

# FAUNA *of* AUSTRALIA

Volume 4A

## POLYCHAETES & ALLIES

The Southern Synthesis

### 2. CLASS MYZOSTOMIDA

MARK J. GRYGIER



© Commonwealth of Australia 2000.  
All material CC-BY unless otherwise stated.

At night, *Eunice Aphroditois* emerges from its burrow to feed.  
Photo by Roger Steene



## DEFINITION AND GENERAL DESCRIPTION

Myzostomes are soft-bodied marine worms that are almost all commensal with, or parasites of echinoderms, especially crinoids but also ophiuroids and asteroids (Pls 10.1–10.4). They have diverse body forms (see Fig. 2.1): some are elongate, oval or disc-like; others are irregular. They are superficially unsegmented, but the repetition of certain body parts has usually been considered an indication of metamerism. A coelom is lacking or, interpreted otherwise, is represented only by the internal spaces of the female and male reproductive systems. A proboscis or introvert is often present (Figs 2.2A, 2.13B, 2.15, 2.19A), derived ontogenetically either from the entire anterior end of the body (in the order Proboscidea) or from the rear of the oral cavity (in the order Pharyngidea). Five pairs of unarticulated, unbranched legs or parapodia are present, each containing a protrusible hook, usually some replacement hooks and a support rod (or aciculum) (Fig. 2.4A). The hook apparatus is almost always present even when the parapodia are rudimentary (Figs 2.10B, 2.12, 2.13B, 2.14E). Most species have sucker- or pit-like lateral organs which are usually protrusible; their number and location vary (Figs 2.11A, 2.14B, 2.15, 2.17A, 2.18, 2.19A). The body margin often bears cirri (Figs 2.1A–C, E, F, 2.2B).

The epidermis is overlain by a thin cuticle and is usually a myo-epithelium with a basal membrane (Fig. 2.3A) or a syncytium with sunken nuclei. It may be ciliated. The dermis surrounding the internal organs consists of obliquely striated muscles and parenchyma cells (Fig. 2.3A).

The gut is entire, but the locations of the mouth (or, alternatively, the proboscis pocket opening) and anus are variable: dorsal, marginal or ventral in different taxa. The pharynx is surrounded by a muscle bulb (Figs 2.2A, 2.10A, 2.11A, B; 2.12, 2.14A, E, 2.16B, 2.17B, 2.18, 2.19B); jaws and teeth are absent. One to three (rarely more) pairs of branched or, rarely, anastomosing diverticula extend from the stomach (Figs 2.2C, 2.12, 2.14D, 2.17A, 2.18), except in one species. The intestine usually resembles a cloaca (Figs 2.2A, C, 2.11B, 2.17B, 2.18, 2.19B) in that it receives one pair (rarely more) of ducts, sometimes partly fused, from the anterior part of the uterus; in one genus the common pore of the ducts is external (Fig. 2.14A, E); in a few species the ducts are absent. These ducts have been most commonly called metanephridia, but any role in excretion or gamete release is doubtful. However, five pairs of protonephridia are known from one species. The nervous system (see Figs 2.6, 2.11A, C; 2.16D; 2.18) has a circum-oesophageal ring with poorly developed cerebral ganglia, a peribulbar or a prebulbar nerve ring in the proboscis, and a ventral nerve cord that is, fundamentally, long and ladder-like, but most often is condensed to a single cord or a compact mass; five pairs of major lateral nerves serve the parapodia, and up to six pairs of intermediate nerves may be present.

Myzostomes are almost all protandric hermaphrodites. In the female system, lateral diverticula branch off the anterior part of the unpaired dorsal uterus (Figs 2.2C, 2.14E); these diverticula lie dorsal (rarely ventral) to the gut diverticula or enclose the latter. The posterior part of the uterus, or oviduct, lies dorsal to the intestine and opens close to the anus (Figs 2.2A, 2.14A, 2.17B, 2.19B).

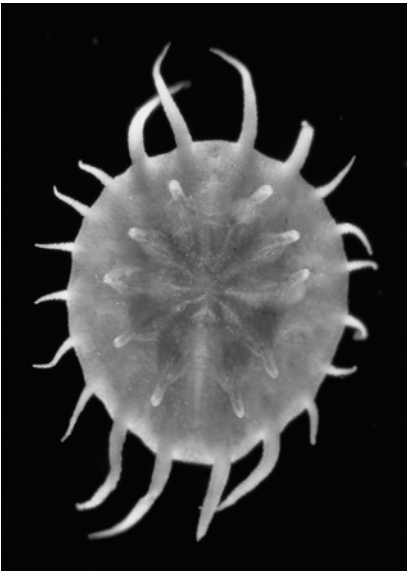
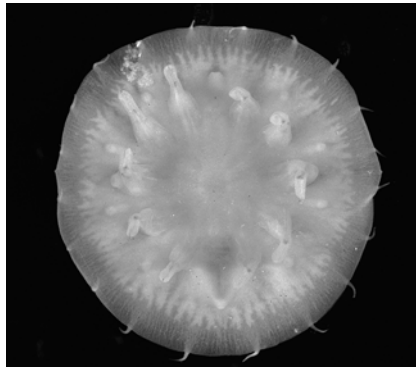
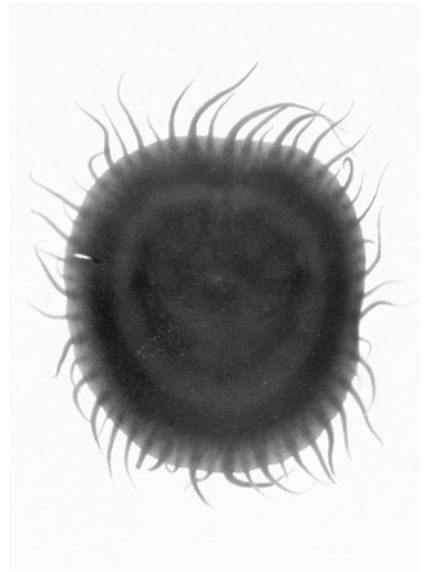
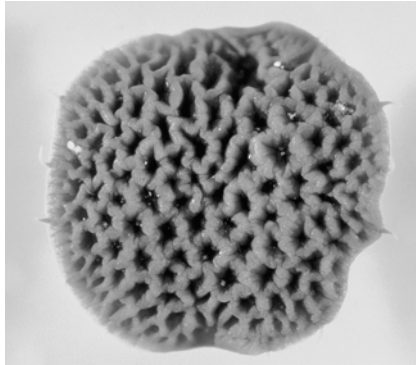
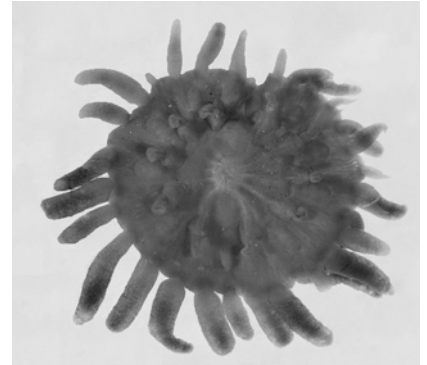
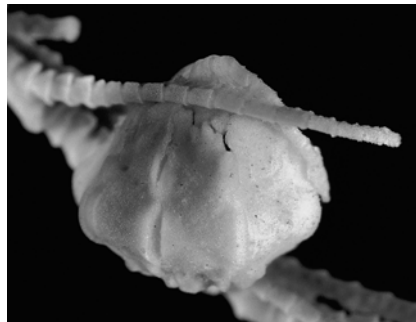
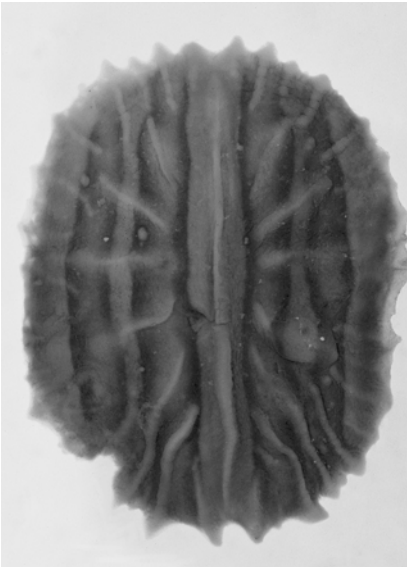
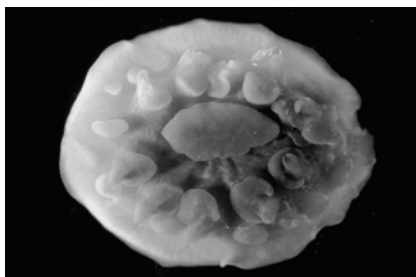
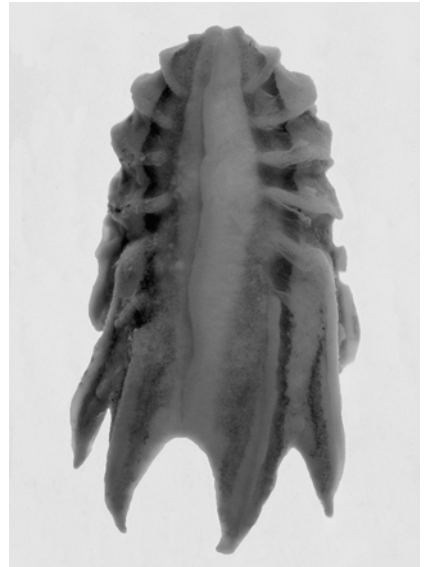
The ovaries, which may be single or double, paired or unpaired, lie dorsal to the gut on the floor of the anterior part of the uterus (Figs 2.2C, 2.11B) or ventro-lateral to the gut in the uterine diverticula (Figs 2.12, 2.14B, E). Oocytes accompanied by two accessory cells implant and grow in the epithelium of the diverticula and are later released into the lumen.

The male system is paired (Figs 2.2B, 2.11A, 2.12, 2.14D, 2.16C, 2.18). The testes are diffuse or compact and usually lie ventral to the digestive system, but occasionally are dorsal. The seminal ducts empty through one or two pairs of vasa deferentia into a pair of seminal vesicles (sometimes absent) that exit lateral to the third pair of parapodia. A pair of protrusible penes may be present. Spermatozoa develop in vacuoles inside spermiocysts. In the mature spermatozoon (Fig. 2.7A–C), the flagellum passes alongside and outside the main cell body and has a centriolar derivative at its free end; there is no nuclear membrane, and the chromatin is condensed into one or more rows of bead-like bodies.

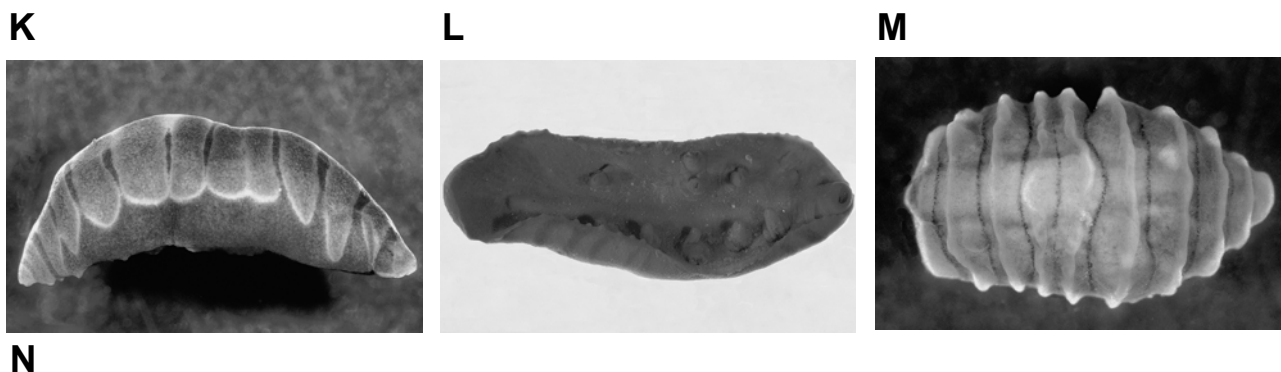
Hypodermic internal fertilisation takes place by means of a spermathecal syncytium derived from spermiocysts that are transferred in a spermatophore (Fig. 2.7D).

The larva (Fig. 2.8) is a trochophore that temporarily develops two clusters of chaetae and a retractable caudal process.

The Myzostomida comprises two orders and eight families. Two families, Myzostomatidae and Endomyzostomatidae, are known from Australian waters.

**A****B****C****D****E****F****H****G****J****I**





**Figure 2.1** Species of Myzostomida known from Australian waters (A–M) or likely to occur in the Australian Antarctic Territory (N). Photographs are of preserved specimens. **A**, *Myzostoma ambiguum* from *Oxycomanthus bennetti*, Bohol, Philippines; occurs on *Oxycomanthus bennetti* and *Comatella stelligera* in Western Australia and Queensland. **B**, *Myzostoma* species aff. *Myzostoma stochoeides*, host unknown, from Vernon Island, Northern Territory. **C**, *Myzostoma polycyclus* from *Comanthus timorensis*, Mindoro, Philippines; occurs on *Comanthus timorensis*, *Comanthus parvicirrus*, *Comanthus mirabilis* and *Comatula pectinata* var. *purpurea* in Western Australia and

Queensland. **D**, *Myzostoma insigne* (synonym of *Myzostoma echinus* according to Grygier 1990), host unknown, from Holothuria Bank, Western Australia; also known from *Comanthus parvicirrus* in Queensland. **E**, *Myzostoma* species aff. *Myzostoma cirricostatum*, host unknown, from Halmahera, Indonesia; occurs on *Lamprometra palmata* and *Comanthus* species in Western Australia. **F**, *Myzostoma mortenseni*, host unknown, from Lizard Island, Queensland (same specimen photographed in life by Stamman *et al.* 1985); also known from *Comanthina schlegeli*, *Comanthus briareus*, *Comaster gracilis* and perhaps *Himerometra* species in Queensland. **G**, *Myzostoma plicatum* from *Lamprometra palmata*, Houtman Abrolhos, Western Australia; also known from *Lamprometra palmata*, *Stephanometra spinipinna* and *Comatella stelligera* in Queensland. **H**, gall of *Myzostoma willemoesii* on *Glyptometra tuberosa*, Negros, Philippines; occurs on *Glyptometra inaequalis* off New South Wales. **I**, *Myzostoma fissum* (synonym: *Myzostoma striatum*; see Eeckhaut *et al.* 1998) from *Lamprometra palmata*, Houtman Abrolhos, Western Australia; widespread in Australia on *Lamprometra palmata*. **J**, *Notopharyngoides aruensis* from *Oxymetra erinacea*, Sunda Strait, Indonesia; occurs in Northern Territory and Queensland, on *Stephanometra oxyacantha* in the latter instance. **K**, *Hypomyzostoma* species (*Myzostoma* species 4 of Grygier 1988) from *Lamprometra palmata*, Cobourg Peninsula, Northern Territory; also known from *Lamprometra palmata* in Western Australia. **L**, *Hypomyzostoma nanseni* from *Stephanometra spicata*, Cobourg Peninsula, Northern Territory; also known from *Stephanometra oxyacantha* in Queensland and *Lamprometra palmata* in Western Australia. **M**, *Hypomyzostoma sulcatum*, host unknown, Darwin, Northern Territory; also known from *Oligometrides adeonae* in Western Australia. **N**, *Asteromyzostomum* species of Grygier (1988) from sea star *Labidiaster* species, near McMurdo Sound, Antarctica. The specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (A, C, E, L, M, N), the Natural History Museum, London (F, G, H), the Australian Museum, Sydney (D), and the Northern Territory Museum of Arts and Sciences, Darwin (B, I, J, K). [M.J. Grygier]

## HISTORY OF DISCOVERY

Myzostome worms were first discovered on crinoids (*Antedon* species) in European seas in the 1820s. Pioneering studies on the two common species, *Myzostoma cirriferum* and *M. glabrum*, were published from the 1840s through to the mid-1860s (see citations in Graff 1877 and Nansen 1885). In his worldwide monographic studies, Graff (1877, 1883, 1884a, 1884b, 1884c, 1885a, 1885b, 1887) described more than half of the known species of crinoid-associated myzostomes. Works by other authors include: regional taxonomic studies by McClendon (1906), Boulenger (1913), Remscheid (1918) and Atkins (1927); a controversy about the sexual system between Beard (1884, 1898) and Wheeler (1896, 1899), and; anatomical studies of *Myzostoma*, *Asteriomyzostomum* and *Protomyzostomum* by Nansen (1885, 1887), Stummer-Traunfels (1903) and Fedotov (1912, 1914, 1916, 1925, 1929), respectively. Stummer-Traunfels (1926) comprehensively reviewed the earlier literature and Jägersten (1936, 1937,

1939a, 1939b, 1940a, 1940b) studied the histology, reproductive biology and taxonomy of several genera, with particular attention to *M. cirriferum*. Jägersten's (1940a) systematic synthesis largely inspired the review by Prenant (1959) and represented the state of the art in myzostome studies for decades except for a few significant, but isolated works (see for example, Kato 1952; Wagin 1954). In the 1980s, taxonomic studies on the group were revived (for example, Grygier 1989, 1990, 1992; Eeckhaut, VandenSpiegel & Grygier 1994; Eeckhaut & Jangoux 1995; Eeckhaut 1998; Eeckhaut, Grygier & Deheyn 1998) and electron microscopical studies of the reproductive biology, spermatology and general anatomy were initiated (for example, Afzelius 1983, 1984; Pietsch & Westheide 1987; Mattei & Marchand 1988; Eeckhaut & Jangoux 1992, 1993a, 1993b, 1995, 1997; Eeckhaut 1995; Eeckhaut, Dochy & Jangoux 1995).

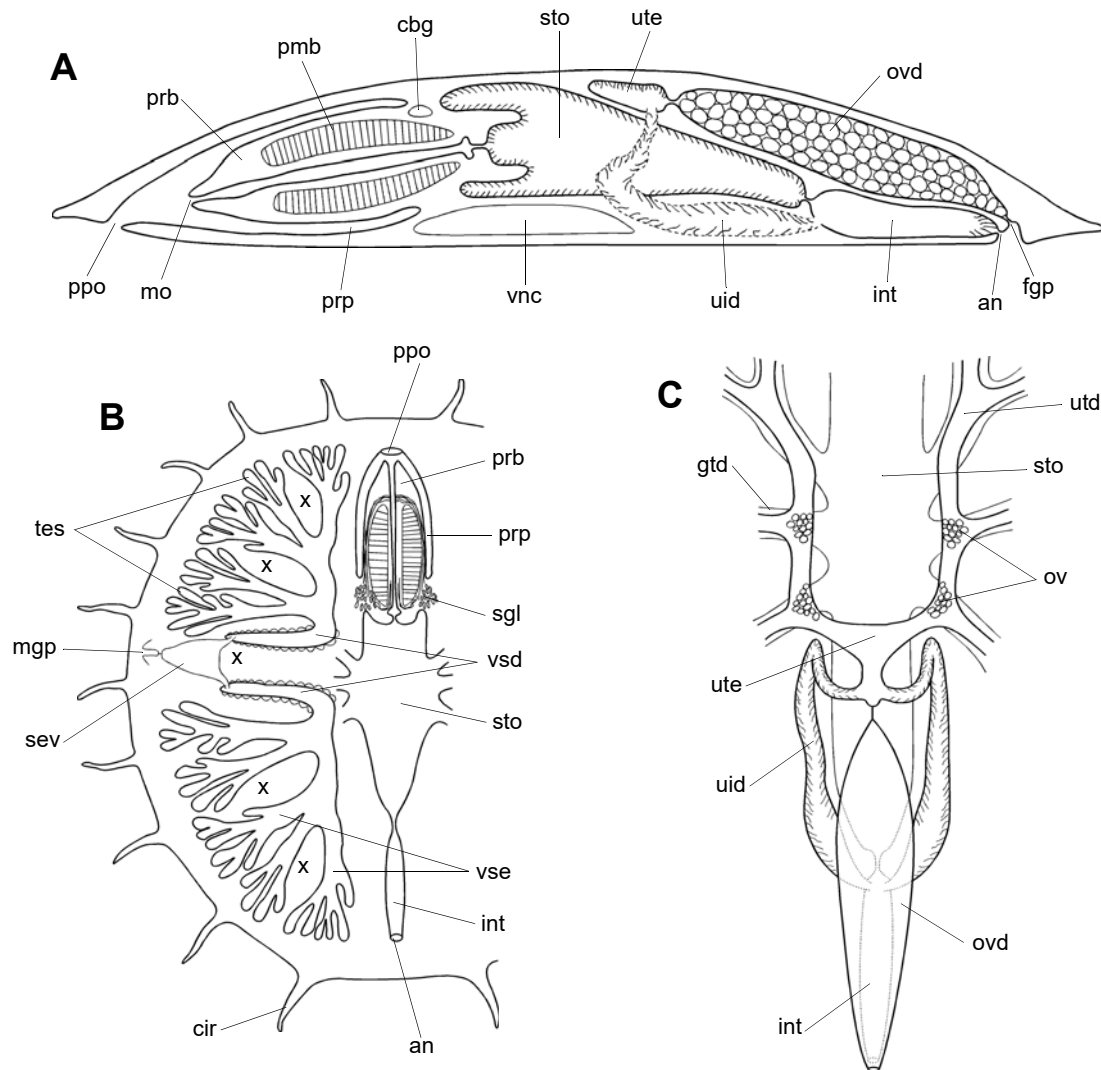
Very little work has been done on Australian Myzostomida. Graff (1884b, 1887) described a few species collected by the *Challenger* Expedition in the Torres Strait and Arafura Sea; most of his material is housed in The Natural History Museum, London. Potts (1915) studied the coloration of specimens from Murray Island, Torres Strait, in relation to their hosts' coloration, and Atkins (1927) described the species involved; efforts to locate this collection have failed. Day & Hutchings (1979) listed the Australian species based on the earlier papers, and Jangoux (1987, 1990) listed the cysticolous and gallicolous species. Stamman, Phillips, Phillips & Segar (1985) published a colour photograph of a living Australian specimen on its host, and Eeckhaut *et al.* (1998) identified it (Fig. 2.1F herein). Lester & Sewell (1989) reported unidentified myzostomes on five species of comatulid crinoids at Heron Island. Fabricius & Dale (1993) documented the presence and relative abundance of myzostomes on 15 species of comatulids from the central part of the Great Barrier Reef, especially Davies Reef; efforts to locate this large collection have also been unsuccessful. Grygier's (1990) summary of literature records and unpublished museum collections showed the presence of at least 20 species in Queensland, 17 in the Northern Territory and one in South Australia; Grygier (1989, 1992) gave detailed distribution data for two of these species. Eeckhaut *et al.* (1998) described, illustrated and provided distribution maps and new Australian records for eight species of myzostomes, one of them new. Most of these Australian myzostome specimens are in the National Museum of Natural History, Smithsonian Institution, the Museum of Comparative Zoology, the Australian Museum, the Western Australian Museum and the Northern Territory Museum of Arts and Sciences. In order to prepare the present review, the author examined additional unpublished collections housed in some of these museums.

No myzostomes have been reported from the Australian External Territories. Six species of *Myzostoma*, *Proto-myzostomum*, *Endomyzostoma* and *Asteromyzostomum* have been recorded from crinoid, ophiuroid and asteroid hosts in Antarctic waters (Stummer-Traunfels 1908; Boulenger 1916; Fauvel 1936; Grygier 1988, 1989; Bartsch & Faubel 1995), but from the Antarctic Peninsula and the Weddell, Bellinghausen and Ross Seas, not the Australian Antarctic Territory.

## MORPHOLOGY AND PHYSIOLOGY

### External Characteristics

Myzostomes are basically bilaterally symmetrical, often with a superficial, superimposed radial symmetry. They are not segmented *per se*, but there is a certain repetition of body parts. The body form varies from elongate and 'worm-shaped', as in *Mesomyzostoma* species (Fig. 2.12), to oval, shield-shaped or circular, as in many species of *Myzostoma* (Fig. 2.1A–F). Species of *Asteriomyzostomum*, and especially those of *Contramyzostoma* (Fig. 2.15) and *Asteromyzostomum* (Figs 2.1N, 2.18), have a body that is broader than it is long. The worms are usually flat and thin, but may also be thick and dome-shaped, semi-cylindrical or even mushroom-shaped. Diverse elaborations of the posterior end of the body are common in species of *Myzostoma* (Fig. 2.1H) and *Asteromyzostomum* (Figs 2.1N, 2.18). Radial or transverse dorsal ridges are present in many Myzostomatidae (Fig. 2.1G, I, M), and some species of *Myzostoma* have plate-like thickenings, prominent papillae or reticulate ridges on the dorsal side (Fig. 2.1E). The body margin of most myzostomatids and some endomyzostomatids bears cirri; their numbers and lengths are important diagnostic features. Typically 10 pairs (Fig. 2.1A, B), often more (Fig. 2.1C, F), and sometimes fewer or none (Fig. 2.1J) are present. Some myzostomatids, particularly *Hypomyzostoma* species (Fig. 2.1K, L), have numerous large or small marginal scallopings or irregular margins instead of discrete cirri.



**Figure 2.2** Anatomy of *Myzostoma cirriferum* (Myzostomatidae, Proboscidea). **A**, internal organs, sagittal view. **B**, digestive tract and male reproductive system, ventral view. **C**, digestive tract and female reproductive system, dorsal view. **an**, anus; **cbg**, cerebral ganglion; **cir**, marginal cirrus; **fgp**, female genital pore; **gtd**, gut diverticula; **int**, intestine; **mo**, mouth; **mgp**, male genital pore; **ov**, ovaries; **ovd**, oviduct; **pmb**, pharyngeal muscle bulb; **ppo**, proboscis pocket opening; **prb**, proboscis; **prp**, proboscis pocket; **sev**, seminal vesicle; **sgl**, salivary gland; **sto**, stomach; **tes**, testes; **uid**, utero-intestinal duct; **utd**, uterine diverticula; **ute**, uterus; **vnc**, ventral nerve cord (or mass); **vsd**, vas deferens; **vse**, vas efferens; **x**, sites of parapodia. (After Jägersten 1939b) [I. Hallam]

Members of the Myzostomatidae have a retractable proboscis that often bears several pairs of buccal papillae (Fig. 2.1D). The proboscis of *Pulvinomyzostomum* and *Endomyzostoma* species is not homologous with this and is never so armed.

