

COMPARATIVE ANATOMY OF THE STOMACH OF BUCCINOIDEA (NEOGASTROPODA)

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ABSTRACT

Stomach anatomy of 15 species from five families of Buccinoidea has been examined. Stomach anatomy does not depend upon diet, but reflects phylogenetic relationships. Therefore, a combination of stomach characters [presence or absence of the posterior mixing area; presence and degree of development of longitudinal fold(s), separating gastric chamber into ventral and dorsal channels; presence and degree of development of lateral sulcus; position of the digestive gland ducts, and others] allows discrimination of all families of Buccinoidea, except for the closely related Buccinidae and Buccinulidae. The current familial position of the genera *Clea*, *Busycon* and *Nassaria* is questioned from evidence of stomach anatomy. The function of the neogastropod stomach is discussed, with emphasis on food absorption. Observations on the ciliary currents in the stomachs of live specimens suggest that food absorption occurs through the stomach walls, rather than in the tubules of the digestive gland.

INTRODUCTION

The order Neogastropoda is one of the most abundant and diverse groups of marine gastropods, encompassing more than 5200 species (Taylor, Morris & Taylor, 1980). The number of families recognized within Neogastropoda varies greatly, from 15 (Ponder & Warén, 1988) to 34 (Golikov & Starobogatov, 1988). It is generally accepted that evolution of the order, as well as that of other caenogastropods, was determined mainly by the changes in the anatomy of the digestive system (Kohn, 1983), while similarity of shells is often the result of convergence. Much attention has been paid to the anatomy of the digestive system (e.g. Ponder, 1974) and current phylogenetic analyses of the higher classification of Neogastropoda have been based mainly on anatomical characters of the digestive system (e.g. Kantor, 1996; Taylor, Kantor & Sysoev, 1993; Kantor & Taylor, 2002), especially on the foregut. Similarly, discrimination of the families within the Neogastropoda has traditionally been based on radular and other foregut characters.

The stomach of neogastropods remains a poorly studied structure. Only two publications (Smith, 1967; Medinskaya, 1993) are dedicated entirely to stomach morphology and its comparative analysis. There are also a number of descriptions of stomachs of different species in scattered publications (e.g. Graham, 1949; Marcus & Marcus, 1962a,b; Brown, 1969; Ponder, 1970; Lus, 1981[Q1]). Nevertheless, scarcely more than 30 species have been described in any detail. This can be explained by the relative difficulty of studying stomach anatomy, since in preserved specimens it is usually too poorly fixed for examination.

Buccinoidea is one of the generally accepted monophyletic groups within neogastropods. It is an abundant and diverse group of carnivorous marine gastropods, which encompasses about 1000 species (Taylor *et al.*, 1980). Up to seven families are usually included into this superfamily: Buccinidae, Fascioliariidae, Nassariidae, Melongenidae, Buccinulidae, Columbelloidae and Colubrariidae. In an extreme view, Ponder & Warén (1988) classified all but one, Columbelloidae, as subfamilies of Buccinidae.

One of the reasons for the differences in taxonomy of the group is that their foregut (including the radula) is rather uniform and poor in taxonomic characters. At the same time, characters of the foregut have generally been used for the fami-

lial discrimination of neogastropods. Thus, examination of the stomach may provide an important set of additional characters that could be useful for taxonomic discrimination at both generic and familial levels.

MATERIAL AND METHODS

Material for this study was collected over a number of years in different parts of the world, mainly in Florida, India, Vietnam and in the White Sea. When possible, dissections of stomachs of live molluscs were conducted and the ciliary currents traced with carmine particles. For general morphology, the shell was either removed before fixation or cracked with a vice. Different fixatives (alcohol and formalin) were used with similar results. The best results were obtained when stomachs were opened before fixation, although the outer wall became rather contracted in these specimens. In general, if the animals were fixed with a full stomach, preservation was poor, probably due to self-digestion, and the specimens unsuitable for detailed examination. Therefore, it is worthwhile starving animals for several days prior to fixation. For examination of the stomach by scanning electron microscopy (SEM), it was opened, mucus removed by washing and the material fixed in 10% glutaraldehyde in seawater.

All the stomachs were opened in a standard way by a dorsal longitudinal cut along the upper border with the digestive gland (Fig. 1B; position of cut marked with dashed line). This is the easiest way to open the stomach and may be done without separating it from the underlying digestive gland. In a few cases, when openings of the ducts of digestive gland were not clearly seen on dissection, it was necessary to examine the inner side of the stomach adjoining the digestive gland. This can be done on preserved specimens only by removing the digestive gland piece by piece.

It should be mentioned that the general appearance of the stomach differs significantly, depending on the position of the incision, and whether live or preserved specimens are examined. When living snails are dissected, the outer wall contracts and reflects outwards, thus appearing shorter than it actually is.

