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The genus *Thalia* Blumenbach, 1798 (Tunicata, Thaliacea), with descriptions of two new species

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ABSTRACT

Investigations of the marine pelagic tunicate genus *Thalia* Blumenbach, 1798, resulted in the description of two new species, *T. cicar* and *T. sibogae*. In addition the three known subspecies of *Thalia democratica* (Forskål, 1775) are considered full species. The distribution of these species, including *Thalia longicauda* (Quoy & Gaimard, 1824), is given and a key to the solitary and aggregate zooids of the species is added. The specific status of the six taxa of the genus is discussed.

INTRODUCTION

Until 1937 *Thalia democratica* (Forskål, 1775), one of the two representatives of the genus *Thalia* Blumenbach, 1798, at that time, was considered a monotypical species, although its great variability was frequently noted. In 1937, Tokioka described from Japanese waters a variety of this species, which he named *orientalis*, as Tokioka was of the impression that this variety was limited to oriental waters, while the "typical variety" was supposed to be limited to the Atlantic. At the same time Tokioka (1937) described a forma *echinata*, forming part of the variety *orientalis*. Borgelt (1968a, 1968b), after having studied southeast African material and having compared this with the descriptions of Tokioka (l.c.), concluded that three different taxa were involved, which he considered to be subspecies: *Thalia democratica democratica* (= Tokioka's typical variety), *T.d. intermedia* (= partly Tokioka's var. *orientalis* including its forma *echinata*) and *T.d. orientalis* (= also partly Tokioka's var. *orientalis* including its forma *echinata*).

It is not clear why Borgelt (l.c.) decided to describe the three taxa as subspecies in spite of their sympatric occurrence in Japanese and South African waters. To explain his difficulties in distinguishing the aggregate zooids of the three subspecies he stated that this is probably caused by the "continuous gene flow" (Borgelt, 1968a: 58) which would diminish the mor-

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phological differences. It is hard to understand how morphological differences could be maintained notwithstanding a continuous gene flow. It is proposed here, until further information on ecology and microdistribution has become available, to treat the taxa of the genus *Thalia* as separate species. The present study is part of an investigation of samples of Thaliacea from all over the world, which will result in an inventory of the known and undescribed forms.

Material

The localities of the samples studied are represented in the map of figure 1. Rough positions of the sampled stations and collectors are listed below, accompanied by abbreviated indications of the museums in which the material is deposited. ZMA = Zoological Museum of Amsterdam, BMNH = British Museum (Natural History) in London, ZMUC = Zoological Museum of Copenhagen, USNM = United States National Museum, Washington, U.S.A., and RMNH = Rijksmuseum van Natuurlijke Historie at Leiden, the Netherlands.

Atlantic Ocean and Mediterranean:

Plymouth (50°N, 04°W), Marine Biology Laboratory, BMNH. — South Devon coast (50°N, 03°W), Marine Biology Laboratory, BMNH. — Valencia, Ireland (52°N, 10°W), Marine Biology Laboratory, BMNH. — W. Mediterranean (37°—41°N, 01°—12° E), USNM. Mediterranean Cruises, Dr. Gibbs, USNM/ZMA. — Villefranche-s-Mer (43°N, 03°E), Ihle, ZMA. — Naples (40°N, 15°E), Ihle, ZMA. — Triest (46°N, 14°E), Ihle, ZMA. — Newport (Rhode Island, USA, 42°N, 72°W), Norman, BMNH. — North Central Atlantic, st. Juliette 4 (37°N, 38°W), HMS "Snellius", ZMA. — st. India 3

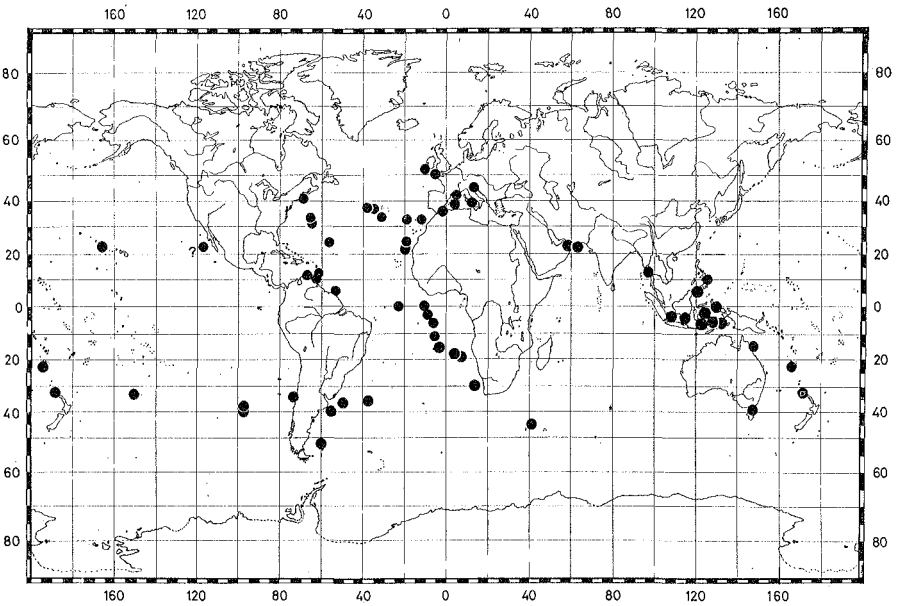

Fig. 1. Oceanic localities from which the studied specimens of *Thalia* originated. Question mark indicates sample of which the locality is uncertain.

(34°N, 30°W), HMS "Snellius", ZMA. — st. India 6 (34°N, 65°W), HMS "Snellius", ZMA. — st. India 1 (33°N, 13°W), HMS "Snellius", ZMA. — st. India 2 (33°N, 19°W), HMS "Snellius", ZMA. — st. Navado F-h-03 (25°N, 57°W), HMS "Snellius", ZMA. — st. Navado 7-01 (25°N, 19°W), HMS "Snellius", ZMA. — st. Echo 1 (22°N, 20°W), HMS "Snellius", ZMA. — (37°N, 36°W), Chazalie Exp., ZMA. — (26°N, 20°W), Terra Nova Exp., st. 16, BMNH. — Bermuda (32°N, 65°W), Ocean Acre Project Cruises 10, 11, 12, 13, USNM/ZMA. — Southern Caribbean (12°—13°N, 68°—70°W), CICAR Project Cruises 12B, 13, 14, 15, 18, 19, ZMA. — (10°—11°N, 61°—62°W), CICAR Project Cruise 15, ZMA. — (06°—08°N, 52°—57°W), CICAR Project Cruises 15, 16/17, ZMA. — St. Vincent (13°N, 61°W), HMS "Rodney", BMNH. — Equatorial Atlantic (01°S, 23°W), Kruizinga, RMNH. — Southeastern Atlantic (0°S, 11°W), Dana Exp., st. 4000 I, VII, ZMUC. — (03°S, 10°W), Dana Exp., st. 3999 III, ZMUC. — (07°S, 08°W), Dana Exp., st. 3998 II, IV, V, IX, X, XI, ZMUC. — (11°S, 07°W), Dana Exp., st. 3997 III, ZMUC. — (15°S, 06°W), Dana Exp., st. 3996 V, VIII, ZMUC. — (30°S, 13°E), Dana Exp., st. 3978 VII, VIII, IX, X, XI, ZMUC. — Off Angola (17°S, 03°E), coll.?, BMNH. — Off Angola (19°S, 05°E), coll.?, BMNH. — Southwestern Atlantic (36°S, 47°W), Challenger Exp., BMNH. — (37°S, 37°W), Challenger Exp., BMNH. — (37°S, 50°W), Challenger Exp., st. 324, BMNH. — (40°S, 55°W), Challenger Exp., st. 319, BMNH. — Falkland Islands (52°S, 60°W), Wright, BMNH.

