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MYZOSTOMIDA (ANNELIDA) FROM SINGAPORE, WITH RELATED INDO-PACIFIC DISTRIBUTION RECORDS AND DESCRIPTIONS OF THREE NEW SPECIES

Igor Eeckhaut, Didier VandenSpiegel and **Mark J. Grygier**

ABSTRACT. - Seven myzostomidan species of the genus *Myzostoma* F.S. Leuckart, 1836, were observed alive in association with comatulid crinoids collected in the territorial waters of Singapore. An eighth species from Singapore was found in a museum collection. All eight species are described and most are illustrated by color photographs from life and by scanning electron micrographs. Three of the species are new to science: *M. jaegersteni*, *M. capitocutis* and *M. singaporense*; *M. brachiatum* Graff, 1877, is recorded for the second time and a lectotype is designated for it. Other new Indo-West Pacific distribution records of four of the eight species are listed.

INTRODUCTION

The Myzostomida are represented by about 140 species of obligate symbionts of echinoderms which have unsettled taxonomic affinities. Most of them look like flatworms on account of their dorsoventrally flattened body shape, but their parapodia and cirri suggest that they are close to Polychaeta (see Graff, 1877; Jägersten, 1940a; Prenant, 1959). The genus *Myzostoma* F.S. Leuckart, 1836, is the largest in the Myzostomida. It accounts for about 120 species, most of which are ectocommensals, although a few form galls or cysts on crinoids (Graff, 1884, 1887; Jangoux, 1990). The present paper reports on eight species of *Myzostoma* recently found infesting comatulid crinoids from the waters of Singapore, including three undescribed species, and also lists additional new records outside Singapore for many of them. Until now, just two species of *Myzostoma* have been known from Singapore, *M. attenuatum* Grygier, 1989 (q.v.) and, in a summary report which shall be fully documented herein, *M. longicirrum* Graff, 1887 (see Grygier 1990).

Igor Eeckhaut, Didier VandenSpiegel - Laboratoire de Biologie Marine, Université de Mons-Hainaut, 19 ave. Maistriau, B-7000 Mons, Belgium. **Mark J. Grygier** - Sesoko Marine Science Center, University of the Ryukyus, Sesoko, Motobu-cho, Okinawa, 905-02 Japan.

MATERIAL AND METHODS

Crinoid hosts with myzostomes representing seven species were collected either by SCUBA diving or dredging at various sites in the territorial waters of Singapore. Once collected, they were maintained alive in an aquarium with recirculating seawater in the Department of Zoology of the National University of Singapore. Myzostomes were observed and counted on their hosts under a binocular microscope. Some specimens (the holotype and paratypes for new species; one specimen for known species) of each observed species have been deposited in the Zoological Reference Collection (ZRC) of the Department of Zoology (National University of Singapore); some others were used for histology.

For the observations of parapodial hooks, support rods, and replacement hooks, one individual of each species was digested in a weak solution of sodium hypochlorite for a few minutes. Once most of the tissue was dissolved, the specimens were dried and mounted on slides. Microscopic observations were made with an Olympus IMT-2 phase contrast microscope.

For histological observations (semi-thin sections), individuals were fixed for 3-24 h at 4°C in a solution of 3% glutaraldehyde in cacodylate buffer (0.1 M, pH 7.8). They were washed in buffer, post-fixed for 1 h with 1% osmium tetroxide in 0.1 M cacocylate buffer, and washed again in buffer. After dehydration, specimens were embedded in Spurr and cut into 1 µm thick serial sections. Sections were stained in a 1:1 solution of Methylene Blue/ Azur II according to the procedure of Ganter & Jollès (1969-1970).

For SEM observations, individuals fixed either in Bouin's fluid or glutaraldehyde were dehydrated in graded concentrations of ethanol and dried by the critical point method using liquid CO_2 as the transition fluid. Then they were mounted on aluminium stubs, coated with gold in a sputter coater, and observed with a JEOL JSM 6100 scanning electron microscope.

Additional specimens of some of the species mentioned above, as well as one additional species from Singapore, had been isolated during a survey of myzostomes at many natural history museums (Grygier, 1990). Most of the specimens were sorted, drawn, sometimes photographed, and later catalogued in the National Museum of Natural History, Smithsonian Institution, Washington D. C. (USNM); two were among loaned specimens from the Northern Territory Museum of Arts and Sciences, Darwin (NTMAS) and the Uppsala Universitets Zoologiska Museum (UUZM). Relevant type specimens from The Natural History Museum in London (BMNH) and the Naturhistorisches Museum Wien (NMW) were also examined. One microscopic preparation was made by exposing dissected parapodia to dilute sodium hypochlorite as described above and mounting the exposed hook apparati in glycerine jelly on a glass slide.

TAXONOMIC ACCOUNT

Myzostoma brachiatum Graff, 1877
(Figs. 1, 20A-C, 27A-B)

Myzostoma brachiatum Graff, 1877: 16-17, 23, 72, 79, Taf. II, Fig. 2; Graff, 1884: 8, 16, 20, 24, 55, 80.

Myzostomum brachiatum - Clark, 1921: 667.

Material examined. - Host: *Heterometra savignii* (J. Müller, 1841). Locality: Johore Shoal (collected by dredging), Singapore, 30 m, coll. xii.1991. No. of hosts examined: 5 (3 infested). No. of myzostomes obtained: 4 (1-2 myzostomes per host). One specimen deposited as voucher (ZRC 1993-7279). Additional material: whole mount of Graff's (1877) illustrated syntype (NMW Inv. No. 2909), herein designated as lectotype. Other syntype not found.

Previously recorded distribution. - Bohol, Philippines (type locality) (Graff, 1877).

Previously recorded host. - *Comatella nigra* (P. H. Carpenter, 1888).

Description of specimens from Singapore. - The body is ovoid and flat (Fig. 1). The length varies from 0.7 to 1 mm and the width from 0.4 to 0.7 mm. The body margin is surrounded by 29 to 32 cirri of unequal lengths (Fig. 1). Short cirri no more than 70 μm long and long cirri 200-500 μm long are irregularly distributed around the body margin, the long cirri being more numerous posteriorly (Fig. 1). The parapodia (five pairs) are 200 μm long and are closer to the body margin than to the midpoint (Fig. 1). The support rods of the parapodia are as long as the parapodial hooks (ca. 200 μm long in the 0.8 mm long individual that was examined) but a little thinner (Figs. 20B-C). The curvature of the tip of the hook is slight (Fig. 20B). The tip of the support rod is bent 45° relative to the shaft; the manubrium lies on both sides of the shaft, its external part (viz. the part opposite to the parapodial hook) being rounded and its internal part (viz. the part facing the hook) ending with three to four parallel lobes (Fig. 20C). One replacement hook 40 μm long occurs in each parapodium (Fig. 20A). The lateral organs (four pairs) look like small slits and lie halfway between the parapodia and the margin. The penes and introvert were not exposed. The opening of the introvert pouch is antero-ventral, that of the cloaca is postero-ventral; and both are close to the body margin.

Remarks. - In its current state, the lectotype differs from Graff's (1877) figure in having much shorter marginal cirri, in missing most of the left-hand cirri, and in having three additional short cirri along the posterior half of the right margin (Fig. 27A). The present specimens from Singapore agree with it morphologically except for having a weaker distal curvature of the parapodial hooks (Figs. 20B, 27B).

Myzostoma horologium Graff, 1884
(Figs. 2, 3, 14, 21A-C)

Myzostoma horologium Graff, 1884: 7, 9, 13, 19-20, 22, 27-29, 79, Pl. I, Figs. 1-17
Myzostomum horologium - Clark, 1921: 658-659.