Intraspecific variability was not large, and concerned mainly the position and prominence of the minor folds. However, folds

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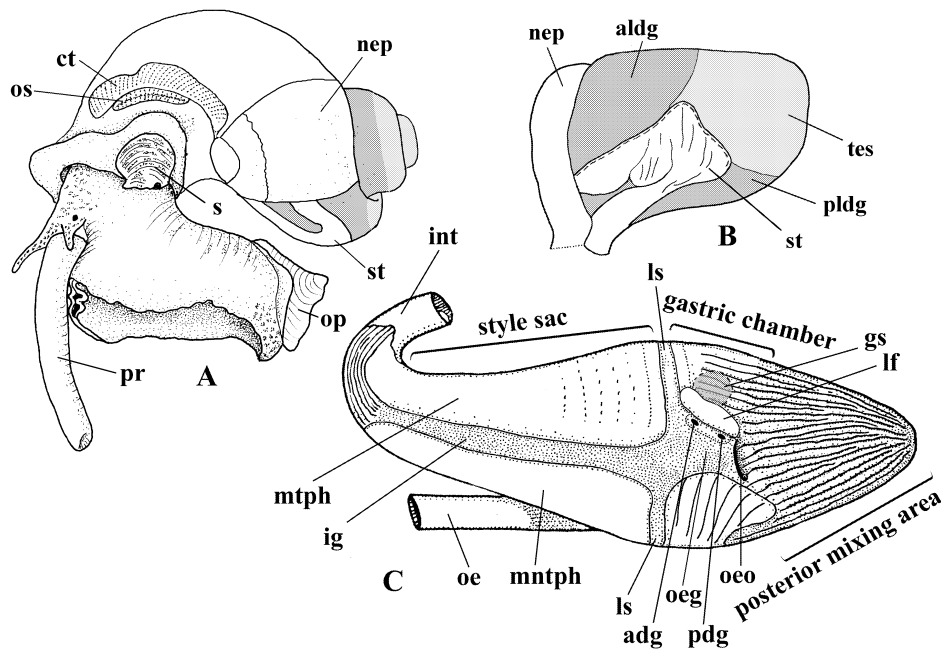


Figure 1. General morphology of the buccinoidean stomach. A. Schematic view of the generalized crawling buccinoidean gastropod without a shell from the left side. B. Schematic view of the whorls of the visceral mass to show the position of the stomach in relation to the digestive gland, gonad and nephridium (*Buccinum undatum*). C. Diagram of the buccinoidean stomach, opened by dorsal cut. Abbreviations (for all figures): adg = opening of anterior duct of digestive gland; aldg = anterior 'lobe' of digestive gland; ct = ctenidium; cz = cuticularized zone; dg = digestive gland; dp = duct pouch; gon = gonad; gs = gastric shield; ig = intestinal groove; int = intestine; lf = longitudinal fold on the inner stomach wall; lf1 = longitudinal fold on the outer stomach wall; ls = lateral sulcus; mntph = minor typhlosole; mtph = major typhlosole; nep = nephridium; oe = oesophagus; oeg = oesophageal groove; oeo = oesophageal opening into gastric chamber; op = operculum; os = osphradium; pdg = posterior opening of duct of digestive gland; pldg = posterior 'lobe' of digestive gland; pma = posterior mixing area; pr = proboscis; psf = pad-shaped fold; sf = striated fold; st = stomach; tes = testis; tfl = tile-like folds; tg = transverse groove; tph = typhlosole.

were usually less prominent in living animals than in preserved ones of the same species. Folds were usually most pronounced when the stomach was opened in living snails and then fixed.

RESULTS

General neogastropod stomach morphology

The stomach can be divided into two main regions (Fig. 1C). The proximal region, usually referred to as the gastric chamber ('globular part' of Fretter & Graham, 1994), receives the opening of the oesophagus and duct(s) of the digestive glands. The distal region is more or less cylindrical and is usually called the style sac. Smith (1967) and Medinskaya (1993) named the latter the compacting area. The site of passage of the style sac into the intestine is usually marked by a well-defined curve, as well as by the disappearance of the minor typhlosole. The gastric chamber may have a more or less long, blind, posterior extension, which is sometimes called the caecum (e.g. Brown, 1969) or posterior mixing area (e.g. Smith, 1967; Fig. 1C). In order to avoid confusion with the caecum of the primitive vetigastropod stomach, I prefer the term posterior mixing area.

The stomach is embedded in the digestive glands and borders the nephridium (Fig. 1A), which sometimes covers the anterior part of the style sac. There is no consistency in the literature with regard to the designation of dorsal and ventral parts of the stomach. Here, the inner wall (facing the digestive glands) and outer, exposed, wall (facing the shell) are distinguished. Placing the visceral hump with the apex directed upward (as is shown in Fig. 1B), the upper side of the stomach is referred to as the dorsal side (marked with a dashed line). The lower side is designated as ventral, although these may not correspond to dorsal

and ventral sides of the animal, especially when the stomach is situated at an angle to the visceral whorl (Fig. 8B).