INDIAN OCEAN:

S.W. Indian Ocean (45°S, 41°E), Discovery Antarctic Exp. 1910, BMNH. — Arabian Sea (23°N, 64°E), John Murray Exp., st. 61, BMNH. — Gulf of Oman (24°N, 59°E), John Murray Exp., st. 76, BMNH. — Maungmagan (Birma, 14°N, 98°E), Meggitt, BMNH. — Indonesian Archipelago (07°N—10°S, 105°—135°E), Siboga Exp., st. 93, 98/99, 106, 109, 136, 138, 144, 146, 165, 184, 186, 189a, 213, 217 and 223, ZMA. — Java Sea (113°E, 03°—07°S), Delsman, st. 6A, 10B, 12B, 14A, 16A, 21A, 23, 28, 36, ZMA.

PACIFIC OCEAN:

Between Bohol and Limosana Island (Philippine Archipelago, 10°N, 124°E), Albatross Exp., st. 5233, USNM. — Northern Great Barrier Reef area (14°—16°S, 144°—146°E), Grt. Barrier Reef Exp., st. 7, 13, 14, 16, 18, 19, 21, 22, 23, 26, BMNH. — Nouméa (New Caledonia, 22°S, 167°E), Meryon, BMNH. — Idem, Wijsman-Best, ZMA. — North of New Zealand (34°S, 172°E), Terra Nova Exp., st. 93, BMNH. — Between Laysan and Honolulu (20°—25°N, 158°—172°E), Schauinsland, ZMA. — E. Pacific (?), MLR-Cruise, st. 5805—9470, BMNH. — Southern Pacific (33°S, 151°W), Challenger Exp., BMNH. — (37°S, 94°W), Challenger Exp., BMNH. — (39°S, 94°W), Challenger Exp., st. 295, BMNH. — (34°S, 72°W), Challenger Exp., BMNH.

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Koperdraat sorted the CICAR samples, financially supported by the Netherlands Organisation of Pure Research (ZWO). Mr. J. Zaagman assisted with the preparation of the distribution maps.

Terminology

In literature dealing with *Thalia* there is some confusion about the names given to the various projections of the test of the animals. To avoid misunderstanding of the descriptions given below the terms used are defined as follows (see fig. 2):

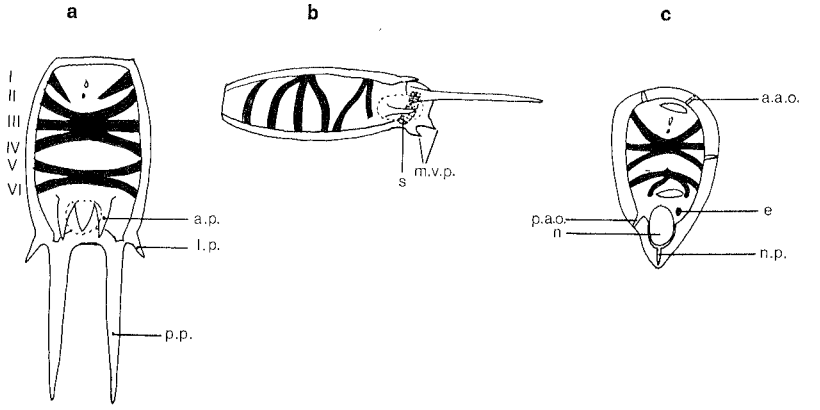

Fig. 2. Terminology of the morphological characters distinguishing the species of *Thalia*. a. solitary zooid, dorsal view (I—VI = body muscles; a.p. = atrial palp; l.p. = lateral projection; p.p. = posterior projection). b. solitary zooid, lateral view (m.v.p. = medioventral projections; s = stolon). c. aggregate zooid, dorsal view (a.a.o. = anterior attachment organ; p.a.o. = posterior attachment organ; e = embryo; n.p. = nucleus projection).

Solitary zooids: "Posterior projections" (called "lateral projections" by Ritter, 1905) are the long stiff projections protruding beyond the posterior part of the animal. At their base a slight ingrowth of the body wall is present. Posterior projections are characteristic of all members of the genus *Thalia*.—"Lateral projections" (called "ventrolateral projections" by Borgelt, 1968b) are the small sideward protruding projections on the posterior part of the test. They fail in some of the species of *Thalia*.—"Medioventral projections" are the two small protrusions crowning the thickened part of the test ventral to the nucleus. Size and shape of them differ in the various species of *Thalia*. —"Atrial palps" (called "dorsolateral projections" by Borgelt, 1968b) are the two small projections flanking the triangular atrial valve. They may be straight and simple, bifurcate or absent depending on the species.

Aggregate zooids: The "nucleus projection" is a thin sharply pointed extension of the body wall posterior to the nucleus. This nucleus projection is present in two of the six species of *Thalia*.—"Attachment organs" are thin

protrusions of the body wall traversing the test, by which the individuals of a chain are attached and — presumably — keep in nervous contact. The shape and length of some of these attachment organs, particularly the anterior and posterior ones, may have some taxonomic significance.

Thalia Blumenbach, 1798

Nomenclatorial note. — *Thalia* Blumenbach, 1798, seems to be used first for specimens of what is now known to be *Cyclosalpa pinnata* (Forskål, 1775). By strict application of the Law of Priority *Thalia* Blumenbach, 1798, is a senior synonym of *Cyclosalpa* De Blainville, 1827, as was pointed out by Waal (1968). Waal proposed to the International Commission on Zoological Nomenclature to designate *Salpa democratica* Forskål, 1775, as the type species of the genus *Thalia*. It is assumed here that the commission will eventually decide in favour of this proposition.

Type species. — *Salpa democratica* Forskål, 1775.

Description. — Solitary zooids: Test elongately cylindrical, thickened ventrally around the nucleus, with two long, more or less stiff posterior projections. Oral aperture placed anteriorly, atrial aperture dorso-posteriorly. Body musculature consisting of one prominent intermediate muscle (I) which is interrupted dorsally and five body muscles proper (II-VI), of which the fifth is interrupted ventrally. Dorsal tubercle simple and small, dorsal languet present, nucleus compact, stolon coiled around nucleus.

Aggregate zooids: Test egg-shaped, rounded or pointed posteriorly. Body equipped with five body muscles (I-V), fused dorsally into two groups (I-III and IV-V); all muscles interrupted ventrally. Nucleus compact, testis arranged in four lobes. Dorsal tubercle simple and small, dorsal languet present.

