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

Yuri I. Kantor & John D. Taylor

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 raphitomines, although not found in every species, are a rhynchostomial introvert, a rhynchoideal septum, the needle-like radial teeth and the muscular bulb consisting of a single muscle layer. In Kornia harnandi and Paramontana raphitoma 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 Pseudadaphna granovitata the venom apparatus persists but the radula is absent. Teretifus 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 sectorial means. Raphitomines have the most disparate foregut configurations of any conoidean subfamily. The rhynchostomial introvert is otherwise found only in Terebridae and the rhynchoideal introvert found in many terebrids and some Conus species. Tubular salivary glands are also found in Mangeliniae and some Crassispireinae. Phylogenetic analysis suggests that the Raphitominae have closest similarity with the Coninae and Mangeliinae.

RIASSUNTO
Le Raphitomine (precedentemente note come Daphnellinae) sono, dal punto di vista conciliante, la più disparata delle sottofamiglie di conoidi, 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, posizione e morfologia delle maggiori strutture come la proboscide, la massa boccale, il setto, le ghiandole e gli aliferi del tubo boccale. Caratteristiche distinctive delle Raphitominae, anche se non riscontrabili in tutte le specie, sono un introvertino ricinocostale, i denti radulari aghiformi ed il bulbo muscolare costituito in un singolo strato muscolare. In Kornia harnandi e Paramontana raphitoma c’è una struttura situata proprio posteriormente alla massa boccale somigliante alla “valle di 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 velefero possono essere presenti o assenti. Normalmente la perdita della radula è correlata con la perdita della ghiandola del veleno, ma in Pseudadaphna granovitata, l’apparato velefero persiste pur essendo la radula assente. Specie di Teretifus mancano della proboscide, della radula, dell’apparato velefero o delle ghiandole salivari. Tre tipi principali di modalità alimentari sono proposti 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 velefero senza colpire con la radula; 3) cattura della preda senza radula e uso del veleno, probabilmente per attività sottomarina. Le Raphitominae possiedono anche la più disparata serie di configurazioni del canale alimentare anteriore di tutte le sottofamiglie di conoidi. L’introvertino ricinocostale si ritrova altrove solo tra le Terebrideae e l’introvertino ricinoideale si trova in molte terebridi e in alcune specie di Conus. Le ghiandole salivari sono presenti anche nelle Mangeliniae e in alcune Crassispireinae. Un’analisi filogenetica suggerisce che le Raphitominae hanno stretta similitudine con le Coninae e le Mangeliinae.

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 & Sysoev, 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 Mangeliniae. Fifty-seven Recent genera and subgenera are listed by Taylor et al. (1993). Raphitomines have a world-wide distribution and inhabit a wide range of habitats from the

> 83 <
Figure 1. Gymnolea pyrgogrammus (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. Gymnolea amertoni (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 the smallest and largest conoidea ranging from around 1.5 mm to 136 mm shell height (Powell, 1966). Notable are some of the large deeper water taxa, such as Pontinthanna, Spergo and Thaiberta. 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 Paleogene 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 conoidea currently classified in the Mangeliidae 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 Clisthomangelia (Oliverio, 1995) and Hemilienardia (Taylor et al., 1993 and herein). For Philiberta and Caenodagmites, 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 rhynchodal introvert and septum which had otherwise been found only in species of Terebridae. Initial phylogenetic analysis identified the Raphitominae along with the Taraniidae as the most derived groups of conoidea (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 conoidea.

**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
- br - buccal tube
- "bct" - cylinder of the buccal tube
- bts - buccal tube sphincters
- cf - circular fold
- cm - columnar muscle
- cmf - circular muscle fold
- con - circumesophageal nerve ring
- dasg - duct of the accessory salivary gland
- dsg - duct of salivary gland
- dvg - duct of the venom gland
- epp - epithelial pad
- gld - glandular cells
- glf - glandular fold
- dvg - duct of venom gland
- int - introvert
- mb - muscular bulb of the venom gland
- oe - oesophagus
- pr - proboscis
- prr - proboscis retractors
- rdc - radular caecum
- rch - rhynchocoel (rhynchodal cavity)
- rnh - rhynchostomal funnel
- rns - rhynchone
- rs - radular sac
- rps - 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 - vestibial 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 pyrgogramma** (Dautzenberg & Fischer, 1896) (Figures 1, 3 A-B, 20A)

