



Foregut anatomy and relationships of raphitomine gastropods (Gastropoda: Conoidea: Raphitominae)

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KEY WORDS: Conoidea, Raphitominae, anatomy, foregut, feeding mechanism, phylogeny.

ABSTRACT

The Raphitominae (formerly Daphnellinae) are, from shell characters, probably the most morphologically disparate of the conoidean subfamilies, including both some of the smallest and largest species of the superfamily. A study by serial sections of 14 species revealed considerable variation in the configuration of the foregut. Species differ in the presence, position and morphology of the major structures such as proboscis, buccal mass, septum, glands and sphincters of the buccal tube. Distinctive features of raphitomes, although not found in every species, are a rhynchostomal introvert, a rhynchodeal septum, the needle-like radular teeth and the muscular bulb consisting of a single muscle layer. In *Kermia barnardi* and *Paramontana rufozonata* there is a valve situated just posterior to the buccal cavity resembling the valve of Leiblein of *Rachiglossa* and *Nematoglossa*. A remarkable feature of the Raphitominae is the independent reduction and loss of major foregut organs - the proboscis may be long, reduced, vestigial or totally absent. The radula, salivary glands and venom apparatus may be present or absent. Usually radula loss is correlated with the loss of the venom gland but in *Pseudodaphnella granocostata* the venom apparatus persists but the radula is absent. *Teretiopsis* species lack a proboscis, radula, venom apparatus or salivary glands. Three main types of feeding are proposed for the Raphitominae: 1) normal toxoglossan feeding with use of teeth at the proboscis tip for stabbing and envenomation of prey. 2) envenomation of the prey without stabbing by radular teeth. 3) capture of prey without stabbing and envenomation, probably by suctorial means. Raphitomes have the most disparate foregut configurations of any conoidean subfamily. The rhynchostomal introvert is otherwise found only in Terebridae and the rhynchodeal introvert found in many terebrids and some *Conus* species. Tubular salivary glands are also found in Mangeliinae and some Crassispirinae. Phylogenetic analysis suggests that the Raphitominae have closest similarity with the Coninae and Mangeliinae.

RIASSUNTO

Le Raphitominae (precedentemente note come Daphnellinae) sono, dal punto di vista conchiliare, la più disparata delle sottofamiglie di conoidei, comprendendo alcune tra le più piccole e le più grandi specie della superfamiglia. Uno studio condotto con sezioni seriali su 14 specie ha rivelato una variabilità considerevole nella configurazione del canale alimentare anteriore. Le specie differiscono nella presenza, la posizione e la morfologia delle maggiori strutture come la proboscide, la massa boccale, il setto, le ghiandole e gli sfinteri del tubo boccale. Caratteristiche distintive delle Raphitominae, anche se non riscontrabili in tutte le specie, sono un introveto rincostomale, i denti radulari aghiformi ed il bulbo muscolare consistente in un singolo strato muscolare. In *Kermia barnardi* e *Paramontana rufozonata* c'è una struttura situata proprio posteriormente alla massa boccale somigliante alla "valve of Leiblein" di *Rachiglossa* e *Nematoglossa*. Una caratteristica rimarchevole delle Raphitominae è la riduzione e/o la perdita indipendente dei maggiori organi del canale alimentare anteriore - la proboscide può quindi essere lunga, ridotta, vestigiale o totalmente assente. La radula, le ghiandole salivari e l'apparato velenifero possono essere presenti o assenti. Normalmente la perdita della radula è correlata con la perdita della ghiandola del veleno, ma in *Pseudodaphnella granocostata*, l'apparato velenifero persiste pur essendo la radula assente. Specie di *Teretiopsis* mancano della proboscide, della radula, dell'apparato velenifero o delle ghiandole salivari. Tre tipi principali di modalità alimentari sono proposte per le Raphitominae: 1) normale alimentazione toxoglossa con uso dei denti radulari all'apice della proboscide per colpire ed iniettare il veleno nella preda; 2) uso dell'apparato velenifero ma senza colpire con la radula; 3) cattura della preda senza radula né uso del veleno, probabilmente per attività suttoriale. Le Raphitominae possiedono anche la più disparata serie di configurazioni del canale alimentare anteriore di tutte le sottofamiglie di conoidei. L'introveto rincostomale si ritrova altrove solo tra le Terebridae e l'introveto rincostomale si trova in molte terebre e in alcune specie di *Conus*. Le ghiandole salivari sono presenti anche nelle Mangeliinae e in alcune Crassispirinae. Un'analisi filogenetica suggerisce che le Raphitominae hanno stretta similarità con le Coninae e le Mangeliinae.

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INTRODUCTION

Gastropods of the superfamily Conoidea are notable for the possession of a large, coiled venom gland, together with highly modified radular teeth used to inject venom into the prey. Although *Conus* is the most well known taxon (Kohn, 1990; Olivera *et al.* 1990), it represents only a small part of the total diversity of the group. Classifications have largely been based on shell and radular characters (Powell, 1966; McLean, 1971) but recent studies are providing anatomical criteria, mainly derived from characters of the foregut, for the definition of suprageneric taxa of conoideans (Taylor, Kantor & Sysøev, 1993; Kantor, Medinskaya & Taylor, 1977; Medinskaya, 1999). Amongst the species studied so far a wide disparity in the

configuration of the various organs of the foregut has been revealed and new arrangements are continually being discovered. Preliminary studies of the diverse subfamily Raphitominae (formerly Daphnellinae) suggested a wide variation in foregut anatomy, including the apparent loss of major structures (Smith, 1967a; Sheridan, Bouillon & Van Mol, 1973; Taylor *et al.*, 1993). For this reason we decided to investigate the anatomy of the Raphitominae in more detail.

The Raphitominae is probably one of the most species-rich of all the conoidean subfamilies, exceeded only by the Mangeliinae. Fifty-seven recent genera and subgenera are listed by Taylor *et al.* (1993). Raphitomes have a world-wide distribution and inhabit a wide range of habitats from the

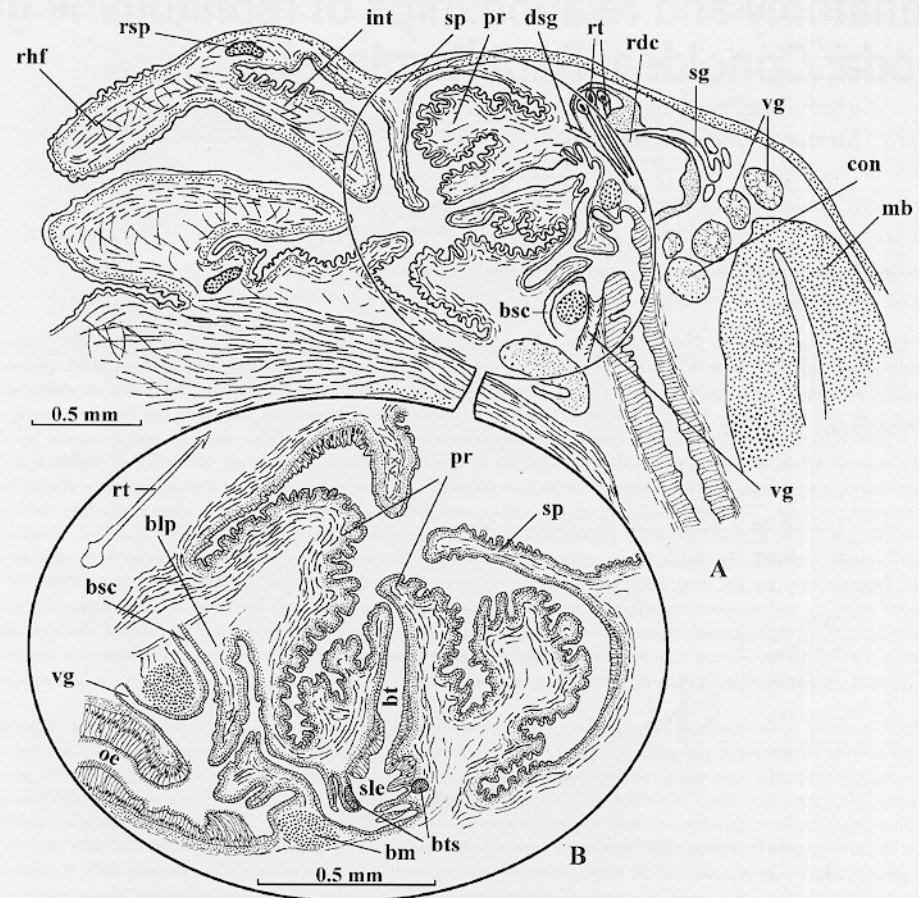


Figure 1. *Gymnobela pyrrhogramma* (Dautzenberg & Fischer, 1896). A. Semidiagrammatic longitudinal section of the foregut. B. Enlarged region of the proboscis and buccal mass (the single marginal tooth is drawn in the same scale to the left of the proboscis).

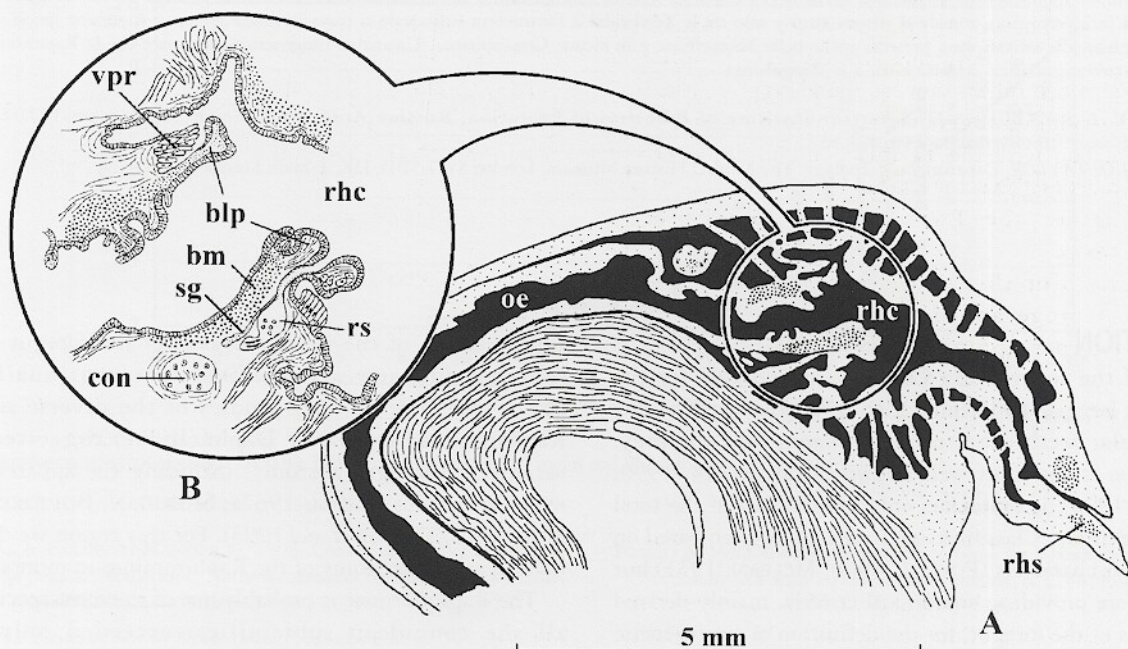


Figure 2. *Gymnobela emertoni* (Verrill & Smith, 1884) [after Taylor *et al.*, 1993, slightly modified]. A. Semidiagrammatic longitudinal section of the foregut (rhynchocoel — solid black). B. Enlarged region of the proboscis and buccal.



intertidal boulders of coral reefs (KAY, 1990) to abyssal depths (BOUCHET & WARÈN, 1980) including hydrothermal vents (SYSOEV & KANTOR 1995; BECK, 1996). The group encompasses some of both the smallest and largest conoideans ranging from around 1.5 mm to 136 mm shell height (POWELL, 1966). Notable are some of the large deeper water taxa, such as *Pontiothauma*, *Spergo* and *Thatcheria*. Apart from brief accounts of anatomy and habitat little is known about the biology of any species. Raphitomines also have a rich fossil record in the Cenozoic, PACAUD & LE RENARD (1995) for instance, record 80 species from the Palaeogene of the Paris Basin.

Despite the wide disparity in shell form Raphitominae are usually recognised by two shell characters, namely, the diagonally cancellate larval shell and the shape of the posterior apertural canal which is located at the suture in the form of reversed L shape (POWELL, 1966; McLEAN, 1971). These characters are, however, not present in all species. Raphitomines also lack an operculum. Many small species of conoideans currently classified in the Mangeliinae and other subfamilies are very poorly known and on investigation some of these have been shown to possess both raphitomine shell and anatomical characters as exemplified by recent studies of *Clathromangelia* (OLIVERIO, 1995) and *Hemilienardia* (TAYLOR *et al.* 1993 and herein). For *Philbertia* and *Caenodagreutes*, SMITH (1967b) showed how species with very similar shells possess very different internal anatomies.

Previous anatomical studies of a few raphitomine species have indicated a puzzling disparity of foregut anatomy (KANTOR & SYSOEV, 1986; 1989; OLIVERIO, 1995; PACE, 1903; SMITH, 1967a; SHERIDAN *et al.*, 1973; SYSOEV & KANTOR 1995; TAYLOR, *et al.* 1993). Some species possess a full range of conoidean foregut organs including the venom apparatus, salivary glands, proboscis and radula whilst in others some or all these structures are absent. Additionally, some species have been described with structures such as the rhynchodeal introvert and septum which had otherwise been found only in species of Terebridae. Initial phylogenetic analysis identified the Raphitominae along with the Taraninae as the most derived groups of conoideans (TAYLOR *et al.* 1993), however, it was uncertain whether the Raphitominae constituted a monophyletic group.

The objectives of this study were to establish the morphological range and disparity of the foregut in Raphitominae, to reappraise previous descriptions of raphitomine anatomy, and to use an analysis of foregut characters to explore relationships both within family and with other conoideans.

MATERIAL AND METHODS

Details of the species studied are listed in Table 1. For all species, longitudinal serial sections were made of the foregut, cut at 8–10 µm and mostly stained in Masson's trichrome. Radulae were cleaned in a dilute sodium hypochlorite solution, washed in distilled water, and air dried onto circular glass coverslips. These were then glued to stubs, sputter coated and then examined by SEM.

Abbreviations used on anatomical figures:

asg - accessory salivary gland
bc - buccal cavity
blp - buccal lip
bm - buccal mass
bsc - buccal sac
bt - buccal tube
"btc" - cylinder of the buccal tube
bts - buccal tube sphincters
cf - circular fold
cm - columellar muscle
cmf - circular muscle fold
con - circumoesophageal nerve ring
dasg - duct of the accessory salivary gland
dsg - duct of salivary gland
dvg - duct of the venom gland
epp - epithelial pad;
glc - glandular cells
glf - glandular fold
dvg - duct of venom gland
int - introvert
mb - muscular bulb of the venom gland
oe - oesophagus
pr - proboscis
pr - proboscis retractors
rdc - radular caecum
rhc - rhynchocoel (rhynchodeal cavity)
rhf - rhynchostomal funnel
rns - rhynchostome
rs - radular sac
rsp - rhynchostomal sphincter
rt - radular tooth
sg - salivary gland
sle - sac-like enlargement of the buccal tube
sng - snout gland
sp - septum
tm - transverse muscles
vg - venom gland
vl - valve
vpr - vestigial proboscis

SPECIES DESCRIPTIONS

In this section we describe and illustrate the foregut anatomy and radulae of each of the species examined. Nomenclature of organs and structures largely follows TAYLOR *et al.* (1993) and KANTOR *et al.* (1997). Although we have studied only a small proportion of the living genera and species, our coverage includes gastropods of very different sizes and from widely different habitats, ranging from the shallow intertidal to abyssal depths and hydrothermal vents.

