

# MYZOSTOMES FROM PAPUA NEW GUINEA, WITH RELATED INDO-WEST PACIFIC DISTRIBUTION RECORDS AND DESCRIPTION OF FIVE NEW SPECIES

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## ABSTRACT

Eighteen species of myzostomes were found in association with crinoids collected in Papua New Guinea. Thirteen of the former are described by means of in vivo, light microscopical, and SEM-based observations. Five are new to science: *Myzostoma cuniculus*, *M. laingense*, *M. nigromaculatum*, and *M. longitergum* are ectocommensals; *Contramyzostoma sphaera* is a parasite living in a soft cyst induced upon its host. The eight previously described species, six of which are redescribed in detail, include *Myzostoma ambiguum* Graff, *M. capitocutis* Eeckhaut, VandenSpiegel and Grygier, *M. fissum* Graff, *M. mortenseni* (Jägersten), *M. polycyclus* Atkins, and *M. stochoeoides* Atkins, as well as *Hypomyzostoma crosslandi* (Boulenger) and *Notopharyngoides aruensis* (Remscheid). Most are ectocommensals but the last is an intradigestive symbiont. New Indo-West Pacific distribution and host records for all eight are listed, based on surveys of museum collections, and their entire range are mapped. *Hypomyzostoma* Perrier, 1897 (type species *Myzostoma folium* Graff) is resurrected for one of the species-groups previously recognized within *Myzostoma*, and a lectotype is selected for *H. crosslandi*. Specimens from Singapore previously identified as *M. elegans* Graff are reassigned to *M. capitocutis*.

The Myzostomida include about 140 species of obligate symbionts of echinoderms, principally crinoids. They are usually considered to be very close to Polychaeta (they possess chaetae and their development includes a trochophoral stage), although they also have non-annelidan characters (their epidermis is a myoepithelium and their spermatozoons grow inside spermicysts) (Eeckhaut et al., 1990; Eeckhaut, 1995; Haszprunar, 1996).

Most myzostomes are ectocommensals of comatulid crinoids but a few are parasites and infest the integument, digestive system, or gonads of crinoids, ophiuroids, or asteroids (Jangoux, 1990). The majority of taxonomic papers on myzostomes date from before the Second World War (e.g., Graff, 1877, 1883, 1884, 1887; Remscheid, 1918; Atkins, 1927; Jägersten, 1937, 1940), but a few records of known and new species, some with SEM-based descriptions, have recently been published (Grygier, 1989; 1992; Eeckhaut and Améziane-Cominardi, 1994; Eeckhaut et al., 1994; Eeckhaut and Jangoux, 1995). Several species of myzostomes have been described from the Torres Straits (Graff, 1884, 1887; Atkin, 1927), but until now none has been recorded from any other waters bordering Papua New Guinea (PNG hereafter). The present paper reports on 18 species of myzostomes, five of them new to science and six others redescribed in detail, found infesting comatulid crinoids in a bay on the north coast of PNG, and also lists additional new records outside PNG for most of them.

## MATERIALS AND METHODS

Crinoid hosts with myzostomes were collected by hand by the Belgian team during dives at 10–30 m depth in July, 1994, at various sites in Hansa Bay (Madang Province, PNG). During collec-

tions, crinoids were placed separately in plastic bags. Once in the laboratory at the Biological Station King Léopold III, each crinoid was placed in a dish filled with 70% ethanol and shaken vigorously. The myzostomes fallen from their hosts were counted under a binocular microscope and put into fixatives for morphological studies.

For histological observation, individuals were fixed either in Bouin's fluid for 24 h or in a solution of 3% glutaraldehyde in cacodylate buffer (0.1 M, pH 7.3) for 3 h at 4°C. Bouin's fluid-fixed individuals were dehydrated, embedded in Paraplast, cut into 5 µm sections with an HM 340E Microm microtome, and stained with Masson's trichrome according to the procedure of Gabe (1968). Glutaraldehyde-fixed individuals were washed in cacodylate buffer, postfixed for 1 h with 1% osmium tetroxide in 0.1 M of the same buffer, and washed again in buffer; after dehydration, specimens were embedded in Spurr and cut into 1 µm serial sections, which were stained in a 1:1 solution of Methylene Blue/Azur II according to the procedure of Ganter and Jollès (1969, 1970).

For SEM observation, individuals were fixed in Bouin's fluid for 24 h, then dehydrated in graded concentrations of ethanol and dried by the critical point method using CO<sub>2</sub> as the transition fluid. Samples were mounted on aluminium stubs, coated with gold in a sputter coater, and observed with a JEOL JSM 6100 scanning electron microscope.

Descriptions of the parapodial hooks, replacement hooks, and support rods were based on individuals, the soft tissues of which were digested in weak bleach. Once most of the tissues were dissolved, the hooks and support rods were dried and mounted on slides. Microscopic observations were made with an Olympus IMT-2 phase contrast microscope.

The type lots of the new species were divided between the Institut Royal des Sciences Naturelles de Belgique (IG hereafter) and the Laboratory of Marine Biology at the University of Mons-Hainaut, Belgium (UMH hereafter).

Additional records of many of these same species were compiled on the basis of extensive surveys of museum collections of myzostomes and crinoids, as outlined by Grygier (1990), including further large collections from the Western Australian Museum, the Australian Museum, the Museum of Comparative Zoology, the Osaka Museum of Natural History, and the Department of Chemistry, Biology and Marine Science, College of Science, University of the Ryukyus. Some specimens were photographed and individuals of two of the species were examined by SEM. Also, collections were made in 1988 near Sesoko Island, Okinawa, using the technique described above except for washing the crinoids in 5–10% ethanol in sea water; in these cases, the myzostomes were fixed in buffered seawater formalin and then transferred to 80% ethanol, and bleach-digested parapodia were mounted in glycerine jelly on slides for examination using a Nikon Optiphot microscope equipped with a drawing tube.

#### TAXONOMIC ACCOUNT

Eighteen species of myzostomes were found on 25 species of crinoids (Table 1). Out of these 18, five are new to science and eight are already known but, for the most part, incompletely described. The last five species (four *Myzostoma* and one *Cystimyostomum*) are represented by too few specimens to determine them accurately and they are not included in the following descriptions.

#### *Myzostoma cuniculus*, sp. nov.

(Figs. 1A–B, 2A, 3, 9, 10)

*Material examined*.—Type lot, Hansa Bay, PNG: 15 specimens (1–7 per host) from 6 of 12 examined *Clarkcomanthus albinotus* Rowe, Hoggett, Birtles and Vail, 1986. Type specimens: holotype (IG28342-10); 7 paratypes (IG28342-11): 2 intact specimens in alcohol, 1 sectioned, 1 dissolved in bleach for observation of parapodial hook apparatus, and 3 used for SEM observation; remaining 7

Table 1. List and numbers of the crinoids and their associated myzostomes sampled in Hansa Bay (Madang Province, Papua New Guinea) in July, 1994.

Crinoids	Myzostomes
<i>Comaster multifidus</i> (9)	<i>Myzostoma capitocutis</i> (14), <i>M. nigromaculatum</i> (34)
<i>Comaster gracilis</i> (4)	<i>M. capitocutis</i> (6), <i>M. nigromaculatum</i> (8)
<i>Comanthus parvicirrus</i> (8)	<i>M. polycyclus</i> (3), <i>M. capitocutis</i> (2), <i>Myzostoma</i> sp. A (6)
<i>Comanthus alternans</i> (7)	<i>M. ambiguum</i> (5), <i>Notopharyngoides aruensis</i> (2)
<i>Comanthus mirabilis</i> (2)	<i>M. ambiguum</i> (1)
<i>Comanthus suavius</i> (1)	<i>M. polycyclus</i> (3)
<i>Clarkcomanthus littoralis</i> (4)	<i>M. polycyclus</i> (1)
<i>Clarkcomanthus albinotus</i> (12)	<i>M. mortenseni</i> (3), <i>M. cuniculus</i> (15), <i>Myzostoma</i> sp. B (1)
<i>Oxycomanthus bennetti</i> (21)	<i>M. ambiguum</i> (339)
<i>Comatella stelligera</i> (8)	<i>Contramyzostoma sphaera</i> (128), <i>Myzostoma</i> sp. C (1)
<i>Capillaster multiradiatus</i> (139)	<i>M. stochoeides</i> (5), <i>M. capitocutis</i> (1), <i>M. polycyclus</i> (1), <i>Cystimyzostomum</i> sp. A (1)
<i>Comanthina schlegelii</i> (1)	<i>M. longitergum</i> (15)
<i>Himerometra robustipinna</i> (6)	<i>M. ambiguum</i> (1)
<i>Dichrometra flagellata</i> (13)	<i>M. fissum</i> (13), <i>H. crosslandi</i> (2), <i>Myzostoma</i> sp. D (2)
<i>Lamprometra palmata</i> (1)	<i>M. nigromaculatum</i> (1)
<i>Stephanometra oxyacantha</i> (5)	<i>M. laingense</i> (5)
<i>Comaster multibrachiatus</i> (2),	no myzostomes
<i>Comanthus gisleni</i> (2),	
<i>Comanthus wahlbergi</i> (1),	
<i>Comanthina audax</i> (2),	
<i>Alloeocomatella pectinifera</i> (2),	
<i>Cenometra bella</i> (5),	
<i>Colobometra perspinosa</i> (2),	
<i>Heterometra savignii</i> (1),	
<i>Stephanometra spicata</i> (3)	

paratypes retained at UMH and used or reserved for histological work.

*Additional records*.—Hansa Bay, PNG: 2 specimens on 1 *Clarkcomanthus littoralis* Rowe, Hoggett, Birtles and Vail, 1986, 1 July 1996, D. VandenSpiegel and I. Eckhaut. Australian Museum: 1 specimen (W 18553) on arm of brown and cream crinoid, Lizard Is., 14°40'S, 145°28'E, 29 November 1979, R. Muffley. Museum and Art Gallery of the Northern Territory: 1 specimen (NTM WM.00040) from *Comanthus samoanus*, i.e., *C. wahlbergi* J. Müller, 1843, McCluer Is., Northern Territory, Australia, 11°05'S, 133°00'E, 8–9 m, 16 Oct. 1982, R. Hanley.

*Etymology*.—Noun in apposition from Latin *cuniculus*, rabbit, based on the resemblance imparted by the two caudal processes.

*Diagnosis*.—Small myzostome with ovoid body ending in two broad, furred, acirrate caudal processes approximately equal in length to body proper. Ten pairs of small, thin cirri, all of equal length; cirri 2–9 grouped in doublets flanking lateral organs. Parapodia small, thin, acirrate, located closer to body margin than to ventral midline. Hook shaft thick, ending in large, open, rounded hook. Support rod as long as hook but thinner; manubrium as small, low, isosceles triangle. Lateral organs located halfway between parapodia and body margin on paired ventral humps alternating with parapodia. Introvert pouch opening close to first pair of parapodia. Common exit of digestive tract and female genital duct at level of bifurcation between caudal processes. Relative lengths of pharynx,

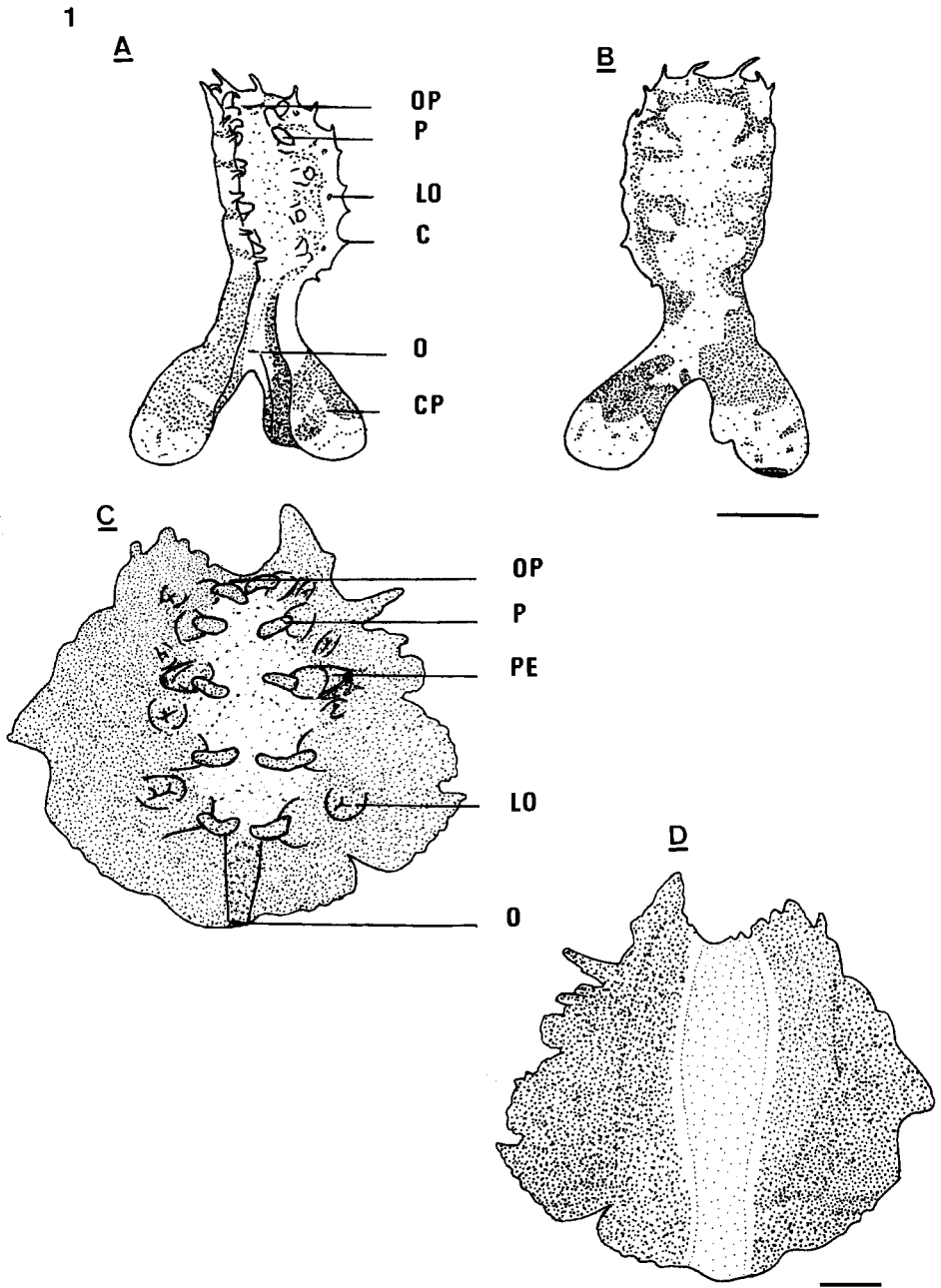
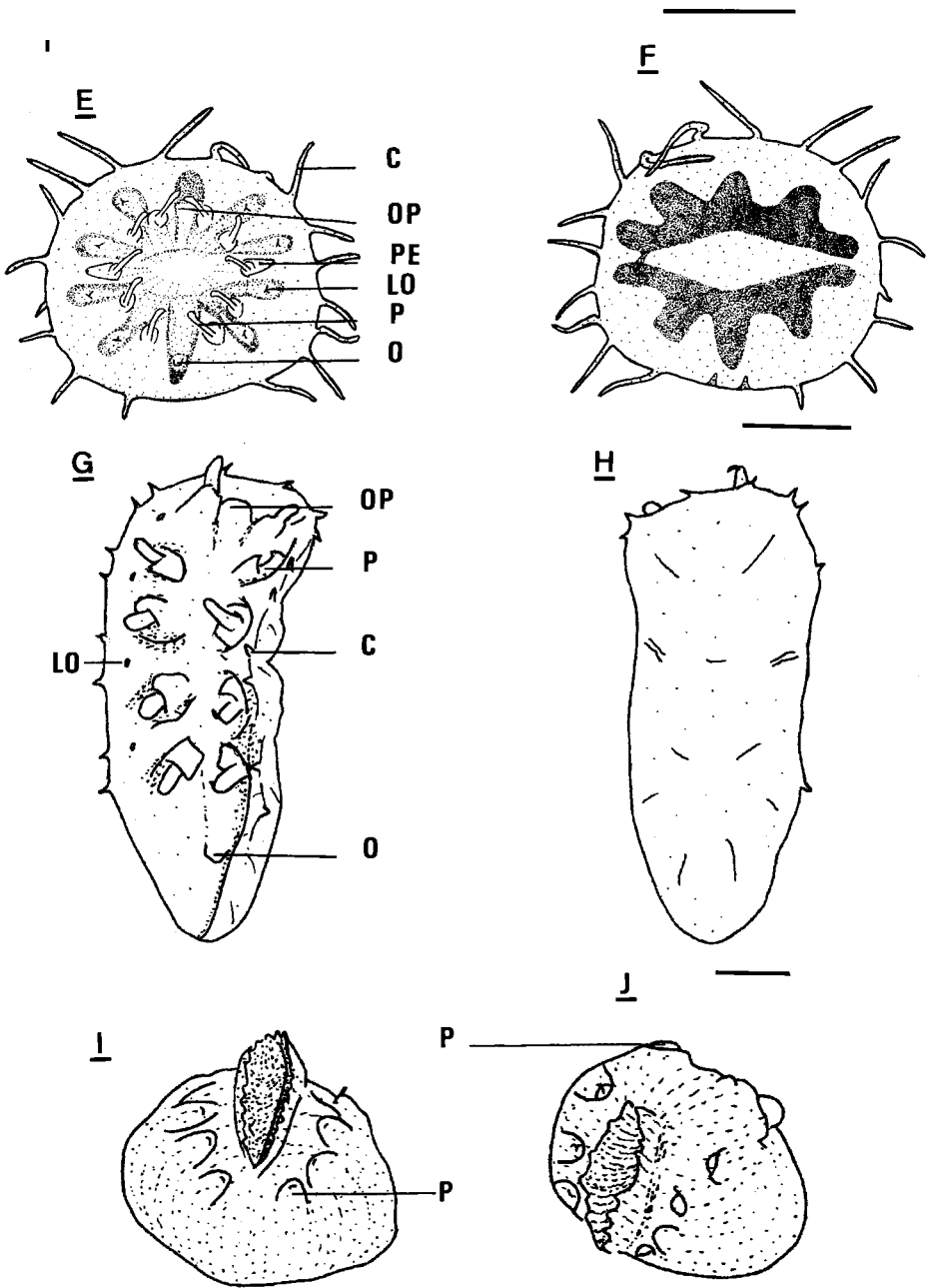
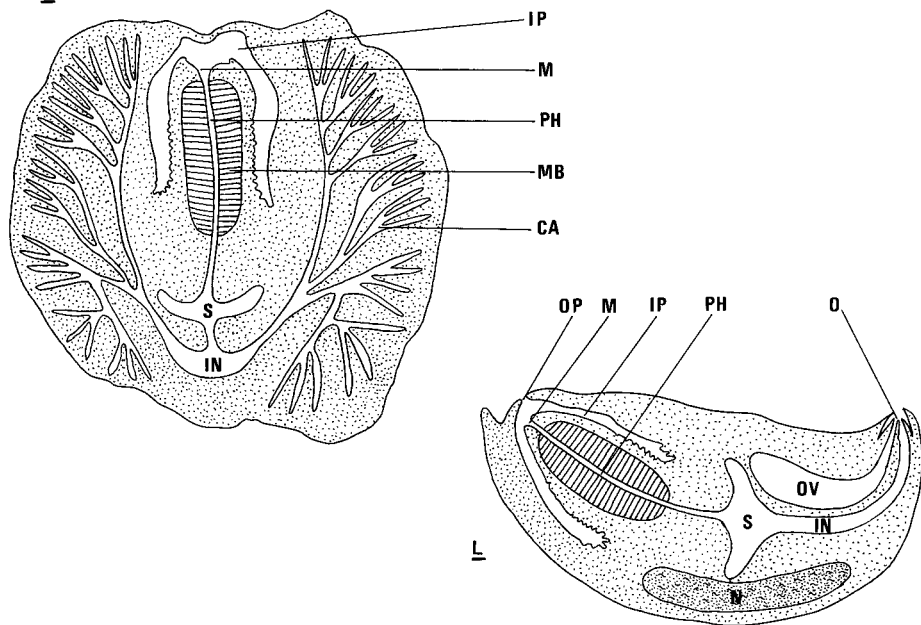


Figure 1. Drawings of eight Indo-West Pacific species of myzostomes (the first five drawings are based on specimens from Papua New Guinea, the last three are based on specimens from Okinawa). Ventral and dorsal sides of *Myzostoma cuniculus* (A,B, respectively), *M. laingense* (C,D), *M. nigromaculatum* (E,F), *M. longitergum* (G,H); front and left sides of *Contramyzostoma sphaera* (I,J); idealized frontal and sagittal sections of *C. sphaera* (K,L); dorsal and ventral sides of *Myzostoma mortenseni* (M,N), *M. polycyclus* (O,P) and *Notopharyngoides aruensis* (Q,R). Scale bars in figures A to J = 500  $\mu\text{m}$ ; Scale bars in figures M to R = 700  $\mu\text{m}$ .