The stomach in neogastropods receives two openings of the ducts of the digestive glands, each corresponding to a gland. More rarely, the ducts fuse to enter the stomach through a single opening (e.g. *Oliva*, Kantor & Tursch, 2001). Digestive glands are paired organs, sometimes clearly separate, but more often fused without a visible border.

There is a differences of terminology applied to the ducts. They are usually (e.g. Smith, 1967) called anterior (corresponding to the anterior digestive gland and lying closer to the style sac) and posterior (corresponding to the posterior digestive gland and lying closer to the opening of the oesophagus), and this is followed here. Openings of the ducts are often situated in a separate depression, referred to as the duct pouch (Smith, 1967).

The gastric chamber in most neogastropods is subdivided, although not completely, into ventral and dorsal chambers by a longitudinal fold passing along the inner wall (Fig. 1C: lf); sometimes there is also a corresponding fold on the outer wall. The ventral chamber is often referred to as the 'oesophageal groove' (Fig. 1C: oeg). The style sac is also subdivided by major and minor typhlosoles into ventral (intestine groove) and dorsal channels. The major typhlosole is closer to the inner wall and passes into the intestine (Fig. 1C: mtph).

At the border between the gastric chamber and style sac in neogastropods there is often a transverse canal, sometimes only on the inner wall, which is a communication of the dorsal chamber with the mid-ventral, longitudinally-directed, intestinal groove (Fig. 1C: ls). This canal was called the lateral sulcus by Brown (1969), a term accepted here. Smith (1967) did not recognize it, and when the anterior duct of the digestive gland

opened in this area, he sometimes called it the 'duct pouch' or, in other cases, a transverse groove.

Anatomical descriptions

Buccinidae ***Buccinum* spp.** (Figs 1B and 2)

Material examined: *Buccinum undatum* Linnaeus, 1758. White Sea, Kandalaksha Bay, intertidal, coll. Y. I. Kantor, 2000, three live specimens dissected for stomach morphology; Britain, France, market samples, two specimens dissected.

Buccinum glaciale Linnaeus, 1761. White Sea, Kandalaksha Bay, 5–10 m, coll. M.V. Pluscheva, one preserved specimen.

Buccinum elatior (Middendorff, 1849). White Sea, Kandalaksha Bay, 5–10 m, coll. Y. I. Kantor, 2000, one preserved specimen dissected.

Description: Stomach morphology is very similar in the three species studied and is exemplified by *B. undatum*, the most well-studied species.

The stomach is large and spans about one-third of the whorl from the nephridium border (Fig. 1B). Posteriorly, the stomach borders the gonad. Digestive glands are separate, with the anterior (right; Fig. 1B: *aldg*) situated dorsal to the stomach, while the posterior (left; Fig. 1B: *pldg*) is located posteroventral to the stomach. The oesophagus opens into the stomach ventrally mid-way along its length. The posterior mixing area is rather long, its outer wall lined with strong oblique folds, visible through the outer stomach wall, while inner wall possesses nearly longitudinal folds. The posterior duct of the digestive gland is small and situated at the entrance of the oesophagus. The anterior duct of the digestive gland opens at the junction of the intestinal groove and lateral sulcus. At the level of the posterior opening a short, but rather wide, longitudinal fold (Fig. 2: *lf*), originates and runs along the length of the gastric chamber bordering the oesophageal groove. The inner wall of the gastric chamber is lined with strong longitudinal folds, which are continuous with those of the posterior mixing area. The outer wall is lined with broad, low, transverse folds. The oesophageal groove (Fig. 2: *oeg*) is narrow and deep. The lateral sulcus (Fig. 2: *ls*) is distinct and rather deep, present only on the inner stomach

wall. The style sac is long, with the inner wall of the posterior part of the dorsal channel lined with low transverse folds, while the anterior part has distinct longitudinal folds. Typhlosoles are prominent.

The stomach of *Buccinum* is characterized by complex and powerful ciliary currents. A very strong ciliary current leads from the oesophagus into the posterior mixing area and currents from the oesophagus are also directed dorsally along the outer stomach wall. From the posterior mixing area there are currents along the inner stomach wall that are directed forwards and then ventrally along the lateral sulcus towards the anterior duct. There is also a current leading from the posterior duct, and bearing a string of mucus along the transverse fold and across the lateral sulcus. Near the anterior duct, this mucous string is mixed with the mucus from the anterior duct. Carmine particles added to the stomach in this area are quickly bound together with this mucus. There are turbulent currents in the oesophageal groove and strong currents along the intestinal groove. Along the typhlosoles, there are weak currents leading from the intestinal groove into the ventral stomach chamber.