Gymnobela pyrrhogramma (Dautzenberg & Fischer, 1896)
(Figures 1, 3 A-B, 20A)

Rhynchodaenum and proboscis

The rhynchostomal sphincter is small and located posteriorly

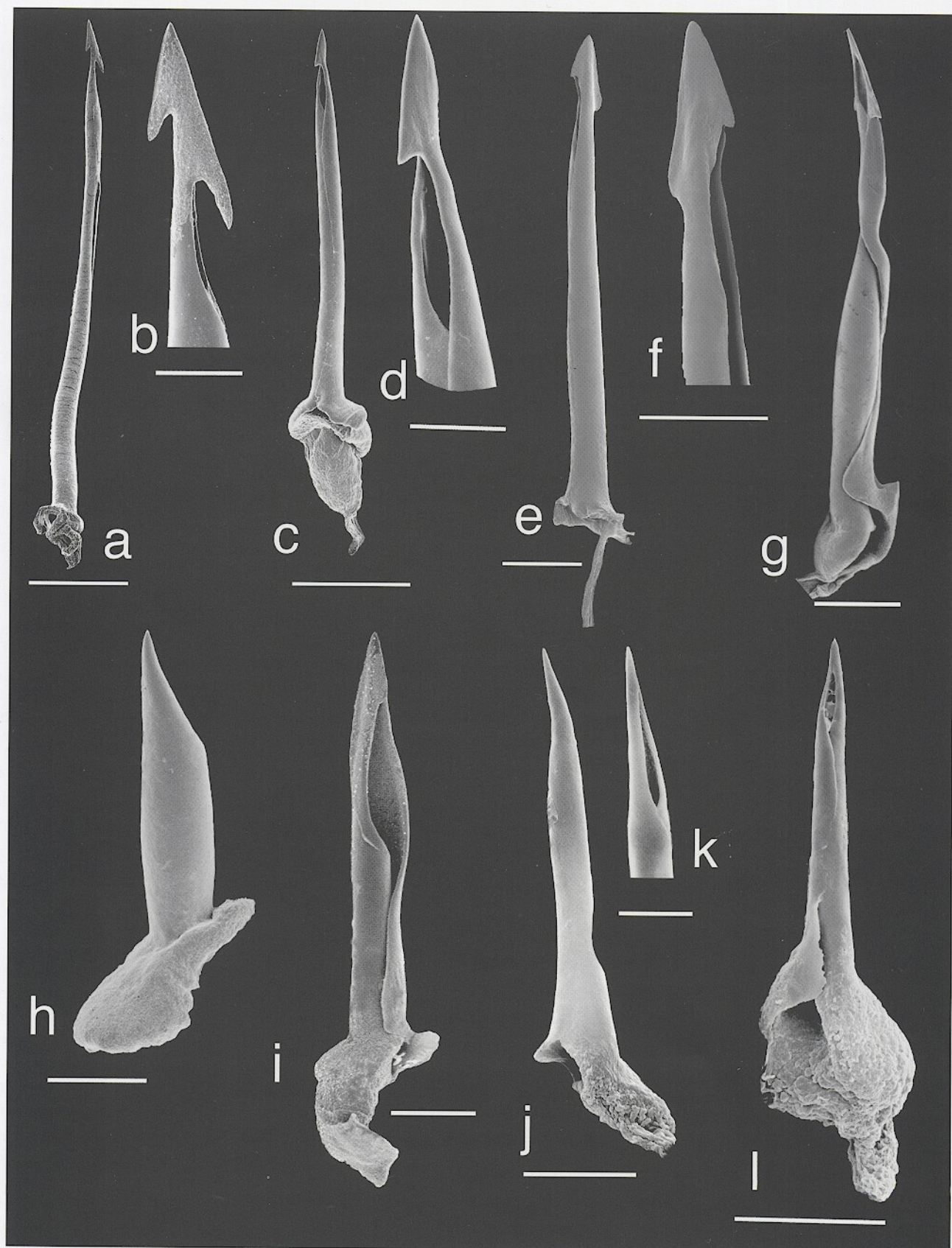


Figure 3. Marginal radular teeth of Raphitominae and *Conus bobolensis*. A. *Gymnobela pyrrogramma*. Scale bar = 100µm. B. detail of tip of A. Scale bar = 20µm. C. *Phymorhynchus moscalevi*. Scale bar = 50µm. D. detail of tip of C. Scale bar = 10µm. E. *Pontiotbauma mirabile*. Scale bar = 50µm. F. detail of tip of E. Scale bar = 50µm. G. *Conus bobolensis*. Scale bar = 100µm. H. *Hemilienardia malleti*. Scale bar = 20µm. I. *Thatcheria mirabilis*. Scale bar = 50µm. J. *Paramontana rufozonata*. Scale bar = 10µm. K. Detail of tip of H. Scale bar = 5µm. L. *Gymnobela emertoni*. Scale bar = 20µm.



within the rhynchostome. There is large rhynchostomal introvert which lacks a sphincter at the tip. The introvert when withdrawn occupies slightly more than half the length of the rhynchocoel. The epithelium of the body wall is cuticularized and composed of low, columnar cells. These are replaced by tall, columnar, ciliated cells at the proximal end of the retracted introvert and then by a tall, columnar, cuticularized epithelium near the introvert tip. Thus, when everted the introvert would have a ciliated epithelium, while its inner surface would be cuticularized. A thin but muscular, rhynchodeal septum with a narrow orifice divides the rhynchocoel medianly.

The proboscis, when retracted, is very short, and lies posterior to the septum. Its walls form numerous, large, circular folds, which indicate a potential for great extension of proboscis length on protraction. The mouth is very narrow. Powerful proboscis retractor muscles run along the proboscis walls. The buccal tube forms numerous long circular folds at the base of

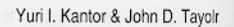
the proboscis, which probably straighten when the proboscis is protracted. Within the buccal tube there is a prominent, sac-like enlargement at some distance behind the mouth opening. This is lined by a tall columnar epithelium which forms a pad. A small anterior sphincter lies at the base of this sac-like enlargement. The distance from the mouth opening to the sphincter is about equal to the length of a radular tooth and therefore this sphincter is able to hold the base of a tooth. The buccal tube is lined with a very low epithelium, bearing short cilia, and has relatively thick walls only slightly thinner than those of the proboscis.

Buccal mass and oesophagus

The buccal mass is very short, with thin walls, and a possible sphincter just at the junction with the oesophagus. There are medium-sized, extensible buccal lips which may be inverted posteriorly into the buccal cavity. The oesophagus is wide and lined with a tall ciliated epithelium with glandular cells.

Table 1. Details of Raphitominae specimens sectioned for analysis.

<i>Gymnobela emertoni</i> (Verrill & Smith, 1884). 4706 m, North Atlantic, Biogas station CP17. 46°31' N, 10°20' W. The Natural History Museum, London.
<i>Gymnobela pyrrhogramma</i> (Dautzenberg & Fischer, 1896). 590 m, N. Atlantic, BIACORES station 161, 37°40' N, 25°51' W. The Natural History Museum, London.
<i>Gymnobela</i> sp. unnamed. see Kantor & Sysoev. 1996. 3610 m, E. Tasman Sea, 44°18' S, 166°46' E, Galathea station 607, Zoological Museum of University of Copenhagen, uncatalogued.
<i>Teretia teres</i> (Forbes, 1844), 250 m Sörendsvik, Norway. coll. J.D. George, 1973. The Natural History Museum, London.
<i>Teretiopsis abyssalis</i> Kantor & Sysoev, 1989. Sectioned holotype, 5510 m, 39°57' N, 165°07' E, (E. of Japan), R/V Vityaz stn 3156, Zoological Museum of Moscow State University, Moscow, Lc-5680.
<i>Teretiopsis levicarinatus</i> Kantor & Sysoev, 1989. Sectioned holotype, 2800m, 5°02' N, 20°50' W off Liberia, Zoological Museum of Moscow State University, Moscow, Lc-5679.
<i>Kermia barnardi</i> (Brazier, 1876). Intertidal rocks, Pointe Ouen Toro, Near Nouméa, New Caledonia. Coll. J.D. Taylor, 1989. The Natural History Museum, London.
<i>Hemidaphne reeveana</i> (Deshayes, 1863). Intertidal reef edge, Asan Bay, Guam. Coll. J.D. Taylor 1986. The Natural History Museum, London.
<i>Hemilienardia malleti</i> (Récluz, 1852). Intertidal reef edge, Asan Bay, Guam. Coll. J.D. Taylor 1986. The Natural History Museum, London.
<i>Pseudodaphnella granicostata</i> (Reeve, 1846). Intertidal reef edge, Asan Bay, Guam coll. J.D. Taylor 1986. The Natural History Museum, London.
<i>Paramontana rufozonata</i> (Angas, 1877). Intertidal rocks, Cape Vlamingh, Rottnest Island, Western Australia. Coll J.D. Taylor 1996. The Natural History Museum, London.
<i>Thatcheria mirabilis</i> Angas, 1877. 440 m, W. of Lacepede Archipelago, Western Australia, 16°54' S, 119°52' E. The Natural History Museum, London.
<i>Phymorhynchus moscalevi</i> Sysoev & Kantor, 1995. Sectioned paratype, 3680m, Mid-Atlantic Ridge, 26°08' N, 44°49' W, Zoological Museum of Moscow State University, Moscow, Lc-22458.
<i>Phymorhynchus wareni</i> Sysoev & Kantor, 1995. Sectioned paratype, 1483m. Edison Seamount, S. of Lihir Island, W. Pacific, 3°18.85' S, 152°34.9' E, Canadian Museum of Nature, Ottawa, CMN 92955.
<i>Pontiothauma mirabile</i> Smith 1895. 2540m, Indian Ocean, 6°59' N, 78°50' E SAFARI Stn. CP5. Radula only. The Natural History Museum, London.
Also
<i>Conus bobolensis</i> Petuch, 1979. New Caledonia, Muséum national d'histoire naturelle, Paris.



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radular teeth (Fig. 3L) are 60-70 μm long, enrolled, simple, awl shaped with pointed tip and a large club-shaped base.

Gymnobela sp.
(Figures 4, 20C)

This is an undescribed species, provisionally assigned to *Gymnobela* on the basis of shell characters, which possesses an unusual anatomy with the description modified from Kantor & Sysoev (1996). Only the anterior part of the digestive system was serially sectioned after removal from the body haemocoel.

Rhynchodaeum and proboscis

Rhynchostomal introvert absent. There is no rhynchodeal septum present. The proboscis is very long, folded several times within the rhynchodeal cavity and rather broad at the base (in the figure the proboscis is shown straight and somewhat shorter). The proboscis is thin-walled and lined with tall, goblet-shaped cells, which are cuticularized in the posterior part of the proboscis. Powerful proboscis retractor muscles run along the proboscis walls. The border between the muscles and the wall is unclear so that retractors give the appearance of a thick proboscis wall. The wall of anterior part of the proboscis forms an invagination, into which the anterior part of the buccal tube protrudes like a cylinder (Figure 4B "btc"). The opening of the buccal tube, which should be considered as the mouth, is very small. The epithelium lining the anteriormost part of the buccal tube is formed by tall, elongated, probably glandular cells (Figure 4B - glc). The buccal tube is rather thick-walled, and lined with a low epithelium. The wall of the buccal tube is composed of a layer

of connective tissue, underlain by a layer of circular muscle fibres. A large sphincter is located approximately mid-way along the length of the proboscis. At the proboscis base the buccal tube forms a low circular fold (Figure 4A - cf).

Buccal mass and oesophagus

The large, oval, buccal mass is situated at the base of the proboscis. The walls of the buccal cavity are moderately thin and formed by circular muscle fibres.

Glands

A single, convoluted, tubular, salivary gland opens through a moderately long duct into the anterior part of the radular sac. There is rather large accessory salivary gland, which is oval with broad lumen. The inner layer of epithelium is very thin and comprises no more than 1/5 of the thickness of the gland wall. The layer of muscle fibres is also very thin. The duct of the gland opens into the buccal tube mid-way along the length of the proboscis near to the buccal tube sphincter.

The venom gland is well developed, of uniform histology, long, convoluted, and opens into the posterior part of the buccal cavity close to the opening of the radular sac. The large, oval, muscular bulb is formed by an outer, very thin layer of longitudinal muscle fibres, a layer of connective tissue and thick, inner layer of longitudinal muscle fibres.

Radula

A small radular sac opens into the right side of the posterior part of the buccal cavity. The radular sac is thin-walled, without a pronounced caecum. No radular teeth were present in the sac.

Pseudodaphnella granicostata (Reeve, 1846)
(Figures 5, 20M)

Rhynchodaeum and proboscis

The rhynchostomal introvert absent. The rhynchostomal sphincter is medium-sized and located rather to the posterior of the rhynchostome. Anterior to the sphincter there is a large, fold of circular muscles (Fig. 5A - cmf). The rhynchostomal lips are poorly muscular and extend to form a rhynchostomal funnel. The epithelium of the anterior part of the rhynchocoel between the rhynchostome and the sphincter bears long cilia, while in the sphincter area the epithelium is cuticularized and similar to that lining the rest of the rhynchocoel. The epithelium of the rhynchodaeum is folded. In the posteriormost part of rhynchocoel there is low septum, (fig. 5B - sp), the epithelium behind this changing to tall, columnar cells.

The proboscis is very reduced, short, and represented only by a circular fold, through which long and muscular buccal lips are protruded.

Buccal mass and oesophagus

The epithelium lining the anterior third of the buccal lips externally and the buccal mass and oesophagus bears very long cilia (9-15 μm). The buccal mass is not differentiated from the buccal lips and extends to the base of the proboscis. The buccal tube is absent because of the reduction of the proboscis.

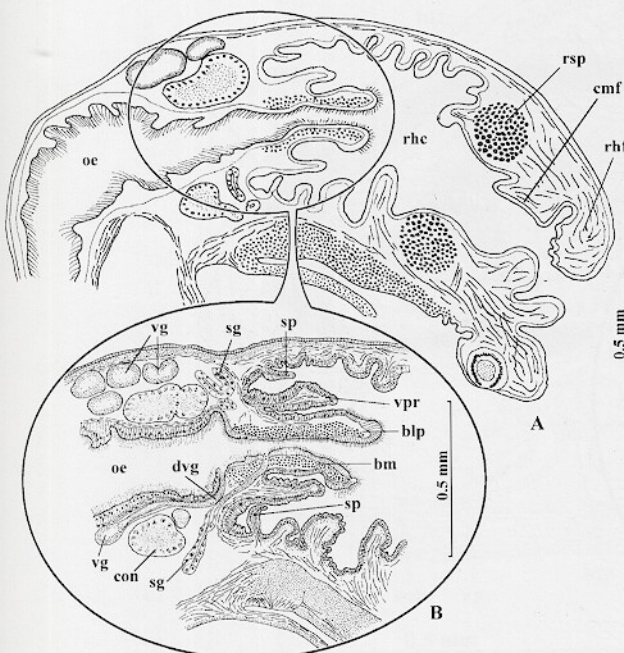


Figure 5. *Pseudodaphnella granicostata* (Reeve, 1846). A. Semidiagrammatic longitudinal section of the foregut. B. Enlarged region of the posterior rhynchodaeum and buccal mass.



Glands

The unpaired salivary gland is large, tubular and highly convoluted. The walls of the gland are formed by a single type of large, oval cell with granulated cytoplasm, which bears long cilia. Anteriorly, the gland gradually passes into a narrow ciliated duct, which opens ventrally at the border of posterior third of the buccal mass.

The venom gland is long and convoluted, with a change in histology prior to its anteriorwards passage through the nerve ring into a narrow ciliated duct, which opens just posterior to the buccal mass. The diameter and histology of the venom duct are similar to that of the salivary duct. The muscular bulb is very small, of the same diameter as the venom gland and with the wall formed from a single, thin layer of longitudinal muscle fibres. Internally the bulb is lined with an low epithelium bearing very long cilia.

Radula

The radula is absent.

Thatcheria mirabilis Angas, 1877

(Figures 3 I, 6, 20F)

Rhynchodaeum and proboscis

The rhynchostomal sphincter is large and located posteriorly within the rhynchostome. To the anterior there is a well-

developed rhynchostomal funnel, rhynchostomal introvert absent. The epithelium lining the anterior half of the rhynchocoel consists of tall, columnar, ciliated cells but in the posterior half this is gradually replaced by low, smooth epithelium. The rhynchodaeum is thick-walled and folded.

In the posterior part of the rhynchocoel there is a thin but highly muscular septum with a relatively narrow orifice. While the outer side of the septum is lined with an epithelium of low, cubical cells, the inner side, as well as the rest of rhynchodaeum and proboscis walls is lined with tall, columnar, non-ciliated cells. In the retracted state the proboscis can appear very short, lying posterior to the septum, but it is capable of significant extension and in one dissected specimen was seen protruding through the septum orifice and occupied more than half the length of the rhynchocoel.