Material examined. - Host: *Comatula purpurea* (J. Müller, 1843). Locality: Johore Shoal (dredging), Singapore, 30 m, coll. viii.1992. No. of hosts examined: 51 (10 infested). No. of myzostomes obtained: 15 (1-3 myzostomes per host). One specimen deposited as voucher (ZRC 1993-7280). Additional material: one specimen (USNM 167400) found on preserved *Comatula purpurea* (USNM 34904), "Albatross" sta. 5276, South China Sea near southern Luzon, Philippines (13°49'15"N, 120°14'15"E, 33 m, coll. 17.vii.1908); syntypes (BMNH 89.11.8-1, 89.11.8-2, and 89.11.8-3) from "Challenger" sta. 186 and 187.

Previously recorded distribution. - "Challenger" sta. 186 and 187 in the Torres Strait (Graff, 1884), probably also "Challenger" sta. 190 in the Arafura Sea (Graff, 1884).

Previously recorded hosts. - Uncertain but, according to Graff (1884), probably *Comatula rotalaria* Lamarck, 1816, *Comatula solaris* Lamarck, 1816, and *Comaster sp.*; Clark (1921)

inferred from circumstantial evidence pertaining only to station 190 that the hosts might really have been *Zygometra microdiscus* (Bell, 1882) and *Z. elegans* (Bell, 1882).

Description of specimens from Singapore. - The body is discoid and stout (Fig. 2). Its diameter varies from 0.8 to 3 mm. The body margin is surrounded by numerous, very short, closely spaced cirrus-like nubs in two size classes, 10 µm and 20 µm long (Fig. 3). The acirrate parapodia (five pairs) are 350 µm long and are closer to the body margin than to the midpoint (Figs. 2, 3). The parapodial hooks and support rods are equal in length (ca. 550 µm long in the 1.2 mm long individual that was examined), but the former are 1.5-2 times thicker than the latter (Fig. 21B-C). The tip of the hook is long and nearly straight beyond the rather sharp curve connecting it to the shaft (Fig. 21B). The tip of the support rod is bent 45° with regard to the shaft; the manubrium is large, lying on both sides of the shaft, and its internal part has numerous lobes (Fig. 21C). One replacement hook 0.25 mm long occurs in each parapodium (Fig. 21A). The lateral organs (four pairs), each of which has a diameter of 150 µm when protruded, lie halfway between the parapodia and the margin (Figs. 2, 3). The two small penes are 50 µm long and are situated close to the third pair of parapodia (Fig. 2). The introvert is large and possesses buccal papillae. The opening of the introvert pouch lies between the first pair of parapodia, while the cloacal opening lies outside the ring of parapodia at the level of the lateral organs (Fig. 2).

The ventral colouring is whitish. The dorsal colouring is variable but the most common pattern is shown in Fig. 14. It looks like a watch dial divided into ten sectors. The center of the dial is a white or yellow patch surrounded by a large, brown to purple ring. Ten brown to purple lines extend out from the center to the similarly coloured body margin. The spaces between the radial lines are white. Individual variability is expressed by occasional branchings of the radial lines. The smallest individuals are differently coloured, being whitish and spotted with many small, brown to purple patches. One large individual is totally black.

Remarks. - As described by Graff (1884), the syntypes differ from the Singaporean specimens by the absence of marginal cirri (represented only by minute nubs in the present material) and by the shape of the manubrium of the parapodial support rod, the internal part of which was drawn as though bissected. The present Philippine specimen, with a diameter of 4.3 mm, is bigger than the Singaporean ones, and, in contrast to the syntypes, has a thick and disc-like rather than hemilenticular body shape. The flat, wrinkled dorsal surface forms the top of the disc and the lateral organs and cloacal papilla lie on the side.

Myzostoma jaegersteni, new species
(Figs. 4-6, 15, 22A-C)

Material examined. - Host: *Heterometra savignii*. Locality: Johore Shoal (dredging), Singapore, 30 m, coll. xii.1991 and viii.1992. No. of hosts examined: 5 (3 infested). No. of myzostomes obtained: 7 (1-3 myzostomes per host). Type specimen: holotype (ZRC 1993-7281); 2 paratypes (ZRC 1993. 7281); other paratypes used for histology. Additional specimens: three non-type specimens (USNM 167401) found loose in jar with *Neometra multicolor* (A. H. Clark, 1907) (USNM 35465), collected by A. Owston, R/V "Golden Hind", Uraga Channel, Tokyo Bay, Japan, 46 m, coll. 26.v.1901; more than 100 specimens associated with *Tropiometra carinata* (Lamarck, 1816) collected by M. Ortiz near the coast of Mozambique (Barreira Rosa), coll. 13.iv.1987.

Diagnosis. - Small, thin *Myzostoma* with flat, elongated body ending in six cirrate caudal processes. About ten pairs of marginal cirri, the most anterior pair being 2-3 times longer than the others. Parapodia acirrate, closer to body margin than to midpoint. Support rods as

long but thinner than hooks, manubrium of former developed on one side of shaft and ending in 3-5 parallel lobes. Lateral organs small, located nearly at body margin. Penes small. Introvert small and thin; opening of introvert pouch very close to anterior body margin. Ciliation sparse, with capitate cilia. Relative lengths of pharynx, stomach, and intestine 2:1:2; three pairs of lateral caeca starting from the stomach.

Description of type lot. - The holotype is 1 mm long (including the caudal processes but not their cirri) and 0.67 mm wide. The lengths of the paratypes range from 1.0 to 2.7 mm and their widths from 0.6 to 0.8 mm. There are six caudal processes measuring 150-400 μm long, those closer to the midline being the longest (Fig. 4). One or several caudal processes were lost from most of the paratypes. There are about ten pairs of marginal cirri around the body in addition to those which arise from the tips of the caudal processes (Fig. 4). The former are about 100 μm long except the most anterior pair, which is 300 μm long, and the latter are 200 μm long (Figs 4, 5). The parapodia (five pairs) are 100 μm long. The support rod in each is as long as the hook (ca. 150 μm long in the 0.8 mm long specimen which was examined) but a little thinner (Fig. 22B-C). The tip of the hook is more or less evenly curved and medium-sized relative to the length (Fig. 22B). The tip of the support rod is bent 30° relative to the shaft; the manubrium is only developed on one side of the shaft and resembles a more or less quadrangular flag ending in 3-5 parallel lobes (Fig. 22C). One replacement hook 30 μm long occurs in each parapodium (Fig. 22A). There are four pairs of lateral organs that look like small slits and are only 20 μm long (Fig. 5); the lateral organs were only observed in a retracted condition. The introvert was not exposed; its pocket opens closer to the anterior body margin than to the first pair of parapodia (Fig. 5). The cloacal opening is postero-ventral, close to the bases of the most median caudal processes. Cilia occur sparsely all over the body and are unusual in that the tips of all the cilia are curled (Fig. 6). The animal is very translucent in life, the dorsal and ventral colouring being a dull white (Fig. 15).

The digestive system in the 2.5 mm long sectioned individual (caudal processes included) consists of a straight tube 850 μm long and probably three pairs of blind digestive caeca. The tube consists of a pharynx (325 μm long), a stomach (175 μm long), and an intestine (350 μm long). The three pairs of caeca start from the stomach and divide to penetrate into the lateral parts of the body.

Individuals are hermaphrodites. Both the female and male genital systems are similar to those of other species of *Myzostoma*. The female genital system lies dorsal to the digestive system and consists of a diffuse ovary and a branched oviduct. The ovary of the sectioned specimen is well developed and consists of numerous female gametes at different stages of development (viz. oogonia, previtellogenetic and vitellogenetic oocytes) lying in the parenchyma. Developing female gametes occur in the trunk and the caudal processes. The male genital system lies ventrolateral to the digestive system and consists of a diffuse testis, probably four short deferent ducts, two seminal vesicles, and two penes. The testis is poorly developed in the sectioned specimen and consists of male gametes which develop within cyst cells, viz. spermatocysts, these latter lying within the parenchyma [see Afzelius (1983, 1984) for a detailed explanation of myzostomidan spermiogenesis].