Feeding of *Buccinum undatum* was studied in detail by Taylor (1978). It is a generalist species, mostly consuming polychaetes, gastropods, bivalves and other animals. In stomachs opened in this study, the food, when present, usually consisted of large fragments.

***Pisania tinctoria* (Conrad, 1846)** (Fig. 3)

Material examined: Sebastian Inlet, Brevard County, Florida; coll. Y. I. Kantor, 1999, five specimens dissected (two live).

Description: The stomach is long and extends slightly more than half of the whorl from the nephridium border (Fig. 3F). The dorsal side of the stomach borders the gonad. Integuments of the visceral mass, covering the digestive gland, are strongly black-pigmented. The oesophagus opens into the stomach near its posterior end. The posterior mixing area is short and lined with strong transverse folds, visible through the outer stomach wall (Fig. 3G,H: *pma*). The posterior opening of the digestive gland is small and situated at the entrance of the oesophagus (Fig. 3H: *pdg*). A narrow, distinct, longitudinal fold (Fig. 3G,H: *lf*), originates at the level of the posterior opening and runs the length of the stomach bordering the oesophageal groove. It is white in contrast to the rest of the stomach, which is lined with a

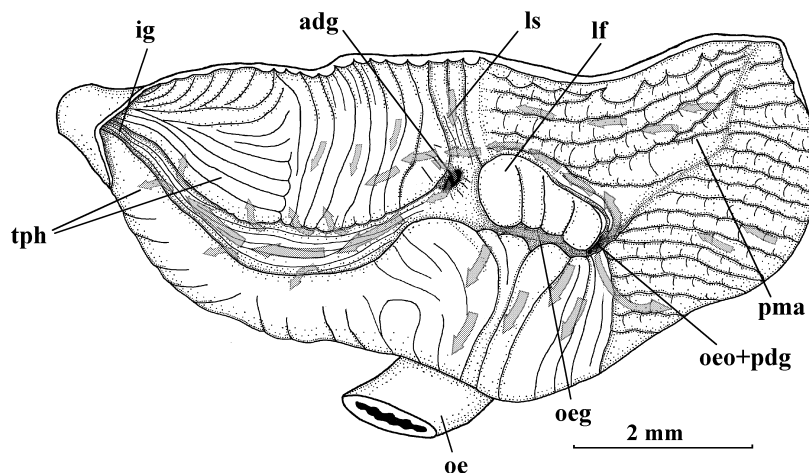


Figure 2. *Buccinum undatum*. Stomach opened along the dorsal line, outer wall reflected. Arrows indicate the main ciliary currents. See Fig. 1 legend for explanation of abbreviations.

dark grey epithelium. The inner and part of the outer walls are covered with low, narrow, parallel, oblique folds. In some specimens the mucus string was observed running along the mid-portion of the inner wall into the intestine. This string envelops the food remains in the intestinal groove and forms the faecal string. The oesophageal groove (Fig. 3H: oeg) is dark grey and in some specimens is nearly smooth, while in others it is covered with oblique folds. The outer stomach wall has an oblique, distinct fold that is transversely striated (Fig. 3G,H: sf). This is directed ventrodorsally and disappears at the border with the style sac. In some specimens the fold originates near the entrance of the oesophagus (Fig. 3H), in others at the level of the anterior opening of the digestive gland. Ventral to the fold there is a rather broad zone of thick epithelium, covered with mucus and forming irregularly spaced transverse folds. The lateral sulcus (Fig. 3G: ls) is very shallow, and is seen on the inner and outer stomach walls. It is also visible through the outer wall of the stom-

ach. The style sac area is very short and partially covered by the nephridium. The opening of the anterior duct of the digestive gland is very small and situated in the oesophageal groove. The diameter of the anterior duct itself, as it passes inside the digestive gland, is large and similar to that of the stomach. Typhlosoles are low and indistinct. The inner wall of the posterior part of the dorsal channel of the style sac is lined with low transverse folds, while the anterior part has distinct longitudinal folds.

In transverse sections, it is seen that the gastric chamber is divided into dorsal and ventral channels by the longitudinal fold and transversal striated fold (Fig. 3B–D), which are connected by the lateral sulcus at the point of transition to the style sac.

Strong ciliary currents are absent. Weak flow was observed from the oesophagus into the posterior mixing area and dorsally along the inner wall of the stomach. In the oesophageal groove there were stronger turbulent currents, as well as dorsally directed currents along the striated fold, draining the groove.