The mouth is broad. The buccal tube has neither sphincters nor any sac-like enlargement. The thin walls of the tube are lined with a low, smooth epithelium and highly folded due to the great contraction of the proboscis. The muscles of the proboscis walls are equally developed along their length. Defined proboscis retractor muscles absent.

Buccal mass and oesophagus

The buccal mass is large, broad, very thin-walled, and lies behind and outside of the proboscis. In the sectioned specimen, the buccal mass was distorted due to the great proboscis

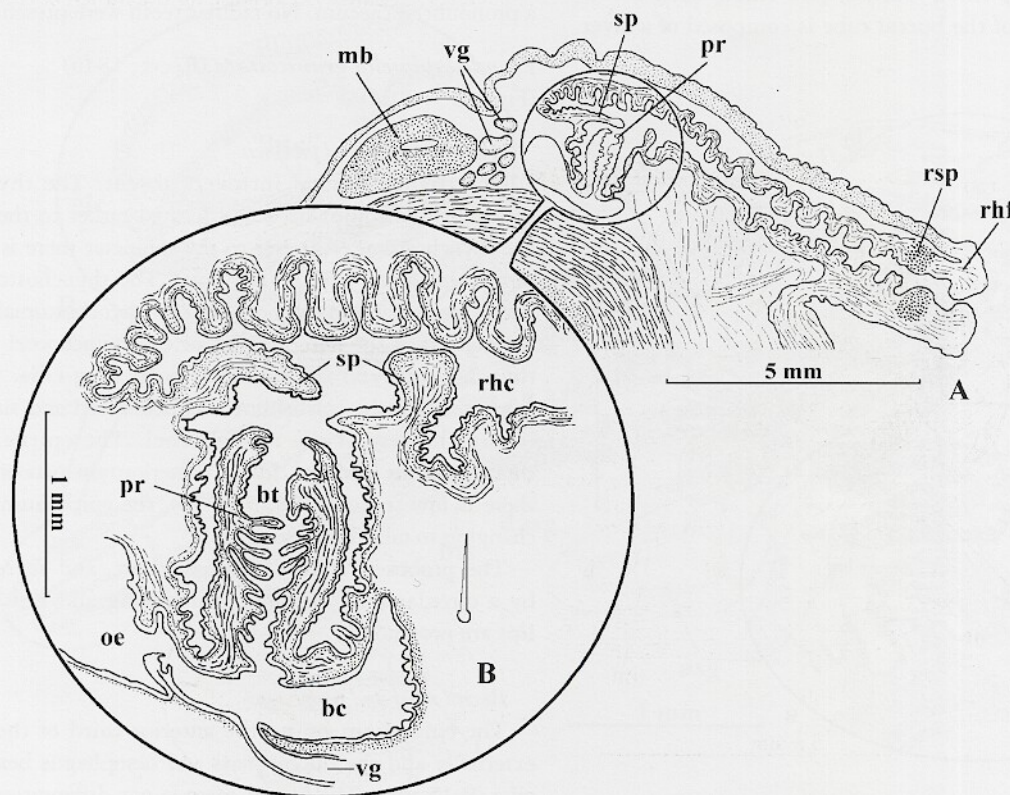


Figure 6. *Thatcheria mirabilis* Angas, 1877. A. Semidiagrammatic longitudinal section of the foregut. B. Enlarged region of the proboscis and buccal mass (the single marginal tooth is drawn in the same scale to the right of the proboscis).



contraction. The buccal mass gradually passes into a wide oesophagus without an obvious border. It is lined with a medium-tall, ciliated epithelium.

Glands

The salivary glands are paired, tubular, long, highly convoluted and wide (about 100 μm in diameter). The epithelium, lining the glands comprises uniform, very low, non-ciliated cells. The glands gradually pass into the ducts, which are much narrower (about 30 μm in diameter) and lined with ciliated epithelium. The ducts open into the radular sac close to its entry into the buccal cavity.

The venom gland opens ventrally at the posterior border of the buccal cavity and does not change in histology after passing anteriorly through the nerve ring. The muscular bulb is large, long and oval, with the wall formed from a single, thick layer of circular muscle fibres. The lumen of the bulb is narrow and lined with a low, non-glandular epithelium.

Radula

The radular sac is small and short, and situated laterally to the buccal cavity, opening on the right side through a short but wide buccal sac. The radular teeth (Fig. 3I) are very small, about 280 μm long in a specimen with a shell length 88 mm, that is 0.3% of the shell length. The teeth are enrolled, and awl shaped with a large adapical opening and an extended base.

Hemilienardia malleti (Récluz, 1852)

(Figures 3H, 7, 8, 20L)

Rhynchodaeum and proboscis

The rhynchostomal sphincter is medium-sized and long. There is very large rhynchostomal introvert (Fig. 7) which, in the retracted position, occupies nearly the entire length of the rhynchocoel. There is no rhynchodeal septum.

The retracted proboscis is narrow, long, highly convoluted and probably exceeds the rhynchocoel in length (it is shown less coiled and shorter on the figure). The proboscis is attached near the middle of the ventral wall of the rhynchodaeum. The proboscis lumen is filled with oval cells with large nuclei. Defined proboscis retractor muscles absent. The mouth is very narrow. The buccal tube is thin-walled, with a small sac-like enlargement near the mouth, which is lined by tall columnar epithelium, forming a small pad. A single radular tooth was seen held at the proboscis tip with the base adhering to the pad. Prominent buccal tube sphincters are absent. The buccal tube is lined with very low, non-ciliated epithelium.

Buccal mass and oesophagus

The buccal mass is poorly defined, short and thin walled. It is lined with a columnar epithelium with very long cilia and passes gradually into the oesophagus.

Glands

The salivary glands are paired, tubular, long and highly convoluted and relatively rather thick (about 22 μm in diameter). The epithelium, lining the glands is of uniform, columnar, ciliated cells, completely occupying the lumen of the gland.

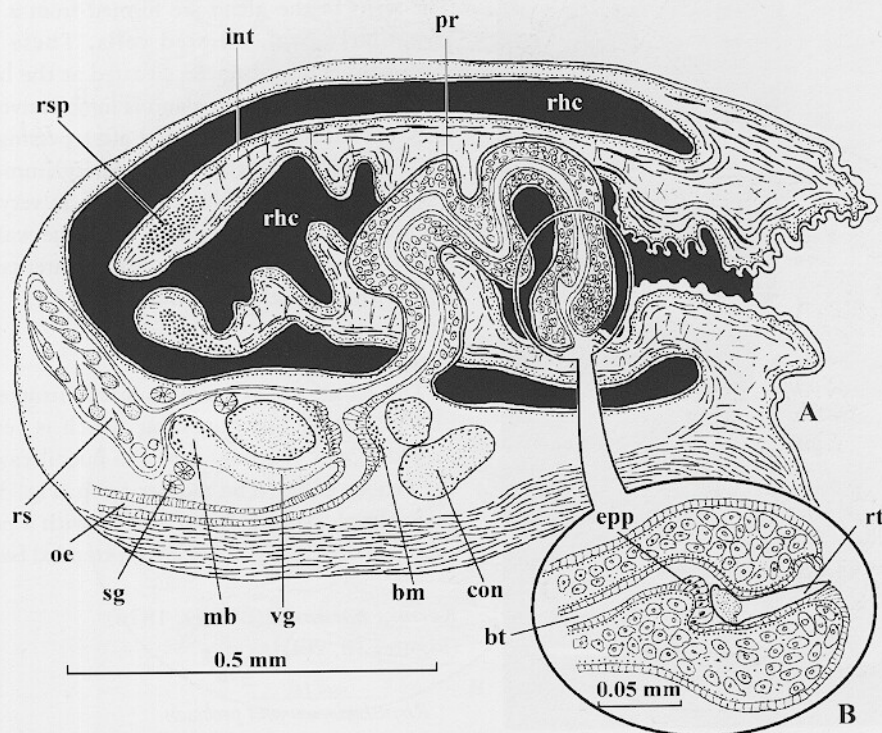


Figure 7. *Hemilienardia malleti*. A. Semidiagrammatic longitudinal section of the foregut (rhynchocoel - solid black). B. Enlarged proboscis tip with the marginal tooth.



The venom gland is very short (entire gland is shown on figure 7A - vg), of uniform histology, and slightly coiled with a diameter of about 45 μm . It opens into the buccal cavity in the area of the nerve ring, so that the gland itself does not pass through the ring. The muscular bulb is small and oval, with a diameter about the same as the gland, and the wall formed by a single, thin layer of muscle fibres.

Radula

The radular sac is relatively large and long and the radular caecum small. The buccal sac is long, narrow and curved. The radular teeth (Fig. 3H) are robust, relatively long (80 μm), broad, with a pointed tip and a large extended base.

Paramotana rufozonata (Angas, 1877)
(Figures 3J, 9, 20K)

Rhynchodaeum and proboscis

The rhynchostomal sphincter is medium-sized and positioned posteriorly within the rhynchostome. Rhynchostomal introvert or funnel absent. The tall, columnar

epithelium of the rhynchocoel is cuticularized, with very large oval cells. There is a septum in the posterior part of rhynchocoel. The epithelium, lining the outer surface of the septum is continuous with that of the rhynchodaeum, while on the inner surface it is replaced by similar but lower epithelium, which is continuous with that of the proboscis wall. Between the body wall and dorsal wall of the rhynchocoel there are numerous very large, irregularly oval cells with granulated cytoplasm and large oval nuclei (Fig. 9A - glc). These cells are probably glandular.

The proboscis is short and in the contracted state occupies less than half the length of the rhynchodaeum. Defined proboscis retractor muscles absent. The mouth opening is very narrow and surrounded by a circular fold of the proboscis wall. The buccal tube is narrow, thin-walled and widens at the proboscis base. It is lined with a low cuticularized epithelium. There are no sphincters.

Buccal mass and oesophagus

The buccal mass is very small, with rather thin walls, forming large buccal lips which protrude into the buccal tube (Fig. 9B - blp). The buccal cavity is lined with medium-tall cells possessing long cilia. To the posterior and before passing into oesophagus the walls of the buccal cavity form a posteriorly-projecting circular fold. This is lined with tall, columnar, epithelial cells, which bear extremely long cilia, that form a valve (Fig. 9C). The epithelium of the oesophagus is low and ciliated.

Glands

The salivary gland is probably unpaired, tubular and coiled. The walls of the gland are formed from a single type of large, irregularly oval, ciliated cells. These have a granulated cytoplasm and oval nuclei situated at the base or in the middle of the cells. The venom gland is long, convoluted and thick, and does not change in histology after passing through the nerve ring. It opens into the buccal cavity immediately posterior to the buccal sac. The muscular bulb is very small, of the same diameter as the venom gland, with the wall formed of a single thin layer of circular muscle fibres. Internally the bulb is lined with a low, smooth epithelium.

Radula

The radula sac is medium-sized, situated to the left of the proboscis base. The buccal sac which is very narrow, long and curved, opens ventrally into the buccal cavity, just anterior to the venom gland. The radular teeth (Fig. 3J) are about 40 μm long, simple, enrolled, awl shaped with a pointed tip, a narrow channel near the tip and a large extended base.

Kermia barnardi (Brazier, 1876)
(Figures 10, 20I)

Rhynchodaeum and proboscis

The rhynchostomal sphincter is medium-sized, and located posteriorly in the rhynchostome. Rhynchostomal introvert or

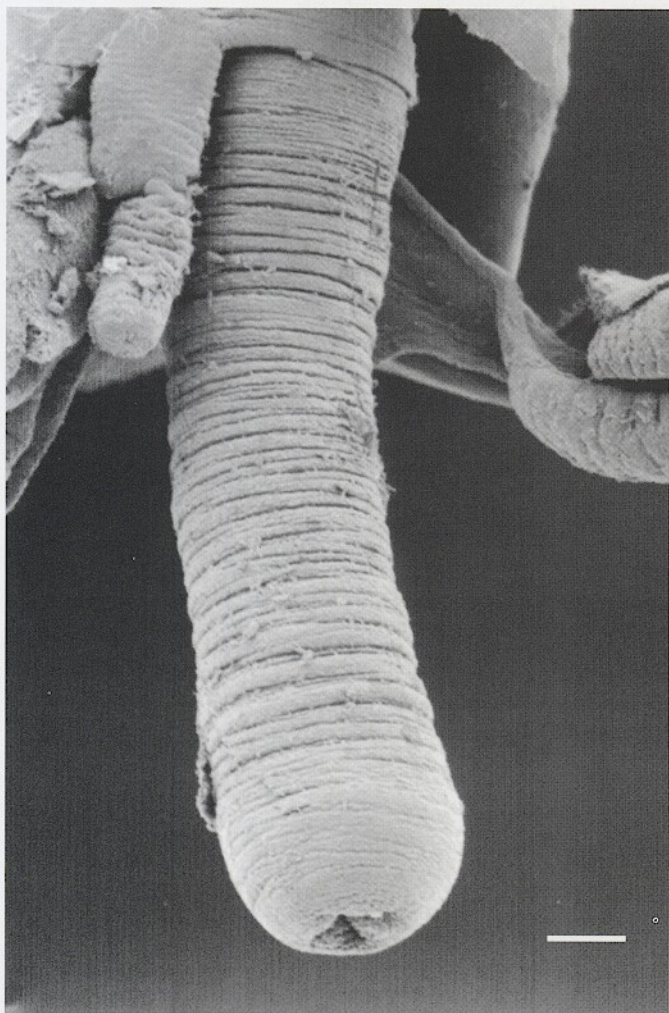


Figure 8. *Hemilienardia malleti*. Extended rhynchodeal introvert, relaxed specimen, critical point dried. Scale bar = 100 μm .

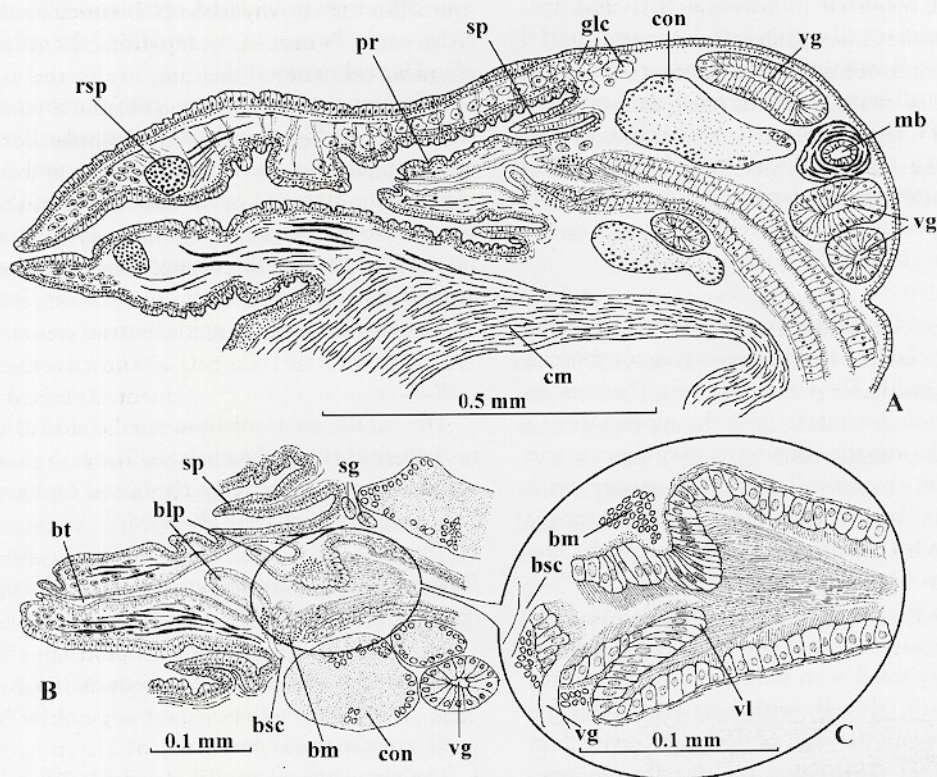


Figure 9. *Paramotana rufozonata* (Angas, 1877). A. Semidiagrammatic longitudinal section of the foregut. B. Enlarged proboscis and buccal mass. C. Enlarged buccal mass with the valve.

