV.

Two taxa are recognized: *P. confoederata* (Forskål, 1775) and *P. bicaudata* (Quoy & Gaimard, 1826). The latter has been considered a subspecies of the former by most previous authors. In view of the apparent sympatry of both taxa they are considered separate species in the present study.

***Pegea confoederata* (Forskål, 1775)**

Synonymy:

- Salpa confoederata* Forskål, 1775: 115, pl. 36 fig. A; Bruguière, 1789: pl. 75 figs. 2—4 (after Traustedt, 1885); Gmelin in Linnaeus, 1791: 3130; Bosc, 1802 (after Traustedt, 1885); Lamarck, 1816: 117; Risso, 1826 (after Traustedt, 1885); de Blainville, 1827: 111; Apstein, 1894: 12, fig. 16; Apstein, 1906a: 255; Apstein, 1906b: 172, pl. 8 figs. 10—11, pl. 9 figs. 12—18; Stiasny, 1919: 14, figs. 6—8. (Non: Streiff, 1908: figs. 23—25 (= *P. bicaudata*)).
- Salpa gibba* Bosc, 1802 (after Traustedt, 1885).
- Salpa socia* Bosc, 1802 (after Traustedt, 1885).
- Salpa scutigera* Cuvier, 1804: 379, pl. 68 figs. 4—5; Lamarck, 1816: 118; Cuvier, 1817: 18; figs. 4—5; de Blainville, 1827: 110.
- Salpa octophora* Cuvier, 1804: 379, pl. 68 fig. 7; Lamarck, 1816: 118; Cuvier, 1817: 20, fig. 7; de Blainville, 1827: 110; Meyen, 1832: 417.
- Salpa vivipara* Péron & Lesueur, 1807 (after Traustedt, 1885).
- Pegea octophora*; Savigny, 1816: 124, pl. 24 fig. 1 (after Traustedt, 1885).
- Salpa ferruginea* Chamisso, 1819 (after Traustedt, 1885); de Blainville, 1827: 110; Meyen, 1832: 417.
- Salpa femoralis* Quoy & Gaimard, 1833: pl. 88 figs. 1—5, 1834: 577.
- Salpa scutigera-confoederata*; Vogt, 1854: 6; Traustedt, 1885: 362, pl. 2 figs. 23—24, 46; Traustedt, 1893: 5; Apstein, 1904: 656.
- Salpa quadrata* Herdman, 1888: 84, pl. 9 figs. 1—8.
- Pegea scutigera-confoederata*; Herdman, 1891 (after Metcalf, 1918).
- Salpa confoederata-scutigera*; Ritter & Byxbee, 1905: 196.

Salpa (Pegea) confoederata; Metcalf, 1918: 127, figs. 119—127; Sewell, 1926: 100, figs. 28—33; Berrill, 1950: 297.

Pegea confoederata; Ihle & Ihle-Landenberg, 1938: 107, figs. 1—5; Belloc, 1938: 324, figs. 14—17; Thompson, 1948: 143, pl. 60 figs. 1—2, pl. 61 figs. 1—4, pl. 62 figs. 1—5; Yount, 1954: 317 (in part), figs. 24—25; Van Zijl, 1959: 14; Fagetti, 1959: 217, pl. 4 figs. 1—2; Bary, 1960: 109, fig. 13; Godeaux, 1962: 29; Godeaux & Goffinet, 1968: 67 (in part); Dossman, 1970: 73, fig. 4; Kashkina, 1973: 202; Kahskina, 1974: 194.

Type locality: Eastern Mediterranean.

Diagnosis (fig. 15a):

Solitary zooids: Length: up to 81 mm (n=58); according to Traustedt (1885) it may reach 120 mm. No differences other than the number of muscle fibres and the arrangement of the atrial musculature have been found between the solitary zooids of this species and those of *P. bicaudata*. Furthermore the difference in number of muscle fibres is only clear in warmer waters (30°N-30°S) as *P. confoederata* shows clinal variation in this character, whereas this has not been found in *P. bicaudata*. Muscle fibre number of M I to M IV is 61—158 (m = 88.1, n = 71). In warmer waters this number is 61—118 (m = 85.7, n = 64). Oral musculature: exactly like that of *P. bicaudata*. Metcalf's (1918) statement that the intermediate muscle terminates above the oral retractor in *P. confoederata*, whereas it reaches beyond the oral retractor in *P. bicaudata* is not confirmed by the present material. In both species the intermediate muscle joins the oral retractor. Atrial musculature (fig. 8): there seems to be considerable difference in the number and the arrangement of atrial muscles. The two dorsal and three ventral incomplete sphincters observed in full grown specimens of *P. confoederata* have been shown (by Metcalf, 1918) to be derived from an embryonic set of four

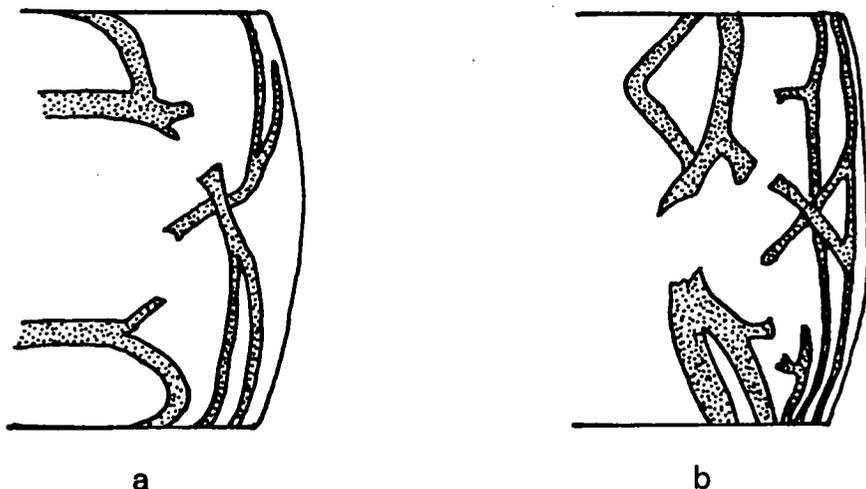


FIG. 8. The arrangement of the atrial musculature in the solitary generation of *P. confoederata* (a) and *P. bicaudata* (b).

each. Parallel to the fourth body muscle runs an extra muscle giving off two dorsal longitudinal stretches of muscle directed to the mid-dorsal line. This same extra muscle seems to be present in a modified form in *P. bicaudata*. In contrast to the situation in *P. bicaudata* sol., small forwardly directed branches of the second and third sphincters are absent.

