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FOREGUT ANATOMY OF THE LARGER SPECIES OF TURRINAE, CLAVATULINAE AND CRASSISPIRINAE (GASTROPODA: CONOIDEA) FROM HONG KONG

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ABSTRACT

The anatomy of the foregut is described for ten species of the gastropod family Turridae collected from shallow waters around Hong Kong. Anatomical characters including the length of the proboscis, the position of the buccal mass, the epithelium of the rhynchodeum, the size of the buccal lips, the morphology of the radular teeth and the looping of the oesophagus, were used to define five different types of foregut organization. The two species of Turrinae have an anatomy, which apart from the radular teeth, departs little from the plesiomorphic condition for the Conoidea. The two species of *Turricula* (Clavatulinae) are very different, with a buccal mass located near the distal tip of the proboscis. Most variation is found among the six species of Crassispirinae which have three different proboscis and radular types. The hollow hypodermic-style teeth of *Ptychobela* represent another evolutionary pathway to the toxoglossan feeding mechanism.

INTRODUCTION

The prosobranch gastropod superfamily Conoidea comprises the three families Conidae, Terebridae and Turridae united by the possession of the toxoglossan feeding mechanism involving the venom gland and modified radular teeth. The Turridae are by far the most diverse of the three families, with perhaps more than 4000 living species and 336 genera. Turrids are particularly abundant in soft-substrate habitats from shallow subtidal to abyssal depths, but their biology is poorly known. The family is also in a state of some taxonomic confusion with seventeen subfamilies in current use. Most of these taxa are rather poorly defined on the basis of a few shell and/or radular characters (Powell 1966; McLean 1971).

Recently, Taylor *et al.* (1993) have proposed a new classification of the Conoidea, based mainly upon characters of foregut anatomy and radula. However, even now relatively few species have been studied anatomically, with amongst these a rather heavy

bias towards species from high latitudes. For most subfamilies, the anatomy is known for only a few species. Nevertheless, it is now clear that conoidean gastropods show a surprisingly wide diversity of foregut anatomy, which reflects a diversity of feeding methods and behaviour. Hollow, barbed, harpoon-like radular teeth have been independently evolved several times (Taylor *et al.* 1993) and even so-called 'primitive' turrids are capable of using single radular teeth at the proboscis tip (Kantor and Taylor 1991).

In Hong Kong, several species of larger Turridae from three subfamilies, Turrinae, Clavatulinae and Crassispirinae, are common in shallow sublittoral habitats. One of these, *Turricula nelliae spurius*, (Hedley) is particularly abundant in the north-western part of Mirs Bay (Taylor 1992), and its anatomy, diet and feeding behaviour has been described by Taylor (1986) and Miller (1989, 1990). However, there are a further nine larger species for which the anatomy is unknown. Six species can be classified in the subfamily Crassispirinae, a poorly known taxon from which widely disparate radular morphologies have been reported. For instance, Kilburn (1988, 1989) has demonstrated that the genera *Inquisitor*, *Funa* and *Ptychobela* have very similar shells, but very different radular teeth.

The objective of this paper is to describe the foregut anatomy and radulae of the common larger species of turrid gastropods from around Hong Kong. These data will contribute to an improved understanding of phylogenetic relationships among the conoidean suprageneric taxa, and also the evolution of the toxoglossan feeding mechanism.

MATERIALS AND METHODS

Most of the gastropods used in this study (Table 1) were collected in April 1992 during the trawl sampling programme around southern Hong Kong. Details of the stations, distribution and abundance of the species are given in Taylor (this volume). Additional material was derived from collections made from previous trawl surveys of Tolo Channel and Mirs Bay (details in Taylor and Shin 1990; Taylor 1992) and now housed in The Natural History Museum, London.

The foreguts of a least two specimens of each species were dissected and drawings

Table 1
List and classification of species examined anatomically.

Family Turridae
Subfamily Turrinae
Lophiotoma leucotropis (Adams and Reeve, 1850)
Gemmula deshayesii (Dournet, 1839)

Subfamiiy Clavatulinae
Turricula nelliae spurius (Hedley, 1922)
Turricula javana (Linnaeus, 1767)

Subfamily Crassispirinae
Funa jeffreysii (Smith, 1875)
Funa latisinuata (Smith, 1877)
Inquisitor latifasciata (Sowerby, 1870)
Cheungbeia mindanensis (Smith, 1877)
Cheungbeia robusta (Hinds, 1843)
Ptychobela suturalis (Gray, 1838)

made using camera lucida. Longitudinal serial sections were made of the foregut of each species (except *Ptychobla suturalis*). Preparations of at least two radulae for each species were examined by scanning electrom microscopy.

RESULTS

The definition and nomenclature of the foregut organs and structures and the classificaton of genera follows Taylor *et al.* (1993).

Turrinae

Lophiotoma leucotropis (Adams and Reeve, 1850)

(Plates 1a, 2; Figs 1–2)

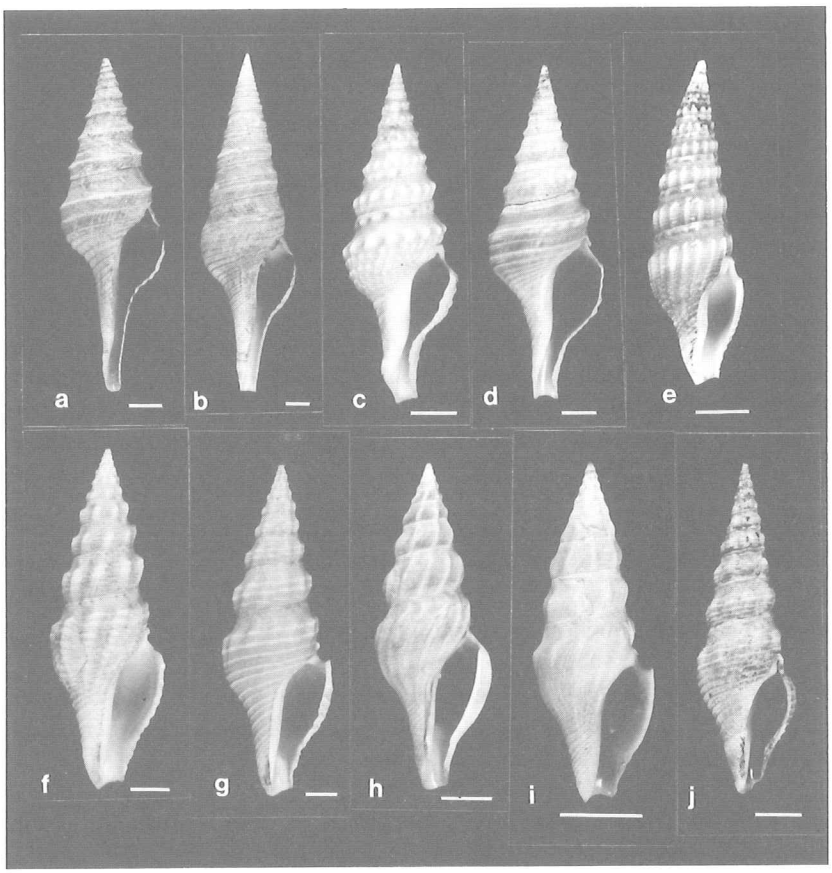

Plate 1. Shells of species studied in this paper. A, *Lophiotoma leucotropis*; B, *Gemmula deshayesi*; C, *Turricula nellie spurius*; D, *Turricula javana*; E, *Inquisitor latifasciata*; F, *Funa flavidula*; G, *Funa latisinuata*; H, *Cheungbeia mindanensis*; I, *Cheungbeia robusta*; J, *Ptychobela suturalis*. Scale bar 5 mm in each case.

Taxonomy. This species is described and illustrated by Powell (1964, p. 312).

Distribution. Around Hong Kong, this species is commonly found in north-western Mirs Bay and Tolo Channel and less commonly off Cape d'Aguilar. More widely, it is known from China, Taiwan southern Japan and the northern Philippines

Foregut anatomy. There is a large rhynchocoel (Fig. 1) lined almost entirely by glandular epithelium with only the extreme posterior end not glandular. The rhynchostomal sphincter is located in a posterior position, with glandular epithelium in the anterior part of the rhynchostome. The proboscis is robust, medium-long and capable of protraction through the rhynchostome. Within the buccal tube, there is a single, annular sphincter near the tip, but anterior to this there is a sac-like enlargement, lined by tall epithelial cells. In thin section, a single marginal radular tooth of the wishbone type is seen gripped by the tall epithelium. Relaxed specimens show that the anterior part of the buccal tube can be everted (Fig. 1), which would expose the radular tooth at the proboscis tip. The buccal mass is located just within the base of the proboscis. There is a large odontopore, with two large, unfused cartilages. The radular sac is long (Fig. 2). There are two large, separate, acinous, salivary glands each with ducts which enter the buccal cavity on either side of the buccal sac. The venom gland is fairly short and glandular throughout most of its length, becoming duct-like only in the section immediately before insertion into the buccal cavity, in a position just to the posterior of the radular sac. The venom gland terminates proximally in the muscular bulb, which is composed of two layers of longitudinal muscle separated by a thin connective tissue layer and with the interior lined by a layer of epithelial cells.

Radula. The radula ribbon is robust, with two marginal teeth in each radular row (Plate 2). Lateral and central teeth are absent. The marginal teeth are of the 'wishbone' type, with the proximal half of the tooth bifid. The two limbs of the tooth are approximately equal in size. The distal end of each tooth is dagger-like and sharply pointed, with a knife-like edge along either side.

Gemmula deshayesii (Doumet, 1839)
(Plates Ib,3; Figs 3-5)

Taxonomy. This species is described and illustrated by Powell (1964, p. 270-1).

Distribution. Around Hong Kong, this species has been found in Tolo Channel, northern Mirs Bay and in the southern area around Cape d'Aguilar. Elsewhere, it is known from southern Japan, Taiwan and China.