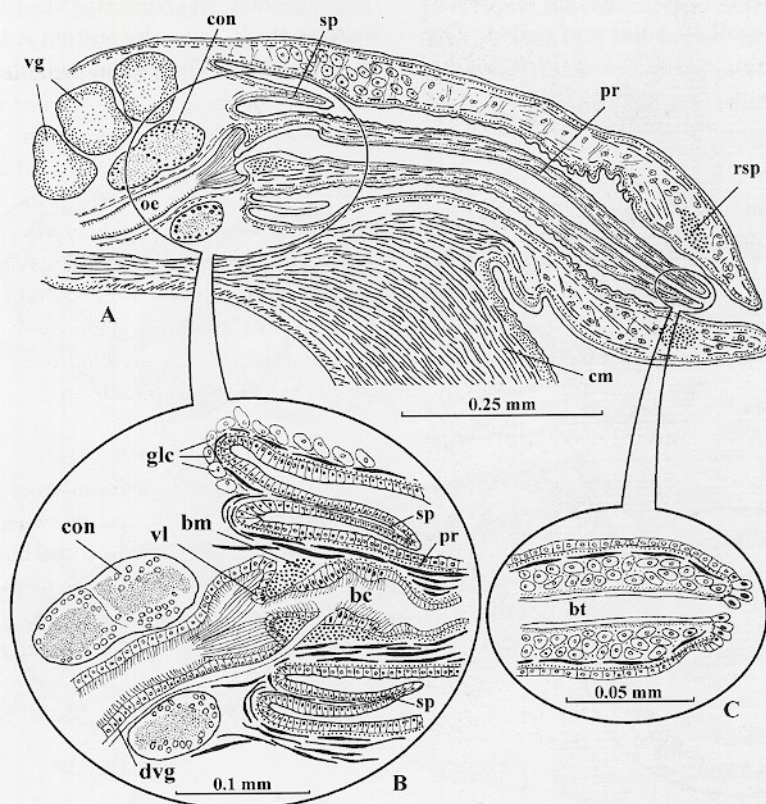


Figure 10. *Kermia barnardi* (Brazier, 1876). A. Semidiagrammatic longitudinal section of the foregut. B. Enlarged proboscis base and buccal mass (opening of the buccal sac not shown). C. Enlarged proboscis tip.

funnel absent. The rhynchocoel possesses a cuticularized, epithelium of tall, columnar cells with very large oval nuclei that occupy most of the cell length. In the posterior part of the rhynchocoel there is a small septum. The epithelium lining the septum and proboscis is continuous with that of the rhynchodaeum. Between the body wall and dorsal wall of rhynchocoel there are numerous very large, irregularly oval cells with a granulated cytoplasm and relatively small oval nuclei (Figure 10B - glc). These are probably glandular cells.

The proboscis is long and in the contracted state occupies the entire length of the rhynchodaeum. Proboscis retractor muscles run along the proboscis walls. The border between the muscles and the wall is unclear so that retractors give the appearance of a thick proboscis wall. The mouth opening is very narrow and surrounded by tall goblet-shaped cells, possibly sensory, with large oval nuclei and granulated protoplasm. The buccal tube is very narrow and thin-walled anteriorly but becomes wider and thicker walled posteriorly. There is no anterior sphincter.

Buccal mass and oesophagus

The buccal mass is very small with rather thin walls, and the buccal cavity is lined with tall cells with long cilia. Near the boundary with the oesophagus, the walls of the buccal cavity form a posteriorly-projecting fold. This is lined with tall, columnar, epithelial cells, with extremely long cilia, that form a valve. The epithelium of the oesophagus is composed of low, ciliated cells.

Glands

The salivary gland (s?) is small, tubular and coiled. The gland walls are formed from a single type of large, irregularly-

oval cells with granulated cytoplasm and oval nuclei situated either at the base or in the middle of the cells. The lumen of the gland is very narrow.

The venom gland is long, convoluted and thick. There is a change in histology just prior to its passage through the nerve ring where it forms a much narrower, ciliated duct, which passes through the ring and opens into the buccal cavity immediately posterior to the buccal sac. The muscular bulb is small, of slightly larger diameter than the venom gland, with the wall formed from a single thin layer of circular muscle fibres. Internally the bulb is lined with a low, smooth epithelium.

Radula

The radular sac is medium-sized and situated latero-ventrally to the left of the proboscis base. The buccal sac is short, narrow and straight and opens into the buccal cavity ventrally.

No radular teeth were obtained.

Phymorhynchus wareni Sysoev & Kantor, 1995
(Figures 11, 20D)

The description is modified from SYSOEV & KANTOR (1995).

Rhynchodaeum and proboscis

The rhynchodeal cavity is long, with a large, posteriorly located, rhynchostomal sphincter, and with very large, rhynchostomal funnel. The walls of the funnel are highly folded and capable of great extension. There are well-developed transverse muscles connecting the rhynchodaeum with the body walls. A thick, muscular septum is located in the posterior part of rhynchocoel. The proboscis is short and occupies about one

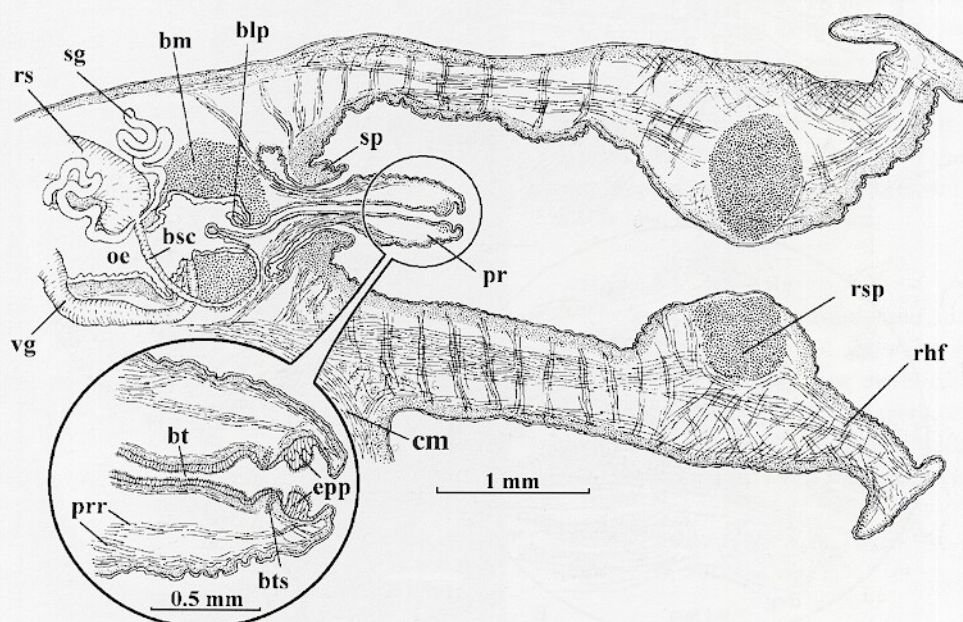


Figure 11. *Phymorhynchus wareni* Sysoev & Kantor, 1995 [after Sysoev & Kantor, 1995, slightly modified]. A. Semidiagrammatic longitudinal section of the foregut. B. Enlarged proboscis tip.



third of the length of the rhynchodeal cavity. Its walls are covered by a low, cubic, cuticularized epithelium and internally formed by thin outer layer of circular muscle fibres and an inner layer of longitudinal fibres. The posterior quarter of the proboscis and the inner side of septum are lined with a tall, columnar epithelium. Massive proboscis retractor muscles are attached to the walls of the proboscis about half way along its length. In the posterior part of the proboscis, the retractor muscles occupy the whole inner lumen and after leaving it are then attached to the columellar muscle and roof of the body haemocoel. The proboscis retractor muscles give rise to smaller muscle bundles which run to the wall of the sac-like enlargement of the buccal tube.

The mouth opening is small and rounded and this leads to a sac-like enlargement of the buccal tube. The epithelial cells lining the enlargement are tall, bear long cilia, and form a pad. There is a small sphincter of the buccal tube at the base of the sac-like enlargement (Fig. 11B – bts). The buccal tube itself is rather thick-walled and lined with a ciliated epithelium. The wall of the buccal tube is formed of circular muscle fibres, underlain by a thin layer of longitudinal fibres. A single radular tooth was observed within the lumen of the buccal tube near the proboscis base.

Buccal mass and oesophagus

The large, bulb-shaped, buccal mass is situated at the base of the proboscis. There are small and thin-walled, buccal lips, inverted inside the buccal cavity. The oesophagus is wide, lined with tall cells with very long cilia and opens in the U-shaped stomach. The buccal cavity and the oesophagus are filled with unrecognisable food content.

Glands

Long, convoluted, tubular, salivary glands open by short, poorly differentiated ducts into the base of the long buccal sac.

The venom gland is long and convoluted and opens into the posterior part of the buccal cavity. There is no change in histology of the gland anterior to the nerve ring. The medium-sized, oval, muscular bulb is formed by a single, thick layer of circular muscle fibres.

Radula

The buccal sac opens in the anteriormost part of the buccal cavity. The sac is very long and narrow and runs along the right side of the buccal mass. The length of the sac is about eight times longer than a single radular tooth. The radular teeth have a rather short, slender shaft (mean tooth length = $0.380\mu\text{m}$) with a prominent single barb at the distal tip and a complex base divided into a haft and three spurs (SYSOEV & KANTOR, 1995; Fig. 5 A-C).

Phymorhynchus moscalevi SYSOEV & KANTOR, 1995
(Figures 3 C-D, 12, 20E)

Description is based on SYSOEV & KANTOR (1995).

Rhynchodaeum and proboscis

The rhynchodeal cavity is long with a large rhynchostomal sphincter. Anteriorly, there is a large, highly muscular, rhynchostomal funnel with muscle fibres orientated in several directions. This structure resembles a muscular hydrostat (Kier, 1988) and the funnel is probably very mobile. Well-developed transverse muscles connect the rhynchodaeum with the body walls. At the posterior end of the rhynchocoel there

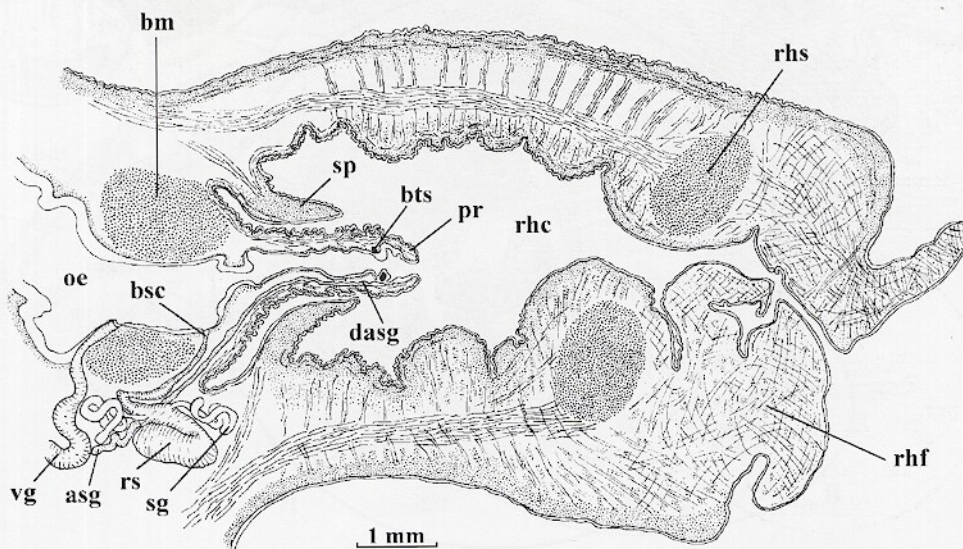


Figure 12. *Phymorhynchus moscalevi* Sysoev & Kantor, 1995 [after Sysoev & Kantor, 1995, slightly modified]. Semidiagrammatic longitudinal section of the foregut.



is a thick and muscular septum through which the proboscis can be protracted. The rhynchocoel and outer side of the septum are lined with an epithelium of tall columnar cells with large oval nuclei. This epithelium is replaced at the tip of the septum by one of low cubic cells, which is continuous with the proboscis epithelium.

The proboscis is very small and occupies about one-third the length of the rhynchodeal cavity. Well-developed retractor muscles run for almost the entire length of the proboscis and occupy nearly the whole inner lumen of the posterior part. To the posterior, they are attached to the columellar muscle and roof of the body haemocoel. A small and rounded mouth opening leads to a sac-like enlargement of the buccal tube. The epithelial cells, lining the enlargement are taller than that of the rest of the buccal tube and form a pad. There is a very small sphincter at the base of the sac-like enlargement. The thick wall of the buccal tube is formed of circular muscle fibres, with an underlying thin layer of longitudinal fibres. In the sectioned specimen the lumen of the tube was filled with particles of pyrites.

Buccal mass and oesophagus

The large bulb-shaped buccal mass is situated at the base of the proboscis. The buccal cavity is wide and only slightly narrower than the oesophagus.

Glands

A pair of long, highly convoluted, tubular, salivary glands open by short, poorly differentiated ducts into the base of the long buccal sac. Additionally, there is a small, tubular, convoluted, accessory salivary gland, situated below the buccal mass. The gland has histology typical of the Conoidea (SCHULTZ, 1983; TAYLOR & MILLER, 1990) and is formed of two epithelial layers divided by a thin layer of circular muscle fibres. It opens by a duct into the anterior, ventral part of the buccal tube.

The venom gland is long and convoluted and opens into the posterior part of the buccal cavity. The large, oval, muscular bulb is formed by a single thick layer of circular muscle fibres and has a wide lumen.

Radula

The buccal sac is long and narrow, forming a sharp bend

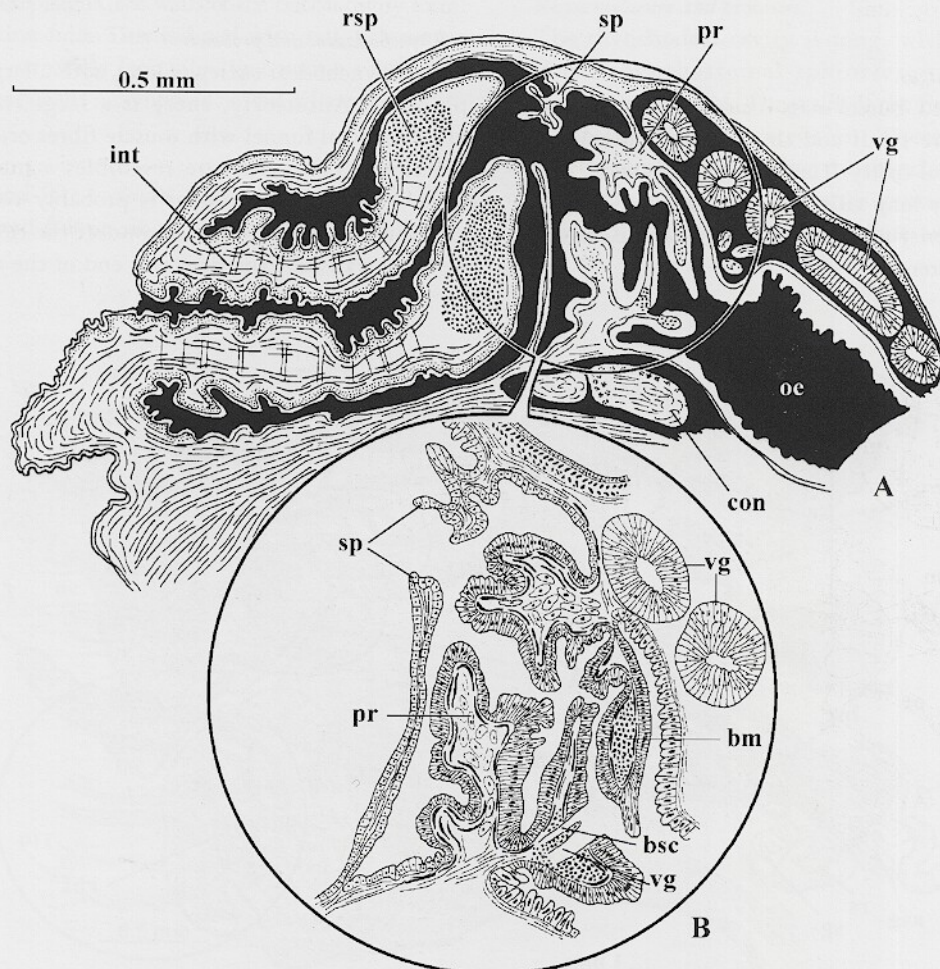


Figure 13. *Hemidaphne reeveana* (Deshayes, 1863) [after Taylor *et al.*, 1993, slightly modified]. A. Semidiagrammatic longitudinal section of the foregut. B. Enlarged region of the proboscis and buccal mass.



after leaving the radular diverticulum and opens in the very anterior part of the buccal cavity. The radular sac is small, situated below the buccal mass. The radular teeth are long and slender (200 μ m) with a narrow tip with a single barb and an extended complex base.