Aggregate zooids: Animal without posterior projections or protuberances. Length: up to 101 mm ($n=291$); according to Traustedt (1885) it may reach 150 mm. Muscle fibre number of M I to M IV is 38—143 ($m = 65.5$, $n = 291$). There is a distinct clinal variation in this character: in warm waters (30°N — 30°S) the number of muscle fibres is 38—78 ($m = 54.3$, $n = 238$), in cold waters 93—143 ($m = 122.1$, $n = 43$). Apparently linked to this clinal variation the body muscles generally fuse in the mid-dorsal line in warmer waters, while they are merely approaching or barely touching in colder waters. This is particularly clear in M III - M IV. More attention to this phenomenon will be given in a future paper. Oral musculature: almost identical to that of the solitary zooid. The only difference is the extent of the intermediate muscle: it does not reach the oral retractor. Atrial musculature: three dorsal and three ventral sphincters. The second and the third dorsal sphincters are laterally interrupted. The third ventral sphincter joins the fourth body muscle and may thus be considered partly as the atrial retractor muscle. Parallel to this retractor M IV gives off a branch which encircles the ventral part of the atrial aperture. There is a short ventral interruption of this branch. According to Metcalf (1918) the atrial musculature of *P. confoederata* greg. differs from that of *P. bicaudata* greg. firstly by the absence of the lateral interruption of the first dorsal sphincter, and secondly by the absence of the second ventral sphincter (which in his fig. 125 apparently fuses with the first ventral sphincter). These observations are not confirmed by the present material. Both species are exactly alike in their atrial musculature.

Distribution (fig. 9):

P. confoederata has a wide-spread occurrence from 50°N to 45°S in all oceans. It is one of the more common species.

***Pegea bicaudata* (Quoy & Gaimard, 1826)**

Synonymy:

Salpa bicaudata Quoy & Gaimard, 1826: 124, fig. A-1; Quoy & Gaimard, 1833: pl. 89 figs. 1—5, 1834: 585.

Salpa nephodea Lesson, 1830 (after Metcalf, 1918).

Pegea confoederata; Lahille, 1892: fig. 3; Yount, 1954: 317 (in part).

Salpa confoederata; Streiff, 1908: 32, figs. 23—25.

Salpa (Pegea) confoederata subsp. *bicaudata*; Metcalf, 1918: 139, figs. 128—132.

Pegea confoederata bicaudata; Haneda & Tokioka, 1954: 369, figs. 16—17; Furuhashi & Tokioka, 1966: 117, figs. 1—3; Braconnot, 1973: 13, pl. 8 figs. A-B.

Pegea confoederata subsp. *bicaudata*; Godeaux & Goffinet, 1968: 68.

Type locality: Straits of Gibraltar.

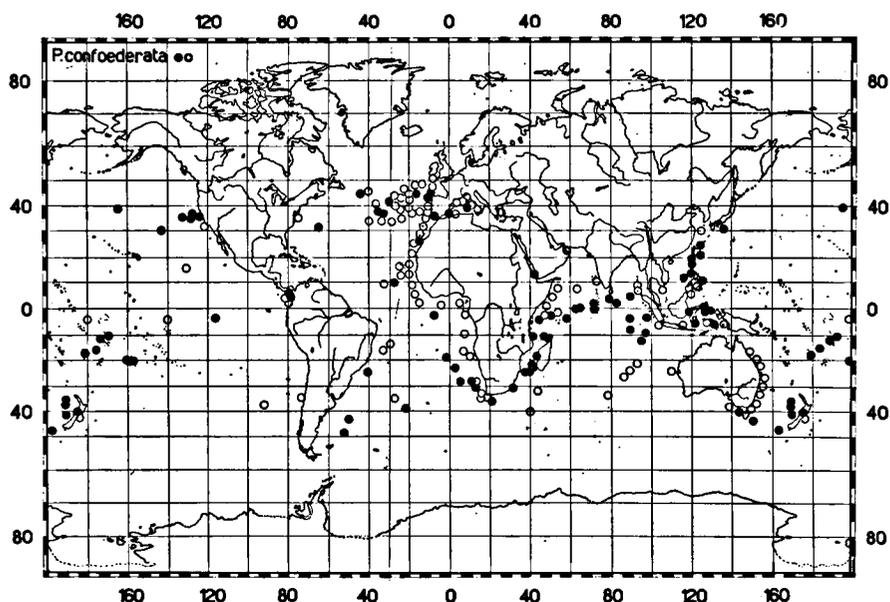


FIG. 9. Distribution of *Pegea confederata*.

Diagnosis (fig. 15b):

Solitary zooids: Up till now the solitary zooid of *P. bicaudata* has been distinguished from that of *P. confederata* only by Metcalf (1918). The present study has revealed no other differences than the number of muscle fibres and the arrangement of the atrial musculature in solitary zooids found associated with aggregate *P. bicaudata*. Length of these specimens: up to 70 mm ($n=9$). The number of muscle fibres of M I to M IV is 103—154 ($m = 124.0$, $n = 9$); all these specimens originated from warm waters and are clearly separated from those of *P. confederata* from warm waters. Oral musculature exactly as described by Streiff (1908), who apparently also studied *P. bicaudata*. The arrangement of the atrial musculature (fig. 8) seems to be a good diagnostic character, although the need for an extensive study of the variation of oral and atrial musculature in salps is apparent.