Foregut anatomy. There is a large rhynchocoel cavity (Fig. 3), which, except for the extreme posterior end is lined with glandular epithelium. The rhynchodeal sphincter is located in a posterior position within the rhynchostome. A glandular epithelium lines the anterior part of rhynchostome. The proboscis is moderately long, and in the retracted state occupies most of the length of the rhynchocoel. The buccal tube has an annular sphincter situated a short distance to the posterior of the proboscis tip. Anterior to the sphincter is a sac-like enlargement containing tall epithelial cells, where detached mar-

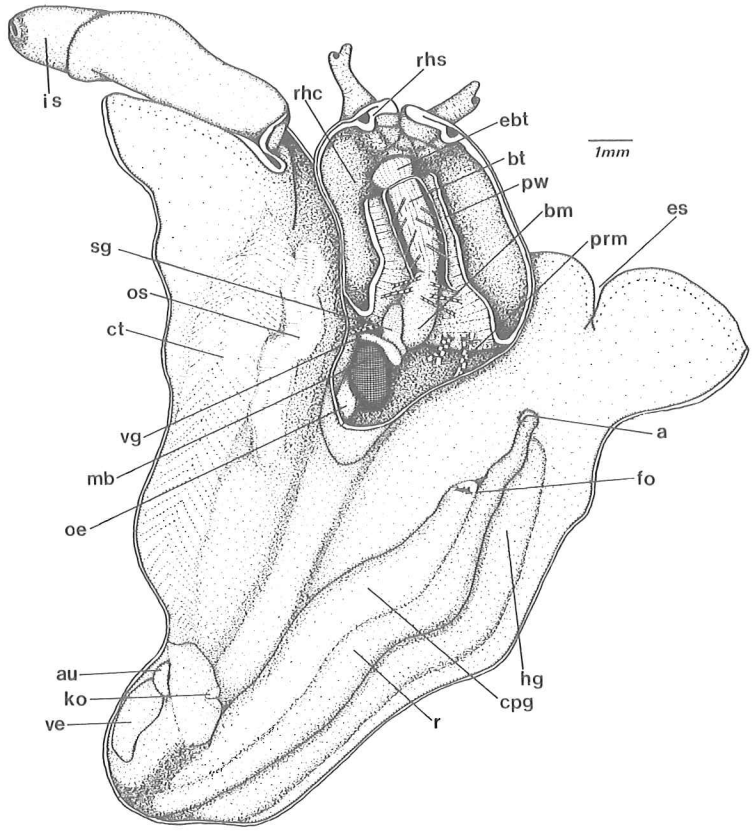

Fig. 1. *Lophiotoma leucotropis*, general anatomy of the foregut.

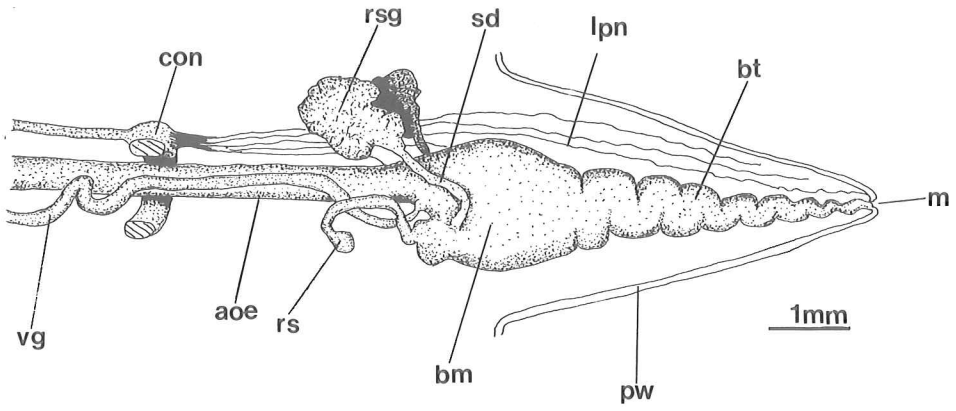

Fig. 2. *Lophiotoma leucotropis*, diagram showing details of the foregut within the proboscis walls.

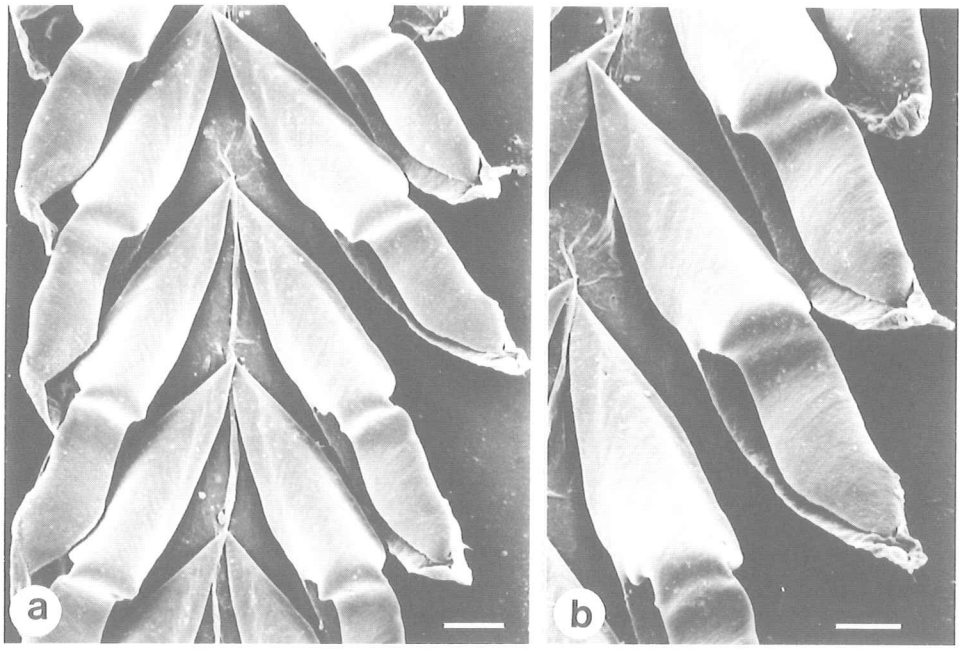

Plate 2. Radula of *Lophiotoma leucotropis*. A, portion of radular ribbon with two marginal teeth in each row. Scale bar 10 μm. B, marginal tooth. Sale bar 15 μm.

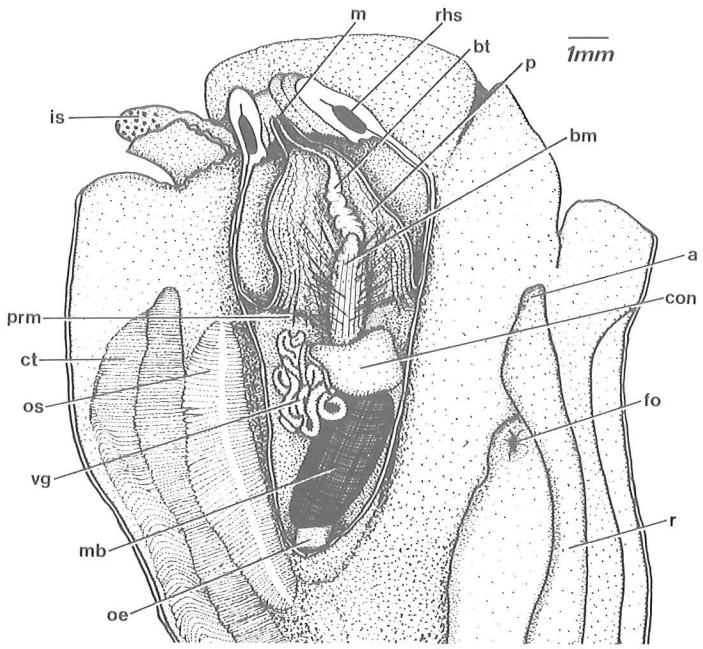

Fig. 3. *Gemnula deshayesii*; general view of the foregut.

ginal teeth are held (Fig. 5). As in *Lophiotoma*, it is likely that the anterior part of the buccal tube can evert, thereby exposing the tooth. The buccal mass is contained within the base of the proboscis. The walls of the buccal mass are highly muscular, with two short muscular lips at the anterior opening into the buccal tube (Fig. 4). The odontophore is large with two unfused cartilages. Ducts from two large acinous salivary glands enter to either side of the buccal sac. The venom gland is long and has a uniformly glandular histology, except for a short, duct-like tract immediately before its entry into the buccal cavity, just to the posterior of the radular sac. The muscular bulb is large and somewhat cylindrical in shape, composed of two layers of longitudinal muscle separated by a thin connective tissue layer. The outermost muscle layer is about twice as thick as the innermost.

Radula. There are three teeth in each radular row, consisting a central and two marginal teeth set on a robust radular ribbon (Plate 3). The central tooth is broad and rectangular with a central cusp. and except for the leading edge, the tooth has a low profile and is poorly defined. The marginal teeth are robust and of the 'wishbone' type with the proximal portions bifid. The innermost limb of the tooth is slightly larger and thicker than the outer limb, which has a knee-like bend. The distal end of the tooth is dagger-like, sharply pointed with a knife-like inner blade.

Clavatulinae

Turricula nelliae spurius (Hedley, 1922)

(Plates 1c, 4; Figs. 6 and 7a)

Taxonomy. Powell (1969, pp. 238-40) has described and discussed the the nomenclature of this species in some detail. Taylor *et al.* (1993) have recently advocated removing *Turricula* from the Turriculinae (now Cochlespirinae) and placing it in the Clavatulinae. This decision is based on a suite of anatomical characters shared between the taxa, the similarity of the radulae and the mediolateral position of the nucleus of the operculum.

Distribution. Around Hong Kong, this species is very abundant in northern Mirs Bay and Tolo Channel, but less abundant off the southern coast around Cape d'Aguilar. Elesewhere, it is known from the northern Indian Ocean, Indonesia, New Guinea, and China.

Foregut anatomy. The foregut anatomy of this species has already been described by Taylor (1986) and Miller (1990). However, some further details are now available and these and the major features are summarized below.

There is a posteriorly-located sphincter to the rhynchostome. The rhynchocoel is lined with glandular epithelium, except at the posterior where the rhynchodeal wall has the same histology as the proboscis wall. There is a large proboscis capable of long protraction through the rhynchostome (Fig. 6). The buccal tube is very short with two annular sphincters at the anterior tip. The buccal mass and radular sac are situated near the distal end and entirely within the proboscis. The buccal cavity is muscular with short anterior buccal lips. The odontophore is large with two separate cartilages. The pair of acinous salivary glands are elongate and lie alongside the oesophagus and are contained within the proboscis. Two salivary ducts enter on either side of the buccal sac. Poste-

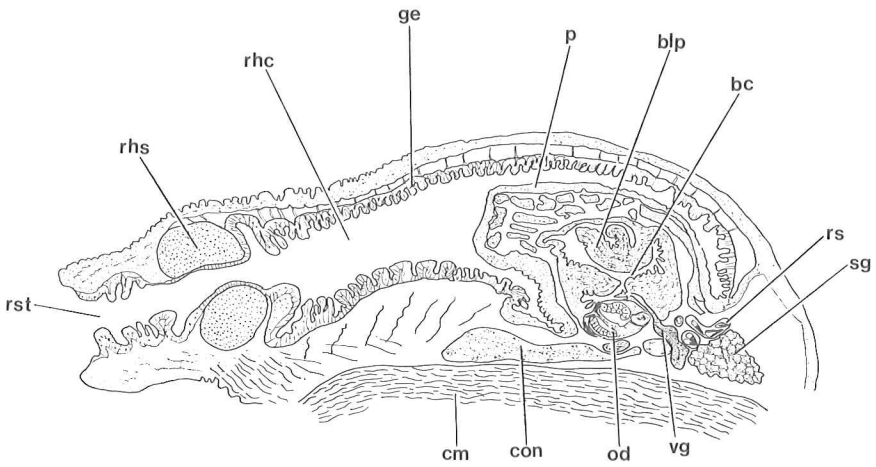

Fig. 4. *Gemmula deshayesii,* longitudinal section through the foregut.