- **Rhynchodeaum and proboscis**
  The rhynchostomal sphincter is small and located posteriorly
within the rhynchostome. There is large rhynchosomal introvert which lacks a sphincter at the tip. The introvert when withdrawn occupies slightly more that 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, rhynchoideal 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.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Details</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gymnoba emortonii</td>
<td>(Verrill &amp; Smith, 1884). 4706 m, North Atlantic, Biogas station CP17, 46°31’ N, 10°20’ W. The Natural History Museum, London.</td>
</tr>
<tr>
<td>Gymnoba sp. unnamed.</td>
<td>see Kantor &amp; Sysoev. 1996. 3610 m, E. Tasman Sea, 44°18’ S, 166°46’ E, Galathea station 607, Zoological Museum of University of Copenhagen, uncatalogued.</td>
</tr>
<tr>
<td>Teretopis abyssalis</td>
<td>Kantor &amp; 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.</td>
</tr>
<tr>
<td>Teretopis levicarinatus</td>
<td>Kantor &amp; Sysoev. 1989. Sectioned holotype, 2800 m, 5°02’ N, 20°50’ W off Liberia, Zoological Museum of Moscow State University, Moscow, Lc-5679.</td>
</tr>
<tr>
<td>Thatcheria mirabilis</td>
<td>Angas, 1877. 440 m, W. of Lacepede Archipelago, Western Australia, 16°54’ S, 119°52’ E. The Natural History Museum, London.</td>
</tr>
<tr>
<td>Phymorhynchus mosalevi</td>
<td>Sysoev &amp; Kantor, 1995. Sectioned paratype, 3680 m, Mid-Atlantic Ridge, 26°08’ N, 44°49’ W, Zoological Museum of Moscow State University, Moscow, Lc-22458.</td>
</tr>
<tr>
<td>Pontiathaoa mirabile</td>
<td>Smith 1895. 2540 m, Indian Ocean, 6°59’ N, 78°30’ E SAFARI Stn. CP5. Radula only. The Natural History Museum, London.</td>
</tr>
</tbody>
</table>

Also
Glands
The salivary glands are paired, tubular, long and highly convoluted, although very narrow, measuring about 30 μm in diameter. The epithelium, lining the glands comprises uniform, tall, columnar, ciliated cells. The ducts are not differentiated from the glands and open into proximal part of the radular caecum.

The venom gland does not change in histology after passing anteriorly through the nerve ring and opens ventrally into the posterior part of the buccal mass. 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 large and long and situated dorsally to the oesophagus (only the radular caecum is shown on Figure 1A). The radular caecum is medium sized. The buccal sac (i.e. that portion of the radular sac lying between the entrance of the salivary ducts and the buccal cavity) is long and narrow (Fig. 1B - bsc). It passes downward along the right side of the buccal mass, and then gradually turns towards its narrow ventral opening into the buccal cavity just to the anterior of the of the buccal mass "sphincter". The radular teeth (Fig. 3 A-B) are hollow, long (630 μm), slender, slightly curved and with an enlarged base. The distal tip of the tooth has two distinct barbs with the apical opening located behind the second barb.

Gymnobela emertoni (Vetrill & Smith, 1884) (Figures 2, 3L, 20B)

Rhynchodaemum and proboscis
The rhynchostomal sphincter is medium-sized and anteriorly located. Rhynchostomal introvert absent. There is no rhyncheal septum present. There are well-developed transverse muscles connecting the rhynchodaemum with the body walls. The proboscis is vestigial and represented by a low circular fold with an epithelium of tall, columnar cells.

Buccal mass and oesophagus
The buccal mass is small and thin-walled. There are small buccal lips, which are longer than the proboscis itself. The buccal tube is absent due to the near complete reduction of the proboscis.

Glands
The unpaired salivary gland is very small, tubular and straight. The venom gland is absent.

Radula
The radula sac is very short and contains very few teeth. The buccal sac opens ventrally near the tip of the buccal lip. The

---

Figure 4. Gymnobela sp. [after Kantor, Syslov, 1996, slightly modified]. A. Semidiagrammatic longitudinal section through the proboscis and buccal mass region; nervous ring not shown. B. Enlarged proboscis tip. C. Head.
radular teeth (Fig. 3D) 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.