Most myzostomes have five pairs of legs or parapodia (examples in Fig. 2.1), all of which have a protrusible, hook-shaped chaeta (Figs 2.2B, 2.4). The parapodia tend to be inconspicuous except in myzostomatids, in which they are well developed, lobiform and often highly extensile. Sometimes they bear a button-like or pointed cirrus on the medial side of their proximal fold.

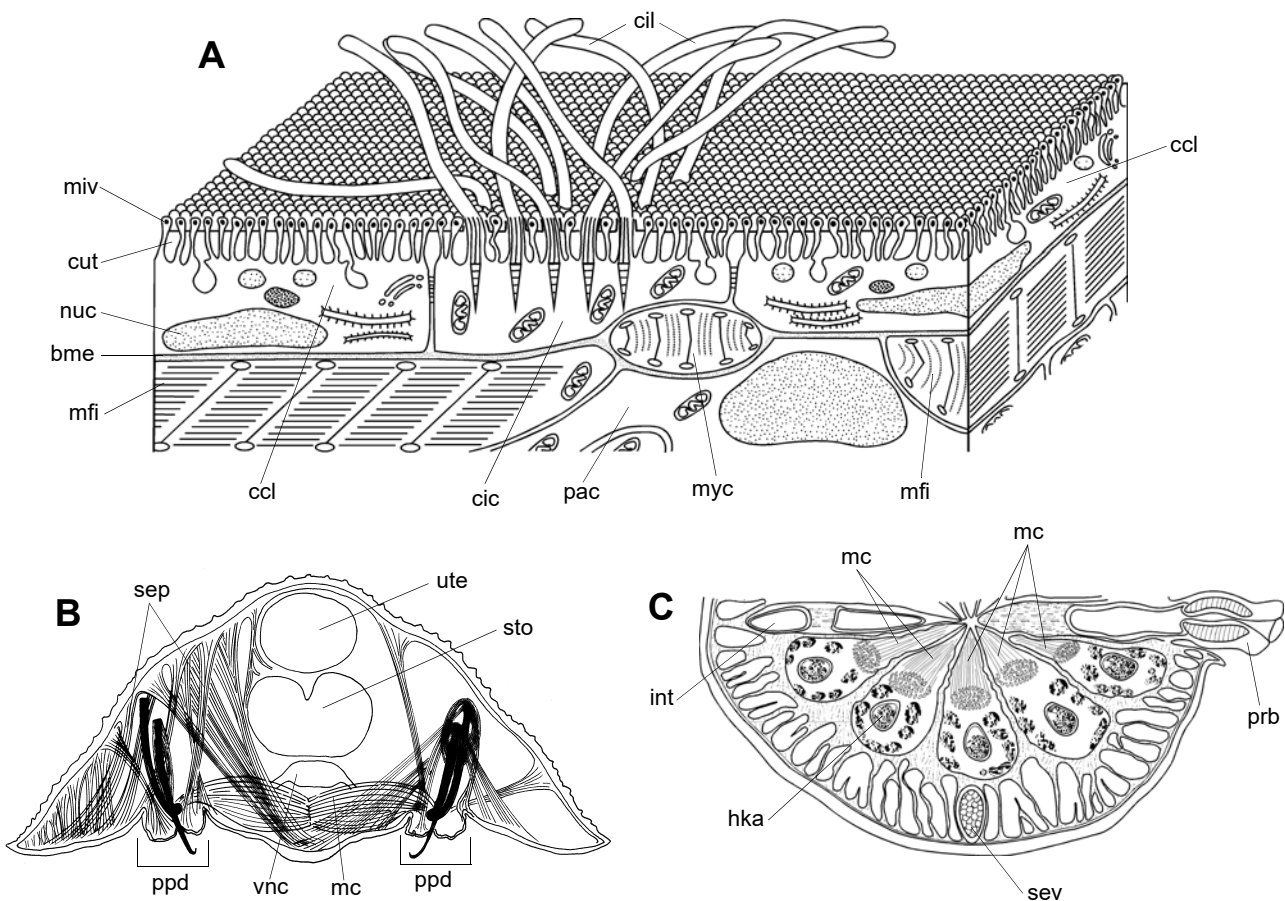
Most myzostomes also have sucker- or pit-like lateral organs that are often protrusible and sensory in function. Myzostomatids have four pairs of lateral organs, each pair alternating with the parapodia (Fig. 2.1B). However, in other families they are located in different positions, or in greater or lesser numbers (Figs 2.11A, 2.15, 2.17A, 2.18) or may even be absent.



## Body Wall and Musculature

Many histological studies of the integument have been made, but transmission electron microscopical studies are few and concern only *Myzostoma cirriferum* and *Contramyzostoma bialatum* (see Eeckhaut & Jangoux 1993a, 1995; Eeckhaut 1995). The following description is based on the former species.

The epidermis, bounded by a cuticle and basement membrane (Fig. 2.3A), consists of sensory-secretory areas and non-innervated, myo-epithelial areas. Sensory-secretory areas are found on the cirri, body margin, buccal papillae, parapodia and parapodial folds (see nervous system section below). Myo-epithelial areas (Fig. 2.3A) comprise covering cells, ciliated cells and myo-epithelial cells. The covering and ciliated cells are covered densely with microvilli that protrude nearly all the way through the four-layered cuticle, and are joined together by a zonula adhaerens and a septate desmosome. The ciliated cells are dispersed and each has a tuft of simple or paddle-shaped cilia (see Eeckhaut *et al.* 1994) with  $9 \times 2 + 2$  axonemes and ciliary rootlets. The myo-epithelial cells lie beneath the other cells, perpendicular to the antero-posterior axis of the body and in contact with the basement membrane; the myofibrils within them, although parallel, show no regular arrangement in cross section. Species of *Contramyzostoma* also have covering cells, myo-epithelial cells and patches of cilia.



**Figure 2.3** **A**, microanatomy of the non-sensory integument (three cell types underlain by a basal membrane) of *Myzostoma cirriferum*. **B**, **C**, musculature of *Myzostoma glabrum*: **B**, semi-transverse view showing muscular septum on left and parts of parapodial musculature on left and right; **C**, half a horizontal section showing ventral musculature. **bme**, basement membrane; **ccl**, covering cell; **cic**, ciliated cell; **cil**, cilia; **cut**, cuticle; **hka**, parapodial hook apparatus; **int**, intestine; **mc**, musculus centralis; **mfi**, muscle fibre in dermis; **miv**, microvilli; **myc**, myo-epithelial cell; **nuc**, nucleus; **pac**, parenchyma cell; **ppd**, parapodium; **prb**, proboscis; **sep**, septa; **sev**, seminal vesicle; **sto**, stomach; **ute**, uterus; **vnc**, ventral nerve cord (or nerve mass). (A, after Eeckhaut & Jangoux 1993a; B, C, after Graff 1877)

The integument is unciliated in most pharyngidean genera, but is ciliated in patches in *Endomyzostoma* species and uniformly ciliated in *Pulvinomyzostomum* and male *Mycomyzostoma*. The cuticle of *Asteriomyzostomum asteriae* is uniquely formed from the individual caps on each epidermal cell. The integumental musculature in all myzostomes comprises circular and longitudinal fibres. These lie below the uninterrupted basement membrane of the epidermis in *Myzostoma* (Fig. 2.3A). In contrast, in *Proto-myzostomum* and *Stelechopus*, in which the epidermal cells reportedly form a syncytium and, at least in the former genus, there is no basement membrane, the epidermis nuclei are sunken below the integumental muscles (Fedotov 1914; Jägersten 1940a; Nigmatullin 1970; Bartsch & Faubel 1995). In species of *Asteromyzostomum*, the epidermal cell nuclei are sunken through *holes* in the basal membrane (Wagin 1954).

Beneath the epidermis and filling the spaces around the gonads and digestive system is a dermis consisting of double obliquely striated muscle fibres and parenchyma cells that are variable in form (Fig. 2.3A). In some species, the dorsal part of the dermis includes a thick collagenous layer (Rao & Sowbhagyavathi 1974).

The musculature of motile forms like *Myzostoma* species (Fig. 2.3B, C; see Graff 1877) includes, in addition to the integumental muscles, dorso-ventral muscles that form the septa, the muscles of the parapodia and lateral organs, the longitudinal retractor muscles of the proboscis, sheaths of circular and longitudinal muscle fibres around the internal organs and muscle sheets above and below the nervous system. In *Myzostoma*, a ventral muscle mass composed of radially directed fibres is especially well developed (Fig. 2.3C). The mass includes: the five pairs of muscoli centrales of the parapodia; the anterior proboscis retractor; the posterior muscles that surround the intestine, and; twelve primary septa. These septa alternate with the parapodia and divide distally to encompass the lateral organs and then form a connected web of secondary radial septa near the margin.

The ten lateral body chambers defined by the primary septa are open to the main longitudinal chamber in which the uterus, gut and nervous system lie (Fig. 2.3B). The more central dorso-ventral muscles that make up the septal walls converge on the ventral muscle mass, whereas those nearer the margin converge ventrally outward (Fig. 2.3B); the muscles that make up the secondary septa run straight up and down. In a very robust species, such as *M. glabrum* (Fig. 2.3B), the gaps between the component muscles of the septa are small, whereas in others, such as *M. cirriferum*, the gaps are great, there are no real body chambers, and most of the muscles run directly dorso-ventrally.

There is no mineralised skeleton nor any evidence of a hydrostatic skeleton. The only hard parts are the parapodial hook apparatus described below.

## Locomotion

Some species are more motile than others. Cysticolous, gallicolous and endoparasitic forms are immotile. In motile members of the Myzostomatidae, the parapodia are capable of great extension and have a powerful, complex musculature. They consist of two parts (Fig. 2.4A): the parapodial fold, which is a low, obliquely conical continuation of the ventral body wall that may have a cirrus on its medial face, and the parapodium itself. The support rod (aciculum) within provides support for the limb, and the rod's distal manubrium guides the hook that provides traction; the hook can be withdrawn inside the parapodium. The support rod is permanent, but one or more replacement hooks are constantly being secreted.

Stummer-Traunfels (1903, 1910) described in great detail the internal structure of the parapodia of *Asteriomyzostomum asteriae* and *Myzostoma gigas* (for the latter, see Fig. 2.4A). The external integument, minus most muscles except for sphincters, continues inside the parapodium as the hook sheath. Parapodial glands presumably empty a lubricating fluid into the sheath pocket, a diverticulum of the hook sheath. More proximally is the chaetal gland or chaetal sac, consisting of several follicles that secrete the support rod, the hook in use, and a varying number of replacement hooks. The support rod's core and manubrium are secreted by the proximal and distal parts, respectively, of one follicle (two distinct follicles in *M. gigas*; Fig. 2.4A); the intervening part of the rod passes through parenchyma, which presumably secretes the mantle layer (see below). A row of replacement hook follicles in sequential stages of development leads up to the follicle of the hook in use. The hook's shaft passes first through a lumen into which accessory gland cells empty; in *M. gigas* there is a distinct accessory gland sac (Fig. 2.4A). The shaft then passes through a tube defined by the manubrium into the hook sheath,



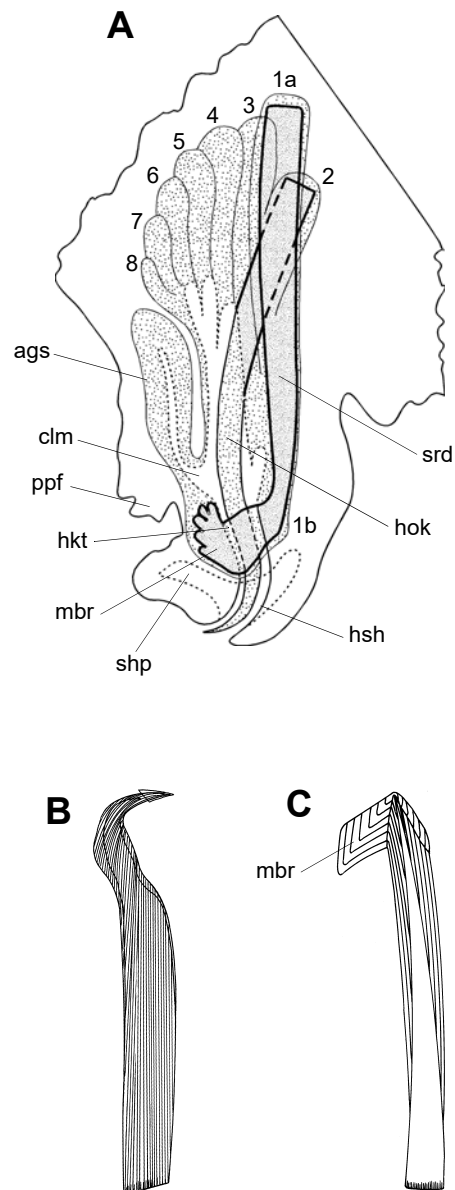
from which its tip can be protruded or retracted by muscular action. The smallest replacement hook follicles are completely enclosed, but those with more fully developed replacement hooks open into the accessory gland lumen.

Jägersten (1936) provided the most detailed light microscopical study of the microstructure of the hooks and support rods; they have generally been supposed to be chitinous structures. Both appear superficially to consist of a tapered, fibrillar core surrounded by a homogeneous mantle except near the base. In addition, the support rod has a curved manubrium attached at the tip (Fig. 2.4B, C). However, only the support rod truly has a mantle; the core of the support rod corresponds structurally to an entire hook, except that the tip of the hook has a thin protective sheath. The hooks and the support rod cores have a substructure of tightly packed, parallel tubes. At the base, processes of the basal secretory cell of the follicle penetrate into the tubes. The tubes are uniform in the support rods, but in the hooks their lumen becomes narrower nearer the sides and the material itself becomes harder; nonetheless, there is no precise boundary between the inner and outer regions. In the curved, distal part of the hook, the tubes are generally oriented obliquely relative to the long axis (Fig. 2.4B). The mantle layer of the support rod, which is secreted by cells other than the basal cell, has no tubes, but is made of several concentric, cylindrical (not conical) layers of homogeneous material (Fig. 2.4C). The manubrium consists of inner and outer secreted layers, both of which show growth lines; the irregular distal end apparently grows by the addition of small clumps of material.

The musculature of the hook apparatus is not attached directly to the hook and support rod, but to a membrane bordering the chaetal sac that is derived from the integumental basal membrane. This musculature has been described in detail for some species of *Myzostoma* (Fig. 2.3B; Graff 1877; Stummer-Traunfels 1910) and *Asteriomyzostomum* (Stummer-Traunfels 1903). The principal difference between the Myzostomatidae and the other families is the lack of a strong musculus centralis in the latter, whereas in the former it generally contributes to the formation of a powerful ventral muscle mass (Fig. 2.3B, C).

## Feeding and Digestive System

Myzostomes associated with crinoids (except the endoparasitic *Mesomyzostoma* and stalk-dwelling *Mycomyzostoma*) all feed by means of their proboscis on particles entrained in the ambulacral grooves of their host's pinnules, arms, or disc, or, for *Pulvinomystomum*, in the host's gut. However, it is exceedingly uncommon to find identifiable gut contents in these worms.



**Figure 2.4** Parapodium, hook and support rod structure in *Myzostoma*. **A**, chaetal gland of parapodium of *Myzostoma gigas*. **B**, a hook of *Myzostoma* species (reported as *Myzostomum ambiguum*) with artificially loosened sheath at tip and internal tubes shown as striae. **C**, support rod of *Myzostoma gigas* showing central core of shaft (structurally equivalent to hook), concentric layers of mantle around core and growth lines of distal manubrium. **ags**, accessory gland sac; **clm**, central lumen; **hkt**, hook tube; **hok**, hook; **hsh**, hook sheath; **mbr**, manubrium; **ppf**, parapodial fold; **shp**, sheath pocket; **srd**, support rod; **1a**, **1b**, support rod follicles; **2–8**, hook and replacement hook follicles. (A, after Stummer-Traunfels 1926; B, C, after Jägersten 1936) [I. Hallam]

The digestive system consists of a mouth, pharynx, stomach with usually two or three pairs of branching diverticula, and an intestine and anus. Jägersten (1940c), Platel (1962), Eeckhaut (1995), and Eeckhaut, Dochy & Jangoux (1995) have studied in detail the digestive system of *M. cirriferum* (Fig. 2.2A, B). In this species and other Myzostomatidae, the mouth, at the tip of a retractable proboscis that represents the anterior portion of the body, is encircled by a lip that in different species often bears several pairs, or a corona, of ciliated, sensory, buccal papillae (Fig. 2.1D). In members of the Pharyngidea, the proboscis is a protrusion of the rear of the oral cavity and lacks buccal papillae, or it is absent and the mouth is terminal (see Figs 2.10A, 2.11A, B, 2.12, 2.13B, 2.14A, D, 2.15, 2.16B, 2.17B, 2.18, 2.19). The circum-oral tentacles of *Asteromyzostomum* species are much longer than buccal papillae (Fig. 2.18); they are probably not their homologues, and serve primarily to anchor the myzostome to its host sea star's integument.

In *Myzostoma*, the pharynx traverses the proboscis and is unciliated (Fig. 2.2A). It is lined with glandular cells and is surrounded in part by a basement membrane-bounded muscle bulb with alternating radial and circular muscles. Such a muscle bulb is present in all myzostomes and serves for ingestion; the mechanism is described by Eeckhaut *et al.* (1995). Processes from salivary gland cells, deeply sunken into the parenchyma at the base of the proboscis (Fig. 2.2B), pass both inside and outside the muscle bulb to open into the pharynx at the bulb's anterior end (according to Platel 1962) or onto the lip (according to Eeckhaut *et al.* 1995); they secrete acid mucopolysaccharides (Platel 1962). Salivary glands open into the homologous region, the mouth cavity, in *Mesomyzostoma*, *Protomyzostomum* (Fig. 2.11B) and *Asteriomyzostomum* (Fig. 2.17B); no such glands occur in *Pulvinomyzostomum* and *Mycomyzostoma*.

The midgut, comprising the stomach and its diverticula (Figs 2.2A, 2.11B, 2.17B, 2.19B), is separated from the pharynx and intestine by sphincters. Diverticula are absent from female *Mycomyzostoma*; males lack a gut. In *Myzostoma*, the epithelium of the stomach, diverticula and intestine each consists of a different kind of cell; none is glandular. The stomach epithelium is ciliated (Fig. 2.2A); these cilia have a 9x2+2 axoneme and no rootlets. Such cilia are also present in *Endomyzostoma*, but are absent in *Protomyzostomum* and *Asteriomyzostomum*. Platel (1962) implied that the presence of ciliated low epithelium or unciliated high epithelium, or a mixture of the two, in the stomach of *M. cirriferum* depends on the recency of feeding. In this species, the cells of the diverticula and intestine bear microvilli, but cilia are absent except for those around the anus (Fig. 2.2A); in contrast, the entire intestine is ciliated in *Protomyzostomum* (Fig. 2.11B) and *Asteriomyzostomum*. The cells of the diverticula are vacuolated and serve both for intracellular digestion of food particles and the excretion of digestive wastes (see excretion section below).

## Circulatory System and Respiration

There is no special circulatory system. The midgut diverticula, however, ramify throughout the body (Figs 2.1B, 2.12, 2.14D, 2.17A, 2.18) and serve to distribute nutriment, at least. Gills are absent, and respiration apparently takes place through the entire body surface. Some myzostomes, however, have been observed to pump sea water in and out through the anus (Nansen 1885); this may indicate an additional site of oxygen uptake. Most cysticolous and gallicolous forms maintain two openings to their domicile, which might allow for a respiratory current.

## Excretion

The gut diverticula of *Myzostoma cirriferum* are the principal site of excretion of waste derived from the intracellular digestion of food (Jägersten 1940c; Platel 1962; Eeckhaut 1995; Eeckhaut *et al.* 1995). Each epithelial cell develops a large vacuole that fills with yellow-green concretions of excreta contributed by smaller endocytotic digestive vacuoles. The apical part of the cell with the vacuole buds off into the lumen as an excretory vesicle. Vesicles then accumulate in the rear of the stomach, becoming cemented together by a mucopolysaccharide into a mass that is eventually transferred into the intestine and expelled. In *Protomyzostomum*, the excreta simply fills the inside of the cell, not a special vacuole, and is released into the lumen when the cell disintegrates (Jägersten 1940a).

Five pairs of protonephridia have been found in *M. cirriferum* (Pietsch & Westheide 1987); they are located anterior to each pair of parapodia and spaced equidistantly across the midline. Each protonephridium comprises three terminal cells and a tubule cell (Fig. 2.5). Each terminal cell has six to nine flagella, each of which is encircled by 10 cytoplasmic rods, and the tubule cell is ciliated. Fenestrated regions of the terminal cells connect the lumen to the surrounding parenchyma and presumably serve for filtration. The presence of protonephridia has not yet been confirmed for any other species.

The single pair of ciliated utero-intestinal ducts (multiple sets in *Protomyzostomum polynebris*, absent in *Mycomyzostoma* and *Stelechopus*), termed nephridia by many authors, usually connect the uterus to the anterior part of the intestine; in *Endomyzostoma* these ducts pass directly to the exterior. These ducts are discussed below in connection with reproduction; they are probably not filtratory organs, but may serve to expel waste material from the uterus.

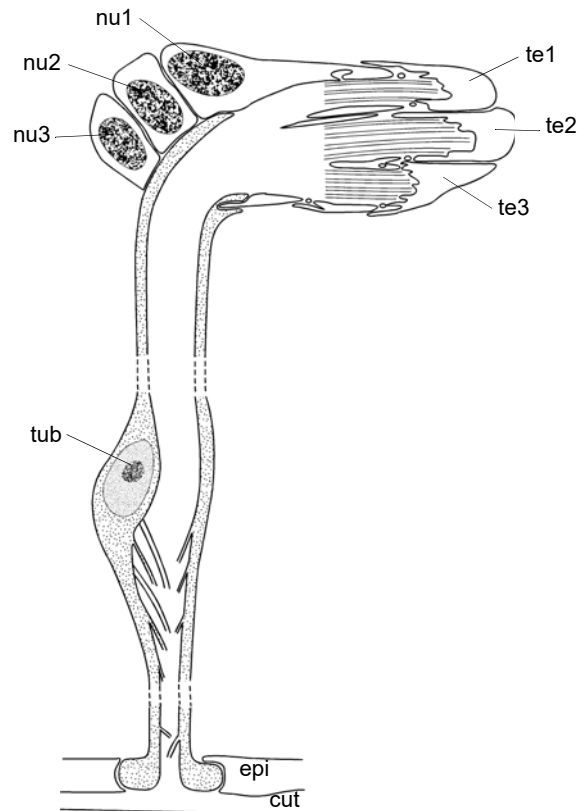
## Nervous System and Sense Organs

The nervous system has been described most thoroughly for several species of *Myzostoma* (Fig. 2.6), in which it consists of a circum-oesophageal ring, proboscis nerves, a ventral nerve mass and peripheral nerves (Nansen 1885, 1887; see also Boulenger 1913). Three pairs of nerves connect a prebulbar ring, located distally in the proboscis, with the circum-oesophageal ring posteriorly; in the latter, the cerebral ganglia are very poorly developed. Nerves pass anteriorly from the prebulbar ring into each buccal papilla and two pairs of nerves travel posteriorly along the pharynx towards the base of the proboscis. The ventral nerve mass is compact and consists of ganglion cells that are located between and dorso-lateral to two longitudinal commissures. An intermediary longitudinal nerve and five major and six minor pairs of lateral nerves are also present. The longitudinal commissures are connected by a major transverse commissure at the anterior and posterior ends, four thick transverse commissures alternating with the major lateral nerves, and five minor commissures at the levels of the major lateral nerves.

Each of the five main lateral nerves on each side splits into two outer, one intermediate and two inner nerves. The two outer nerves branch extensively near the body margin and each also innervates a marginal cirrus. The two inner nerves serve the muscles and glands of the respective parapodium. The intermediate nerve bifurcates, one branch going to the musculus centralis of the respective parapodium, and the other to the body margin.

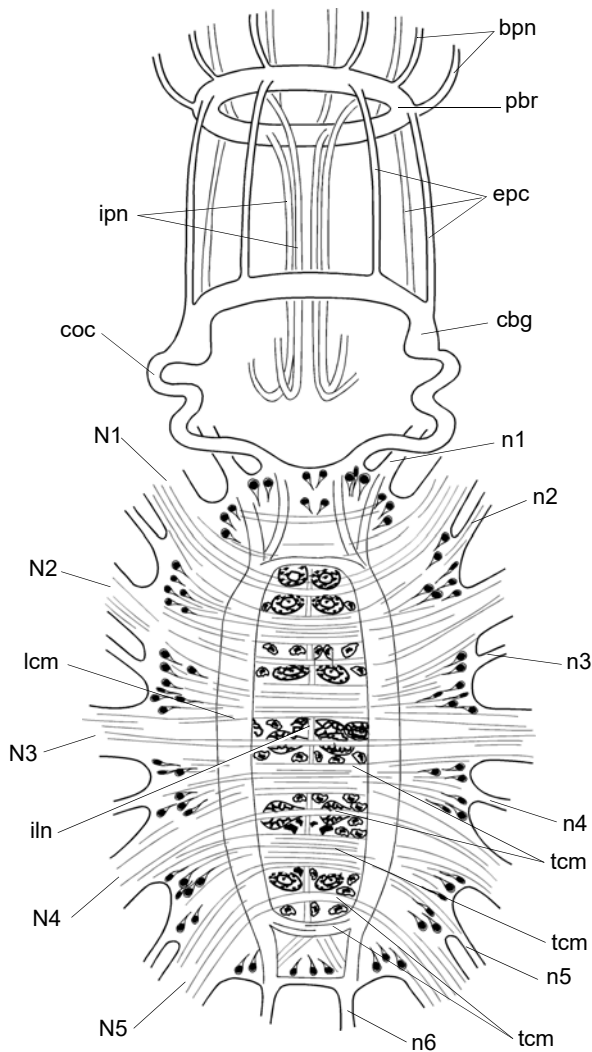
The six pairs of minor lateral nerves innervate muscles and the gonads. The first pair innervates the anterior body margin, and the sixth pair the posterior part of the body; the others each split into an upper and lower main branch and several ventrally directed branches.