Six species are known. For descriptions of *T. democratica, T. rhomboides* and *T. orientalis* one is referred to Borgelt (1968b). For the description of *T. longicauda,* see Godeaux (1967).

1. **Thalia democratica** (Forskål, 1775)

Salpa democratica Forskål, 1775: 113, pl. 36: fig. G; Heider, 1895: 368 (after Borgelt, 1968b); Russell & Colman, 1935: 210 (in part).
Salpa mucronata Forskål, 1775: 114, pl. 36: fig. D; Ihle, 1910: 47 (in part); Streiff, 1908: 38, fig. 26—30.
Biphora democratica; Bruguière, 1789: 180.
Biphora mucronata; Bruguière, 1789: 181.
Salpa spinosa Otto, 1823: 303, pl. 42; fig. 1.
Dubreuillia cirrhosa Lesson, 1830: 278 (after Borgelt, 1968b).
Salpa caboti Desor, 1848: 75 (after Borgelt, 1968b).
Salpa democratica-mucronata; Traustedt, 1885: 365, pl. 2: fig. 25—28; Herdman, 1888: 79, pl. 8: fig. 1—10.
Thalia mucronata; Lahille, 1890: 11 (after Borgelt, 1968b).
Thalia democratica; Metcalf, 1919: 109; Stiasny, 1927: 441, fig. 37—42; Thompson, 1948: 139, pl. 56—59; Tokioka, 1955: 77, fig. 20; Fagetti, 1959: 215, fig. 1—2; Bary, 1960: 108; Amor, 1966: table I; Esnal, 1970b: 126; Dossman, 1970: 75, fig. 5.

? *Thalia democratica*; Philippine form, Metcalf, 1919: 118.
Thalia democratica var. *orientalis* Tokioka, 1937: 226 (in part).
Thalia democratica f. *typica* Sewell, 1953: 25; Tokioka, 1964: table 2; Bernard, 1958: 218, table I, fig. 8d.
Thalia democratica ssp. *democratica* Borgelt, 1968b: 68, fig. 1.

Type locality. — near Mallorca, Western Mediterranean.

Comments. — To the extensive description of Borgelt (1968b) might be added that the total number of muscle fibres in solitary zooids (M I-VI) is 37-86. This wide variation is due to clinal variation in the same way as described for *Salpa fusiformis* Cuvier, 1804 (see Van Soest, 1972). In aggregate zooids the test is bluntly pentagonal and never echinate.

Diagnostic characters. — Solitary zooids: atrial palps simple and straight, test smooth; lateral projections small, medioventral projections small and of unequal length, the anterior one being smallest; all test projections echinate. Muscle fibre number M I-VI is 37-86 (n = 118). Body muscles II-IV and V-VI touch or fuse over a short distance only. Aggregate zooids: nucleus bears a posterior projection; test pentagonal posteriorly; number of muscle fibres in M I-V is 15-17, normally 16.

Size: Length of solitary zooids 2.3-11.7 mm (posterior projections excluded) (n = 208), aggregate zooids 1.8-18.2 mm (n = 234).

Distribution. — The distribution data presented here are mostly based on material studied by the author, as previous records did not discriminate between the different taxa of the genus. Only when literature records were accompanied by descriptions or figures, from which the taxon could be

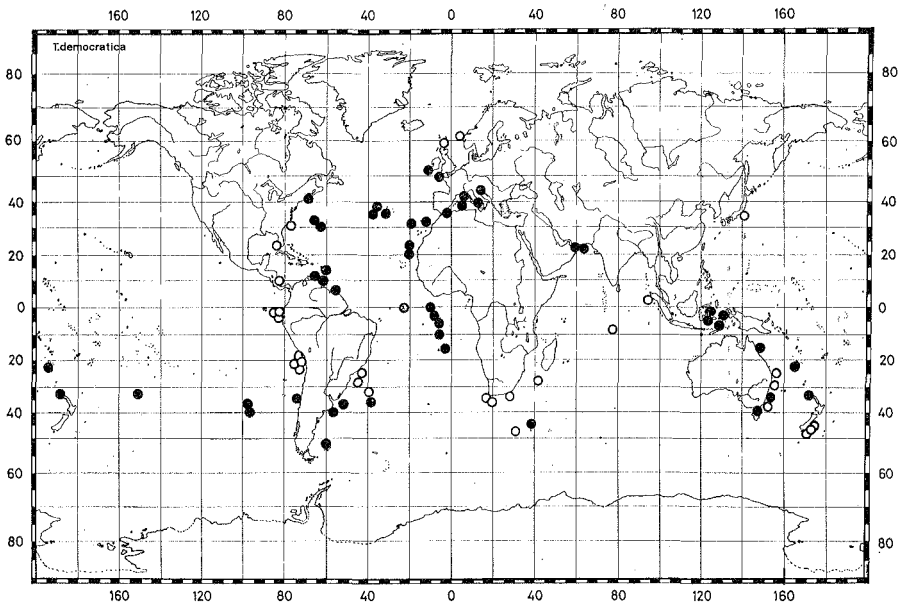

FIG. 3. Distribution of *Thalia democratica* (Forskål, 1775). Black dots: records examined by the author; open circles: records based on literature data.

recognized, they were included in the present distribution maps (open circles on the maps). *Thalia democratica* (fig. 3) has been found seasonally in the northern North Sea (Apstein, 1894), in the Faroe-channel and west of Scotland (Fraser, 1960) and near the southern coasts of England and Ireland. It has been found off the east coast of the U.S.A. near Rhode Island, in the central north Atlantic, in the western Mediterranean, near Villefranche and Naples, in the Adriatic (Triëst), in the Gulf of Mexico (Metcalf, 1919) in the southern Caribbean, off the Surinam coast, in the central south Atlantic, the western south Atlantic (not in the Benguela current area), near Cape of Good Hope and in southeast African waters (Borgelt, 1968b), in the northern Indian Ocean (Arabian Sea, Andaman Sea), in Indo-Australian waters, north of New Zealand, off the east coast of New Zealand (Bary, 1960), off Nouméa (New Caledonia), off the east coast of Australia (Thompson, 1948), in the Bass Strait area, off the Pacific Coast of Middle Japan (Tokioka, 1937), in the south Pacific (35°-40° S, 70°-150° W) and off the west coast of South America (Fagetti, 1959, and Dossman, 1970). No samples were available from the central Indian Ocean and the north Pacific, and only a few from the central Pacific. Northernmost record (not examined): northern North Sea (Apstein, 1906: near Bergen, Norway, 61°N); southernmost record: Falkland Islands (52°S; BMNH. 1842.2.24.77), a surprising record as this area is generally presumed to fall outside the normal distribution of *T. democratica*; it is probably a seasonal occurrence, just as the northernmost records.