**Rhynchoidea 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 - gle). 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)

**Rhynchoidea and proboscis**  
The rhynchostomal introvert absent. The rhynchostomal sphincter is medium-sized and located rather to the posterior of the rhynchosome. 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 rhynchosome 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 rhynchodea 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.
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 rhynchoeel 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 rhynchoeel 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 rhynchoeel.

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 0.5% of the shell length. The teeth are enrolled, and awl shaped with a large adapical opening and an extended base.

Hemileiotardia malleti (Récluz, 1852)
(Figures 3H, 7, 8, 20L)

Rhynchodeaum and proboscis
The rhynchosomal sphincter is medium-sized and long. There is very large rhynchosomal 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 rhynchodeaum. 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. Hemileiotardia 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.

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

**Rynchodaecum and proboscis**
The rynchostomal sphincter is medium-sized and positioned posteriorly within the rynchostome. Rynchostomal introvert or funnel absent. The tall, columnar epithelium of the rynchocoele is cuticularized, with very large oval cells. There is a septum in the posterior part of rynchocoele. The epithelium, lining the outer surface of the septum is continuous with that of the rynchodaecum, 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 rynchocoele 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 rynchodaecum. 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.

*Keremia bernardi* (Brazier, 1876)
(Figures 10, 201)

**Rynchodaecum and proboscis**
The rynchostomal sphincter is medium-sized, and located posteriorly in the rynchostome. Rynchostomal introvert or
Figure 9. *Paramuta ruficornata* (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 rhynchoceol 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 rhynchoceol there is a small septum. The epithelium lining the septum and proboscis is continuous with that of the rhynchodeaum. Between the body wall and dorsal wall of rhynchoceol there are numerous very large, irregularly oval cells with a granulated cytoplasm and relatively small oval nuclei (Figure 10B - gnc). These are probably glandular cells.

The proboscis is long and in the contracted state occupies the entire length of the rhynchodeaum. Proboscis retractor muscles run along the proboscis walls. The border between the muscles and the wall is unclear so that retractor cells 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 warreni* Sysoev & Kantor, 1995
(Figures 11, 20D)

The description is modified from *Sysoev & Kantor* (1995).

*Rhynchodeaum 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 rhynchodeaum with the body walls. A thick, muscular septum is located in the posterior part of rhynchoceol. The proboscis is short and occupies about one

---

Figure 11. *Phymorhynchus warreni* 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, curricularized 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 columnellar muscle and roof of the body haemocoeel. 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 = 0.380μm) 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 muscareli** SYSOEV & KANTOR, 1995
(Figures 3 C-D, 12, 20E)

Description is based on SYSOEV & KANTOR (1995).

**Rhynchodeaen 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 rhynchodeaen with the body walls. At the posterior end of the rhynchocoel there

---

Figure 12. Phymorhynchus muscareli 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 columnellar 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 niveata* (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.](image-url)
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 μm) with a narrow tip with a single barb and an extended complex base.

**Hemidaphne reeveana** (Deshayes, 1865)
(Figures 13, 20L)

**Rhynchodaenum 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 rhynchocele. Towards the posterior of the rhynchocele there is a thin, poorly muscular, rhynchocele 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.

**Rhynchodaenum and proboscis**
The rhynchostomal sphincter is large and located posteriorly within the rhynchozome. There is medium-sized rhynchostomal funnel. The epithelium of the rhynchocele is tall, columnar and brown. There is no septum. The rhynchodaenum 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 rhynchodaenum wall.](image-url)
Glands
There are no foregut glands present.

Radula
Absent.

_Teretipsis leviarinatus_ Kantor & Sysoev, 1989
(Figures 15, 20G)

Description modified from Kantor & Sysoev, 1989.

_Rhynchodaenae 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 rhynchodaenae 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 maxillae_

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).

_Rhynchodaenae 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. _Teretipsis leviarinatus_ 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 & WAREN (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 Pontithauma mirabile Smith, 1895 (PAECE 1903, and radular details Fig. 3E); Philibertia purpurea (MONTAGU, 1803), P. linearis (MONTAGU, 1803) (details in SHERIDAN et al., 1973); Caenogastropus asthen 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 rhynchoideal cavity but extends as a tube when protruded. 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 extension of the anterior part of the rhynchostome (Fig. 11A, 12 - rf). The rostrum of some Conus species is a similar structure.