Nervous connections to the lateral organs have been followed in *Protomyzostomum*, where the main lateral nerves serve these organs and the parapodia (Fedotov 1914); in *Asteriomyzostomum* branches of the intermediate nerves probably serve the lateral organs (Stummer-Traunfels 1903).



**Figure 2.5** A single protonephridium of *Myzostoma cirriferum* (Myzostomatidae, Proboscidea); five pairs have been observed. **cut**, cuticle; **epi**, epidermal cell; **nu1–nu3**, nuclei of terminal cells; **te1–te3**, terminal cells; **tub**, tubule cell. (After Pietsch & Westheide 1987) [I. Hallam]





**Figure 2.6** Central nervous system of *Myzostoma giganteum* (Myzostomatidae). **bpn**, buccal papillae nerves; **cbg**, cerebral ganglion; **coc**, circum-oesophageal connective; **epc**, external proboscideal connectives; **iln**, intermediary longitudinal nerve; **ipn**, internal proboscideal nerves (pharyngeal nerves); **lcm**, longitudinal commissure; **n1–n6**, minor lateral nerves; **N1–N5**, major lateral nerves; **pbr**, prebulbar nerve ring; **tcm**, transverse commissure. (After Nansen 1887) [I. Hallam]

parapodia (see Fig. 2.1B). Such a lateral organ consists of a ciliated, villose dome surrounded by, and either retracted within or protruding from, an integumental fold. The inner surface of the fold is entirely secretory; its gland cells resemble those of the parapodial integument. The epidermis of the dome comprises vacuolated cells together with an admixture of ciliated sensory cells and a distinct kind of secretory cell. The microvilli of the vacuolated cells project well beyond the cuticle. Each process from the sensory cells ends in a cilium. The cell body of the secretory cells, similar to those in the cirri, lies below the general epidermis.

In other families, lateral organs may be absent (most species of *Endomyzostoma* and *Mycomyzostoma*) or present, as: two ventral pairs (*Stelechopus*); four ventral pairs alternating with the parapodia (other *Endomyzostoma* and *Asteriomyzostomum* species – in the latter sometimes with a posterior medial one present; Fig. 2.17A); five dorsal pairs directly opposite the parapodia (*Protomyzostomum*; Fig. 2.11A);

Similar compact nervous systems are found in some pharyngidean genera (Figs 2.17B, 2.18). However, elongate ones have been described in *Mesomyzostoma* and *Stelechopus*, both with a single nerve cord, and in *Protomyzostomum* species and males of *Mycomyzostoma calcidicola*, with either a single or a double nerve cord (Figs 2.11A, 2.16D); details for each genus are given in the family sections below. All have five pairs of major lateral nerves, but there are fewer minor pairs in species of *Stelechopus* and *Protomyzostomum* than in *Myzostoma*.

Sense organs are principally tactile and/or olfactory; eyes are absent. The marginal cirri and buccal papillae are evidently sensory, but in *Myzostoma cirriferum* and some other species the cirri may also have an additional function. A ventral groove lined with supposed adhesive cells runs along each marginal cirrus. Two similar grooves run along the edges of the triangular marginal processes in species such as *M. furcatum*.

Except in some pharyngidean genera, the body is ornamented with patches of cilia. Cilia over the general body surface are evidently non-sensory (Fig. 2.3A; Eeckhaut & Jangoux 1993b), but in *M. cirriferum*, at least, those on the marginal cirri, buccal papillae, lateral organ domes, parapodia and parapodial folds, and in dorsal and ventral bands near the body margin have a sensory function. In these regions of sensory/secretory epithelium, branched nerve endings project through the basal membrane and between the basal parts of the epidermal cells. Each nerve process ends in a single cilium, presumably a mechanoreceptor.

The lateral organs, sucker-like processes found near the body margin, are now interpreted as mechano- and chemosensory structures rather than as attachment devices. Their ultrastructure has been investigated only in *M. cirriferum* (Eeckhaut & Jangoux 1993a). In this species and other myzostomatids, there are almost always four pairs ventrally, outside of, and alternating with, the

10 ventral pairs alternating with the parapodia (*Pulvinomyzostomum*; Fig. 2.19A); or up to 40 lateral organs scattered mostly along the lobed posterior body margin (*Asteromyzostomum*; Fig. 2.18). Further details are given in the family sections.

## Endocrine and Exocrine Systems

Nothing is known about possible endocrine function in myzostomes and reports on exocrine glands are entirely anatomical, with a little histochemistry; they principally concern arrays of secretory cells. The parapodial glands, accessory glands and chaetal glands of the parapodia are described under Locomotion. Salivary glands are described in the Feeding and Digestive System section. The secretory cells of the integument and lateral organs are described in the Body Wall and Musculature and Nervous System and Sense Organs sections above, respectively.

## Reproduction

Most, if not all, myzostomes are protandric hermaphrodites, passing through a functional male stage to a hermaphroditic stage and, in some species, on to a functional female stage (Wheeler 1896). Only *Mycomyzostoma calcidicola* is considered to be dioecious (Eeckhaut 1998), although there is some question regarding *Endomyzostoma* species.

According to the prevailing histological interpretation, the ovaries are usually located on or are sunken into the floor of the uterus above the stomach in the vicinity of the origin of the midgut diverticula, either as one or two unpaired organs or as one or two pairs (Figs 2.2C, 2.11B, 2.12). The ovaries are found ventral to the gut in uterine diverticula in a few Myzostomatidae, for example, in *Myzostoma adhaerens* (synonym of *M. furcatum* according to Grygier 1990) and *Notopharyngoides platypus*, and perhaps all species of *Endomyzostoma* (Fig. 2.14B, C, E; Wheeler 1896; Stummer-Traunfels 1908; Remscheid 1918). The ovaries produce triplet cells consisting of an oocyte together with two accessory cells. These are given off into the lumen, travel out into the diverticula (uterus lumen and diverticular spaces being considered the coelom); they attach to or possibly penetrate the epithelium, which in *Myzostoma* is ciliated dorsally. According to Wheeler (1896), the accessory cells are then absorbed by the oocyte, but their nuclei remain distinct until yolk begins to develop. However, according to Jägersten (1939b), the accessory cells transform into follicle cells and eventually several layers of follicles become attached to each side of the dorsal ciliary band, displacing and obscuring the original epithelial cell lining. In either case, the oocytes enlarge, detach from the epithelium and accumulate in the uterus; the posterior portion of the latter, lying dorsal to the intestine, is often referred to as the oviduct (Fig. 2.2A). The female gonopore is located just behind the anus and may be very closely associated with it.

Eeckhaut (1995) presented a different interpretation of the female reproductive system, based on ultrastructure. Like Wheeler (1896) and Jägersten (1939b), he studied *Myzostoma cirriferum*. A single diffuse ovary containing oogonia and previtellogenic and vitellogenic oocytes overlies all the uterine diverticula; this area is not merely a zone for maturing cells. The diverticula have an epithelium with a basement membrane, and the latter separates the developing ova and their surrounding parenchyma cells from the lumen, which is considered a branched oviduct rather than a coelom.

The anatomy and histology of the male reproductive system have been most closely studied in *Myzostoma cirriferum* (see Jägersten 1934, 1939b), including by transmission electron microscopy (Eeckhaut 1995). Less detailed observations have been made on many other species. In typical species of *Myzostoma*, the male system consists of testes, two pairs of vasa deferentia (anterior and posterior on each side), and a pair each of seminal vesicles and penes that open lateral to the third pair of parapodia (Fig. 2.2B). The testes occur as two pairs, comprising many follicles scattered diffusely in the parenchyma at the ends of dendritic vasa efferentia, mostly below the gut diverticula though some extend dorsally (most are dorsal in *M. 'ambiguum'* and *M. longimanum*; Jägersten 1939b) and with their outer border falling far short of the body margin. A basal membrane, or tunica propria, bounds the follicles, at least in *M. cirriferum*, and also the vasa efferentia, which have no cellular lining. The basal membrane bounds the vasa deferentia and seminal vesicles, too, both of which have an epithelium. In *M. cirriferum*, this epithelium consists of vesicular gland cells in the vasa deferentia, spumous gland cells in most of the seminal vesicle and vacuolated gland cells near the exit of the latter. The epithelium-lined spaces have often been considered a coelom, but Wheeler (1896) disagreed with that interpretation and Jägersten (1939b) noted that the relevant embryological information is lacking. A short canal leads from the seminal vesicle to the gonopore at the end of the penis. The penis, which varies greatly in length among

species, is ordinarily retracted into the body as an ectoderm-lined penial tract, which is ciliated around the gonopore. The aperture seen at the body surface or on a distinct papilla when the penis is retracted is the outer end of this temporary penial tract. The tract disappears when the penis is fully extended; it has often been misnamed the ejaculatory duct (see discussion in Jägersten 1939b). In some species, such as *M. cirriferum*, the extended penis may reach well beyond the body margin.

According to Jägersten (1939b), the innermost end of a follicle is lined with stem cells that give rise to spermatogonia and spermiocyst cells. The latter engulf the former to form spermiocysts, and spermatogenesis proceeds in intracellular vacuoles (see below). Eeckhaut (1995) did not observe stem cells; his records began with formed spermiocysts. The spermiocysts are aligned in single file in the distal parts of the follicles and in the vasa efferentia, which thus are solid cell-strings with no lumen. When the spermiocysts enter the vasa deferentia, the spermatids mature into spermatozoa. Other small cells are present in the ducts and seminal vesicles. They have been regarded by various authors as, for example, abortive spermiocysts (Nansen 1885; Stummer-Traunfels 1903; Eeckhaut 1995), nurse cells (Fedotov 1914) or lymphocytes (Jägersten 1934). The vasa deferentia have rings of muscle fibrils that give them a segmented appearance and cause peristalsis. The entrance to the seminal vesicle is closed by a muscular sphincter, and spasmodic contractions of the distal end of the duct force quantities of spermiocysts into the vesicle, where formation of the spermatophore takes place (see below).

The seminal vesicle is covered by a layer of circular muscles; external to them a discontinuity in the parenchyma, which extends proximally to include the vasa deferentia, allows the vesicle to slide outward into the penis when the latter is extended. A ventral sheet of vesicle retractor muscles bends around the distal end of the discontinuity. The penis retractor muscles originate dorsally and pass beneath the seminal vesicle to a point near the inverted end of the penis.

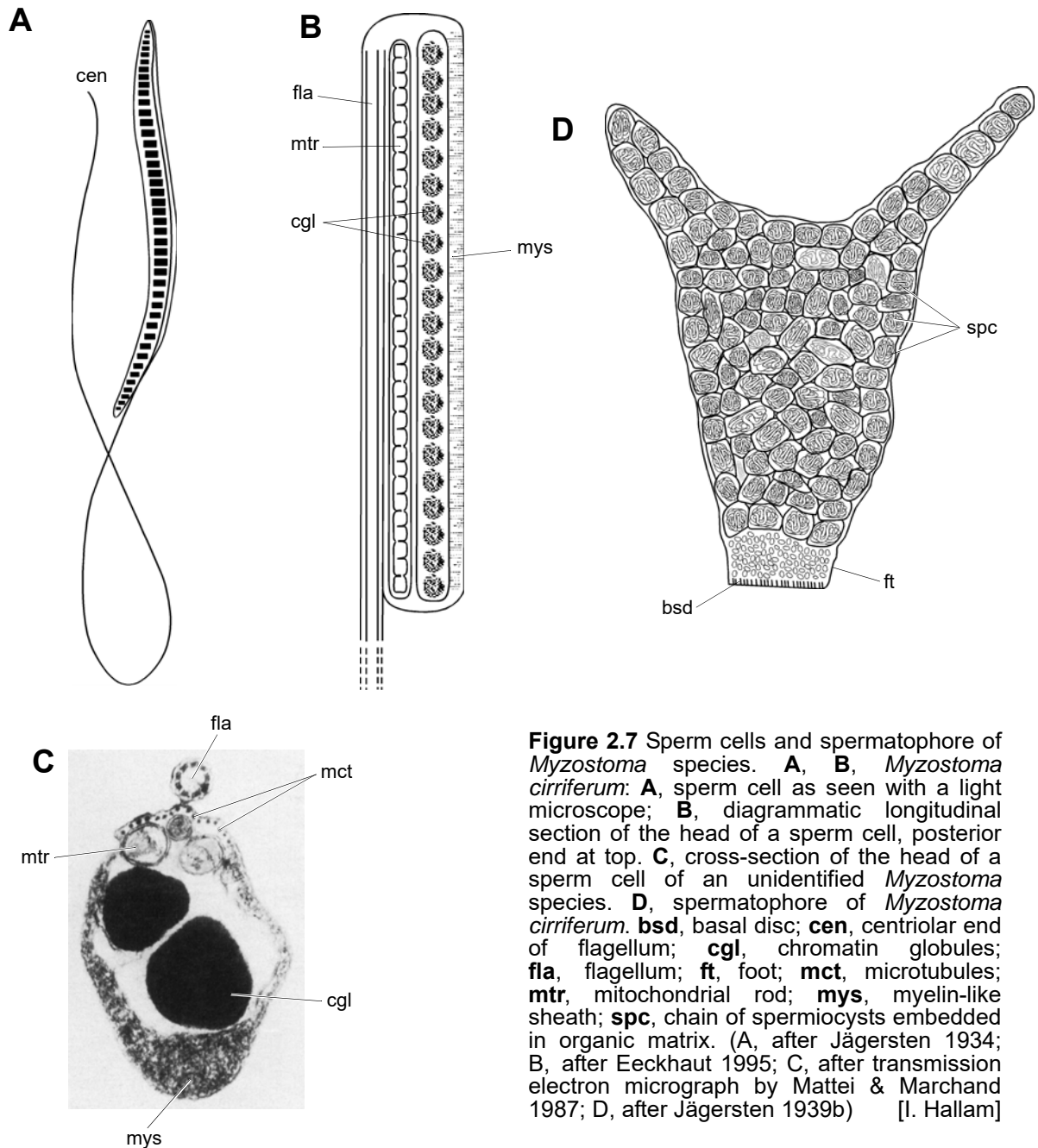
Structural differences in the male system among the Myzostomatidae most often involve the length of the penes, whether or not they form distinct papillae when retracted, and the location of the aperture of the penial tract. *Myzostoma* ‘*ambiguum*’ of Jägersten (1939b) and *M. longimanum* additionally have the seminal vesicle divided into a proximal narrow duct and a distal sac-like portion, unlike in *M. cirriferum*. In most members of this family, the penis on each side protrudes from the angle at the outer base of the third parapodium, but in *M. cirriferum* and a few other species (for example, *M. glabrum*, *M. fissum* and *M. plicatum*) the penial tract opens close to the body margin, with a fixed integumental tube extending from near the third parapodium to the aperture. Jägersten (1939b) stated that *M. cirriferum* is unusual in displaying a well-defined boundary between the vasa efferentia and vasa deferentia. In other species, the epithelium (or possibly connective tissue) continues to varying degrees into the former ducts (for example, lining the whole system except the follicles in *M. ‘ambiguum’*); or else no epithelial lining is found at all (for example, in *M. cuniculus* and *M. longitergum*; Eeckhaut *et al.* 1998).

Details of the male system in pharyngidean myzostomes are given individually in the family sections below. In the Pharyngidea, protrusible penes are absent and sometimes (for example, *Mycomyzostoma calcidicola*) seminal vesicles are also lacking. Compact, rather than diffuse, testes occur in many Endomyzostomatidae and also in *Stelechopus hyocrini*.

Literature on the ultrastructure of myzostomidan spermatozoa and their spermatogenesis is extensive (see Bargalló 1977; Afzelius 1983, 1984; Mattei & Marchand 1988; Eeckhaut 1995). In *Myzostoma cirriferum*, the cell body is 30 µm long and the free part of the flagellum is 70 µm long (Fig. 2.7A). The sperm cell has a flagellum, but the flagellar centriole is at the free end, which is therefore anterior. The nucleus is not bounded with a nuclear membrane, but sits within an open, myelin-like sheath (Fig. 2.7C); it contains a string of darkly staining, bead-like chromatin bodies, varying from 40 to 60 in different populations of *M. cirriferum* (Fig. 2.7A, B). Usually two rod-shaped mitochondria lie parallel to each other by the open side of the nucleus. The mitochondria (Fig. 2.7C) are surrounded on the outside by 22 to 24 microtubules (fewer in the species studied by Mattei & Marchand 1988), two of which (the ‘dorsal rods’) are attached to the plasma membrane and thus to the flagellum alongside. The flagellum has a 9x2+0 axoneme structure and, except for its most posterior end, lies outside the main body of the cell (Fig. 2.7C); it freely extends anteriorly beyond the cell body to a sharp spine derived from a pre-centriolar vesicle. The spermatozoon can swim flagellum foremost by flagellar undulations, or, more efficiently, flagellum hindmost by undulations of the cell body.

The spermatids develop within vacuoles inside host cells called spermiocysts. All sperm in the same spermiocyst are at the same stage of development. Originally the spermatid nucleus has a typical nuclear membrane, but this later opens and allows the nucleoplasm and cytoplasm to mix. The chromatin has





**Figure 2.7** Sperm cells and spermatophore of *Myzostoma* species. **A**, **B**, *Myzostoma cirriferum*: **A**, sperm cell as seen with a light microscope; **B**, diagrammatic longitudinal section of the head of a sperm cell, posterior end at top. **C**, cross-section of the head of a sperm cell of an unidentified *Myzostoma* species. **D**, spermatophore of *Myzostoma cirriferum*. **bsd**, basal disc; **cen**, centriolar end of flagellum; **cgl**, chromatin globules; **fla**, flagellum; **ft**, foot; **mct**, microtubules; **mtr**, mitochondrial rod; **mys**, myelin-like sheath; **spc**, chain of spermiocysts embedded in organic matrix. (A, after Jägersten 1934; B, after Eeckhaut 1995; C, after transmission electron micrograph by Mattei & Marchand 1987; D, after Jägersten 1939b) [I. Hallam]

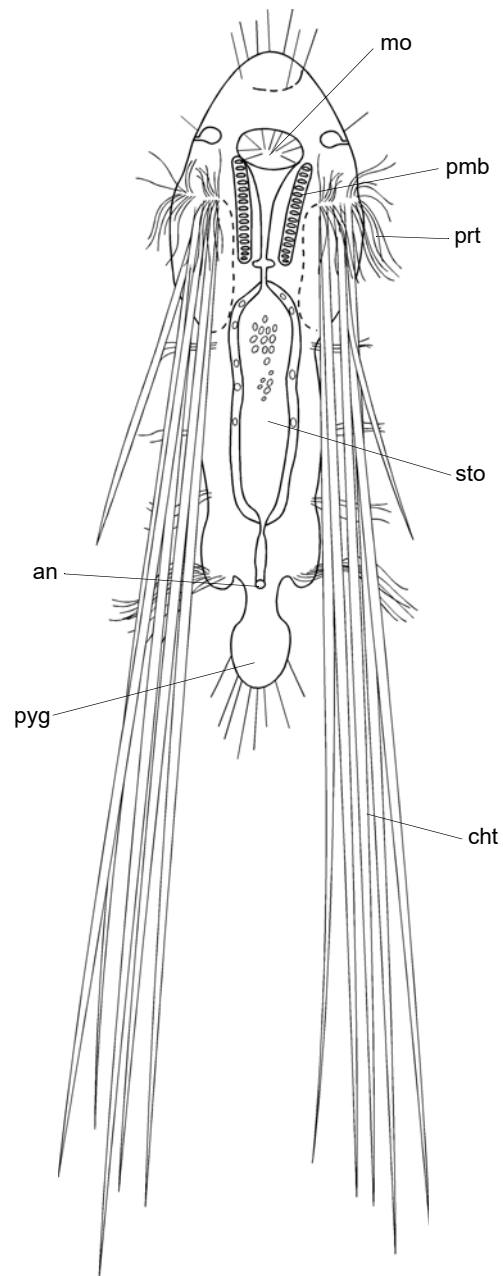
already begun condensing into small spheres at the earliest stages; the spheres get larger and more numerous and later form a row. The multilayered, myelin-like sheath is presumably derived from the Golgi apparatus. Typical small mitochondria fuse to form the rod-shaped mitochondria of the mature sperm (Fig. 2.7B). The two ‘dorsal rods’ appear against the plasma membrane before being joined by the remainder of the intracellular microtubules, which had earlier formed a manchette around the nucleus. The development of the flagellum is very peculiar. According to Mattei & Marchand (1988), the centriole and a vesicle atop it first migrate up a cytoplasmic canal away from the original posterior end of the sperm, then the canal ruptures for most of its length, leaving most of the flagellum outside the cell body, but in contact with it. The centriole continues to migrate until the anterior end of the axoneme, tipped with a vesicle-derived spine, extends well beyond the originally anterior end of the cell body (Fig. 2.7B), and the posterior end of the axoneme has been drawn up within the originally posterior end of the cell body. This explanation differs from earlier descriptions (Jägersten 1939b; Afzelius 1984), which assumed that the free part of the flagellum is always the original posterior end.

Copulation is effected hypodermically by the transfer of a spermatophore from one individual to another, a process that has been studied most thoroughly in *Myzostoma cirriferum* (Jägersten 1939b; Eeckhaut & Jangoux 1991; Eeckhaut 1995). A specimen of any size can receive a spermatophore, but only larger individuals can deposit one. Spermatophores of *M. cirriferum* are up to 0.5 mm long and each have two short arms (Fig. 2.7D); arms are absent from the spermatophores of '*M. ambiguum*' (Kato 1952) and *M. alatum* (Eeckhaut & Jangoux 1992). A spermatophore is formed within one of the seminal vesicles and is expelled through the gonopore at the end of the everted penis, thus becoming attached to the surface of the recipient worm. The body and arms of the spermatophore contain chains of spermiocysts coated by or enclosed in an extracellular matrix (Eeckhaut & Jangoux 1992); each spermiocyst consists of a large cyst cell and one to three coiled clumps of spermatozoa in vacuoles inside. The foot of the spermatophore contains chains of smaller spermiocysts with abortive germ cells; the contents of vesicles in the basal disc probably act in penetrating the recipient worm's integument. The spermio-cysts enter the worm as a large, digitate, motile syncytium, which delivers the sperm to the oocytes in the uterus, presumably by breaking through the wall of the latter. The entire copulatory process lasts at most a few hours.

The pair of ciliated ducts connecting the uterus to the intestine in most species (Figs 2.2A, C, 2.17B, 2.18, 2.19B) probably serves to expel the spent syncytium and excess gametes after fertilisation. These ducts may be completely separate or be fused at either the proximal or distal end. *Protomyzostomum polynephris* has supernumerary ducts on each side (Fig. 2.11B). In species of *Endomyzostoma*, the ducts' common pore is external near the anus, not inside the intestine (Fig. 2.14A, E). Although these ducts do not serve for excretion in the same sense as nephridia (see excretion section above), their superficial resemblance to metanephridia of many polychaetes is one factor in the prevailing interpretation of the internal spaces of the female reproductive system as a coelom (disputed by Eeckhaut 1995).

## Embryology and Development

Embryological studies have been conducted on four species of European and Japanese myzostomes. Newly spawned, fertilised eggs are no more than 50 µm in diameter; the maximum number obtained from a single female of *M. cirriferum* kept in the laboratory was close to 500 eggs (Eeckhaut & Jangoux



**Figure 2.8** Planktonic larva (late metatrochophore) of *Myzostoma glabrum*. **an**, anus; **cht**, chaetae; **mo**, mouth; **pmb**, pharyngeal muscle bulb; **prt**, prototroch; **pyg**, pygidium; **sto**, stomach. (After Jägersten 1939a) [I. Hallam]

1993b). The egg membrane becomes the larval cuticle, so no hatching occurs. Brooding of the eggs and early larvae occurs only in some species of *Endomyzostoma*, in which the upturned lateral edges of the body form a dorsal brood chamber.

The following sequence of events follows spawning in a species of *Myzostoma* (misidentified as *M. ambiguum*) (Kato 1952) and in *M. cirriferum* (Eeckhaut & Jangoux 1993b; Eeckhaut 1995). The maturation divisions produce two polar bodies. A polar lobe forms at the vegetal pole and fuses with the CD blastomere after the first cleavage. A second polar lobe forms and fuses with the D blastomere after the second cleavage. A third polar lobe forms, blastomere D divides, blastomeres A–C divide (a spiral division) and the polar lobe fuses with blastomere 1D (the last two stages are reversed in '*M. ambiguum*').

From this point on, four larval stages are distinguishable in *M. cirriferum*: (1) the spherical protrochophore with a prototroch and an apical tuft; (2) the pyriform trochophore; (3) the pyriform metatrochophore (Fig. 2.8) with two tufts of four denticulate chaetae, a ventral mouth just anterior to the prototroch, the prototroch divided into tufts, and an eventually retractile post-anal pygidium with a ciliary band and terminal cilia, and; (4) the metamorphic larva that loses the cilia and chaetae. The larvae reach a final length of 100–120  $\mu\text{m}$ , excluding the chaetae. This entire process takes about 5 days in the plankton. Basically, the same series of larval stages occurs in *M. glabrum*, but with usually six chaetae per tuft in the metatrochophore (Jägersten 1939a, as *M. parasiticum*), and also in *M. alatum* (Eeckhaut & Jangoux 1992). '*Myzostoma ambiguum*' differs primarily in having several additional ciliary bands, and it takes at least 8 days to reach the late metatrochophore stage.

The metatrochophores of *M. cirriferum* are captured by the tube feet of their eventual host crinoid as potential food particles, and the denticulate chaetae catch onto the host. If too young, the larva is rejected or occasionally swallowed. The metamorphosing worms become embedded in temporary cysts in the walls of the ambulacral grooves of the host's pinnules, where they remain through the young male stage. The cysts are formed from fused tube feet and ambulacral lappets.