Remarks. - *Myzostoma jaegersteni*, new species, is characterised by its cirrate caudal processes. All three Japanese specimens agree with the specific diagnosis by having three pairs of cirrate caudal processes and ten pairs of marginal cirri, the first pair longer than the others. Unlike the Singaporean specimens, the preserved Japanese specimens are brown. The morphology of the specimens from Mozambique matches exactly that of the Singaporean

specimens but preserved specimens from Mozambique are light brown. The hook apparatus of individuals in the two lots is similar.

Two other species of *Myzostoma* recorded from the Torres Strait (Australia) have from four to six cirrate caudal processes: *M. quadrifilum* Graff, 1884 and *M. intermedium* Graff, 1884. The former species differs from *M. jaegersteni* in always having four caudal processes, the most anterior pair of marginal cirri being the same length as the others, and its brown colouring. Only one specimen of *M. intermedium* was known and it was so badly preserved that Graff (1884) only observed the outline of the body. It differs from *M. jaegersteni* in its circular body shape and dark colouring. Furthermore, among the specimens examined in the preparation of Grygier's (1990) survey, some that were quite distinct from *M. jaegersteni* could be assigned to *M. intermedium*. *Myzostoma tentaculatum* (Jägersten, 1940b), recorded from Nagasaki Prefecture, Japan (33°08'N, 129°20'E), also has cirrate caudal processes and one long anterior pair of marginal cirri like *M. jaegersteni*, but there is only one pair of very large caudal processes.

Etymology. - Dedicated to Professor Gösta Jägersten, who produced very impressive works on myzostomidan taxonomy, anatomy, and biology during the first part of this century.

Myzostoma capitocutis, new species
(Figs. 7-9, 16, 23A-C)

Material examined. - Host: *Comaster gracilis* (Hartlaub, 1890). Locality: collected by SCUBA diving at Pulau Satumu (Raffles Lighthouse), Singapore, 0-15 m, coll. viii.1992. No. of hosts examined: 32 (7 infested). No. of myzostomes obtained: 9 (1-3 myzostomes per host). Type specimen: holotype (ZRC 1993. 7282); 2 paratypes (ZRC 1993-7282); other paratypes used for histology.

Diagnosis. - Small *Myzostoma* with flat, discoid body bearing 44-48 cirri of unequal length. Parapodia acirrate, lying in a circle, and located a little closer to midpoint of the body than to margin. Support rods a little longer than hooks but half as thick; manubrium of former only developed on one side of the shaft, large and triangular. Lateral organs star-shaped, located about halfway between parapodia and body margin. Penes large. Introvert large with buccal papillae. Opening of introvert pouch between first pair of parapodia. Many long, hair-like papillae, i.e., body wall extensions, covering the whole dorsal surface. Ciliation sparse, with straight cilia. Relative lengths of pharynx, stomach, and intestine 1:1:1; three pairs of lateral caeca starting from stomach.

Description. - The diameter of the holotype is 1.9 mm, and those of the paratypes range between 1.9 and 2.7 mm. The marginal cirri are 100-240 µm long (Figs 7, 8). The dorsal surface of the body bears several dozen elongate, cylindrical papillae measuring between 10 and 250 µm long (up to 500 µm in one individual), the shortest ones being confined to a zone near the body margin (Fig. 8). The parapodia (five pairs) are 200 µm long (Fig. 7). In each the hook is a little shorter than the support rod (former 450 µm long and latter 500 µm long in the 2.7 mm long specimen that was examined), but the support rod is only half as thick as the hook (Fig. 23B-C). The hook has a medium-sized, rounded tip (Fig. 23B). The tip of the support rod is not bent but follows the slight curvature of the shaft; the manubrium is only developed on one side of the shaft and looks like a large, pleated, triangular flag (Fig. 23C). One replacement hook 300 µm long occurs in each parapodium (Fig. 23A). The penes are about as long but considerably thicker than the third pair of parapodia, from the lateral base of which they arise. The lateral organs (four pairs) measure 150 µm in diameter when

protruded and are formed of a central villous mass surrounded by a serrated fold which gives the organs a star-shaped appearance (Figs. 7, 9). The introvert bears four pairs of buccal papillae (Fig. 7). The opening of the introvert pouch is located between the first pair of parapodia, and the cloacal papilla is midway between the fifth parapodia and the posterior body margin (Fig. 7). The dorsal colouring in life is dirty white to brown, always spotted with numerous dark brown patches (Fig. 16). The ventral colouring is whitish.

The digestive system in the 1.8 mm long sectioned individual consists of a straight tube 950 μm long and probably three pairs of blind digestive caeca. The tube includes a pharynx (325 μm long), a stomach (275 μm), and an intestine (350 μm). The three pairs of caeca start from the stomach and divide to penetrate into the lateral parts of the body. Individuals are hermaphrodites with a well developed ovary and testis. The gross anatomy of the genital systems is similar to that of other species of *Myzostoma*.

Remarks. - *Myzostoma capitocutis*, new species, is characterized by the occurrence of long, cylindrical dorsal papillae. Four other species have dorsal papillae: *M. gigas* Graff, 1884, *M. giganteum* Nansen, 1885, *M. tuberculatum* (Jägersten, 1937), and *M. holotuberculatum* (Jägersten, 1940). They all differ from *M. capitocutis* by the fact that their papillae are low and more or less hemispherical and in having just 10 pairs of marginal cirri. None of the known disc-like species of *Myzostoma* with many marginal cirri (e.g., *M. elegans* Graff, 1877, *M. polycyclus* Atkins, 1927, *M. evermanni* McClendon, 1907) have dorsal processes of any kind.

Etymology. - From the Latin *cutis capitis*, scalp, based on the resemblance imparted by the hair-like dorsal papillae.

Myzostoma singaporense, new species
(Figs. 10, 11, 17, 24B-C)

Material examined. - Host: *Comaster gracilis*. Locality: collected by SCUBA diving around Pulau Satumu (Raffles Lighthouse), Singapore, 0-15 m, coll. viii.1992. No. of hosts examined: 32 (7 infested). No. of myzostomes obtained: 16 (1-6 myzostomes per host). Type specimen: holotype (ZRC 1993-7283); all paratypes used for histology.

Diagnosis. - Small *Myzostoma* with flat, ovoid body. Ten pairs of marginal cirri of nearly same length, two most anterior and two most posterior pairs being slightly longer. Parapodia acirrate, slightly closer to body margin than midpoint. Parapodial hooks and support rods of same length and thickness, manubrium of latter developed on one side of shaft, like small triangular flag with spur at its base. Lateral organs closer to body margin than to parapodia. Penes small. Introvert large, with opening of introvert pouch closer to body margin than to first pair of parapodia. Ciliation sparse with straight cilia; 4-10 tufts of cilia along body margin in intervals between adjacent cirri. Relative lengths of pharynx, stomach, and intestine 2:1:2; two pairs of lateral caeca starting from stomach.

Description. - The holotype is 0.86 mm long and 0.78 mm wide. The paratypes vary in length from 0.3 to 1.2 mm, in width from 0.2 to 0.7 mm. The 2 anterior and 2 posterior pairs of cirri are the longest and measure 150 μm, while the others are 100 μm long (Fig. 10). There are five pairs of thin, acirrate parapodia which are 100 μm long (Fig. 10), and small penes are associated with the third pair. The parapodial hooks and support rods are of the same length (ca. 200 μm long in the 1.2 mm long individual that was examined) and thickness

(Fig. 24B-C). The tip of the hook has a rather open curvature (Fig. 24B). The tip of the support rod is bent 45° relative to the shaft; the manubrium is only developed on one side of the shaft, as a small triangular flag with a large lobe at the inner corner and a spur at the base (Fig. 24B). No replacement hook was observed. When protruded, the lateral organs (four pairs) are 40 µm in diameter (Figs 10, 11). They and the opening of the introvert pouch and the cloacal opening form a ring quite close to the body margin. The introvert is ca. 300 µm long. The body ciliature is sparse but characterized by 4-10 tufts of cilia between successive cirri along the body margin (Figs 10, 11). The smallest individuals are translucent in life, and it is possible to observe within them the seminal vesicles full of white germinal products and the four red digestive caeca which dichotomise (Fig. 17). The largest individuals are less translucent; their dorsal surface is whitish with red lines.