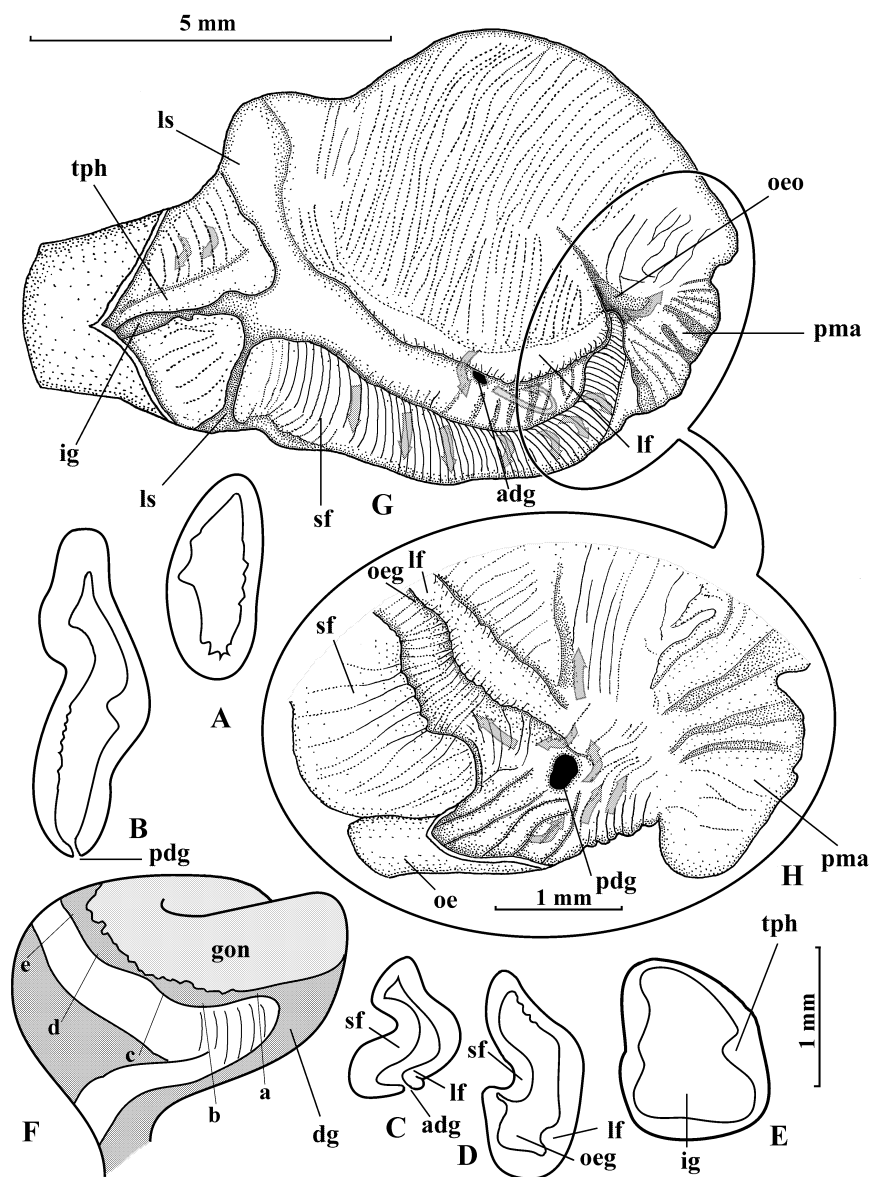


Figure 3. *Pisania tinctoria*. A–E. Schematic transverse sections through the stomach, at the levels indicated by corresponding letters (a–e) on part F. F. Schematic view of the whorls of the visceral mass to show the position of stomach. G. Stomach opened along the dorso-lateral line. H. Enlarged part of stomach, showing opening of oesophagus into gastric chamber. Oesophagus partially opened along ventral line. Arrows indicate the main ciliary currents. See Fig. 1 legend for explanation of abbreviations.

In Sebastian Inlet *Pisania tinctoria* feeds exclusively on barnacles (Kantor & Harasewych, 1994), of which large fragments of legs were found in the stomach and intestine.

***Clea helenae* (Philippi, 1847)**
(Fig. 4)

Material examined: Phuket Island, Thailand, freshwater pond, many specimens coll. R. N. Kilburn & V. Vongpanich, 2000. Two specimens dissected.

Description: The stomach is small, and partially covered by the digestive glands. The posterior mixing area is very long, forming a real 'caecum', which spans nearly three-quarters of the whorl and is equally narrow along its length (Fig. 4A). The posterior mixing area is oval in transverse section, compressed dorso-ventrally, and lined with nine prominent, tall, longitudinal folds, several of which are continuous with the folds of the posterior oesophagus (Fig. 4C). The epithelial cells of these folds are mostly ciliated, with sporadic glandular, non-ciliated cells. The gastric chamber is comparatively short. At the opening of the oesophagus there are small, paired, closely spaced and oval openings of the digestive gland. Each opening is situated in its own, rather deep, depression. The longitudinal fold (Fig. 4B: lf) is rather short, oblique and borders the posterior part of the distinct, although narrow lateral sulcus (Fig. 4B: ls). The lateral sulcus was also visible on the outer stomach wall, although less pronounced. Typhlosoles are well-developed and border the deep intestinal groove. The major typhlosole is narrower and more prominent, while the minor typhlosole is broader, but short, fading at the nephridial border. The inner wall of the dorsal channel of the style sac is lined with transverse folds, which are replaced with inconspicuous longitudinal folds anteriorly.