3. Rhynchoideal septum: 0 = absent (Fig. 7, 14, 15 – sp); 1 = mid-rhynchoideal (Fig. 1, 13 – sp); 2. posterior rhynchoideal (Fig. 5B, 9A, 10A – sp).
   Many raphitomines possess a thin muscular septum that divides the rhynchocele. 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 conoidea have a long proboscis (occupying more than half the length of the rhynchoideal 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 |
| Gymnobela aurantii                            | 0 | 0 | 2 | 2 | ? | ? | ? | ? | 0 | 0 | 2 | 1 | 1 | 1 | ? | ? | 0 | 1 | 0 |
| Gymnobela pycnophyllum                       | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| Gymnobela sp.                                | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| Teretia teres                                | 1 | 0 | 1 | 1 | 0 | ? | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| Teretisophis abyssalis                       | 0 | 1 | 0 | 2 | ? | ? | ? | ? | 0 | 1 | 2 | 1 | 1 | ? | ? | 0 | 1 | 0 |
| Teretisophis levicarinus                     | 0 | 1 | 0 | 2 | ? | ? | ? | ? | 0 | 1 | 1 | 2 | 1 | 1 | ? | ? | 0 | 1 |
| Kerma barnardi                               | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 2 | 0 |
| Hemidaphne reevela                           | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 1 |
| Pseudodaphnella granicosta                   | 0 | 1 | 2 | 2 | ? | ? | ? | ? | 0 | 1 | ? | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 0 |
| Paramontana rufusomata                       | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 2 | 1 | 1 |
| Thaetichia mirabilis                         | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| Pseudorhynchochel muscaeles                  | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 |
| Hemithaenaria mallei                         | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| Pontithauma mirabilis                        | 0 | 1 | 2 | 1 | 0 | ? | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| Philibertia purpurea                         | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| Philibertia linearis                         | 1 | 0 | 0 | 2 | ? | ? | ? | ? | 0 | 1 | 2 | 1 | 1 | ? | ? | 0 | 1 | 0 |
| Caenogastropus asthen                        | 0 | 0 | 2 | ? | ? | ? | ? | ? | 0 | 1 | 2 | 1 | 1 | ? | ? | 0 | 1 | 0 |
| Conus bohokensis                             | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Hastula haecillis                            | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Mangelloidea wheela                          | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| Opisthoderma inermis                         | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Terebra subulata                             | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 |
| Oenopota levadens                            | 0 | 0 | 0 | 1 | 0 | 0 | 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 vestibial proboscis (Fig. 2B, 14B, 15B - vtr). Where the proboscis is vestigial or absent we have coded the following character (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 mangeliineae (TAYLOR et al., 1993, fig. 9).

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

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 conoidea the salivary glands are acinous in histology but in Mangeliineae, Raphitominae and a few species of Cassisspirinae the glands are tubular.

13. Accessory salivary glands: 0 = present; 1 = absent.
   A well-known apomorphy of the Neugastropoda (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 conoidea 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 nervous 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 conoidea 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 Mangeliineae 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 Leiblinia of Rachiaglossa (GRAHAM, 1941) although the homology is uncertain.

18. Operculum: 0 = present; 1 = absent.

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

Outgroup

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. Semidigrammatic longitudinal section of the anterior foregut (after Taylor et al. 1993 modified).
Coninae:
Conus boboleensis Petuch, 1979 (Fig. 17)
Conus ventricosus Gmelin, 1791 (Taylor et al., 1993 and Fig. 16)
Clathurellinae:
Ophiocoma inermis (Hinds, 1843)
Mangeliniae:
Mangelia nebula (Montagu, 1803) (Sheridan et al., 1973)
Oeopontinae:
Oenopota letidensis (Dall, 1919) (Shirek, 1975)
Terebridae:
Hastula bacillus (Deshayes, 1859) (Taylor & Miller, 1990)
Teremira subalata Linnaeus, 1767 (Taylor 1990)

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

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

Rhynchoidea and proboscis

The rhynchoideal cavity is long, with an anterior rhynchostral sphincter of medium-size. A pronounced rhynchostral funnel is absent, although the rhynchostral lips are large. Transverse muscles, connecting the rhynchoidea with the body walls are absent. In the medial part of the rhynchooeel there is a thin septum with a rather narrow orifice. The anterior part of the rhynchooeel 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 rhynchooeel.