Abbreviations: AF, anterior sagittal fold; C, cirrus; CA, caecum; CP, caudal process; I, introvert; IN, intestine; IP, introvert pouch; LO, lateral organ; LOF, lateral organ fold; M, mouth; MB, muscular bulbus; MF, marginal fold; O, common opening of digestive system and female genital tube; OP, opening of the introvert pouch; OV, oviduct; P, parapodia; PE, penis; PH, pharynx; S, stomach

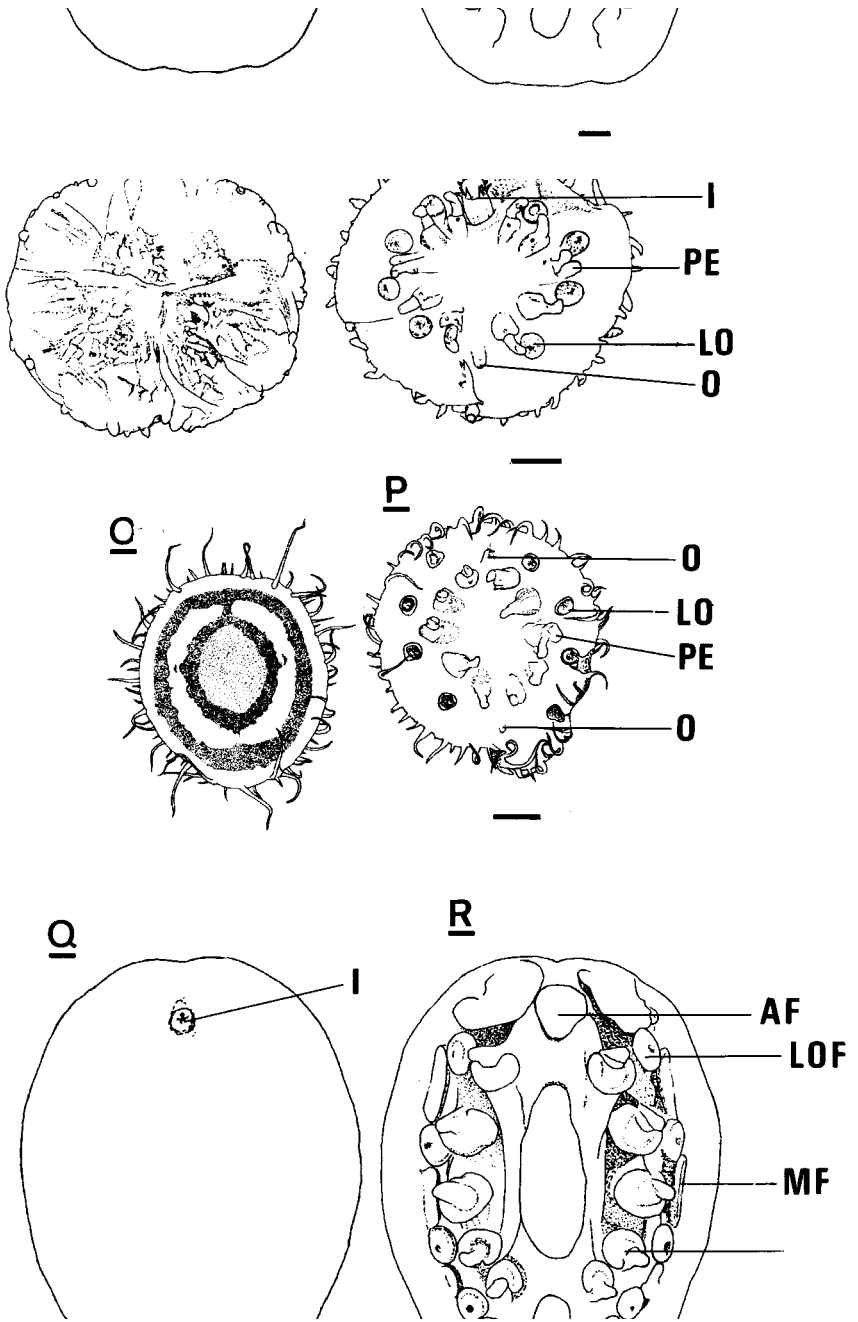
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stomach, and intestine 3:2:4. Two pairs of digestive caeca. Adults hermaphrodites. Ectocommensals.

*Description of type lot.*—Holotype 3 mm long (including caudal processes) and 1.4 mm wide (Figs. 1A,B). Paratypes ranging in length from 1 to 3 mm and in width from 0.6 to 1.4 mm. Larger specimens provided with 2 broad, acirrate, caudal processes, these 1.4 mm long and 0.8 mm wide in holotype (Figs. 1A,1B,3), with edges often furled, thus resembling rabbit ears. These processes and their common base trailing posteriorly. Smaller individuals with only one wide, flat caudal process, incipiently bifid in some. Ten pairs of small, fine cirri 100  $\mu$ m long (Figs. 3,10). Cirri 2 and 3, 4 and 5, 6 and 7, and 8 and 9 on each side rather closely spaced and flanking lateral organs on distinct lobes of body margin. Color in life dirty white with reddish-brown dorsal patches (Fig. 1B). Ventral side colored dirty white, with darker areas bordering parapodia (Fig. 1A).

Five pairs of parapodia lying in two almost parallel rows close to body margin (Figs 1A,3). Parapodia small, 300  $\mu$ m long, acirrate (Fig. 9). Hook shaft thick, drawn slightly outward in its distal half; tip forming large, open hook and bending more than 90° (Fig. 2A). Support rod as long as hook but less than half as thick (200  $\mu$ m long in 2.3 mm long examined individual); manubrium in form of obtuse isosceles triangle with rounded corners, produced very little on outer side of shaft (Fig. 2A). One replacement hook present (Fig. 2A).

Four pairs of lateral organs alternating with parapodia, located on humps halfway between latter and body margin (Fig. 10). Opening of introvert pouch a small slit between first pair of parapodia (Fig. 9). Common posteroventral exit pore for digestive tract and female genital duct at level of bifurcation between caudal processes; digestive system



fused with oviduct over last 10  $\mu\text{m}$ . Penes not protruding, but two male genital pores opening just outside third pair of parapodia.

Digestive system in 3 mm long sectioned individual (caudal processes included) consisting of straight tube 1400  $\mu\text{m}$  long and two pairs of blind digestive caeca. Tube consisting of pharynx (300  $\mu\text{m}$  long) included within protrusible introvert, stomach (400  $\mu\text{m}$  long), and intestine (700  $\mu\text{m}$  long). Caeca starting from sides of stomach, anterior pair going to anterior part of body, posterior pair going back to ends of caudal processes; caeca dividing into numerous secondary and tertiary branches.

Hermaphroditic. Female genital system lying dorsal to digestive system and consisting of diffuse ovary and oviduct with branches. Oviduct consisting of sagittal cavity dorsal to stomach and intestine; its anterior portion giving rise to thin, branched channels extending out dorsal to digestive caeca. Ovary found dorsal to these channels and consisting of numerous female germinal cells (oogonia, previtellogenic oocytes, and vitellogenic oocytes) lying in parenchyma. Male genital system lying ventrolateral to digestive system, consisting of diffuse testis, numerous efferent ducts, and two seminal vesicles. Testis well developed, extending throughout ventral part of body, including caudal processes, and consisting of male germinal cells developing within cyst cells (spermiocysts), these latter lying in parenchyma (see Afzelius, 1984, and Mattei and Marchand, 1988, for detailed but contradictory descriptions of spermiogenesis in myzostomes). Spermiocysts passing through efferent ducts and accumulating in pair of ovoid seminal vesicles, latter 200  $\mu\text{m}$  long and located just outside third pair of parapodia. No deferent ducts nor penial ducts observed; seminal vesicles opening to exterior through two simple pores.

*Description of other specimens.*—Specimens from Hansa Bay found on *C. littoralis* similar to large type lot specimens but colored green in life (rather than dirty white) with black patches.

Specimen from Lizard Island with caudal processes 1.3 mm long, equal to or slightly shorter than body proper. Right caudal process folded longitudinally; left one split in two and each secondary lobe also folded. Body dorsum with faint brown submarginal ring and cross-band; caudal process mottled brown. Dorsal cuticle apparently minutely spinulose. Nine pairs of cirri around main body, those flanking each lateral organ spaced slightly closer together. Parapodia lacking medial cirri. Introvert pouch opening halfway between first parapodia and anterior body margin.

Northern Australian specimen 2.3 mm long, 1.0 mm wide, 0.9 mm high. Posterior quarter as caudal lobe partly folded in two and upraised about 45°. Front end of specimen damaged; no buccal papillae seen on exposed introvert. Ventral structures not observed, but 9 or 10 pairs of short, tapered marginal cirri present; at least left cirri 4-5, 6-7, 8-9 spaced as couplets flanking subcircular lateral organs with tiny apertures.

*Remarks.*—*Myzostoma cuniculus* is mainly characterized by its caudal process that eventually develops into two large, furred, acirrate lobes. The marginal humps bearing the lateral organs and couplets of cirri are also characteristic. Several other species have a single pair of large processes: *M. bicaudatum* Graff, 1883, *M. filicauda* Graff, 1883 (sensu Graff, 1884; see Grygier (1989) for attendant nomenclatural problem), *M. filiferum* Graff, 1884; *M. divisor* Grygier, 1989, and *M. tentaculatum* Jägersten, 1937. However, the first four species have a round main body trailing a pair of short or long, uniformly cylindrical processes that end bluntly or in a cirrus, and the last has a pair of relatively very large processes shaped like artillery shells, each ending in a cirrus. One of us (MJG) has seen specimens of four undescribed species very close to *M. cuniculus*: the first, from Okinawa,



has only one broad caudal process furled into a cone with several posterior notches and lobes; the second, from Enewatak, has an elongate body with single upturned and folded but rather short caudal process and a thick, rugose cuticle; the third has an upturned caudal process thrown into multiple folds in a manner similar to *Asteromyzostomum* (see Grygier, 1988); and the fourth, from southern PNG, is quite like *M. cuniculus* but with 3 of the pairs of cirri tremendously elongated. The closest relatives of *M. cuniculus* will certainly be found among these forms.

*Myzostoma laingense*, sp. nov.

(Figs. 1C–D, 2B, 4, 11)

*Material examined*.—Type lot, Hansa Bay, PNG: 5 specimens (1–2 per host) from 4 of 5 examined *Stephanometra oxyacantha* (Hartlaub, 1890). Type specimens: holotype (IG28342-20); 4 paratypes (IG28342-21): 1 intact specimen in alcohol, 1 specimen sectioned, 1 dissolved in bleach for observation of the parapodial hook apparatus, and 1 used for SEM observation.

*Etymology*.—Referring to Laing I., the type locality.

*Diagnosis*.—Large myzostome with thick body broader posteriorly than anteriorly. Numerous small, knob-like, closely spaced marginal cirri, all of about equal size. Parapodia long, stout, located halfway between body margin and ventral midpoint. Hook shaft thick, ending in long, sharp tip. Support rod slightly longer but thinner than hook. Manubrium large, quadrangular. Lateral organs closer to parapodia than to body margin. Introvert pouch opening close to first pair of parapodia. Common exit of digestive tract and female genital duct located very close to posterior body margin. Relative lengths of pharynx, stomach, and intestine 1:1:2. Adults hermaphrodites. Ectocommensals.

*Description*.—Holotype 4.5 mm long and 4 mm wide (Figs. 1C,D). Paratypes ranging from 2.7 to 4.5 mm long and 2.2 to 4 mm wide. From level of third pair of parapodia, body broadening posteriorly (Figs. 1C,D). Body margin irregular: in some specimens posterior end grossly pleated, giving impression of 2 to 5 posterior processes (Fig. 4). Numerous knob-like marginal cirri 50  $\mu$ m long (Figs. 4, 11). Dorsal texture smooth to sandpapery. Dorsal coloration consisting of reddish mid-dorsal stripe flanked by pair of narrow light stripes; more lateral regions dark reddish-brown or black (Fig. 1D).

Five pairs of parapodia in 2 slightly diverging rows (Fig. 1C). First, 2nd and 3rd pairs of parapodia located halfway between body margin and body midpoint; 4th and 5th pairs located closer to body midpoint due to lateral extension of posterior body part. Parapodia stout, 400  $\mu$ m long, with probably a small, knob-like medial cirrus on their basal fold (Figs. 4, 11). Shaft of hook thick and nearly straight; long, nearly straight tip bent sharply at about 120° (Fig. 2B). Support rod a little longer than hook (rod 500  $\mu$ m long in 2.7 mm long examined individual, hook 450  $\mu$ m long); manubrium expanded on both sides of shaft, inner portion as distally broadening, flag-like quadrangle (Fig. 2B). Two replacement hooks in each parapodium (Fig. 2B).

Four pairs of hemispherical, hump-like lateral organs located closer to parapodia than to body margin, their size increasing from front to rear (1st pair 250  $\mu$ m in diameter; 4th pair 500  $\mu$ m in diameter) (Figs. 4, 11). Introvert pouch opening between first pair of parapodia (Fig. 4). Common exit pore of digestive tract and female genital duct evident as small posteroventral slit located very close to posterior body margin. Two conical penes up to 100  $\mu$ m long at outer margins of third pair of parapodia.

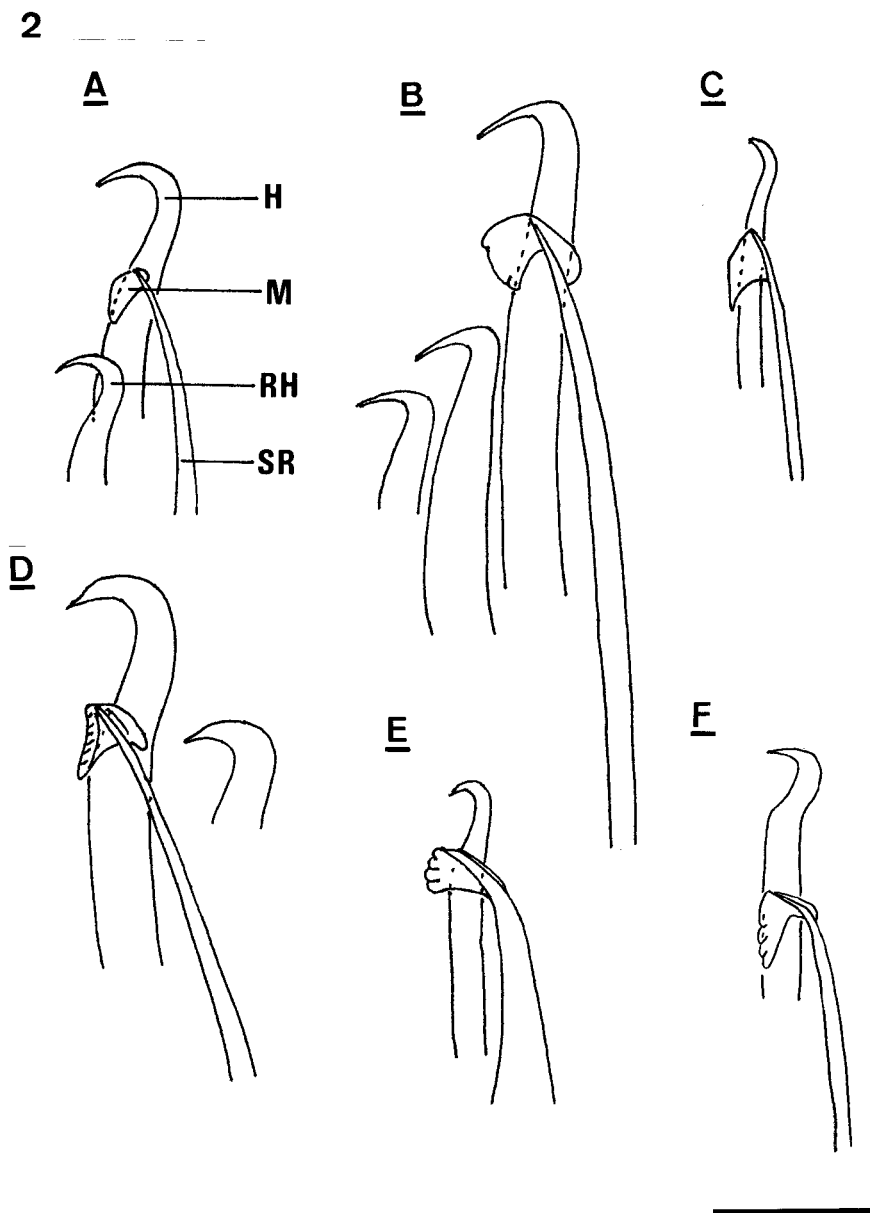
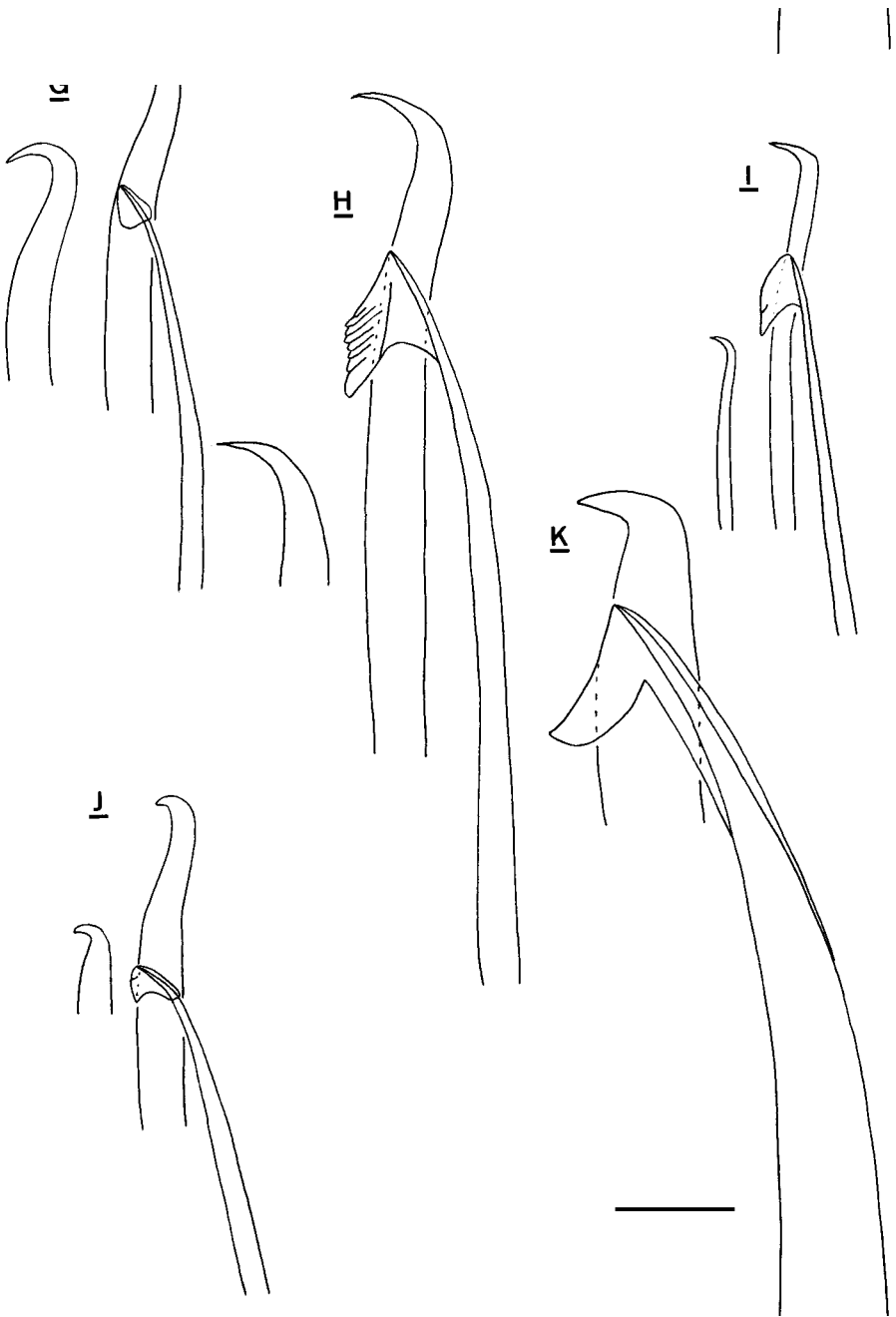


Figure 2. Drawings of the myzostome parapodial hook apparatus based on specimens from Papua New Guinea. *Myzostoma cuniculus* (A), *Myzostoma laingense* (B), *Myzostoma nigromaculatum* (C), *Myzostoma longitergum* (D), *Contramyzostoma sphaera* (E), *Myzostoma ambiguum* (F), *Myzostoma fissum* (G), *Myzostoma mortenseni* (H), *Myzostoma polycyclus* (I), *Hypomyzostoma crosslandi* (J), *Notopharyngoides aruensis* (K). Scale bars = 120  $\mu\text{m}$ . Abbreviations: M, manubrium; H, hook; RH, replacement hook; SR, support rod



Digestive system in 4 mm long sectioned individual consisting of straight tube 2000  $\mu\text{m}$  long and paired, blind digestive caeca. Tube consisting of pharynx (500  $\mu\text{m}$  long) included in protrusible introvert, stomach (500  $\mu\text{m}$  long), and intestine (1000  $\mu\text{m}$  long). Number of pairs of caeca and their extent of branching not established. Both male and female genital systems poorly developed: female germinal cells lying in dorsal parenchyma, male germinal cells lying inside cysts in ventral parenchyma. No seminal vesicles observed.