Hemidaphne reeveana (DESHAYES, 1863)
(Figures 13, 20L)

Rhynchodaeum and proboscis

The rhynchostomal sphincter is large, situated at the tip of a large rhynchostomal introvert, which in the inverted position occupies most of the length of the rhynchocoel. Towards the posterior of the rhynchocoel there is a thin, poorly muscular, rhynchodeal septum with a relatively narrow orifice.

The proboscis, when retracted, is very short and lies posterior to the septum. Its walls are folded, which suggests the possibility of a great extension of proboscis length on protraction. Defined proboscis retractor muscles absent.

The mouth is broad and leads to a sac-like enlargement of the buccal tube at some distance from the mouth opening, which is lined by tall columnar epithelium, forming a pad. The buccal tube is thin-walled and folded, without sphincters and lined with columnar epithelium.

Buccal mass and oesophagus

The buccal mass is short and thin-walled. There are medium sized extensible buccal lips.

Glands

The salivary glands are paired, tubular, long and convoluted.

The venom gland does not change histology after passing anteriorly through the nerve ring and opens ventrally into the buccal cavity immediately posterior to the buccal sac. The wall of the muscular bulb is formed of single thin layer of circular muscle fibres.

Radula

Radula present but no details as only a single specimen was available for study.

Teretiopsis abyssalis KANTOR & SYSOEV, 1989
(Figure 14, 20H)

Description modified from KANTOR & SYSOEV, 1989.

Rhynchodaeum and proboscis

The rhynchostomal sphincter is large and located posteriorly within the rhynchostome. There is medium-sized rhynchostomal funnel. The epithelium of the rhynchocoel is tall, columnar and brown. There is no septum. The rhynchodaeum is connected to the body wall by numerous transverse muscles (Figure 14C - tm).

The proboscis is vestigial and represented by only a low circular fold at the base of the small extensible buccal lips. The proboscis is lined with a low epithelium. The buccal tube is absent due to the reduction of the proboscis.

Buccal mass and oesophagus

The buccal mass is medium-sized with rather thick walls. The buccal cavity is very narrow and lined with a low, smooth epithelium. The oesophagus is wide and lined with tall epithelium.

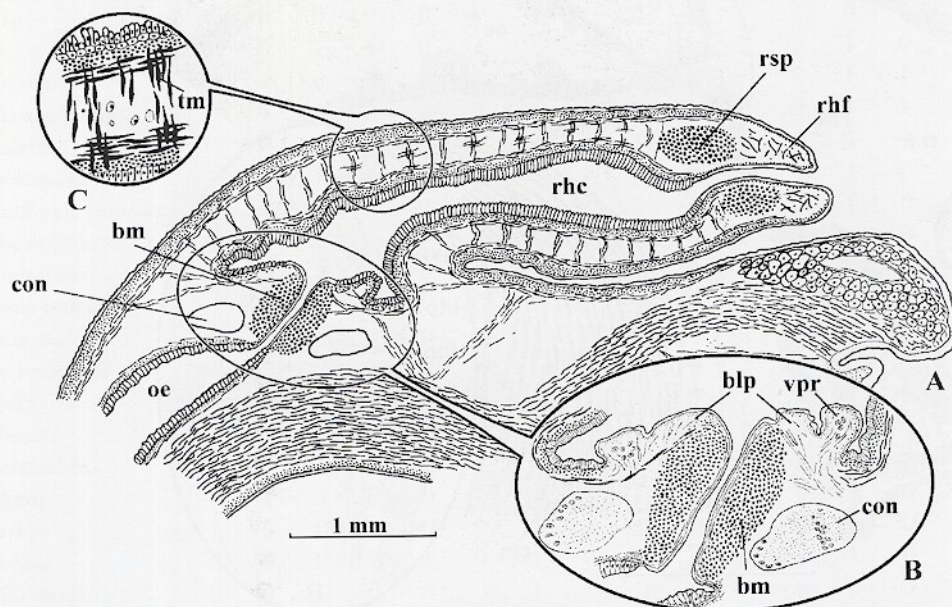


Figure 14. *Teretiopsis abyssalis* Kantor & Sysoev, 1989 [after Kantor & Sysoev, 1989, modified]. A. Semidiagrammatic longitudinal section of the foregut. B. Enlarged region of the proboscis and buccal mass. C. enlarged part of the rhynchodaeum wall.

*Glands*

There are no foregut glands present.

Radula

Absent.

Teretiopsis levicarinatus KANTOR & SYSOEV, 1989
(Figures 15, 20G)

Description modified from KANTOR & SYSOEV, 1989.

Rhynchodaeum and proboscis

The rhynchostomal sphincter is large and located to the posterior of the rhynchostome. There is medium-sized rhynchostomal funnel. The epithelium of the rhynchocoel is tall, columnar and dark-brown. There is no septum. The rhynchodaeum is connected with the body wall by numerous transverse muscles.

The proboscis is vestigial and represented by only a low circular fold at the base of the small extensible buccal lips. The proboscis and anterior surface of the buccal lips are lined with a rather tall epithelium of goblet-shaped cells. A buccal tube is absent due to the reduction of the proboscis.

Buccal mass and oesophagus

The buccal mass is very small with thin walls. The buccal cavity is very narrow and lined with very low epithelium. The epithelium of the oesophagus is dark brown and tall, somewhat similar to that of the rhynchocoel.

Glands

There are no foregut glands.

Radula

Absent.

Teretia teres (Forbes, 1844)
(Figure 20N)

The sectioned specimen was rather poorly fixed but some details of the anatomy are given below and characters included in the matrix (Table 1).

Rhynchodaeum and proboscis

There is a long rhynchodeal introvert which in the retracted state, occupies about 2/3 of the rhynchocoel. The rhynchostomal sphincter is large and situated at the introvert tip. A prominent septum with a narrow central aperture is situated towards the posterior of the rhynchocoel. The proboscis is short and occupies about 1/4 of the rhynchocoel. A distal buccal tube sphincter is present.

Buccal mass and oesophagus

The buccal mass is short and thin walled. No buccal lips were observed.

Glands

The salivary glands are paired and tubular. The venom gland is prominent with no change in histology anterior to the nerve

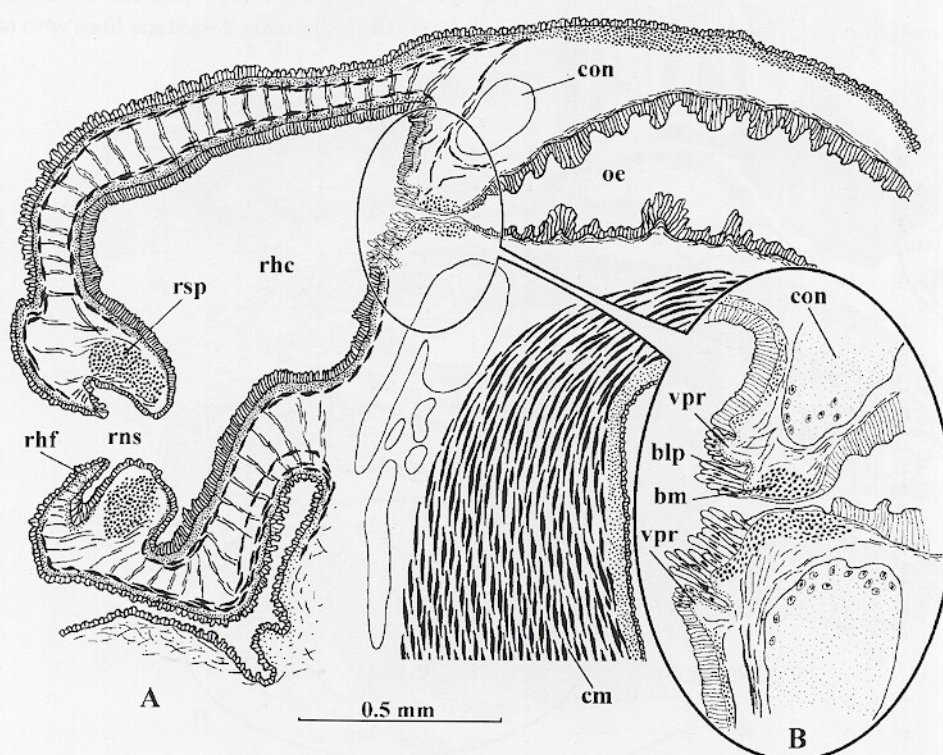


Figure 15. *Teretiopsis levicarinatus* Kantor & Sysoev, 1989 [after Kantor & Sysoev, 1989, modified]. A. Semidiagrammatic longitudinal section of the foregut. B. Enlarged region of the proboscis and buccal mass.



ring. The muscular bulb consists of a single layer of circular muscle with the lumen lined with a low epithelium.

Radula

BOUCHET & WARÉN (1980 p. 82) state that the radula is absent in this species but the radular sac and teeth are clearly seen in the thin sections. The individual radular teeth are short, enrolled and with large bases.

CHARACTER STATES AND PHYLOGENETIC ANALYSIS

In addition to the species described and illustrated above, a few other species of Raphitominae for which sufficient anatomical details have been published have also been included in the analysis. These species are *Pontiothauma mirabile* Smith, 1895 (PACE 1903, and radular details Fig. 3E); *Philbertia purpurea* (MONTAGU, 1803), *P. linearis* (MONTAGU, 1803) (details in SHERIDAN *et al.*, 1973); *Caenodagreutes aethus* Smith, 1967 (SMITH, 1967a). The characters and their states are briefly reviewed below and their distribution amongst the taxa shown in Table 2. A particular difficulty with raphitomines is the reduction or absence loss of foregut organs and this causes problems in the coding of inapplicable character states. Following STRONG & LIPSCOMB (1999) we have coded inapplicables as "?" (reductive coding). Moreover, a major limitation of the analysis is the fact that only a very small proportion of the living genera and species have been studied.

1. Rhynchostomal introvert (Fig. 1A, 7A - int): 0 = absent; 1 = present

The introvert is a mobile elongation of the rhynchostomal lips which when retracted lies within the rhynchodeal cavity but extends as a tube when protracted. Other than some species of raphitomines an introvert has been otherwise recorded only in the Terebridae.

2. Rhynchostomal funnel: 0 = absent; 1 = present

The funnel is formed by a muscular extensions of the anterior part of the rhynchostome (Fig. 11A, 12 - rhf). The rostrum of some *Conus* species is a similar structure.

3. Rhynchodeal septum: 0 = absent (Fig. 7, 14, 15 - sp); 1 = mid-rhynchodaeum (Fig. 1, 13 - sp); 2. posterior rhynchodaeum (Fig. 5B, 9A, 10A - sp).

Many raphitomines possess a thin muscular septum that divides the rhynchocoel. This is situated either towards the middle of the cavity or more usually at the posterior. Similar septa are found in some Terebridae and a few *Conus* species (Fig. 16, 17A - sp).

4. Proboscis: 0 = long; 1 = short; 2 = vestigial; 3 = absent

Most conoideans have a long proboscis (occupying more than half the length of the rhynchodaeum when retracted) but in raphitomines and some Terebridae it may be reduced or absent.

Table 2. Matrix of characters and character states for raphitomine species and outgroups.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Taxon																			
<i>Gymnobela emertoni</i>	0	0	2	2	?	?	?	?	0	0	2	1	1	1	?	?	0	1	0
<i>Gymnobela pyrrhogramma</i>	1	1	1	1	0	0	1	1	0	0	2	1	1	0	0	2	0	1	0
<i>Gymnobela</i> sp.	0	0	0	0	0	1	0	1	0	1	?	1	0	0	0	1	0	1	?
<i>Teretia teres</i>	1	0	1	1	0	?	1	1	?	0	2	1	1	0	0	2	0	1	0
<i>Teretiopsis abyssalis</i>	0	1	0	2	?	?	?	?	0	1	?	2	1	1	?	?	0	1	0
<i>Teretiopsis levicarinatus</i>	0	1	0	2	?	?	?	?	0	1	?	2	1	1	?	?	0	1	0
<i>Kermia barnardi</i>	0	0	2	0	0	1	1	1	1	0	2	1	1	0	1	2	1	1	0
<i>Hemidaphne reeveana</i>	1	0	1	1	0	1	1	1	0	0	2	1	1	0	0	2	0	1	0
<i>Pseudodaphnella granicostata</i>	0	1	2	2	?	?	?	?	0	1	?	1	1	0	1	2	0	1	0
<i>Paramontana rufozonata</i>	0	0	2	1	0	1	1	1	0	0	2	1	1	0	0	2	1	1	1
<i>Thatcheria mirabilis</i>	0	1	2	1	0	1	1	1	1	0	2	1	1	0	0	2	0	1	0
<i>Phymorhynchus moscalevi</i>	0	1	2	1	0	0	1	1	1	0	2	1	1	0	0	2	0	1	?
<i>Hemilienardia malleti</i>	1	0	0	0	0	1	1	1	1	0	2	1	1	0	0	2	0	1	?
<i>Pontiothauma mirabile</i>	0	1	2	1	0	?	1	1	1	0	2	1	1	0	0	2	0	1	0
<i>Philbertia purpurea</i>	1	0	1	0	0	1	1	1	0	0	2	1	1	0	0	2	0	1	0
<i>Philbertia linearis</i>	1	0	0	3	?	?	?	?	0	1	?	2	1	1	?	?	0	1	0
<i>Caenodagreutes aethus</i>	0	0	?	2	?	?	?	?	0	1	?	2	1	1	?	?	0	1	0
<i>Conus bobolensis</i>	0	1	1	0	0	1	0	1	1	0	3	0	1	0	0	0	0	0	1
<i>Hastula bacillus</i>	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1
<i>Mangelia nebula</i>	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0	1	0	0	1
<i>Ophiodermella inermis</i>	0	0	0	0	0	0	1	1	0	0	3	0	0	0	0	3	0	0	1
<i>Terebra subulata</i>	1	0	1	0	0	0	1	1	1	0	3	0	0	0	0	3	0	0	1
<i>Oenopota levidensis</i>	0	0	0	1	0	1	1	1	0	0	2	1	1	0	0	1	0	0	1

In some species, the low cylinder of muscular tissue surrounding the entrance to the buccal cavity represents a vestigial proboscis (Fig. 2B, 14B, 15B - vpr). Where the proboscis is vestigial or absent we have coded the following characters (5 - 8) as inapplicable "?".

5. Buccal tube introvert: 0 = absent; 1 = present.

This is a muscular flap-like structure located at the distal end of the buccal tube in the outgroup *Mangelia nebula* and other mangeliinae (TAYLOR *et al.* 1993, fig. 9)

6. Anterior buccal tube sphincter (Fig. 1B, 11B, 12 - bts): 0 = present 1 = absent

Most conoideans have a sphincter located in a distal position within the buccal tube.

7. Mid-buccal tube sphincter: 0 = present; 1 = absent

A sphincter in a middle position of the buccal tube found in *Conus* species (Fig. 1, 17B - bts).

8. Posterior (or basal) buccal tube sphincter (TAYLOR *et al.*, 1993, fig. 9 - ps): 0 = present; 1 = absent.

A basal buccal tube sphincter is present in the outgroup *Mangelia nebula* (SHERIDAN *et al.*, 1973) and other Mangeliinae.

9. Buccal lips (Fig. 1B, 2B, 5B, etc. - blp): 0 = present; 1 = absent.

These are muscular extensions of the anterior walls of the buccal mass which project as a tube into the buccal tube. In some species they can be inverted into the buccal cavity. Buccal lips occur sporadically throughout the Conoidea (TAYLOR *et al.* 1993; KANTOR *et al.* 1997).