The digestive system in the 0.8 mm long sectioned individual consists of a straight tube 750 µm long and two pairs of blind digestive caeca. The tube includes a pharynx (300 µm long), a stomach (150 µm), and an intestine (300 µm). The two pairs of caeca start from the stomach and divide to penetrate into the lateral parts of the body. Individuals are hermaphrodites; the sectioned individual had a poorly developed ovary with only a few oocytes in the vitellogenic stage, and a well developed testis. The gross anatomy of the genital systems is similar to that of other species of *Myzostoma*.

Remarks. - The most distinctive external features of *M. singaporense*, new species, are the presence of ten pairs of marginal cirri, the first and last two pairs of which are a little longer than the other cirri, and the presence of tufts of cilia around the body margin. *Myzostoma fimbriatum* Graff, 1884 has similar tufts of cilia around its body margin but does not otherwise much resemble *M. singaporense* and is an arctic or subarctic species. Several described species have ten pairs of cirri with longer anterior and posterior pairs (e.g. *M. vastum* Graff, 1883, *M. antennatum* Graff, 1884, *M. ambiguum* Graff, 1887, *M. longicirrum* Graff, 1887 (see below), and *M. longimanum* (Jägersten, 1937)). However, all of these have: 1) longer cirri than *M. singaporense* or 2) a considerably greater disparity in length between the long and short cirri or 3) a round rather than oval body.

Etymology. - Referring to Singapore, the type locality.

Myzostoma elegans Graff, 1877
(Figs. 12, 18, 25B-C)

Myzostoma elegans Graff, 1877: 12-13, 22, 72, 79, Taf. X, Figs. 1-3; Graff, 1884 (*partim*): 16, 19, 20, 24, 54, 80; Graff, 1887: 5; Grygier, 1990: 184, 189.
Myzostomum elegans - Clark, 1921 (*partim*): 666.

Material examined. - Host: *Comaster gracilis*. Locality: collected by SCUBA diving around Pulau Satumu (Raffles Lighthouse) and Pulau Semaku, Singapore, 0-15 m, coll. viii.1992. No. of hosts examined: 32 (14 infested). No. of myzostomes obtained: 27 (1-4 myzostomes). One specimen deposited as voucher (ZRC 1993-7284). Additional material: one specimen (USNM 167402) found loose in jar with *Comaster gracilis* (USNM E34588), collected by D. L. Meyer, Fiji, 1976; one specimen (USNM 167403) found loose in jar with *Comanthina schlegelii* (Carpenter, 1881) (USNM E34847), collected by D. L. Meyer, north side of Kraka Island, Banda Islands, Indonesia (4°30'09"S, 129°52'57"E, 3-18 m, coll. 1975); seven specimens (USNM 167404), host unknown, International Indian Ocean Expedition, "Anton Bruun" Cr. I., sta. 47b, northern Bay of Bengal (19°50'N, 92°55'E, 22-30 m, coll. 5.iv.1963); one specimen (USNM 167405) found loose in jar with 3 *Comanthus parvicirrus* (USNM 34994), "Albatross" sta. 5147, vicinity of Siasi, Sulu Archipelago (5°41'40"N, 120°47'10", 37m, coll. 16.ii.1908).

Previously recorded distribution. - Bohol, Philippines (type locality) (Graff, 1877); Banda Islands (Grygier 1990); Fiji (Grygier, 1990).

Previously recorded hosts. - Species refered to as the *nomen nudum Comatula triquetra* Lütken (in manuscript) by Graff (1877), true identity of which is unknown according to Clark (1931; therein spelled *C. triqueta*); species refered to *Actinometra armata* Semper MS (i.e., *Comanthus parvicirrus*) by Graff (1877) and *A. parvicirra* (J. Müller, 1841) (i.e., *Comanthus parvicirrus*) by Graff (1884), true identity uncertain due to complex nomenclatural history which also involves *A. polymorpha* Carpenter, 1879 (see Clark 1921, 1931, Rowe *et al.* 1986); three unspecified species of Comasteridae.

Description of specimens from Singapore. - The body is flat, almost discoidal, slightly wider than long (Fig. 12). The diameter is from 0.8 to 1.75 mm. The body margin is lined with 36-49 cirri of unequal length, varying from 10 to 150 μm long (Fig. 12). Generally, a short cirrus alternates with a long one. The acirrate parapodia are 120 μm long and lie halfway between the body margin and the midpoint (Fig. 12). The parapodial hooks and support rods are of the same length (ca. 200 μm in the 1.2 mm long individual that was examined) and width (Fig. 25B-C). The hook narrows sharply at the tip, which smoothly traces a 90° curve (Fig. 25B). The tip of the support rod is not bent but follows the slight curve of the shaft; the manubrium is only developed on one side of the shaft in the shape of a pleated, triangular flag (Fig. 25C). No replacement hook was observed. Two large penes which are 150 μm long are associated with the third pair of parapodia. The lateral organs (four pairs), which are 30 μm in diameter when retracted, lie halfway from the parapodia to the body margin (Fig. 12). The introvert is large and the opening of the introvert pouch lies halfway between the first pair of parapodia and the anterior body margin (Fig. 12). The cloacal opening lies halfway between the fifth parapodia and the posterior body margin. The ventral colouring in life is whitish and the dorsal colouring is also whitish but spotted with brown dots (Fig. 18). Sometimes the dots are concentrated to form brown dorsal patches situated in a ring halfway between the midpoint and the body margin.

Description of other specimens. - The Indonesian specimen is 2.56 mm long and 2.40 mm wide with at least 55 marginal cirri (part of margin damaged). The Fijian specimen is 1.88 mm long and 1.68 mm wide with about 42 marginal cirri. Both are brown in the preserved state, with a translucent marginal zone. Of the two, the Fijian specimen has relatively shorter cirri which are more even in length. The circle of acirrate parapodia is centered anterior of the body's midpoint, with a radius 40-50% that of the body. The low, round, mound-like lateral organs are a little closer to the parapodia than to the body margin and are well within the inner boundary of the marginal zone. The opening of the introvert pouch is in the ring defined by the lateral organs, but, unlike the specimens from Singapore, the cloacal opening lies outside that ring. The specimens collected in the Bay of Bengal are brown and range in diameter from 0.8 to 2.8 mm. The smallest one has its rather long and slender introvert extended and there are four pairs of fine buccal papillae. The specimen collected in the Sulu Archipelago is about 3.2 mm in diameter and its color is quite faded. It has more than 53 marginal cirri. There is no fourth parapodium on the left side, but the body is not otherwise deformed.

Remarks. - *Myzostoma elegans* is characterized by cirri that are numerous and of different lengths. The species was originally reported from Bohol, Philippines (Graff 1877). The syntypes were not found in the NMW in 1987, although some other myzostome types collected by Semper and described by Graff (1877) are housed there. No lectotype is designated. The identity of Graff's (1884) Carribean specimen of *M. elegans*, which was neither described

nor illustrated and has been lost, must be considered questionable. One of Graff's two syntypes was four mm long with 80-86 marginal cirri, therefore larger and bearing more cirri than the present specimens. Graff's smaller syntype had relatively shorter cirri than the larger. Like some of the present specimens, the colouring was brown with a distinct marginal zone; like all of them, no cirri were observed on the parapodia, and the ring of lateral organs was well medial to the boundary of the marginal zone. The penis was described as emerging from the body medial to the parapodia and extending outwards between the third and fourth parapodia, but this must be an error. The lateral organs were described as oval; the present ones are round but the retracted part inside the body is oval.

It is quite possible that differences among individuals are due to allometric growth of the region between the parapodia and the inner border of the marginal zone, and to the addition of marginal cirri with growth.