In the stomach of one specimen there were unidentifiable food remnants containing sediment particles.

Nassariidae
***Nassarius vibex* (Say, 1822)**
(Fig. 5)

Material examined: Florida Keys, coll. Y. I. Kantor, 1999, five specimens dissected (three live).

Description: The stomach is long and narrow, spanning more than half of the whorl from the nephridium border and at least half of it is represented by a very long posterior mixing area. The gastric chamber and style sac are situated at an angle to the upper border of the whorl of the visceral mass, while the posterior mixing area is situated parallel to it. The posterior mixing area lies in the upper third of the height of the whorl of the visceral mass. At the opening of the oesophagus into the stomach there are paired, slit-like openings of the digestive gland. The ducts are situated in the shallow duct pouch, that has slightly thickened edges and which serves as a sphincter that can close both ducts simultaneously. Longitudinal folds of the posterior oesophagus lead to the posterior mixing area, in which the folds are also orientated parallel to the main stomach axis. There is a short longitudinal fold that separates the ducts and the oesophageal opening from the dorsal chamber of the stomach. The lateral sulcus is deep and lined with a low epithelium with inconspicuous transverse folds, or without obvious folds. The typhlosoles are well-developed, thick and border the deep intestinal groove. This part of the stomach is sometimes slightly darker than the rest. The inner wall of the dorsal channel of the style sac is lined with well-marked transverse folds, which are replaced with inconspicuous longitudinal folds anteriorly. A gastric shield is absent.

In empty stomachs, currents running out of the ducts are clearly seen. Strong ciliary currents lead from the oesophageal opening into the posterior mixing area along its ventral side. There is also a current leading from the oesophageal opening to the outer stomach wall and anteriorly along the horizontal fold.

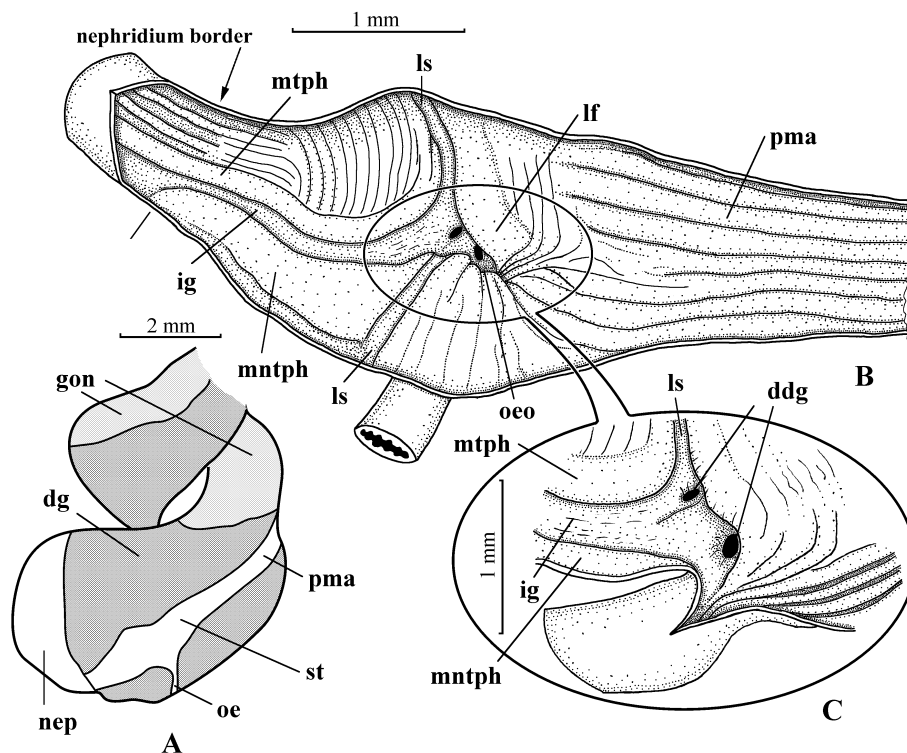


Figure 4. *Clea helenae*. **A.** Schematic view of the whorls of the visceral mass to show position of stomach. **B.** Stomach opened along dorsal line and outer wall reflected. Only short portion of posterior mixing area is shown. **C.** Enlarged area of opening of the posterior oesophagus into stomach. Outer stomach wall cut off, oesophagus opened along mid-line. See Fig. 1 legend for explanation of abbreviations.