Aggregate zooids: Animal bearing two long, rather limp posterior projections of unequal length. Sometimes one of them is so short as to appear wholly absent. Length: up to 66 mm ($n=45$). Muscle fibre number of M I to M IV is 80—160 ($m = 102.9$, $n = 45$). There appears to be some clinal variation in this character: in warm waters the number is 80—128 ($m = 97.6$, $n = 35$), in temperate waters 109—160 ($m = 121.4$, $n = 10$). Oral and atrial musculature found to be exactly like that of *P. confederata* greg. The differences between the species observed by Metcalf (1918) cannot be confirmed.

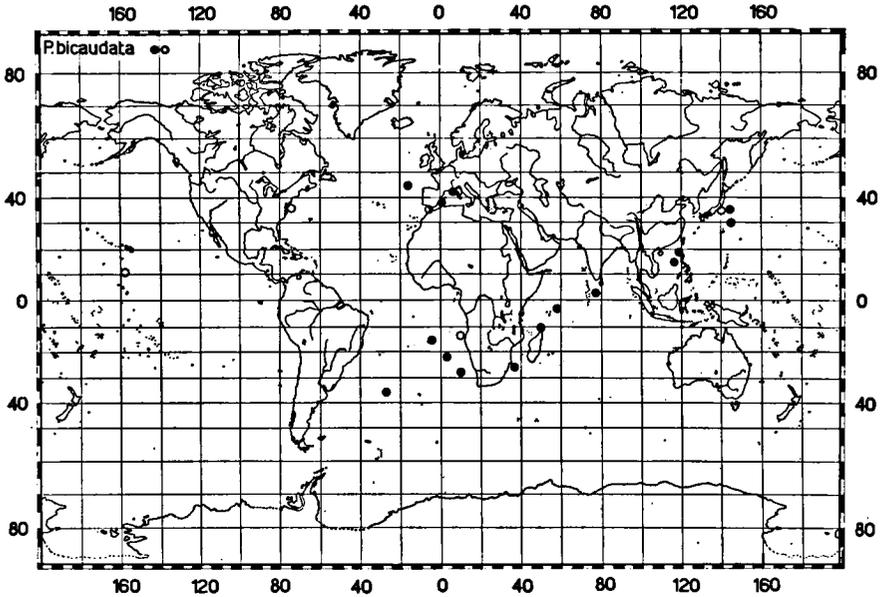


FIG. 10. Distribution of *Pegea bicaudata*.

Distribution (fig. 10):

P. bicaudata is apparently rare, but its distribution seems as wide as that of *P. confederata*. Metcalf (1918) mentions specimens from the east coast of North America. Haneda & Tokioka (1954) and Furuhashi & Tokioka (1966) found specimens near Japan. Yount (1954) found specimens south of Hawaii. Godeaux & Goffinet (1968) report the species to occur off the coast of Angola. There are many records from the Mediterranean where it seems to be moderately common (e.g. Streiff, 1908; Metcalf, 1918; Braconnot, 1973; present material). To these distributional data can be added: North Atlantic (45°N, 16°W), eastern and western South Atlantic, western and northern Indian Ocean and western North and South Pacific.

Remark: Furuhashi & Tokioka (1966) described a chain of 9 aggregate specimens of this species in which they found a different orientation of the posterior projections of both sides of the chain. Braconnot (1973) also described and figured chains of this species, but could not discover any different orientation. In the present material a chain of four specimens is present; no difference in orientation of the individuals is apparent.

Genus *Ritteriella* Metcalf, 1919

Type species: *Salpa amboinensis* Apstein, 1904.

Diagnosis:

Solitary zooids: Animal elongately cylindrical with the oral and atrial aperture terminal. Test very thin and flabby, entirely smooth, without projections or elevations. The number of body muscles varies from 9–31;

this number also varies within the species. The body muscles form almost complete loops, but are all ventrally interrupted, except for the first three or four body muscles in *R. amboinensis*, which are continuous ventrally. The ventral interruption is barely visible in the anterior part, but widens towards posterior. The body muscles frequently anastomose in the mid dorsal region, often causing a different number of muscles on both sides of a single individual. The oral musculature is differently arranged in the different species, although observations of various authors are contradictory (cf. Metcalf, 1918; Yount, 1954; Meurice, 1970; Kashkina, 1973). It consists of 2—4 dorsal and 5 ventral sphincters, a pair of oral retractors, which are often partly divided into two or three partly separate muscles. The second dorsal sphincter crosses the first. The intermediate muscle touches the third sphincter laterally. Sphincters are either continuous or interrupted ventrally. The atrial musculature consists of a large number of continuous sphincters (up to 10) and a pair of atrial retractors. Dorsal tubercle: a simple S-shape in all species. Intestine: varying from a loosely coiled to an uncoiled, longitudinally extended form. Associated with the intestine (on the left side) is a blood-forming organ of a rounded or longitudinally extended shape. Stolon: at first reaching forward to about halfway the body, then curving backwards. **Aggregate zooids:** Animal fusiform with a distinct anterior and posterior projection comparable to that of the aggregate zooid of *Salpa* species. The posterior projection is notably longer than the anterior one. Test voluminous, but thin, and very adhesive. Test bulging slightly over nucleus. Six body muscles, which are continuous dorsally, but widely separated ventrally. M I - M IV fused in the dorsal region as are M V and M VI. This pattern resembles that of the aggregate zooids of *Salpa*, but it differs clearly in the fusion of M I and M II, which extends to the lateral parts, giving the impression, that in the anterior dorsal region only three body muscles are fused in stead of four. M IV and M V widely separated and not approaching laterally. A branch of M VI encircles the atrial aperture. The arrangement of the body muscles is distinctly asymmetrical. Oral musculature: there are three dorsal and two or three ventral sphincters, and a pair of oral retractors. The intermediate muscle is fused laterally with the third dorsal sphincter. Atrial musculature: there are five atrial sphincters and a pair of atrial retractors. Dorsal tubercle: a simple stick. Intestine coiled into a tight nucleus. Ovary and embryo positioned between M V and M VI on the right side.

Three species are recognized, one of which (*R. retracta*) has been currently considered synonymous with *R. picteti*. Sufficient data are presented below to show they are different taxa and that synonymizing is unjustified.