The proboscis is medium-sized, and in the contracted stage occupies about half of the rhynchooeel. Its walls are highly folded so that when protracted the proboscis is long. The proboscis is lined with a curricularized, 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 rhynchoidea. 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 boboleensis Petuch, 1979. A. longitudinal section of foregut. Snout gland situated at the left side of the rhynchoidea is seen as if the rhynchoidea is transparent. B. Enlargement of posterior rhynchoidea 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 T) and 50% majority rule (b †) trees derived from 64 equally parsimonious trees with a length 52 steps. Consistency Index = 0.54, Rescaled C.L. = 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 rhynchoideal septum is located in the posterior part of the rhynchoideal 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...
sculpture of the protoconch whorls (absent in *Paramontana*), the single muscle layer of the muscular bulb and the rhynchoideal septum (absent in several species). Clade 3 is supported in all trees by the possession of a rhynchoideal introvert, but this state is also found in *Philiberta linearis* (Clade 8). In Clade 4 the rhynchoideal 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 conoidans 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 *Pseudaphelina graniosottata*, of longitudinally orientated fibres). The exception is *Gymnobella 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 rhynchoidea into two parts. Beside the raphitomines, the septum is found only in the subfamily Conininae and family Terebridae. The septum in raphitomines is usually positioned in the very posterior part of the rhynchoeel where it often resembles a circular fold at the proboscis base. In other species it is situated close to the middle of the rhynchoeel as in *Gymnobella pyrrobragma*, *Hemidaphne reeseana*, *Terezia 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 rhynchoideal wall (*P. graniosottata*, *Philiberta 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 rhynchoeel, while that on the inner side is confluent with the epithelium of proboscis wall. Thus the division of the rhynchoeel into two portions is probably of some functional significance. It is uncertain whether the septum is a plesiomorphic character for all Conoidae 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 rhynchostral introvert. This structure is present in *Gymnobella pyrrobragma*, *Hemidaphne reeseana*, *Hemiellenbergia rolliet*, *Teretia teres* (our data), along with *Philiberta purpurea* and *P. leutroyii bouchi* (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 some species without an introvert, the rhynchoeel is usually characterised by the formation of the so called “rhynchostral 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 rhynchoidea with the body walls. KANTOR & SYSOEV (1989) suggested, that during the contraction of the transverse muscles, the inner volume of the rhynchoeel increases and thus a negative pressure arises in the rhynchoeel. This possibly facilitates the suction of the prey through the rhynchoeel.

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 *Kremia barnardi* and *Pseudaphelina graniosottata*, 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 pyrhographe (Dautzenberg & Fischer, 1896), 20.9mm. B, Gymnobela emeriti (Verrill & Smith, 1884), 25.3mm. C, Gymnobela sp. unnamed. see Kantor & Sysoev, 1995, 26.6mm. D, Phymorhynchus varoni Sysoev & Kantor, 1995, 56.3mm. E, Phymorhynchus muscosa Sysoev & Kantor, 1995, 32.1mm. F, Thaleobus mirabilis Angas, 1877, 82.2mm. G, Toretispius licarinae Kantor & Sysoev, 1989, 10.7mm. H, Toretispius abysalis Kantor & Sysoev, 1989, 14.5mm. I, Kermia hernardi (Brazier, 1876), 4.8mm. J, Homilinaria mullati (Récluz, 1852), 4.8mm. K, Paramontana rufonata (Angas, 1877), 4.5mm. L, Hemidaphne roranae (Deshayes, 1865), 6.6mm. M, Pseudaphonella gracilis (Reeve, 1846), 11.9mm. N, Toretis toro (Forbes, 1844), 11.5mm.
or 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 protrusion of the proboscis. Nevertheless, in at least two species of Crassispirinae with the modified gland (*Antigualus morganus* and *Haedropleura septangularis*) (Kantor et al. 1997) and in both the abovenamed raphitomines the oesophageal loop is absent.

Only in *Phymorphynchus moschavi* 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 *Terebriidae*, *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, *Kernia barnardi* and *Paramonotana rafsonata*. This valve resembles the valve of Leiblein, found in Rachiglossa and Nematoglossa (Graham, 1941; 1966). Robinson (1960) supposed, that in *Mangelia brachytesoma* 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 (= Cancellarioidae) (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 minure, 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 *Kernia barnardi*, *Hemiteleuria malleti* and *Philbertia purpurea*. It is reduced in size in *Thatcheria mirabilis* and *Gymnobela pyrrhogramma*. While in other species, *Pseudodaphnella granicostata*, *Gymnobela emertoni*, *Tereitopsis ssp.*, 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*, *Tereitopsis ssp.*, *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*, *Tereitopsis ssp.*, *Raphitoma linearis*, *Abyssobela atoxica* (Kantor & Sysoev, 1986) and *Claithromangelia granum* (Oliverio, 1995).