2. **Thalia rhomboides** (Quoy & Gaimard, 1824)

Salpa rhomboides Quoy & Gaimard, 1824: 510, pl. 74: fig. 3—4.
? *Salpa monotoma* Quoy & Gaimard, 1834: 591; 1833: pl. 89: fig. 11—14.
Salpa pyramidalis Quoy & Gaimard, 1834: 593; 1833: pl. 89: fig. 15—18.
Salpa mucronata; Apstein, 1906: 252, pl. 28: fig. 19—22 (in part); Ihle, 1910: 47 (in part).
Salpa democratica; Russell & Colman, 1935: 210 (in part).
Thalia democratica; Sewell, 1926: fig. 28; Ihle & Ihle-Landenberg, 1935: 19, table I.
Thalia democratica var. *orientalis* Tokioka, 1937: 226, fig. 1 (in part).
Thalia democratica var. *orientalis* f. *echinata* Tokioka, 1937: 229 (in part).
Thalia democratica f. *orientalis*; Sewell, 1953: 33 (in part).
Thalia democratica echinate form; Yount, 1954: 323, fig. 28a—d, fig. 29a—d.
Thalia democratica ssp. *intermedia* Borgelt, 1968b: 70, fig. 2.

Borgelt (1968b) was apparently unaware of *Salpa rhomboides* and *Salpa pyramidalis* of Quoy & Gaimard (1824, 1834), when he described the new subspecies *intermedia.*

Type locality. — Between Réunion ("Ile de Bourbon") and Australia ("Nouvelle Hollande").

Comments. — To the extensive description of Borgelt (1968b: 70, *T. democratica intermedia*) must be added, that in solitary specimens the number of muscle fibres is 77-106. In the aggregate zooid the test is sharply ridged, see for instance Apstein (1906: fig. 19) and Yount (1954: fig. 29a). In some specimens, e.g. in the samples of Siboga-Expedition st. 104, 136, 138, 144, and

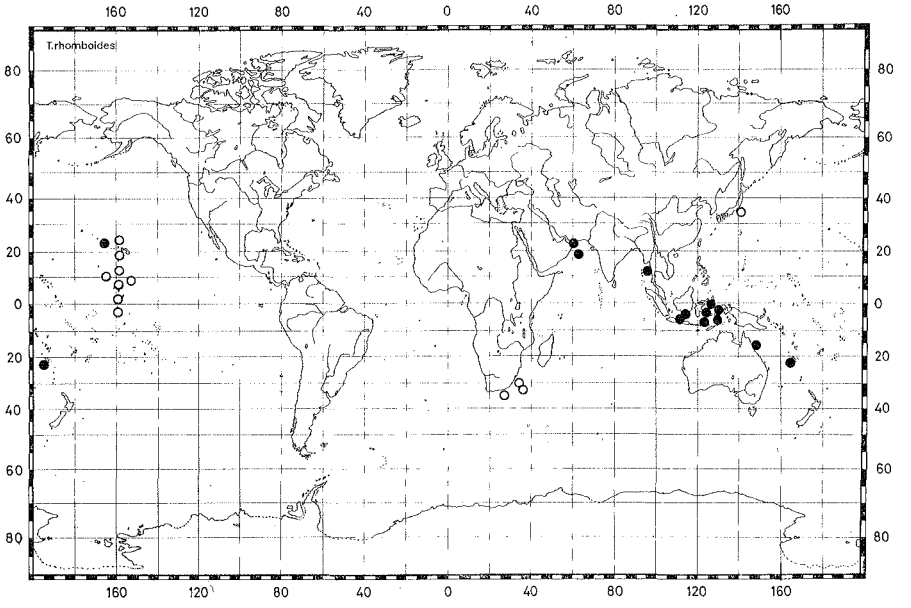

FIG. 4. Distribution of *Thalia rhomboides* (Quoy & Gaimard, 1824). Black dots: records examined by the author; open circles: records based on literature data.

213 the test posterior to the nucleus is strongly elongated into a "tail"; this was already noted by Apstein (1906: fig. 20) and Sewell (1926: fig. 24).

Diagnostic characters. — Solitary zooids: atrial palp bifurcated. Strongly papillated all over the test. Fairly long lateral projections, strongly developed medioventral projections of unequal length; all test projections echinate. Muscle bands very wide, number of muscle fibres 77-106 (n = 64); body muscles II-IV and V-VI touch. Aggregate zooids: Nucleus projection absent, test bearing longitudinal and transversal ridges with numerous papillae; posterior part of the test pentagonal, sharply pointed. Number of muscle fibres 15-17, normally 16.

Size: Length of solitary zooids 3.0-13.5 mm (n = 72) (posterior projections excluded), aggregate zooids 1.8-10.4 mm (n = 98).

Distribution (fig. 4) —. *T. rhomboides* seems to be restricted to Indo-Pacific waters, as it has not been found in the Atlantic so far. Borgelt (1968b) records it from southeast African waters, as did Quoy & Gaimard (1834: *Salpa pyramidalis* on Agulhas Bank). It has been found in the Gulf of Arabia, the Indo-Australian archipelago, off the east coast of middle Japan (Tokioka, 1937), in the central Pacific (Yount, 1954), between Laysan and Honolulu (Hawaii Islands), off Nouméa (New Caledonia: Tokioka, 1960) and off the north-eastern coast of Australia (Great Barrier Reef area).

3. **Thalia orientalis** Tokioka, 1937

Thalia democratica var. *orientalis* Tokioka, 1937: 226 (in part).
Thalia democratica var. *orientalis* f. *echinata* Tokioka, 1937: 229 (in part).
Salpa democratica; Ritter, 1905: 73.
Salpa mucronata; Ihle, 1910: 47 (in part).
Thalia democratica smooth form; Yount, 1954: 323, fig. 28e, fig. 29e.
Thalia democratica f. *orientalis*; Bernard, 1958: 217, fig. 7, 8a, table I.
Thalia democratica ssp. *orientalis*; Borgelt, 1968b: 72, fig. 3.

Type locality. — Misaki, east coast of middle Japan. Type specimens are lost (personal communication by Prof. T. Tokioka).

Comments. — In Borgelt's extensive description (1968b: 72) the word "usually" should be omitted in reference to characters of the test, as it implies a variation of characters not found by the present author. The number of muscle fibres in solitary zooids of M I-VI = 30-36.