Ritteriella amboinensis (Apstein, 1904)

Synonymy:

Salpa amboinensis Apstein, 1904: 651, pl. 12 figs. 2—10; Ihle, 1910: 34, figs. 7—15 (Non: Apstein, 1906a: 250, pl. 27 figs. 8—14 (=probably *R. retracta*); nec: Apstein, 1906b: 166, fig. 18 (=probably *R. retracta*)).

Salpa (Ritteria) amboinensis; Metcalf, 1918: 56, figs. 29—32; Sewell, 1926: 85, figs. 15—16.

Salpa (Ritteriella) amboinensis; Metcalf, 1919: 19.

Ritteriella amboinensis; Thompson, 1948: 126, pl. 46 figs. 1—2, pl. 47 figs. 1—4, pl. 48 figs. 1—3; Yount, 1954: 307, fig. 18a-c; Fenaux & Godeaux, 1970: 207; Meurice, 1970: 194, figs. 1—10; Kashkina, 1973: 198, fig. 1; Kashkina, 1974: 191.

Type locality: near the Island of Ambon (Indonesia).

Diagnosis (fig. 15c):

Meurice (1970) redescribed this species excellently.

Solitary zooids: Length: up to 30 mm ($n=9$); according to Meurice (1970) it may reach 50 mm. Number of body muscles varying from 9 to 12 ($m = 10.6$, $n = 9$); often a different number can be counted on both sides, due to irregular anastomosing in the mid dorsal region. The first three or four body muscles are continuous ventrally. Muscle fibres barely distinguishable in most specimens. Because of the great number of fibres per muscle only those of MI + MII were counted. In five more or less distinct specimens the number of MI + MII appeared to be: 138—229 ($m = 188.0$). Oral musculature: all ventral sphincters and the intermediate muscle are continuous ventrally. The oral retractor does not reach the first body muscle. Intestine loosely coiled. The blood-forming organ is bean-shaped and compact.

Agregate zooids: Length (excluding projections): up to 11 mm ($n=29$); according to Meurice (1970) it may reach 30 mm. Number of muscle fibres of MI to MVI is 31—47 ($m = 37.3$, $n = 29$). Oral musculature: three dorsal and two ventral sphincters.

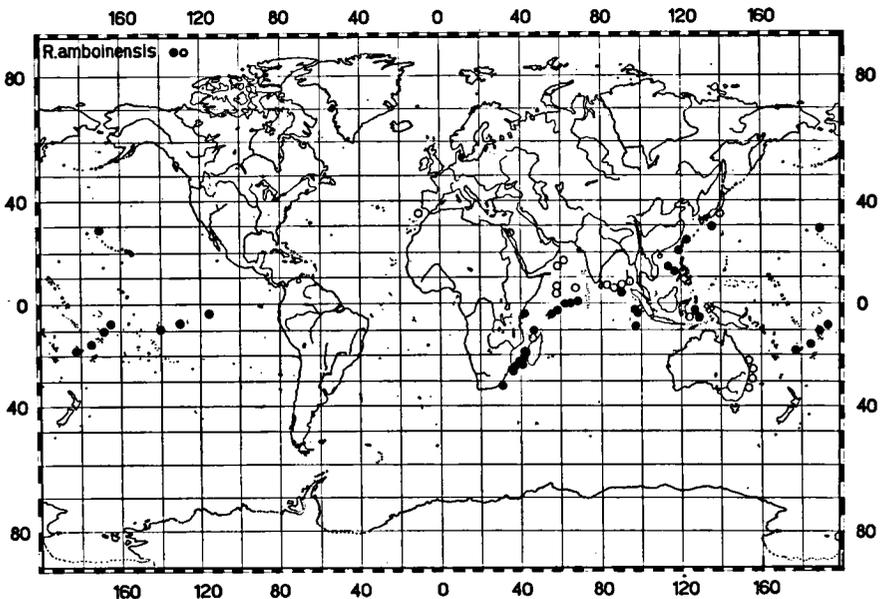


FIG. 11. Distribution of *Ritteriella amboinensis*.

Distribution (fig. 11):

Ritteriella amboinensis is widely distributed and not uncommon in the whole of the Indo-Pacific. Meurice (1970) notes that it seems to be absent from the eastern Pacific, but the present material contains specimens of this species from 04°20'S, 116°46'W; 07°45'S, 131°22'W and 09°06'S, 140°21.5'W (Dana expeditions). There is one certain record from the Atlantic (Meurice, 1970): 33°12'N, 11°17'W. Apstein's (1906a) records of this species from the Gulf of Guinea (included in the distribution charts of Meurice (*l.c.*) and Kashkina (1974)) are doubtful, as the figures he gives are probably of *R. retracta*.

Ritteriella picteti (Apstein, 1904)

Remark: The present study has shed new light on the variation of *R. picteti* and *R. retracta* (Ritter, 1906). In the opinion of the present author they are not synonymous as has been thought by most previous authors, but ought to be treated as closely related separate species.

Synonymy:

Salpa picteti Apstein, 1904: 655, pl. 12 figs. 12—14; Apstein, 1906a: 252, pl. 28 figs. 18, 18a; Apstein, 1906b: 168, fig. 22; Ihle, 1910: 43, fig. 16.

Salpa (*Ritteria*) *picteti*; Metcalf, 1918: 55, figs. 26—28; Sewell, 1926: 86, fig. 17.

Salpa (*Ritteriella*) *picteti*; Metcalf, 1919: 19 (Non: Komai, 1932: 65, fig. 1 (= *R. retracta*)).

Ritteriella picteti; Thompson, 1948: 124 (in part), pl. 44 figs. 2—3; Yount, 1954: 308 (in part), fig. 19a; Kashkina, 1973: 199 (in part), fig. 1b (Non: Thompson, 1948: 124 (in part), pl. 44 fig. 1, pl. 45 figs. 1—2 (= *R. retracta*); nec: Berner, 1954: 121, figs. 1—4 (= *R. retracta*); nec: Fraser, 1955: 247 (= *R. retracta*); nec: Fagetti, 1959: 213, pl. 2 figs. 1—2 (= *R. retracta*); nec: Godeaux, 1969: 74 (= *R. retracta*); nec: Kashkina, 1974: 192 (= *R. retracta*)).