*Remarks.*—*Myzostoma laingense* is characterized by its stout, broad body with an irregular margin armed with many small cirri. These features are shared with *M. furcatum* Graff, 1887 (= *M. adhaerens* Remscheid, 1918; Grygier, 1990), which was collected on *Actinometra* sp. near the Moluccas. The new species differs by the absence of true caudal processes (two small, triangular pairs with marginal grooves in *M. furcatum*), the absence of longitudinal and radial dorsal ridges, and the presence of dorsal stripes (color a solid maroon or dark brown in *M. furcatum*).

*Myzostoma nigromaculatum*, sp. nov.

(Figs. 1E–F, 2C, 5, 12)

*Material examined.*—Type lot, Hansa Bay, PNG: 34 specimens from 7 of 9 examined *Comaster multifidus* (J. Müller, 1841). Type specimens: holotype (IG28342-30); 21 paratypes (IG28342-31): 10 intact specimens in alcohol, 5 sectioned, 1 dissolved in bleach for observation of the parapodial hook apparatus, and 5 used for SEM observation; 12 remaining paratypes retained at UMH and used or reserved for histological work.

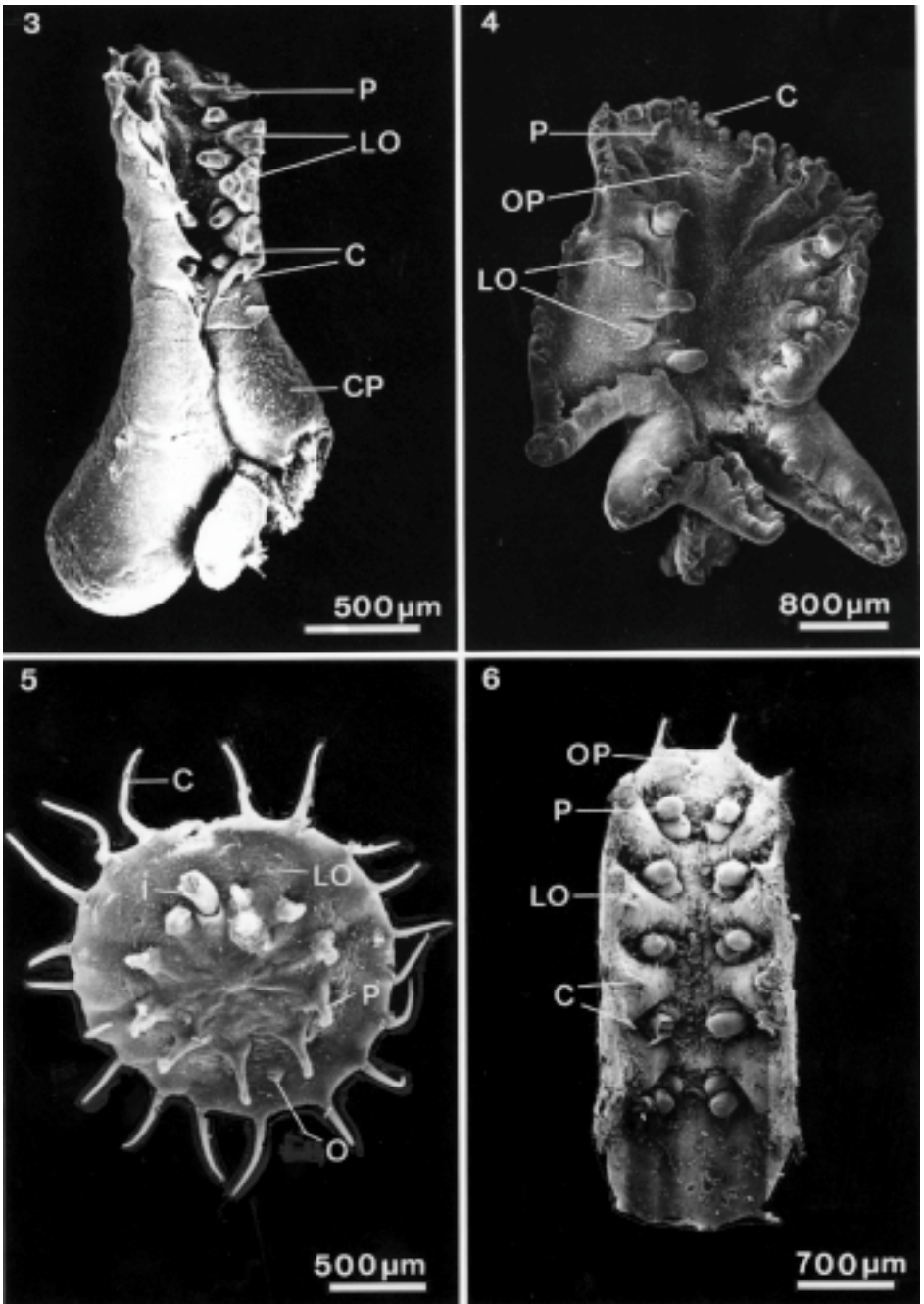
*Additional records.*—Hansa Bay, PNG: 8 specimens from 2 of 4 examined *Comaster gracilis* (Hartlaub, 1890), and 1 specimen from 1 examined *Lamprometra palmata* (J. Müller, 1841); all retained at UMH.

*Etymology.*—Adjective from Latin *niger*, black, and *maculus*, spot, referring to the characteristic dorsal color pattern.

*Diagnosis.*—Small myzostome with flat, round body. Ten pairs of moderately long, thin cirri, slightly longer anteriorly than posteriorly. Parapodia small, thin, acirrate, located halfway between body margin and ventral midpoint. Hook shaft thin and ending in small, sharp tip. Support rod as long as hook but thinner; manubrium large, quadrangular. Lateral organs and introvert pouch opening located closer to parapodia than to body margin. Common exit of digestive tract and female genital duct located halfway between last pair of parapodia and body margin. Relative lengths of pharynx, stomach, and intestine 3:2:2. Three pairs of digestive caeca. Adults hermaphrodites. Penes small. Ectocommensals.

*Description of type lot.*—Body round often slightly curved with ventral part concave and dorsal part convex. Holotype 1.7 mm in diameter (Figs. 1E,F). Diameters of paratypes ranging from 0.9 to 2 mm. Ten pairs of fine, straight cirri with two most anterior pairs (three most anterior in some paratypes) up to 2 times longer than others, these being all of same length (ca. 300  $\mu\text{m}$ ) (Figs. 1E,F,5). Dorsal coloration of large individuals consisting of 2 pale brown to red transverse arcs, each being made of 5 oblong patches. Dorsal coloration in small individuals consisting of more-or-less irregular ring. Same pattern as dorsal occurring less vividly ventrally in all specimens (Fig. 1F).

Five pairs of parapodia lying in circle halfway between body margin and ventral midpoint and centered on this midpoint (Figs. 1F,5). Parapodia thin, 200  $\mu\text{m}$  long, with no



Figures 3 to 29. SEM views of myzostomes from Papua New Guinea.  
 Figures 3 to 7. General view of the ventral side of *Myzostoma cuniculus* (3), *Myzostoma laingense* (4), *Myzostoma nigromaculatum* (5), *Myzostoma longitergum* (6), *Contramyzostoma sphaera* (7).  
 Abbreviations on p. 860.

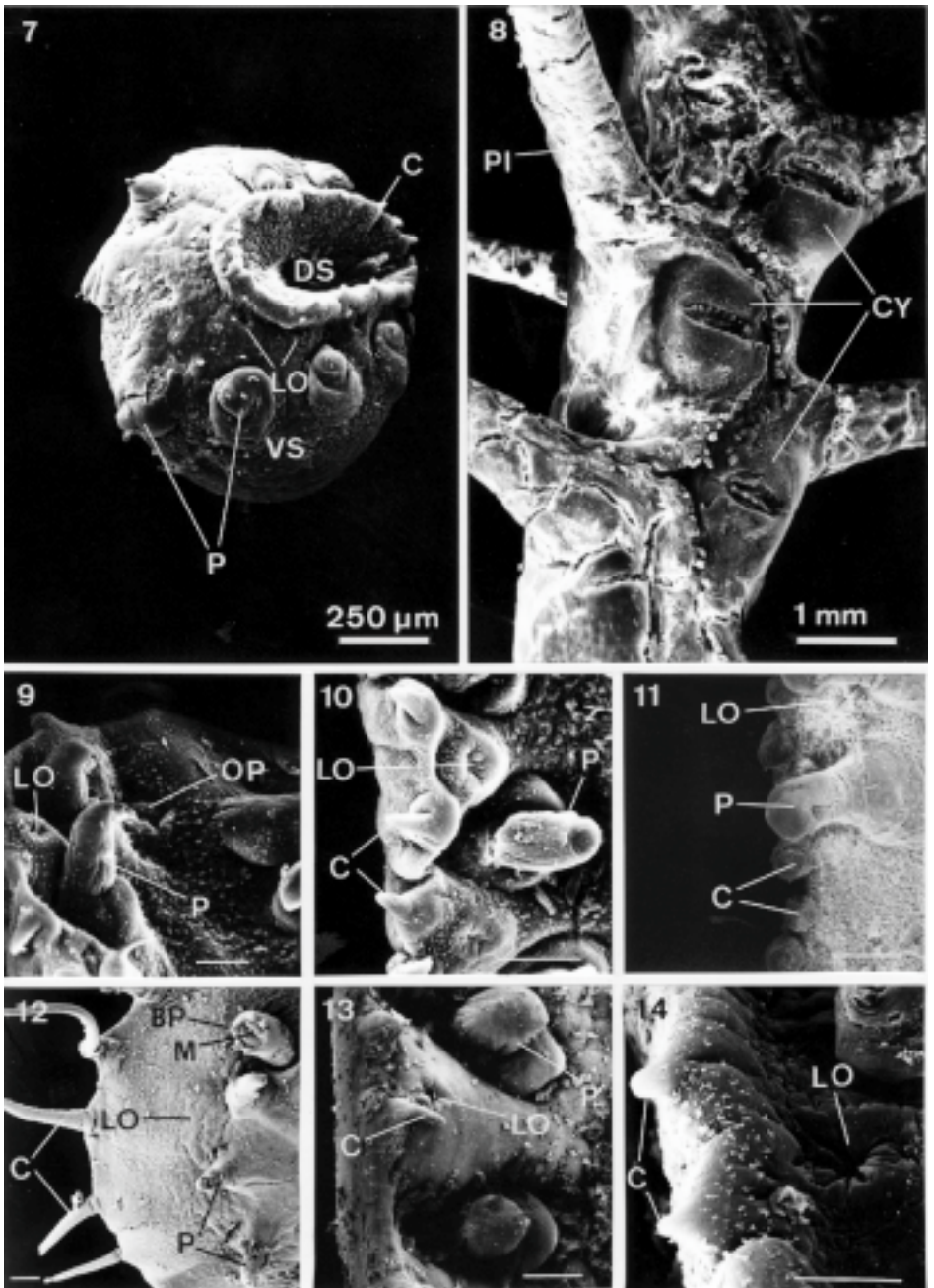


Figure 8. General view of three cysts induced by *C. sphaera*.

Figures 9 to 14. detailed views of the ventral appendages of *Myzostoma cuniculus* (9,10), *Myzostoma laingense* (11), *Myzostoma nigromaculatum* (12), *Myzostoma longitergum* (13), *Contramyzostoma sphaera* (14). Scale bar = 100 µm. Abbreviations on p. 860.

medial cirrus. Hook shaft thin, slightly bowed outward in distal quarter, with small, weak tip curving less than 90° (Fig. 2C). Support rod of each parapodium as long as hook but even thinner (200 µm long in 2.3 mm long examined individual) (Fig. 2C). Manubrium developed only on inner side of shaft, almost quadrangular like drooping flag (Fig. 2C). No replacement hooks observed.

Four pairs of lateral organs located a little closer to parapodia than to body margin (Figs. 1E,5,12). Lateral organs small, flat and oval. Opening of introvert pouch lying between first pair of parapodia (Figs. 1E,5). Introvert provided with 3 pairs of buccal papilla 20 µm long. Common exit pore of digestive tract and female genital duct lying halfway between fifth pair of parapodia and body margin (Fig. 1F). Two penes weakly developed as short nozzles 50 µm long, thicker than but almost hidden by third pair of parapodia.

Digestive system in 1.2 mm long sectioned individual consisting of straight tube 700 µm long and 3 pairs of blind digestive caeca. Tube consisting of pharynx (300 µm long) included within protrusible introvert, stomach (200 µm long), and intestine (200 µm long). Gross anatomy of female genital system similar to that of other species of *Myzostoma*. Male genital system consisting of diffuse testis, numerous efferent ducts, 2 pairs of short deferent ducts leading to 2 ovoid seminal vesicles 150 µm long, and 2 penial ducts.

*Remarks.*—The most distinctive features of *Myzostoma nigromaculatum* sp. n. are the 10 pairs of long marginal cirri that are slightly longer anteriorly than posteriorly and the dorsal color pattern. The morphologically most similar species are those belonging to the *Myzostoma ambiguum*-group defined by Grygier (1990) and *Myzostoma stochoeides* Atkins, 1927. All myzostomes of the former group differ from *M. nigromaculatum* in having at least the two most posterior pairs of cirri, as well as some anterior cirri, considerably longer than the lateral cirri. *M. stochoeides* specimens (discussed later on in the present paper) differ from *M. nigromaculatum* specimens of the same size in having a different color pattern, longer buccal papilla, a thicker introvert and more curled cirri (though a few specimens assigned to *M. stochoeides* have straight cirri; see the remarks about the problematic polymorphism of that species).

***Myzostoma longitergum*, sp. nov.**  
(Figs. 1G–H,2D,6,13)

*Material examined.*—Type lot, Hansa Bay, PNG: 15 specimens from 1 *Comanthina schlegelii* (Carpenter, 1879). Type specimens: holotype (IG28342-40); 5 paratypes (IG28342-41); 2 intact specimens in alcohol, 1 sectioned, 1 dissolved in bleach for observation of the parapodial hook apparatus, and 1 used for SEM observation; 9 remaining paratypes retained at UMH and used or reserved for histological works.

*Etymology.*—Noun in apposition, from Latin *longus*, long, and *tergum*, back, referring to the elongate posterior region.

*Diagnosis.*—Medium-sized myzostome with hemicylindrical, ventrally concave body exhibiting elongation posterior to eighth pair of marginal cirri. Nine to ten pairs of small, thin cirri, all of equal length; cirri 2-9 grouped in doublets flanking lateral organs. Parapodia small, thin, acirrate, located a bit closer to ventral midline than body margin. Hook shaft thick, ending in a long, stout tip. Support rod as long as hook but thinner; manubrium large and triangular. Lateral organs located on ventral humps halfway between parapodia

and body margin. Introvert pouch opening close to anterior body margin. Common exit of digestive tract and female genital duct located 60–65% of way from fifth parapodia to posterior body margin. Relative lengths of pharynx, stomach, and intestine: 2:2:3. Three pairs of digestive caeca. Adults hermaphrodites. Ectocommensals.

*Description.*—Holotype 4 mm long, 1.4 mm wide (Figs. 1G,H). Paratypes ranging from 2.5 to 4.3 mm long and 0.8 to 1.6 mm wide. Most specimens with nine pairs of small, fine cirri 100  $\mu\text{m}$  long, Cirri 2 and 3, 4 and 5, 6 and 7, and 8 and 9 on each side rather closely spaced and flanking lateral organs on distinct lobes of body margin. (Figs. 1G,H,6). Tenth pair (when present) separated farther from ninth and located laterally, not terminally. Color in life uniform light brown.

Five pairs of parapodia lying in 2 parallel rows a bit closer to ventral midline than body margin (Figs. 1G,6), last pair at about 60–70% body length, 2 to 3 times farther from posterior body margin than first pair from anterior body margin (Figs. 1G,6). Parapodia stout, 100  $\mu\text{m}$  long, with no medial cirri (Figs. 6,13). Hook shaft thick, its distal third bowed outward; thick, crochet-like tip curving a little more than 90° (Fig. 2D). Support rod of each parapodium as long as hook but less than half as thick (300  $\mu\text{m}$  long in 2.8 mm long examined individual); manubrium triangular and well developed on both sides of shaft, with small basal spur on outer side and ca. 7 small lobes along drawn out inner margin (Fig. 2D). One replacement hook found in each parapodium (Fig. 2D).

Four pairs of lateral organs alternating with parapodia, on low mounds halfway between parapodia and body margin (Fig. 6). Opening of introvert pouch ventral but adjacent to body margin (Figs. 6,13). Common exit pore of digestive tract and female genital duct located nearly two-thirds of way from fifth parapodia to body margin. No penes observed, but 2 male genital openings present outside third pair of parapodia.

Digestive system in 2.7 mm long sectioned individual consisting of straight tube 2100  $\mu\text{m}$  long and 3 pairs of blind, branched digestive caeca. Tube consisting of pharynx (600  $\mu\text{m}$  long) included within protrusible introvert, stomach (600  $\mu\text{m}$  long), and intestine (900  $\mu\text{m}$  long). Gross anatomy of female genital system similar to that of other species of *Myzostoma*. Male genital system consisting of diffuse testis, numerous efferent ducts, and 2 ovoid seminal vesicles 350  $\mu\text{m}$  long. No deferent ducts nor penial ducts observed.

*Remarks.*—*Myzostoma longitergum* is superficially similar to members of the “crosslandi-group” defined by Grygier (1990) (equivalent to *Hypomyzostoma* Perrier, 1897; see section on *H. crosslandi* below), which includes species with moderately to very elongate bodies and often with a long posterior end. The new species differs from the species of that group (recognized as a genus herein) by the presence of ten pairs of thin cirri, the others having a dentate or scalloped margin, and by the nearly marginal opening of the introvert pouch. Furthermore, in species of *Hypomyzostoma* the lateral organs are not on mounds but are located, often very inconspicuously, very close to the body margin. *Myzostoma longitergum* is also similar in form to, though less slender than, *M. chelonoideum* McClendon, 1906, but it lacks that species’ polygonal cuticular thickenings.