Diagnostic characters. — Solitary zooids: Eight longitudinal rows of minute echinae on the surface of the soft, pliable test; posterior projections very long (sometimes exceeding the length of the test), lateral projections absent, atrial palp bifurcate, medioventral projections strongly developed, of unequal length, the anterior one being smallest; all test projections echinate. Muscle bands narrow, number of muscle fibres 30-36 (n = 42). Muscles II and III touch or fuse barely, muscle III-IV and V-VI strongly fused dorsally. Aggregate zooids: Nucleus projection absent; the posterior and two anterior attachment

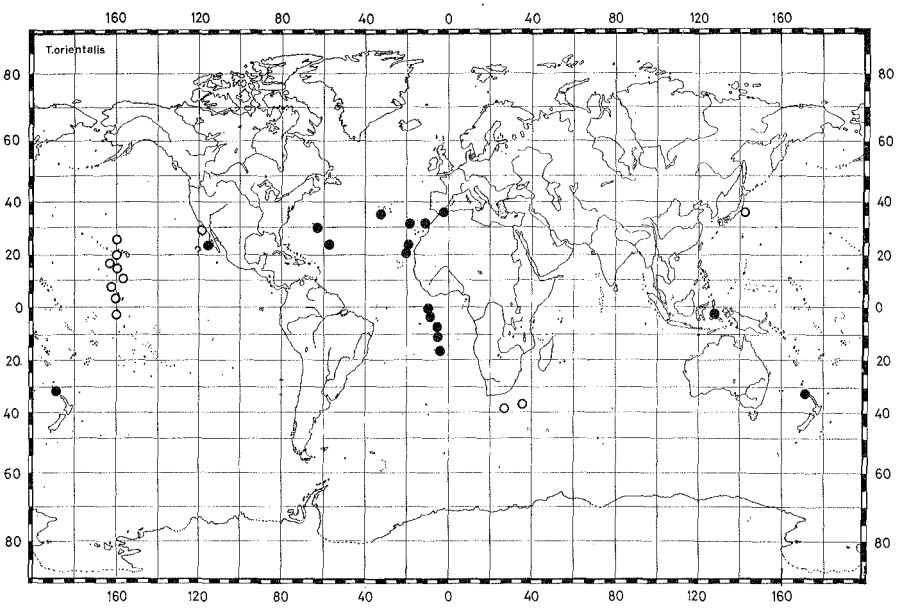

FIG. 5. Distribution of *Thalia orientalis* Tokioka, 1937. Black dots: records examined by the author; open circles: records based on literature data. Question mark indicates uncertain record.

organs protruding beyond test wall; test bluntly pointed posteriorly, possibly tetra- or pentagonal, but very weakly so. Number of muscle fibres 15-17, normally 16.

Size: Solitary zooids 3.0-6.8 (n = 42) (posterior projections excluded), aggregate zooids 2.1-4.5 mm (n = 15).

Distribution (fig. 5). — This species seems to have a wide distribution in the warm and temperate parts of all oceans; it has been found in the western Mediterranean, in the central north Atlantic, in the central south Atlantic, in southeast African waters (Borgelt, 1968b), in Indo-Australian waters, north of New Zealand, near Japan (Tokioka, 1937), in the Hawaii region, and off the west coast of the U.S.A. (San Diego area: Ritter, 1905).

4. **Thalia cicar** nov. spec.

Salpa mucronata; Ihle, 1910: 47—48 (in part).
Salpa democratica; Russell & Colman, 1935: 210—217 (in part).
Thalia democratica var. *orientalis* Tokioka, 1937: 226—228 (in part).
Thalia democratica f. *orientalis*; Sewell, 1953: 33—36 (in part); Godeaux, 1960: 12, fig. 3.

Holotype (fig. 6a). — a solitary zooid from CICAR st. 18-004/203 (12°40.5′N-12°40.9′N, 68°55′W-69°02.6′W, north of Curaçao, 18-XI-1970, collected by HMS "Luymes", surface), ZMA. TU. 1355.

Paratypes. — nine solitary zooids and ten aggregate zooids (one of which has been pictured in fig. 6c), all from the same locality and date as the holotype, ZMA. TU. 1356/1357.

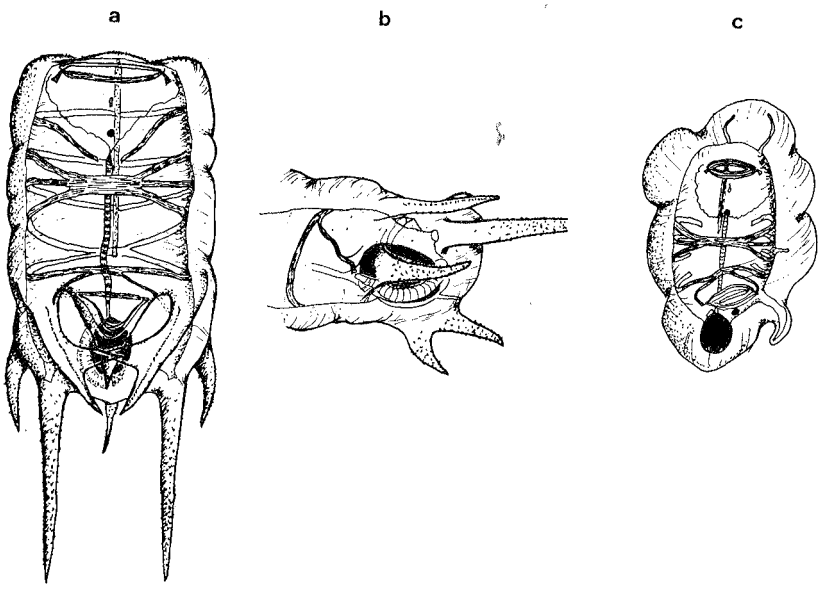

FIG. 6. *Thalia cicar* nov. spec. a. holotype (ZMA. TU. 1355), dorsal view of entire animal. b. holotype, lateral view of posterior part. c. agregate zooid (paratype ZMA. TU. 1356), dorsal view of entire animal.

Description. — Solitary zooids: Test: bulky, flabby, relatively short when compared with height and width (length : height : width = 3:2:2). Test projections strongly developed; atrial palps bifurcate and very large, lateral projections relatively long, posterior projections relatively short when compared to other species of *Thalia*. Echinations only on projections and ridge surrounding the oral aperture, not on the test proper. Internal organs: Dorsal tubercle, gill, endostyl, intestine, vascular and nervous system the same as in the type species (see Borgelt, 1968b).

Musculature: M II-VI dorsally fused into two groups (II-IV and V-VI) over a wide area. Muscle bands narrow, number of muscle fibres M I-VI 26-37 (n = 34).

Size: Length of the holotype 4.0 mm, range of the holotype and nine paratypes 2.2-4.4 mm (posterior projections excluded). Maximal size encountered in the known range of the species: 7.7 mm.

Aggregate zooids: Test: bulky, flabby, with many roundish depressions and elevations; rounded posteriorly or slightly pointed, but not pentagonally. Attachment organs: number variable, on the average fairly long; posterior attachment organ protrudes considerably beyond the test wall.

Internal organs: The same as in the type species (see Borgelt, 1968b). Nucleus projection absent, nucleus rounded or flattened posteriorly.

Musculature: Muscle bands fused into two groups (I-III and IV-V) dorsally. Muscle bands narrow, fusion over a wide area. Number of muscle fibres 16.