10. Radula: 0 = present; 1 = absent.

11. Radula - type of marginal teeth: 0 = semi-enrolled; 1 = semi-enrolled with large base; 2 = enrolled with extended base; 3 = enrolled with narrow base.

The marginal teeth of raphitomines and the outgroups used in this analysis can be divided into 4 types. In *Hastula bacillus* the teeth are semi-enrolled with a narrow base (TAYLOR *et al.*, 1993, fig. 22b); *Mangelia nebula* has semi-enrolled teeth with a large base (TAYLOR *et al.*, 1993; fig. 23 e & f). Most raphitomines have enrolled teeth with an extended base whilst *Conus* and *Terebra subulata* have enrolled teeth with a narrow base (Fig. 3G).

12. Salivary glands: 0 = acinous; 1 = tubular; 2 = absent.

In most conoideans the salivary glands are acinous in histology but in Mangeliinae, Raphitominae and a few species of Crassispirinae the glands are tubular.

13. Accessory salivary gland: 0 = present; 1 = absent.

A well-known apomorphy of the Neogastropoda, (PONDER, 1974; BALL, TAYLOR & ANDREWS, 1997), accessory glands are patchily distributed amongst the Conoidea.

14. Venom gland and muscular bulb: 0 = present; 1 = absent.

15. Histology of anterior venom gland: 0 = uniform histology; 1 = changes to a duct after passage through nerve ring.

In most conoideans the venom gland has a uniform histology along its entire length. In a few species of Turridae and some raphitomine species the gland changes to a ciliated duct after passing anteriorly through the circumoesophageal nerve ring.

16. Muscular bulb layers: 0 = 2 equal layers; 1 = very thin outer layer; 2 = single layer; 3 = outer layer thicker than inner.

In most conoideans the terminal muscular bulb of the venom apparatus consists of two muscle layers of more or less equal thickness divided by a thin connective tissue layer. In Mangeliinae the bulb comprises two layers but the outermost is very thin. Most raphitomines have a bulb composed of a single layer only. In *Terebra subulata* (an outgroup) the outer layer is much thicker than the inner.

17. Oesophageal valve (Fig. 9C, 10B - vl): 0 = absent; 1 = present.

The oesophageal valve was present only in two species of raphitomines. It occupies a similar position and has some structural similarity to the valve of Leiblein of Rachiglossa (GRAHAM, 1941) although the homology is uncertain.

18. Operculum: 0 = present; 1 = absent

19. Protoconch ornament: 0 = cancellate ornament; 1 = non-cancellate ornament

Outgroups

Except for *Conus bobolensis* (described below) and *Conus ventricosus* (Fig. 16, modified from TAYLOR *et al.* 1993, fig. 7) details of the species used as outgroups in the analysis may be found in TAYLOR *et al.* (1993) and the other references cited. Two species of Terebridae were included in the analysis because of the presence of the rhynchodeal introvert and septum in some species of the family.

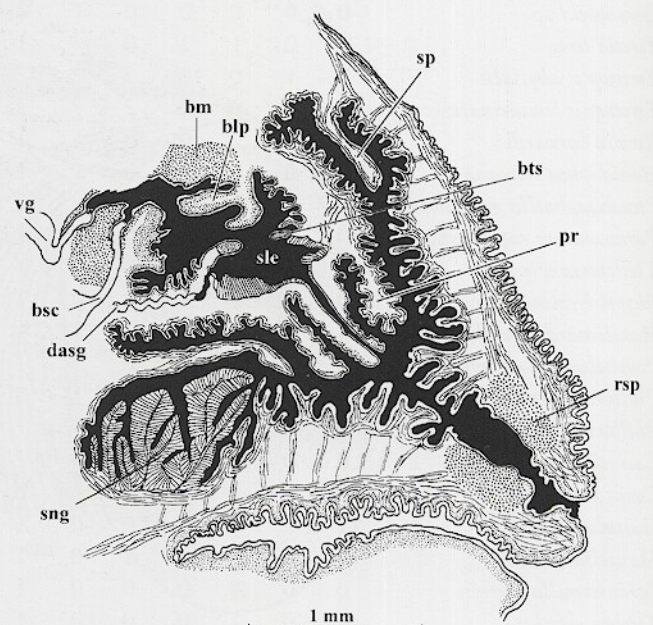


Figure 16. *Conus ventricosus*. Semidiagrammatic longitudinal section of the anterior foregut (after Taylor *et al.* 1993 modified).



Coninae:

Conus bobolensis Petuch, 1979 (Fig. 17)

Conus ventricosus Gmelin, 1791 (Taylor *et al.*, 1993 and Fig. 16)

Clathurellinae:

Ophiodermella inermis (Hinds, 1843)

Mangeliinae:

Mangelia nebula (Montagu, 1803) (Sheridan *et al.*, 1973)

Oenopotinae:

Oenopota levidensis (Dall, 1919) (Shimek, 1975)

Terebridae:

Hastula bacillus (Deshayes, 1859) (Taylor & Miller, 1990)

Terebra subulata Linnaeus, 1767 (Taylor 1990)

Description of *Conus bobolensis* Petuch, 1979
(Figures 3G, 17)

This species has a tall spire, a character usually considered primitive within the Coninae and also there is a rhynchodeal septum a hitherto unrecorded structure in *Conus*.

Rhynchodaeum and proboscis

The rhynchodeal cavity is long, with an anterior rhynchostomal sphincter of medium-size. A pronounced rhynchostomal funnel is absent, although the rhynchostomal lips are large. Transverse muscles, connecting the rhynchodaeum with the body walls are absent. In the medial part of the rhynchocoel there is a thin septum with a rather narrow orifice. The anterior part of the rhynchocoel and the outer side of septum are lined with a very tall glandular epithelium. This epithelium forms high folds, that nearly

completely fill the cavity. The epithelial cells are ciliated with small oval nuclei. At the tip of the septum there is a sharp change to the low and non-glandular epithelium that lines the posterior part of the rhynchocoel.

The proboscis is medium-sized, and in the contracted stage occupies about half of the rhynchocoel. Its walls are highly folded so that when protracted the proboscis is long. The proboscis is lined with a cuticularized, cubical epithelium. The mouth opening is small and rounded and leads to a sac-like enlargement of the buccal tube. The epithelial cells, lining the enlargement are taller than that of the rest of the buccal tube. There is no anterior buccal tube sphincter. At the proboscis tip a single radular tooth was observed protruding through the mouth opening. This tooth is probably held in place by contraction of muscular walls of the anterior proboscis as well as by the epithelium of the of the sac-like enlargement. There is a small intermediate sphincter of the buccal tube.

Buccal mass and oesophagus

The buccal mass is short, with rather thick walls and lies posterior to the proboscis. Small buccal lips are present. The oesophagus is narrow, lined with ciliated epithelium and forms a very long curve between the buccal mass and the nerve ring.

Glands

The salivary glands are fused, very large, acinous and lie to the left of the rhynchodaeum. The salivary ducts are paired, long and highly convoluted. The venom gland does not change in histology after passing anteriorly through the nerve ring and

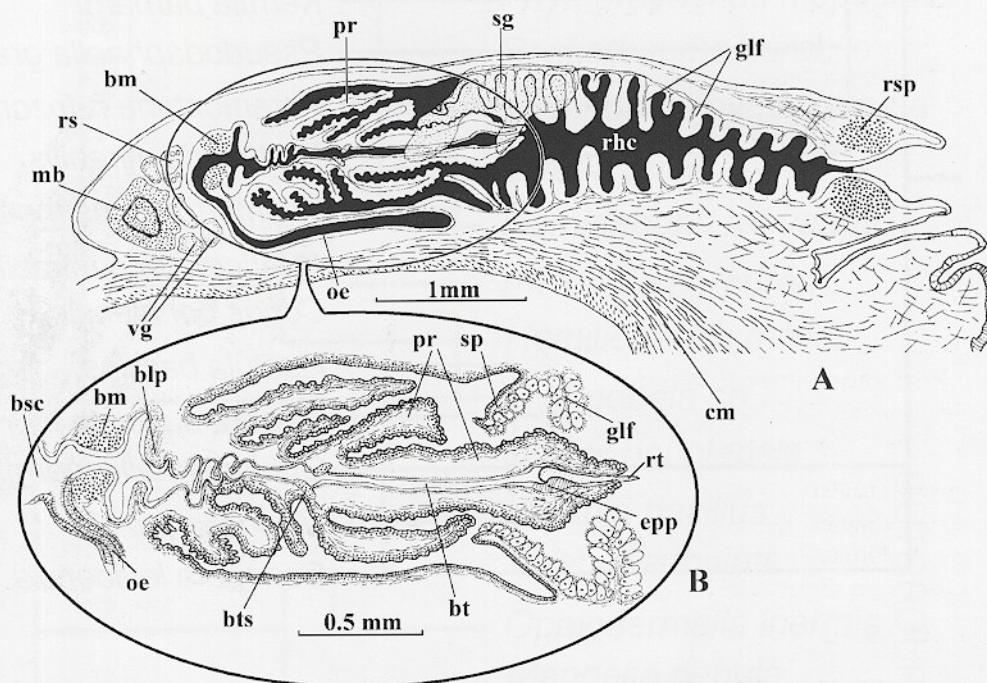


Figure 17. *Conus bobolensis* Petuch, 1979. A. longitudinal section of foregut. Snout gland situated at the left side of the rhynchodaeum is seen as if the rhynchodaeum is transparent. B. Enlargement of posterior rhynchodaeum and buccal mass.



opens ventrally posterior to the buccal mass. The muscular bulb is very large, with its wall formed by two subequal layers of longitudinal muscle fibres, separated by a thick layer of connective tissue.

Radula

The radular sac is broad and long, and situated dorsally to the oesophagus (only the radular caecum is shown on Fig. 17A). It

opens into the buccal cavity on the left side. The radular caecum is medium sized. The buccal sac (i.e. the portion of the radular sac between the entrance of the salivary ducts and the buccal cavity) is very long, narrow, and runs downward along the right side of the buccal mass, and then gradually turns towards its narrow opening ventrally into the buccal cavity just anterior to the sphincter of the buccal mass. The radular teeth (Fig. 3G) are long, at least 630 µm, slightly curved and hollow with two distal barbs.

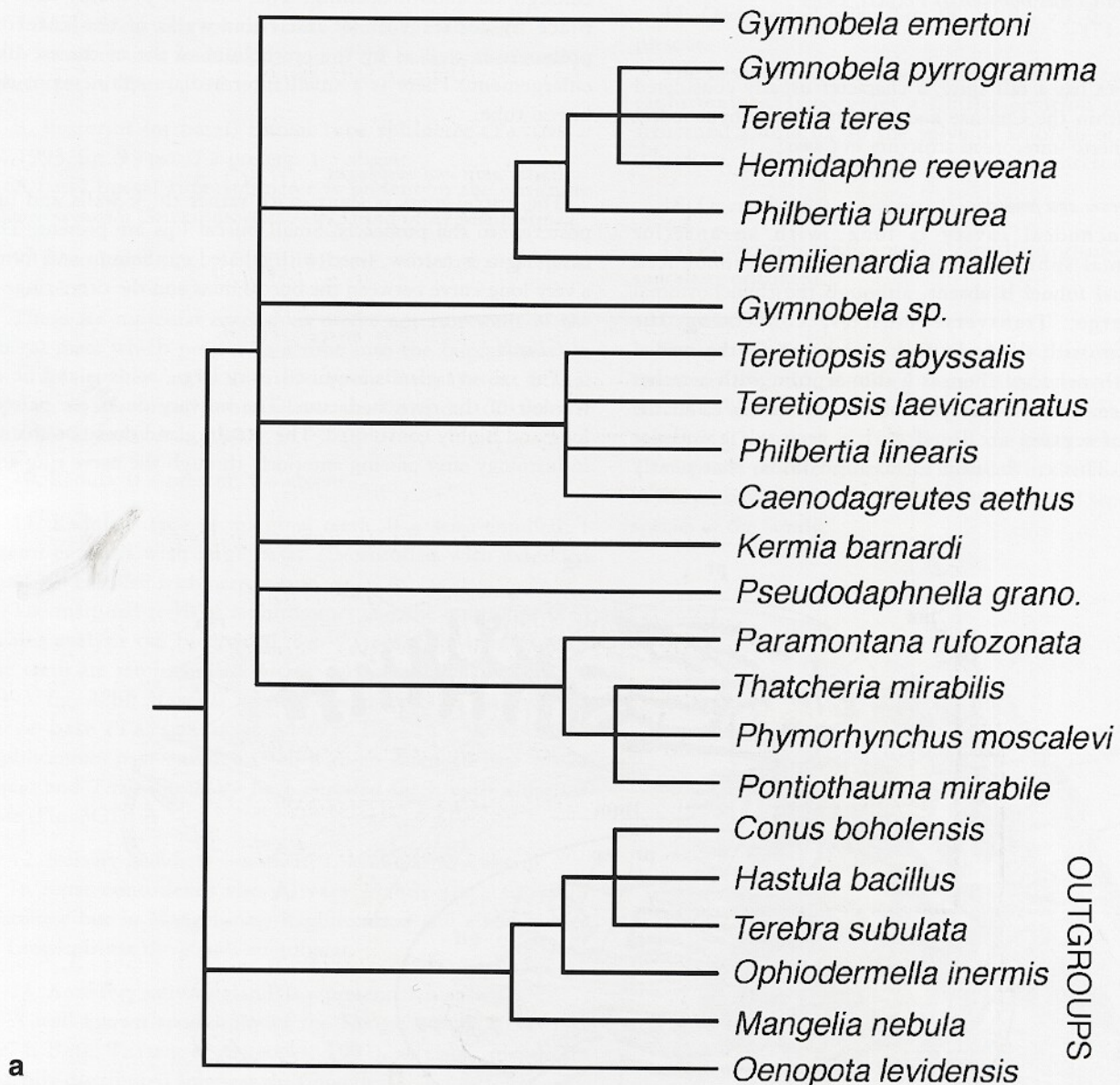


Figure 18. Strict consensus (a ↑) and 50% majority rule (b →) trees derived from 64 equally parsimonious trees with a length 52 steps. Consistency Index = 0.54, Rescaled C.I. = 0.74 and Retention Index = 0.4. Plain numbers indicate percentage occurrence of each clade in the set of equally parsimonious trees. Shaded numbers identify particular clades for reference.