In the Indo-West Pacific, the only species similar to *Myzostoma elegans* is *M. polycyclus* Atkins, 1927 (q.v.), the body of which is also a flat, round disc with numerous marginal cirri. It is possible that these nominal species are synonymous even though typical specimens of the latter are easily recognizable. *Myzostoma polycyclus* has a distinctive dorsal colouring of dark and light rings (cf. color photographs in Uchida, 1992: pl. 72, figs. 6-7), although in small specimens these may be faint, and its parapodia bear medial cirri. Despite the absence of dark markings on the specimen of *M. elegans* reported by Jägersten (1940b) from Jolo, Philippines, the presence of parapodial cirri leads us to suggest that it is really *M. polycyclus*. On the other hand, Chesunov *et al.*'s (1989) supposed *M. irregulare* Graff, 1884 (sic; really 1883), found infesting *Capillaster multiradiatus* (Linnaeus, 1758) in the Maldives, may really be *M. elegans*. The specimens were 1.5-2 mm in diameter and coloured light beige. The illustrated specimen had 55 marginal cirri, and no parapodial cirri appear in the drawing or are mentioned in the text.

Myzostoma stochoeides Atkins, 1927
(Figs. 13, 26A-C)

Myzostoma stochoeides Atkins, 1927: 344-346, Text-Figs 5-6, Pl. I, Figs 1-3.

Material examined. - Host: *Comaster tenellus* A. H. Clark, 1931. Locality: Johore Shoal (dredging), Singapore, 30 m, coll. viii.1992. No. of hosts examined: 8 (5 infested). No. of myzostomes obtained: 11 (1-6 myzostomes per host). One specimen deposited as voucher (ZRC 1993-7285).

Previously recorded distribution. - Badu Island, Torres Strait (type locality) (Atkins, 1927).

Previously recorded host. - *Comanthus annulatus* (Bell, 1882), now synonymised with *Comanthus parvicirrus* (see Rowe *et al.*, 1986).

Decription. - The body is discoid and flat (Fig. 13). It measures 0.9-3 mm in diameter. Ten pairs of cirri, all the same length, surround the body margin (Fig. 13). They are 140 µm long when retracted and 300 µm long when extended. The parapodia (five pairs) are situated closer to the body midpoint than to the margin (Fig. 13). Their support rods are as long (0.35 mm in the 1.7 mm long individual that was examined) but a little thinner than their hooks (Figs. 26B-C). The tip of the hook turns abruptly at a right angle and is almost straight thereafter (Fig. 26B). The tip of the support rod is not bent but follows the slight curvature of the shaft, and its manubrium is only developed on one side of the shaft, looking like a drooping flag

(Fig. 26C). One replacement hook 0.2 mm long occurs in each parapodium (Fig. 26A). The lateral organs (four pairs), which are 50 μm in diameter when retracted, are much closer to the parapodia than to the body margin (Fig. 13). The opening of the introvert pouch lies closer to the first pair of parapodia than to the anterior body margin and the papilla bearing the cloacal opening lies halfway between the fifth pair of parapodia and the rear body margin (Fig. 13). There are tufts of cilia over the ventral surface except for a narrow bare band near the margin (Fig. 13). The ventral colouring in life is yellow. The dorsal colouring is yellow to orange, dotted with brown spots.

Remarks. - The principal difference between Atkins' (1927) type specimens of *Myzostoma stochoeides*, which have not been located for reexamination, and the present specimens is the colouring: the dorsal surface of the former was ornamented with dark and clear rings.

Another species resembling the present specimens is *M. agassizii* Graff, 1883, which was recorded from Florida, Montserrat, and St. Vincent in the tropical western Atlantic (see Graff, 1884). Unlike the present specimens, it has a ventral furrow on each marginal cirrus and the introvert pouch opens more anteriorly. It is possible that the 2 mm wide, beige specimens identified by Chesunov *et al.* (1989) as *M. agassizi* (sic) from *Capillaster multiradiatus* in the Maldives are really *M. stochoeides*.

Myzostoma longicirrum Graff, 1887
(Fig. 19, 28A-G)

Myzostoma longicirrum Graff, 1887: 10, Pl. I, Fig. 4; Grygier, 1990: 184, 189.
Myzostomum longicirrum - Clark, 1921: 664.

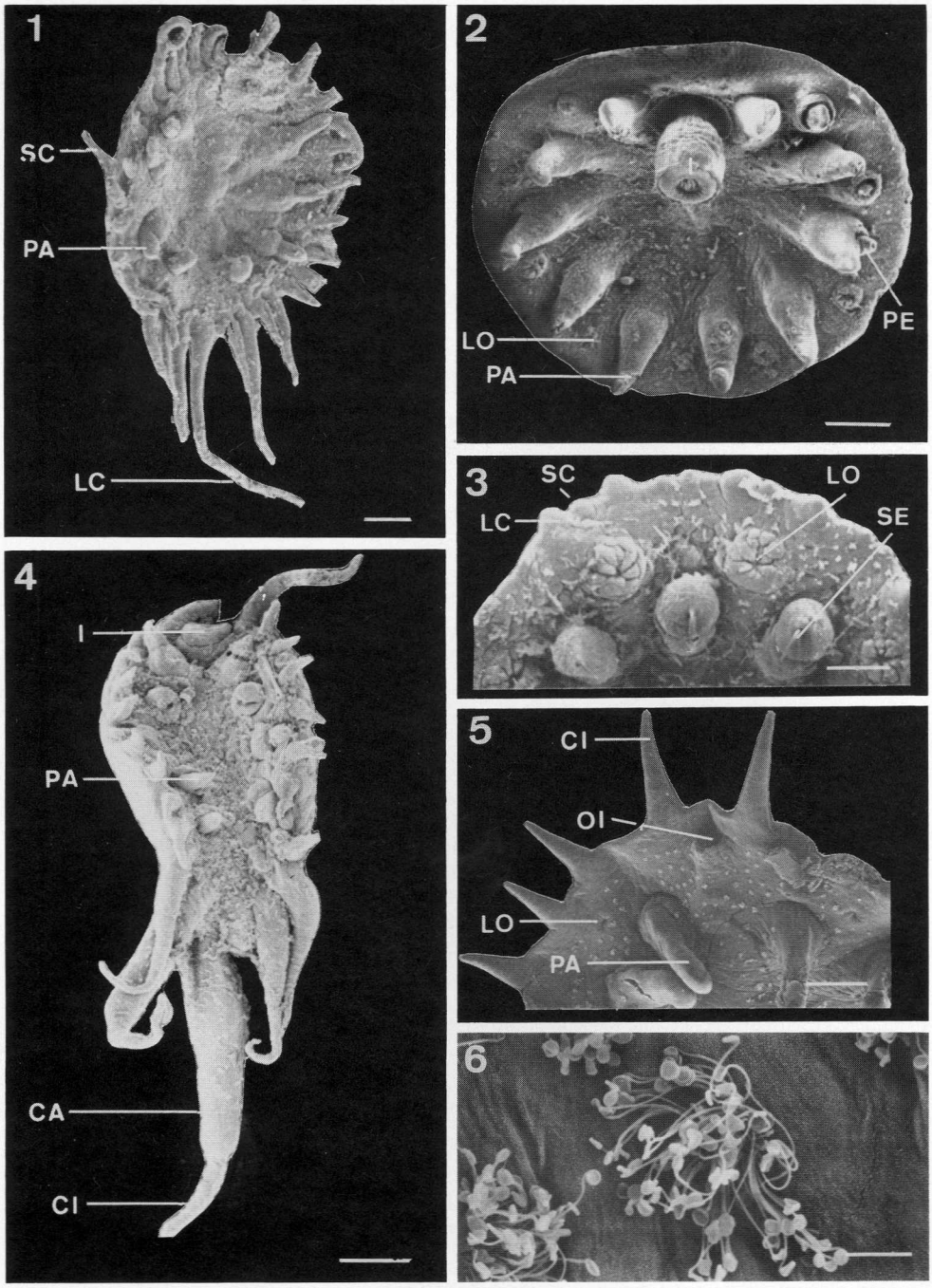
Material examined. - Four specimens (UUZM) on *Capillaster sentosus* (Carpenter, 1888), Singapore, coll. 23.x.1910; five specimens (USNM 167406) found loose in jar with 1 *C. sentosus* (USNM 34844), and 1 specimen (USNM 167407) found loose in jar with 1 *Pontiometra andersoni* Carpenter, (USNM 35222), "Albatross" sta. 5146, near Siasi Island, Sulu Archipelago (5°46'40"N, 120°48'50"E, 44 m, coll. 16.ii.1908); one specimen (USNM 167408) found loose in jar with 1 *C. sentosus* (USNM 34850), "Albatross" sta. 5249, Gulf of Davao, Philippines (7°06'06"N, 125°40'08"E, 42 m, 18 May 1908); one specimen (USNM 167409) found loose in jar with 6 *Capillaster* sp. (USNM E18308), Th. Mortensen's Pacific Expedition 1914-16, off Jolo, Sulu Archipelago, 46 m, coll. 19.ii.1914; five specimens (USNM 167410) found loose in bottle with 1 *C. sentosus* (USNM E19975) and one specimen (USNM 167411) found loose in bottle with 3 *Comatula pectinata* (Linnaeus, 1758) (USNM E19981), Th. Mortensen's Pacific Expedition 1914-16, off Jolo, Sulu Archipelago, 37 m, coll. 17.iii.1914.