The sectioned *M. longitergum* is parasitized by a flatworm which infests the left posterior caecum. The worm is almost totally cylindrical and measures 700  $\mu\text{m}$  long and 300  $\mu\text{m}$  in diameter.



*Contramyzostoma sphaera*, sp. nov.

(Figs. 11–L, 2E, 7–8, 14)

*Material examined*.—Type lot, Hansa Bay, PNG: 128 specimens from 5 of 8 examined *Comatella stelligera* (10–48 myzostomes per host). Type specimens: holotype (IG28342-50); 22 paratypes (IG28342-51): 10 intact specimens in alcohol (some still in cysts), 1 sectioned, 1 dissolved in bleach for observation of the parapodial hook apparatus and 10 used for SEM observation; remaining 105 paratypes retained at UMH and used or reserved for histological works.

*Etymology*.—Noun in apposition from Greek *sphaera*, sphere, referring to the unusual body shape.

*Diagnosis*.—Very small myzostome with almost spherical body a little wider than long. Ventral side convex, highly developed; dorsal side concave, highly reduced. Ten pairs of nub-like cirri, all of equal length. Parapodia small, stout, closer to body margin than to ventral midpoint. Hook shaft thin and ending in short, stout tip. Support rod as long and thick as hook; manubrium large and triangular. Lateral organs located halfway between parapodia and body margin. Introvert pouch opening located anterodorsally. Common exit of digestive tract and female genital duct located posterodorsally on retractile anogenital cone. Relative lengths of pharynx, stomach, and intestine: 4:1:4. One pair of digestive caeca arising from intestine. Adults hermaphrodites. Penes long, retractile. Parasites, living in soft cysts on host arms.

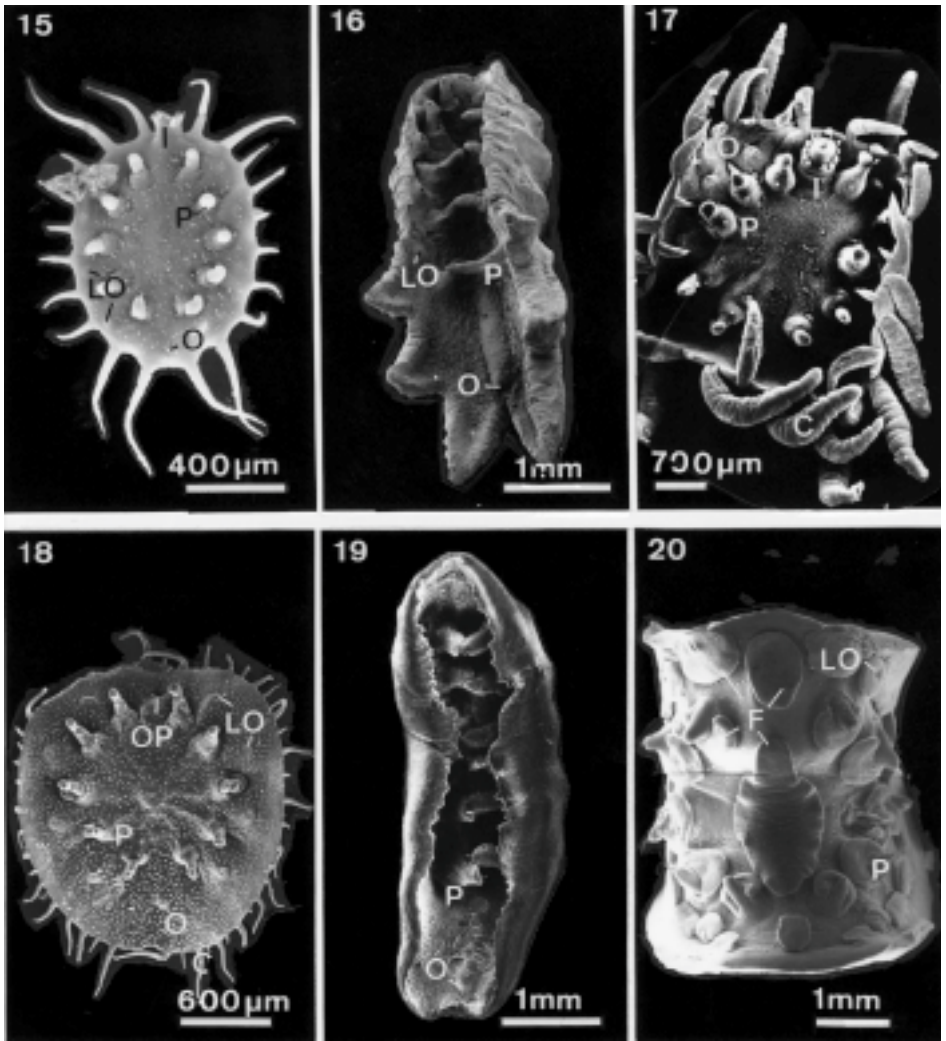
*Description*.—Holotype 1.2 mm wide and 0.8 mm long (Figs. 11, J). Paratypes ranging from 0.7 to 1.1 mm long and from 0.8 to 1.3 mm wide. Ten pairs of small, fine cirri 50  $\mu\text{m}$  long (Figs. 11, J, 7, 14). Color in life uniform reddish-brown.

Five pairs of parapodia 100  $\mu\text{m}$  long, lying far from ventral midpoint of body due to hypertrophy of ventral side (Fig. 7). Last pair of parapodia pointing posteriorly and remaining 4 pairs pointing dorsally (Figs. 1J, 7). Hook shaft thin, nearly straight, its tip curving ca.  $110^\circ$  as small, rounded crook (Fig. 2E). Support rod of each parapodium as long as hook but thicker (200  $\mu\text{m}$  long in 1.3 mm long examined individual); manubrium well developed on one side of strongly curved shaft and ending in 4 to 5 lobes (Fig. 2E). No replacement hooks observed.

Four pairs of lateral organs appearing as small slits halfway between parapodia and body margin (Figs. 7, 14) and alternating with former. Introvert pouch opening dorsally, very close to anterior body margin. Common exit pore of digestive tract and female genital duct lying on retractile cone on dorsal surface close to posterior body margin. Two penes retracted in fixed individuals, but often protruded in life, ca. 700  $\mu\text{m}$  long and extending from 2 penial pouches located close outside third pair of parapodia.

Digestive system in 1.2 mm long sectioned individual consisting of U-shaped tube 900  $\mu\text{m}$  long and pair of blind digestive caeca (Figs. 1K, L). Tube consisting of pharynx (400  $\mu\text{m}$  long) included within protrusible introvert, stomach (100  $\mu\text{m}$  long), and intestine (400  $\mu\text{m}$  long) (Figs. 1K, L). Caeca peculiar in starting from sides of intestine (not stomach, as usual) and extending into anterior part of body (Fig. 1K). Caeca dividing first into 3 secondary branches, these then splitting into numerous tertiary branches (Fig. 1K).

Individuals hermaphroditic. Female genital system lying dorsal to digestive system and consisting of diffuse ovary and branched oviduct (Figs. 1K, L). Oviduct consisting of sagittal cavity dorsal to stomach and intestine and thin, branched channels starting from anterior end of sagittal cavity and running dorsal to digestive caeca (Figs. 1K, L). Ovary



Figures 15 to 20. General views of the ventral side of *Myzostoma ambiguum* (15), *Myzostoma fissum* (16), *Myzostoma mortenseni* (17), *Myzostoma polycyclus* (18), *Hypomyzostoma crosslandi* (19), *Notopharyngoides aruensis* (20). Abbreviations on p. 20.

located dorsal to these channels and consisting of numerous female germinal cells (oogonia, previtellogenic oocytes, and vitellogenic oocytes) lying in parenchyma (Fig. 22). Male genital system lying ventrolateral to digestive system and consisting of diffuse testis, numerous efferent ducts, and 2 penial ducts (Figs. 1K,L). Testis consisting of male germinal cells developing within spermiocysts. No seminal vesicles nor deferent ducts present, but spermiocysts accumulated in pair of penial ducts situated outside third pair of parapodia (Figs. 1K,L). Each penial duct long and running down center of very well developed, muscular penis. Penial duct highly contorted when penis retracted and straight when penis protruded.

This species found living singly inside soft cysts it induces on host's arms. Viewed externally, each cyst hemispherical and located close to ambulacral groove (Fig. 8), with slit-like aperture linking internal cyst cavity (the myzostome's abode) to exterior (Fig. 8). Cysts located close to each other and cavities of neighbouring cysts communicating, thereby allowing myzostomes to reproduce (penes of individuals being able to contact the integument of their neighbours; see Eeckhaut and Jangoux (1991) for information about the myzostome reproduction). Worms feeding on particles diverted from host ambulacral grooves, not on host tissues, but considered as parasites because of alteration to hosts' normal structure.

*Remarks.*—*Contramyzostoma* is a genus recently proposed by Eeckhaut and Jangoux (1995) with the type species *C. bialatum*. That species was observed on *Comaster gracilis* in Singapore. It is characterized by its unusual, superficially inverted morphology: all its external appendages, the opening of the introvert pouch and those of the digestive system and the female genital system are located on a small dorsal field. The hypertrophied ventral surface, as well as the locations of the introvert pouch and common exit of the digestive system and female genital duct, link *C. sphaera* to *C. bialatum*. There are, however, some important differences between the 2 species: the location of the cirri, parapodia, and lateral organs (not on the dorsal field in *C. sphaera*), the number of cirri (just 2 pairs in *C. bialatum*), the sexual condition (*C. bialatum* is either dioecious or a protandrous hermaphrodite), the structure of the ovary (in *C. bialatum* the ovary fills the whole body), and the structure of the digestive system (in *C. bialatum* the single pair of caeca start from and loop back to the stomach). The situation of the digestive caeca within the branches of the oviduct is common to *Contramyzostoma bialatum*, *Cystimyzostomum*, *Pulvinomyzostomum*, and *Protomyzostomum polynephris* Fedotov, 1912 and might therefore be attributed great weight in classification, but it is not the case in the present new species. As a result, our assignment of the new species to *Contramyzostomum* is tentative, and will be subject to revision after the anatomical study of other superficially similar forms, such as *Myzostoma willemoesii* Graff, 1883, *M. aureolatum* Graff, 1883, and several undescribed cysticoles and gallicoles. The possibility that *C. sphaera* represents the encysted juvenile stage of some more conventional adult form (for examples see Remscheid, 1918; Grygier, 1989; Eeckhaut et al., 1990) is refuted by the mature state of development of both the male and female reproductive systems in the present specimens.

*Myzostoma ambiguum* Graff

(Figs. 2F,15,21–22,30A)

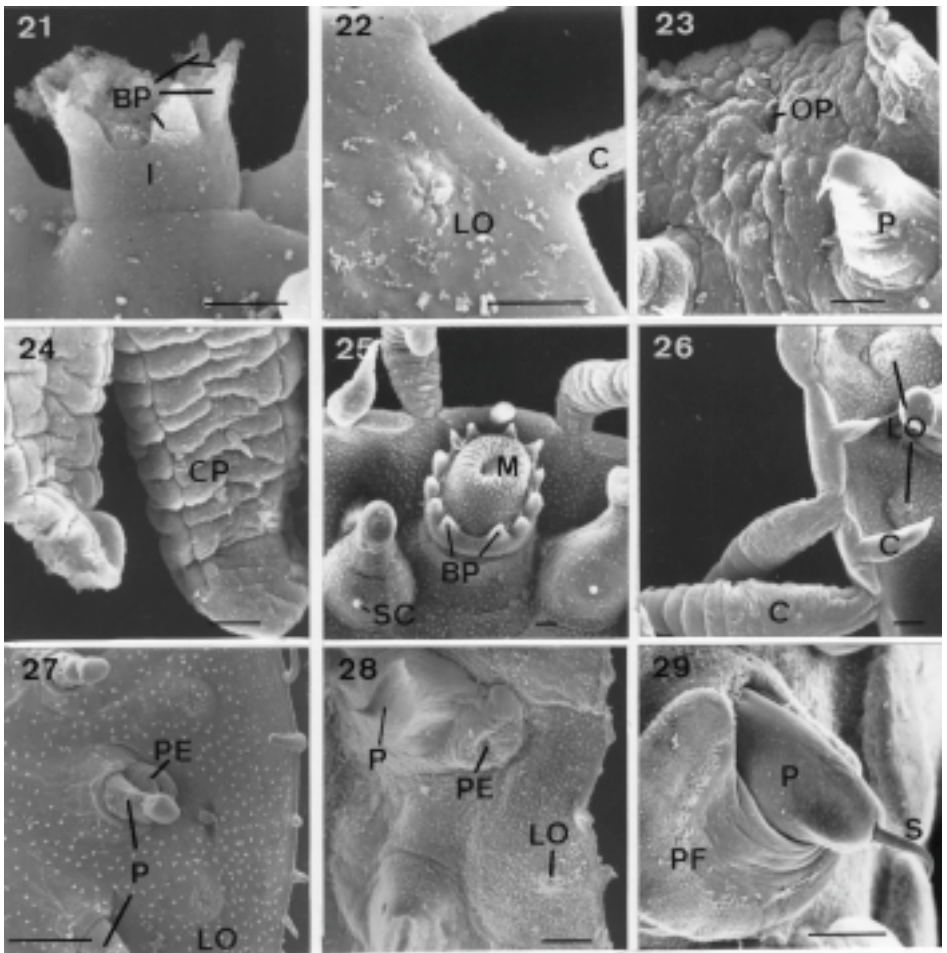
*Myzostoma ambiguum* Graff, 1887: 10, 11, pl. II, fig. 1; Grygier 1990: 184, 185, 186, 189; Grygier 1994: 176.

*Myzostomum ambiguum* — Clark 1921: 666, pl. 41, fig. 1266.

*Myzostoma* sp. 1 — Zmarzly, 1985: 97, 120, 143, 145, 147.

Not *Myzostomum ambiguum* — Jägersten 1937: 2–6, figs 1, 2, 3a, 4a, 5, 6; Kato 1952: 2, 4, 10, 12, 15, pls I–III; Kato 1960: 149, pl. 74, fig. 6; Okada and Kato 1965: 575; Nishimura and Suzuki 1971: 52, pl. 19, fig. 6; Imajima 1975: 87, 264; Okada and Kato 1979: 206; Imajima 1983: 87, 270.

*Type lot and misidentifications.*—From the older literature only the type specimen described by Graff (1887) is admitted as being correctly identified. The holotype was from the collections of the K. Zool. Genootschap, Amsterdam, which is long defunct; the type is not now housed in either the Zoölogisch Museum in Amsterdam nor the Nationaal



Figures 21 to 29. Detailed views of the ventral appendages of *M. ambiguum* (21,22), *M. fissum* (23,24), *M. mortenseni* (25,26), *M. polycyclus* (27), *H. crosslandi* (28), *N. aruensis* (29). Scale bar = 100  $\mu$ m.

Abbreviations: BP, buccal papilla; C, cirrus; CP, caudal process; CY, cyst; D, dorsal side; F, fold; I, introvert; LO, lateral organ; O, common opening of digestive system and female genital duct; OP, opening of introvert pouch; P, parapodium; PE, penis; PI, pinnule; S, seta; SC, small cirrus; VS, ventral side

Natuurhistorisch Museum in Leiden. Specimens from Japan identified either as *M. ambiguum* or *M. antennatum* Graff, 1884 (e.g., Jägersten, 1937; Fedotov, 1938; Kato, 1952) all apparently belong to at least two different species. Those from *Oxycomanthus japonicus* (J. Müller, 1841) correspond perhaps to *M. vastum* Graff, 1883 (sensu Graff 1884), which is, in fact, unnamed because Graff's (1883) original specimens of *M. vastum* from the Caribbean are a different species entirely (Grygier, unpubl. data). Those from *O. pinguis* (A. H. Clark, 1909) are quite likely *M. longimanum* (Jägersten, 1937), which is supposedly specific to that host (Grygier, 1989). This problem requires separate treatment and is beyond the scope of the present report. *Myzostoma ambiguum* is easily

recognizable based on the original description and it is a tropical form with a wide distribution. Zmarzly (1985) presented data on "*Myzostoma* sp. 1" at 5 sites in Micronesia and Australia; those from *Oxycomanthus bennetti* at Enewetak Atoll and Lizard Island have been examined in the present study and confirmed to be *M. ambiguum*.

*Previously recorded distribution.*—Moluccas (Graff, 1887); Enewetak, Kwajalein, Truk, Palau, Lizard Is. (Zmarzly, 1985); Bohol, Moluccas, Marsegoe Is. off Ceram, Great Banda Is., Lizard Is., Fiji, Enewetak (Grygier, 1990; details given below).

*Previously recorded hosts.*—Either *Actinometra solaris* (i.e., *Comatula solaris* Lamarck, 1816), *Actinometra bennetti* (i.e., *Oxycomanthus bennetti* (J. Müller, 1841)), or one of 5 species of so-called *Antedon* (Graff 1887); *Comanthus bennetti* - i.e., *Oxycomanthus bennetti*, and *Comaster multifidus* (Zmarzly, 1985); 8 species of crinoids in 4 families: 4 of Comasteridae, 2 of Mariametridae, 1 each of Colobometridae and Himerometridae (Grygier, 1990; details below).

*Material examined.*—Hansa Bay, PNG: 346 specimens from 2 of 7 examined *Comanthus alternans* (Carpenter, 1881), 1 of 2 *Comanthus mirabilis* Rowe, Hoggett, Birtles and Vail, 1986, 1 of 12 *Clarkcomanthus albinotus*, 19 of 21 *Oxycomanthus bennetti*, and 1 of 6 *Himerometra robustipinna* (Carpenter, 1881) (97% from *O. bennetti*; Table 1). 20 voucher specimens (IG28342-60), others retained at UMH and reserved for histology.

National Museum of Natural History, Smithsonian Institution, collected by D. L. Meyer unless otherwise stated: 49 specimens (5 used for SEM but 2 lost in preparation process) (USNM 173692) from *Oxycomanthus bennetti*, Bohol, Philippines, 10°17.9'N, 124°10.9'E, 40 m, 22 Sept. 1975, A. G. Humes; 35 specimens (USNM 173693) from several *O. bennetti*, Lizard Is., Queensland, Australia, 14°40'S, 145°28'E, June 1981, D. L. Zmarzly; 5 specimens (USNM 173694) loose in jar with *Comaster multibrachiatus* (Carpenter, 1888) (host: USNM E34720), Fiji, 1976; 1 specimen (USNM 173695) loose in jar with *Dichrometra* sp. cf. *D. bimaculata* (Carpenter, 1881) (host: USNM E34798), N side of Marsegoe Is., off Ceram, Indonesia, 2°59'48"S, 128°3'E, 0–15 m, 1975; 1 specimen (USNM 173696) loose in jar with *Heterometra cf. crenulata* (Carpenter, 1882) (host: USNM E34583) from Lizard Is., 1976 [date based on external evidence]; 3 specimens (USNM 173697) loose in jar with *Comanthina schlegelii* (host: USNM E34751), NE side of Great Banda Is., Indonesia, 3–24 m, 12 April 1975; 4 specimens (USNM 173698) loose in jar with *Colobometra perspinosa* (Carpenter, 1881) (host: USNM E34573), Fiji, 1976; 1 specimen (USNM 173699) loose in jar with *Comanthina schlegelii* (host: USNM E34750), Naira, Great Banda Is., Indonesia, 27 March 1975 [year based on external evidence]; 1 specimen (USNM 173699) loose in jar with *Stephanometra* sp. (host: USNM G2551), Lizard Is.; 2 specimens (USNM 173701) loose in jar with *Comaster multifidus* (host: USNM E34538), Lizard Is.; 7 specimens (USNM 173702), host unknown, SIPHILEXP-78 Exped., Cr. no. sp-5-3, between Negros and Cebu, Philippines, 9°19'40"N, 123°18'50"E, 1–7 m, 13 May 1978, not D. L. Meyer.