Type locality: near the Island of Ambon (Indonesia).

Diagnosis (fig. 15d):

Solitary zooids: Length: up to 78 mm (n=13). Number of body muscles varying between 19 and 31 (m=24.7). The largest difference in number on both sides of one individual was found to be three muscles. All body muscles interrupted ventrally. The muscle fibres are clearly visible and fairly easy to count. Analogous to the procedure in *R. amboinensis* at first only the number of muscle fibres of M I + M II was counted: 139—231 (m = 186.6, n = 13). In five specimens also the total number of fibres was counted: 1768—2268 (m=1942.6). Oral musculature: the fifth sphincter and the intermediate muscle are ventrally interrupted (in contrast to the situation in *R. amboinensis*); the oral retractor reaches the first body muscle. Intestine not coiled into a nucleus but stretched out longitudinally in the posterior part of the animal. Blood-forming organ of variable size and form, but not bean-shaped; generally it is a forwardly pointing, longish object.

Aggregate zooids: Found associated with the above described solitary zooids, were some big aggregate specimens quite similar to *R. retracta* greg., but their muscle fibre number seemed higher: 110—169 ($m = 134.2$, $n = 10$). Just as in *R. retracta* greg. their oral musculature differs from that in *R. amboinensis* greg. by the presence of a third ventral sphincter (which is absent in *R. amboinensis*). Length of these specimens (excluding posterior projections): up to 51 mm.

Distribution (fig. 12):

R. picteti seems quite rare, but its distribution is apparently wide, covering the Indian Ocean and the western Pacific Ocean. It is absent from the Atlantic.

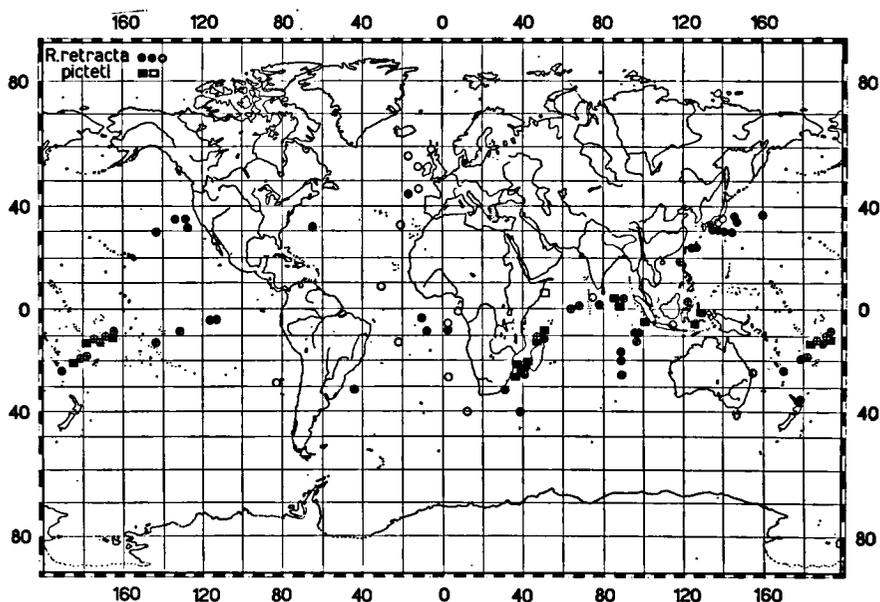


FIG. 12. Distribution of *Ritteriella picteti* (black and open rectangles) and *R. retracta* (black dots and circled crosses). Black dots represent specimens with a high number of muscle fibres, circled crosses represent specimens with a low number of muscle fibres.

Ritteriella retracta (Ritter, 1906)

Remark: The main reason for synonymizing *R. retracta* with *R. picteti* is the description by Komai (1932) of what is considered an intermediate solitary zooid. His specimen possessed 15 body muscles on the left side and 18 on the right side. Until then, *R. picteti* was reported to possess 21—27 muscles and *R. retracta* 11—14, so Komai's specimen had all the appearances of being indeed an intermediate. However, in the present study a specimen with 19

and one with 18 muscles were encountered, which had to be assigned to different species, as their total number of muscle fibres turned out to be 1794 and 987 respectively. Komai's specimen falls within the variation of *R. retracta*, as it will be presented here.

Synonymy:

Cyclosalpa retracta Ritter, 1906: 1, figs. 1—2.

?*Salpa amboinensis*; Apstein, 1906a: 250, pl. 27 figs. 8—14; Apstein, 1906b: 166, fig. 18.

Salpa retracta; Ihle, 1910: 40, fig. 5; Stiasny, 1919: 8.

Salpa (Ritteria) retracta; Metcalf, 1918: 53, fig. 25.

Salpa (Ritteriella) retracta; Metcalf, 1919: 19.

Salpa (Ritteriella) picteti; Komai, 1932: 65, fig. 1.

Ritteriella picteti; Thompson, 1948: 124 (in part), pl. 44 fig. 1, pl. 45 figs. 1—2; Berner, 1954: 121, figs. 1—4; Yount, 1954: 308 (in part), fig. 19b; Fraser, 1955: 247; Fagetti, 1959: 213, pl. 2 figs. 1—2; Godeaux, 1969: 74; Kashkina, 1973: 199 (in part), fig. 1b; Kashkina, 1974: 192.

Type locality: near Japan.

Diagnosis (fig. 15e):

Solitary zooids: Length: up to 70 mm ($n=95$). Number of body muscles varying from 10 to 18 ($m = 12.9$, $n = 92$). All body muscles interrupted ventrally. Number of muscle fibres of M I + M II is 66—204 ($m = 139.7$, $n = 95$). Also the total number of muscle fibres in 16 specimens was counted: 485—1283. A further analysis of the variation of this character is given below. Oral musculature: exactly as in *R. picteti*. Intestine likewise as in *R. picteti*. Although there is a great variation in the shape and the position of the blood-forming organ, it seems to be in general more arched and pointing dorsally rather than forward.