Following metamorphosis (Eeckhaut & Jangoux 1993b), the smallest, barrel-shaped juveniles of *M. cirriferum* have a non-retractile proboscis and only the third pair of parapodia. The remaining four pairs of parapodia, the lateral organs and the anus appear later. The proboscis gradually retracts into a pocket in the anterior end of the trunk and the buccal papillae appear. At the same time, the animal becomes wider and flatter, and has developed marginal cirri and penes by the time it reaches the male stage. Previously, similar observations were made on this species (Jägersten 1940a) and on the larvae of '*M. ambiguum*' (Kato 1952; including a description of the elaboration of the gut diverticula) and the post-metamorphic stages of *M. divisor* (Grygier 1989).

## NATURAL HISTORY

### Life History

Aside from descriptions of early ontogeny, detailed studies of life history have been made only for *Myzostoma cirriferum* infesting the crinoid *Antedon bifida* in Europe. In Loch Creran, Scotland (Woodham 1992), juveniles begin to appear on the host in October, are numerically dominant from November to April and are mostly replaced by adults from June. In the summer, 100% of the hosts are infested with up to 3200 adult myzostomes each. Infestation rates and abundance drop off sharply in the late autumn, to about 50% and less than 10 per host. The life span is inferred to be less than a year, limited by post-spawning mortality, and only the latest spawned individuals overwinter as adults. At Roscoff, France (Eeckhaut 1995; Eeckhaut & Jangoux 1997), the newly settled juveniles and young males remain encysted in the host's ambulacral integument for no more than 2 months; the older males and hermaphrodites then live freely as ectocommensals for 4–5 months. Reproductive activity is constant through the year. The total life span is about 190 days. The population increases by additional recruitment from mid-January to March, to a maximum of about 71 worms per host. Then the numbers decline, possibly due to predation by facultatively commensal amphipods, but remain steady at a lower level through the summer to the beginning of winter.



## Ecology

Myzostomes are usually regarded as obligate commensals, semiparasites or parasites of echinoderms, especially of crinoids. They have, however, also been isolated from a Japanese hexactinellid sponge (Okada 1920) and found as endoparasites of a Puerto Rican antipatharian coral (Goenaga 1977); the identity of the latter worms as myzostomes has been verified (M.J. Grygier personal observation).

Most species of Myzostomatidae are associated with crinoids and belong to at least three ecological types: (1) vagile forms, which move rapidly and freely over the host (see for example, Fig. 2.1A–C); (2) external sessile species, which include round forms that usually sit on the disc (see for example, Fig. 2.1F) and elongate forms that are usually attached to the arms or pinnules (see for example, Fig. 2.1K, L); and (3) a few species that live in skeletal crypts, soft tissue cysts, pinnule galls (see for example, Fig. 2.1H) or the mouth (see for example, Fig. 2.1J). In addition to these, about six species of *Myzostoma* are ectocommensals of various kinds of ophiuroids.

Species of *Endomyzostoma* and *Contramyzostoma* all inhabit cysts or galls on the disc or arms of their host crinoids (Fig. 2.13A, C). *Mycomyzostoma calcidicola* lives in a spherical cyst of the stalk of a crinoid. *Asteriomyzostomum* species are endoparasites of asteroids, whereas species of *Asteromyzostomum* are ectoparasites of other asteroids. *Pulvinomyzostomum pulvinar* lives in the oesophagus and stomach of its host crinoid. Species of *Mesomyzostoma* and *Protomyzostomum* are also endoparasites, the former in the gonads of crinoids, the latter in the gonads or in external cysts of basket stars or in the coelom of other ophiuroids. Forms, as yet undescribed, inhabit the dorsal coelom of the Antarctic ophiuroid *Ophionotus victoriae* (Bartsch & Faubel 1995) and the connective tissue of the calyx of a comatulid crinoid (Heinzeller, Aschauer, Lange & Welsch 1995).

Woodham (1992) summarised the infestation rates and degrees of infestation for some European species. Eeckhaut & Jangoux (1993b), comparing their own data with those of Platel (1962), noted that the morphology and behaviour of the larvae and juveniles of *Myzostoma cirriferum* favour the maintenance of very high or universal infestation rates and high numbers of myzostomes per host in environments where the host crinoid occurs more densely. The very high values obtained by Woodham (1992), also in a dense crinoid population, support this idea.

In their population study of crinoid symbionts on the Great Barrier Reef, Fabricius & Dale (1993) grouped all species of myzostomes together; about 20% of the symbionts were myzostomes, found on 15 of the 43 crinoid species examined. Stout and nocturnal crinoids, and members of the Comasteridae, were more likely to have symbionts of all kinds than other comatulids. Previously, Grygier (1990) had noted that comasterids were a dominant host family for Indo-Pacific myzostomes and that one species could host a diverse assortment of worms (for example, 10 species of myzostomes on *Comanthus parvicirrus*). Based on the author's present study, the proportion of comasterid host crinoids in a given region of Australia is about 40–60% of the total hosts, and higher in tropical Queensland than elsewhere (Table 2.1).

Fabricius & Dale (1993) noted that comasterids cannot cover their ambulacral grooves and, since myzostomes feed upon particles carried along these grooves, easy food accessibility in this family may favour myzostome infestation. In their study, the greatest numbers of individual myzostomes were found on *Comatula purpurea* (but on not more than 20% of the specimens), *Himerometra crassipinna* and *H. magnipinna*. The highest density followed the crinoids' own density pattern: highest on mid-shelf reefs, lower near the edge of the continental shelf and in the lagoon. Regarding co-occurrence with other non-host-specific crinoid associates, there were more frequent associations of myzostomes with polynoid polychaetes and three species of the pontonine shrimp *Periclimenes* than would be expected by chance, and less frequent associations with the isopod *Cartetolana integra* and the alpheid shrimp *Synalpheus stimpsoni*.

Data on host crinoids of Australian myzostomes are summarised in Table 2.1. In all, 54 species have been implicated as hosts. Host species are more diverse in the tropical regions of Queensland and Western Australia than elsewhere. These two regions have 15 host species in common (of 44 total), four of which are also hosts in the Northern Territory: *Comanthus briareus*, *C. wahlbergi*, *Comatella stelligera*, *Lamprometra palmata*. Together, these four species host 19 or 20 species of myzostomes, just three or four of which are common to all three regions, at most seven being shared by at least two regions.

**Table 2.1** Geographic distribution and host apportionment of Australian Myzostomida, based on literature and on the author's data from museum surveys (Grygier 1990, and subsequent surveys of additional collections). All values are given as numbers of purported species.

Regions <sup>1</sup>	SE	QLD	NT	NW	H-A	SW	TS
All Myzostomida	≈10	≈54	≈15	≈35	≈6	3	≈3
Endomyzostomatidae							
<i>Endomyzostoma</i>	1	1	–	3–4	–	–	–
Myzostomatidae							
<i>Notopharyngoides</i> <sup>2</sup>	–	1	1	–	–	–	–
<i>Hypomyzostoma</i> <sup>3</sup>	1?	≈8	4	≈7	–	–	–
<i>Myzostoma</i>	≈8	≈43	≈10	≈24	≈6	3	≈3
Body typical, thin <sup>4</sup>	4	13	3	7	3	3	2
Body typical, thick <sup>5</sup>	–	9	1	4	–	–	–
With supernumerary cirri <sup>6</sup>	1	4	1	2	1	–	–
With caudal process(es) <sup>7</sup>	1	9	3	5	–	–	–
Other <sup>8</sup>	2	8	2	5	2	–	1
Identified species	≈4	≈24	≈6	≈16	3	1	1
Total host crinoid species	≥10	≥35	≥10	≥27	5	3	3–4
Comasterid species	4	21	4	13	3	2	2
Myzostome species per host species	1–2	1–6	1–2	1–4	1–2	1	1
Myzostome species with 3 or more hosts	–	7 <sup>9</sup>	–	1 <sup>10</sup>	–	–	–
Hosts with 3 or more myzostome species	–	7 <sup>11</sup>	–	–	–	–	–

1. **SE**, Fraser Island, Queensland, to Spencer Gulf, South Australia, and Tasmania; **QLD**, Great Barrier Reef and Torres Straits Islands; **NT**, Northern Territory; **NW**, Western Australia north of Shark Bay, including Indian Ocean banks; **H-A**, Houtman Abrolhos and nearby coast; **SW**, Perth to Recherche Archipelago; **TS**, Lord Howe Island and Elizabeth and Middleton Reefs, Tasman Sea.

2. = *Myzostoma platypus* species-group (Grygier 1990); type: *M. ijimai* (see Fig. 2.1J)

3. = *Myzostoma crosslandi* species-group (Grygier 1990); type: *M. folium* (see Fig. 2.1K, L).

4. round or oval, disc- or shield-shaped, thin-bodied species with 10 pairs of marginal cirri; for example, *M. ambiguum*, *M. stochoeides* (see Fig. 2.1A, B).

5. dome- or puck-shaped bodies with rudimentary or no marginal cirri; for example, *M. echinus*, *M. horologium* (see Fig. 2.1D).

6. species with more than 20 marginal cirri that are clearly differentiated from the body proper; for example, *M. polycyclus* (see Fig. 2.1C, F).

7. species with one or more posterior lobes of the body, bearing cirri or not, into which the internal organs penetrate; for example, *M. fissum*, *M. intermedium* (see Fig. 2.1I).

8. species with other unusual forms or ornamentation (for example, *M. attenuatum*, *M. plicatum*, *M. chelonoides*) (see Fig. 2.1G).

9. *M. mortenseni*, *M. coriaceum*, *M. plicatum*, *M. polycyclus*, *Hypomyzostoma* species (= *M.* species 4 of Grygier 1988), two unidentified or undescribed species.

10. *Hypomyzostoma nanseni*.

11. *Comanthus parvicirrus*, *C. timorensis* (probably synonymous with the former; if so, Australian *C. parvicirrus* hosts nine myzostome species in all, the highest on any single host species), *C. wahlbergi*, *Comanthina schlegelii*, *Comatella stelligera*, *Stephanometra oxyacantha*, *Lamprometra palmata*.

Host specificity for Indo-West Pacific myzostomes, including Australian species, may be species-specific, family-specific, or non-specific (Grygier 1990). In the Australian fauna, few species of myzostomes infest as many as three or four host species in a given geographic region; conversely, few host species are infested by three or more myzostome species (see Table 2.1). The usual number of host or symbiont species for a myzostome or crinoid, respectively, is one or two.

Several endoparasites of myzostomes have been described in the older literature (see review by Jägersten 1941). These include: encysted larvae of a cestode, *Taenia myzostoma*, from *Myzostoma graffi*, and a trematode, *Distoma myzostomatis*, from *Notopharyngoides platypus* (several authors have mentioned undescribed trematode larvae from other myzostome hosts); a supposed amoeba, *Amoeba myzostomatis*, from *M. glabrum* (true nature unclear), and; a fecampiid turbellarian, *Glanduloderma myzostomatis*, from *M. brevilobatum* and, presumably, *M. longimanum*. More recently, Grygier (1989, 1992) reported other unidentified endoparasitic helminths from *M. attenuatum*, *M. lobatum* and *M. bocki*, and so did Eeckhaut *et al.* (1998), from *M. longitergum*, *M. capitocutis* and *M. stochoeides*. Such parasites are not uncommon in museum collections examined by the author. Indications of predator-induced injury, such as asymmetries in body outline and in the number of parapodia or lateral organs, are also common.

## Behaviour

Some species of Myzostomatidae move freely upon their host crinoids. Their marginal cirri are contractile, the lateral organs and proboscis are protrusible, and the parapodia are used for locomotion in any direction. Feeding is accomplished by protruding the proboscis into the host's ambulacral groove and ingesting entrained food particles. Studies on sexual behaviour have been conducted only on *Myzostoma cirriferum* (Eeckhaut 1995), as recounted in the reproduction section above. No ethological studies are available concerning transfer of myzostomes between crinoids, or territoriality upon hosts. Although the larvae of *M. cirriferum* are captured passively and do not seek out their hosts, they do show a preference for grabbing with their parapodia at long, thin substrata, such as crinoid arms or (even) spaghetti of similar dimensions (Eeckhaut 1995). In sessile species, such as *M. glabrum* and *M. alatum*, which are permanently attached to the host's disc, it is common for a protandric male individual to sit on the dorsum of a larger hermaphrodite (Graff 1877; Eeckhaut & Jangoux 1992).

## Economic Significance

Myzostomes have no commercial value, and none is known to infest any pest sea star.

## BIOGEOGRAPHY AND PHYLOGENY

### Distribution

Myzostomes occur almost worldwide in marine environments, from the intertidal to depths of over 3000 m. Their greatest diversity naturally corresponds to regions of greatest crinoid diversity, namely the tropical Indo-West Pacific and, to a considerably lesser degree, the tropical Western Atlantic. In temperate waters, they are probably most diverse in Japan, perhaps because of the influence of the warm Kuroshio Current in supporting a high diversity of crinoids. In deeper waters of the western Pacific, the fauna of myzostomes on stalked crinoids is relatively rich. Regions of low crinoid diversity may nonetheless be home to a relatively diverse assortment of myzostomes (north-western Europe) or to only a few species (California). None is yet known from the eastern tropical and south-eastern Pacific.

Grygier, in 1990, indicated that the myzostome fauna of Queensland seemed to be part of a widespread Tropical Indo-West Pacific fauna, whereas that of the Northern Territory seemed to be different. At the time, the Western Australian fauna was almost unknown, and only one species was noted from the south-eastern coast. Since then, additional collections (principally those of the Australian Museum, the Western Australian Museum and the Museum of Comparative Zoology) have been examined and an up-to-date summary of the distribution of Myzostomatidae and Endomyzostomatidae around Australia is presented in Table 2.1. About two thirds of the species are of uncertain identity or new. Of the 10 species of *Myzostoma* from the Northern Territory, six are known within Australia only from the Territory; the other four also occur in both Queensland and Western Australia. The latter two regions alone, with a total count of 54 species of *Myzostoma*, share an additional nine species, thus having about 13 in common. Given such a degree of faunistic overlap, it appears that all myzostomes of tropical Australia belong, after all, to the Indo-West Pacific biogeographical province.

In comparison with the tropical regions, relatively few species are recorded for the temperate coasts of Australia (Table 2.1). Some of these are tropical outliers and one is amphitropical (*M. bocki* is known from Perth and Japan: Grygier 1992), but the south-east in particular has a different and as yet undescribed fauna.

A few myzostome records from islands and reefs in the Tasman Sea constitute the first positive records from any Australian External Territory (Table 2.1).

## Affinities with Other Groups

Early assignments of myzostomes to the Trematoda, Crustacea or Stelehopoda (with Tardigrada and Penta-stomida) are no longer considered seriously. Fedotov (1929, 1938) regarded the Myzostomida as true annelids with affinities to polychaetes and archiannelids, whereas placement as a class in Annelida was adopted by Kato (1952), on the basis of ontogenetic evidence. Consequently, authors of textbooks and encyclopedias typically have placed the group as an order of Polychaeta or class of Annelida, citing as evidence the parapodia with support rods and hooks (similar to polychaete parapodia with acicula and chaetae), the trochophore-type larva and the supposed metamerism. A position within the Polychaeta among the phyllodocidan families is also favoured in a cladistic analysis of polychaetes by Rouse & Fauchald (1997). However, several alternative hypotheses are still current and being debated, and no biochemical systematic studies of nucleic acid sequences have been published.

Jägersten (1940a) combined the Myzostomida and Annelida as two classes within a coelomate, protostome group called Chaetophora; the putative defining characters, most of which are not exclusive, include parapodial chaetae, a ventral nerve cord, a hindgut and anus, metanephridia and trochophore larvae.

Wagin (1976, 1979) recognised three superphyla within the Spiralia, of which one, the Trochozoa Oligomera, included molluscs, myzostomes and dinophilids; these all lack so-called primary heteronomy of the metameres in ontogeny. Myzostomes were regarded as more primitive than molluscs. This is probably a paraphyletic classification, because one of the other superphyla, the Trochozoa Polymera, may have originated from among the Trochozoa Oligomera, according to Wagin.

Mattei & Marchand (1987) noted numerous ultrastructural similarities between the spermatozoa of Myzostomida and Acanthocephala (spiny-headed worms). They regarded these two taxa as sister groups linked by synapomorphic sperm and placed them in a single phylum, the Procoelomata.

Eeckhaut (1995) compared myzostomes to turbellarians and polychaetes. The only synapomorphy shared by myzostomes and polychaetes could be the cirri; the dorsal and ventral parapodial cirri of polychaetes might correspond to the marginal cirri and medial parapodial cirri of myzostomes, but homologies of these various structures have yet to be proven. Eeckhaut denied the presence of both metameres and a coelom in myzostomes. He thus considered the Myzostomida as an acoelomate phylum, not closely related to polychaetes, but with advanced features (such as the trochophore larva and a myo-epidermis) that set them apart from flatworms.

Haszprunar (1996), in a cladistic study aimed at establishing the relations of the Mollusca, estimated that the Myzostomida arose between the molluscan lineage and a eucoelomate group including sipunculans, echiurans and ordinary annelids, but he cautioned that this result was probably not very stable. A similar result, but with the sipunculans removed to the molluscan lineage, was obtained in a cladistic study of the entire Metazoa (Zrzavý *et al.* 1998).

## Affinities Within the Taxon

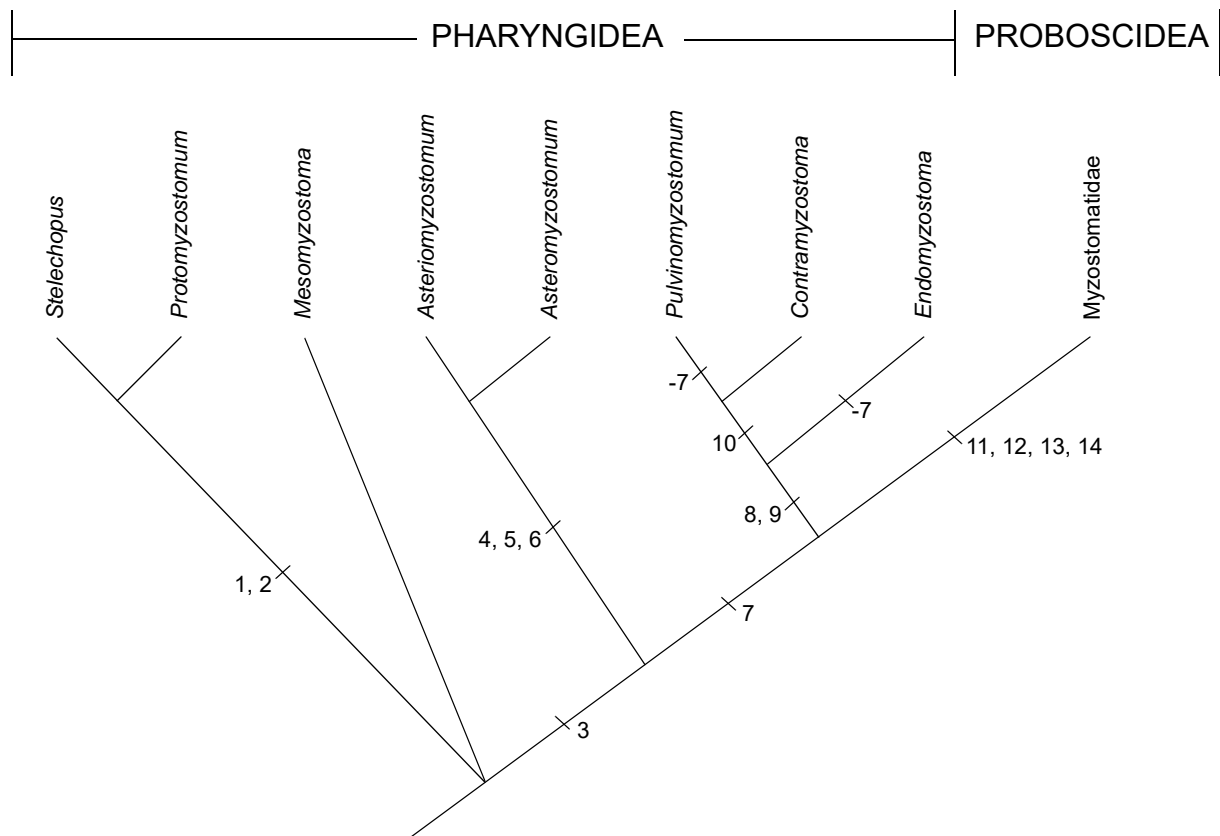
Jägersten (1940a) published a phylogenetic tree for the genera of Myzostomida (modified here as Fig. 2.9). It shows the purportedly advanced, or at least characteristic, features distal to each branch point or node. Homoplasy is evident, and the order Pharyngidea is paraphyletic with respect to the Proboscidea. *Protomyzostomum* and *Stelechopus* are separated from the remaining genera on the basis of having several, rather than three, pairs of midgut diverticula (both conditions being apomorphic compared to an unbranched gut in a hypothetical ancestor), and the presence of sunken epidermal nuclei.

*Mesomyzostoma* branches off separately in Jägersten's (1940a) tree, but no synapomorphy links it to the remaining genera; thus, Figure 2.9 shows it as part of a basal polytomy. The habitat within the host's reproductive system can serve as an autapomorphy for this genus; no particular unique and advanced



morphological character was noted by Jägersten. The remaining group of genera is characterised by having a shortened ventral nerve cord. *Asteriomyzostomum* branched off next in Jägersten's (1940a) tree, also without supporting autapomorphies (though again, habitat, namely ectoparasitism on sea-stars, may serve). *Asteriomyzostomum* can be accommodated in the vicinity, and perhaps as the sister group of *Asteriomyzostomum* (Fig. 2.9), on the basis of the reduced number of midgut diverticula (one or two pairs), the laterally broadened body and the common host class.

*Pulvinomyzostomum* and *Endomyzostoma* (synonym: *Cystimyza*) are related, according to Jägersten (1940a), by both having a pharynx-derived proboscis. We can add that the branches of the uterus surround the gut diverticula in these two genera (also true, convergently, in *Protomyzostomum polynephris*). The same is true for *Contramyzostoma*, which formally remains *incertae sedis* because of the nature of its proboscis is not known. However, if it does belong to the clade here under discussion, the U-shaped gut with dorsal mouth and anus suggests a close relationship to *Pulvinomyzostomum* (Fig. 2.9). This potential three-genus clade is joined to the final branch, the order Proboscidea (that is, *Myzostoma* and allies), by the presence of marginal cirri, which are presumed to have been lost secondarily in *Pulvinomyzostomum* and some species of *Endomyzostoma*. The protrusible penis of the Proboscidea is interpreted here as an apomorphy, not a plesiomorphy lost independently four times in all the other genera, as in Jägersten's (1940a) scheme.



**Figure 2.9** An estimate of phylogenetic relationships among the genera of Myzostomida, based in part upon characters discussed by Jägersten (1940a). The order Pharyngidea is paraphyletic. Putative apomorphies supporting this tree morphology are: **1**, more than three pairs of gut diverticula; **2**, epidermis a syncytium with its nuclei sunken below the muscle layer; **3**, ventral nerve cord shortened antero-posteriorly; **4**, gut diverticula reduced to one or two pairs; **5**, body expanded laterally (but by different means in the two genera); **6**, parasites of Asterozoa; **7**, marginal cirri present (-7, represents sporadic independent losses); **8**, large proboscis derived as protruded pharynx (homology not confirmed for *Contramyzostoma*); **9**, uterine branches enclosing gut diverticula (convergently so in one species of *Protomyzostomum*); **10**, mouth and anus both dorsal and gut U-shaped; **11**, pair of protrusible penes; **12**, well-developed lobiform parapodia with muscoli centrales forming mid-ventral muscle mass; **13**, large proboscis derived ontogenetically from entire anterior end of juvenile's body, and; **14**, prebulbar nerve ring.

[M. Grygiel]

## Fossil Record

Deformities on fossil crinoids and occasionally other fossil echinoderms have been attributed to myzostomes by many authors since the first observations by Graff (1885a); a heterogeneous form genus, *Myzostomites*, has been proposed for some of them. The great majority of supposed myzostome traces from fossil crinoids involve the columns of stalked crinoids; they are most often seen as barrel-shaped swellings that sometimes have slits, apertures or internal hollows. Franzén (1974) noted that almost none of these fossils resembles the impressions left by activity of extant myzostomes.

All myzostome-induced deformities in Recent crinoids concern the arms, pinnules or disc, except for the cysts of *Mycomyzostoma calcidicola*, which involve the column and cirri of *Saracrinus nobilis* (Eeckhaut 1998). Several authors (see Meyer & Ausich 1983) have, therefore, recognised only certain arm deformities, none older than Pennsylvanian, as fossil traces of cysticolous or gallicolous myzostomes (see for example, Welch 1976, text-fig. 2). However, Eeckhaut (1998) believes that the discovery of *M. calcidicola* ought to revive the debate about older Palaeozoic column deformities.

## CLASSIFICATION

The classification outlined in Table 2.2 and adopted here is based on that of Jägersten (1940a) with modifications to reflect the current state of knowledge. Six of the eight families, marked with an asterisk, are not known from Australian waters. However, members of the Protomyzostomatidae, Asteromyzostomatidae and Pulvinomyzostomatidae have been recorded from Antarctic waters and are likely to occur in the Australian Antarctic Territory.

For the group as a whole, Graff's (1877) name Myzostomida has precedence over Perrier's (1897) name Philocrinida. Jägersten (1940a) proposed a division into two orders: Proboscidea and Pharyngidea. Proboscidea includes one family, Myzostomatidae, with a single genus *Myzostoma*. The Pharyngidea comprise six families, each with one genus: Stelechopodidae (*Stelechopus*), Protomyzostomatidae (*Protomyzostomum*), Mesomyzostomatidae (*Mesomyzostoma*), Cystimyzo-stomatidae (*Cystimyza*; see nomenclatural remarks below), Asteriomyzostomatidae (*Asteriomyzostomum*) and Pulvinomyzostomatidae (*Pulvinomyzostomum*). Of these seven families, only the Myzostomatidae and Cystimyzo-stomatidae (as Endomyzostomatidae here, see below) are known to occur in Australian waters.