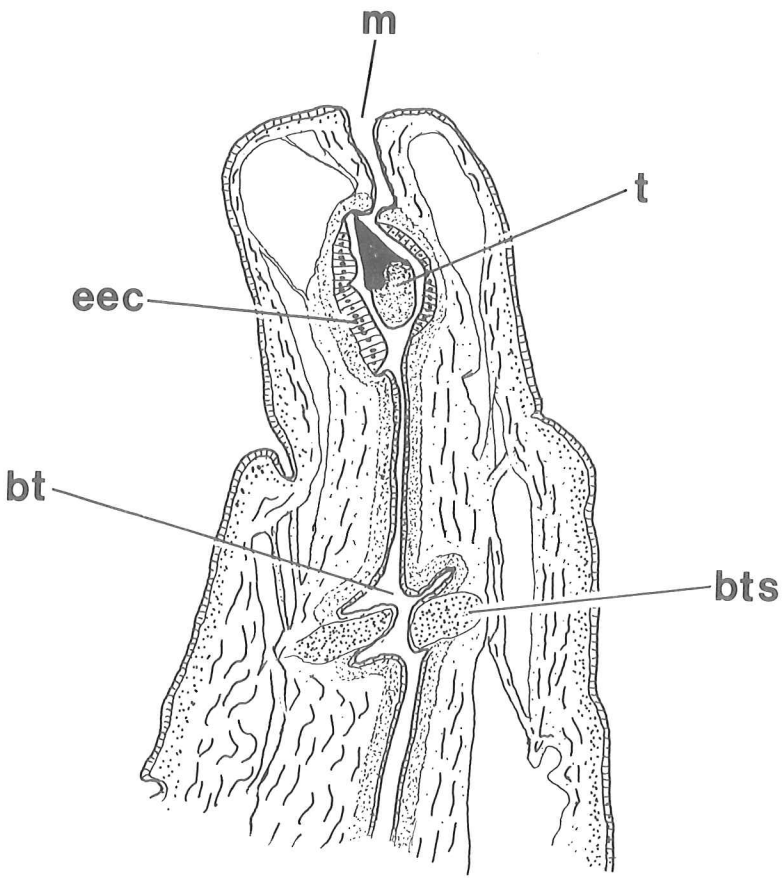

Fig. 5. *Gemmula deshayesii*, section through the proboscis tip showing single radular tooth held in sac-like enlargement of the buccal tube.

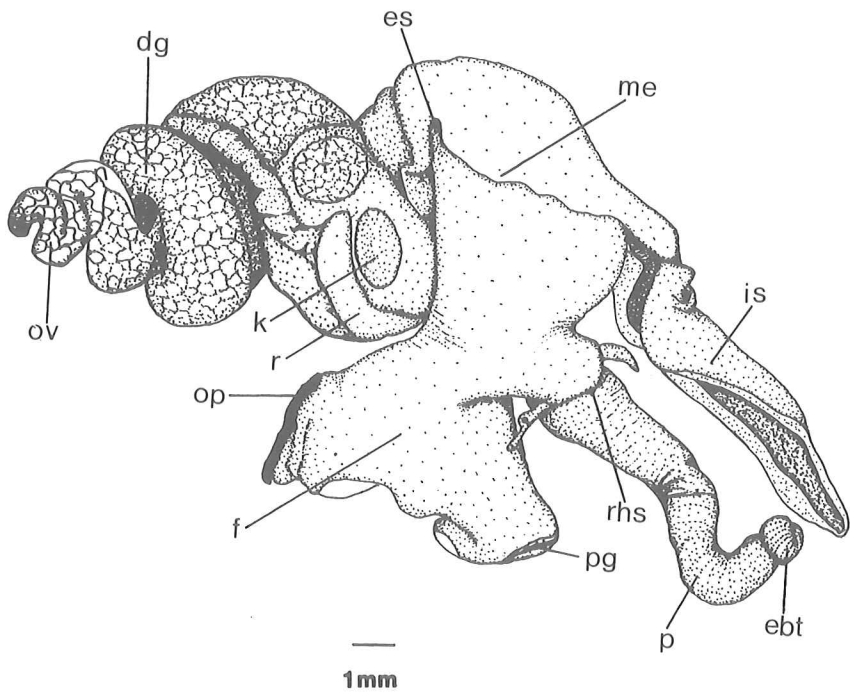

Fig. 6. *Turricula nelliae spurius*, general view of a relaxed animal showing the extended proboscis (p) and the everted tip of the buccal tube (ebt).

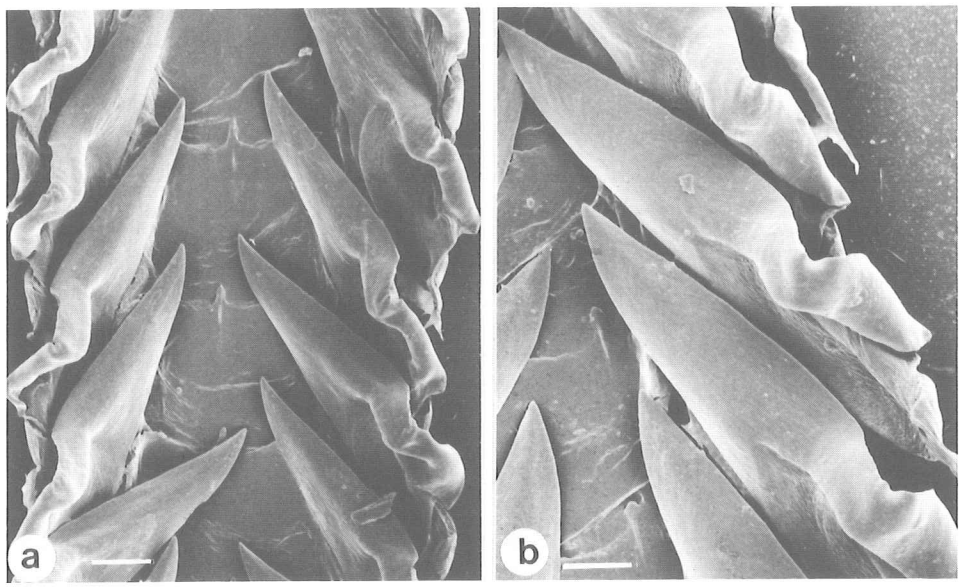

Plate 3. Radula of *Gemmula deshayesii*. A, portion of radular ribbon with two rows of marginal teeth and central tooth of low relief. Scale bar 20 μm. B, detail of marginal tooth. Scale bar 20 μm.

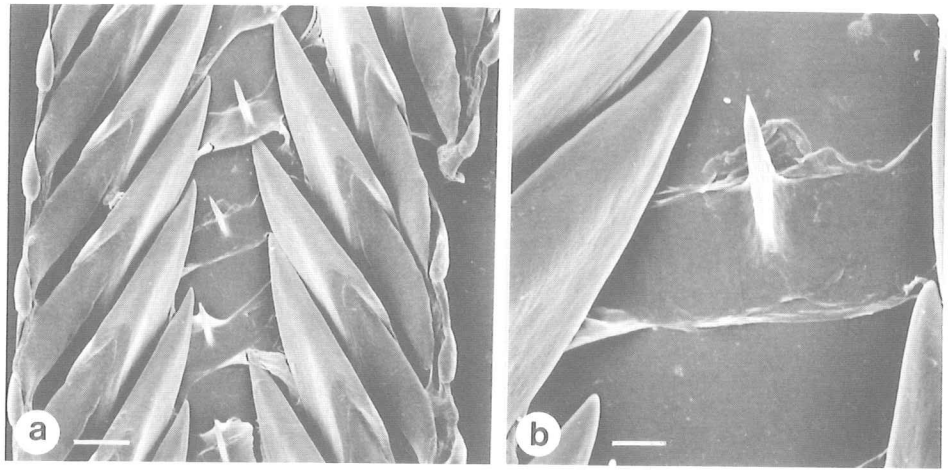

Plate 4. Radula of *Turricula nelliae spurius*. A, portion of radular ribbon with two marginal teeth and one central tooth in each row. Scale bar 25 μm. B, central tooth. Scale bar 7 μm.

rior to the circum-oral nerve ring the venom gland is dular, but the anterior portion within the proboscis is ciliated and duct-like. The muscular bulb is ovoid in section with two layers of circular muscle, separated by a very thin connective tissue layer. The outer muscle layer is about twice as thick as the inner.

Miller (1990) has shown how the anterior part of the buccal tube of *T. nelliae* can be everted to form a ciliated pad, and also how the radula can be protracted through the mouth to bite through the tube of pectinariid polychaetes. However, the double sphincter arrangement at the tip of the buccal tube, is similar to that seen in other turrids which are capable of holding single radular teeth at the tip of the proboscis (Kantor and Taylor 1991). These observations suggest that *Turricula nelliae* probably has some flexibility in its feeding behaviour, which may be relected in the wide diversity of polychaetes eaten (Taylor 1986).

Radula. There is a robust radular ribbon with two rows of marginal teeth and a central tooth. The marginal teeth are of the robust 'wishbone' type, with the larger inner limb forming the dagger-like distal half of the tooth. This has a pointed tip and a slightly curved, knife-like inner blade. The outer limb is smaller and inserts into the inner limb about half-way up the tooth. The central tooth is broad, short, and rectangular in shape, with a generally low profile. However, there is a long, prominent, spine-like central cusp.

Turricula javana (Linnaeus, 1767)
(Plates Id, 5; Fig. 7b)

Taxonomy. This species is described and illustrated by Powell (1969, pp. 235-7).

Distribution. It is uncommon around Hong Kong and only a few specimens have been found in Mirs Bay and the southern area around Cape d'Aguilar. Elsewhere, it is known from the northern Indian Ocean and northwest Pacific from Karachi to Japan.

Foregut. The foregut of this species (Fig. 7b) is very similar to that of *Turricula nelliae spurius*, with the same type of proboscis and also having the buccal mass located near the distal tip.

Radula. This consists of a robust radular ribbon with two rows of marginal teeth and a central tooth. The marginal teeth are of the robust 'wishbone' type with a large inner limb which forms the dagger-like distal end of the tooth. This has a sharply pointed tip and knife-like edges. The smaller, outer limb of the tooth slots into a groove about one third down the length of the inner limb. The central tooth is broad and short with a prominent, spine-like, central cusp and lateral 'wings' which arc to the anterior. The form of the 'wings' in Plate 5b suggests that the broad central tooth may, in fact, be formed from plate-like lateral teeth fused with the true smaller central tooth, which has a base with a quadrate outline.