**The salivary glands.** The tubular salivary glands can be paired or single (*Thatcheria mirabilis*, *Pseudodaphnella granicostata*) or completely absent as in *Tereitopsis ssp.*, *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; Simoné, 1999). Some species have a complete set of foregut organs including rhynchoidal 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 Mangeliniae) 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 Pthymorrhynchus to the simple awl shaped teeth of Paramontana. During ontogeny the teeth of Conus become progressively more elaborate (NYBÄKEN, 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 raphitomines 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 conoidea 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 known 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 Pthymorrhynchus spp. and Gymnoba lata, 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 Crassispininae (Turruidae), namely Burchia spectabilis and Inquisitor latissimilis (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 subarantaeosa (DAUTZENBERG & FISCHER, 1896) the radula of the rissoid gastropod Bentho nectra tenuis was found (BOUCHET & GARÈN, 1980). An undescribed species Pthymorrhynchus from the East Pacific Rise was reported with fragments of the gastropod Neomphalus fritterneri in its gut (WARÉN & BOUCHET, 1989), whilst it has also been observed, that Pthymorrhynchus moscali, living on the hydrothermal vents, feeds on the bivalve Bathymodiolus (A. WARÉN, personal communication). The food being at least partially digested within the rhyechnocoele. 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 have examined: Gymnoba sp., Gymnobela pyrrhogramma, Pthymorrhynchus sp., Helminthidida melleti and probably Paramontana rugosa. 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 Philberia 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 Helminthidida melleti. Although Paramontana rugosa 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 radial stabbing.

Species belonging to this group including Hemidaphne rosea, Thatcheria mirabilis, Pseudoaphnella granostata, Philberia leufoyi boothi, either lack a radula but possess a venom gland (P. granostata) or lack any mechanisms for holding radular teeth at the proboscis tip. Thus, in T. mirabilis and D. rosea the mouth opening is very wide and without sphincters or an epithelial pad. In Philberia leufoyi 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 Kornia 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 (Teripitisi sp., Raphitoma linearis, Clathromangia granum, Abyssobius atossica), or, like Gymnobela envorii possess only a vestigial radula. In all these species, there is well-developed cavity between the rhynochoean and the body wall and prominent radial muscles cross this cavity. KANTOR & SYSOY (1989) have proposed previously that contraction of the radial muscles increase the inner volume of the rhynochoeal and causes negative pressure within it. This facilitates a suctorial engulfment of the prey into the rhynochoeal.

The rhynochostomal introtaxis 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 rhynochostomal introtaxis 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 Mangelinae and Coninae. Both Mangelinae 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 Mangeliniae 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). Proctochora 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 probosics, radular sac without radular teeth), while the muscular bulb of the venom gland is very similar to that of Mangeliniae (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 Mangeliniae.

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 rhynchocoe as in Conus boholensis, 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 pleiomorphic conditions, found in most groups of Turridiidae and Conidae. The cladistic analysis also supposes that Coninae are the sister group of Raphitominae.

CONCLUSIONS

This study confirms our initial impression that the foreroot of the Raphitominae exhibits more structural variation than any other conoidea family or subfamily excepting the Terebridae. The range of variation extends from species which possess a full complement of conoidae foreroot organs (probosics, venom apparatus, salivary glands, radula) to those in which most or all of these structures are absent. Despite this variation in foreroot configuration, monophyly of the Raphitominae is supported by several apomorphies such as the cancellate proctochora, the single layer to the muscular bulb and the rhynchodal septum. The division of conoidae foreroots into just two categories, the intraembolic and polyembolic types (Smith, 1967a) is a gross oversimplification. As more and more conoidea 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 foreroot 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.

ACKNOWLEDGMENTS

We thank Philippe Bouchez for the generous donation of some of the specimens used in this study and Fred Wells for the specimen of Thacheria mirabilis. Yuri Kantor is grateful for support from the Department of Zoology at the NHM, London. We also thank Dave Cooper who made many of the serial sections and Mark Wilkinson for advice on coding of inapplicable characters.

REFERENCES