Wagin (1954) proposed a new genus, *Asteromyzostomum*, in a new subfamily, outside the context of Jägersten's classification. He considered it to be derived from a *Myzostoma*-like ancestor. However, it lacks the characteristic *Myzostoma* proboscis, which is the defining character of the order Proboscidea. Accordingly, Wagin's subfamily is elevated here provisionally to family Asteromyzostomatidae in the Pharyngidea. Eeckhaut (1995) placed the genus in the Asteriomyzostomatidae with no explanation; Figure 2.9 shows that there might be some justification. *Asteromyzostomum* is not known from Australia.

Species-groups like those diagnosed by Grygier (1990) within the heterogeneous genus *Myzostoma* were implicit already in Graff's (1884b) *Challenger* Expedition monograph. Several available genera have been proposed by Perrier (1897) and Uchida (1992) for subsets of *Myzostoma sensu lato*: *Cercomyzostoma*, *Polymyzostoma*, *Hypomyzostoma* (= *M. crosslandi*-group; type: *M. folium*), *Notopharyngoides* (= *M. platypus*-group; type: *M. ijimai*); the last two have been accepted by Eeckhaut *et al.* (1998) and Grygier & Nomura (1998), and are thus adopted here.

**Table 2.2** Classification of the extant Myzostomida. Families marked with an asterisk (\*) have not been recorded from Australian waters. †See Affinities with Other Groups for discussion concerning the position and rank of Myzostomida.

---

### Class MYZOSTOMIDA†

#### Order PROBOSCIDEA

Family Myzostomatidae

#### Order PHARYNGIDEA

Family Stelechopodidae\*

Family Protomyzostomatidae\*

Family Mesomyzostomatidae\*

Family Endomyzostomatidae

Family Asteriomyzostomatidae\*

Family Asteromyzostomatidae\*

Family Pulvinomyzostomatidae\*

---

Perrier (1897) proposed two additional genera, *Endomyzostoma* and *Hetero-myzostoma*, for species subsequently included by Jägersten (1940a) in *Cystimyzostomum*, a junior synonym and thus invalid. Grygier in Eeckhaut (1998) recognised *Endomyzostoma* (type: *M. pentacrini*) as the valid name of this genus; elevated to family level, Perrier's (1897) subfamily, now as Endomyzostomatidae, thus has priority over Cystimyzostomatidae and is to be used instead.

Eeckhaut & Jangoux (1995) placed their new genus *Contramyzostoma* in the Cystimyzostomatidae (that is, Endomyzostomatidae), but this assignment was based on the relation with the host, not on morphology, and may not withstand closer scrutiny. Another new genus, *Mycomyzostoma*, was described in the same family by Eeckhaut (1998), and possibly yet another (family assignment uncertain) has been discovered by Heinzeller *et al.* (1995). None of these new forms is known from Australia, although *Saracrinus nobilis*, the host of *Mycomyzostoma calcidicola*, occurs off the north-western coast.

### Key to the orders and families of Myzostomida

- 1 (a) Marginal cirri usually present in ten or more pairs (Figs 2.1A–C, E, F, 2.2B), but sometimes body margin even, irregular or scalloped (Fig. 2.1G, I–L). Parapodia usually well developed (Fig. 2.3B; 2.4A). Proboscis present, movable and retractable (Figs 2.1D, 2.2A, B). Prebulbar nerve ring present anterior to pharyngeal muscle bulb; connected to, but not incorporating cerebral ganglia (Fig. 2.6). Diverticula of female reproductive system generally located dorsal to and following the midgut diverticula (Fig. 2.2C). Protrusible penis on each side lateral to third parapodium (Fig. 2.1B). Mostly living externally on crinoids or ophiuroids as adults ..... Order Proboscidea, Myzostomatidae
- (b) Marginal cirri absent or fewer than 10 pairs. Parapodia small to vestigial. Proboscis present or absent. Prebulbar nerve ring absent or represented by plexus. Cavities of female reproductive system usually broadened, sometimes enclosing midgut diverticula (Fig. 2.14B). Penes absent or rudimentary. Adults mostly encysted (Fig. 2.13A, C), gallicolous, inquiline or endoparasitic ..... Order Pharyngidea, 2
- 2 (a) Body margins upturned dorsally in functional female or hermaphrodite stage (Figs 2.14B, C, 2.19A). Proboscis present (Figs 2.13B, 2.19). Marginal cirri present in some. Midgut diverticula at least in part passing through or contained within uterine diverticula (Fig. 2.14B). Testes almost always compact (Fig. 2.14D) ..... 3
- (b) Body margins not upturned (Figs 2.10; 2.11A, 2.12), or, if so, also thrown into complex folds (Figs 2.1N, 2.18). Proboscis absent. Marginal cirri absent. Stomach and midgut diverticula ventral to uterus and its diverticula [except *Protomyzostomum polynephris* as in 2(a)]. Testes diffuse (Fig. 2.11A) or as large, open sacs ..... 4
- 3 (a) Mouth and anus both dorsal (Fig. 2.19). Lateral organs present, 10 pairs (Fig. 2.19). Ovaries found dorsal to gut. Living within oesophagus and stomach of crinoids ..... Pulvinomyzostomatidae†
- (b) Mouth and anus both terminal (Fig. 2.14A). Lateral organs absent, or four pairs. Ovaries found ventral to gut (Fig. 2.14B, C). Living in cysts or galls on crinoids (Fig. 2.13A, C) ..... Endomyzostomatidae†† (synonym: Cystimyzostomatidae)
- 4 (a) Body longer than wide. Parapodia positioned more or less along body margins (Figs 2.11A, 2.12). Mostly endoparasites of crinoids or ophiuroids ..... 5
- (b) Body wider than long (Figs 2.1N, 2.17A, 2.18). Parapodia found ventrally, close to but not along margins. Parasites of asteroids ..... 7
- 5 (a) Lateral organs absent. Epidermis of discrete cells. Two pairs of uniserially branched midgut diverticula. Ventral nerve cord running whole length of body. Endoparasites of crinoid reproductive system (Fig. 2.12) ..... Mesomyzostomatidae
- (b) Lateral organs present. Epidermis a syncytium with nuclei sunken below integumental muscle layer. Stomach with three or more pairs of diverticula (Fig. 2.11A) or as large, open sac (Fig. 2.10A). Ventral nerve cord not longer than one-half body length (Fig. 2.11A) ..... 6

- 6 (a) Anus not protruded. Parapodia slightly protruding with ring-like cuticular thickenings. Two pairs of lateral organs far anteriorly and far posteriorly. Midgut and uterus as large, open sacs; oviduct and utero-intestinal ducts absent. Associates of deep-sea stalked crinoids. (Fig. 2.10A, B) .....Stelechopodidae
- (b) Anus protruded on conical process. Parapodia not protruding, sometimes found in indentations of body margin. Five pairs of lateral organs found dorsally, more or less opposite parapodia. Midgut with numerous lateral diverticula which sometimes anastomose. Oviduct and at least one pair of utero-intestinal ducts present. Endoparasites or cysticoles of basket stars and brittle stars (Ophiuroidea) (Fig. 2.11A, B) ..... Protomyzostomatidae
- 7 (a) Body flat and oval with simple margin. Mouth ventral and anus dorsal. Parapodia arranged in oval. Four pairs of lateral organs alternating with parapodia; one extra medial posterior lateral organ sometimes present. Male genital openings lateral. Endoparasites. (Fig. 2.17A, B) ..... Asteriomyzostomatidae
- (b) Body fungus-like, posterior margin thrown into complicated lobular folds that bear many supernumerary lateral organs. Mouth and anus terminal, former surrounded by circum-oral tentacles. Parapodia located along anterior margin. Male genital openings on anterior margin. Ectoparasites. (Figs 2.1N, Fig. 2.18)..... Asteromyzostomatidae
- † *Contramyzostoma* (Fig. 2.15), assigned to the Cystiomyzostomatidae by Eeckhaut & Jangoux (1995), probably has affinities to both Pulvinomyzostomatidae and Endomyzostomatidae (see Fig. 2.9) and is considered *incertae sedis* herein.
- †† *Mycomyzostoma* (Fig. 2.16), assigned to the Endomyzostomatidae by Eeckhaut (1998), is morphologically so simplified as to defy family assignment; it is considered *incertae sedis* herein.

## Order PROBOSCIDEA

Members of the Proboscidea are distinguished by the presence of a movable and protrusible proboscis in which a prebulbar nerve ring is present; the peribulbar nerve ring, when present, is incomplete. The proboscis is derived ontogenetically from the anterior part of the juvenile's body; thus, the salivary glands empty into the anterior end of the pharynx or onto the tip of the proboscis. The parapodia are usually well developed, sometimes each with a medial cirrus. Ten or more pairs of marginal cirri are usually present, but by no means universal. The uterine diverticula follow dorsally along the midgut diverticula. A protrusible penis is present on each side of the body.

The Proboscidea comprises the single family Myzostomatidae.

## Family Myzostomatidae

The Myzostomatidae are a large family of commensal or semi-parasitic marine worms (Pls. 10.1–10.4). They mostly live externally on crinoids, but a few live in galls on crinoids or externally on ophiuroids. The distinguishing features of the family are those of the order.

The family name was originally proposed as Myzostomidae, an 'incorrect' spelling that has been widely used. However, from 1989 the nomenclaturally correct spelling Myzostomatidae has been used consistently by the author. The grammatical root for the formation of the family name based on *Myzostoma* is 'Myzostomat-', not 'Myzostom-', for it is derived from '*stomatos*', the genitive form of the Greek word '*stoma*'. The other family names used in this chapter similarly represent corrections of original misspellings.

The family comprises several nominal genera: *Myzostoma*, *Hypomyzostoma* and *Notopharyngoides* are recognised here. The principal genus, *Myzostoma* (junior synonyms *Myzostomum* and *Cyclocirra*), includes about 100 validly described species; its type, *M. cirriferum*, is the best known and studied of all myzostome species. *Myzostoma* comprises a heterogeneous collection of species and will probably become more restricted as well-defined subsets are removed as distinct genera; Grygier (1990) has briefly defined unnamed species-groups. Recognition seems premature for some of the genera proposed by Perrier (1897), for example *Cercomyzostoma* for species with caudal processes and *Polymyzostoma*



for those with more than 20 marginal cirri. Fishelson (1974) used a *nomen nudum*, *Eumyzostomum*, for specimens identified by V.L. Wagin (L. Fishelson personal communication); no published work by Wagin defining the genus has been found.

The Australian myzostomatid fauna is very diverse and includes representatives of all three genera (see Table 2.1). About 71 species of *Myzostoma* are recognised from Australia by the author, although only about 24 can be identified with certainty. Most live in the tropical regions of Australia; 14 have been found in two or more of the six tabulated geographic regions (Table 2.1). These 71 purported species can be grouped by body form: typical and thin-bodied (23 species), typical and thick-bodied (18), multi-cirrate (5), having one or more caudal processes (12), and other (13). In addition, three or four species of *Myzostoma* occur on a similar number of comatulids at Lord Howe Island and the Elizabeth and Middleton Reefs in the Tasman Sea (Table 2.1). Three Antarctic species, *M. antarcticum* and *M. divisor*, from comatulid crinoids, and *M. gerlachei* from an ophiuroid, have not yet been reported from the Australian Antarctic Territory, but are likely to occur there. Only one species of *Notopharyngoides*, *N. aruensis*, has been reported from Australian waters; it lives on an unidentified host in the Northern Territory and on *Stephanometra oxyacantha* in Queensland. Some 15 species of *Hypomyzostoma* have been noted by the author, possibly an over-estimate due to the abundance of transversely banded or ridged forms similar to *H. fasciatum* and *H. dodecaphalcis*; almost all are tropical.

The morphology of *Myzostoma* species (as represented mostly by *M. cirriferum*) is covered extensively above in the general introduction to the Myzostomida; this section briefly characterises the other two genera and describes the range of morphological variation within *Myzostoma*.

The genus *Notopharyngoides* has three described species from the Indo-West Pacific: *N. platypus*, *N. aruensis* (Fig. 2.1J) and *N. ijimai*. They live singly or in pairs in soft cysts on the host's arms or disc, or freely on the host, or in the host's mouth (Grygier & Nomura 1998; Eeckhaut *et al.* 1998). The body is round or oval, but the margins may be upturned; cirri may be present or absent. The proboscis pocket opens either ventrally (*N. platypus*) or dorsally. Two to four low, steep-sided protuberances are present along the ventral midline; the anus is at the rear of the posterior one. The parapodial folds are wide, flat, kidney-shaped lobes; the lateral organs are in the centre of similar round lobes. A ventral submarginal shelf (*N. ijimai*) or ring of lappets (the other species) may coalesce with some of the lateral organ lobes. Aspects of the internal morphology were described by Wheeler (1896) for *N. platypus* and Remscheid (1918) for *N. aruensis*.

The genus *Hypomyzostoma* (Fig. 2.1K–M) comprises at least 11 described species, including representative species such as *H. folium*, *H. crosslandi*, *H. elongatum*, *H. dodecaphalcis* and *H. nanseni*. They live extended lengthwise along the arms or pinnules of crinoids. The body form is elongate with a convex dorsum and, generally, a concave ventral side. The parapodia lie at equal intervals in two parallel rows; the first pair is much closer to the anterior end than the fifth is to the rear. The lateral organs lie very near the margin; the first two pairs tend to be displaced anteriorly and the last two posteriorly with respect to the nearby parapodia. Cirri are absent; however, the margin may have numerous large, rounded projections or scallopings, or may bear denticle-like processes, or be nearly smooth. Transverse dorsal colour stripes or ridges may be present. The parapodial fold usually bears a button-like medial cirrus, and the parapodium itself typically bears a villose pad and a longitudinal groove. The proboscis pocket and the anus both open ventrally; buccal papillae are absent. Aspects of the internal morphology were described by Graff (1877) for *H. elongatum*, Boulenger (1913) for *H. crosslandi* and Remscheid (1918) for *H. taeniatum* and *H. sulcatum*. Encysted juveniles have been noted for two species (Remscheid 1918; Grygier 1988).

As a 'catch-all' genus including about 100 described species, *Myzostoma* shows an enormous range of morphological variation. Commonly the body shape, ignoring any caudal processes, is round, shield-shaped or oval (Fig. 2.1A–G); oval-elongate or bullet-shaped bodies are uncommon. Caudal processes may comprise a single upturned or furled lobe, several finger-like lobes (Fig. 2.1I), pairs of small, triangular lobes, or two or four or more grossly enlarged cirral bases with or without apical cirri. The body varies in thickness from membranous (Fig. 2.1B) to robust (Fig. 2.1E); hemispherical (Fig. 2.1D) or hemicylindrical body forms occur. A thin, translucent marginal zone not penetrated by the internal organs may be present (Fig. 2.1B). Colour patterns vary and can include contrasting circles or stripes (Fig. 2.1C). Many species have a dorsal longitudinal ridge and numerous radiating ridges (Fig. 2.1G, I); less commonly, dorsal tubercles or other kinds of sculpturing are present (Fig. 2.1E). The margin usually bears cirri, which may be long or short or of variable lengths (if the latter, usually the anterior and

posterior several pairs are longer than the lateral ones; Fig. 2.1A). The cirri may taper or be even in diameter, or they may be minute nubs. The number of cirri is usually 20 (10 pairs; Figs 2.1A, B, E, 2.2B), but some species have up to 100 or more (Fig. 2.1C). The 10 pairs are usually spaced evenly, but in several species they are distributed in pairs flanking each lateral organ. A considerable number of species lack cirri, but may have numerous rounded projections (Fig. 2.1G), or a lobed, membranous fringe; in others the margin is simple. The parapodia vary in relative size, extensibility, shapes and relative sizes of the hooks and support rods, presence or absence of medial cirri, distance of the array from the centre or the midline and extent of anterior displacement of the array. The size, shape and relative position of the lateral organs vary; a few species have more than the usual four pairs (five or six). The proboscis usually has buccal papillae that vary in number from four to at least 30 (Fig. 2.1D), but some species have none. The proboscis pocket usually opens ventrally, but may open marginally. The anus is ventral, marginal or, rarely, dorsal. When everted, the penes usually protrude directly from the lateral bases of the third parapodia; however, in certain species the apertures from which they protrude are displaced close to the body margin (Fig. 2.2B). Internally, the pattern of midgut diverticula, and thus also of uterine diverticula, varies greatly. There may be either two or three pairs of main gut diverticula (Fig. 2.2C), and their subsequent branching may be very limited or very extensive (Fig. 2.1B). The ovaries are located either in the uterus dorsal to the stomach or in a pair of uterine diverticula at different levels lateral or ventro-lateral to the stomach (Fig. 2.2C). The pair of utero-intestinal ducts may be separate or they may be fused at either the uterine end or the intestinal end.

## Order PHARYNGIDEA

Members of Pharyngidea are distinguished by the absence of a myzostomatid-type proboscis. If present, the proboscis is formed as a protrusion of the posterior wall of the oral cavity; thus the salivary glands, when present, empty into the oral cavity. A peribulbar nerve ring, incorporating the cerebral ganglia, is sometimes present. Compared to proboscideans, marginal cirri are fewer or absent, the parapodia are poorly developed, penes are generally absent, and the female reproductive system usually consists of broad spaces rather than narrow diverticula; gut diverticula often penetrate these spaces. Most pharyngideans are enclosed or otherwise permanently fixed to their host; they do not live freely upon their hosts.

The Pharyngidea comprises seven families. Only species of one family, Endomyzostomatidae, are found in Australian waters. Descriptions of the other six families are provided as several may yet be found in Australia or its external territories.

## Family Stelechopodidae

The family Stelechopodidae is represented by the single species *Stelechopus hyocrini*. It was first collected during the *Challenger* Expedition off the Crozet Islands in the Indian Ocean (Graff 1884b); animals were found on stalked crinoids, *Hyocrinus* and *Bathocrinus* species, at depths of 750–875 m. The precise relationship between *S. hyocrini* and its hosts is unknown. Jägersten (1940a) redescribed the species, giving details of its histology.

The following summary of the morphology of *Stelechopus hyocrini* is primarily based on Jägersten's (1940a) study. The body is flat and elongate, reaching a size of 3.5 x 0.9 mm (Fig. 2.10A). The unusually thick (60 µm) cuticle is papillose. The nuclei of the epidermal syncytium are sunken beneath the longitudinal and circular integumental muscle strands. There is very little parenchyma. The small parapodia are usually positioned ventro-laterally along the length of the body (Fig. 2.10B), or sometimes marginally or dorso-laterally; their integument has circular folds. The third pair of parapodia is the largest, and the first and fifth pairs the smallest; the first pair or one of its members is occasionally absent. Although parapodial musculature is present, but there is no musculus centralis, nor a ventral muscle mass. Marginal cirri are absent. Only two pairs of lateral organs have been observed: simple, deep invaginations in front of the first pair of parapodia and behind the fifth pair.

The mouth is at the end of a very small, apparently non-retractile, anterior process (Fig. 2.10A), behind which the pharynx passes through a small muscle bulb. The midgut is a large, open space interrupted by trabeculae that enclose dorso-ventral muscles; it may represent the combined stomach and gut diverticula of other myzostomes (Jägersten 1940a). The short intestine leads to the anus beneath the posterior end of the body.

The female reproductive system comprises a uterus with anastomosing diverticula. It is dorsal to, and co-extensive with the midgut and, like the latter, is interrupted by dorso-ventral trabeculae (Fig. 2.10A). Ovaries were not found, but young oocytes were present on the dorsal wall, and rather small, ripe oocytes (60–100 µm) were free in the lumen. Histological examination has shown that the thin wall separating this cavity from the midgut breaks down, thus allowing ripe oocytes to enter the midgut. Neither a lateral pair of ducts from the uterus nor a medial oviduct was found; the eggs may be expelled via the gut.

The male reproductive organs are paired and lie ventral to the midgut; on each side is a long, folded, generally open sac that shows very little differentiation into follicles and ducts. It has a few trabeculae like those of the midgut and a laterally directed exit duct that opens through a weak sphincter on the body margin just above the third parapodium. There appear to be no protrusible penes and no certain evidence of spermio cysts.

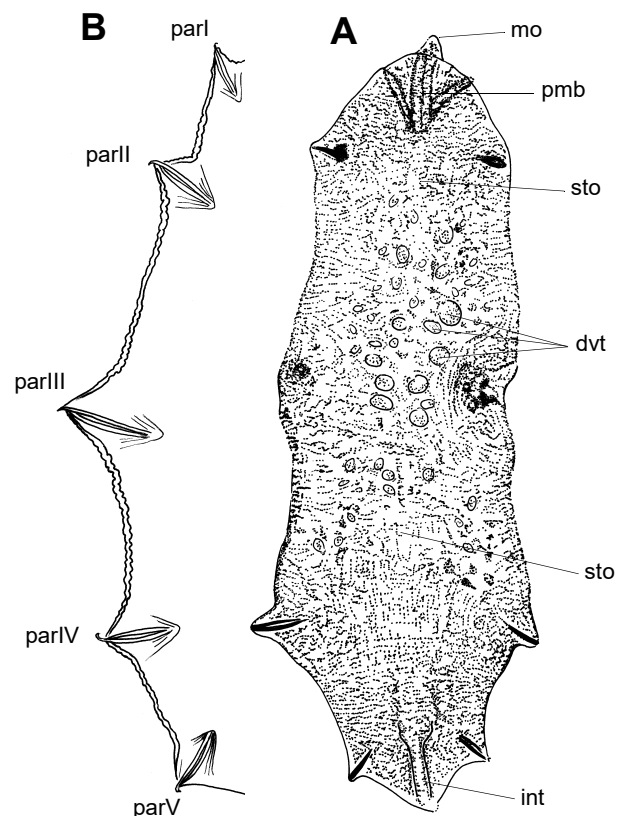
The ventral nerve cord is elongate and single-stranded, reaching nearly the length of the body. It gives rise to about eight pairs of lateral nerves, one opposite each of the five parapodia, and the third, fifth and seventh between the parapodia. An anterior nerve ring was not observed.

### Family Protomyzostomatidae

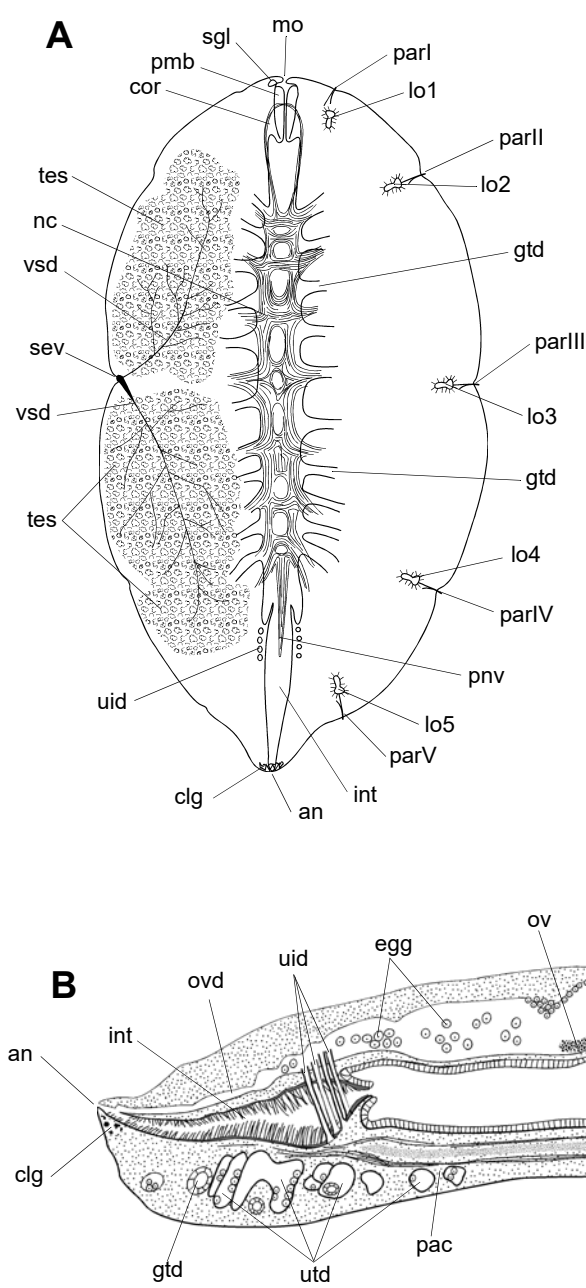
Protomyzostomatids are endoparasites or cyst dwellers of ophiuroids and usually live in temperate to cold seas. The single genus *Protomyzostomum* includes five described species, of which four are found in the Russian Arctic, Bering Sea, Sakhalin and Japan; they are endoparasites of the gonads or cyst-dwellers on the arms or discs of basket stars (Ophiuroidea) (Fedotov 1912, 1914, 1916, 1925; Okada 1922; Jägersten 1940a; Nigmatullin 1970). The fifth species, *P. glanduliferum*, occurs in the Antarctic. It inhabits the ventral coelom (rarely the dorsal) of the brittle star *Ophiacantha disjuncta*. An undescribed myzostome that may belong to this family is an endoparasite of the large antarctic brittle star *Ophionotus victoriae* (Bartsch & Faubel 1995). Both species have been found only in the Weddell Sea, but they may also live in the Australian Antarctic Territory.

The following account is based primarily on *Protomyzostomum polynephris* (see Fedotov 1912, 1914), an endoparasite that consumes the genital sacs in the affected gonad lobes of *Gorgonocephalus eucnemis*. Such feeding leads to partial or full castration of the host, depending on the intensity of the infestation. Up to five adult individuals of *P. polynephris* live together in capsule-like cysts that eventually become calcified. Young worms occur in the bursal cavities or beneath the bursal epithelium. Infestations of up to half the population of the host species occur, with from one to at least 119 parasites per host. The Antarctic *P. glanduliferum* also shows a host prevalence of about 50% (Bartsch & Faubel 1995).