Australian Museum: 1 specimen (W21866) from unidentified crinoid (host: J22900), off Bird Islet, Lizard Is., Queensland, Australia, 14°40'S, 145°28'E, 27 m, 11 Feb. 1987, R. T. Springthorpe and M. J. Grygier; 1 specimen (W22076) from *O. bennetti* (host: J12723), One Tree Reef, Queensland, Australia, 23°30'S, 152°05'E, 18 m, 28 July 1975, L. Owens.

Museum and Art Gallery of the Northern Territory: 14 specimens (NTM WM.00053) (badly decayed) from arms of 3 *O. bennetti*, Enewetak Atoll, Marshall Is., 15–28 m, 21 Sept. 1980, D. L. Zmarzly.

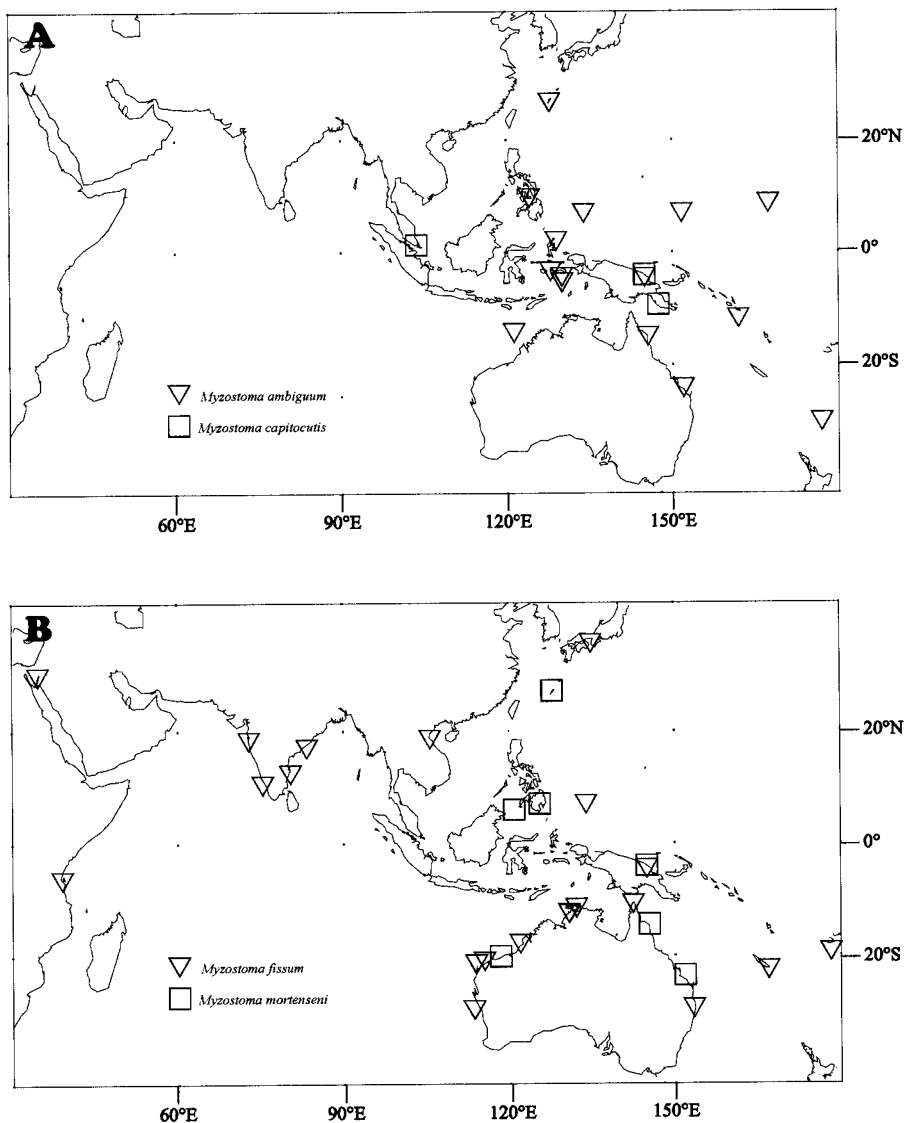
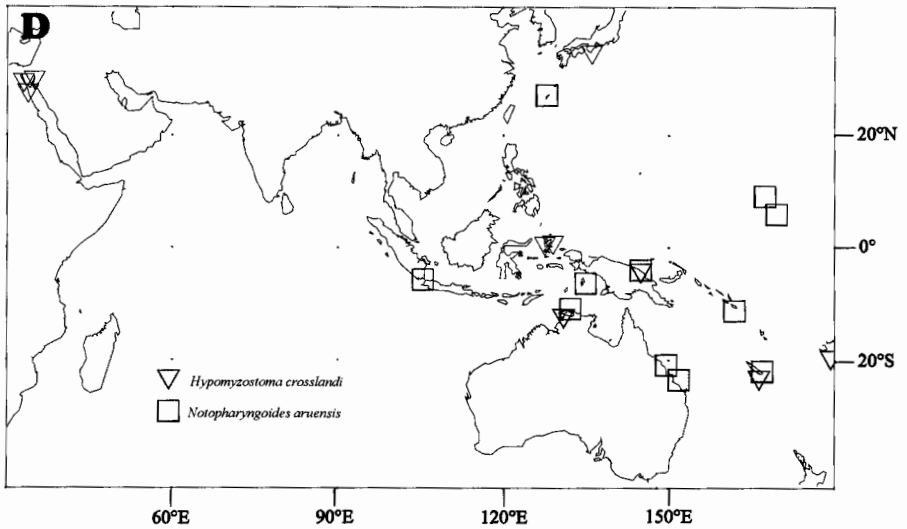
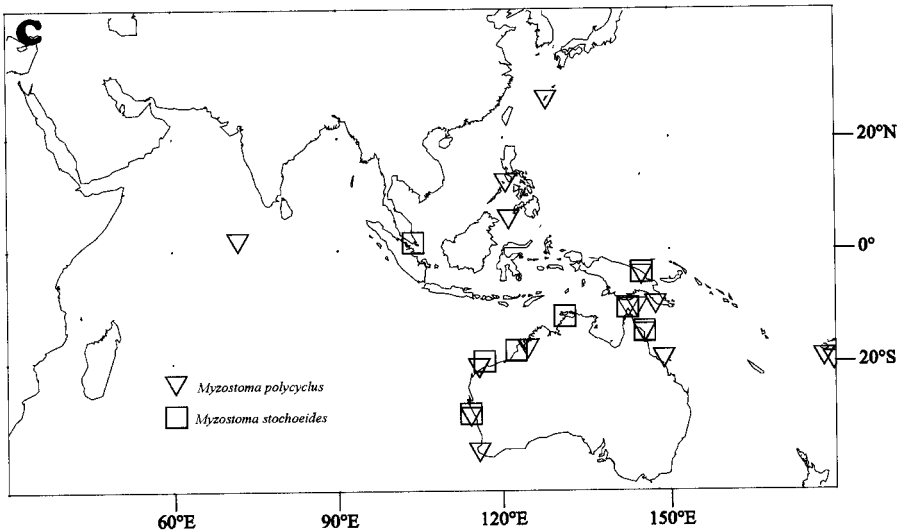


Figure 30. Distribution maps in the Indo-West Pacific of *Myzostoma ambiguum* and *M. capitocutis* (A), *M. fissum* and *M. mortenseni* (B), *M. polycyclus* and *M. stochoeides* (C) and *Hypomyzostoma crosslandi* and *Notopharyngoides aruensis* (D).

Western Australian Museum: 1 specimen (WAM 31-94) from *O. bennetti* (host: WAM 1122-84), E of Sandy Islet, South Scott Reef, off Western Australia, 6–12 m, 8 Sept. 1984, L. Marsh; 2 specimens (WAM 39-94) from *O. bennetti* (host: WAM 1127-84), anchorage W of Sandy Islet, Scott Reef, off Western Australia, 12–15 m, 9 Sept. 1984, L. Marsh.



University of the Ryukyus, Department of Chemistry, Biology and Marine Science: 40, 9, and 12 specimens, respectively, from 3 separately collected host crinoids (one identified as *O. bennetti*), Okinawa, Japan, R. Tamura.

Osaka Museum of Natural History (OMNH-IV 0000-0000; except for some specimens retained by MJG): 103 specimens from 13 *O. bennetti*, W coast of Okinawa (Sunabe, Mizugama, Maeda Misaki, Udoui), 11 Feb.–13 Aug. 1995, 4.0–12.7 m, Y. Fujita (1 to 36 myzostomes per host).

*Description of PNG specimens.*—Small, flat, ovoid body encircled by 10 pairs of cirri (Fig. 15), varying from 0.8 to 2 mm long and 0.6 to 1 mm wide. Cirri of 1st, 2nd, 9th, and 10th pairs up to 8 times longer than other cirri (up to 800  $\mu$ m long) (Fig. 15). Parapodia

thin, 200  $\mu\text{m}$  long, closer to body margin than to ventral midpoint (Fig. 15). Hook shaft thick, making a wide curve in its distal fifth; tip short, sharp, and curving  $90^\circ$  (Fig. 2F). Support rod of each parapodium as long as hook but thinner (150  $\mu\text{m}$  long in 800  $\mu\text{m}$  long examined individual); manubrium more or less triangular, mostly on inner side of shaft, and ending in 6 lobes (Fig. 2F). Four pairs of lateral organs closer to body margin than to parapodia (Figs. 15,22). Mouth surrounded by 4 pairs of buccal papilla (Fig. 21). Opening of introvert pouch and common exit of digestive tract and female genital duct closer to the body margin than to parapodia, former barely submarginal (Fig. 15). No penis observed, but 2 penial apertures seen outside third pair of parapodia.

*Description of other specimens.*—Body 0.6–1.8 mm long, width 69–93% of length (usually about 80%), greatest width anterior of midlength. Color of preserved specimens gray-blue, purplish brown, dark brown with dorsal mottling, light brown, or colorless (in decayed specimens). Dorsum low but convex with variably expressed cruciform uplift above pharynx and seminal vesicles. Ventral side ciliated and flat with stellate array of thin ridges extending from center to parapodia. In relaxed specimens posterior end narrower than anterior, with bases of front 4 cirri defining an arc, rear 4 a trapezoid; margin straight across between 10th pair of cirri or slightly indented. Cirri 1, 2, 9, and 10 much longer and thicker than the others, varying depending of state of contraction from one third body length to a little more than body length. Lateral cirri either all of same length or gradually becoming longer toward front and rear, terminal cirri 3–7 times longer than shortest lateral cirri. Opening of introvert pouch small and ventral, but very close to anterior margin. Introvert capable of protruding 40% of body length, with muscle bulb in distal half and narrower proximal region, but usually only distal half protruded. Probably normally 4 pairs of buccal papillae (7 papillae seen in several specimens, 9 in one). Common opening for digestive tract and female genital duct halfway to two-thirds of way from last parapodia to rear margin.

Parapodia set in oval centered slightly ahead of midlength, each about halfway from center of oval to body margin. Parapodia with conical, acirrate base and slender, finger-like distal part. Pair of penes at lateral bases of parapodia 3 capable of protruding beyond body margin to about 3 times length of parapodium, thicker than distal part of parapodium. Four pairs of very inconspicuous lateral organs alternating with parapodia, their openings visible as tiny round holes a little more than halfway from parapodia to body margin; in some cases opening located at outer end of small oval rise. In some decayed specimens lateral organs protruded as round buttons somewhat larger than apertures.

Proximal parts of gut diverticula not observed, but 10 pairs of main distal branches present, leading toward bases of each marginal cirrus and bifurcating once at level of lateral organs.

Some specimens exhibiting abnormalities. Of those from Bohol, one lacking a parapodium 4, another a parapodium 5; another with 11 cirri on one side and no parapodium 5 on the other; one with extra cirrus at front and rear, another with 9 cirri on one side due to injury. One specimen collected by Meyer missing some posterior cirri and with deformed parapodium 5, due to injury.

*Remarks.*—The only difference between typical present specimens and Graff's (1887) holotype is that the common exit of digestive system and female genital duct in the latter is supposedly a little closer to parapodia 5 than to the rear body margin. However, Graff's description was based on a damaged specimen. The narrow, trapezoidal rear end and the extreme frontal position of the opening of the introvert pouch are sufficient to distinguish



*M. ambiguum* from most of its close relatives mentioned above; *M. antennatum* has a similar posterior profile, but its introvert pouch opens between the first pair of parapodia and its 9th cirri are shorter.

Including the new records and older records fully documented herein, this species is distributed from Okinawa through the Philippines, eastern Indonesia, and PNG to NE and NW Australia, and also in Fiji (Fig. 30A). It has 12 confirmed host species, 8 in the Comasteridae, 2 in the Mariametridae, and 1 each in the Himerometridae and Colobometridae.

*Myzostoma capitocutis* Eeckhaut, VandenSpiegel and Grygier  
(Fig. 30A)

*Myzostoma capitocutis* — Eeckhaut et al., 1994: 674–675, figs. 7, 9, 16, 23A–C.

*Myzostoma elegans* — Eeckhaut et al. 1994: 676–678, figs. 12, 18, 25B–C (partim).

*Previously recorded distribution.*—Singapore (Eeckhaut et al., 1994).

*Previously recorded host.*—*Comaster gracilis* (Eeckhaut et al., 1994).

*Material examined.*—Hansa Bay, PNG: 24 specimens from 4 of 9 examined *Comaster multifidus*, 1 of 4 *Comaster gracilis*, 1 of 8 *Comanthus parvicirrus* and 1 of 139 *Capillaster multiradiatus* (Table 1). More than 50 specimens, all from *C. multifidus*, Hansa Bay, PNG, July 1995, D. VandenSpiegel and I. Eeckhaut.

Australian Museum: 2 specimens (W22042) from *Comaster multifidus* (host: J16893), stn PNG AJB-206, Bootless Bay, Papua New Guinea, 2 Nov. 1980, A. J. Bruce.

*Remarks.*—Some of the Papuan specimens are smaller than those collected at Singapore. The dorsal side of the smallest specimens from Hansa Bay lacks the hair-like papillae that characterize the species, while the dorsal side of medium-sized individuals, including those from Bootless Bay, has short, nub-like papillae. These small specimens are similar to the myzostomes from Singapore erroneously called *M. elegans* by Eeckhaut et al. (1994), which must therefore be considered as young stages of *M. capitocutis* (Fig. 30A) However the other specimens referred to *M. elegans* by Eeckhaut et al. (1994) are not *M. capitocutis*.

One specimen collected in 1994 and 10 specimens collected in 1995 were infested by flatworms. The flatworms occurred single or by pair in the parenchyma of the myzostomes. The parasites induced large, white bulges either on the ventral or dorsal side of the myzostomes. The bulges were most often located close to a parapodium of the third pair, the last being sometimes greatly atrophied (i.e., atrophied parapodia are smaller and thinner than regular parapodia). Parasites were cylindrical, of 400 µm long and 250 µm in diameter and could move in swimming thanks to the beatings of the vibratile cilia which covered their whole surface.

This species is now known from 4 species of Comasteridae.

*Myzostoma fissum* Graff  
(Figs. 2G, 16, 23–24, 30B)

*Myzostoma fissum* Graff, 1884: 55, pl. IV, fig. 1; Graff 1887: 6, pl. I, figs 5, 6. — Grygier 1990: 182, 183, 184, 189, 190; Grygier 1994: 176.

*Myzostomum fissum* — Clark, 1921: 667.

*Myzostoma striata* — George, 1943: 150 (*nomen nudum*); George 1950: 215, 220, figs. 1–5, pl. V, fig. 1; Rao and Sowbhagyavathi 1974: 360–362, fig. 12.

*Myzostomum striatum* — Shyamasundari, 1976:199.

*Myzostomum quadrilobatum* Vagin [*nomen nudum*] — Fishelson, 1974: 189, fig. 7(14); Fishelson 1976: 468, fig. 7a.

*Previously recorded distribution.*—CHALLENGER stn 174 (SW of Fiji) (Graff, 1884); Madras (George, 1943, 1950; Shyamasundari, 1976); Waltair Coast of India (Rao and Sowbhagyavathi, 1974); Eilat (Fishelson, 1974, 1976); Zanzibar, Red Sea (near Eilat), Bombay, Travancore State (India; now part of Kerala State), Madras, Western Australia, Northern Territory, Cauda Nhatrang (Vietnam), Palau (Grygier, 1990; details given below); Kii Peninsula (Japan) (Grygier, 1994).

*Previously recorded hosts.*—Perhaps *Antedon inaequalis* (i.e., *Glyptometra inaequalis* (Carpenter, 1884)) (Graff, 1884); both either *Antedon occulta*, *A. similis* (i.e., either *Stephanometra spicata* (Carpenter, 1881) or *Lamprometra palmata*), or *Antedon tuberculata* (i.e., *S. spicata* (Graff, 1887)) [Clark (1921) noted that the second host could not have come from the listed deep-water station; in hindsight, the first potential host seems unlikely too.]; *Lamprometra palmata* (George, 1943, 1950; Rao and Sowbhagyavathi, 1974; Shyamasundari, 1976; Grygier, 1990); *Lamprometra klunzingeri* (Fishelson, 1974; 1976); 7 different host species, 5 belonging to Mariametridae, 1 each to Comasteridae and Himerometridae (Grygier, 1990; details below).

*Type lots.*—Three synonymous nominal species are involved here. Graff (1884) examined one specimen of *M. fissum* (the holotype) from CHALLENGER stn 174 off Kandavu Is., Fiji. This specimen, which is now in the Natural History Museum, London (Reg. no. 89.11.8.16), was tightly curled and received only a superficial description. One of us (MJG) has examined it and found it in a terribly contorted condition; the caudal processes were barely recognizable and some were broken off. Two specimens supposedly from the same station (impossible according to Clark (1921)) were in better original condition (Graff, 1877) but were not found in London in 1986. George (1943) gave a very brief description of *M. striata* (corrected spelling *striatum*), but with no diagnosis or interspecific comparison; a full and nomenclaturally valid description based on 16 syntypes followed (George, 1950). It lives on *L. palmata* on the Madras and Waltair coasts of India. We have not seen the types. Fishelson (1974, 1976) illustrated a species he called *Myzostomum quadrilobatum* Vagin (i.e., attributed to the late V. L. Vagin of Kazan State University, Russia, to whom Fishelson had sent myzostomes for identification; Fishelson, pers. comm.). The following observations apply to this nominal species and also the one Fishelson (1974, 1976) called *M. quadrilobatum* Vagin (see Remarks below). As far as we have been able to determine, both species were first mentioned, without description and in a biogeographical context, by Vagin (1970b). Vagin mentioned but did not provide a reference for his own 1969 work therein, a work which, by implication, should have contained the formal taxonomic descriptions. However, inspection of the card catalogue of the library of the Zoological Institute in St. Petersburg, Russia, and correspondence with several of Prof. Vagin's acquaintances and former students turned up no evidence of such a publication in 1969 or any other year. This, together with Fishelson's (1974, 1976) papers' lacking statements purporting to differentiate *M. quadrilobatum* and *M. hexalobatum* from other taxa, lead us to consider them *nomina nuda*.

*Material examined.*—Hansa Bay, PNG: 13 specimens from 8 of 13 examined *Dichrometra flagellata* (1 to 4 myzostomes per host). 3 voucher specimens (IG28342-70); others retained at UMH and reserved for histology.

Natural History Museum, London: 1 specimen (ZB 1980.453) from *Heterometra africana* (A. H. Clark, 1911), Zanzibar Harbour, stn 96, 6°9.4'S, 39°10.5'E, 20 m, A. J. Bruce (another specimen from same lot deposited in National Museum of Kenya); 13 specimens (ZB 1980.432-444) from *L. palmata*, Bombay, B. F. Chnapgar and S. R. Sane; 2 specimens (ZB 1980: 449-450) from *L. palmata*, Cape Boileau, Western Australia, March 1930, Mrs. B. Grey; 2 specimens (ZB 1980: 478-479) from *Comatella nigra* (Carpenter, 1888), Rolland Passage, Houtman Abrolhos Is., Western Australia; uncatalogued, from *Lamprometra palmata gyges* (Bell, 1884) (host: 1938.8.23.101), Hermite I., Western Australia.