Previously recorded distribution. - Zamboanga, Philippines (type locality) (Graff, 1887); Gulf of Davao, Siasi, and Jolo (Philippines) (Grygier, 1990); Singapore (Grygier, 1990).

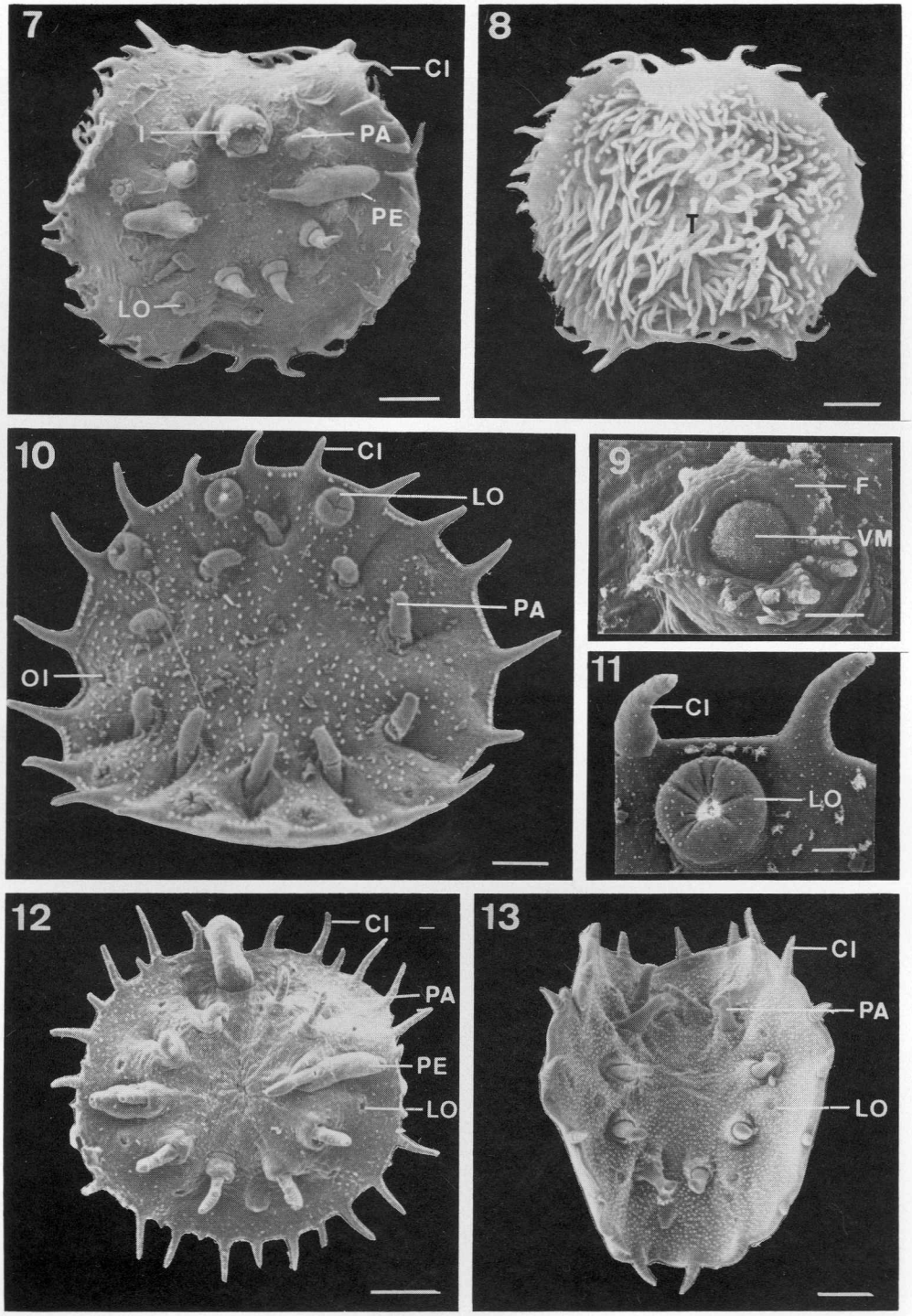
Previously recorded hosts. - *Comanthus parvicirrus*; 4 unspecified species in two unspecified families.

Description. - The most distinctive characteristics are the nearly round, dark brown body with a diameter of 1.0-2.6 mm, the membranous marginal lobes between the marginal cirri, and the first three and last three pairs of cirri being much longer than the rest and attaining nearly the disc diameter (Figs 19, 28A-B).

The disc-like body of the best specimen has a slightly shield-shaped outline, being a bit broader in the front (Figs. 19, 28A-B). The dorsal surface can be smooth or wrinkled, and different specimens show either a weak central hump and radial ridges, a longitudinal ridge,