Aggregate zooids: In all but the number of muscle fibres similar to *R. picteti* greg. Length: up to 39 mm ($n = 42$). Number of muscle fibres of M I to M VI is 60—109 ($m = 88.9$, $n = 42$). A further analysis of the variation of this character is given below.

Distribution (fig. 12):

Although Berner (1954) considers this species rare, it has been found rather frequently in the present material. *R. retracta* has a wide distribution over all three oceans from about 50°N to 40°S. Kashkina (1974) reviewed its distribution in the Atlantic (as *R. picteti*).

Remark: When studying Indo-Pacific samples of *R. retracta* the author got the impression that the specimens could be divided into two groups on the basis of muscle fibre counts. A further analysis confirmed this impression. Muscle fibre counts of *Ritteriella* are represented in fig. 13 and table I. Concerning the solitary zooids of *R. retracta* there is a clear bimodality found in the graph representing the number of fibres of M I + M II. The first group has 66—114 fibres ($m = 88.9$, $n = 27$), the second 128—207 ($m =$

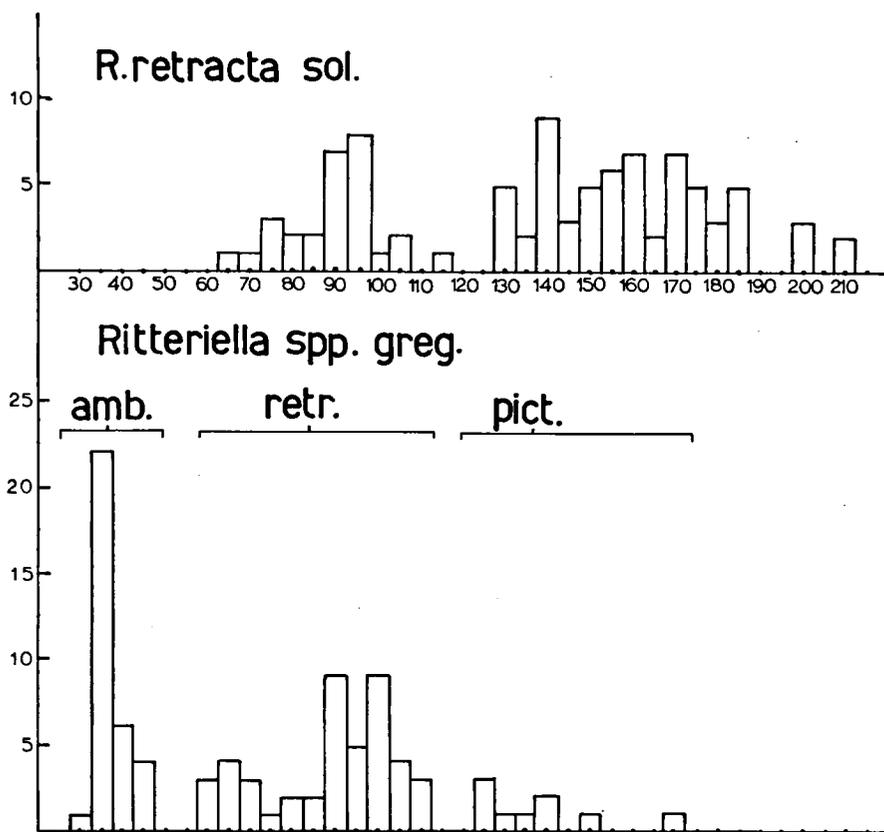


FIG. 13. Frequency diagrams of muscle fibre numbers in *Ritteriella* spp. Top: The no. of fibres of M I + M II in *R. retracta* sol. Bottom: The no. of fibres of M I + M VI in aggregate specimens of *Ritteriella* spp. Vertical axis: no. of specimens, horizontal axis: no. of muscle fibres.

159.9, n = 68). The number of body muscles of both groups apparently do not differ significantly: specimens with a low number of muscle fibres in M I + M II possess an average number of body muscles of 12.1 (10—16, n = 27), those with a high number of muscle fibres 13.3 (11—18, n = 68). Consequently, the total number of muscle fibres should also be quite different. This is confirmed by the counts of 8 specimens with a low number of muscle fibres in M I + M II and 10 specimens with a high number (table I). The first group appeared to possess 485—664 muscle fibres, the second 866—1283. The total number of muscle fibres in five specimens of *R. picteti* are given in table II; they vary from 1768 to 2268. From these countings it is clear that in the genus *Ritteriella* just as in other salp genera the number of muscle fibres is of utmost importance for taxonomical studies. Nevertheless, the present data seem too thin to split *R. retracta* into two taxa. It has to be pointed out, that both forms may occur in the same sample. In the Atlantic

TABLE I. Comparison between the number of body muscles, the number of muscles fibres of M I + M II, and the total number of muscle fibres in 17 specimens of *Ritteriella retracta* sol.

No. of body muscles	No. muscle fibres M I + M II	No. of muscle fibres total
17	142	1283
14	186	1127
13	162	970
14	158	987
15	165	1087
13	145	921
13	151	886
15	136	912
12	157	932
18	131	987
12	95	561
11	94	501
12	82	485
13	106	546
15	73	571
12	95	599
13	114	664

TABLE II. Comparison between the number of body muscles, the number of muscle fibres of M I + M II, and the total number of muscle fibres in 5 specimens of *Ritteriella picteti* sol.