National Museum of Natural History, Smithsonian Institution: 3 specimens (USNM 173703) loose in jar with 6 *L. palmata* (host: USNM E3280), Neendakara Bar, Travancore State (now part of Kerala State), southern India, Feb. 1928, H. S. Rao and M. Sharif; 1 specimen (USNM 173704) loose in jar with 5 *Lamprometra* sp. (host: USNM G2557), Palau, 1976, D. L. Meyer.

Museum of Art Gallery of the Northern Territory, from *Lamprometra palmata* (unless host unknown), Northern Territory, Australia, R. Hanley: 3 specimens (NTM WM.0001, WM.0026), host unknown from Coral Bay, Port Essington, 11°11'S, 132°03'E, 2.5-3.5 m, 17 Oct. 1981; 10 specimens (NTM WM.0008, WM.0009, WM.0038), all from Table Head, Cobourg Peninsula, 11°15'S, 132°11'E, 2-4.5 m, 11 May 1983; 4 specimens (NTM WM.0022), Coral Bay, Port Essington, 2.5 m, 16 May 1983; 1 specimen (NTM WM.0029), Anglers Reef, Darwin, 12°18.7'S, 130°52'E, 5-6 m, 19 July 1982.

Western Australian Museum: 5 specimens (WAM 16-94) from *L. palmata* (host: WAM 729-93), Gannet I., E of Delta Is., Montebello Group, Western Australia, 14 Aug. 1993, L. Marsh et al.; 3 specimens (WAM 17-94) from *L. palmata* (host: WAM 730-93), and 1 specimen (WAM 42-94), host unknown, intertidal sand bank connecting Buttercup Is. and Hermite Is., Montebello Group, Western Australia, 15-16 Aug. 1993, L. M. Marsh et al.; 2 specimens (WAM 21-94) from *L. palmata* (host: WAM 33/1979), top of barrier reef of Mangrove Bay, Northwest Cape, Western Australia, 26 June 1977, L. M. Marsh; 1 specimen (WAM 83-95), host unknown, Montebello Group, Western Australia, Aug. 1993, WAM party.

Australian Museum: 2 specimens (W5858, W194997), former from *L. palmata* (host of other unknown), Stokes Hill Power Station, Darwin, Northern Territory, Australia, 22 Oct. 1965, E. Pope; 3 specimens (W22049) from *D. flagellata* (host: J12041), lagoon at New Caledonia, 22°S, 167°E, 10 m, 28 Nov. 1978, J. Marshall; 1 specimen (W22066) from *L. palmata* (host: J12004), lagoon in New Caledonia, 22°S, 167°E, 12 m, 29 Nov. 1978, J. Marshall; 1 specimen (W22075) from *L. palmata* (host: J12322), end of breakwater, Tweed River, New South Wales, Australia, 28°18'S, 153°27'E, 25 m, Dec. 1978, R. Martin.

Museum of Comparative Zoology: 2 specimens (MY 35) from *Lamprometra gyges* - i.e., *L. palmata gyges* (host: 613), Torres Straits, Australia.

Osaka Museum of Natural History: 1 specimen (OMNH-IV 1454) on arm of *Dichrometra doederleini* (de Loriol, 1900) (host: 264), Nada, Gobo City, Wakayama Prefecture, Japan, 11 Feb. 1969, T. Yamamoto.

Uppsala University Zoological Museum: identification as *M. fissum* somewhat uncertain, from *Lamprometra moorei* (i.e., *Liparometra articulata* (J. Müller, 1847)), Cauda Nhatrang, S. Annam (now Vietnam), C. Dawydoff.

*Description of PNG specimens.*—Large with elongated, stout body ending in 3 pairs of caudal processes (Figs. 16,24), varying from 1.4 to 6.5 mm long, 0.7 to 3.2 mm wide. Body margin bearing 10 pairs of cirri plus caudal processes (Fig. 16). Anterior cirri short, posterior ones becoming longer. Medialmost pair of caudal processes longest; outermost pair shortest (Fig. 16); pair of longitudinal grooves delimiting their ventral surface (Fig. 24). Color in life varying according to that of host: when latter white, myzostomes almost totally white with 4 slightly darker longitudinal dorsal stripes; when hosts reddish, myzostomes colored in purple or red with 4 dark longitudinal dorsal stripes.

Five pairs of parapodia lying in 2 almost parallel rows halfway between body margin and ventral midline (Fig. 16). Parapodia stout, 400  $\mu$ m long, with small medial cirrus 30  $\mu$ m long on base. Hook shaft thick, drawn back slightly in distal third; tip making long, open crook and curving about 135° to sharp point (Fig. 2G). Support rod as long as hook but less than half as thick (400  $\mu$ m long in 3 mm long examined individual); manubrium a small triangle developed on both sides of shaft (Fig. 2G). One replacement hook in each parapodium (Fig. 2G).

Four pairs of lateral organs located on integumental humps halfway between parapodia and body margin (Fig. 16). Opening of introvert pouch and common exit of digestive tract and female genital system located close to front and rear body margins, respectively (Fig. 23). Penes present as two integumental tubes located at the outer edges of the 3rd pair of parapodia and opening close to the margin.

*Description of other specimens.*—Body rounded at front, broadening toward rear, and usually ending in 3 pairs of caudal processes, medial pair longest and outermost pair shortest. Specimens 2.0–9.3 mm long measured to tip of longest caudal process, this length exceeding that along midline by 12–50% (usually 27–36%). Sides of body usually downturned, presumably to enwrap host arm. Nine to 12 finger-like to triangular marginal cirri along each side, but anterior margin sometimes with supernumerary ones, in extreme cases forming a fringe. Caudal processes lacking cirri, ventrally concave due to longitudinal furrow. Lengths of members of a pair often quite different, and aberrations common: one specimen with all 3 right ones rudimentary, 2 others with rudimentary or lost medialmost process, some others with outermost process on one side barely larger than cirrus, one specimen with small extra process between two large ones, another with all processes very broad and divided distally. One specimen from Darwin (W 5858) with only 1 left and 2 right caudal processes well developed, others vestigial; same specimen with round dorsal lump on right side, indicating presence of parasite.

Dorsal sculpturing consisting of high ridge along midline, 4 pairs of laterally radiating primary ridges not reaching lateral margin, 2 posterior pairs of primary ridges extending onto medial and second pairs of caudal processes (former turning at right angle to do so), and numerous secondary and sometimes tertiary ridges near margins. These last mostly continuous with marginal cirri, but longest, rearmost pair extending onto outermost caudal processes, and up to 4 pairs of tertiary ridges found on webs between outermost and second processes.

Dorsal coloration sometimes preserved. Two pairs of dark, longitudinal stripes on white background, each stripe darkest at its edges. Outer stripe just medial to inner ends of secondary ridges, broadening posteriorly to include entire second caudal process. Inner stripe connecting medial parts of primary ridges, broadening posteriorly and splitting to either side of uncolored ridge in medial caudal process. First 4 pairs of primary ridges mostly reaching from medial edge of inner stripe to lateral edge of outer stripe. Two dark,

longitudinal stripes found ventrally as well, one at level of parapodia, other between parapodia and midline. Specimens from Zanzibar different, with white-flecked background and pink stripes; one of these specimens with some solid white ridge crests as well.

Introvert pouch opening generally between front ends of bases of first pair of parapodia, thus near anterior body margin (nearly terminal in smallest USNM specimens). Introvert rarely protruding, as short cylinder lacking buccal papillae. Common exit of digestive system and female genital duct opening on subterminal rise in notch between medial pair of caudal processes, closer to margin than proboscis pocket opening is in most specimens.

Parapodia arranged in posteriorly open U, rear ones spaced a little farther apart than front ones, last pair near level of bases of outermost caudal processes. All parapodia about halfway from midline to margin, consisting of low, crescentic or conical basal fold with small, blunt or pointed medial cirrus (in most specimens examined) and small distal part slightly longer than wide when retracted, finger-like when protruded. Lateral bases of parapodia 3 enlarged to varying degrees, with integumental tube extending away from parapodium and opening near margin, as in *M. cirriferum* (Eeckhaut et al, 1990).

Four pairs of lateral organs situated halfway from parapodia to margin, with raised, round openings; posterior ones larger. First pair right behind first parapodia, 4th nearly even with 5th parapodia, other 2 pairs equidistant between parapodia 2 and 3, and 3 and 4, respectively. One specimen lacking right fourth lateral organ (as well as right medial caudal process), another with only 4 parapodia and 3 lateral organs on left side.

*Remarks.*—The costate dorsum and 3 pairs of caudal processes identify the present specimens as *M. fissum* (at least sensu Graff, 1887, and we assume he correctly identified those specimens). The same features, together with the color pattern observed in some specimens, meet the definition of *M. striatum* as well. George (1950) stated that his specimens had no more than 10 pairs of marginal cirri, while the present ones may have a few more, and he also reported 4 buccal papillae on the introvert, which were not evident in our material. The other main purported differences were the lack of a ventral furrow on the caudal processes of *M. striatum* (but its presence or absence probably depends on fixation technique) and whether or not the main dorsal ridges reach the margin (but it is very difficult to interpret the ridges in Graff's holotype). The present specimens also match Fishelson's (1974, 1976) drawings of *M. quadrilobatum* Vagin [*nomen nudum*] in dorsal sculpturing and coloration and in having 3 pairs of caudal processes. This name implies 2 pairs of processes, and Fishelson's collections, examined by Wagin and now deposited in the Zoological Institute in St. Petersburg, did include a species with 2 pairs, *M. lobatum* Graff, 1877 (see Grygier, 1992). On the other hand, another *nomen nudum* employed by Fishelson (1974, 1976), *M. hexalobatum*, would be more appropriate as a synonym of *M. fissum* in terms of its six implied caudal processes. It seems likely that Fishelson (1974, 1976) confused these two nominal species when he labelled his illustration as *M. quadrilobatum* rather than *M. hexalobatum*.

No previous author has reported parapodial cirri in this species, nor the posterior increase in size of the lateral organs, nor the unusual situation of the male genital openings. The specimens from the Northern Territory commonly co-occur with an elongate species similar to *Hypomyzostoma crosslandi*, referred to as *Myzostoma* sp. 4 by Grygier (1988). Those from Bombay and Western Australia often co-occur with a disc-like, dorsally costate species referable to *M. plicatum* Graff, 1884 (sensu Jägersten, 1940); this has additional similarities to *M. fissum*, such as the 2 pairs of dark bands and tubes leading to

nearly marginal male genital openings. Further study is needed to determine whether *M. fissum* and *M. plicatum* represent morphs of a dimorphic species.

*Myzostoma fissum* ranges from East Africa and the Red Sea through India to Australia, and on to Japan, Palau, and Fiji (Fig. 30B), and must be regarded as a widespread Indo-West Pacific species. Most records involve 4 genera of Mariametridae: *Lamprometra*, *Dichrometra*, *Stephanometra*, and *Liparometra*; but there is also one host each in the Comasteridae, Heterometridae, and, if that of the holotype is correctly identified, Glyptometridae. *M. fissum* thus seems not to be very host-specific, as was already mentioned by Grygier (1989), though it has a clear preference to associate with crinoids of the genera *Lamprometra* and *Dichrometra*.

*Myzostoma mortenseni* (Jägersten)

(Figs. 1M–N, 2H, 17, 25–26, 30B)

*Myzostomum mortenseni* Jägersten, 1940: 107–109, Text-fig. 4, Taf. 1, fig. 3.

a myzostomid bristleworm — Stamman et al. 1985: 15, color photograph on p. 14. sp. 31, n. sp. — Grygier 1990: 184, 189.

*Previously recorded distribution.*—Jolo (Philippines) (Jägersten, 1940); Gulf of Davao (Philippines), Lizard Is. and Heron Is. (Queensland) (Grygier, 1990; details below).

*Previously recorded hosts.*—White *Actinometra* without cirri (Jägersten, 1940); 4 species of Comasteridae (Grygier, 1990; details below).

*Type lot.*—Jägersten (1937) described the external and internal anatomy of this species on the basis of 5 syntypes, one of which was sectioned. The four intact syntypes have been examined (by MJG) in the Universitets Zoologisk Museum, Copenhagen.

*Material examined.*—Hansa Bay, PNG: 3 specimens from 3 of 12 examined *Clarkcomanthus albinotus*. 1 voucher specimen (IG28342-80); others retained at UMH and used for histology.

Australian Museum: 1 specimen (W201142) from green crinoid (this specimen photographed in life by Stamman et al. (1985)) and 1 specimen (W201146) from brown and white crinoid, 5–10 m, Lizard Is., Queensland, Australia, 7 July 1984, D. J. H. Phillips.

Western Australian Museum: 3 specimens (WAM 38-94) from *Comantheria briareus* (i.e., *Comanthus briareus* (Bell, 1882)) (host: WAM 1120-82), 20.4 km NW of Port Hedland, Western Australia, 20°12'S, 118°25'E, 14 m, 3 Aug. 1982, J. Fromont on SOELA.

National Museum of Natural History, Smithsonian Institution, uncatalogued: 1 specimen (USNM 173767) loose in jar with 2 *Comantheria polycnemis* (i.e., *Comanthus alternans*) (host: USNM 34999), ALBATROSS stn 5254, SW of Linao Pt., Gulf of Davao, Mindanao, Philippines, 7°5'42"N, 125°39'42"E, 11.5 m, 18 May 1908; 1 specimen (USNM 173768) loose in jar with at least 2 *Comanthina schlegelii* (host: USNM E34745), Heron Is., Queensland, Australia, D. L. Meyer; 1 specimen (USNM 173769), host unknown, 1 specimen (USNM 173770) associated with *Comanthus briareus*, and 1 specimen (USNM 173771) associated with *Comaster gracilis*, all from Heron Is., 6–9 May 1975, D. B. Macurda and D. L. Meyer.

University of the Ryukyus, Department of Chemistry, Biology and Marine Science: 1, 1, and 15 specimens, respectively, from 3 *C. briareus*, Okinawa, Japan, R. Tamura.

M. J. Grygier's personal collection: 8 and 2 specimens, respectively, from 2 *Oxycomanthus japonicus* (identified from field guides), patch reef N of Sesoko Bridge, Okinawa, Japan, 3 m, 7 July 1988, S. Nakamura and M. J. Grygier; 11 specimens from *O.*

*japonicus*, patch reef N of Sesoko Bridge, 3–5 m, 31 Oct. 1988, S. Nakamura and M. J. Grygier.

*Description of PNG specimens.*—Large with round, stout body surrounded by numerous cirri (Fig. 17), diameter ca. 4 mm. Body margin bearing ca. 32 cirri of 2 lengths: small cirri fine, 300  $\mu\text{m}$  long, and often alternating with large ones; latter club-shaped and up to 1.2 mm long (Fig. 17). Color in life dark red (or black) and white. All cirri totally dark. Dorsum resembling chessboard, white background with wide, dark, sagittal stripe; thin, dark ring located closer to body margin than to dorsal midpoint; and numerous thin, radial, dark stripes going from ring either to body margin or sagittal stripe.

Five pairs of parapodia lying in circle halfway between body margin and ventral midpoint (Fig. 17). Parapodia stout, 500  $\mu\text{m}$  long, with small medial cirrus 30  $\mu\text{m}$  long on their base (Fig. 17). Hook shaft thick, bent slightly outward in distal third; long, sharp, nearly straight tip bent less than 90° relative to shaft (Fig. 2H). Support rod as long as hook but half as thick (750  $\mu\text{m}$  long in 5 mm long examined individual); manubrium triangular with concave proximal margin, developed only on inner side of shaft (Fig. 2H). One replacement hook in each parapodium (Fig. 2H).

Four pairs of lateral organs round with star-shaped aperture at center (Fig. 17). Opening of introvert pouch close to first pair of parapodia. Introvert wide, 400  $\mu\text{m}$  in diameter, with 6 pairs of buccal papillae around its apex (Fig. 25). Common exit of digestive tube and female genital system opening halfway between fifth parapodia and body margin. Penes less than 100  $\mu\text{m}$  long, starting from outer edges of 3rd pair of parapodia.

*Description of Okinawan specimens* (Fig. 1M,N).—Diameter 2.3–9.3 mm, most slightly wider than long. Dorsum smooth in smaller specimens, but large specimens leathery (Fig. 1M) or lightly to heavily nubbled, with small, central raised knob and ill-defined, bumpy radiating ridges (sometimes defined by absence of bumps in between) stopping at half radius. Color dark red in life, fading to cream on most of body in alcohol but remaining pink on major marginal cirri and some parapodial cirri.

Number of cirri ranging from ca 55 to 85, in 3 size classes. Cirri arranged in repeating pattern of subunits as follows (with reference to Fig. 26), but exceptions (especially missing small cirri) common: subunit bounded by 2 thick and usually long cirri arising from indentations in margin and directed initially dorsally or laterally (longest of these cirri 0.3–2.1 mm long in different specimens, usually about 1.2 mm, all either broadest near base and gradually tapering, or cylindrical with rounded or pointed tips); marginal lappet defined by these indentations bearing similar but smaller cirrus at slight indentation in middle, and 2 very small, conical cirri (or nub-like rudiments thereof) halfway between middle cirrus and each large cirrus; lappet generally bent ventrally, so these small cirri generally pointing ventrally. Growth of smaller classes of cirri, together with intercalation of new cirri in between, apparently ongoing.

Five pairs of broad-based parapodia in circle halfway from center to body margin or slightly inward from that level (Fig. 1N). Basal fold forming a well-defined, full ring and bearing conical medial cirrus, size of latter varying among specimens (Fig. 1N). Penes usually retracted as small lobes at lateral bases of third parapodia, but capable of protruding to at least same length as distal part of parapodium (as thick as or narrower than parapodium when protruded). Partly protruded penis together with basal fold of parapodium resembling ladle with distal part of parapodium arising from bowl. Hooks and support rods of equal length, hook twice as thick. Tip of hook long and sharp, making open 90° curve. Two to 4 replacement hooks present, but at most 1 of substantial size, others

minute. Manubrium of support rod with short proximal spur on outer side and quadrangular inner process with groove for hook and elongate lower angle.

Four pairs of very large (about 2/3 diameter of bases of parapodia), round lateral organs closer to parapodia than to body margin, their inner margins at about same level as outer edges of parapodia (Fig. 1N). Various forms as closed, round swellings; higher, partly open, fluted swellings; crater-like formations with rounded pad either deep within outer wall fold or raised to rim of latter (alternatively, with wall fold open and barrel-like, with round pad visible inside); or with pad produced externally and flattened out to diameter wider than that of now hidden wall fold, with dimple in middle (Fig. 1N).

Opening of introvert pouch between levels of parapodia and lateral organs or slightly forward of that point (Fig. 1N). Introvert shaped like poppy pod, proximal end as isthmus much narrower than distal portion with muscle bulb; crown of 11–18 conical buccal papillae surrounding mouth except for ventral gap (arc tilted so dorsal side farther distal than ventral part), basically 6 pairs with intercalary small ones added on dorsal side (Fig. 1N). Common exit of digestive tube and female genital system opening at level of outer margins of lateral organs.

One aberrant specimen with all 4 pairs of lateral organs but only 7 parapodia: 4 on left (first missing), 3 on right (second and third, including penis, missing).

*Description of Philippine specimen.*—Body 3.7 mm long, 3.5 mm wide. Right leg 5 vestigial. About 59 cirri, longest 0.8 mm (i.e., rather short).

*Description of Australian specimens.*—Western Australian specimens with disc diameters of 1.3–3.0 mm. Most of longer cirri of smallest specimen not swollen, except for basal parts of some.

Queensland specimens 3.5–6.2 mm wide. Color in life (see Stamman et al., 1985) yellow dorsally with translucent major cirri banded in black and resembling stained chromosomes; preserved specimens orange-brown with turquoise major cirri. Greatest number of cirri counted 48. Longest cirri in 2 best preserved specimens 1.4 mm and 2.7 mm; in former, major cirri plump; in latter, major cirri outstretched and slender. Largest specimen with low bumps covering dorsum, with radial spokes formed of higher bumps. Ventral details as in Okinawan specimens, although no introvert fully protruded.