Conus ventricosus Gmelin, 1791
(Figure 16)

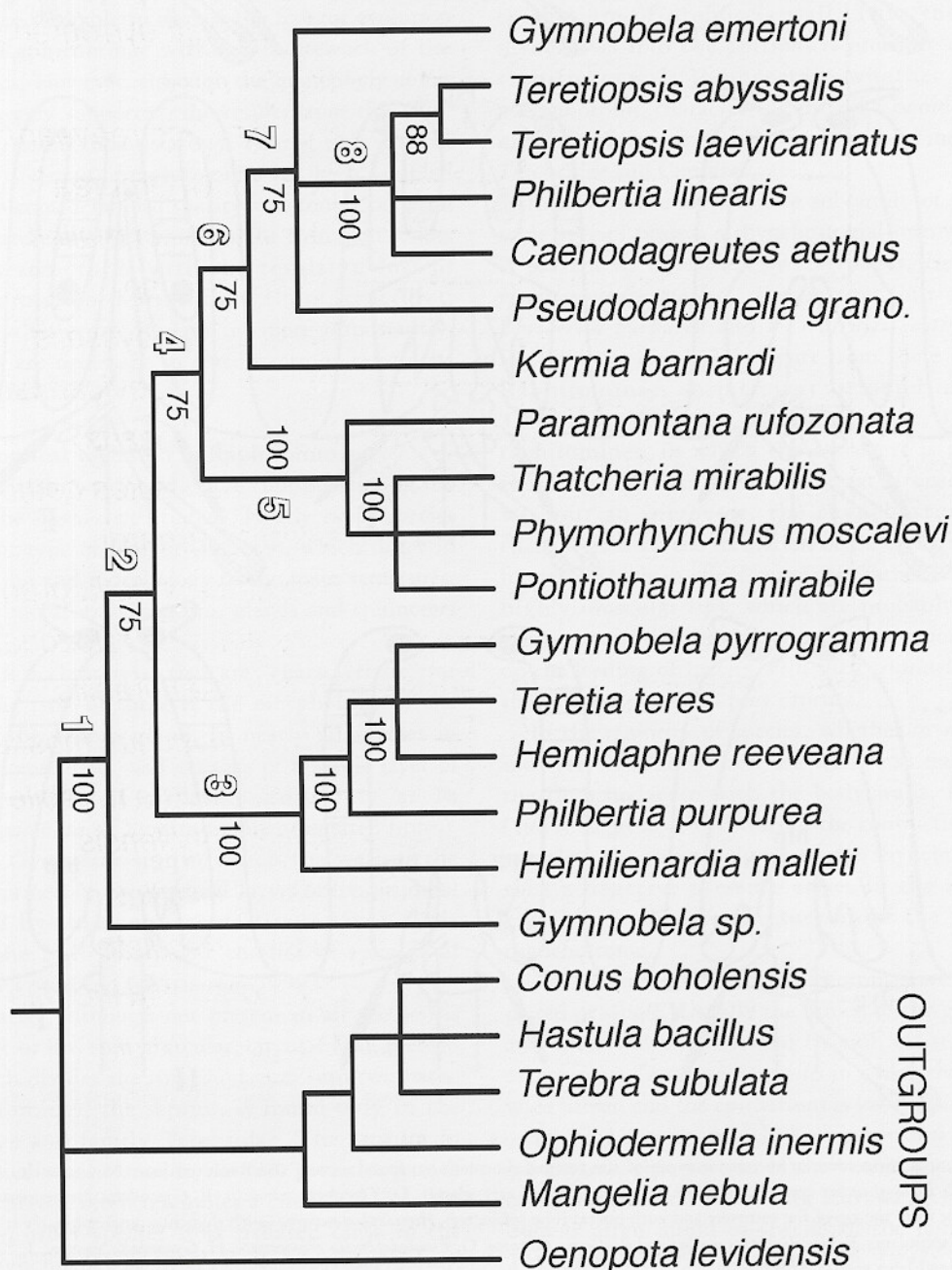
The foregut anatomy of *Conus ventricosus* is generally similar to *C. bobolensis*, but the rhynchodeal septum is located in the posterior part of the rhynchodeal cavity. This structure was previously interpreted as a fold of the proboscis wall (TAYLOR *et al.*, 1993, fig. 7).

Parsimony analysis

The characters listed above and their states in the 17 species of Raphitominae and six outgroup species are given in Table 2.

The analysis was performed using PAUP version 3.1.1. Multistate characters were treated as unordered. The heuristic search option was used with tree bisection-reconnection, branch swapping in effect and with ten replicates of a random addition sequence of taxa. The analysis produced 64 equally parsimonious trees of length 52 steps. The resulting strict consensus and 50% majority rule trees are shown in Fig. 18.

The monophyly of the Raphitominae is supported at Clade 1 by the presence of radula teeth with large bases and the lack of an operculum. Clade 2 which includes all the Raphitomines examined, except *Gymnobela* sp., is supported by the three character states namely, the presence of diagonally cancellate



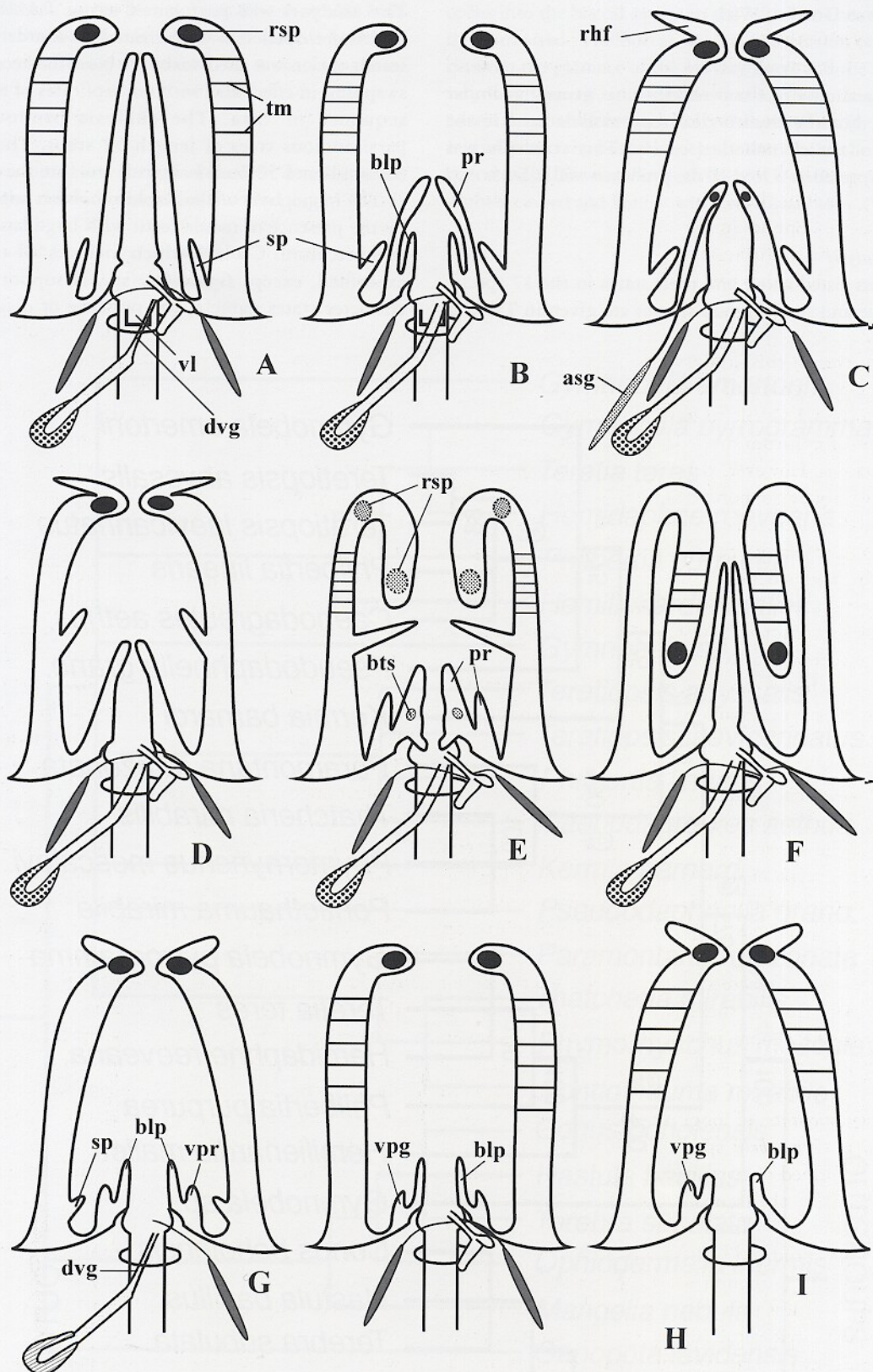


Figure 19. Diagram summarising some of the major types of the foregut morphology, found among the Raphitominae. Not to scale. A, *Kermia barnardi*. B, *Paramotana rufozonata*. C, *Phymorhynchus* spp. (*P. moscalevi* with accessory salivary gland). D, *Thatcheria mirabilis*. E, *Gymnobella pyrbogramma* (with rhynchostomal sphincter shifted posterior from the tip of the introvert and with buccal tube sphincter), *Hemidaphne reeveana* (with rhynchostomal sphincter at the tip of the introvert and without buccal tube sphincter). F, *Hemilienardia malleti* and *Philbertia purpurea*. G, *Pseudodaphnella granicostata*. H, *Gymnobella emertoni*. I, *Teretiopsis* spp., *Philbertia linearis*, *Abyssobela atoxica* (without vestigial proboscis).



sculpture of the protoconch whorls (absent in *Paramontana*), the single muscle layer of the muscular bulb and the rhynchodeal septum (absent in several species). Clade 3 is supported in all trees by the possession of a rhynchodeal introvert, but this state is also found in *Philbertia linearis* (Clade 8). In Clade 4 the rhynchodeal septum is situated in a posterior position and lost in some of the terminal members of the clade. Clade 6 is supported by the anterior change in the histology of the venom gland in some species. Species in Clades 7 and 8 have lost major foregut organs (the radula, salivary glands and venom apparatus) and it is likely that this is not a natural grouping.

DISCUSSION

Our main objectives in this study were to describe details of foregut anatomy in a group of poorly known conoideans and normally it would be desirable to discuss the foregut evolution and traits of the Raphitominae within a framework of the phylogenetic analysis. However, although the monophyly of the Raphitominae is largely supported, the results from this (Fig. 18) are for several reasons, unsatisfactory. Firstly, only a small subset of the total diversity of raphitomines has been sampled and amongst these considerable disparity was found between taxa. Secondly, a feature of raphitomines is the reduction or loss of major foregut structures with the resulting loss of phylogenetic information derived from those structures. Thirdly, study of other organ systems or, more importantly, molecular analyses are necessary to corroborate or refute the results presented here.

Summary of anatomical variation in Raphitominae

Considerable variation was found in the configuration of the foregut amongst the species we studied. Nearly every species possesses a different type of foregut (Fig. 19), which differ in the presence, position and morphology of the main structures, such as proboscis, buccal mass, septum, glands and sphincters of the buccal tube.

There are very few characters, that are "characteristic" for the subfamily. The first of these is the morphology of the muscular bulb of the venom gland. In nearly all species in which the bulb is present its wall consists of a single layer of muscle fibres (usually of circular and rarely as in *Pseudodaphnella granicostata*, of longitudinally orientated fibres). The exception is *Gymnobela* sp., in which the wall of the muscular bulb is formed of two unequal layers of longitudinal fibres, separated by thin connective tissue layer. This morphology of the bulb is similar to that of species of Mangeliinae we have studied (TAYLOR *et al.*, 1993).

The other character (although not present in all species) is the septum, a more or less thin muscular, circular fold, pierced by an orifice, which divides the rhynchodaeum into two parts. Beside the raphitomines, the septum is found only in the subfamily Coninae and family Terebridae. The septum in raphitomines is usually positioned in the very posterior part of the rhynchocoel where it often resembles a circular fold at the proboscis base. In other species it is situated close to the middle of the rhynchocoel as in *Gymnobela pyrrhogramma*,

Hemidaphne reeveana, *Teretia teres* and *Thatcheria mirabilis*. In this case the proboscis, in the retracted position, lies behind the septum, but can be protruded through the orifice when protracted (this was observed at least in *T. mirabilis*). In these species, it is likely that complete closure of the septal orifice is possible. In other species the septum may be greatly reduced and represented by very low fold of the rhynchodeal wall (*P. granicostata*, *Philbertia purpurea* (SHERIDAN *et al.* 1973), or be completely absent. The presence, position and degree of development of septum do not correlate with any other characters of the foregut. At present the function of the septum is obscure. In most species there is a change in the epithelial lining at the tip of the septum; the epithelium of the outer side of the septum is continuous with that of the rhynchocoel, while that on the inner side is confluent with the epithelium of proboscis wall. Thus the division of the rhynchocoel into two portions is probably of some functional significance. It is uncertain whether the septum is a plesiomorphic character for the all Conoidea and lost in the majority of taxa or if it has been evolved independently in the Terebridae and Conidae.

Raphitominae are the sole subfamily of Conidae, in which some species possess a rhynchostomal introvert. This structure is present in *Gymnobela pyrrhogramma*, *Hemidaphne reeveana*, *Hemilienardia malleti*, *Teretia teres* (our data), along with *Philbertia purpurea* and *P. leufroyii boothi* (SMITH, 1967a; SHERIDAN *et al.*, 1973). Apart from these occurrences in the Raphitominae, an introvert is found in most species of Terebridae (TAYLOR, 1990; SIMONE, 1999). Species of raphitomines, in which the introvert is absent are usually characterised by a greatly elongated head. Also in species without an introvert, the rhynchostome is frequently characterised by the formation of the so called "rhynchostomal funnel", which in effect comprises rather enlarged and usually highly muscular lips, which are probably capable of active movements. Although no direct observations have been made on the feeding of species with such a funnel, it is highly likely that it is employed in prey capture.

In the majority of species, whether or not they possess an introvert or funnel, there are transverse muscles, that connect the rhynchodaeum with the body walls. KANTOR & SYSOEV (1989) suggested, that during the contraction of the transverse muscles, the inner volume of the rhynchocoel increases and thus a negative pressure arises in the rhynchocoel. This possibly facilitates the suction of the prey through the rhynchostome.

The salivary glands of raphitomines are tubular and either paired or single. Usually the lumen of the gland is very narrow and their walls are formed by tall, ciliated epithelium. An exception is *Thatcheria mirabilis* in which the glands have a very wide lumen and the epithelium is low, cubic and non-ciliated.

In some species, namely *Kermia barnardi* and *Pseudodaphnella granicostata*, that portion of the venom gland situated in front of the circum-oral nerve ring narrows to form a duct. Such a duct is often found in species of the family Turridae (*sensu* TAYLOR *et al.*, 1993; KANTOR *et al.*, 1997). This transformation

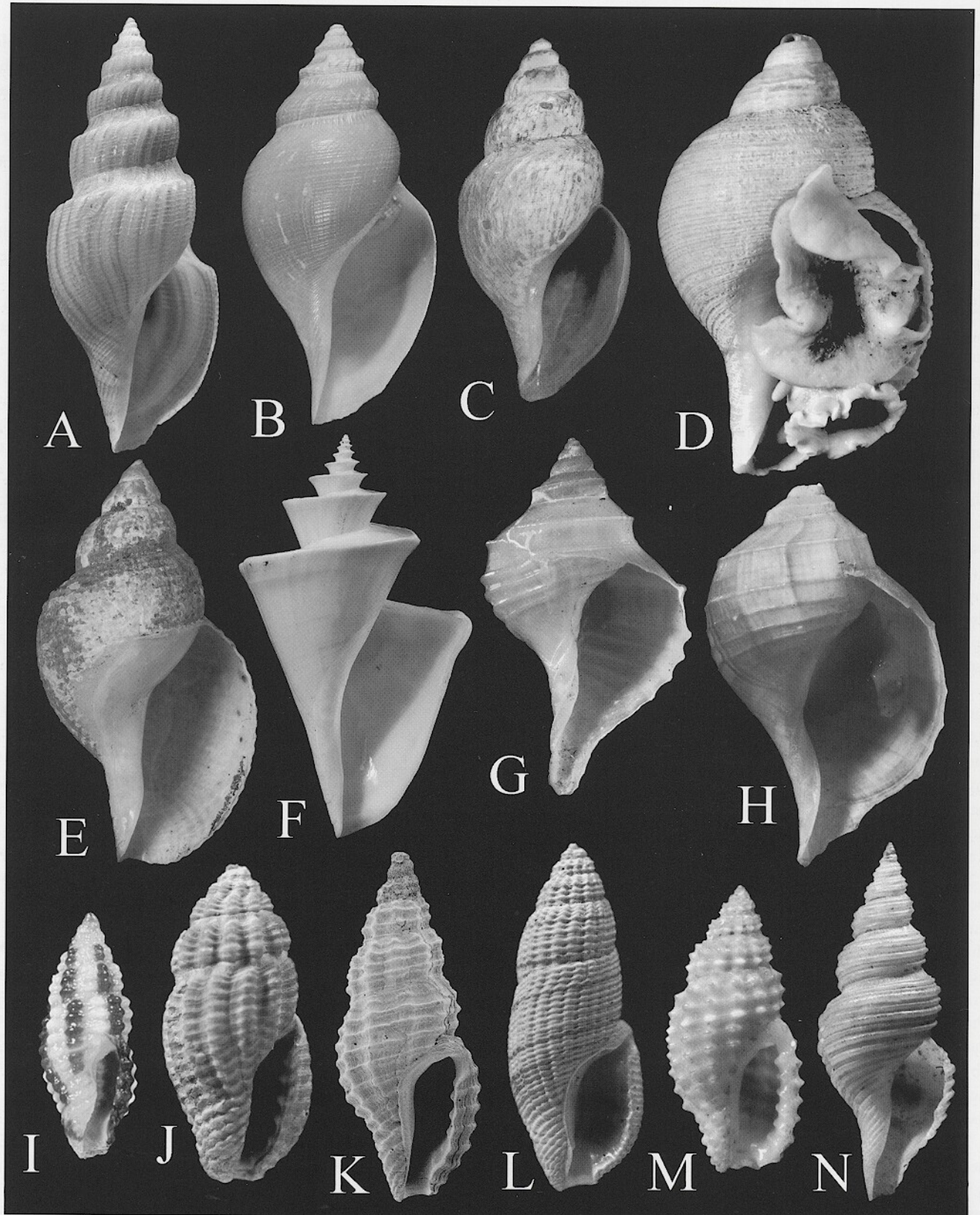


Figure 20. Shells of species described anatomically. Locality details in Table 1. Shell heights (mm). A, *Gymnobela pyrrhogramma* (Dautzenberg & Fischer, 1896), 20.9mm. B, *Gymnobela emertoni* (Verrill & Smith, 1884), 25.3mm. C, *Gymnobela* sp. unnamed. see Kantor & Sysoev, 1996, 26.6mm. D, *Phymorhynchus wareni* Sysoev & Kantor, 1995, 56.3mm. E, *Phymorhynchus moscalevi* Sysoev & Kantor, 1995, 32.1mm. F, *Thatcheria mirabilis* Angas, 1877, 82.2mm. G, *Teretiopsis levicarinatus* Kantor & Sysoev, 1989, 10.7mm. H, *Teretiopsis abyssalis* Kantor & Sysoev, 1989, 14.3mm. I, *Kermia barnardi* (Brazier, 1876), 4.8mm. J, *Hemilienardia malleti* (Récluz, 1852), 4.8mm. K, *Paramontana rufozonata* (Angas, 1877), 4.5mm. L, *Hemidapbne reeveana* (Deshayes, 1863), 6.6mm. M, *Pseudodapbnella granocostata* (Reeve, 1846), 11.9mm. N, *Teretia teres* (Forbes, 1844), 11.5mm.



of the venom gland is usually associated with the elongation of the oesophagus between the buccal mass and the nerve ring, forming the oesophageal loop. This loop allows forward movement of the buccal mass on protraction of the proboscis. Nevertheless, in at least two species of Crassispirinae with the modified gland (*Antiguraleus morganus* and *Haedropleura septangularis*) (KANTOR *et al.* 1997) and in both the above-mentioned raphitomines the oesophageal loop is absent.