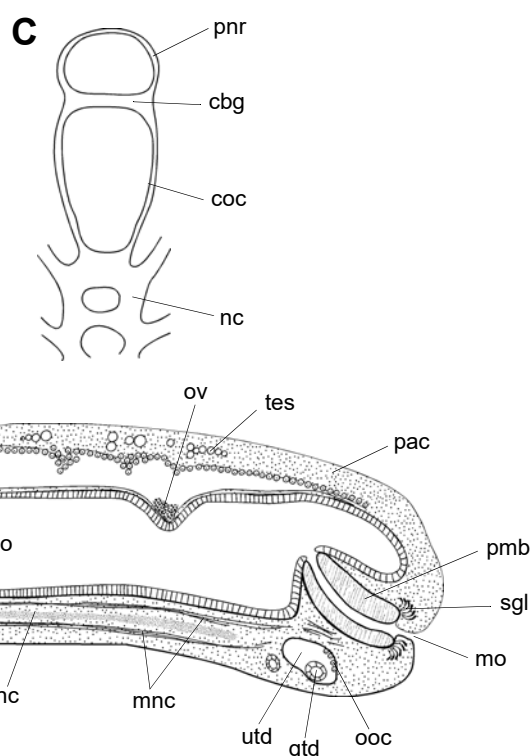
Adult *Protomyzostomum polynephris* (Fig. 2.11A, B) are the largest of all myzostomes and may reach a size of 32 mm long by 15 mm wide and a thickness of 2–3 mm. The body is oval and flat, but in life is either rolled up or irregularly folded within its capsule. There is a thin cuticle, but no external cilia. The epidermal cells are sunk beneath a muscular layer, with no basal membrane; their distal portions form a syncytium through which criss-crossing circular and longitudinal muscles pass. Integumental gland



**Figure 2.10** Family Stelechopodidae. *Stelechopus hyocrini*. **A**, entire animal flattened on slide. **B**, body margin showing parapodia. **dvt**, dorso-ventral trabeculae; **int**, intestine; **mo**, mouth; **parI–parV**, parapodia I–V or their hook apparatus; **pmb**, pharyngeal muscle bulb; **sto**, stomach. (A, after photomicrograph by Jägersten 1940a; B, after Graff 1884b) [I. Hallam]



**Figure 2.11** Family Protomyzostomatidae. Anatomy of *Protomyzostomum polynephris*. **A**, female with reproductive system mostly omitted. **B**, mid-sagittal section. **C**, anterior section of central nervous system. **an**, anus; **cbg**, cerebral ganglion; **clg**, cloacal gland cells; **cm1–10**, commissures; **coc**, circum-oesophageal connective; **cor**, circum-oesophageal nerve ring; **egg**, eggs; **gtd**, gut diverticula; **int**, intestine; **lo1–5**, lateral organs 1–5; **mnc**, muscles associated with nerve cord; **mo**, mouth; **nc**, nerve cord; **ooc**, oocytes; **ov**, ovaries; **ovd**, oviduct; **pac**, parenchyma; **parI–parV**, parapodia I–V or their hook apparatus; **pmb**, pharyngeal muscle bulb; **pnr**, peribulbar nerve ring; **pnr**, posterior nerve; **sev**, seminal vesicle; **sgl**, salivary glands; **sto**, stomach; **tes**, testes; **uid**, utero-intestinal duct; **utd**, uterine diverticula; **ute**, uterus; **vsd**, vas deferens. (A, B, after Fedotov 1914; C, after Jägersten 1940a). [I. Hallam]



cells occur only near the anus and sometimes the mouth. The body musculature is weak and includes dorso-ventral muscles, muscles above and below the nerve cord, and muscles sheathing the gut and female reproductive system.

The poorly-developed parapodia are present on the body margin in the young, but close to the ventral margin in older individuals; they often occupy indentations of the margin (Fig. 2.11A). Only those of mid-sized individuals have replacement hooks. The musculature of each parapodium is independent. Marginal cirri are absent in all species. The five pairs of lateral organs are small and inconspicuous except in *P. cystobium*, and they are located dorsally, more or less directly opposite the parapodia (Fig. 2.11A). Each lateral organ has a ciliated floor and a central part surrounded by gland cells; in *P. polynephris* a canal leads inward from the floor. The musculature of the lateral organs includes sphincters, retractors, dilators and protractors, but there is no surrounding capsule formed from dorso-ventral muscles. The mouth and anus are terminal, the mouth opening on a distinct, small or large, conical papilla (Fig. 2.11A, B). A proboscis and buccal papillae are absent, but the pharynx can be protracted and retracted to some extent. A sphincter and dilator muscles surround the mouth. The small pharyngeal muscle bulb (Fig. 2.11B) has two layers of circular fibres and irregularly arranged radial fibres. Salivary gland cells empty into the posterior part of the mouth cavity. Eight to 13 (most often 10) more or less ramifying diverticula branch irregularly off the long stomach on each side in *P. polynephris*.



(Fig. 2.11A). *Protomyzostomum sagamiense* has 16 to 25 such diverticula on each side; only three or four are present on each side in *P. cystobium* and *P. glanduliferum*. Posterior to the stomach there is a shorter, ciliated intestine.

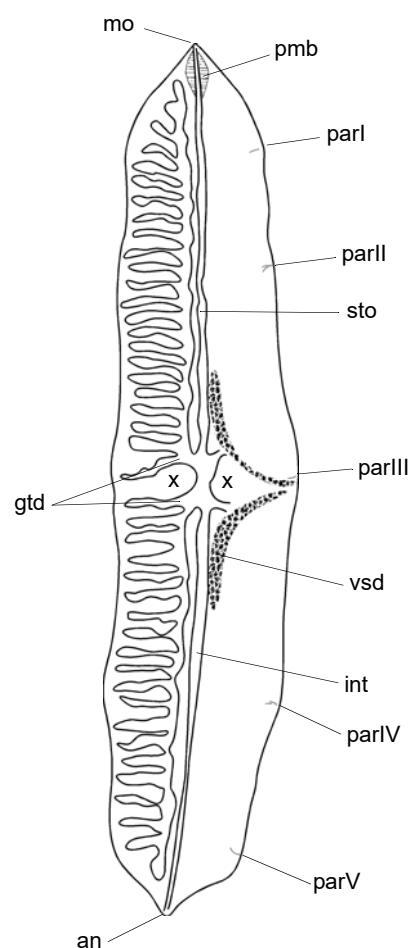
Protomyzostomatids are hermaphrodites, the smaller ones being more actively male, the larger ones more female. Two diffuse ovaries are usually present, one behind the other, on the ventral side of the uterus over the gut (Fig. 2.11B); *P. glanduliferum* has one ovary. The uterus has to eight to 18 diverticula per side irregularly along its anterior two-thirds, often parallel to and, in *P. polynephris*, sometimes enclosing the midgut diverticula; some enter the ventral part of the body (Fig. 2.11B). In *P. cystobium* they all pass ventrally between the gut diverticula and can anastomose. The oviduct empties into the intestine internally just before the anus. Ciliated ducts run dorso-ventrally between the lower part of the uterus and the lower or middle part of the anterior portion of the intestine; they number three to seven per side in *P. polynephris* (Fig. 2.11B); *P. cystobium* has only one pair. The diffuse testicular follicles (Fig. 2.11A) are dorsal to the female organs in *P. polynephris* and *P. glanduliferum* and dorsal to the gut diverticula in *P. cystobium*, but mostly lie ventral to the gut diverticula in *P. sagamiense*. The testes lead into an anterior and posterior pair of vasa deferentia. These empty, via small seminal vesicles and non-protrusible, nipple-like penes, through a pair of marginal slits between the third parapodia and third lateral organs.

The nervous system in *P. polynephris* and *P. cystobium* is ladder-like with a circum-oesophageal ring and peribulbar ring (Fig. 2.11C) and a widely separated pair of ventral nerve cords (Fig. 2.11A). The cords are joined by 10 commissures and give off eight main pairs of lateral nerves and an unpaired posterior nerve. Pairs 3, 5 and 7 are thinner than the others and innervate the sex organs, whereas the other pairs each split into two branches that serve the respective parapodium and lateral organ (and penis). The nervous system is quite different in *P. astrocladi* (Jägersten 1940a). The ventral nerve cord is unpaired, although two fibrous tracts are present within it. Besides the main lateral nerves, innumerable other interconnected nerve tracts forming a plexus are present. They are more developed ventrally than dorsally, and supposedly Fedotov (1925) mistook these for muscles.

### Family Mesomyzostomatidae

The two known mesomyzostomatid species are endoparasites of the reproductive organs of comatulid crinoids. The better known species, *Mesomyzostoma reichenspergi*, was collected from *Amphimetra discoidea* in the Aru Islands, Indonesia (Remscheid 1918). It can be assumed to occur in northern Australia. It lives in the sterile longitudinal canals of the crinoid arm, and not in the gonads themselves. *Meso-myzostoma kato* is found in the gonads of *Oxycomanthus japonicus* in Japan (Okada 1933).

The body of *M. reichenspergi* (Fig. 2.12) is vermiform, up to 1.91 mm long and 3 to 6.5 times longer than wide; *M. kato* reaches a size of 4.5 x 0.45 mm. A cuticle is present, but external cilia are absent. The integumental musculature



**Figure 2.12** Family Mesomyzostomatidae. Morphology of *Mesomyzostoma reichenspergi*; ovary sites indicated by x. an, anus; gtd, gut diverticula; int, intestine; mo, mouth; parl-parV, parapodia I-V or their hook apparatus; pmb, pharyngeal muscle bulb; sto, stomach; vsd, vas deferens. (After Remscheid 1918) [I. Hallam]

includes outer circular and inner longitudinal muscles. Other longitudinal muscles encompass the pharynx, stomach and gut diverticula, and circular muscles ensheath the cloaca and uterus. Muscles also surround the ventral nerve cord.

Parapodia are represented only by slight lateral protrusions. Five pairs of independent hook apparatus are present in *M. reichenspergi* and three to four pairs in *M. katoi* (Fig. 2.12). Each consists of one or two hooks and a support rod. Marginal cirri and lateral organs are absent.

A proboscis and proboscis pocket are absent. From the terminal mouth the pharynx passes through a small pharyngeal muscle bulb and a sphincter into the long, narrow stomach. At about mid-body in *M. reichenspergi* and three-quarter body length in *M. katoi*, two pairs of diverticula branch off to the anterior and posterior ends of the body (Fig. 2.12); each diverticulum gives rise to a single row of closely spaced, laterally directed side branches. The long, narrow intestine extends to the terminal anus.

The female reproductive organs overlie the digestive organs. A pair of short utero-intestinal ducts branch off the uterus and enter the intestine through a common ventral pore. Also branching from the uterus are two pairs of diverticula that overlie the gut branches; they often bulge with ova released from their dorsal wall. The two ovaries lie in ventral pouches of the uterus between the two pairs of diverticula. The oviduct overlies the intestine and empties terminally. The testes generally lie beneath the gut diverticula. In *M. reichenspergi*, the anterior and posterior vas deferens on each side (Fig. 2.12) join at a small, well-muscled seminal vesicle that exits through a sphinctered ejaculatory duct dorsal to the third pair of parapodial hooks. Supposedly, male gonopores are absent in *M. katoi*.

The circum-oesophageal nerve ring encircles the end of the mouth tube in front of the pharyngeal muscle bulb. The single ventral nerve cord runs the length of the body and gives rise to five pairs of large nerves to the parapodia, an undetermined number of finer nerves between these, and some terminal nerves.

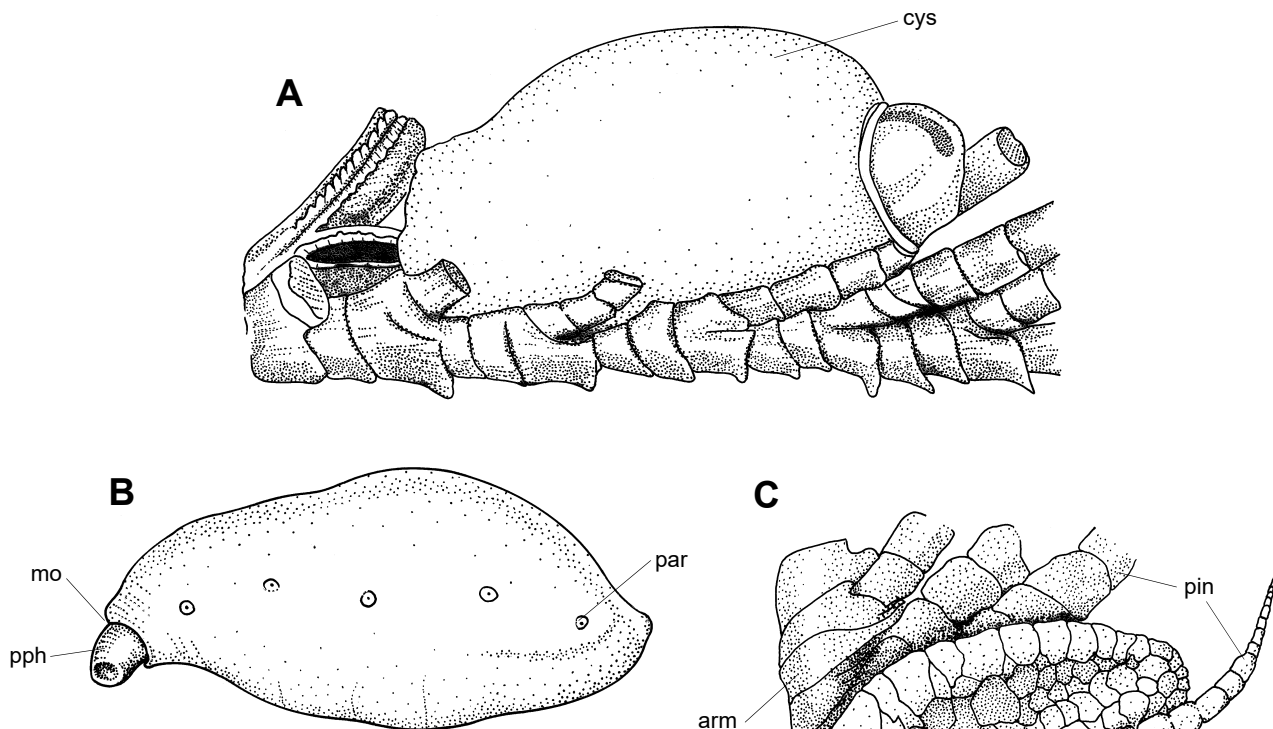
### Family Endomyzostomatidae

Members of the Endomyzostomatidae live in cysts or galls on crinoids. Galls are formed from enlarged and deformed crinoid ossicles, whereas cysts are fleshy or incorporate many supernumerary ossicles.

Until recently, this family supported one genus concept with three available names, each with a different type species: *Endomyzostoma* (*Myzostoma pentacrini*), *Heteromyzostoma* (*M. tenuispinum*), and *Cystimyostomum* (*M. cysticolum*). The name *Endomyzostoma* only is recognised as valid here (see discussion under Classification). Eeckhaut & Jangoux (1995) assigned the new genus *Contramyzostoma* to this family, as did Eeckhaut (1998) for *Mycomyzostoma*, but these are treated here separately because the true affinities of these genera are uncertain. The family is also known as Cystimyostomatidae.

The boundaries of the Endomyzostomatidae are not firmly established. Jägersten (1940a) included at least 10 nominal species in *Cystimyostomum*, comprising the majority of gallicolous and cysticolous myzostomes from crinoids. Jangoux (1987, 1990), however, returned the gallicoles, including *M. pentacrini* and *M. tenuispinum*, to *Myzostoma* and restricted *Cystimyostomum* to cysticoles. He also transferred into *Cystimyostomum* some species from the Myzostomatidae that are otherwise referable to *Notopharyngoides* (*N. platypus*, *N. iijimai*), *Hypomyzostoma* (*H. taeniatum*) and *Myzostoma* (*M. willemoesii*; see Fig. 2.1H). Jangoux's classification is not supported by comparative morphology and is here considered artificial. The species-level taxonomy also appears to be artificial. *Endomyzostoma cysticolum* has been reported to form different types of cysts on different parts of the body of an assortment of crinoid species from the Caribbean, Red Sea, Japan, Indonesia and Antarctica, and it almost certainly comprises several distinct species, despite opinions to the contrary by Stummer-Traunfels (1908). Histological study of this genus has not been as thorough as for most of the other myzostome genera (see works by Graff 1884b; Wheeler 1896; McClendon 1906; Stummer-Traunfels 1908).

The domicile of endomyzostomatids takes several forms (see Graff 1884b; Boulenger 1916; Remscheid 1918; Eeckhaut & Améziane-Cominardi 1994): a crypt hollowed out between and within enlarged arm ossicles; a cavity within swollen pinnules; a relatively soft cyst with some calcified elements along the ambulacrum of a pinnule, arm or disc (Fig. 2.13A); a hard, bean-shaped gall involving one or two arm ossicles; a hard, sac-like or liver-shaped, multi-plated cyst of the arms, pinnules or disc (Fig. 2.13C). Cysts may have a single opening, as in *Endomyzostoma deformatior*, but usually two are present, one of which faces into the ambulacral groove and the other is near the posterior end of the body.



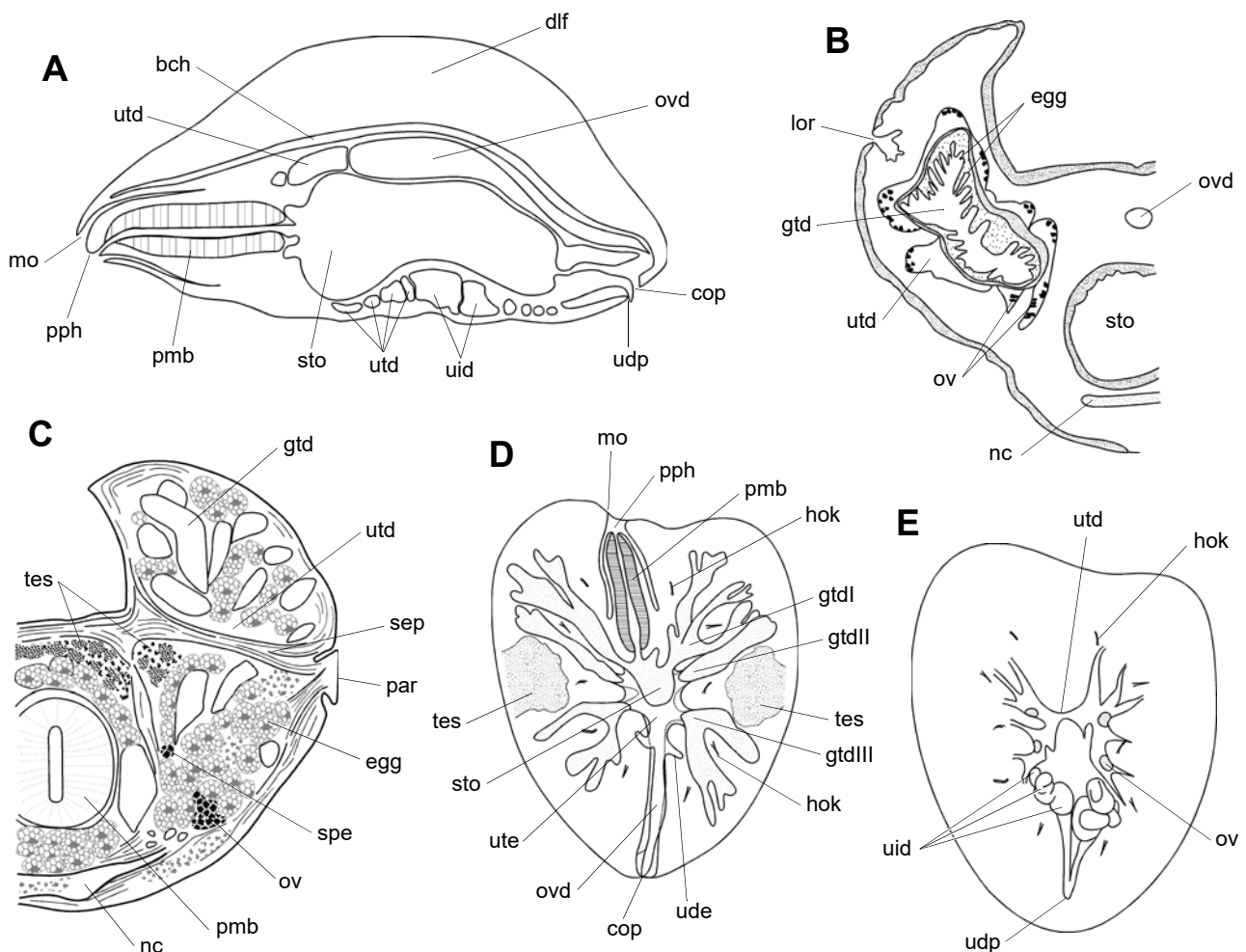
**Figure 2.13** Family Endomyzostomatidae. **A, B**, *Endomyzostoma* species (reported as *Myzostoma cysticolum*): **A**, animal *in situ* in soft cyst on arm of host, Antarctic *Promachocrinus kerguelensis*; **B**, female removed from cyst. **C**, plated cyst of *Endomyzostoma* species (reported as *Myzostoma cysticolum*) on pinnule of Indonesian *Amphimetra tessellata discoidea*, similar to cysts found on several tropical Australian comatulids. **arm**, arm of host; **cys**, cyst; **mo**, mouth; **par**, parapodium; **pin**, pinnules; **pph**, proboscis (protrusible pharynx). (A, B, after Boulenger 1916; C, after Remscheid 1918) [I. Hallam]

The Australian fauna investigated by the author includes at least three species of *Endomyzostoma*. A form referable to *E. clarki* lives in galls on the arms of at least two species, including *Metacrinus cyaneus* and unidentified specimens, of metacrinine stalked crinoids off north-western and south-eastern Australia. Another, which might be referred to *E. cysticolum* of Remscheid (1918) (Fig. 2.13C) or may be polytypic, lives in a liver-shaped, multi-plated cyst on the arms or pinnules of several species of comatulids in tropical Australia, including *Himerometra robustipinna*, *Heterometra crenulata* and *Pontiommetra andersoni*. An undescribed species that resembles *E. deformatior* lives in a small, soft cyst along the arm ambulacra of *Comatella stelligera* at Barrow Island, Western Australia. In addition, *E. cysticolum* of Stummer-Traunfels (1908) and Boulenger (1916), an Antarctic species that forms a soft cyst on the arms and discs of *Promachocrinus kerguelensis* and *Antedon adriani* (Figs 2.13A, B, 2.14A, D, E), undoubtedly occurs in the Australian Antarctic Territory; such cysts have been seen on crinoids from off Adélie Land (M.J. Grygier personal observation).

The female body is 2–11 mm long and round in outline when flattened, but in life it is typically trough-shaped or folded in two with the lateral margins upturned and even meeting or overlapping (Fig. 2.14A–C). In *E. deformatior*, all margins are upturned, so the true dorsum is obscured. The dorsal cavity so formed serves in some species as a brood chamber for the fertilised eggs and early larvae. The proboscis (a protruded pharynx) and the anal papilla are both terminal (Figs 2.13B, 2.14A). The five pairs of small parapodia form an arc on the upturned surface on each side (Fig. 2.13B) and may protrude slightly, be discoidal, or be reduced to the hook apparatus alone, depressed into grooves. *Endomyzostoma*

*inflator* supposedly has no parapodia at all. Most species reportedly have no lateral organs, except for *E. clarki* (McClendon 1906) and *E. tenuispinum* (Eeckhaut & Améziane-Cominardi 1994), both of which have four pairs alternating with the parapodia. Marginal cirri are absent or reduced in number; at most five to seven pairs, in *E. tenuispinum*. The body surface bears tufts of cilia (Jägersten 1940a; Eeckhaut & Améziane-Cominardi 1994). The dorso-ventral musculature is well developed (Fig. 2.14C), but the parapodial musculature is feeble and there is no mid-ventral muscle mass.

The mouth cavity extends as a shallow proboscis pocket to about midlength of the pharyngeal muscle bulb (Fig. 2.14A). The stomach is ciliated and surrounded by a sheath of longitudinal and circular muscles, and the gut diverticula are highly branched. *Endomyzostoma tenuispinum* has 20 to 30 branched gut diverticula on each side, but far fewer are present in *E. deformatior*. There is no anal sphincter in the female stage; a flap is present.



**Figure 2.14** Family Endomyzostomatidae. **A**, female of Antarctic *Endomyzostoma* species (reported as *Myzostoma cysticola*), sagittal section just off midline. **B**, one half of a cross-section, dorsal side up, of a female *Endomyzostoma clarki*, a gallicolous species from Japan, and, evidently, also from Australia. **C**, one half of a cross-section of a female *Endomyzostoma belli*, sectioned more anteriorly than in **B**. **D**, **E**, morphology of a male Antarctic *Endomyzostoma* species (reported as *Myzostoma cysticola*), **E** more ventral than **D**. **bch**, mid-dorsal 'brood chamber'; **cop**, common anal and female genital opening; **dlf**, dorso-lateral fold; **egg**, eggs; **gtd**, gut diverticula; **gtdI–III**, main gut diverticula I–III in **D**; **hok**, parapodial hooks; **lor**, lateral organ; mouth; **nc**, nerve cord; **ov**, ovaries; **ovd**, oviduct; **par**, parapodium; **pmb**, pharyngeal muscle bulb; **pph**, proboscis (protrusible pharynx); **sep**, muscular septum; **spe**, sperm; **sto**, stomach; **tes**, testes; **ude**, entrance to utero-intestinal duct; **udp**, common external exit pore of utero-intestinal ducts; **uid**, utero-intestinal duct; **utd**, uterine diverticula; **ute**, uterus. (A, D, E, after Stummer-Traunfels 1908; B, after McClendon 1906; C, after Wheeler 1896) [I. Hallam]



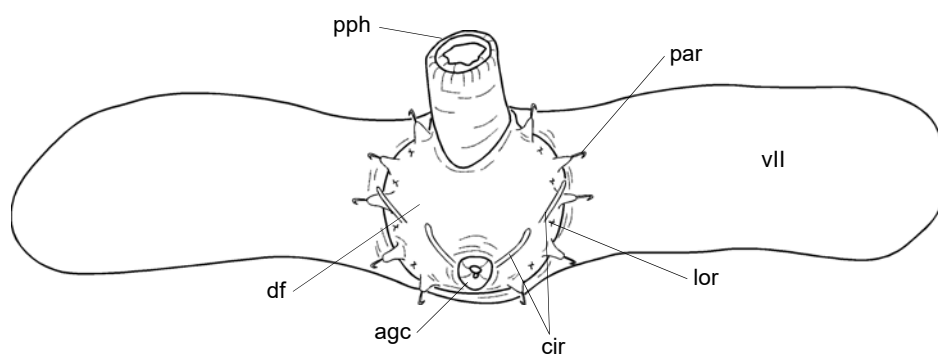
Sexuality may be variable, and there is some question about whether supposed testes have been correctly identified in some species (Jägersten 1939b). In *Endomyzostoma pentacrini* and *E. deformatior*, two or three hermaphrodites usually occur together in separate cavities in a gall; the male system is developed only unilaterally, with the testicular follicles in a compact mass. Pairs occur in other species: a large functional female and a dwarf, protandric male. Both sexual systems supposedly occur in all individuals, but only one system is active (Wheeler 1896; McClendon 1906; Stummer-Traunfels 1908).