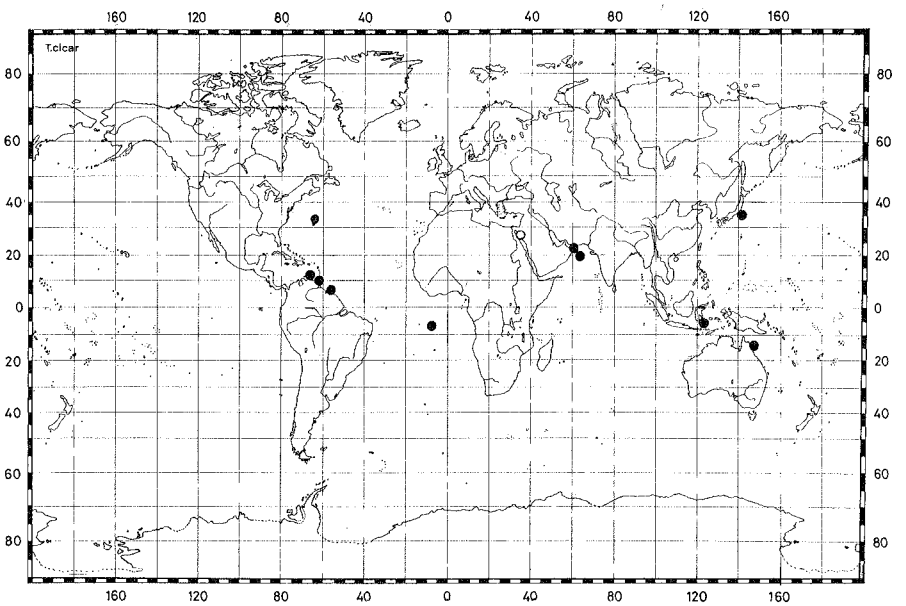

FIG. 7. Distribution of *Thalia cicar* nov .spec. Black dots: records examined by the author; open circles: records based on literature.

Size: Of the figured paratype 3.4 mm, size range of ten paratypes 1.9-4.0 mm. Maximal size encountered in the distributional range of the species: 4.6 mm.

Distribution (fig. 7). — *T. cicar* is the commonest salp species in the area around Curaçao, Aruba and Bonaire, and off the Surinam coast. A few specimens have been found near Bermuda and in the central south Atlantic (Dana-Exp. st. 3998: 07°S, 08°W). It occurs in the Arabian Sea, in the Gulf of Elat (Godeaux, 1960: fig. 3), in the Indo-Australian archipelago, off the Pacific coast of middle Japan (Tokioka, 1937) and off the northeastern coast of Australia (Great Barrier Reef area).

5. **Thalia sibogae** nov. spec.

Salpa mucronata; Ihle, 1910: 47 (in part).
Thalia democratica var. *orientalis*; Tokioka, 1967: 230 (in part).

Holotype. — A solitary specimen (fig. 8a) from Siboga Exp. st. 93 (ca 05°N, 120°E), Pulu Sanguisapio, Tawi-Tawi Island, Sulu-archipelago, 24/25-VI-1899, bottom depth 12 m. ZMA. TU. 1358.

Paratypes. — Nine solitary zooids and ten aggregate zooids (one of which has been pictured in fig. 8c) from the same locality as the holotype, ZMA. TU. 1359/1360.

Description. — Solitary zooids: Test: bulkily rounded, quite firm, smooth except for test projections and ridge around oral aperture. Atrial palps bi-

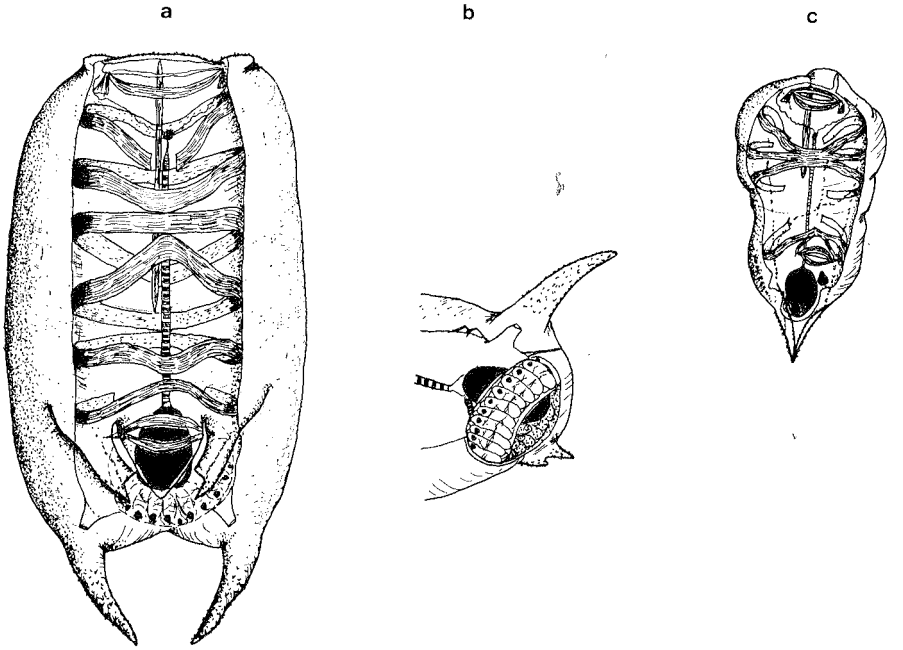

FIG. 8. *Thalia sibogae* nov. spec. a. holotype (ZMA. TU. 1358), dorsal view of entire animal. b. holotype, lateral view of posterior part. c. aggregate zooid (paratype ZMA. TU. 1359), dorsal view of entire animal.

furcate, fairly small. Lateral projections absent. Posterior projections very short, situated at an angle to the surface of the test. Medioventral projections small and of unequal length; sometimes the anterior one fails. Internal organs: The same as in the type species (see Borgelt, 1968b).

Musculature: M II-IV touch dorsally, M V-VI near but do not touch dorsally. Muscle bands very wide, number of muscle fibres 56-84 (n = 11).

Size: Length of the holotype 8.1 mm, size range of holotype and nine paratypes 4.6-11.1 mm (posterior projections excluded).

Aggregate zooids: Test: bulkily rounded anteriorly, sharply pointed pentagonally posteriorly. Test surface traversed by weakly developed echinated ridges.

Attachment organs: One or two anteriorly, possibly also laterally; posterior attachment organ very small, never protruding beyond the test wall.

Nucleus projection: Absent, nucleus rounded posteriorly. Internal organs: The same as in the type species (see Borgelt, 1968b).

Musculature: Body muscles M I-III and M IV-V fused over a short stretch. Muscle bands wide, number of muscle fibres 16. Size: Length of the figured paratype 5.2 mm, size range of ten paratypes 3.5-6.5 mm.

Distribution (fig. 9). — This species in only known from a very rich sample from the type locality and from one solitary specimen captured by the Albatross-expedition, 1908 at st. 5233, between Bohol and Limosana Island (Philippine archipelago), 10°N, 124°E, USNM. cat. no. 11750. Tokioka (1967) identified this specimen as *Thalia democratica* var. *orientalis* Tokioka, 1937.

6. **Thalia longicauda** (Quoy & Gaimard, 1824)

Salpa longicauda Quoy & Gaimard, 1824: 507, pl. 73: fig. 8; Ihle, 1911: 588.
Salpa democratica-mucronata var. *flagellifera* Traustedt, 1885: 369, pl. 1: fig. 12—13.
Salpa flagellifera; Apstein, 1894: 13; Apstein, 1906: 253—254, fig. 9.
Thalia longicauda; Metcalf, 1919: 119—121; Krüger, 1939: 126—127; Amor, 1966: table I, fig. 1; Godeaux, 1967: 91—102; Esnal, 1970a: 248.