No. of body muscles	No. of muscle fibres M I + M II	No. of muscle fibres total
28	231	2016
26	150	1768
30	227	2268
24	185	1867
19	212	1794

Ocean only solitary zooids with a high number of muscle fibres have been found. Concerning the aggregate zooids the occurrence of two groups of specimens is less clear. In the graph representing the number of muscle fibres of aggregate zooids of all *Ritteriella* species (fig. 13b) the first peak consists of *R. amboinensis* specimens, separable from the others by the absence of a third ventral oral sphincter. Between these and the other specimens a clear gap is found. A similar gap exists between what is considered the aggregate stock of *R. picteti* and *R. retracta*. The remaining central part of the graph concerns both *R. retracta*-groups. Although the number of specimens studied is quite small, it seems likely that the first group, corresponding to the solitary zooids with a low number of muscle fibres, has a range of the number of fibres of M I - M VI of 60—78 ($m = 67.3$, $n = 11$), while the second group

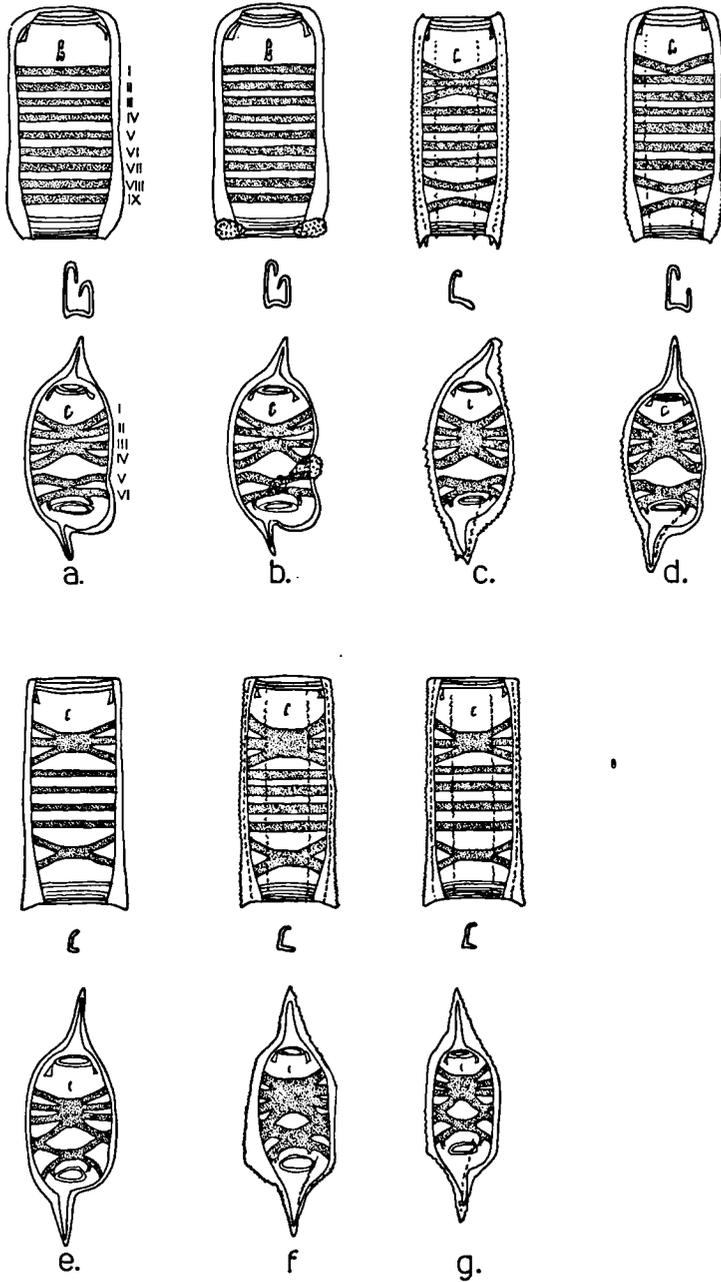


FIG. 14. Schematic representation of the species of the genus *Salpa*. Top row: solitary zooids, middle row: dorsal tubercle of solitary zooids, bottom row: aggregate zooids. a. *S. maxima*, b. *S. tuberculata*, c. *S. aspera*, d. *S. younti*, e. *S. fusiformis*, f. *S. thompsoni*, g. *S. gerlachei*.

corresponding to the solitary zooids with a high number of muscle fibres, have a range of 81—109 ($m = 96.6$, $n = 31$). One Atlantic specimen has a number of fibres of M I - M VI of 96. Finally it cannot be overlooked that the phenomenon described above has much in common with the situation found in Indo-Pacific *Salpa aspera* specimens.

KEY TO THE SPECIES OF THE GENUS SALPA

Solitary zooids:

1. — All body muscles parallel dorsally 2
— Not all body muscles parallel dorsally 3
2. — Test entirely smooth *Salpa maxima* (fig. 14a)
— Test bearing echinated oval cushions on posterior part
. *S. tuberculata* (fig. 14b)
3. — M VIII and M IX fused in the mid dorsal region 4
— M VIII and M IX approaching, but not touching or fused in the mid
dorsal region 6
4. — Test echinated 5
— Test smooth *S. fusiformis* (fig. 14e)
5. — Number of muscle fibres of M IV = 70—130
. *S. thompsoni* (fig. 14f)
— Number of muscle fibres of M IV = 36—71 *S. gerlachei* (fig. 14g)
6. — M I approaching M II in the mid dorsal region, M III parallel to M II
. *S. younti* (fig. 14d)
— M I - M III approaching, touching or fused in the mid dorsal region
. *S. aspera* (fig. 14c)

Aggregate zooids:

1. — M IV and M V approaching but not fused laterally 2
— M IV and M V fused laterally 5
2. — M I + M II and M III + M IV fused, M II and M III touching in the
mid dorsal line 3
— M I - M IV fused strongly in the mid dorsal region 4
3. — Test entirely smooth *S. maxima* (fig. 14a)
— Test bearing two echinated cushions dorsally *S. tuberculata* (fig. 14b)
4. — Both anterior and posterior projections echinated; posterior projection
has a cut off or bifid appearance *S. aspera* (fig. 14c)
— Only posterior projection echinated; it is tapering into a point
. *S. younti* (fig. 14d)
5. — Test smooth *S. fusiformis* (fig. 14d)
— Test echinated 6
6. — Number of muscle fibres of M I - M VI = 137—235; muscles broad
. *S. thompsoni* (fig. 14e)
— Number of muscle fibres of M I - M VI = 113—159; muscles narrow
. *S. gerlachei* (fig. 14g)