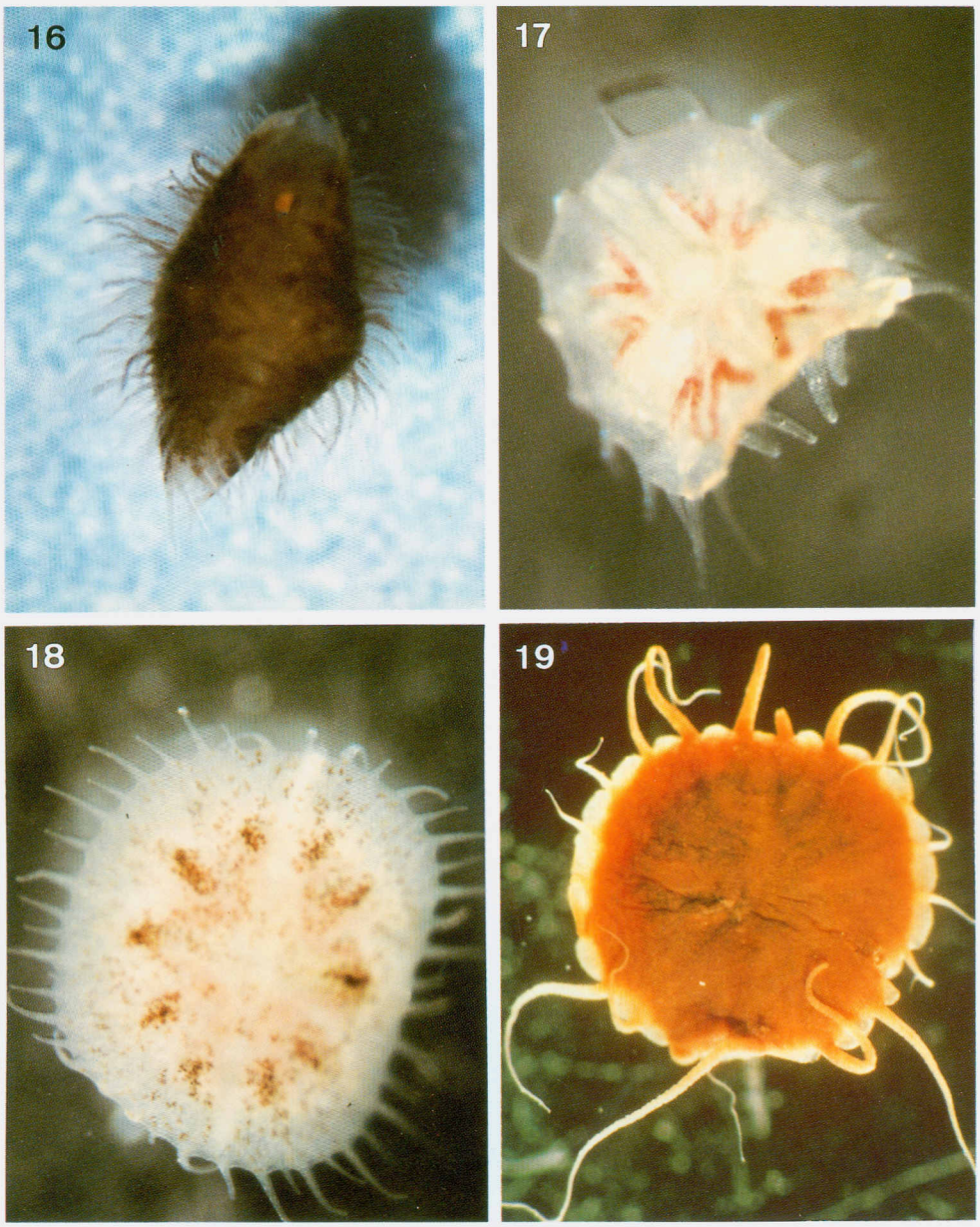


Figs. 1-6. SEM views of Singaporean *Myzostoma* species. Fig. 1. *M. brachiatum* Graff, 1877, ventral view, scale bar 100 μm. Figs 2-3. *M. horologium* Graff, 1884: ventral view and detail of body margin, respectively; scale bars 300 μm and 100 μm, respectively. Figs 4-6. *M. jaegersteni*, new species: ventral view (one of the caudal processes is missing), detail of body margin, and ciliature, respectively; scale bars 100 μm, 150 μm, and 10 μm, respectively. Abbreviations: CA, caudal process; CI, cirrus; I, introvert; LC, large cirrus; LO, lateral organ; OI, opening of introvert pouch; PA, parapodium; PE, penis; SC, small cirrus; SE, seta.

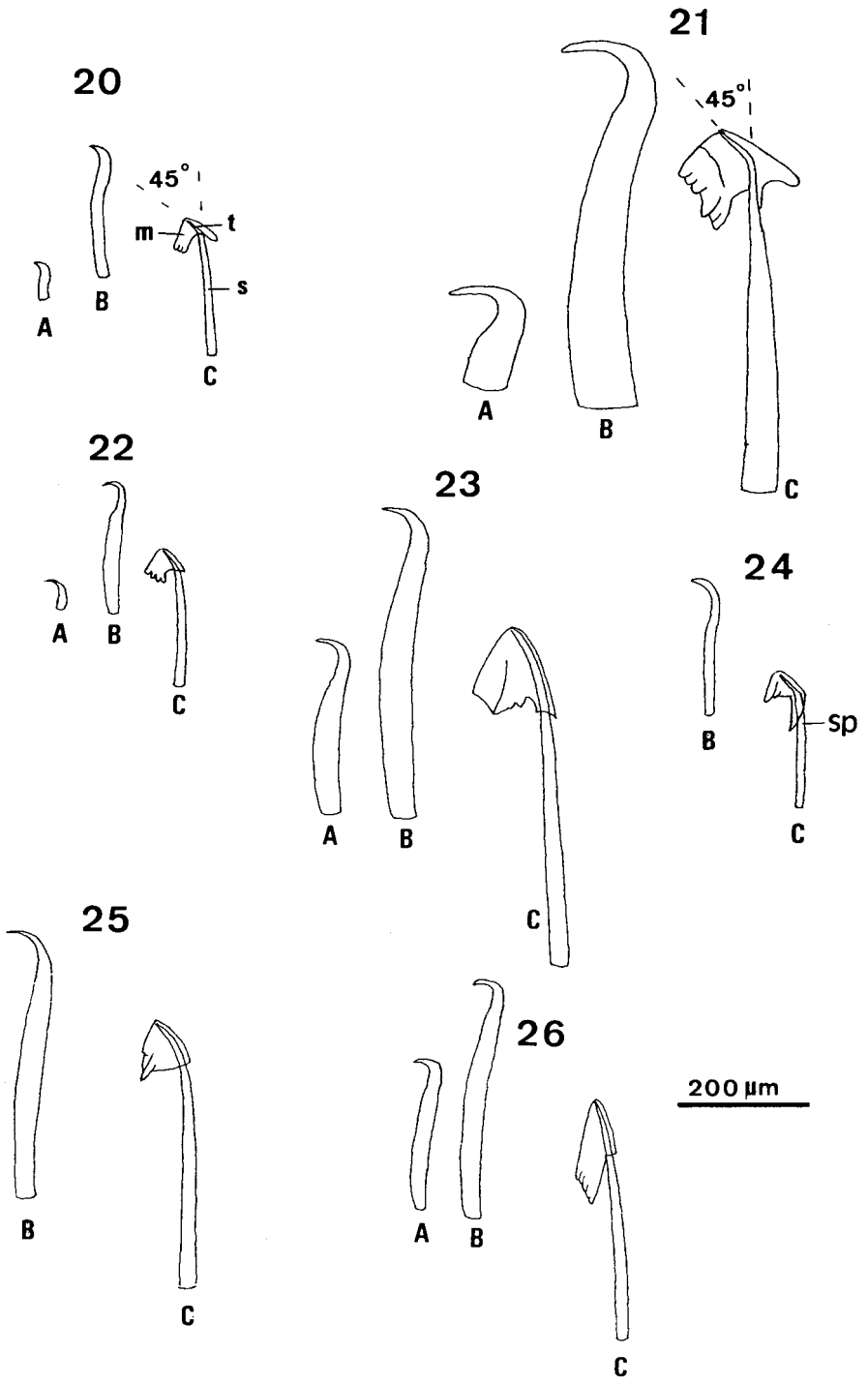


Figs. 7-13. SEM views of Singaporean *Myzostoma* species. Figs 7-9. *M. capitocutis*, new species: ventral view, dorsal view, and detail of lateral organs, respectively; scale bars 400 μm, 400 μm, and 50 μm, respectively. Figs 10-11. *M. singaporense*, new species: ventral view and detail of body margin, respectively; scale bars 100 μm and 20 μm, respectively. Fig. 12. *M. elegans* Graff, 1877, ventral view, scale bar 300 μm. Fig. 13. *M. stochoeides* Atkins, 1927, ventral view, scale bar 400 um. Abbreviations: CI, cirrus; F, fold; I, introvert; LO, lateral organs; OI, opening of the introvert pouch; PA, parapodium; PE, penis; T, tubercle; VM, villous mass.

Figs. 14-15. Optical micoscope views of Singaporean *Myzostoma* species. Fig. 14. *M. horologium* Graff, 1884 (seen from dorsal side). Fig. 15. *M. jaegersteni*, new species (seen from lateral side).