Type locality. — Near Port Jackson, E. Australia.

Note. — The description and the figure of Quoy & Gaimard (1824) are not very specific. Their species could be synonymous with one of the preceding species of *Thalia*. Material from the type locality collected by the Challenger expedition only contained *Thalia democratica*, which of course does not prove a thing. However, as the area near Port Jackson is typically devoid of colder, subantarctic influences the possibility of occurrence of this species in that area is not too likely, when one considers the distribution of the species (fig. 9). Moreover, it has not been found by Thompson (1948). To decide in this matter examination of the type material is necessary. For a full description one is referred to Godeaux (1967).

Diagnostic characters. — Solitary zooids: Atrial palps absent apart from two vestigial elevations of the test on both sides of the atrial aperture. Lateral and medioventral projections absent; posterior projections thin, not stiff as in the other species of *Thalia*, not particularly long; echinations on the

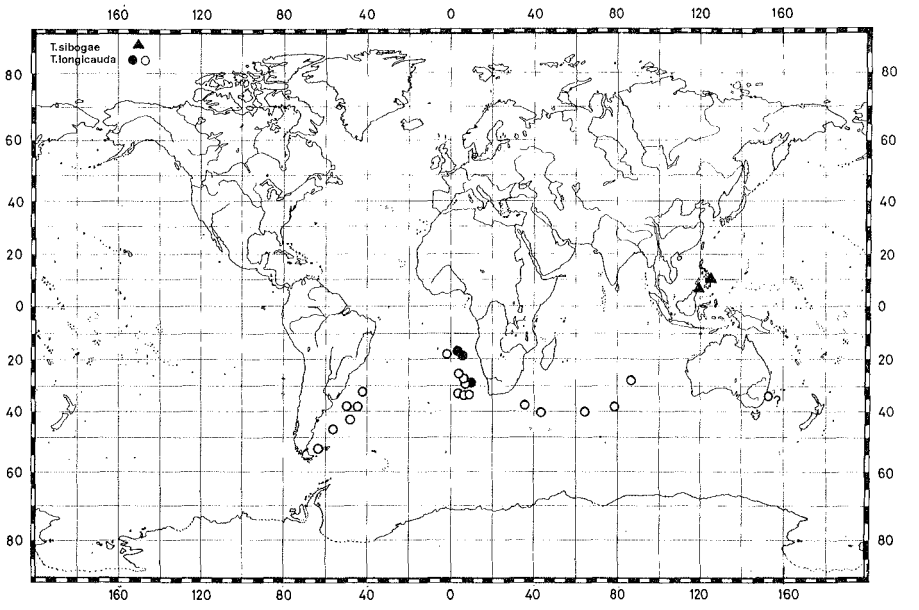

FIG. 9. Distribution of *Thalia sibogae* nov. spec. (black triangles) and *Thalia longicauda* (Quoy & Gaimard, 1824) (black dots and open circles). Question mark indicates doubtful occurrence.

posterior projections very delicate. Test smooth. Muscle bands not fused into groups, but running parallel dorsally. Muscle fibre number 75-80. Maximal size encountered 11.6 mm (n = 10). Aggregate zooids (after Godeaux, 1967, as no specimens were available for the present study): Nucleus bearing posterior projection; test smooth, rounded, but pointed posteriorly; muscle fibre number M I-V = 29-38.

Distribution (fig. 9). — The species has been found in the Benguela current area (17°S-35°S, 3°W-20°E: present material; Traustedt, 1885; Krüger, 1939), off the Atlantic coast of South America (31°S-54°S: Amor, 1966; Esnal, 1970b), south east of South Africa (Apstein, 1906), near the islands of New Amsterdam and St. Paul (Traustedt, 1885; Godeaux, 1967), central Indian Ocean (27°S, 83° E: Apstein, 1906) and off the east coast of Australia (type locality of Quoy & Gaimard, 1824). According to Michaelsen (1914) the species was found at 01°S, 07°E by the Deutschen Tiefsee-Expedition. The report of Apstein (1906) on the salps of this expedition does not mention this record, so it is probably a mistake.

Discussion

The taxonomic status of the various forms of the genus *Thalia*, presented here as species, remains a matter of consideration. Viewed geographically, all taxa with the possible exception of *Thalia longicauda*, are of sympatric occurrence over a wide area. Moreover, in many instances two or more taxa have been found to occur in the same plankton samples, which makes reproductive isolation seem improbable, were they of subspecific level. Only in one instance an intermediate solitary zooid has been found. It is probably a hybrid of *T. democratica* and *T. cicar* from Great Barrier Reef st. 13 (16°S, 145°E). The hybrid has been pictured in figure 11c; 11a and 11b are the local

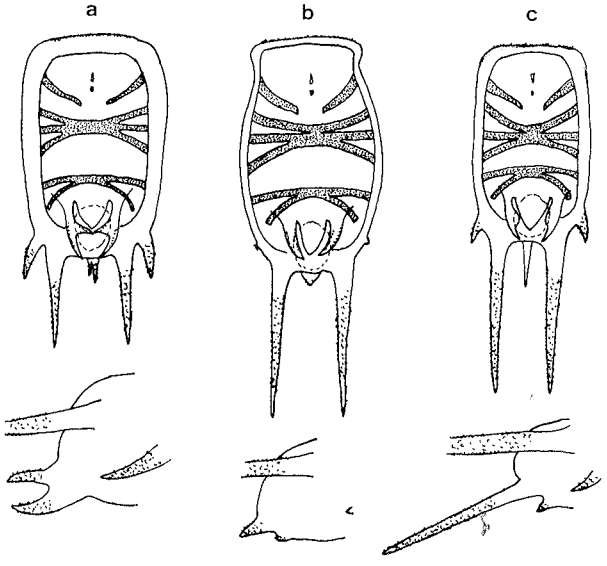

Fig. 11. Presumed hybridization of *Thalia cicar* (a) and *T. democratica* (b) from the Great Barrier Reef area. The presumptive hybrid, a solitary specimen (c), shows intermediate characters in the shape and size of the test projections.

T. democratica and *T. cicar*. The possibility is not excluded that the presumed hybrid specimen in reality belongs to a new, undescribed taxon of the genus *Thalia*. More specimens are needed to decide in this matter. Hybridization would indicate that occasionally reproductive contact between the taxa of the genus *Thalia* is possible; whether this denies their specific status is hard to decide from this single record. In all other instances the species could be readily recognized, at least as far as the solitary zooids are concerned. Aggregate zooids are difficult to distinguish in some parts of the oceans, due, no doubt, to clinal and other variations. This will be a subject of future papers.