Subfamily Crassispirinae
Funa jeffreysii (Smith, 1875)
(Plates 1f, 6a; Figs 8. and 9)

Taxonomy. The shell is illustrated and described and the nomenclature reviewed by Wells and Taylor (1994). Kilburn (1988) introduced the subgeneric name *Fùna* for *Inquisitor*-like gastropods, but with broad-bladed radular teeth. This and the anatomical differences warrant full generic status for *Funa*.

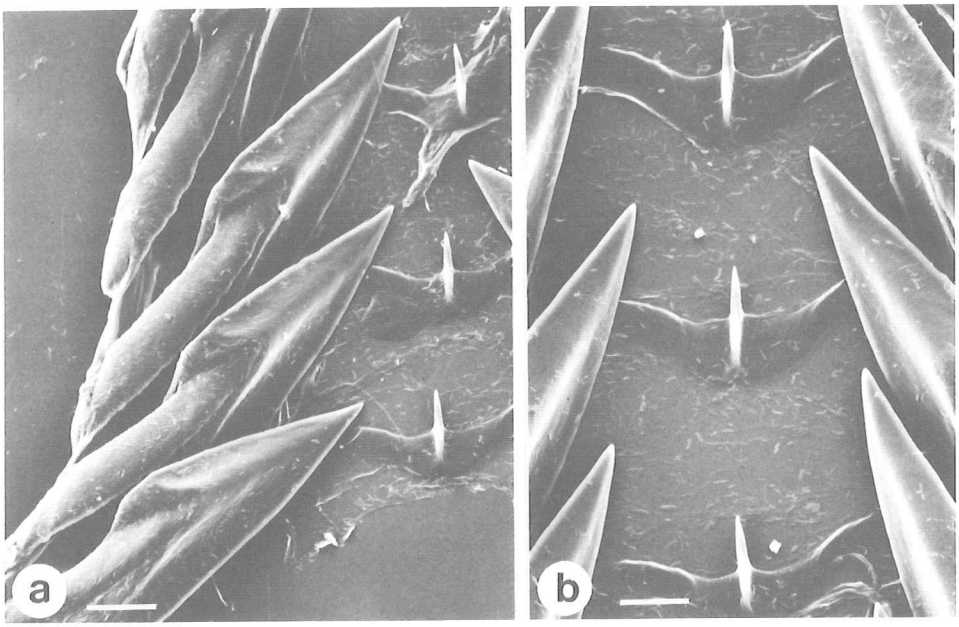

Plate 5. Radula of *Turricula javana*. A, portion of radular ribbon with two marginal and one central teeth. Scale bar 40 μm. B, detail of central teeth. Scale bar 30 μm.

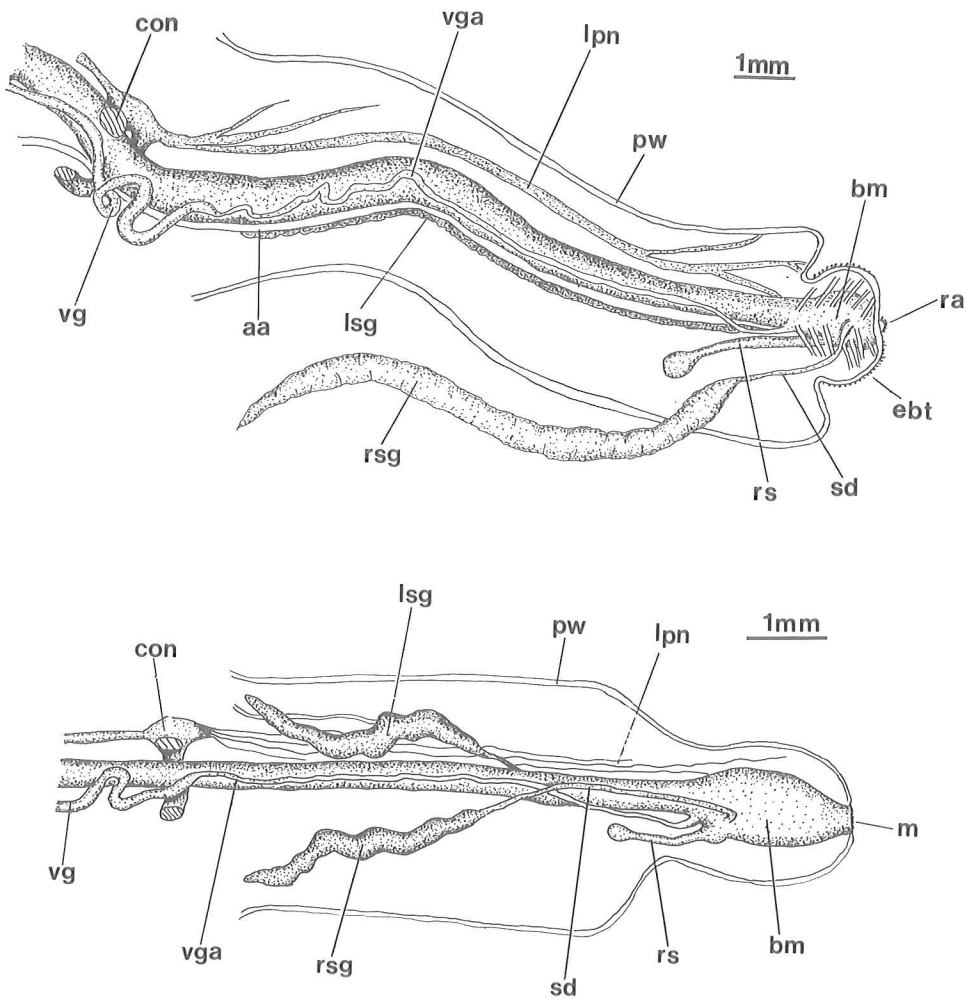

Fig. 7. Diagram of the proboscis in *Turricula* species showing the distally situated buccal mass and the elongate salivary glands contained within the proboscis. A, *Turricula nelliae spurius*; B, *Turricula javana*.

Distribution. This species is common in Mirs Bay and Tolo Channel and southern Hong Kong. Elsewhere it is known from China and Japan.

Foregut anatomy. The rhynchostome has a large anteriorly situated sphincter (Fig. 8). The anterior part of the rhynchocoel is lined with glandular epithelium, while the posterior has a epithelium similar to and continuous with the proboscis wall. There is a well-developed proboscis, which in the contracted state occupies about half the length of the rhynchocoel. The buccal tube has a single anterior sphincter and in sections a single, detached radular tooth is seen to be held at the sphincter. In specimens where

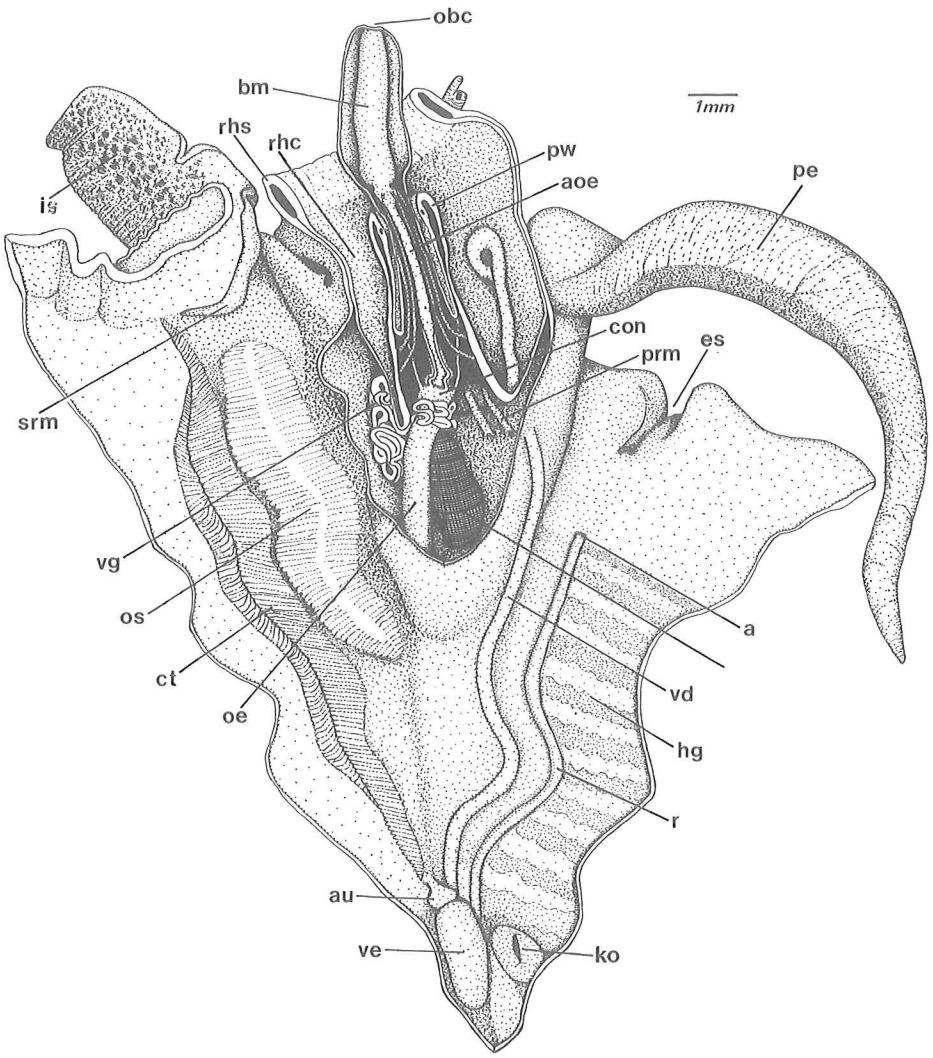

Fig. 8. *Funa jeffreysii*, general view of foregut anatomy of relaxed animal with extended proboscis and protracted buccal mass.

the proboscis is retracted, the buccal mass lies within its base (Fig. 9), but in relaxed gastropods the buccal mass can be protracted way byond the probocis tip and out through the rhynchostome (Fig. 8). There is a small odontophore with two small, separate cartilages. Two elongate, acinous salivary glands have ducts which enter the buccal cavity to either side of the buccal sac. The venom gland is long and glandular behind the circum-oral nerve ring, but ciliated and duct-like to the anterior of the ring. The muscular bulb is relatively large, consisting of two muscle layers of more or less equal thickness separated by a conspicuous connective tissue layer. In gastropods with a retracted proboscis, the oesophagus is bent into a large loop between the buccal mass and the nerve ring (Fig. 9). This loop is straightened when the proboscis is protracted.