*Remarks.*—The specimens assigned to *M. mortenseni* herein may not all truly belong to the same species. The different colorations of specimens from Okinawa, PNG, and Queensland and the differences in size (and to some degree in shape) of the major cirri among specimens from Okinawa and the Philippines on the one hand, and Queensland on the other, suggest that a species complex might be involved. The apparent alternation of two size classes of cirri in PNG specimens instead of three, as in Okinawan specimens, also may be a species-level difference. There is little doubt, though, that the type lot from Jolo, which have only nub-like major cirri, and the specimens from Okinawa belong to the same species; the range in size variation of the major cirri in the latter population, from nubs under 0.3 mm long to sausage-like structures up to 1.3 mm long, shows this. For the Queensland population to have even larger cirri and a different coloration is perhaps not beyond the pale of intraspecific variation. With the present records, this species (or species-group) is now known to be widespread in the Western Pacific, from Okinawa to tropical Australia (Fig. 30B); it has so far been reported from 6 species of Comasteridae in 5 genera.



*Myzostoma polycyclus* Atkins

(Figs 10–P,2I,18,27,30C)

*Myzostoma polycyclus* Atkins, 1927: 340–344, text-figs. 1–4, pl. I, Figs 1–3; Grygier 1990: 184; Grygier 1994: 176.

*Myzostomum polycyclus* - Uchida 1992: 372, pl. 72–6, 72–7.

*Myzostomum elegans* - Jägersten 1940: 104–107, fig. 1; Iwase et al. 1990: 91.

*Myzostomum irregulare* Chesunov et al. 1989: 172–3, fig. 1.

*Previously recorded distribution.*—Murray Is. and Badu Is., Torres Straits, Australia (Atkins 1927); Jolo, Philippines (Jägersten, 1940); Mindoro and Jolo (Philippines), Torres Straits, SW of Fiji (Grygier, 1990); Ryukyu Is., Japan (Iwase et al., 1990; Uchida, 1992; Grygier, 1994); possibly Maldives (Chesunov et al., 1989).

*Previously recorded hosts.*—*Comanthus annulatus* (i.e., *Comanthus parvicirrus* (J. Müller, 1841)) (Atkins 1927); *Comanthus parvicirrus* (Iwase et al., 1990; Uchida, 1992; Grygier, 1994).

*Type lot and other historic specimens.*—Atkins (1927) described this species on the basis of 22 syntypes, which could not be located in 1986 either at Bedford College or in the Natural History Museum, London.

Three specimens from Jolo, Philippines, referred to *M. elegans* by Jägersten (1940) and now housed in the Zoological Museum, University of Copenhagen, were reexamined.

*Material examined.*—Hansa Bay, PNG: 8 specimens (1–3 per host) from 3 of 8 examined *Comanthus parvicirrus*, 3 specimens on 1 *Comanthus suavius* Rowe, Hoggett, Birtles and Vail, 1986, 1 specimen on 1 of 139 examined *Capillaster multiradiatus* (Linnaeus, 1758), and 1 specimen on 1 of 4 *Clarkcomanthus littoralis* (Carpenter, 1888) (Table I). 1 voucher specimen from *C. parvicirrus* (IG28342-80); other specimens retained at UMH and used or reserved for histology.

Western Australian Museum: 2 specimens (WAM 44-94) from *Comanthus parvicirrus* (host: WAM 743-93), stn MB1, E side of patch reef in lagoon W of Hermite Is., Montebello Group, Western Australia, 20°27'S, 115°29.3'E, 6–7 m, 10 Aug. 1993, L. Marsh et al.; 1 specimen (dried into a barely recognizable film) (WAM 33-95) from *C. parvicirrus* (host: WAM 1149-84), stn 17, intertidal reef flat SE of North Passage, E side of North Scott Reef, off Western Australia, 14 Sept. 1984, L. Marsh; 4 specimens (WAM 34-95) from *C. parvicirrus* (host: WAM 1092-88), SW side of Long Is., Wallabi Group, Houtman Abrolhos Is., Western Australia, 6–9 m, 25 March 1988, L. Marsh; 1 specimen (WAM 35-95), host unknown, stn 9, intertidal reef flat at George Water, Kimberley, Western Australia, 17 July 1980, L. M. Marsh; 2 specimens (WAM 36-95), host unknown, Montebello Group, Western Australia, Aug. 1993, WAM party.

Australian Museum: 1 specimen (W22047) from *C. suavius* (host: J17011), stn PNG AJBV-206, Bootless Bay, Papua New Guinea, 1980, A. J. Bruce; 4 specimens (W22056) from *C. parvicirrus*, channel between Carter and Yonge Reefs, Queensland, Australia, 14°33'S, 145°35'E, 9 m, 15 Oct. 1982, L. Vail and A. Hoggett. Tentatively assigned to this species: specimens (W 22057) from *Oxycomanthus perplexus* (H. L. Clark, 1916) (host: J12296), off Kirra Beach, Queensland Australia, 4 m, 12 May 1979, J. Marshall.

National Museum of Natural History, Smithsonian Institution: 1 specimen (USNM 173705) in vial in bottle with 1 *Comanthus timorensis* (i.e., *C. parvicirrus*) [But according to Rowe et al. (1986), *C. timorensis* sensu A. H. Clark subsumed 4 species while

representing in principal *Clarkcomanthus littoralis*.] (host: USNM E18353), Puerto Galera, Mindoro, Philippines, 8 Feb. 1914, Th. Mortensen's Pacific Expedition 1914–16; 4 specimens (USNM 173706), host unknown, Mbulia Is., Fiji, International Indian Ocean Expedition, Cruise 1, stn 27, 18°50'30"S, 178°32'10"E, depth "-", 28 Aug. 1963, R/V TE VEGA; 2 specimens (USNM 173707), host unknown, Fiji, 30 April 1975, probably D. L. Meyer.

Museum of Comparative Zoology, all from Carnegie Expedition at Mer, Murray Is., Torres Straits, Australia, Oct. 1913, H. L. Clark: 22 specimens (MY 28, 30, 44, 45) loose in bottles with many *Comanthus timorensis* (i.e., 1 of 4 other nominal species, probably *C. parvicirrus*; see remarks above) (hosts: 570, 571, 574, 575); 1 specimen (MY 27) from *C. parvicirrus* (host: 582); 1 specimen (MY 34) from *Comatula pectinata* (Linnaeus, 1758) var. *purpurea* (J. Müller, 1843) (host: 561); 1 specimen (MY 39) from *Comatella stelligera* (host: 557).

Museum of Victoria, uncatalogued: 1 specimen on back of arm base of unidentified host, Britomart Reef, Queensland, Australia.

University of the Ryukyus, Department of Chemistry, Biology and Marine Science: 1 lot tentatively assigned to this species from *Comanthus parvicirrus*, Okinawa, Japan, R. Tamura.

M. J. Grygier's personal collection: 1 specimen from *Comanthus parvicirrus*, patch reef N of Sesoko Bridge, Okinawa, Japan, 3 m, 7 July 1988, S. Nakamura and M. J. Grygier; 1 specimen from *C. parvicirrus*, patch reef N of Sesoko Bridge, Okinawa, Japan, 2–5 m, 31 Aug. 1988, S. Nakamura and M. J. Grygier.

*Description of PNG specimens.*—Medium-sized, round, flat body surrounded by numerous cirri (Fig. 18), diameter varying from 1.2 to 2.7 mm. Up to 50 fine cirri of unequal sizes (100–600  $\mu$ m long) (Fig. 18), small cirri often alternating with longer ones. Background color in life whitish-green, with dorsal pattern of central solid circle and two outer concentric rings; circle colored yellow or orange, rings dark green to black.

Five pairs of parapodia lying in circle closer to ventral midpoint than to body margin and centered slightly anterior of midlength (Fig. 18). Parapodia slender, 300  $\mu$ m long with inconspicuous medial cirri on their basal fold. Hook shaft thin, bent very slightly outwards at midlength, with short, sharp, straight tip bent at less than 90° (Fig. 2I). Support rod of each parapodium as long and nearly as thick as hook (350  $\mu$ m long in 1 mm long examined individual); manubrium more or less quadrangular like drooping flag, developed only on inner side of shaft (Fig. 2I). One replacement hook in each parapodium (Fig. 2I).

Four pairs of lateral organs evident as small, star-shaped slits alternating with parapodia and halfway between them and body margin (Fig. 27). Opening of introvert pouch and the common exit of digestive tract and female genital duct halfway between parapodia and body margin, in same circle as lateral organs. Two penes 100  $\mu$ m long at outer bases of third parapodia (Fig. 27).

*Description of other specimens.*—USNM Philippine specimen (basically similar to Okinawan specimens illustrated in Figure 10-O-P) disc-like, flat, very thin, 3.1 mm long, 3.0 mm wide, wider in front than rear, with 56 slender marginal cirri of variable length. Longest cirri (1.5 mm) found anteriorly, other longer cirri about 0.8 mm. Dorsal coloration consisting of dark brown central spot with darker border, and dark brown ring equidistant between spot edge and body margin. Parapodia in ring closer to center than to margin, centered anterior of midlength. Medial cirrus on base distal to shallow trough; distinct radial ridges leading from parapodial bases toward center of disc. Distal part of

parapodium short and cylindrical, with oval tip. Penes evident as protrusible nozzles at outer bases of parapodia 3. Four pairs of lateral organs closer to parapodia than to disc margin, 0.13 mm in diameter, appearing as round, raised discs with grooves radiating from central aperture. Introvert pouch opening in circle defined by lateral organs; common opening of digestive system and female genital duct closer to parapodia 5 than to rear margin, just outside this circle.

Fijian specimens 1.5–2.7 mm long, similar in outline to the above, but dorsal markings faded and number of marginal cirri varying from 42 to 55; cirral lengths irregular. Parapodia and lateral organs projecting farther than in above specimen; lateral organs cylindrical, higher than wide. Circles of parapodia and lateral organs relatively closer to margin in smaller specimens than in larger ones. Translucent marginal zone present; anterior lateral organs even with its inner edge, but posterior ones well inward from it.

MCZ specimens demonstrating change in dorsal color pattern with growth: bulls-eye pattern of large specimens gradually replacing dense brown speckles of small specimens. Specimen from Papua New Guinea (W22047) pale with hint of dark central spot and ring.

*Remarks.*—The combination of a flat, disc-like body, supernumerary marginal cirri, parapodial cirri, and distinctive dorsal markings makes misidentification of *M. polycyclus* nearly impossible. The possibility of synonymy with *M. elegans* exists, however. The types of the latter have not been located, but the specimens assigned to that species by Eeckhaut et al. (1994) that were not from Singapore (i.e., those not reassigned to *M. capitocutis* herein) have no parapodial cirri, and this is provisionally considered the most important distinction from *M. polycyclus*. The Philippine specimens assigned to *M. elegans* by Jägersten (1940) have 45–60 marginal cirri and correspond to the Philippine *M. polycyclus* described above in coloration and the presence of parapodial cirri, as already pointed out by Eeckhaut et al. (1994). The specimen referred to *M. irregulare* Graff, 1883 by Chesunov et al. (1989) from *Capillaster multiradiatus* in the Maldives must be either *M. polycyclus* or *M. elegans*; Eeckhaut et al. (1994) favored the latter assignment.

The Caribbean *M. evermanni* McClendon, 1907 also has supernumerary marginal cirri and medial cirri on the parapodia, and is probably very closely related to *M. polycyclus*. Based on an examination of type and newly identified material at the National Museum of Natural History, Smithsonian Institution (Grygier, unpubl. data), it differs from the latter in the absence of dorsal dark rings, the much shorter marginal cirri, and the lateral organs being positioned farther out from the parapodia in large specimens.

The known range of *M. polycyclus* now extends from Okinawa to tropical Australia, with outliers in Fiji and, perhaps, the Maldives (Fig. 30C). It has at least 7 hosts (the taxonomic status of some being uncertain), all of which belong to the Comasteridae.

#### *Myzostoma stochoeides* Atkins

(Fig. 30C)

*Myzostoma stochoeides* Atkins, 1927: 344–346, text-figs. 5–6, pl. 1, fig. 4; Eeckhaut et al. 1994: 678–679, figs 13, 26 A–C.

*Previously recorded distribution.*—Badu Is., Torres Straits, Australia (Atkins, 1927); Singapore (Eeckhaut et al., 1994).

*Previously recorded hosts.*—*Comanthus annulatus* (i.e., *C. parvicirrus*) (Atkins, 1927); *Comaster tenellus* A. H. Clark, 1931 (Eeckhaut et al., 1994).

*Type lot*.—The history of this species was reviewed by Eeckhaut et al. (1994); as with *M. polycyclus*, the 5 syntypes have not been located.

*Material examined*.—Hansa Bay, PNG: 5 specimens, 1 each from 5 of 139 examined *Capillaster multiradiatus*. 3 voucher specimens (IG28342-90); other specimens retained at UMH and used or reserved for histology.

Museum and Art Gallery of the Northern Territory Museum, 5 specimens (NTM WM.00030), host unidentified, NW Vernon I., Northern Territory, Australia, 12°2.5'S, 131°4.5'E, 20 m, 28 Sept. 1982.

Western Australian Museum: 2 specimens (WAM 64-94) loose in jar with *Comanthina variabilis* (Bell, 1882) (host: WAM 602-83), SOELA stn SO 5/82/27, 90.6 km NNW of Dampier, Western Australia, 19°51.8'-52.2'S, 116°30.0'-24.0'E, 62 m, 29 Sept. 1982, L. Marsh and M. Bezant; 3 specimens (WAM 65-94) from *C. variabilis* (host: WAM 1094-82), SOELA stn SO 4A/82/02, 23.2 km NW of Port Hedland, Western Australia, 20°10'S, 118°25'E, 16 m, 26 July 1982, J. Fromont; 1 specimen (WAM 56-94) from *C. variabilis* (host: WAM 562-83 or 562-82), 100 km WNW of Port Hedland, Western Australia, 19°58.1-58.3'S, 117°42.0-43.8'E, 42 m, 26 Sept. 1982, L. Marsh and M. Bezant on SOELA. Tentatively assigned to this species: 4 specimens (WAM 52-94) loose in jar with *Capillaster multiradiatus* (host: WAM 654-83), NW of SOELA stn SO 5/82/15, 18.5 km NW of Delambre I., Dampier Archipelago, Western Australia, ca. 20°17.0-18.3'S, 117°00.2-01.3'E, 32-36 m, 28 Sept. 1982, L. Marsh and M. Bizant; 2 specimens (WAM 49-94) from *Comanthina variabilis* (host: WAM 1095-82), SOELA stn SO 4A/82/02, 23.2 km NW of Port Hedland, Western Australia, 20°10'S, 118°25'E, 16 m, 26 July 1982, J. Fromont; 2 specimens (WAM 48-94) from *C. variabilis* (host: WAM 546-83), SOELA stn SO 5/82/09, 50 km NNE of Cape Lambert, Western Australia, 20°11.9-13.5'S, 117°23.9-24'E, 27 Sept. 1982; 13 specimens (WAM 23-94), from *Comanthina belli* (i.e., *C. variabilis*) (host: WAM 564-81), Sandy Is., Houtman Abrolhos Is., Western Australia, 12 m, 31 March 1981, J. Marshall.

Australian Museum: 1 specimen (W22054) from *Comanthina variabilis* (host: J6538), Cape Villaret, Western Australia, 18°20'S, 122°04'E, 10 Sept. 1929, H. L. Clark. Tentatively assigned to this species: 1 specimen (W22045) from *Comaster multifidus* (host: J17443), South Is., Lizard Is., Queensland, Australia, 14°40'S, 145°28'E, 9 m, 21 Feb. 1983, L. Vail.

Museum of Comparative Zoology: 1 specimen (MY 50) from *Comanthina belli* (i.e., *C. variabilis*) (host: 845), Cable Beach near Broome, Western Australia.

*Supplementary description*.—Papuan specimens not all alike, but with differently formed cirri. Small specimens of ca. 1.6 mm in diameter similar to WAM 52-94: individuals light brown with translucent margin, cirri very straight, one-eighth of body diameter. Large specimens of ca 1.9 mm similar to WAM specimens found on *C. variabilis*: individuals light to dark brown with translucent margin, cirri very curled, one-eighth of body diameter.

Northern Territory Museum specimens very thin, translucent discs, circular or a little longer than wide (2.1-3.6 mm long, 1.9-3.6 mm wide), with very wide marginal zone free of internal organs. One with dorsal hump well off center, presumably due to helminth parasite. Color creamy with gray translucent marginal zone and slight brownish midventral tinge. Ten pairs of marginal cirri, not all equal but lateral ones not necessarily shortest; ratio of cirral length to body size varying by factor of 2, longest ones typically 250-330  $\mu$ m long in small specimens, 350-600  $\mu$ m long in large ones. Parapodia located halfway

from center of disc to margin or very slightly closer to center, long and lacking medial cirrus. Penis as small, conical nozzle at outer base of parapodium 3. Introvert pouch opening in circle defined by lateral organs, common exit of digestive tube and female genital organ opening just outside this circle. Lateral organs closer to parapodia than to margin but more than halfway from parapodia to edge of marginal zone; round, 100–200  $\mu\text{m}$  in diameter in different specimens, with tiny central aperture. Gut diverticula giving rise to about 100 terminal branches.

MCZ specimen from Broome very thin, translucent, disc-like, with pale brown center. Introvert with 4 pairs of buccal papillae. Protruded penis as long and a little thicker than parapodium.

Western Australian Museum specimens light brown, 1.9–3.9 mm in diameter. Introvert pouch opening, small lateral organs, and cloacal opening all in same circle. Buccal papillae present, at least 6 in one specimen, 7 in another. Parapodial cirri absent. Of tentatively identified specimens, WAM 52-94 with relatively longer cirri, WAM 48-94 too small to be sure of identity (1.2–1.6 mm diameter; same problem for Australian Museum W22045, diameter 1.2 mm), and WAM 26-94 with 12 buccal papillae.

*Remarks.*—The tentatively assigned specimens, at least those from *Comanthina variabilis*, probably all belong to the same species as the positively identified ones (WAM 49-94 is even from same station as WAM 65-94!), but small individuals pose a problem of confusion with young *M. coriaceum* Graff, 1884, which, however, have much bigger, suction cup-like lateral organs (M. J. Grygier, unpubl. data). Whether any of these specimens, or those from Singapore reported by Eeckhaut et al. (1994), truly belong to *M. stochoeides* is hard to judge in the absence of type specimens. It will probably prove necessary to designate a neotype to fix the species concept. For now, any thin, translucent, disc-like myzostomes with 10 short to medium-long, tendril-like marginal cirri, a wide marginal zone, no parapodial cirri, and small lateral organs, and with the introvert pouch opening and common opening of intestine and female genital duct more or less in the lateral organ circle can be assigned to this species.

*Myzostoma stochoeides* seems to have a somewhat restricted distribution: Singapore, PNG, and the northern coast of Australia (Fig. 30C), although some tentatively identified specimens range farther south along the east and west coasts of Australia. It occurs on four or five species in four genera of Comasteridae, perhaps most commonly on *Comanthina variabilis*.

#### *Hypomyzostoma crosslandi* (Boulenger, 1913)

(Figs. 2J, 19, 28, 30D)

*Myzostoma crosslandi* Boulenger, 1913: 102–107, text-fig. 23, pl. VI, figs 2, 3, pl. VII, figs. 1–5, pl. VIII, fig. 1; Wagin 1968: 19; Grygier 1990: 183, 184, 189.

*Myzostomum crosslandi* — Clark 1921: 670, pl. 40, figs. 1251–1253; Fishelson 1974: 189, fig. 7(13); Fishelson 1976: 468, fig. 6a; Wagin 1969: 65; Wagin 1970a: 31; Wagin 1970b: 17, fig. 3 (map).

Grygier (1990) informally recognized a *crosslandi* species-group within *Myzostoma*. *Hypomyzostoma*, a generic name proposed by Perrier (1897) but since unused, herewith is applied to this species-group, which, according to Grygier (1990), also includes *M. folium* Graff, 1877, the type-species by monotypy of *Hypomyzostoma*.

*Previously recorded distribution.*—Red Sea: Ul Shubuk, Suez Bay, and unspecified locality (Boulenger, 1913; Fishelson, 1974; Grygier, 1990); E of Halmahera, Fiji (Grygier, 1990).