Thalia cicar seems to have some preference for neritic surroundings. Most of the records are from offshore localities. The same can be said of *T. sibogae*,

KEY TO THE SPECIES OF THE GENUS *Thalia* BLUMENBACH, 1798

A. Solitary zooids.

1. — Body muscles running parallel dorsally; atrial palps and medioventral projections absent . . . . . *longicauda* (fig. 10f)
   — Body muscles fused into two groups (II-IV and V-VI) dorsally; atrial palps and medioventral projections present 2
2. — Atrial palps simple and straight . . . . . *democratica* (fig. 10a)
   — Atrial palps bifurcate 3
3. — Test papillated 4
   — Test smooth 5
4. — Test papillated strongly, number of muscle fibres M I-VI = 70-110, lateral projections present . . . . . *rhomboides* (fig. 10b)
   — Eight longitudinal ridges of very delicate echinations, muscle fibres M I-VI = 28-39, lateral projections absent . . . *orientalis* (fig. 10d)
5. — Lateral projections present, muscle fibres M I-VI = 25-37 . . . . . *cicar* (fig. 10c)
   — Lateral projections absent, muscle fibres M I-VI = 56-84 . . . . . *sibogae* (fig. 10e)

B. Aggregate zooids.

1. — Number of muscle fibres M I-V = 29-38 . . *longicauda* (fig. 10f)
   — Number of muscle fibres M I-V = 16 (15-17) 2
2. — Test papillated 3
   — Test smooth 4
3. — Test prismatic in appearance, echinated ridges sharp . . *rhomboides* (fig. 10b)
   — Test roundish, echinated ridges barely visible . . *sibogae* (fig. 10e)
4. — Posterior part of test rounded, not pentagonal . . . *cicar* (fig. 10c)
   — Posterior part of test pentagonally pointed 5
5. — Nucleus bearing posterior projection, anterior attachment organs not protruding beyond test wall . . . . . *democratica* (fig. 10a)
   — No posterior projection on nucleus, anterior attachment organs protruding beyond test wall . . . . . *orientalis* (fig. 10d)

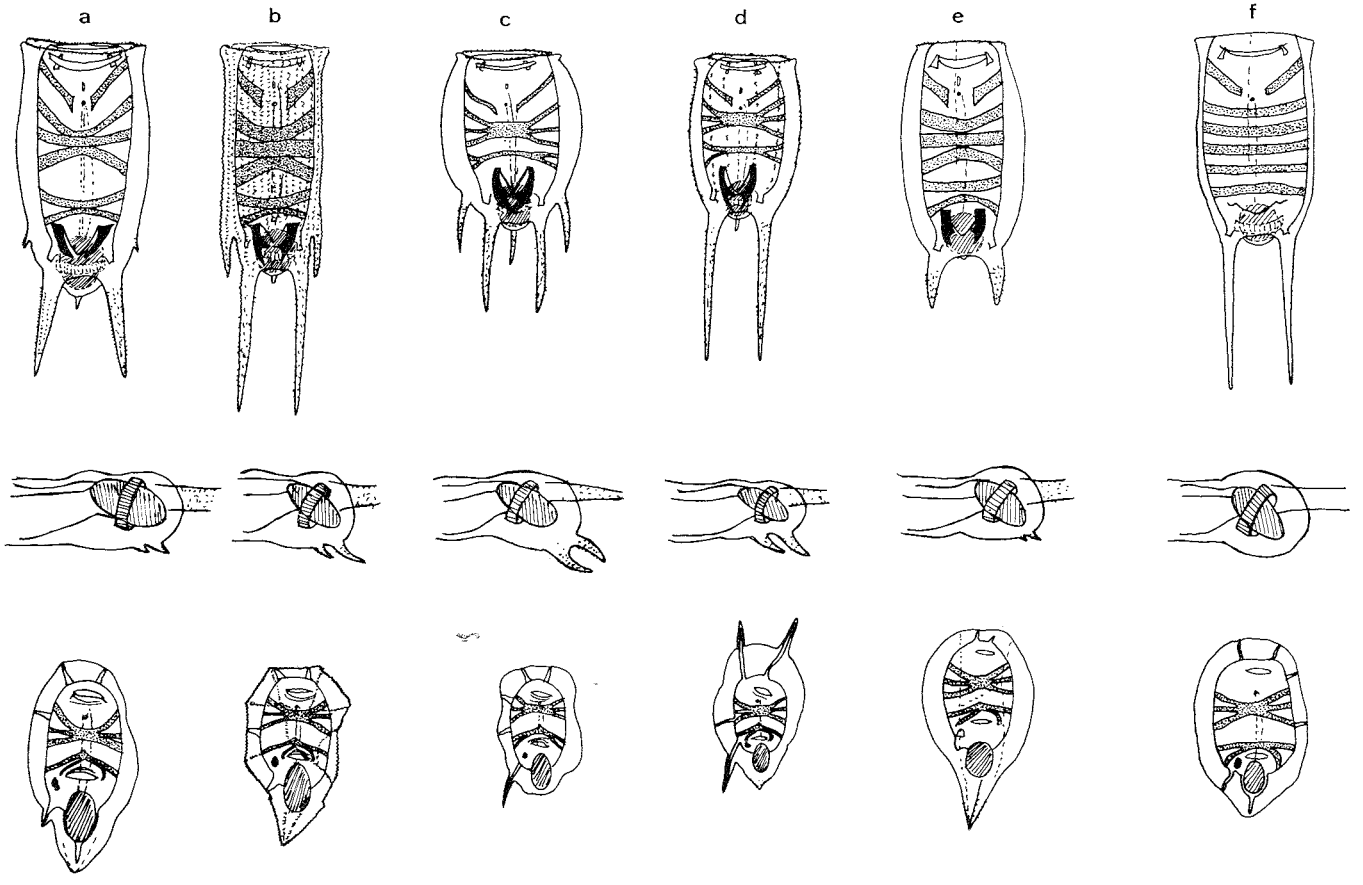

FIG. 10. Schematic representation of the six species of the genus *Thalia*. Top row: solitary zooids, dorsal view; middle row: solitary zooids, lateral view of posterior part; bottom row; aggregate zooids. a. *T. democratica*, b. *T. rhomboides*, c. *T. cicar*, d. *T. orientalis*, e. *T. sibogae*, f. *T. longicauda*.

although it is only known from two localities. By and large *T. rhomboides* also is found mostly in continental seas and lagoons. *T. orientalis* seems to be typically oceanic: it has not been found in the Curaçao area, nor in the Arabian Sea or the Great Barrier Reef area. *T. democratica* is apparently indifferent in this respect, although most of its neritic records are from areas where oceanic currents run along the coasts. *T. longicauda* is definitely associated with the subantarctic waters. In the one area where it penetrates far north (Benguela current), the other species of *Thalia* fail. In fact *T. longicauda* has never been found in any sample together with other *Thalia* species. However, the distributional ranges of *T. longicauda* and *T. democratica* do have some overlap, for instance along the Atlantic coast of South America and south east of South Africa. It is assumed that this overlap is only seasonal: in the summer season with increased sea temperatures *T. longicauda* presumably moves to higher latitudes, while its winter range is partly taken over by *T. democratica.* In winter both species probably will move north, without actually meeting. Apart from being allopatric, *T. longicauda* is also morphologically clearly separated from its five relatives, which can be indicated conveniently as the "*Thalia democratica*-group".

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