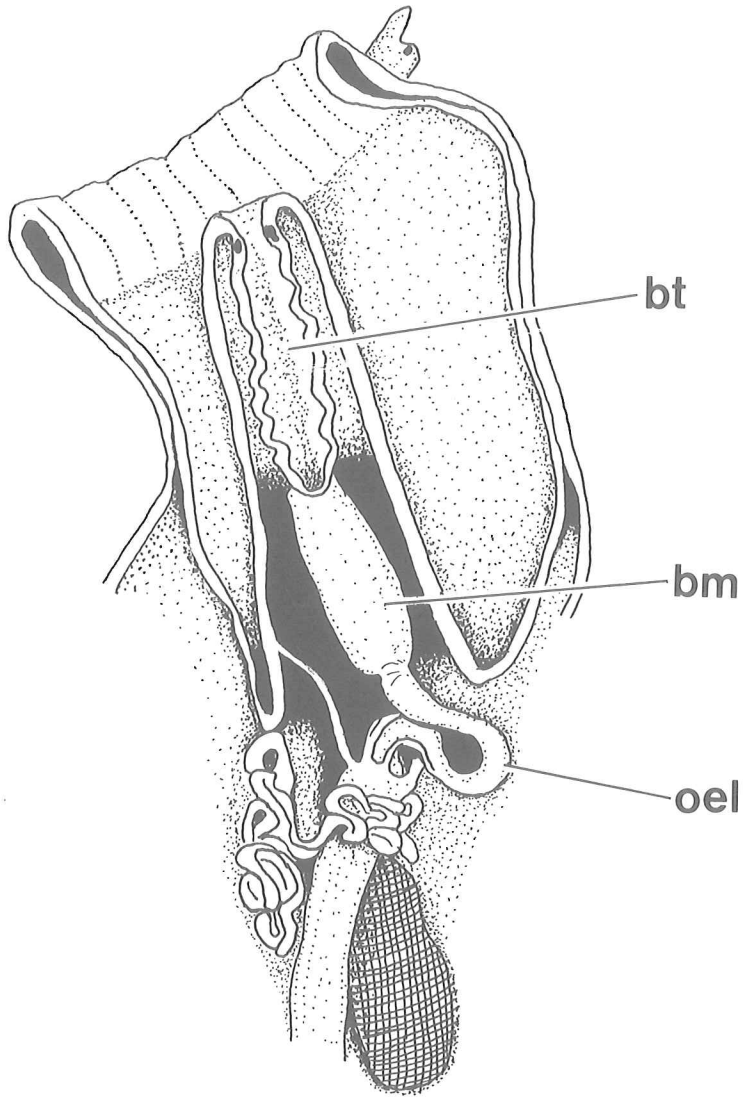

Fig. 9. *Funa jeffreysii*, with proboscis in retracted state and buccal mass situated near the base of the proboscis.

Funa jeffreysii is known to feed upon nemerteans and polychaetes (Miller 1990, as *Inquisitor latisinuata*) and although the feeding process has not been directly observed, a possible feeding mechanisn has been suggested by Taylor *et al.* (1993). It is proposed that prey are initially stabbed by means of the single radular teeth held at the tip of the extended proboscis and simultaneously envenomated. The buccal mass is then everted from the proboscis tip and through the rhynchostome and pulls in the prey, probably with direct use of the radula and odontophore.

Radula. The radular ribbon is relatively weak and the radula consists of two rows of marginal teeth only. The teeth are elongate (Plate 6a) and paddle-shaped, with a long, narrow shaft and a flattened distal end. The distal tip is pointed, with knife-like edges on either side and a blunt barb. An inconspicuous, thin secondary limb lies along the margin of the main shaft of the tooth.

Funa latisinuata (Smith, 1877)
(Plate 1 g, 6b; Fig. 10)

Taxonomy. This species, which is very similar to *F. jeffeysii* is described, illustrated and discussed by Wells and Taylor (1994).

Distribution. China.

Foregut anatomy. The anatomy of the foregut (Fig. 10) is very similar to that described above for *Funa jeffreysii*.

Radula. The radula consists of marginal teeth only (Plate 6b) which are similarly paddle-shaped to those of *F. jeffreysii*, but with a more angular distal termination and pronouced knife-like edges to the blade and no blunt barb. A thin accessory limb lies along the shaft of the tooth. The basal membrane of the radula is insubstantial.

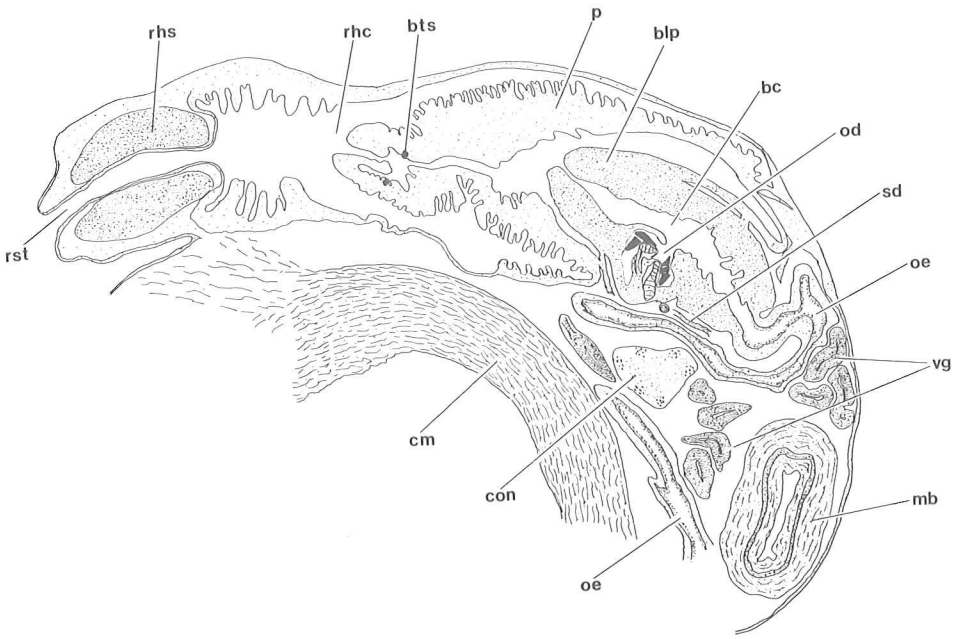

Fig. 10. *Funa latisinuata*, longitudinal section through the foregut of a specimen with retracted proboscis.

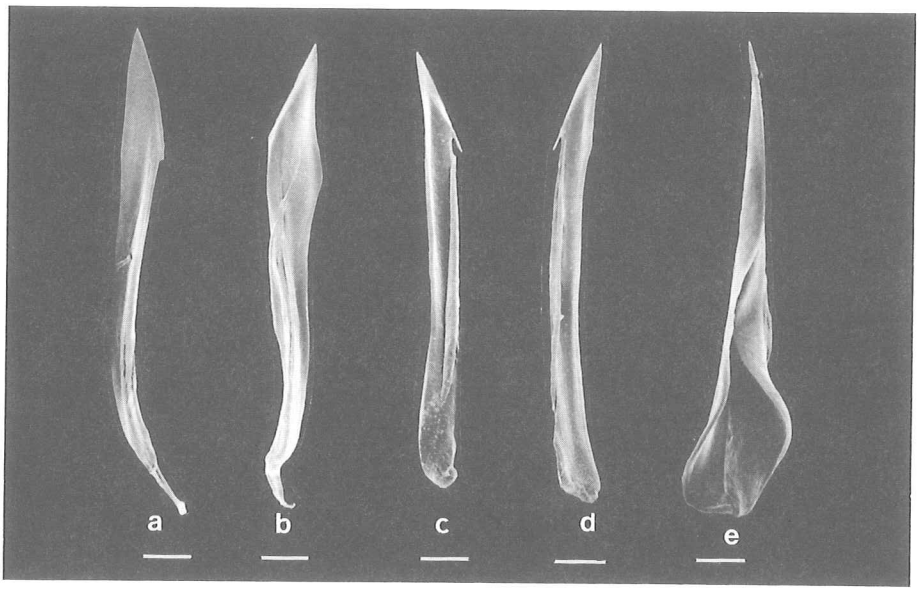

Plate 6. Single marginal teeth of Crassispirinae. A, *Funa jeffreysii*. Scale bar 50 μm. B, *Funa latisinuata*. Scale bar 50 μm. C, *Cheungbeia robusta*. Scale bar 20 μm. D, *Cheungbeia mindanensis*. Scale bar 25 μm. E, *Ptychobela suturalis*. Scale bar 20 μm.

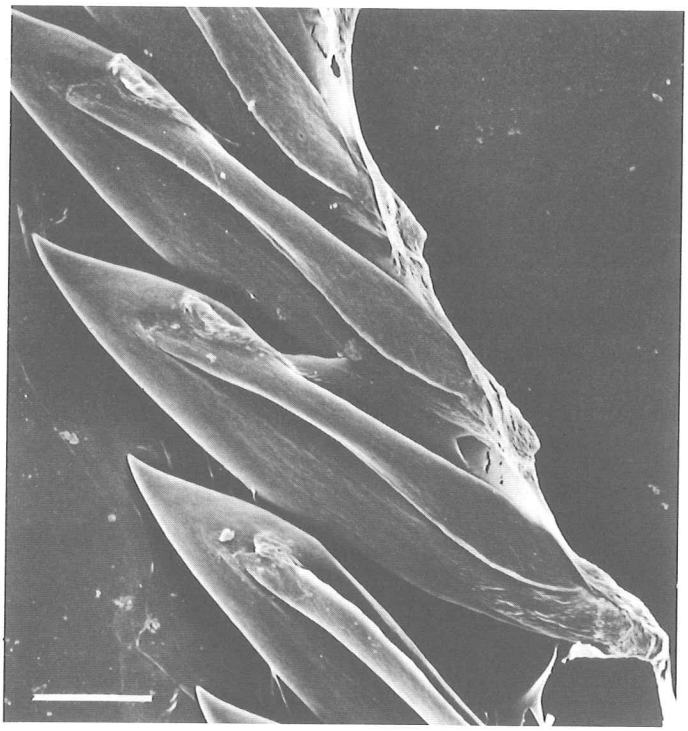

Plate 7. Marginal radular teeth of *Inquisitor latifasciata*. Scale bar 15 μm.

Inquisitor latifasciata (Sowerby, 1870)
(Plate 1e, 7; Figs 11–12)

Taxonomy. The species is described and illustrated by Wells and Taylor (1994).

Distrubition. Originally described from Hong Kong, not known elsewhere.