Male-stage individuals are round and flat, and about 1 mm in diameter; they lack marginal cirri and have stubby parapodia, and most (all?) lack lateral organs (Fig. 2.14D, E). They have three pairs of weakly branched midgut diverticula. The testes are compact (Fig. 2.14D) and located between the second and third pairs of gut diverticula (except for the diffuse testes in *E. inflator*). Each testis has a central collecting space that is directly connected to the male genital aperture on each side of the body; the aperture is usually marginal, but occasionally ventral or dorsal near the margin. The penis is not protrusible. The female reproductive system develops in the males (Fig. 2.14D, E) as an epithelium-lined organ with a dorsal cavity, a pair of ventrally directed passages that surround the bases of the second and third pairs of gut diverticula, and a pair of ventral cavities connected across the midline, from each of which three lateral diverticula arise and follow beneath the gut branches (Stummer-Traunfels 1908). Two pairs of undeveloped ovaries are located at the bases of these diverticula. Precursors of the female gonopore and common utero-intestinal duct pore are also present.

In the female stage, the usual relative positions of the ovaries and testes are inverted (Fig. 2.14C); the ovaries are located ventral to the gut, whereas the testes are dorsal and protrude into the uterus and its diverticula (Wheeler 1896; McClendon 1906; Stummer-Traunfels 1908). According to Jägersten (1939b), though, the dorsal testes of *E. belli* (Fig. 2.14C) are more likely spermatogenic syncytia invading the female after mating (see reproduction section above). The cavities of the female system are only partly lined by an epithelium, the remainder by a pseudoepithelium of reticular connective tissue. The lateral passages have become greatly expanded and fused with the ventral cavities and their diverticula so as to suspend the gut diverticula within capacious lateral sacs (Fig. 2.14B; see also Wheeler 1896). The ventral cavities are connected across the midline between the stomach and ventral nerve mass by several irregular passages. In this stage, the two pairs of ventral ovaries (Fig. 2.14B, C) are much bigger than in the male stage. In females of *E. cysticum*, the male genital openings are found dorsally near the margin, outside the third pair of parapodia (Stummer-Traunfels 1908). The testes no longer produce sperm, and Stummer-Traunfels thus suggested that earlier reports of females lacking testes were mistaken.

A pair of utero-intestinal ducts (Fig. 2.14A, E) begin at the posterior end of the uterus as ciliated canals and then broaden into a pair of contorted, glandular, unciliated end-sacs, the exit ducts of which fuse. The common duct so formed is also glandular and unciliated and opens at a pore just anterior to the anus, not inside the intestine as usual (Wheeler 1896; Stummer-Traunfels 1908).

The ventral nerve cord or mass has not been described in detail.

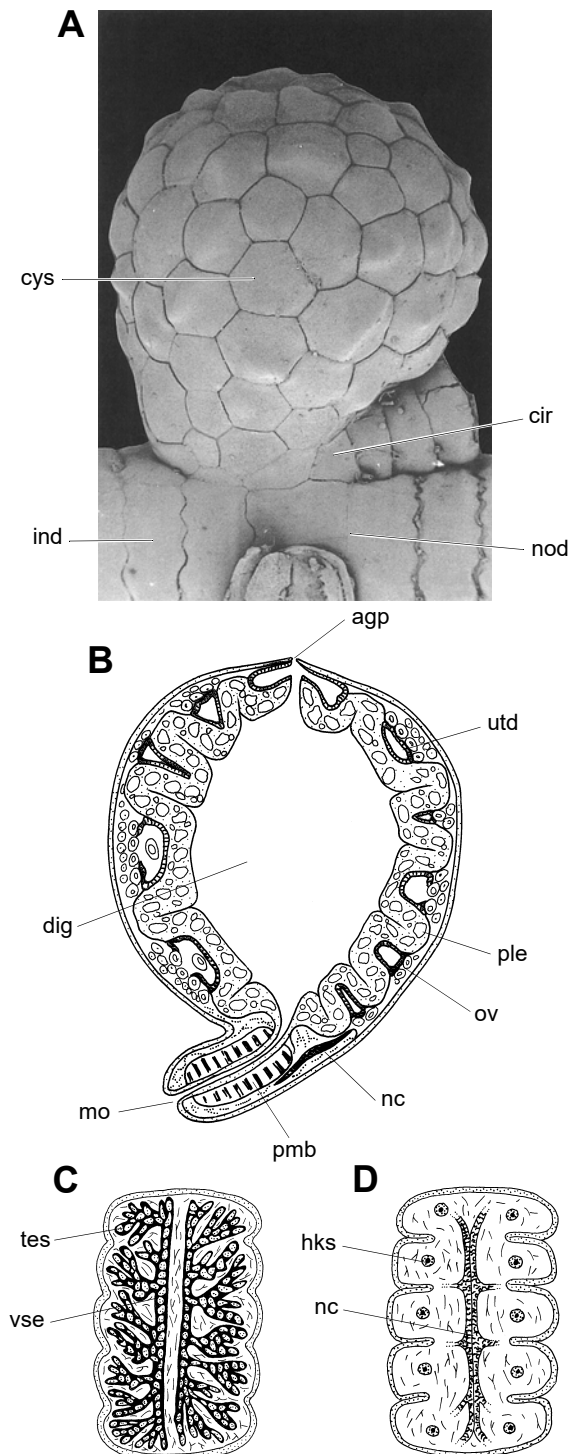


**Figure 2.15** Family Endomyzostomatidae. *Contramyzostoma bialatum* (*incertae sedis*), dorsal view. **agc**, anogenital cone; **cir**, cirri; **df**, dorsal field; **lor**, lateral organ; **par**, parapodium; **pph**, proboscis (protrusible pharynx); **vII**, ventro-lateral lobe. (After Eeckhaut & Jangoux 1995) [I. Hallam]

**Contramyzostoma.** Only a brief mention of this genus will be given here, because its assignment to the Cystimyzo-stomatidae (that is, Endomyzo-stomatidae) by Eeckhaut & Jangoux (1995) is not based on morphology and may be erroneous. The type-species, *C. bialatum*, lives in cysts on the arms and disc of *Comaster gracilis* off Singapore; it is about 2 mm wide. The central part of the anatomically ventral side is produced into two large lateral lobes (Fig. 2.15), such that the outer parts of the ventral side have come to be situated on the small, functionally dorsal side. This 'dorsal field' is round and bears five pairs of parapodia, four pairs of lateral organs and two pairs of posterior cirri; the parapodia are outermost, with their hooks directed outward, and the cirri are innermost. The 'dorsal field', but not the ventral surface, is ciliated. A relatively large proboscis and an anogenital cone arise from the 'dorsal field', connected by a U-shaped gut. Salivary gland cells situated at the pharynx-stomach boundary empty distally on the proboscis. Two diverticula extend from the stomach into each lateral lobe, where they meet to form a loop on each side. The two supposed ovaries are diffuse and lie in the parenchyma of the lateral lobes (as mentioned in the reproduction section above, Eeckhaut's concept of the myzostome ovary differs from that of earlier authors). The mid-dorsal uterus has looped diverticula that enclose the gut diverticula. The nervous system consists of a circum-oesophageal nerve ring and condensed ventral nerve mass.

The lateral protrusions of the mid-ventral surface and the looped diverticula of the stomach and uterus are unique features. The location of the gut diverticula within the cavities of the female system agrees with the structure in *Endomyzostoma* and *Pulvinomyzostomum*. The dorsal positions of the mouth and anus conform with the latter, and most or all parapodia being visible in dorsal view is also a feature shared with *P. pulvinar*. *Contramyzostoma* could be considered an extremely modified *Pulvinomyzostomum*, but differs in having only four pairs of lateral organs and in its location in the host. Unfortunately, the nature of the proboscis remains unknown; the *Myzostoma*-like arrangement of the salivary gland cells suggests, however, that *C. bialatum* belongs to the Proboscidea, not the Pharyngidea.

A second species was described from *Comatella stelligera* in Papua New Guinea by Eeckhaut *et al.* (1998), but it was only tentatively assigned to this genus on the basis of its hypertrophied ventral surface. In many respects it differs considerably from the type-species, and its features were not taken into account in the present treatment of the systematic position of the genus (Fig. 2.9).



**Figure 2.16** Family Endomyzostomatidae. *Mycomyzostoma calcidicola* (*incertae sedis*). **A**, cyst *in situ* on host crinoid, *Saracrinus nobilis*. **B**, mid-sagittal section of female; **C**, horizontal dorsal section of male showing reproductive system. **D**, horizontal ventral section of male showing ventral nerve chain and hook sites. **agp**, ano-genital pore; **cir**, cirrus (extending to right); **cys**, cyst comprising supernumerary ossicles; **dig**, digestive sac; **hks**, site of hook; **ind**, internodal ossicle; **mo**, mouth or entrance to pharynx; **nc**, nerve cord; **nod**, nodal ossicle; **ov**, ovary; **ple**, pleat of digestive sac; **pmb**, pharyngeal muscle bulb; **tes**, testes; **utd**, uterine diverticula; **vse**, vas efferens. (After Eeckhaut 1998) [B–D, I. Hallam]

***Mycomyzostoma*.** Eeckhaut (1998) included this genus in the Endomyzostomatidae because of its cysticolous life style, lack of cirri and lateral organs, and its separate sexes as some species of *Endomyzostoma* supposedly have (although as noted above, so far as is known *Endomyzostoma* species are hermaphrodites). The regression of many characters is extreme. The parapodial hook apparatus and testicular spermocysts of the male and the presence of spermatoc syncytia in the female are all that identify this parasite as a myzostome. Assignment to the Endomyzostomatidae is not supported by the diffuse (instead of compact) testes and by the absence of gut diverticula passing through uterine diverticula. Therefore, *Mycomyzostoma* is treated as *incertae sedis* herein.

The sole species, *Mycomyzostoma calcidicola*, was originally described from specimens collected off New Caledonia, but its host, *Saracrinus nobilis*, also occurs off north-western Australia. A female or a male-female pair lives in a multi-plated, rounded cyst of the stalk of the pedunculate crinoid host (Fig. 2.16A). The cysts are closed or have a single minute opening. Each cyst contacts the base of a cirrus and three or four columnar ossicles, including a nodal ossicle, and the female's proboscis fits a cavity in the side of the stalk. The female has a small proboscis and a large, spherical trunk up to 7 mm across (Fig. 2.16B); the trunk surface is heavily wrinkled except for a flat ano-genital plate, and there are no traces of parapodia, lateral organs or cirri. The pharynx, with a muscle bulb, but no salivary glands, leads into a large, longitudinally pleated digestive sac with no diverticula. The ventral nervous system is condensed. The ovary (*sensu* Eeckhaut 1995) is diffuse, with oocytes developing in the parenchyma. The ciliated diverticula of the reproductive system run between the gut pleats, and they have a common exit with the anus. A uterus and oviduct in the usual sense are evidently absent, and no utero-intestinal ducts were described. The male is much smaller (<1 mm), and is flat and rectangular in outline, with external ciliation and four pairs of lateral indentations (Fig. 2.16C, D). A proboscis, gut, lateral organs and cirri are absent. Five pairs of parapodia are represented by hooks and support rods, the former extending from ventral apertures halfway between the midline and the body margin. The nervous system includes a pair of conjoined ventral longitudinal cords and five pairs of lateral nerves (Fig. 2.16D). The testis is diffuse and marginal (Fig. 2.16C); many ducts join a pair of longitudinal efferent ducts that are assumed to exit near the third pair of parapodia. Vasa deferentia, seminal vesicles and penes are absent.

### Family Asteriomyzostomatidae

The Asteriomyzostomatidae are represented by two species that are endoparasitic in sea stars. The better known species, *Asteriomyzostomum asteriae*, lives in the pyloric caeca of two species of *Sclerasterias* in the Mediterranean (Stummer-Traunfels 1903). *Asteriomyzostomum fisheri* inhabits the body cavity of *Tosia* (*Pentagonaster*) *leptoceramus* off southern California (Wheeler 1905). Australian representatives are unknown.

The body is flat, oval and wider than long: up to 5–6 mm long and 8.5 mm wide (Fig. 2.17A). The five pairs of reduced parapodia are close to the margin ventrally. Marginal and parapodial cirri are absent. The mouth is located ventrally at varying distances from the anterior end; a proboscis and proboscis pocket are absent. The anus and, just before it, the female genital opening, are located dorsally at two-thirds the body length (Fig. 2.17B). Four pairs of lateral organs alternate with the parapodia (Fig. 2.17A); an unpaired ninth, postero-medial one is present in *A. asteriae*.

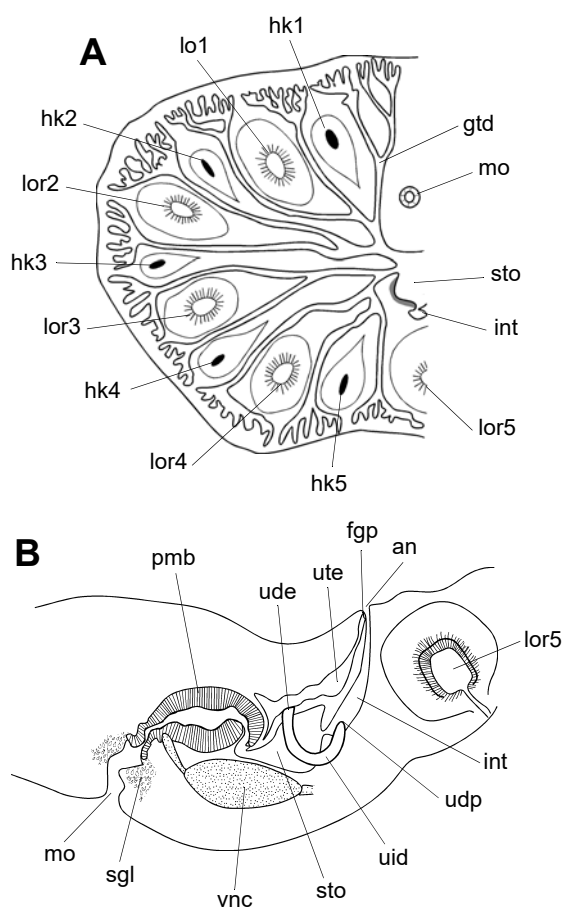
The body wall consists of cuticle, epidermis, basement membrane and muscular sheath. The epidermis consists of cylinder cells and gland cells, the latter being much more abundant ventrally. The cuticle is formed from the 2–3 µm thick caps on each cylinder cell; these caps remain distinct. Except where disturbed by dorso-ventral or parapodial muscles, the integumental musculature consists of an outer layer of radial muscle fibres and an inner layer of concentric ones. The body musculature resembles that of *Myzostoma cirriferum*: two thin layers of mostly transverse muscles above and below the ventral nerve mass, and dorso-ventral muscles, many near the margin and others forming perforated radial septa, especially laterally.

The lateral organs are papilliform, with a sphincter-closed passage leading to an internal cavity (Fig. 2.17B); the integument of the cavity can be protruded as a mushroom-like structure. Beneath the glandular-appearing epithelium of the lateral organ is a thick layer of highly vacuolated connective tissue; surrounding this is a capsule of integumental muscles that is instrumental in the protrusion of the organ and is penetrated by the lateral organ's dorso-ventral retractor muscles and nerves.

The gut is short and its posterior section is bent dorsally (Fig. 2.17B). The mouth cavity is divided into anterior and posterior parts; many salivary gland cells surround and empty into the posterior part. Two principal pairs of gut diverticula are present, and each diverticulum subdivides into five main branches; further subdivision occurs near the body margin (Fig. 2.17A). The intestine is ciliated, but the stomach and its diverticula are not.

All specimens examined were functional hermaphrodites. The uterus and its two pairs of branching diverticula are lined with a ciliated epithelium except for the terminal branches of the diverticula. In *A. asteriae*, each of the paired ovaries lies in a ventral pit at the base of one of the first pair of main diverticula, whereas in *A. fisheri* the ovary is unpaired and lies over the stomach. The uterine diverticula are dorsal to those of the stomach. The ciliated utero-intestinal ducts have an expanded middle section, are separate for their whole length and enter the intestine close behind the stomach (Fig. 2.17B). The male organs are ventral to the gut and its diverticula. They occur mostly in the posterior half of the body in *A. fisheri*. The testes are diffuse. In *A. asteriae*, only one pair of vasa deferentia is present, seminal vesicles are lacking, and the penes are poorly developed. In contrast, *A. fisheri* has an anterior and posterior vas deferens and an ejaculatory duct on each side.

The nervous system consists of a circum-pharyngeal ring around the anterior part of the muscle bulb, with no associated peribulbar or prebulbar ring, and a ventral nerve mass below the stomach, constructed like that of *Myzostoma* (Fig. 2.17B). The peripheral nerves remain undescribed in detail, but the paired lateral organs in *A. asteriae* are quite possibly innervated by branches of the four pairs of intermediate nerves from the ventral mass, and the unpaired one by the most distal pair of nerves, which also serve the intestine and the pair of uterine ducts.

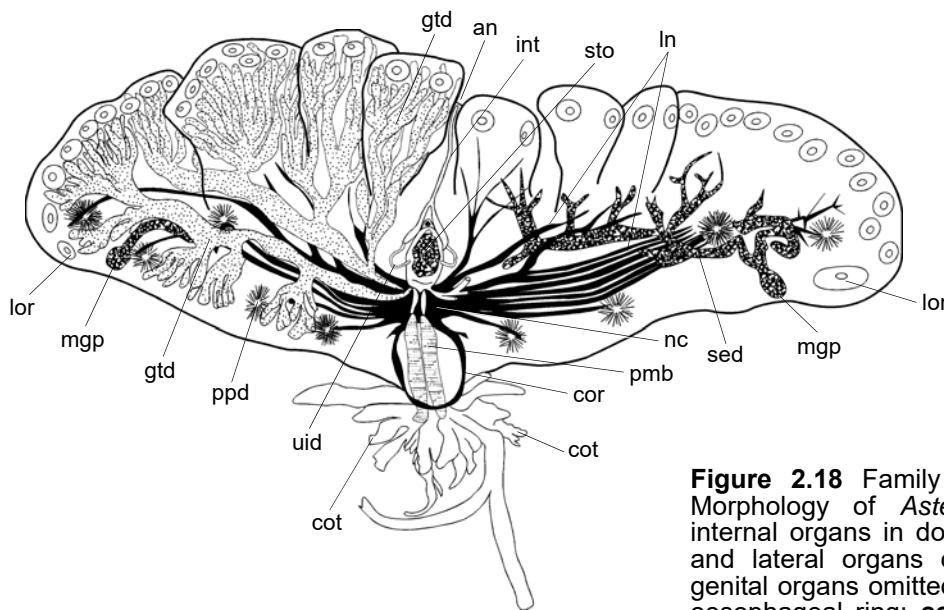


**Figure 2.17** Family Asteriomyzostomatidae. Morphology of *Asteriomyzostomum asteriae*. **A**, ventral view of one side of animal, showing digestive system. **B**, mid-sagittal view, anterior and posterior ends of body omitted. **an**, anus; **fgp**, female genital pore; **hk1–5**, hook apparatus of parapodia 1–5; **int**, intestine; **lor1–5**, lateral organs (**lor5** unpaired); **mo**, mouth; **pmb**, pharyngeal muscle bulb; **sgl**, salivary glands; **sto**, stomach; **ude**, entrance to utero-intestinal duct; **udp**, exit pore of utero-intestinal duct; **uid**, utero-intestinal duct; **ute**, uterus; **vnc**, ventral nerve cord. (After Stummer-Traunfels 1903) [I. Hallam]

### Family Asteromyzostomatidae

The family Asteromyzostomatidae is represented by the single genus *Asteromyzostomum*. Three described species from the Russian Arctic and two unnamed species from the Antarctic and Atlantic have been recorded; four of the species were found ectoparasitic on sea stars, whereas the Atlantic one was disassociated from its host (Wagin 1954; Grygier 1988). The three Russian species, *A. witjasi* (the best known; Fig. 2.18), *A. arcticum* and *A. multiplicatum*, live in the ambulacral grooves of their hosts, *Psilaster pectinatus*, *Urasterias lincki* and *Crossaster papposus*, respectively. *Asteromyzostomum witjasi* is one of the deepest living myzostomes, having been collected from 2260 m in the Bering Sea. The undescribed Antarctic species (Fig. 2.1N), found attached to the sides of the arms of a *Labidiaster* species outside McMurdo Sound, will most likely occur in the Australian Antarctic Territory. In all species, the mouth is inserted through the integument of the host and held in place by numerous circum-oral tentacles (Figs 2.1N, 2.18).





**Figure 2.18** Family Asteromyzostomatidae. Morphology of *Asteromyzostomum witjasi*, internal organs in dorsal view, but parapodia and lateral organs on ventral side; female genital organs omitted. **an**, anus; **cor**, circum-oesophageal ring; **cot**, circum-oral tentacles; **gtd**, gut diverticulum; **int**, intestine; **ln**, lateral nerves; **lor**, lateral organs; **mgb**, male genital pore; **nc**, nerve cord; **pmb**, pharyngeal muscle bulb; **ppd**, parapodium; **sed**, seminal duct; **sto**, stomach; **uid**, utero-intestinal duct. (After Wagin 1954) [I. Hallam]

In *Asteromyzostomum*, the body is wider than long through hypertrophy and lateral spreading of the equivalent of the post-parapodial sector of the body of a typical, disc-shaped species of *Myzostoma* (Wagin 1954). Females of *A. witjasi* are up to 4.2 mm long and 14.5 mm wide, and *A. multiplicatum* reaches 15.2 mm wide. The posterior margin has a great number (up to three orders) of convoluted, lobular folds that resemble a fungus and make up two-thirds to nearly all the body volume (Figs 2.1N, 2.18). The degree of folding is much more pronounced in older females than in young protandric males.

The four (in one species) or five pairs of vestigial, button-like parapodia are all found ventrally along the straight or concave anterior margin on either side of the mouth, with the third pair lying somewhat farther from the edge than the others (Fig. 2.18). The parapodial musculature was not described in detail, but is supposedly well developed and complete when compared to that of *Myzostoma*. Marginal and parapodial cirri are absent. The edges of the posterior folds bear 40 or more oval lateral organs ventrally, each with an opening and inner cavity (Fig. 2.18). A single pair of larger lateral organs lies between parapodia four and five in *A. witjasi*, but none between other parapodia; however, some have been illustrated between the parapodia in *A. arcticum*.

The epithelium consists of cuboidal cells, which overlap like scales on folds of the body and pharynx and on the bases of the circum-oral tentacles. The basal membrane has perforations through which the sunken epithelial cells extend. Within the body, the space between the internal organs and the muscles is filled with stellate and amoeboid parenchyma cells. The musculature has no radial character, but a bilateral one. The many dorso-ventral muscles do not form septa. All the fibres in the well-developed muscle sheets above and below the nervous system are parallel to the front margin of the body, and the very strongly developed postero-ventral regions of these sheets serve to contract the posterior folds.

The mouth leads into the pharynx, which traverses a strong muscle bulb and opens shortly beyond into the broad, sac-like stomach. The single pair of lateral gut diverticula immediately branch into major anterior and posterior diverticula (Fig. 2.18). Side branches of the anterior one bifurcate between the parapodia, whereas the posterior one branches more extensively by bifurcating into the posterior lobes. The stomach protrudes far into the intestine, and the anus opens just ventral to the posterior end of the body.

Wagin's (1954) description provides no clear distinction between uterus and oviduct. The uterus, lying dorsal to the gut, opens just behind the anus; its diverticula lie dorsally parallel to those of the stomach. Two utero-intestinal ducts exit the uterus, abruptly broaden, and merge to form the anterior part of the

intestine (Fig. 2.18). The testes are diffusely distributed in the parenchyma ventral to the gut. Fine seminal canals join into seminal ducts; these empty into the vasa deferentia, which open into a much expanded, deeply situated pair of penes along the anterior margin of the body between the third and fourth parapodia (Fig. 2.18). The description does not say whether the supposed penes are protrusible; perhaps they are merely seminal vesicles.

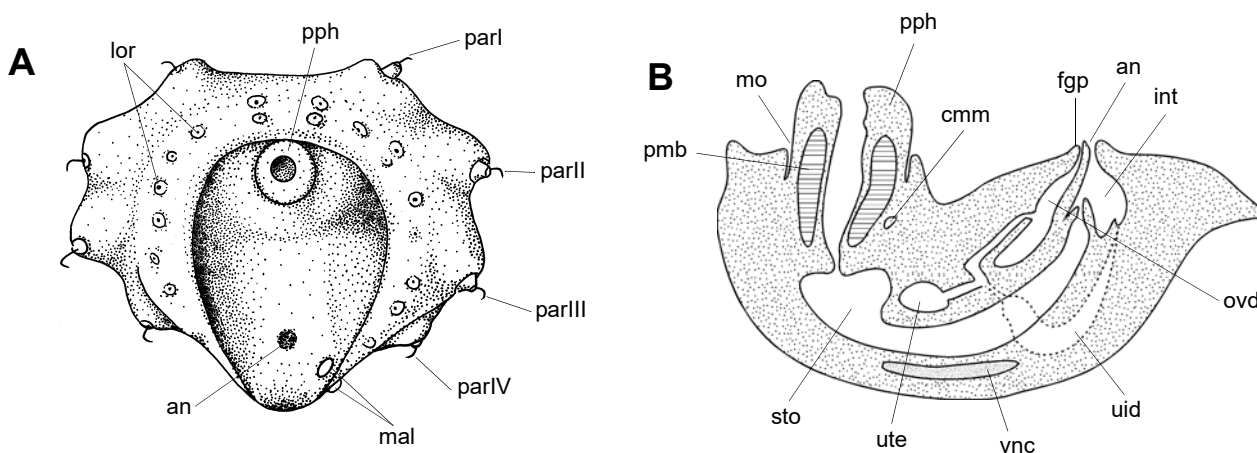
The nervous system consists of a circum-oesophageal ring connected to a laterally extended ventral ganglion or plexus. This plexus is shorter and more concentrated than the ventral nerve mass of *Myzostoma* and gives rise to 10 parallel pairs of lateral nerves (Fig. 2.18).