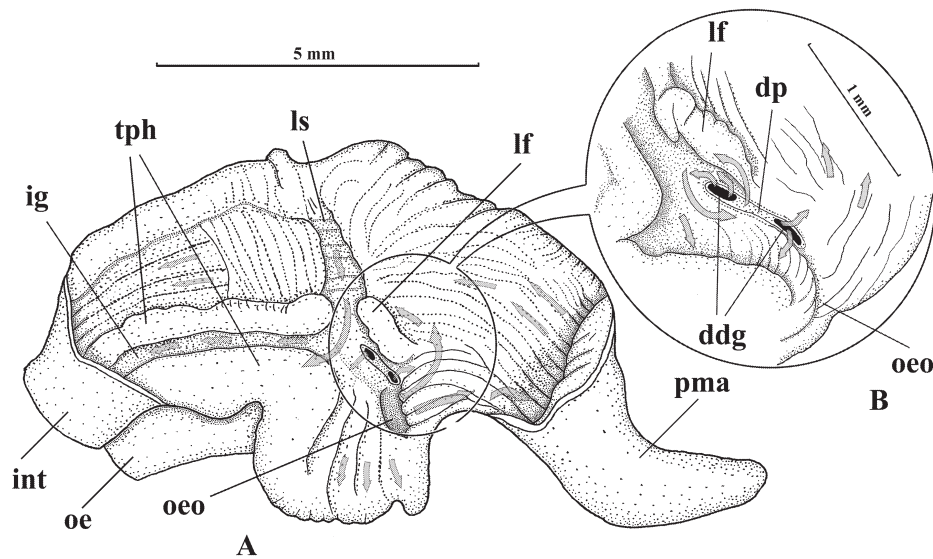


Figure 5. *Nassarius vibex*. **A.** Stomach, opened along dorsal line. **B.** Enlarged part of stomach, showing the opening of oesophagus into gastric chamber. Oesophagus partially opened along ventral line. Arrows indicate the main ciliary currents. See Fig. 1 legend for explanation of abbreviations.

The currents from the posterior mixing area are directed along the dorsal side of the inner wall to the lateral sulcus. In the pouch, the movements of added carmine particles were complex and directed partially towards the outer stomach wall. In the posterior part of the dorsal channel of the style sac there were no obvious movements of particles, but they were present along the longitudinal folds of the sac.

When stomachs of freshly caught specimens were gently squeezed there was an expulsion of yellow, finely particulate material from the ducts.

The stomach contents of three female specimens consisted of sand grains and organic detritus, which in two specimens completely filled the stomach lumen, including the posterior mixing area.

Melongenidae

Melongenella corona (Gmelin, 1791) (Fig. 6)

Material examined: Indian River, Florida, coll. Y. I. Kantor, M. G. Harasewych, three live and two preserved specimens dissected.

Description: The stomach occupies the dorsal part of the body whorl, extending for about one-third to half of the whorl, and is narrow and tubular. The oesophagus is lined with pink epithelium that is replaced by yellow at the transition of the oesophagus to the stomach. The stomach epithelium is uniformly yellowish.

The stomach is simple with poorly defined relief. The gastric chamber is clearly divided into dorsal and ventral channels (oesophageal groove) by two distinct and tall folds (in Fig. 6B: lf, lf2) that are continuous with the typhlosoles. The ducts of the digestive gland are paired, the posterior one very narrow and situated at the entrance of the oesophagus into the stomach. The anterior duct is much broader and is located in a deep pouch (Fig. 6C: adg, shown shallower on the drawing). The lateral sulcus is not defined. Typhlosoles are poorly developed. A mucous string, emerging out of anterior duct of the digestive gland into the intestine, was observed in living specimens.

Ciliary currents from the oesophagus lead to the dorsal channel and then anteriorly along the longitudinal fold towards the compacting area. There are ciliary currents leading from the oesophageal groove into the dorsal channel. Currents carry

fluids out of the anterior duct back into the oesophageal groove, from which they are moved to the dorsal channel. Marking the currents with carmine particles did not reveal any current leading from the dorsal channel or oesophagus into the oesophageal groove.

Melongenella corona feeds on a number of bivalves, including *Crassostrea virginica*, *Ensis minor*, *Tagelus divisus*, large gastropods (such as *Busycon*) and carrion (Gunter & Menzel, 1957).

Pugilina pugilina (Born, 1778) (Fig. 7)

Material examined: Vietnam, Haiphong market, 1999, two preserved specimens examined.

Description: The stomach is very small, tubular, simple, U-shaped, with the long axis directed at about 50° to the whorl (Fig. 7B). The oesophagus is broad, opening ventrally into the posterior part of the stomach. A posterior mixing area is absent.