Foregut anatomy. There is a large rhynchostomal sphincter. The anterior portion of the rhynchocoel is glandular, but the posterior muscular with a similar histology to the proboscis wall. In semi-relaxed animals the proboscis is medium large (Fig. 11) and occupies much of the rhynchocoel, but in retracted specimens (Fig. 12) the proboscis is short and inverted at the tip. There are no buccal tube sphincters. The buccal lips form a muscular tube, which in retracted specimens extends beyond the mouth of the proboscis (Fig. 12). The buccal mass is muscular and in the retracted state lies just within the base of the proboscis, but can clearly be protracted to near the distal tip of the proboscis. The odontophore has two small unfused cartilages. Between the buccal mass and the nerve ring, the oesophagus curves in a large bop. There are two large, acinous, salivary glands with ducts opening into the buccal mass on either side of the buccal sac. The venom gland is duct-like anterior to the circum-oral nerve ring, but grandular to the posterior. The muscular bulb has two longitudinal muscle layers, separated by a relatively thick connective tissue layer.

The lack of any distal sphincter in the buccal tube suggests that single radular teeth are not held at the proboscis tip (Kantor and Taylor 1991). The histology of the posterior rhynchocoel, the loop of the oesophagus and the duct-like anterior venom gland are all features which suggest that the buccal mass is capable of considerable protraction to near the proboscis tip. The muscular extension of the walls of the buccal mass (buccal lips) suggests that this is probably the main organ of prey capture.

Radula. This consists of two rows of marginal teeth only. Each tooth is of the 'wishbone' type (Plate 7) with the inner limb large and robust and the outer limb shorter and thinner. The inner limb terminates in a sharp point. The teeth are very similar to those found in *Inquisitor sterrha* (Watson, 1881) the type species of the genus (personal observation).

Cheungbeia mindanensis (Smith, 1877)
(Plate 1h, 6d; Figs. 13-15)

Taxonomy. This species is described and illustrated by Taylor and Wells (1994).

Distribution. Philippines, China, Japan.

Taxonomy. There is a large, posteriorly situated rhynchostomal sphincter. The anterior two-thirds of the rhynchocoel has a glandular epithelium, while the posterior third has a similar epithelium to that of the proboscis wall. The proboscis is very long and when retracted lies coiled in the rhynchocoel (Fig. 13). The annular folds are conspicuous and the proboscis is clearly capable of considerable extension. The anterior tip of the buccal tube has tall epithelial cell and an anterior sphincter. These are two features as-

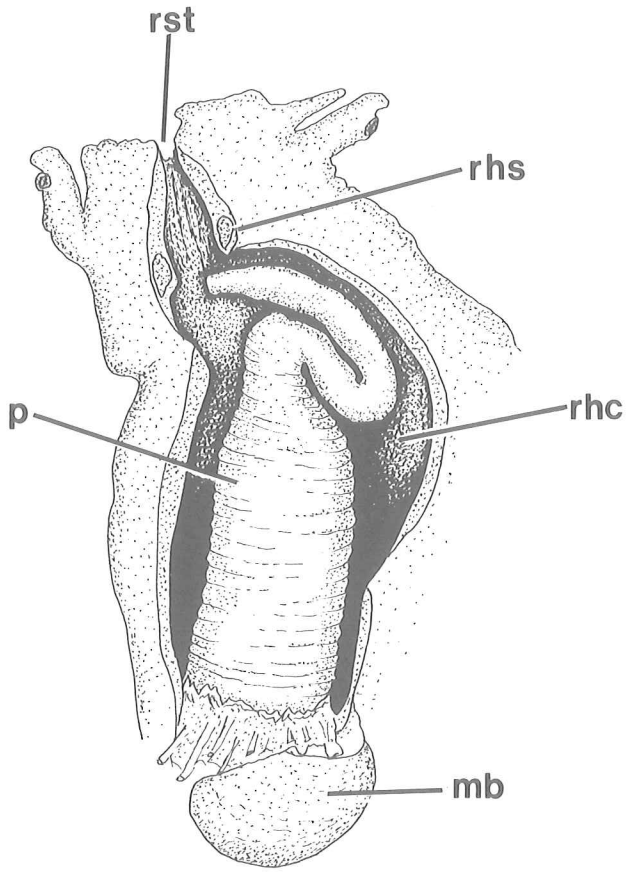

Fig. 11. *Inquisitor latifasciata,* retracted proboscis in the rhynchodeal cavity.

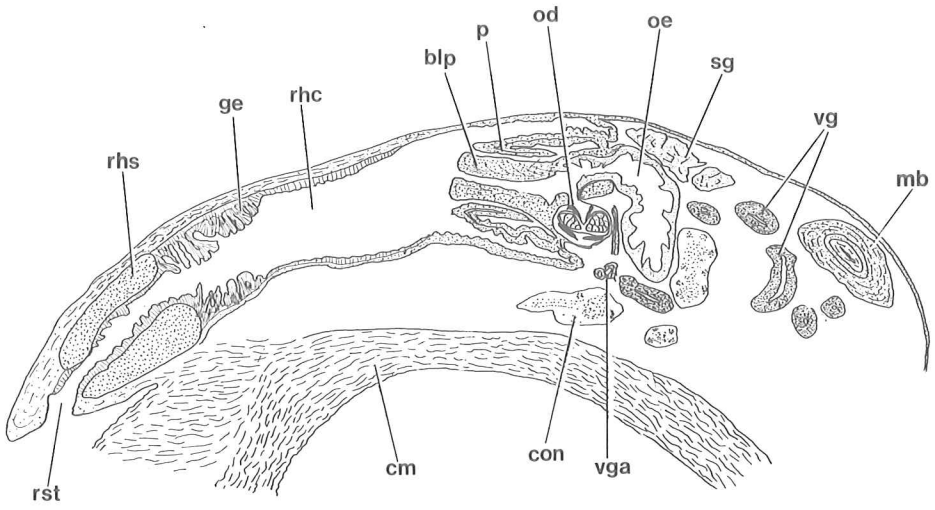

Fig. 12. *Inquisitor latifasciata*, longitudinal section of the foregut.

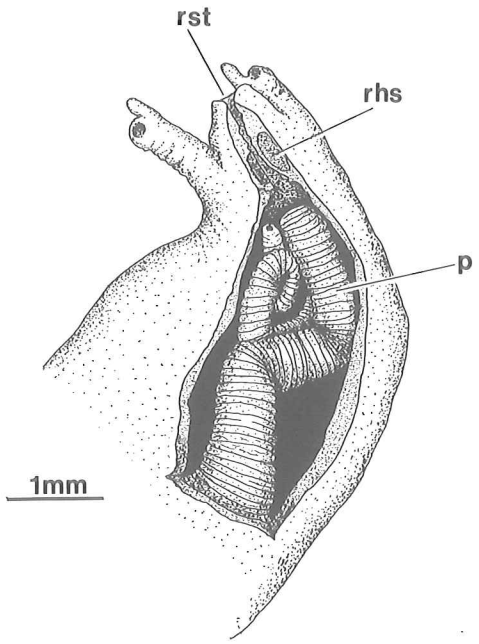

Fig. 13. *Cheungbeia mindanensis*, showing long proboscis coiled within the rhynchodeal cavity.

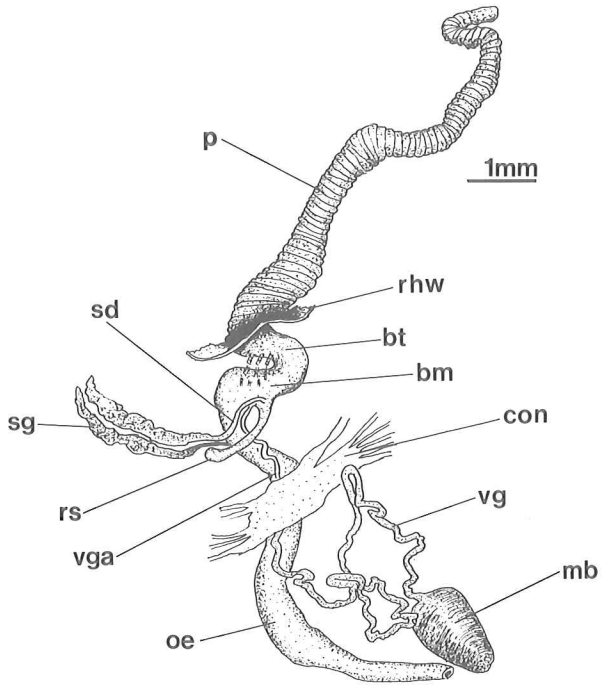

Fig. 14. *Cheungbeia mindanensis*, proboscis and foregut.

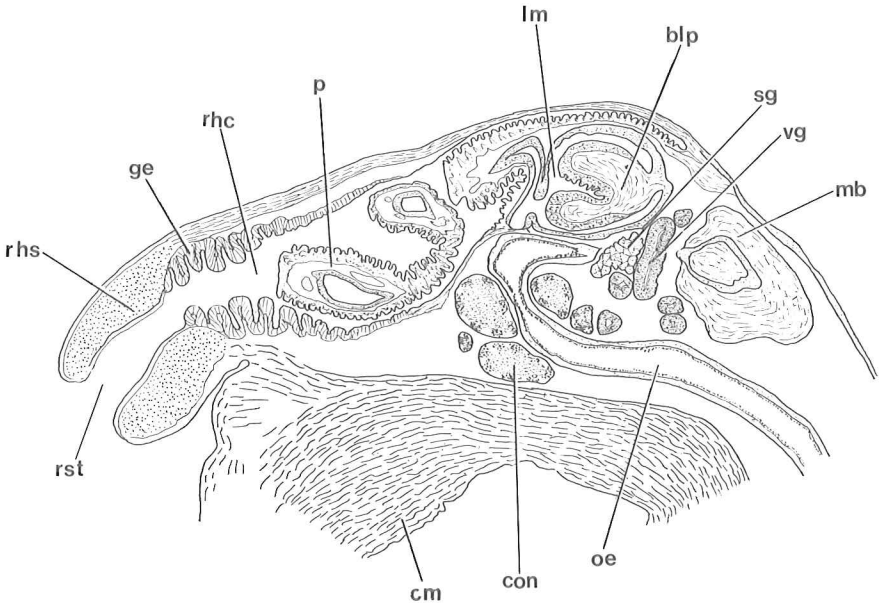

Fig. 15. *Cheungbeia mindanensis*, longitudinal section through the foregut.

sociated with species that hold single radular teeth at the proboscis tip (Kantor and Taylor 1990), but no tooth was observed in section. The buccal mass is situated at the base of the proboscis and has short, anterior, muscular buccal lips. The odontophore has two small cartilages which are fused at the anterior. There are two acinous salivary glands with ducts which enter into the buccal cavity on either side of the buccal sac. The venom gland is duct-like anterior of the circum-oral nerve ring, but to the posterior is glandular and coiled. The muscular bulb is short and posteriorly tapering with two equisize muscle layers separated by a relatively thick connective tissue layer.