### Family Pulvinomyzostomatidae

The Pulvinomyzostomatidae includes one described species, *Pulvinomyzostomum pulvinar* from Europe; it has been extensively studied by Jägersten (1940a). The adult female stage occupies the oesophagus and stomach of its host crinoid of the genus *Leptometra*, often with its posterior end protruding from the mouth. Because of the bowed shape body (Fig. 2.19B), the host's gut is not blocked. Small male-stage individuals are found on the body of the female (Fig. 2.19A), or around the host's mouth if there is no female. A female of an unidentified species of *Pulvinomyzostomum* has been isolated from the Antarctic crinoid *Promachocrinus kerguelensis* collected off South Georgia (M.J. Grygier personal observation); this species may also occur in the Australian Antarctic Territory.

In the female, the anterior and lateral body margins are folded up and inward so the dorsal surface is partly depressed (Fig. 2.19A). The integument is completely ciliated. Both the mouth and anus are dorsal. A retractile, ciliated proboscis arises from a shallow pocket that reaches back only to the anterior end of the pharyngeal muscle bulb (Fig. 2.19B). Marginal parapodial cirri and buccal papillae are lacking. The second and third pairs of the very small parapodia are the most dorsal and are directed laterally; the first pair is more widely separated across the midline than the fifth (Fig. 2.19A). Usually, 10 pairs of non-protrusible lateral organs are present, one pair each in front of, and behind the first and fifth parapodia and two pairs in each space between the parapodia (Fig. 2.19A). Their inner surface consists of reticulate connective tissue underlying a layer of sensory cells.

The 'male' is oval, its length one and a half times its width. The mouth, in the form of a shallow proboscis pocket, opens terminally, and the anus is subterminal and dorsal. Five pairs of papilliform parapodia are present, the third flanked by the male genital openings. Six to 10 pairs of lateral organs are present before sex changes begin (Eeckhaut & Jangoux 1992). Marginal cirri are lacking, but the smallest males have clumps of long cilia at sites that may correspond to reduced cirri; the remainder of the body surface is ciliated, except mid-ventrally in very small specimens. The cilia on the dorsal side beat back to front (that is, opposite to those of *Myzostoma cirriferum*).



**Figure 2.19** Family Pulvinomyzostomatidae. *Pulvinomyzostomum pulvinar*. **A**, female with two males, dorsal view; fifth pair of parapodia present ventrally, but not visible. **B**, female, mid-sagittal view. **an**, anus; **cmm**, commissures; **fgp**, female gonopore; **int**, intestine; **lor**, lateral organs; **mal**, males; **mo**, mouth; **ovd**, oviduct; **parI–parIV**, parapodia I–IV; **pmb**, pharyngeal muscle bulb; **pph**, proboscis (protrusible pharynx); **sto**, stomach; **uid**, utero-intestinal duct; **ute**, uterus; **vnc**, ventral nerve cord. (After Jägersten 1940a)

[I. Hallam]

The transition from the male stage to the female stage occurs in the absence of a female. It involves a broadening and upward bending of the ventral and anterior parts of the body, and downward bending of the posterior end. The mouth is moved to the dorsal side. The proboscis is formed as the rear wall of the original mouth cavity becomes produced like a papilla. The mouth itself widens and its cavity becomes the proboscis pocket as the proboscis grows.

At most, the cuticle is extremely thin. The epidermis consists of one type of cell, the inner ends of which are at different levels. The parenchyma is unusually thick and, although there are many muscles in it, especially near the margin, defined muscle layers are lacking.

The pharynx passes through the muscle bulb into the stomach; salivary glands are absent. The elongate stomach empties into the intestine and also gives rise to three pairs of branching diverticula. For the most part these lie inside (rather than ventral to) the branches of the female reproductive system, either freely inside the lumen or anchored to the wall, and covered with an epithelium.

The uterus bears three pairs of side branches, the distal one of which bifurcates. Subsequent branching gives rise to several large sacs. A pair of ovaries is located at the base of the middle pair of side branches. Developing eggs are attached in follicles to all walls of the side branches. A posterior duct from the uterus bends twice before opening into the dorsal side of the oviduct, and the latter opens dorsally just in front of the anus (Fig. 2.19B). A pair of utero-intestinal ducts exit the uterus just before the posterior duct and occasionally fuse to each other before opening into the ventral side of the intestine (Fig. 2.19B).

The male reproductive system is compact. The testicular follicles lie in a cluster outside the third parapodia and over the genital aperture, with a cavity in between. There is no penis. The female system, including the paired utero-intestinal ducts, develops very shortly before the transition to the female stage.

The nervous system of the female consists of a dorsal cerebral ganglion behind the pharyngeal muscle bulb, linked by a pair of circum-oesophageal connectives to a condensed ventral ganglion about one third as long as the body (Fig. 2.19B). Five pairs of main lateral nerves and six pairs of intermediate nerves are present; three of the latter pairs arise from main nerves and the connectives. The cerebral ganglion and the attached peribulbar nerve ring encircling the muscle bulb branch off about six pairs of nerves anteriorly that merge into a plexus. In the male, the ventral ganglion is narrower and nearly cylindrical. The intermediate nerves arise separately from all the respective main lateral nerves.

## REFERENCES

- Afzelius, B.A. (1983). The spermatozoon of *Myzostomum cirriferum* (Annelida, Myzostomida). *Journal of Ultra-structure Research* 83: 58–68
- Afzelius, B.A. (1984). Spermiogenesis in *Myzostomum cirriferum* (Annelida; Myzostomida). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn* 145: 11–21
- Atkins, D. (1927). Report on the Myzostomida collected by Mr. F.A. Potts in Torres Strait, together with a description of a species obtained by Professor J. Stanley Gardiner from the Maldives. *Proceedings of the Zoological Society of London* 1927: 339–357, plates I–II
- Bargalló, R. (1977). Polimorfisme dels gàmetes masculins. III. Consideracions espermatològiques a propòsit dels Mizostòmids. *Butlletí de la Societat Catalana de Biologia* 2: 33–39, plate
- Bartsch, I. & Faubel, A. (1995). *Protomyzostomum glanduliferum* n. sp., a new myzostomid from the Antarctic ophiuroid *Ophiacantha disjuncta*. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 92: 35–43
- Beard, J. (1884). On the life-history and development of the genus *Myzostoma* (F.S. Leuckart). *Mittheilungen aus dem Zoologischen Station zu Neapel* 5: 544–580, plates 31 & 32
- Beard, J. (1898). The sexual conditions of *Myzostoma glabrum* (F.S. Leuckart). *Mittheilungen aus dem Zoologischen Station zu Neapel* 13: 293–324, plate 10
- Boulenger, C.L. (1913). Report on the Myzostomida collected by Mr. Cyril Crossland in the Red Sea in 1905. *Proceedings of the Zoological Society of London* 1913: 85–108
- Boulenger, C.L. (1916). Myzostomida. *British Antarctic (“Terra Nova”) Expedition, 1910. Natural History Report. Zoology* 2: 135–140, plate I
- Day, J.H. & Hutchings, P.A. (1979). An annotated check-list of Australian and New Zealand Polychaeta, Archiannelida and Myzostomida. *Records of the Australian Museum* 32: 80–161
- Eeckhaut, I. (1995). Cycle vital et biologie de *Myzostoma cirriferum* (Myzostomida), symbiote obligatoire de la comatule *Antedon bifida* (Echinodermata). D.Sc. thesis, Université de Mons-Hainaut, Belgium
- Eeckhaut, I. (1998). *Mycomyzostoma calcidicola* gen. nov., sp. nov., the first extant parasitic myzostome infesting crinoid stalks, with a nomenclatural appendix by M.J. Grygier. *Species Diversity* 3(1): 89–103
- Eeckhaut, I. & Améziane-Cominardi, N. (1994). Structural description of three myzostomes parasites of crinoids and of the skeletal deformities they induce on their hosts. Pp. 203–209 in David, B., Guille, A., Feral, J.-P. & Roux, M. (eds) *Echinoderms through Time. Proceedings of the Eighth International Echinoderm Conference*. A.A. Balkema : Rotterdam
- Eeckhaut, I., Dochy, B. & Jangoux, M. (1995). Feeding behaviour and functional morphology of the introvert and digestive system of *Myzostoma cirriferum* (Myzostomida). *Acta Zoologica, Stockholm* 76: 307–315
- Eeckhaut, I., Grygier, M.J. & Deheyn, D. (1998). Myzostomes from Papua New Guinea, with related Indo-West Pacific distribution records and description of five new species. *Bulletin of Marine Science* 62: 841–886
- Eeckhaut, I. & Jangoux, M. (1991). Fine structure of the spermatophore and introdermic penetration of sperm cells in *Myzostoma cirriferum* (Annelida, Myzostomida). *Zoomorphology* 111: 49–58
- Eeckhaut, I. & Jangoux, M. (1992). Development and behaviour of *Myzostoma alatum* and *Pulvinomyzostomum pulvinar*, two myzostomid symbiotes of the comatulid *Leptometra phalangium* (Echinodermata). Pp. 229–236 in Scalera-Liaci, L. & Canicatti, C. (eds) *Echinoderm Research 1991*. A.A. Balkema : Rotterdam
- Eeckhaut, I. & Jangoux, M. (1993a). Integument and epidermal sensory structures of *Myzostoma cirriferum* (Myzostomida). *Zoomorphology* 113: 33–45
- Eeckhaut, I. & Jangoux, M. (1993b). Life cycle and mode of infestation of *Myzostoma cirriferum* (Annelida), a symbiotic myzostomid of the comatulid crinoid *Antedon bifida* (Echinodermata). *Diseases of Aquatic Organisms* 15: 207–217



- Eeckhaut, I. & Jangoux, M. (1995). *Contramyzostoma bialatum* (Annelida: Myzostomida), a new genus and species of parasitic myzostome infesting comatulid crinoids. *The Raffles Bulletin of Zoology* 43(2): 343–353
- Eeckhaut, I. & Jangoux, M. (1997). Infestation, population dynamics, growth and reproductive cycle of *Myzostoma cirriferum* (Myzostomida), an obligate symbiont of the comatulid crinoid *Antedon bifida* (Crinoidea, Echinodermata). *Cahiers de Biologie Marine* 38(1): 7–18
- Eeckhaut, I., VandenSpiegel, D. & Grygier, M.J. (1994). Myzostomida (Annelida) from Singapore, with related Indo-Pacific distribution records and descriptions of three new species. *The Raffles Bulletin of Zoology* 42: 669–688
- Fabricius, K.E. & Dale, M.B. (1993). Multispecies associations of symbionts on shallow water crinoids of the central Great Barrier Reef. *Coenoses* 8: 41–52
- Fauvel, P. (1936). Polychètes. *Résultats du voyage de la Belgica en 1897–1899 sous le commandement de A. de Gerlache de Gomery*. J.E. Buschmann : Anvers 44 pp.
- Fedotov, D. (1912). *Protomyzostomum polynephris*, eine neue Myzostomidenart. *Zoologischer Anzeiger* 39: 649–653
- Fedotov, D. (1914). Die Anatomie von *Protomyzostomum polynephris* Fedotov. *Zeitschrift für Wissenschaftliche Zoologie* 109: 631–696, plates XIX–XXII
- Fedotov, D.M. (1916). The parasitism of *Protomyzostomum* in the *Gorgonocephalus eucnemis*. *Zoologicheskii Vestnik [Russian Journal of Zoology]* 1: 161–218, plates VIII–X [in Russian with extended English summary]
- Fedotov, D.M. (1925). Über eine neue Art von *Protomyzostomum* (*Pr. astrocladi*, sp. n.) aus *Astrocladus*. *Zoologischer Anzeiger* 73: 183–194
- Fedotov, D.M. (1929). Beiträge zur Kenntnis der Morphologie der Myzostomiden. *Zeitschrift für Morphologie und Ökologie der Tiere* 15: 156–191
- Fedotov, D.M. (1938). Spezialisierung und Degradation im Körperbau der Myzostomiden in Abhängigkeit von der Lebensweise. *Acta Zoologica, Stockholm* 19: 353–385
- Fishelson, L. (1974). Ecology of the northern Red Sea crinoids and their epi- and endozoic fauna. *Marine Biology, Berlin* 26: 183–192
- Franzén, C. (1974). Epizoans on Silurian-Devonian crinoids. *Lethaia* 7: 287–301
- Goenaga, C. (1977). Two new species of *Stichopathes* (Zoantharia; Antipatharia) with observations on aspects of their biology. M.S. thesis, University of Puerto Rico
- Graff, L.v. (1877). *Das Genus Myzostoma* (F.S. Leuckart). Verlag von Wilhelm Engelmann : Leipzig viii 82 pp., plates I–XI
- Graff, L.v. (1883). Verzeichniss der von der United States Coast Survey steamers “Hassler” und “Blake” von 1867 zu 1879 gesammelten Myzostomiden. *Bulletin of the Museum of Comparative Zoology, Harvard College* 11: 125–133
- Graff, L.v. (1884a). On the Myzostomida of the “Porcupine” and “Triton” dredgings. *Proceedings of the Royal Society of Edinburgh* 12: 378–380
- Graff, L.v. (1884b). Report on the Myzostomida collected during the voyage of H.M.S. *Challenger* during the years 1873–76. *Reports on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76, Zoology* 10: 1–82, plates I–XVI
- Graff, L.v. (1884c). Nye Arter af Myzostomider i Universitetets Zoologiske Museum i Kjøbenhavn. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn* (4)6: 81–85
- Graff, L.v. (1885a). Ueber einige Deformitäten an fossilen Crinoiden. *Palaeontographica* 31: 185–191, plate XVI (I)
- Graff, L.v. (1885b). Description of a new species of *Myzostoma*. *Transactions of the Linnean Society of London, 2nd Series, Zoology* 2: 444–446, plate LII (fig. 19)
- Graff, L.v. (1887). Report on the Myzostomida collected during the voyage of H.M.S. *Challenger* during the years 1873–76. Supplement. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76, Zoology* 20: 1–16, plates I–IV

- Grygier, M.J. (1988). Unusual and mostly cysticolous crustacean, molluscan, and myzostomidan associates of echinoderms. Pp. 775–784 in Burke, R.D., Mladenov, P.V., Lambert, P. & Parsley, R.L. (eds) *Echinoderm Biology*. A.A. Balkema : Rotterdam
- Grygier, M.J. (1989). Three new species of *Myzostoma* (Myzostomida). *Proceedings of the Biological Society of Washington* 102: 793–804
- Grygier, M.J. (1990). Distribution of Indo-Pacific Myzostomida and host specificity of comatulid-associated Myzostomida. *Bulletin of Marine Science* 47: 182–191
- Grygier, M.J. (1992). Hong Kong Myzostomida and their Indo-Pacific distributions. Pp. 131–147 in Morton, B. (ed.) *The Marine Flora and Fauna of Hong Kong and Southern China III. Proceedings of the Fourth International Marine Biological Workshop*. Hong Kong University Press : Hong Kong
- Grygier, M.J. & Nomura, K. (1998). Cysticolous Myzostomida, *Notopharyngoides platypus* from *Comanthina nobilis* (Echinodermata : Crinoidea), at Kushimoto, Honshu, Japan. *Species Diversity* 3(1): 17–24
- Haszprunar, G. (1996). The Mollusca: Coelomate turbellarians or mesenchymate annelids? Pp. 3–28 in Taylor, J. (ed.) *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press : Oxford
- Heinzeller, T., Aschauer, B., Lange, A. & Welsch, U. (1995). A myzostomid invading the connective tissue of its host *Comanthus parvicirrus* (Crinoidea). Pp. 3–8 in Emson, R., Smith, A. & Campbell, A. (eds) *Echinoderm Research 1995. Proceedings of the European Echinoderms Colloquium*. A.A. Balkema : Rotterdam
- Jägersten, G. (1934). Studien über den histologischen Bau der männlichen Geschlechtsorgane und die Ausbildung des Spermiums bei *Myzostomum*. *Zoologiska Bidrag från Uppsala* 16: 1–22
- Jägersten, G. (1936). Zur Kenntnis der Parapodialborsten bei *Myzostomum*. *Zoologiska Bidrag från Uppsala* 16: 283–299
- Jägersten, G. (1937). Myzostomiden von Prof. Dr. Sixten Bocks Expedition nach Japan und den Bonin-Inseln 1914. *Arkiv för Zoologi* 29A(17): 1–35
- Jägersten, G. (1939a). Zur Kenntnis der Larvalentwicklung bei *Myzostomum*. *Arkiv för Zoologi* 31A(11): 1–21
- Jägersten, G. (1939b). Über die Morphologie und Physiologie des Geschlechtsapparats und den Kopulationsmechanismus der Myzostomiden. *Zoologiska Bidrag från Uppsala* 18: 163–242, plates I–VII
- Jägersten, G. (1940a). Zur Kenntnis der Morphologie, Entwicklung und Taxonomie der Myzostomida. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* (4)11(8): 1–84, plates I–VII
- Jägersten, G. (1940b). Neue und alte *Myzostomum*-Arten aus dem Zoologischen Museum Kopenhagen. *Videnskabelige Meddelelser fra Dansk Naturhistorisk forening i København* 104: 103–125, plate 1
- Jägersten, G. (1940c). Zur Kenntnis der Histologie und Physiologie (besonders der Exkretion) des Darmes der Myzostomiden. *Zeitschrift für Wissenschaftliche Zoologie* 153: 83–107
- Jägersten, G. (1941). Zur Kenntnis von *Glanduloderma myzostomatis* n. gen., n. sp., einer eigentümlichen, in Myzostomiden schmarotzenden Turbellarienform. *Arkiv för Zoologi* 33A(3): 1–24
- Jangoux, M. (1987). Diseases of Echinodermata. III. Agents metazoans (Annelida to Pisces). *Diseases of Aquatic Organisms* 3: 59–83
- Jangoux, M. (1990). Diseases of Echinodermata. Pp. 439–567 in Kinne, O. (ed.) *Diseases of Marine Animals. Vol. III*. Biologische Anstalt Helgoland : Hamburg
- Kato, K. (1952). On the development of myzostomes. *Science Reports of Saitama University, Series B (Biology and Earth Sciences)* 1: 1–16, plates I–III
- Lester, R.J.G. & Sewell, K.B. (1989). Checklist of parasites from Heron Island, Great Barrier Reef. *Australian Journal of Zoology* 37: 101–128
- Mattei, X. & Marchand, B. (1987). Les spermatozoïdes des Acanthocéphales et des Myzostomides. Ressemblances et conséquences phylétiques. *Comptes Rendus de l'Académie des Sciences, Série III, Sciences de la Vie* 305: 525–529
- Mattei, X. & Marchand, B. (1988). La spermiogenèse de *Myzostomum* sp. (Procoelomata, Myzostomida). *Journal of Ultrastructure and Molecular Structure Research* 100: 75–85

- McClendon, J.F. (1906). The myzostomes of the 'Albatross' Expedition to Japan. *Bulletin of the American Museum of Natural History* 23: 119–130, plates XV–XVII
- Meyer, D.L. & Ausich, W.I. (1983). Biotic interactions among recent and among fossil crinoids. Pp. 377–427 in Tevesz, M.J.S. & McCall, P.L. (eds) *Biotic Interactions in Recent and Fossil Benthic Communities*. Plenum Publishing Corporation : New York
- Nansen, F. (1885). *Bidrag til Myzostomernes Anatomi og Histologi*. Bergens Museum : Bergen 80 pp., plates 1–9
- Nansen, F. (1887). Anatomie und Histologie des Nervensystemes der Myzostomen. *Jenaische Zeitschrift für Naturwissenschaft* 21: 267–321, plate XIX
- Nigmatullin, Ch.M. (1970). *Protomyzostomum cystobium* n. sp. from cysts on the arms and disc of *Gorgonocephalus caryi* Lyman. Pp. 50–66 in Wagin, V.L. (ed.) *Voprosy Evolyutsionnoi Morfologii i Biogeografii* [Questions of Evolutionary Morphology and Biogeography]. Kazan University Press : Kazan [in Russian]
- Okada, Y. (1920). One species of Myzostomida attached to a hexactinellid sponge. *Dobutsugaku Zasshi* [Zoological Magazine, Tokyo] 32: 324–325 [in Japanese]
- Okada, Y. (1922). On a new *Protomyzostomum* (*P. sagamiense*, sp. nov.) from the ovary of *Gorgonocephalus*. *Annotationes Zoologicae Japonenses* 10: 165–169
- Okada, Y. (1933). *Mesomyzostoma katoi*, n. sp., an interesting myzostome found in the gonad of *Comanthus japonicus*. *Annotationes Zoologicae Japonenses* 14: 185–189
- Perrier, E. (1897). Philocrinida. P. 1633 in Perrier, E. *Traité de Zoologie. Fascicule IV. Vers (Suite) – Mollusques – Tuniciers*. Masson et Cie : Paris
- Pietsch, A. & Westheide, W. (1987). Protonephridial organs in *Myzostoma cirriferum* (Myzostomida). *Acta Zoologica, Stockholm* 68: 195–203
- Platel, R. (1962). Histologie du tube digestif de *Myzostomum cirriferum* (Leuckart) (Myzostomides). *Cahiers de Biologie Marine* 3: 261–288
- Potts, F.A. (1915). The fauna associated with the crinoids of a tropical coral reef: with especial reference to its colour variations. *Papers from the Department of Marine Biology of the Carnegie Institution of Washington* 8: 71–96, plate I
- Prenant, M. (1959). Classe des Myzostomides. Pp. 714–784 in Grassé, P.P. (ed.) *Traité de Zoologie, Tome 5*. Masson et Cie : Paris
- Rao, K.H. & Sowbhagyavathi, R. (1974) [dated 1972]. Observations on the associates of crinoids at Waltair Coast with special reference to myzostomes. *Proceedings of the Indian National Science Academy, Part B – Biological Sciences* 38: 360–366
- Remscheid, E. (1918). Beiträge zur Kenntnis der Myzostomiden. *Abhandlungen Herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft* 35: 179–225, plates XII–XIV
- Rouse, G.W. & Fauchald, K. (1997). Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204
- Stamman, E., Phillips, D., Phillips, L. & Segar, D. (1985). Close associations: the sea makes strange bedfellows. *Oceans* 18: 10–17
- Stummer-Traunfels, R.R.v. (1903). Beiträge zur Anatomie und Histologie der Myzostomen. I. *Myzostoma asteriae* Marenz. *Zeitschrift für Wissenschaftliche Zoologie* 65: 495–595, plates XXXIV–XXXVIII
- Stummer-Traunfels, R.R.v. (1908). Myzostomidae. *National Antarctic Expedition, Natural History* 4: 1–26
- Stummer-Traunfels, R.R.v. (1910). Arktische Myzostomen. Mit einer Anhang: Ueber den Bau der Borstendrüsen bei *Myzostoma gigas* Graff. Pp. 75–86 in Römer, F. & Shaudinn, F. (eds) *Fauna Arctica, Vol. 5*. Verlag von Gustav Fischer : Jena
- Stummer-Traunfels, R.v. (1926). Myzostomida. Pp. 132–210 in Kükenthal, W. & Krumbach, T. (eds) *Handbuch der Zoologie, Vol. 3*. Walter de Gruyter & Co. : Berlin
- Uchida, H. (1992). Annelida. Pp. 310–313 in Nishimura, S. (ed.) *Guide to Seashore Animals of Japan with Colour Pictures and Keys, Vol. 1*. Hoikusha Publishing Co., Ltd. : Osaka [in Japanese]

- Wagin, V.L. (1954). *Asteromyzostomum* n. gen. – a new representative of the class Myzostomida (Annelides). *Trudy Leningradskogo Obshchestva Yestestvoispytateley* 72(4): 16–37 [in Russian]
- Wagin, V.L. (1976). On the position of the Myzostomida among the trochophoric animals. Pp. 45–46 in Skarlato, O.A. (ed.) *Evolutsionnaya Morfologiya Bespozvonochnykh Zhivotnykh* [*The Evolutionary Morphology of the Invertebrates*]. Zoological Institute of the Academy of Sciences of the U.S.S.R. : Leningrad [in Russian]
- Wagin, V.L. (1979). On the position of myzostomids among the trochophoric animals. Pp. 124–135 in Wagin, V.L. (ed.) *Voprosy Evolyutsionnoy Morfologii Zhivotnykh* [*Questions on the Evolutionary Morphology of Animals*]. Kazan University Press : Kazan [in Russian]
- Welch, J.R. (1976). *Phosphannulus* on Paleozoic crinoid stems. *Journal of Paleontology* 50: 218–225
- Wheeler, W.M. (1896). The sexual phases of *Myzostoma*. *Mittheilungen aus der Zoologischen Station zu Neapel* 12: 227–302, plates 10–12
- Wheeler, W.M. (1899). J. Beard on the sexual phases of *Myzostoma*. *Zoologischer Anzeiger* 22: 281–288
- Wheeler, W.M. (1905). A new *Myzostoma*, parasitic in a starfish. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 8: 75–78
- Woodham, A. (1992). Distribution and population studies on *Myzostoma cirriferum* Leuckart (Myzostomida) in a Scottish sea loch. Pp. 247–255 in Colombo, G., Ferrari, I., Ceccherelli, V.U. & Rossi, R. (eds) *Marine Eutrophication and Population Dynamics*. Olsen & Olsen : Fredensborg
- Zrzavý, J., Mihulka, S., Kepka, P., Bedzek, A. & Tietz, D. (1998). Phylogeny of the Metazoa based on morphological and 18S ribosomal DNA evidence. *Cladistics* 14: 249–285