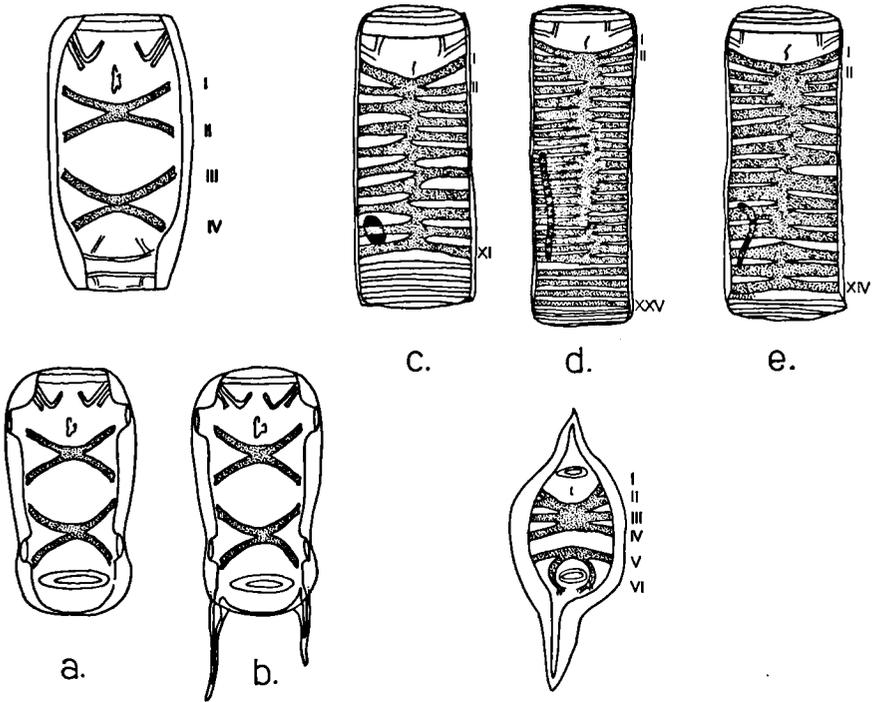


FIG. 15. Schematic representation of the species of the genera *Pegea* and *Ritteriella*. Top row: solitary zooids, bottom row: aggregate zooids. a. *P. confoederata*, b. *P. bicaudata* (for the differences in the solitary zooids cf. fig. 8 and the diagnoses), c. *R. amboinensis*, d. *R. picteti*, e. *R. retracta* (the differences between aggregate zooids of these species are only biometrical).

KEY TO THE SPECIES OF THE GENUS PEGEA

Solitary zooids:

1. — Atrial musculature complicate (cf. fig. 8) *P. bicaudata*
 — Atrial musculature reduced (cf. fig. 8) *P. confoederata* (fig. 15a)

Aggregate zooids:

1. — Two (sometimes one) posterior projections *P. bicaudata* (fig. 15a)
 — No posterior projections *P. confoederata* (fig. 15b)

KEY TO THE SPECIES OF THE GENUS RITTERIELLA

Solitary zooids:

1. — Intestine loosely coiled *R. amboinensis* (fig. 15c)
 — Intestine not coiled, but stretched longitudinally in the posterior part 2
2. — Number of body muscles 10—18 *R. retracta* (fig. 15e)
 — Number of body muscles 19—31 *R. picteti* (fig. 15d)

Aggregate zooids:

1. — Third ventral oral spincter absent; number of muscle fibres of M I - M VI = 31—47 *R. amboinensis*
— Third ventral oral sphincter present; number of muscle fibres of M I - M VI = 60 or more 2
2. — Number of muscle fibres 60—109 *R. retracta*
— Number of muscle fibres 110—169 *R. picteti*

DISCUSSION

From the present study it is again clear, that the number of muscle fibres in salps is of great importance for the distinction of closely related forms. This fact was for the first time appreciated by Foxton (1961). It has presented the solution for the analysis of the relationship between typical specimens of a species and its “varieties”, “forms” or “subspecies”, possessing small morphological differences. In most cases these doubtful deviations from the type appeared to possess a clearly higher or lower number of muscle fibres and through this can be considered separate taxa. The status of these taxa remains, perhaps, a matter of discussion. Anyhow, to designate them as “varieties” or “forms” is quite unsatisfactory, as it is unclear what is meant by these terms. Sympatric “subspecies” seem a *contradictio in terminis*, if there is no apparent mechanism to prevent gene flow, such as different reproductional seasons, different vertical distributions, etc. In a future paper the sympatry of the closely related salp taxa will be treated extensively.

The occurrence of distinctly different species next to closely related ones gives the impression that several “waves” of speciation have taken place in the history of the Salpidae. *Salpa maxima*, *S. aspera* and *S. fusiformis* are clearly separated by a large number of characters and as such might represent fairly old species. *S. tuberculata*, *S. younti* and *S. thompsoni*/*S. gerlachei* differ only barely from the above mentioned species and as such might represent fairly young species, recently split off from the older ones. The same could be argued for the *Ritteriella* species, where *R. picteti* might represent a newcomer. Speculations about the way in which this speciation has taken place will be presented later.

It is in the opinion of the present author not justified to include *S. aspera* (and *S. younti*) in the “*Salpa fusiformis*-group”, compared against *S. maxima* (and *S. tuberculata*), as Foxton (*l.c.*) does. *S. aspera* (and *S. younti*) are clearly intermediate between *S. maxima* (and *S. tuberculata*) and *S. fusiformis* (and *S. thompsoni* + *S. gerlachei*). It is better to speak of three groups within the genus *Salpa*: *S. maxima*-group, *S. aspera*-group and *S. fusiformis*-group.

In view of the many contradictory statements in literature concerning the arrangement of the oral and atrial muscles, which in many cases is thought to be of distinctive value between species, it seems necessary to stress the importance of a thorough study of the variation of these musculatures within the species.

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