The very long proboscis and the anterior sphincter and epithelium of the buccal tube suggest that this species uses single radular teeth at the proboscis tip to stab and envenomate its prey. It is unlikely that the buccal mass can be protracted very far into the proboscis.

Radula. This consists of two rows of marginal teeth only. Each tooth (Plate 6d) is spear-shaped with and elongate shaft and a sharply pointed and barbed tip. The teeth are gutter-shaped in cross section. A thin secondary limb is attached along the inner margin of each shaft.

Cheungbeia robusta (Hinds, 1843)
(Plates li, 6c; Figs. 16-17)

Taxonomy. This species is described and illustrated by Wells and Taylor (1994).
Distribution. Known only from the type locality of Hong Kong.

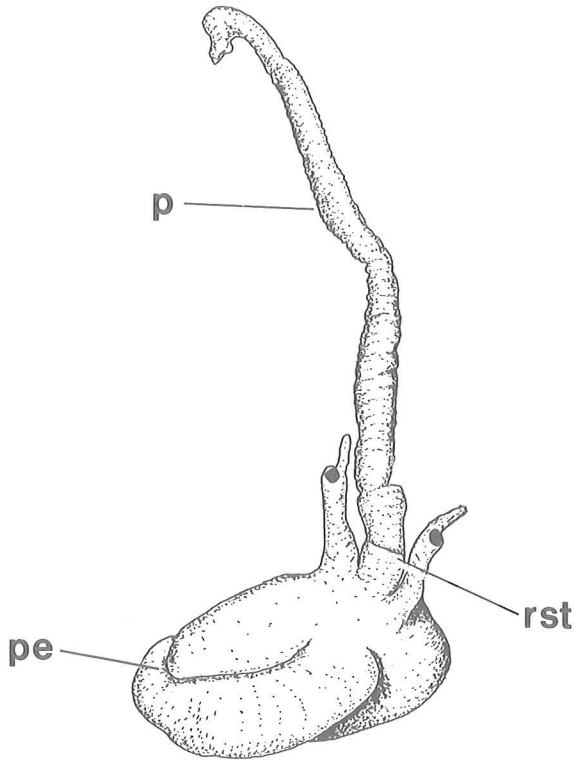

Fig. 16. *Cheungbeia robusta*, relaxed specimen with proboscis extended through the rhynchostome.

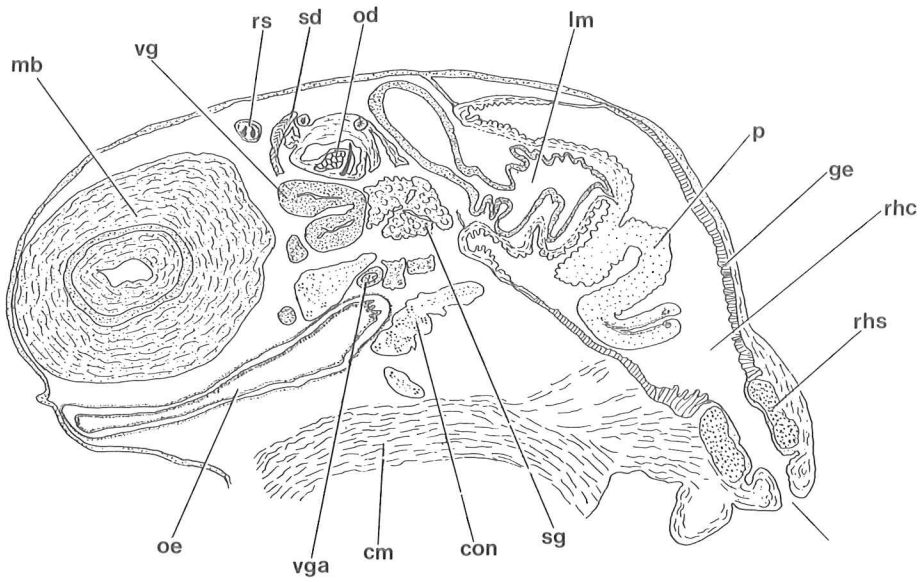

Fig. 17. *Cheungbeia robusta*, longitudinal section through the foregut.

Foregut anatomy. There is a large posteriorly situated sphincter to the rhynchostome. The rhynchocoel is lined with glandular epithelium throughout most of its length, but the posterior part has similar histology to the proboscis wall. The proboscis is long and capable of great extension (Fig. 16) and when retracted lies coiled within the rhynchocoel (Fig. 17). The buccal tube has an anterior sphincter. The buccal mass lies basal to the proboscis. The odontophore has only a single small cartilage. The radular sac is long and coiled at the posterior end. There are two acinous salivary glands which are lightly attached to each other and two salivary ducts enter the buccal cavity to either side of the buccal sac. The venom gland is duct-like and ciliated to the anterior of the circum-oral nerve ring, but coiled and glandular to the posterior. The muscular bulb consists of two layers of circular muscle separated by a relatively thick connective tissue layer.

The long proboscis with the distal sphincter and the harpoon-shaped radular teeth suggest that the teeth are used singly at the proboscis tip to stab and envenomate the prey.

Radula. The radula consists of two rows of marginal teeth only. The individual teeth are long and gutter-shaped, with sharp, barbed tips (Fig. 6c). A thin accessory limb lies along along one side of the shaft. The proximal end of the tooth is slightly twisted. The teeth are very similar to those of *Cheungbeia mindanensis*.

Ptychobela suturalis (Gray, 1838)
(Plates 19, 6e; Figs. 18-19)

Taxonomy. This has been reviewed by Kilbum (1989), see also Taylor and Wells (1994)

Distribution. Rare around Hong Kong; elsewhere from the central Indo-West Pacific, Taiwan to Queensland, Western Australia.

Foregut anatomy. There is a posteriorly situated rhynchostomal sphincter. In retracted animals, the proboscis is short and sections show that the tip is folded inwards around the tube made by the buccal lips which extends beyond the mouth of the proboscis (Fig. 18). In another specimen the proboscis lies partly extended within the rhynchodeum. There is an annular sphincter near the proboscis tip. The muscular buccal lips form a tube with a flaring aperture. The buccal mass lies immediately behind this tube. Another sectioned specimen shows that the bucal lips are very flexible and can be inverted into the buccal cavity. There is a small odontophore with two separate cartilages. Posterior to the buccal mass the oesophagus bends in a large loop before passing through the circum-oral nerve ring. There are two acinous salivary glands with ducts entering the buccal cavity on either side of the anterior end of the radular sac. After passing through the nerve ring, the anterior portion of the venom gland thins considerably and is duct-like rather than glandular. The venom duct joins the buccal mass immediately posterior to the insertion of the radular sac. The muscular bulb is relatively large, and consists of three layers; two thicker longitudinal muscle layers separated by a layer of connective tussue, while a thin circular muscle layer occupies the inside of the bulb.

The morphology of the radular teeth of this species suggests that they are held singly to stab and envenomate the prey and there is a sphincter at the distal tip of the proboscis to grip the tooth.

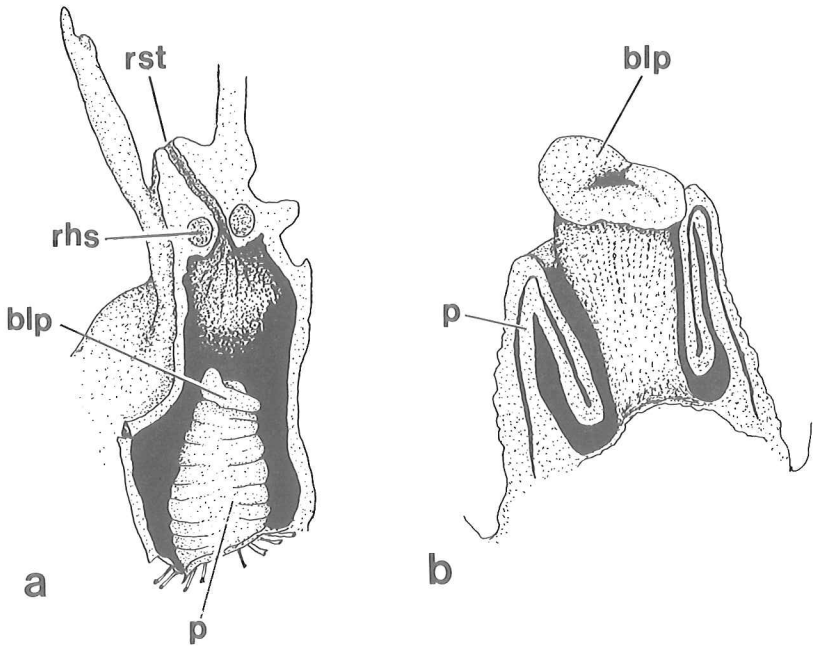

Fig. 18. *Ptychobela suturalis*. A, proboscis within the rhynchodeal cavity; B, section through the proboscis showing the infolded walls and the extended muscular buccal lips.

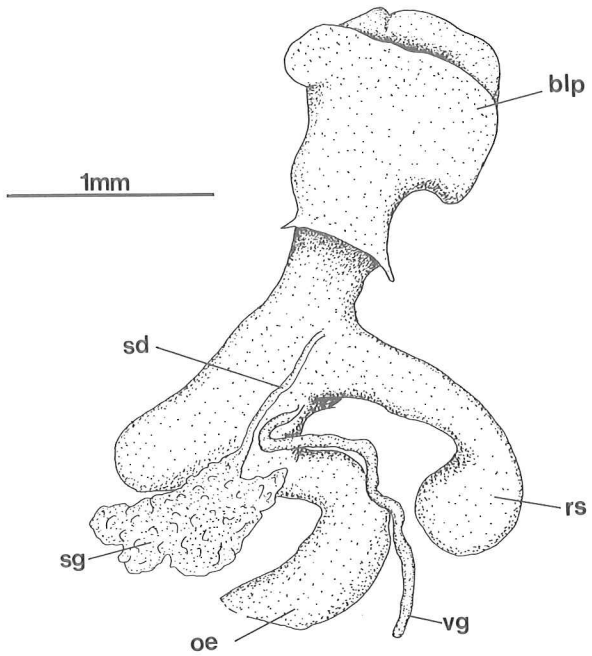

Fig. 19. *Ptychobela suturalis*, anterior part of the foregut.