Only in *Phymorhynchus moscalevi* and *Gymnobela* sp. did we observe an accessory salivary gland. The presence of accessory salivary gland(s) is sporadic within conoideans. They have been recorded in a few species of Terebridae, Turridae (subfamily Cochlespirinae) and Conidae (subfamilies Coninae, Clathurellinae and Raphitominae) (TAYLOR, 1990; TAYLOR *et al.* 1993). Although in Muricidae the gland has been shown to secrete serotonin (ANDREWS *et al.*, 1991) the function in conoideans is unknown.

An outstanding character found in raphitomines is the valve situated just posterior to the buccal cavity. So far, we have observed it in only two species, *Kermia barnardi* and *Paramotana rufozonata*. This valve resembles the valve of Leiblein, found in *Rachiglossa* and *Nematoglossa* (GRAHAM, 1941; 1966). ROBINSON (1960) supposed, that in *Mangelia brachystoma* the sphincter, separating the buccal cavity and oesophagus probably represents the vestiges of the valve (pharynx) of Leiblein. This idea was rejected by SMITH (1967a), his argument mostly based on differences in the position of the radular sac in some turrids compared with the *Rachiglossa* (well anterior to the valve of Leiblein). This objection can now be discounted following the discovery of numerous types of foregut arrangement in the Conoidea (TAYLOR *et al.*, 1993; KANTOR *et al.*, 1997). This point of view was supported by PONDER (1974), who also stated, that the valve may never have evolved past the oesophageal pouch stage in the toxoglossans. Finally, KANTOR (1996) even suggested that the valve of Leiblein may have originated independently twice within the Neogastropoda.

Arguments for the possible homology of the valve in Raphitominae with the valve of Leiblein in *Rachiglossa* concern the position of the valve just in front of the circum-oesophageal nerve ring as is found in other neogastropods and also the presence of the ciliated cone in both groups. The valve in Raphitominae differs in some respects from that of most *Rachiglossa*, principally in the absence of the pad of glandular cells at the base of the ciliated cone. Nevertheless, the description of the valve in *Nematoglossa* (= *Cancellarioidei*) (*Cancellaria*, GRAHAM, 1966), a possible sister group of the Conoidea (TAYLOR & MORRIS, 1988; KANTOR, 1996), resembles the valve of the raphitomines. Moreover, both raphitomine species, in which the valve was found are minute, with a shell length of only several μm , with the valve itself only about 0.1 μm in length and formed by very few cells. This may be a reason for the simplification of the valve and the absence of the glandular pad. The venom gland opens just in front of the valve (Fig. 9C) and therefore the valve does not prevent the use of venom for the immobilisation of the prey.

Evolutionary trends and feeding mechanisms in Raphitominae

A remarkable evolutionary phenomenon seen amongst species of Raphitominae is the independent loss of different foregut structures.

The proboscis. A complete morphological set of transformations of proboscis size is found in Raphitominae. The proboscis is long, occupying nearly the entire rhynchocoel in *Kermia barnardi*, *Hemilienardia malleti* and *Philbertia purpurea*. It is reduced in size in *Thatcheria mirabilis* and *Gymnobela pyrrhogramma*. While in other species, *Pseudodaphnella granicostata*, *Gymnobela emertoni*, *Teretiopsis* spp., it is vestigial and represented only by a low fold. Finally, the proboscis is completely absent in *Raphitoma linearis* and *Abyssobela atoxica* (KANTOR & SYSOEV, 1986).

The venom apparatus. The venom apparatus is absent in *Gymnobela emertoni*, *Teretiopsis* spp., *Raphitoma linearis*, and *Abyssobela atoxica*. Hitherto, it has been supposed that the loss of venom gland was linked with a great reduction or absence of the radula (KANTOR & SYSOEV, 1989; TAYLOR *et al.*, 1993) but in *Pseudodaphnella granicostata* the venom gland persists while the radula is absent.

The radula. A radula is absent in *Pseudodaphnella granicostata*, *Teretiopsis* spp., *Raphitoma linearis*, *Abyssobela atoxica* (KANTOR & SYSOEV, 1986) and *Clathromangelia granum* (OLIVERIO, 1995).

The salivary glands. The tubular salivary glands can be paired or single (*Thatcheria mirabilis*, *Pseudodaphnella granicostata*) or completely absent as in *Teretiopsis* spp., *Raphitoma linearis* and *Abyssobela atoxica*.

Thus, it is seen, that any of the major foregut organs can be lost without relation to the others. A similar loss of foregut structures has been observed in the Terebridae (TAYLOR 1990; TAYLOR *et al.* 1993; SIMONE, 1999). Some species have a complete set of foregut organs including rhynchodeal introvert, proboscis, radula, two pairs of salivary glands, venom apparatus while other species have lost some or all of these organs. In the most derived state the animals feed suctorially using the introvert with all other major structures absent (MILLER, 1975).

The possible role of heterochrony in gastropod evolution has been advocated by LINDBERG (1988) and PONDER and LINDBERG (1997). The trends towards simplification of the foregut observed in Raphitominae may be accounted for by paedomorphosis and it is likely that such changes could have occurred in parallel in different clades. BALL, TAYLOR & ANDREWS (1997) demonstrated that during the ontogeny of *Nucella*, the acinous salivary glands of the adult develop from initial tubular ducts of the embryo. Thus, the tubular salivary glands of raphitomines (and also *Mangeliinae*) likely represent a paedomorphic condition. Similarly, studies of the ontogeny of the neogastropod proboscis (BALL, ANDREWS & TAYLOR 1997) suggest that the reduction or absence of the proboscis in many raphitomines may represent progressively paedomorphic states. Loss of radula and venom apparatus may also be explained by paedomorphosis. In fact the venom gland is one of the last of the major foregut organs to develop during ontogeny (A.D. Ball



personal communication). Amongst those raphitomine species possessing a radula there is considerable variety of tooth form from the elongate barbed, *Conus*-like teeth of *Phymorhynchus* to the simple awl shaped teeth of *Paramontana*. During ontogeny the teeth of *Conus* become progressively more elaborate (NYBAKKEN, 1990), the early post-metamorphic teeth being simple and awl shaped. Thus the simple forms of raphitomine teeth could represent paedomorphic states. It is tempting to suggest that the small size of many raphitomes is also a paedomorphic feature which may be associated with the simplification of the foregut. Although most of the species having the simplified foregut are indeed small there are also small species with proboscis, venom apparatus and radula.

Feeding mechanisms

The remarkable feature of the conoidean feeding mechanism and not restricted just to *Conus*, is the deployment of single radular teeth at the proboscis tip for stabbing and envenomation of the prey. It has been now been demonstrated for a wide range of different conoideans that the teeth are usually held at the proboscis tip by one or more buccal tube sphincters (KANTOR & TAYLOR, 1991; TAYLOR *et al.*, 1993), often in conjunction with an epithelial pad located at the distal end of the buccal tube. In Raphitominae, the buccal tube sphincters are present in only a few of the species possessing a proboscis; these are *Phymorhynchus* spp. and *Gymnobela pyrrhogramma*. In another species, *Hemilienardia malleti*, in which the buccal tube sphincter was absent, the tooth was found at the proboscis tip, probably held by a small pad of epithelial cells. In all other species having a radula and proboscis, the obvious structures for gripping teeth at the proboscis tip were absent. Previously, conoidean species possessing a radula but lacking buccal tube sphincters have been recorded only among Crassispirinae (Turridae), namely *Burchia spectabilis* and *Inquisitor latifasciata* (KANTOR *et al.*, 1997). This absence of a sphincter suggests that teeth are not held at the proboscis tip and therefore no stabbing occurs during prey capture.

The diet of Raphitominae is poorly known. In the stomach of one specimen of *Gymnobela subaraneosa* (DAUTZENBERG & FISCHER, 1896) the radula of the rissoid gastropod *Benthonella tenella* was found (BOUCHET & WARÉN, 1980). An undescribed species *Phymorhynchus* from the East Pacific Rise was reported with fragments of the gastropod *Neomphalus fretterae* in its gut (Warén & Bouchet, 1989), whilst it has also been observed, that *Phymorhynchus moscalevi*, living on the hydrothermal vents, feeds on the bivalve *Bathymodiolus* (A. Warén, personal communication). The food being at least partially digested within the rhynchocoel. Because of this paucity of feeding information, our analysis of the possible feeding mechanisms of the Raphitominae is therefore based on the morphology of the foregut and by comparison with other conoideans where the feeding process is better known. Morphological evidence suggests that there are at least three types of feeding mechanism among Raphitominae.

The normal toxoglossan type (Feeding mechanism type 3 of TAYLOR *et al.*, 1993).

The species belonging to this group probably all use marginal teeth at the proboscis tip for stabbing and envenomation of prey. These include amongst the raphitomine species we examined; *Gymnobela* sp., *Gymnobela pyrrhogramma*, *Phymorhynchus* spp., *Hemilienardia malleti* and probably *Paramontana rufozonata*. In all these species the proboscis and venom apparatus are well developed and there are epithelial pads and sometimes sphincters in the buccal tube for holding radular teeth near the proboscis tip. It is possible that *Philbertia purpurea* belongs to this group as well because according to the drawing of the foregut (SHERIDAN *et al.*, 1973), its anatomy is very similar to that of *Hemilienardia malleti*. Although *Paramontana rufozonata* lacks a buccal tube sphincter or epithelial pad, the mouth opening is very narrow and is surrounded by a circular fold. This fold may be used for holding a radular tooth at the proboscis tip.

Envenomation of the prey without radular stabbing.

Species belonging to this group including *Hemidaphne reeveana*, *Thatcheria mirabilis*, *Pseudodaphnella granicostata*, *Philbertia leufroyi boothi*, either lack a radula but possess a venom gland (*P. granicostata*) or lack any mechanisms for holding radular teeth at the proboscis tip. Thus, in *T. mirabilis* and *D. reeveana* the mouth opening is very wide and without sphincters or an epithelial pad. In *Philbertia leufroyi boothi*, although both radular and venom apparatus are present, the proboscis is vestigial and incapable of holding teeth (SMITH, 1967). It is also possible that *Kermia barnardi* also belongs to this group for its buccal tube also lacks any obvious mechanisms for holding teeth. It is suggested that these animals either envenomate their prey after swallowing or somehow immobilise the prey by squirting venom.

Capture of prey without stabbing and envenomation.

Species, belonging to this group either lack proboscis, radula and venom apparatus (*Teretiopsis* spp., *Raphitoma linearis*, *Clathromangelia granum*, *Abyssobella atoxica*), or, like *Gymnobela emertoni* possess only a vestigial radula. In all these species, there is well-developed cavity between the rhynchodaeum and the body wall and prominent radial muscles cross this cavity. KANTOR & SYSOEV (1989) have proposed previously that contraction of the radial muscles increases the inner volume of the rhynchocoel and causes negative pressure within it. This facilitates a suctorial engulfment of the prey into the rhynchocoel.

The rhynchostomal introvert is present in some species classified into each of the three groups. It likely has a role in prey capture and manipulation. By comparison, in many species of Terebridae the rhynchostomal introvert has taken over the role of the proboscis in prey capture and become the main feeding organ (MILLER, 1975).

Comparison of Raphitominae with other subfamilies of Conidae

Amongst the Conidae, Raphitominae are closest in morphology to Mangeliinae and Coninae. Both Mangeliinae and



raphitomines possess tubular rather than the more usual acinous type of salivary glands. Tubular glands are characteristic for both subfamilies but otherwise are found only in a few Crassispirinae species (KANTOR *et al.*, 1997). The two subfamilies also share a rather similar morphology of the muscular bulb of the venom gland. While in Raphitominae the bulb is single-layered, in Mangeliinae the wall of the bulb has two layers, but the outer is extremely thin and is formed by only a single sheet of muscle fibres.

In this connection the position of *Gymnobela* sp. should be discussed in more detail. This still unnamed species was attributed to Raphitominae on the basis of similarity of general shell shape with some representatives of *Gymnobela* (KANTOR & SYSOEV, 1996). Protoconchs of all available specimens were corroded and therefore its sculpture (which is characteristically diagonally cancellate in *Gymnobela*) is unknown. The anatomy of this species is very unusual within the Raphitominae (e.g. very long proboscis, radular sac without radular teeth), while the muscular bulb of the venom gland is very similar to that of Mangeliinae (still very poorly studied anatomically) in having characteristic very thin outer layer, formed by a single sheet of muscle fibres. Taking this into consideration we suggest, that this species should be transferred to Mangeliinae.

When comparing Raphitominae with Coninae, there are some striking similarities between *Conus* species and some *Gymnobela* species. The characters that are shared by species of both subfamilies are the presence of the septum (which in *Conus* can be both basal as in *Conus ventricosus*, Fig. 16, or situated in the middle sector of the rhynchocoel as in *Conus bobolensis*, Fig. 17; both types of arrangement are found in Raphitominae) and additionally, the shape and size of the proboscis (compare *Gymnobela pyrrhogramma*, Fig. 1 and *Conus* spp., Figs. 16, 17). The main differences are the acinous salivary glands in *Conus* compared with tubular salivary glands in Raphitominae and the multi-layered muscular bulb of *Conus* species. Both these character states represent plesiomorphic conditions, found in most groups of Turridae and Conidae. The cladistic analysis also supposes that Coninae are the sister group of Raphitominae.

CONCLUSIONS

This study confirms our initial impression that the foregut of the Raphitominae exhibits more structural variation than any other conoidean family or subfamily excepting the Terebridae. The range of variation extends from species which possess a full complement of conoidean foregut organs (proboscis, venom apparatus, salivary glands, radula) to those in which most or all of these structures are absent. Despite this variation in foregut configuration, monophyly of the Raphitominae is supported by several apomorphies such as the cancellate protoconch, the single layer to the muscular bulb and the rhynchodeal septum. The division of conoidean foreguts into just two categories, the intraembolic and polyembolic types (SMITH, 1967a) is a gross oversimplification. As more and more conoidean taxa are studied anatomically, for example the Crassispirinae (KANTOR *et al.* 1997), Cochlespirinae (MEDINSKAYA, 1999) or Terebridae (TAYLOR, 1990; SIMONE 1999), an extraordinary disparity of

foregut configurations is being revealed which presumably reflects a great diversity of feeding behaviours and prey capture mechanisms. Unfortunately, little information is available on the biology of these animals.

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