Figs. 16-19. Optical microscope views of Singaporean *Myzostoma* species. Fig. 16. *M. capitocutis*, new species (curled up and seen from ventral side). Fig. 17. *M. singaporense*, new species (seen from dorsal side). Fig. 18. *M. elegans* Graff, 1877. (seen from dorsal side). Fig. 19. *M. longicirrum* Graff, 1887, specimen from Jolo (seen from dorsal side).



Figs. 20-26. Drawings of parapodial hook apparati of Singaporean *Myzostoma* species. In each: A, replacement hook; B, main hook; C, support rod. Fig. 20. *M. brachiatum* Graff, 1877. Fig. 21. *M. horologium* Graff, 1884. Fig. 22. *M. jaegersteni*, new species. Fig. 23. *M. capitocutis*, new species. Fig. 24. *M. singaporense*, new species. Fig. 25. *M. elegans* Graff, 1877. Fig. 26. *M. stochoeides* Atkins, 1927. Abbreviations: m, manubrium; s, shaft; sp, spur; t, tip of hook.

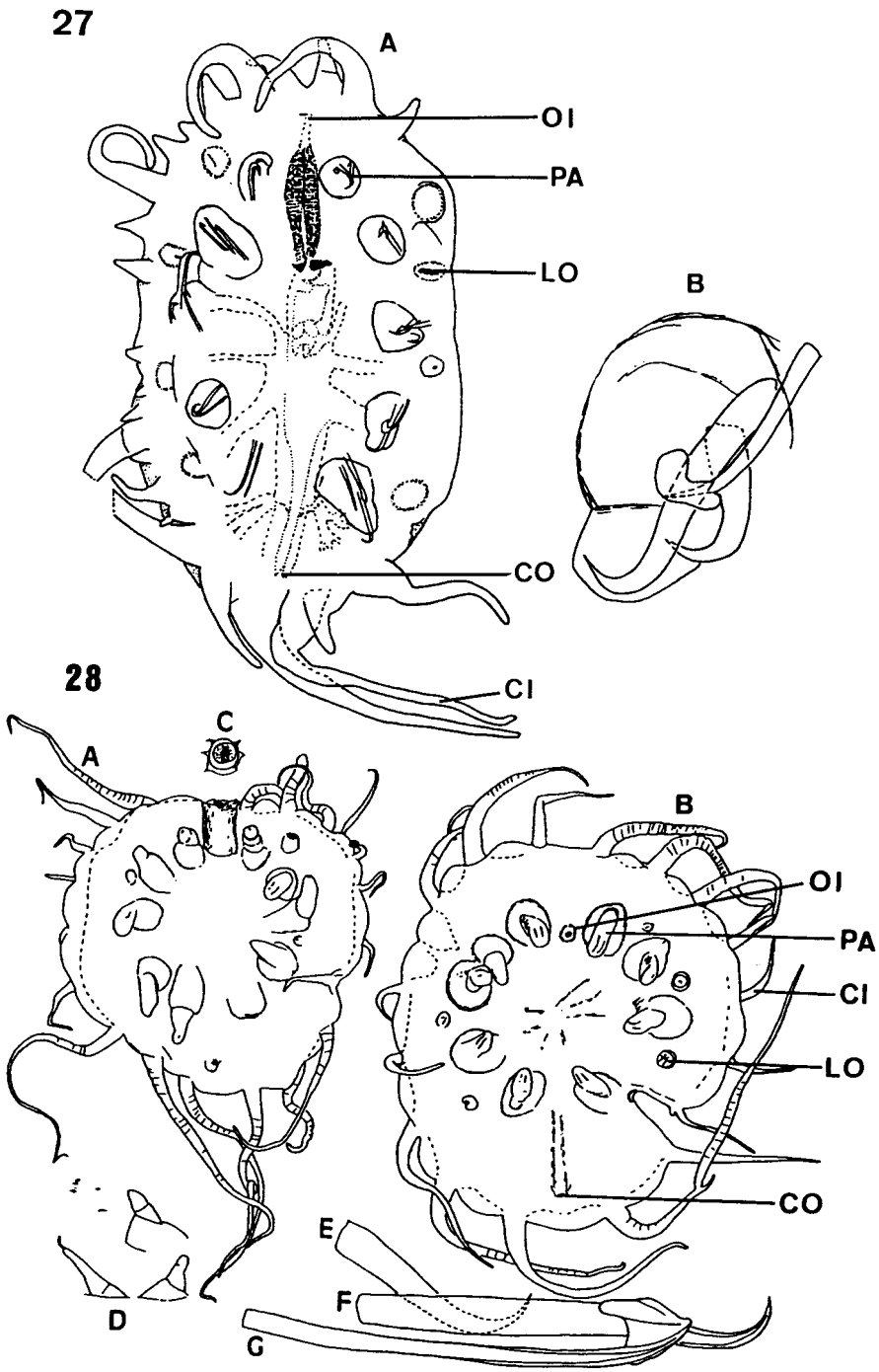


Fig. 27-28. 27. *Myzostoma brachiatum* Graff, 1877, lectotype. A, ventral view, observed on slide; B, left fourth parapodium. 28A-G. *Myzostoma longicirrum* Graff, 1887, specimens from southern Philippines infesting *Capilaster sentosus*. A-B, two specimens seen in ventral view; C, apex of the introvert; D, several parapodia; E-G, parapodial replacement hook, main hook, and support rod, respectively. Abbreviations: CO, cloacal opening; CI, cirrus; F, fold; I, introvert; LO, lateral organs; OI, opening of the introvert pouch; PA, parapodium

or humps over the introvert and seminal vesicles. The convex marginal lobes may be evident all or partway around the body and vary in size and obviousness. The marginal cirri are somewhat annulated.

On the ventral side, the circle of parapodia (five pairs) is centered slightly anterior of the center of the disc, with the parapodia halfway out to the margin but appearing closer to the center when pointing medially (Figs 28A-B). In some specimens, there are radiating ridges inside the ring of parapodia. Spacing between the parapodia is even except slightly wider across the midline for the first and fifth pairs. The parapodia are acirrate and consist of a large but usually low, oval, basal part and a finger-like distal part with a diagonal groove near the base and a aperture at the tip (Figs 28A-B). Either the hook or the support rod may be slightly longer than the other, and there is only one replacement hook (Figs 28E, F, G). The curvature of the hook's tip does not attain 90° (Fig. 28F). The support rod's manubrium is developed only on one side, with its lower angle developed into a blunt spur (Fig. 28G). The opening of the introvert pouch is located in the anterior half of the region between the bases of the first pair of parapodia (Fig. 28A-B). The introvert itself is about twice as long as thick and bears three pairs of buccal papillae that flank the circular, terminal mouth (Fig. 28B-C). The cloacal opening is just inside the border between the body proper and the posterior marginal lobe, from halfway to usually three-quarters or more of the way from the fifth parapodia to the margin (Fig. 28A-B). The lateral organs (four pairs) are round, slightly protruding, and similar in diameter to the distal parts of the parapodia (Fig. 28A-B). They are located just outside the circle of parapodia and alternate with them.

Remarks. - The size and shape, presence of marginal lobes, and pattern of cirral lengths identify these specimens as *M. longicirrum* (cf. Graff, 1887). The holotype was not found in The Natural History Museum in London in 1986 and is presumed to be lost. Graff (1887) noted that the "specimen was much damaged, and the figure given is thus to a large extent a restoration." this may explain discrepancies with Graff's description, in which the lateral organs are placed halfway from the parapodia to the margin and no buccal papillae are shown. The only other described species with a similar general appearance to *M. longicirrum* is *M. crenatum* Graff, 1883, the marginal cirri of which are all short and of equal length (Graff, 1884).

One of the present specimens is missing left leg 4 and left marginal organ 4; it has a deep notch in the body margin, which suggests that it survived an attack by some predator (Fig. 28B). One host jar (*C. sentosa*, USNM 34844) also contained *M. adhaerens* Remscheid, 1916 and *M. attenuatum* Grygier, 1989. The two instances where *M. longicirrum* was found loose with two species of comatulids from the same station suggest that cross-contamination might have occurred.

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