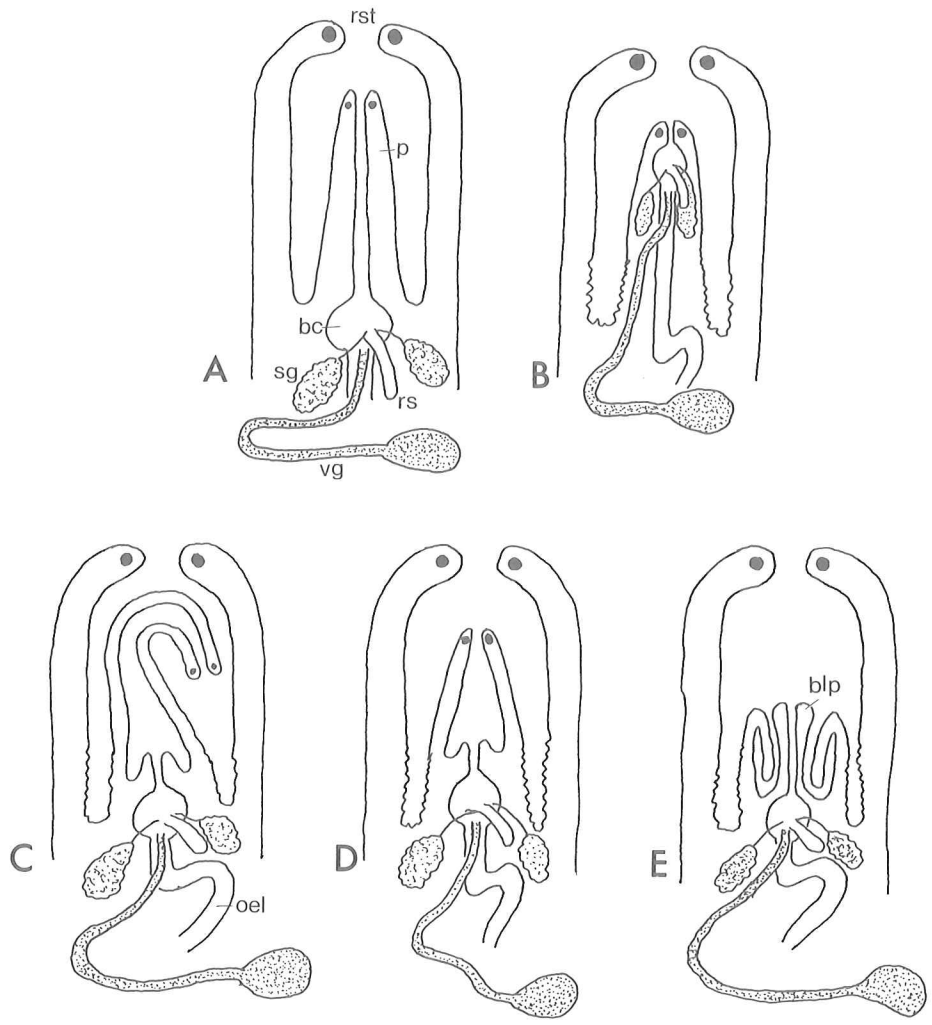

Fig. 20. Diagram summarizing the main types of foregut anatomy found among Hong Kong turrids described in this paper. A, *Lophiotoma* and *Gemmula*; B, *Turricula* species; C, *Cheungbeia mindanensis* and *C. robusta*; D, *Funa* species; E, *Ptychobela suturalis* and *Inquisitor latifasciata*.

Although in retracted animals the buccal mass lies basal to the proboscis, the loop in the oesophagus suggests that it can be protracted a considerable distance forward and probably out beyond the rynchostome.

Radula. The radula consists of two rows of marginal teeth only. Each tooth is hollow and awl-shaped (Plate 6e) with a sharp point. The teeth are composed of two separate pieces which are fused along one edge and loosely twisted together. For further details and illustration see Kilburn (1989, fig. 17) and Wells and Taylor (1994).

DISCUSSION

Recently, Taylor *et al.* (1993) have reviewed the anatomy of the conoidean anterior alimentary system and demonstrated the great variation in foregut structure found among the subfamilies formerly grouped within the Turridae (now divided into five families). On the basis of the character analysis, species of the family Drilliidae (also known as Clavine, Clavusinae or Drilliinae) have been identified as having the least derived foregut anatomy of the whole Conoidea. The buccal mass lies at the base of the proboscis, which is moderately long with a distal sphincter. The posterior of the rhynchodeum is unmodified. There are two acinous salivary glands and a well-developed venom gland which has a uniform histology. There are two odontophoral cartilages and a strong radular ribbon with five teeth in each radular row, consisting of a small central, two comb-like laterals and a pair of flat-bladed marginals. A muscular connection between the radula retractor muscles and the columellar muscle is found in no other conoidean group. All other coniodean foregut patterns are modifications of this basic type.

Among the Hong Kong species examined in this study, there are five different types of foregut which are summarized diagramatically in Figure 20. Type A which is found in *Lophiotoma* and *Gemmula* has the buccal mass located at the base of proboscis and the general arrangement is similar to that found in the family Drilliidae, which is the plesiomorphic state within the Conoidea. The differences are that the muscular connection between the radular retractor muscles and the columellar muscle has been lost in Type A gastropods and also the radula differs from that of the Drilliidae. Type A species have lost the lateral teeth, the central is retained only in *Gemmula* and the marginal teeth have been transformed into the bifid wishbone form. The proboscis can be protracted thraugh the rhynchostome, but the buccal mass moves very little from its basal position. It is known that single detached radular teeth can be held at the proboscis tip, where they are presumably used for stabbing prey with simultaneous envenomation from the well-developed venom apparatus.

The Type B foregut, represented by the *Turricula* species is very different from the preceding type. Here the buccal mass is located near the distal tip of the proboscis, and the Miller (1990) has shown how this may be protracted a considerable distance through the rhynchostome and the buccal tube everted to expose the radular teeth at the site of feeding. The posterior part of the rhynchostome has the same epithelium as the proboscis wall, indicating that the anterior extension is possible. Taylor *et al.* (1993) have shown that the distally-shifted position of the buccal mass in the proboscis is a characteristic feature of species of the subfamily Clavatulinae. *Turricula nelliae* can use the radula as a whole organ at the proboscis tip, in a manner analogous to muricoidean gastropods, but together with other species of Clavatulinae it has distal sphincters in the buccal tube, which indicates the possiblity that single radular teeth can be held and used in stabbling.

The Type C foregut is represented by the *Cheungbeia* species. These have a very long proboscis which lies coiled in the rhynchodeum when retracted, but is capable of considerable protraction. The buccal mass is basal, but is capable of considerable foreward movement, when the proboscis is protracted. *Cheungbeia* species have harpoon-shaped and barbed radular teeth, which are probably held at the proboscis tip when feeding.

Funa species have the Type D foregut. Here, the buccal mass is situated within the

proboscis, but can be moved forward beyond the proboscis tip when feeding. However, single radular teeth have also been found held at the proboscis tip, indicating that they can be used for envenomation. It is likely that prey capture (nemerteans and polychaetes) takes place initially by stabbing and envenonmation; the buccal mass then moves forward out of the proboscis and the prey dragged into the oesophagus.

The Type E foregut is represented by *Inquisitor latifasciata* and *Ptychobela suturalis*. These species have a short proboscis, which is introverted when retracted and it is unclear how far it may be extended. The buccal lips (anterior muscular extension of the buccal mass) are well developed forming a trumpet-shaped tube. There is a loop in the oesophagus behind the buccal mass indicating that the buccal mass can be moved forward and possibly beyond the rhynchostome. Despite the similarity in proboscis, the radular teeth of the last two species are quite different. Those of *Inquisitor latifasciata* are of the bifid wishbone type, while *Ptychobela* has hollow, dart-like radular teeth, formed from two fused components. It is likely that both of types of teeth can be held singly at the proboscis tip.

An apparantly major functional constraint of the Conoidea, is the location of the buccal mass at the base of the proboscis. This means that the radula cannot be used as a whole organ at the proboscis tip as in most other Neogastropoda. Conoideans have evolved various ways of overcoming this problem. In species of the subfamilies Strictispiridae, Clavatulinae and Zonulispirinae the buccal mass has shifted towards the distal end of the proboscis and the whole radula can be used in the primary feeding process. In some Crassispirinae, the buccal mass lies near the base of the proboscis, but a loop in the anterior oesophagus allows it to be protracted forwards out of the proboscis when feeding. The other way of overcoming the problem of the basal buccal mass is to use single detached radular teeth at the proboscis tip to impale and inject prey with venom. This feeding method, which is the most well-known feature of the Conoidea, appears to have evolved independently in at least five different clades of conoideans (Taylor *et al.* 1993). Both the harpoon-like teeth of *Cheungbeia* and the hollow teeth of *Ptychobela* described in this paper, are probably two further independent developments of the hypodermic feeding mechanism.

This study provides new anatomical data for six species of the subfamily Crassispirinae for which very little information was previously available (Maes 1983; Taylor *et al.* 1993). This group shows a considerable diversity of foregut anatomy. The radular teeth vary between the robust wishbone type as found in *Inquisitor*, the large bladed teeth of *Funa*, the harpoon teeth of *Cheungbeia* to the awl-shaped hollow teeth of *Ptychobela*. The proboscis anatomy also varies; *Inquisitor* has a proboscis with a basal buccal mass; *Funa* can protract the buccal mass through the proboscis tip; *Cheungbeia* has a very long proboscis which lies coiled in the rhynchodeum and *Ptychobela* has a short proboscis, but large buccal lips. Given this diversity of anatomy, it is likely that the Crassispirinae is a paraphyletic group, but more of the 39 known genera of need to be examined anatomically before any reclassification is attempted. Shell characters of Crassispirinae would seem to be a poor guide to internal anatomy and relationships.

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KEY TO ABBREVIATIONS USED IN FIGURES.

a	anus
aa	anterior aorta
aoe	anterior oesophagus
au	auricle
bc	buccal cavity
blp	buccal lips
bm	buccal mass
bt	buccal tube
bts	buccal tube sphincter
cm	columellar muscle
con	clrcum-oral nerve ring
cpg	capsule gland
ct	ctenidium
dg	digestive gland
ebt	everted buccal tube
eec	elongate epthelial cells
es	exhalent siphon
f	foot
fo	female opening
ge	glandular epithelium
hg	hypobranchial gland
is	inhalent siphon
k	kidney
ko	kidney opening
lm	lumen of proboscis
lpn	left proboscis nerve
lsg	left salivary gland
m	mouth
me	mantle edge
mb	muscular bulb

obc	opening of buccal cavity
od	odontophore
oe	oesophagus
oel	oesophageal loop
op	operculum
os	osphradium
ov	ovary
p	proboscis
pe	penis
pg	pedal groove
prm	proboscis retractor muscles
pw	proboscis wall
r	rectum
ra	radula
rhc	rhynchocoel
rhs	rynchostomal sphincter
rhw	rhynchodeal wall
rs	radular sac
rsg	right salivary gland
rst	rhynchostome
sd	salivary duct
sg	salivary gland
si	siphon
srm	siphonal retractor muscle
t	radular tooth
vd	vas deferens
ve	ventricle
vg	venom gland
vga	venom gland with changed histology anterior to nerve ring