*Previously recorded hosts.*—*Antedon savignyi* (i.e., *Heterometra savignii* (J. Müller, 1841)) and *Antedon serripinna* (i.e., *Oligometra serripinna* (Carpenter, 1881)) (Boulenger, 1913); *H. savignii*, *Prometra chadwicki* (i.e., *Decametra chadwicki* A. H. Clark, 1909), and an undetermined comatulid (A. H. Clark, 1921); *Lamprometra klunzingeri* Hartlaub, 1890, *H. savignii*, *H. atra* (A. H. Clark, 1911), and *D. chadwicki* (Fishelson, 1974); 5 species in 3 families (Grygier, 1990).

*Type lot.*—Boulenger (1913) described the external and internal anatomy of this species on the basis of 4 large specimens and 2 small, presumably young ones; a large one was sectioned. Only the 2 syntypes illustrated in Boulenger's (1913) pl. VI have been located for examination in the Natural History Museum, London (Reg. no. 1924.3.1.286); they are from an unspecified host at Ul Shubuk. Both were greenish-grey to brown with at least 7 doublets of narrow, lighter colored cross-bands. The shorter one (Boulenger, 1913: pl. VI, figs. 2a, 2b; Clark, 1921: pl. 40, figs. 1252, 1253) is here designated the lectotype.

*Material examined.*—Hansa Bay, PNG: 2 specimens, 1 each from 2 of 13 examined *Dichrometra flagellata* (J. Müller, 1841), 10–30 m, July 1994; 2 specimens, hosts unknown, 10–30 m, July 1988, M.-C. Lahaye and P. Bulteel. 1 specimen (host: *D. flagellata*) used for SEM observations and deposited as voucher (IG28342-100); other specimen dissolved in bleach for parapodial hook observation.

Natural History Museum London: 3 specimens (and soft cyst containing a juvenile; for similar cases see Remscheid (1918) and Grygier (1989)) from *Lamprometra klunzingeri* (BMNH uncatalogued), Ras Buska, Sinai Peninsula, 5 Oct. 1968, L. Fishelson.

Uppsala University Zoological Museum: 1 specimen from *L. klunzingeri*, Ghardagha, Egypt, May 1936, T. Mortensen.

Western Australian Museum: 2 specimens (WAM 18-94) from *Heterometra savignii* (host: WAM 131-82), Eilat, Israel, 29°24'N, 34°57'E, 6 Sept. 1981, J. Marshall; 1 specimen (WAM 19-94) from *Decametra chadwicki* (host: WAM 184-82), Marsa of Mugabila, Gulf of Aqaba, Red Sea, 10–20 m, 15 Sept. 1981, J. Marshall.

National Museum of Natural History, Smithsonian Institution: 1 specimen (USNM 173708) loose in jar with *Lamprometra* sp. (host: USNM G2596), Fiji, 1976, D. L. Meyer; 3 specimens (USNM 173709), host unknown, Fiji, 27 April 1975, D. L. Meyer; 8 specimens (USNM 173710) associated with 2 *L. palmata* (some on aboral sides of arms), HELIX-79 Expedition, stn M116, E of Halmahera, Indonesia, 0°50.0'N, 127°34.0'E, 1.5–6.1 m, 14 July 1979, G. Hendler, R/V ALPHA HELIX (one of these also examined by SEM).

Australian Museum: 1 specimen from *L. palmata*, Stokes Hill Power Station, Darwin, Northern Territory, Australia, 22 Oct. 1965, E. Pope (identification uncertain, possibly "sp. 4" of Grygier (1990)); 1 specimen (W22094) from *D. flagellata* (host: J12041), lagoon at Canal Woodin, New Caledonia, 22°16'S, 166°26'E, 10 m, 28 Nov. 1978, J. Marshall.

Seto Marine Biological Laboratory, Kyoto University: 7 dried specimens (Poly 136) labelled as *Myzostoma crosslandi*, but now only tentatively assignable to this species, host unknown, Kii-Osima (i.e., Ohshima I., Wakayama Prefecture, Japan), 24 July 1937, H. Utinomi.

*Description of PNG specimens.*—Large with elongated, stout body (Fig. 19). Varying from 1.2 to 6.5 mm long and 0.4 to 2.2 mm wide. Body margin surrounded by numerous, very small cirrus-like projections (Fig. 19). Color in life greyish to brown with up to 12 whitish, transverse dorsal stripes.

Five pairs of parapodia lying in 2 almost parallel rows halfway between body margin and ventral midline (Fig. 19). Fifth pair of parapodia lying 3 times farther from posterior body margin than first pair from anterior margin. Parapodia 250  $\mu\text{m}$  long, stout at base but compressed at apex. Hook shaft thick, drawn back slightly in distal third; tip short, stout, curving 90° (Fig. 2J). Support rod of each parapodium as long as hook but half as thick (350  $\mu\text{m}$  long in 1.2 mm long examined individual); manubrium small, developed only on inner side of the shaft (Fig. 2J). One replacement hook in each parapodium (Fig. 2J).

Four pairs of minute, slit-like lateral organs located very close to body margin and far from parapodia (Fig. 28). Opening of introvert pouch halfway between first parapodia and body margin. Common exit pore of digestive tract and female genital duct located close to posterior body margin (Fig. 19). Penes 200  $\mu\text{m}$  long, starting from outer edges of 3rd pair of parapodia (Fig. 28).

*Description of other specimens, supplementing Boulenger (1913).*—Variably-sized, cirrus-like projections often scattered in good numbers along body margin, but some specimens having very few. Lateral organs minute and round, separated by little more than their own diameter from body margin. Introvert lacking buccal papillae. Common exit of digestive tube and female genital duct opening about 80% of way from fifth parapodia to rear margin. Penes at outer bases of third parapodia, extensible to length equalling distal part of parapodium.

Small, button-like, medial parapodial cirrus usually present, as illustrated but not commented upon by Boulenger (1913); absent, however, in at least some present specimens from Fiji. Medial side of distal part of parapodium consisting of villose pad nearly split in two by longitudinal groove. Based on the ALPHA-HELIX specimen illustrated, parapodial hooks more than twice as thick but a little shorter than support rods. Distal half of hook with slight crook and small point bent at 90°. Two replacement hooks present. Manubrium of support rod triangular, bisected by shaft, with inner half bent to form guide for hook.

Coloration of preserved specimens quite varied, but most usually with limited number (7–11) of single or double cross-bands. Three examined Fishelson specimens (5.1–8.0 mm long) all with purple-grey background color; one with 8 slightly darker cross-bands, one with 8 slightly lighter ones, and one with 8 double bands slightly lighter than background. Of Marshall specimens from Red Sea (2.7–7.6 mm long), 2 displaying no color pattern, but third with 10 transverse, dark lines edged in light, on violet background; his New Caledonia specimen (5.4 mm long) chocolate brown with hint of 10–11 lighter cross-bands bordered with light lines. Specimen from Ghardagha (6.9 mm long) white with 11 faint to clear, transverse, indented lines. ALPHA-HELIX specimens (4.2–7.5 mm long) very faded with slight greenish tinge, especially ventrally; best preserved individual exhibiting approximately 10 more-or-less alternating cross-bands of background color and of very light orange, separated by narrower darker bands. Fijian specimens (2.8–5.7 mm long) either brown with 7 narrow, tan, double cross-bands (area between each doublet slightly darker than background), or light greenish-brown with hints of such banding.

*Remarks.*—The variation in color pattern, as long as it is a matter of no more than about 10 often bounded cross-bands, does not provide sufficient cause for recognizing more than one species among the present specimens. Fishelson (1974, 1976) noted pigmented specimens on dark hosts and pale ones on pale hosts. The illustrations of the former show about 9 white cross-bands bounded in black on a dark background; no markings were

illustrated on the pale ones. The extreme posterior position of the cloacal opening and the absence of distinct scalloping along the body margin (a greater or lesser number of small, often pointy projections instead) also help in the recognition of *H. crosslandi*.

*Myzostoma membranaceum* Graff, 1887, a member of the *crosslandi* species-group (Grygier, 1990) and thus assignable to *Hypomyzostoma*, might be a senior synonym of *H. crosslandi*. This would depend on: 1) Graff (1887) having reversed the front and rear ends of the body (but his drawing shows an extended introvert at the purported anterior end), 2) the reported lack of lateral organs being due to their minute size, and 3) the dorsal swellings over the parapodia being artifacts, as sometimes happens in specimens of *H. nanseni* Graff, 1887 (Grygier, unpubl. data). The two syntypes of *H. membranaceum* were collected from *Antedon marginata* (i.e., *Stephanometra spicata*) from CHALLENGER stn 208 off Luzon, but were not found at the Natural History Museum, London, in 1986.

With the new records, the range of *H. crosslandi* is extended from the Red Sea to the Moluccas, New Guinea, northern Australia, New Caledonia, Fiji, and perhaps Japan (Fig. 30D). The 5 species of hosts include 3 of Mariametridae and 1 each of Colobometridae and Himerometridae.

#### *Notopharyngoides aruensis* (Remscheid)

(Figs. 1Q–R, 2K, 20, 29, 30D)

*Myzostoma aruense* Remscheid, 1918: 194–196, 218, pl. 12, figs. 5, 6; Grygier 1990: 184; Grygier 1994: 176.

*Myzostomum aruense* — Jägersten 1937: 25–26 (discussion of affinities).

*Myzostomum ijimai* — Iwase et al. 1990: 91.

*Myzostoma* sp. 2 — Zmarzly, 1985: 97, 99, 120, 143, 145, 147.

“probably an undescribed species” — Grygier 1990: 184 (referring to Zmarzly’s (1985) *Myzostoma* sp. 2).

*Nomenclature and type lot.*—The genus *Notopharyngoides* was introduced by Fishelson (1974) without diagnosis but was validated inadvertently by Uchida (1992) with *N. ijimai* (Hara and Okada, 1921) as the type species (see historical account by Grygier, 1994). Because the Greek root *pharynx* is feminine, the genus name *Notopharyngoides* is also to be treated as feminine (Brown 1956). Remscheid (1918) described the present species based on 2 syntypes, which have not been located at any major museum in Germany. A third species, *N. platypus* Graff, 1887, had long been considered closely related to these (Jägersten, 1937). All have more or less similar arrays of flattened ventral folds and live in integumentary cysts or inside the digestive system of their hosts. *Notopharyngoides aruensis* and *N. ijimai* are characterized by an S-shaped digestive system in which the mouth and anus open dorsally and ventrally, respectively, and by the absence of marginal cirri. In *N. platypus* the mouth is ventral and 10 pairs of marginal cirri are present. Zmarzly (1985) gave an account of the prevalence and incidence of her *Myzostoma* sp. 2 on *Oxycomanthus bennetti* at Enewetak and Kwajalein.

*Previously recorded distribution.*—Aru Is., Indonesia (Remscheid 1918); Enewetak and Kwajalein (Zmarzly 1985).

*Previously recorded hosts.*—*Comantheria briareus* (i. e., *Comanthus briareus*) (Remscheid, 1918); *Tropiometra afra macrodiscus* (Hara, 1895) (Iwase et al., 1990; Grygier, 1994).



*Material examined.*—Hansa Bay, PNG: 2 specimens from 1 of 7 examined *Comanthus alternans*, 10–30 m, July 1994; 4 specimens from *Stephanometra oxyacantha*, 10–30 m, June 1992, I. Eeckhaut and D. VandenSpiegel. One voucher specimen from 1994 lot (IG28342-110); other specimens retained at UMH and used or reserved for histology.

National Museum of Natural History, Smithsonian Institution: 2 specimens (USNM 173711) in mouth of *Oxymetra erinacea* (Hartlaub, 1890) (host: USNM E3189), Danish Expedition to the Kei-Islands, stn 90, N of Sebesi Is., Sunda Strait, Indonesia, 5°55'S, 105°30'E, 36 m, 1 Aug. 1922, T. Mortensen; 2 specimens (USNM 173712) in mouth of *Stephanometra* sp. cf. *S. oxyacantha* (host: USNM E34738) Heron Is., Queensland, Australia, D. L. Meyer.

Australian Museum: 2 specimens (W22081) in mouth of *Stephanometra oxyacantha* (host: J18698), W side of Refuge Bay, Scawfell Is., Queensland, Australia, 20°52'S, 149°37'E, 9 m, 25 Nov. 1983, L. Vail and A. Hoggett.

Uppsala University Zoological Museum: 2 specimens from *Stephanometra protectus* (Lütken, 1874), Sixten Bocks Expedition 1917, Jaluit Is., Marshall Is., 15 Oct. 1917, C. Hessele.

University of the Ryukyus, Department of Chemistry, Biology and Marine Science: 1 specimen from unknown host, Okinawa, Japan, R. Tamura.

M. J. Grygier's personal collection: 2 specimens from *Oxycomanthus japonicus* (identified from field guide), patch reef N of Sesoko Bridge, Okinawa, Japan, 7 July 1988, 3 m, S. Nakamura and M. J. Grygier.

The following specimens are only provisionally included in this species, either because they are juveniles or have been treated as probably separate earlier (Grygier, 1990).

Australian Museum: 1 specimen (AM W22072) from unidentified host (host: J10886), lagoon at Noumea, New Caledonia, 22°S, 167°E, 1977, S. Catala.

Museum and Art Gallery of the Northern Territory: 3 specimens (NTM WM.00051) from mouth of 1 *O. bennetti*, Enewetak Atoll, Marshall Is., 18 m, 21 Nov. 1980, D. L. Zmarzly; 6 specimens (3 pairs) (NTM WM.00052) from mouths of 3 *O. bennetti*, Enewetak Atoll, Marshall Is., 30 July 1980 (15 m), 20 Oct. 1980 (35 m), 19 Nov. 1980 (15 m), D. L. Zmarzly; 1 juvenile (NTM WM.00056), host unknown, Cobourg Peninsula, Northern Territory, Australia, 11°5'S, 132°16.5'E, 14 m, 2 May 1982, R. Hanley.

National Museum of Natural History, Smithsonian Institution, uncatalogued: 5 specimens (USNM 173713), found usually as 1 pair per host in mouth of *O. bennetti*, Eniwetak Atoll, Marshall Is., Oct. 1980, D. L. Zmarzly.

*Description of PNG specimens.*—Very large with ovoid, stout body lacking cirri (Fig. 20), ca 6.5 mm long and 3.8 mm wide. Body folded so dorsal part concave and ventral part convex (Fig. 20). Four types of flattened ventral integumental folds: 1 marginal fold with five pairs of submarginal lappets partially surrounding lateral organs; 4 pairs of folds holding slit-like lateral organs; 3 sagittal folds, middle one longest, posterior one smallest (in one specimen, anterior and middle folds fused); and 5 pairs of folds associated with parapodia (Fig. 20). Color in life uniformly orange to red.

Parapodia stout, 500 µm long (Figs. 20, 29). Hook shaft thick and straight; tip short, stout, and bent almost 90° (Fig. 2K). Support rod of each parapodium as thick (at least basally) as hook but more than twice as long (800 µm long for 300 µm hooks in the 6 mm long examined individual); manubrium developed as narrow blade extending from inner side of shaft (Fig. 2K).

Introvert pouch opening anterodorsally; common opening of digestive tract and female genital duct lying ventrally behind posterior sagittal fold.

Occurring in pairs in host digestive system, one individual located above the other, ventral side of upper individual contacting dorsal side of lower one. However, 2 small specimens observed close to each other inside ambulacral groove of arm near host's mouth, smaller one 400  $\mu\text{m}$  long, larger one 800  $\mu\text{m}$  long. Smaller one not folded, consequently with convex dorsal side and concave ventral side; larger specimen folded as adults.

*Description of other specimens.*—All examined specimens lacking marginal cirri and with opening of introvert pouch dorsal at 7–18% of distance from anterior margin. Ordinarily 3 midventral sagittal lobes, but first 2 often adjacent, confluent, or with minute extra lobe between them; second lobe largest (2–3 times as long as first), third smallest and separated by substantial gap from second, with common exit of digestive tube and female genital duct opening at its rear base. Five pairs of parapodia with basal fold developed into wide, kidney- or heart-shaped plate, open anteriorly in first 3 pairs, posteriorly in posterior 2 pairs. Due to presence of this plate lateral to limb, male genital opening (small knob, never observed protruded) located just anterolateral to parapodium 3; usually plates of parapodia 2 and 3 biggest, that of parapodium 5 smallest. Distal part of parapodium stumpy. Four pairs of lateral organs alternating with parapodia, expressed as dimple or bump in middle of round, disc-like plate with exposed surface of greater diameter than its pedestal (in 1 specimen some plates with deep lateral notch), first and/or fourth pair often confluent with one or both neighboring submarginal lappets (5 pairs of latter; fusion pattern, if any, generally differing on right and left sides of same individual).

Specimens from *Oxycomanthus japonicus* (Figs. 1Q,R) and *O. bennetti* quite large (adult specimens 8.7–10 mm long and 6.7–6.9 mm wide in former, 8.3–10.2 mm in diameter in latter) and flat or with slightly upturned lateral margins, but differing in outline (former oval, latter round), in first pair of submarginal lappets (much wider than remaining pairs in former, all same width in latter), and size and fusion pattern of lateral organ plates (all free and decreasing in size posteriorly in former, all same size in latter but fourth confluent with fourth or with fourth and fifth submarginal lappets). In perfectly flat specimen, lateral organs and submarginal lappets located on bevelled surface between dorsal and ventral surfaces, parapodia and midventral sagittal lobes on latter. Parapodial hook apparatus only described from those infesting *O. japonicus*. Hook and support rod of similar thickness; hook 75% length of latter with nearly straight shaft and short, pointed tip bent at about 50°. Elongate, teardrop-shaped, hollow space within distal half of support rod; manubrium developed on inner side as triangular, basally pointing prong with dentate margin.

Specimens from *Stephanometra oxyacantha* and *Oxymetra erinacea* much smaller and with lateral margins (and to lesser degree anterior and posterior margins) strongly upturned, those from former host nearly round in outline (e.g., 3.3 mm long, 3.1 mm wide), those from latter oval (e.g., 3.3 mm long, 2.5 mm wide). At least those from *S. oxyacantha* differing from larger specimens in shape of parapodial plates: medial portion much wider than lateral and sometimes medial end pointed. Only 1 of 4 specimens examined from these hosts showing any confluence of lateral organs and submarginal lappets (first and fourth lateral organ on one side).

*Remarks.*—The major distinction between *N. aruensis* and *N. ijimai* is that the latter has a pair of continuous submarginal ventral folds, while the former has a series of small, distinct submarginal lappets. We have examined an Okinawan specimen of *N. ijimai* taken

from its type host, *Tropiometra afra macrodiscus*, and the difference is striking. Grygier (1994) noted that an individual from that species of host photographed by Iwase et al. (1990) resembled *N. aruensis* rather than *N. ijimai*. A possible explanation is that the latter was originally reported from integumentary cysts (Hara and Okada, 1921), but Iwase et al.'s (1990) specimen came from the mouth; the Okinawan *N. ijimai* mentioned above also came from a cyst. So perhaps *N. ijimai* is always cysticolous while *N. aruensis* is endosymbiotic, and both can infest the same species of host. Arguing against this, however, is a convincingly illustrated report of *N. ijimai*, which were removed from the throat of the host (Jägersten, 1937). Except for the Papuan specimens, it is not clear that the other present specimens came from their hosts' mouth, although none were found in cysts. Zmarzly (1985) noted that her *Myzostoma* sp. 2 usually occurred as a pair in the mouth of *Oxycomanthus bennetti*, but sometimes 3 adults together or 2 adults and 1 or 2 much smaller juveniles.

The present material quite possibly represents more than one species. Differences are apparent in body size, body shape (round or oval, flat or with margins upturned), shape of the flat parapodial lobes (symmetrical and kidney-shaped or asymmetrical and broadened medially), the relative width of the first pair of submarginal lappets, and whether any lateral organ lobes are confluent with submarginal lappets. If just one species is involved, it is distributed from Okinawa through Indonesia and New Guinea to N and NE Australia, and eastwards to New Caledonia and the Marshall Islands (Fig. 30D). The hosts include representatives of 3 families, Comasteridae, Mariametridae, and Tropiometridae.

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