The posterior oesophagus is lined with well-developed longitudinal folds. The folds on the dorsal side of the oesophagus are continuous with longitudinal folds on the outer stomach wall. The gastric chamber is subdivided into dorsal and ventral channels by a distinct and tall longitudinal fold on the inner stomach wall (Fig. 7A: lf). The ventral channel is represented by the oesophageal groove, occupying a mid-ventral position (Fig. 7A: oeg), which is continuous with the rather deep intestinal groove that is lined with tall, longitudinal, but narrow folds (not seen on the drawing). The dorsal channel of the gastric chamber is lined with oblique, longitudinal folds that are much larger and more raised on the outer stomach wall. In one specimen there was a very narrow and shallow transverse groove (Fig. 7A: tg), absent in the second specimen.

The openings of the ducts of the digestive glands are large and oval. The anterior opening is located just anterior and ventral to the transverse fold, while the posterior one lies at the entrance of the oesophagus into the stomach. Duct pouches are not prominent and the typhlosoles are poorly defined.

Tan & Phuah (1999) examined the feeding of the species in Singapore (under the name *Pugilina cochlidium*, K. S. Tan, personal communication). The species feeds exclusively on the barnacles *Balanus amphitrite* and *B. variegatus*. In feeding experiments, the snails mounted the barnacle and the proboscis

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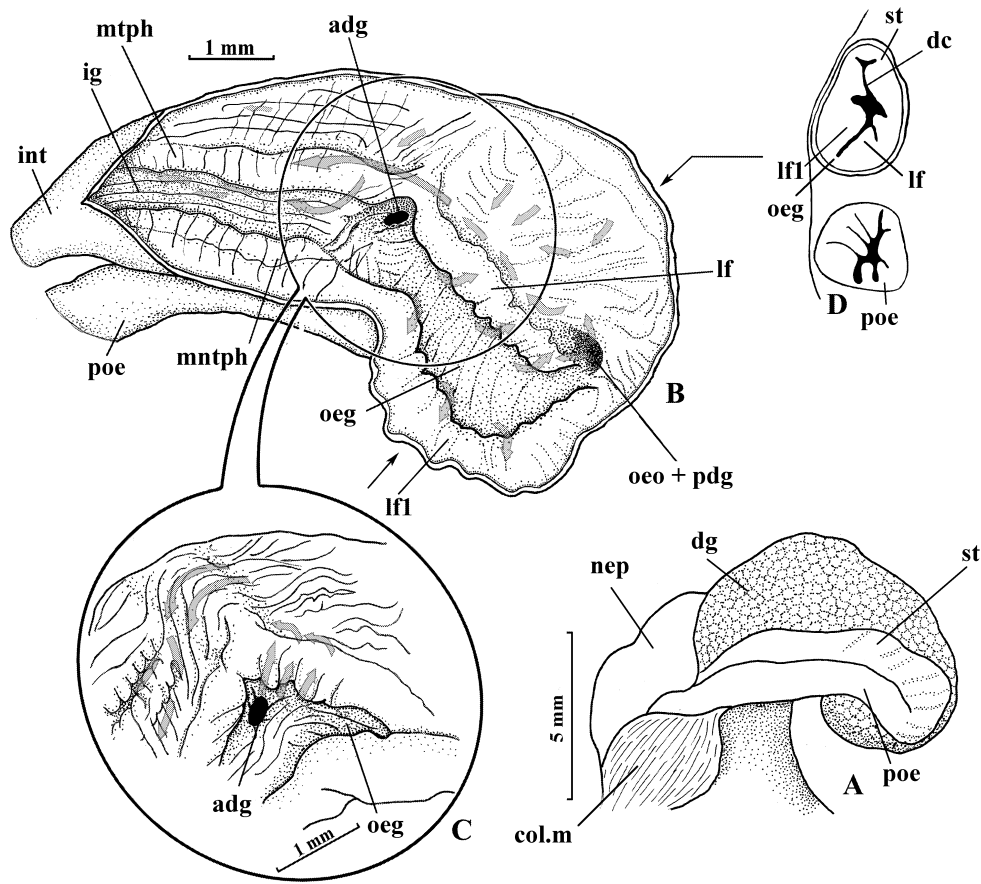


Figure 6. *Melongena corona*. **A.** Schematic latero-ventral view of the whorls of the visceral mass to show position of stomach in relation to digestive gland. **B.** Stomach opened along mid-dorsal line and external wall reflected. **C.** Enlarged part of stomach, showing transition of gastric chamber to style sac. **D.** Schematic section through posterior part of gastric chamber and oesophagus. The position of the section is shown by arrows on **B**. See Fig. 1 legend for explanation of abbreviations.

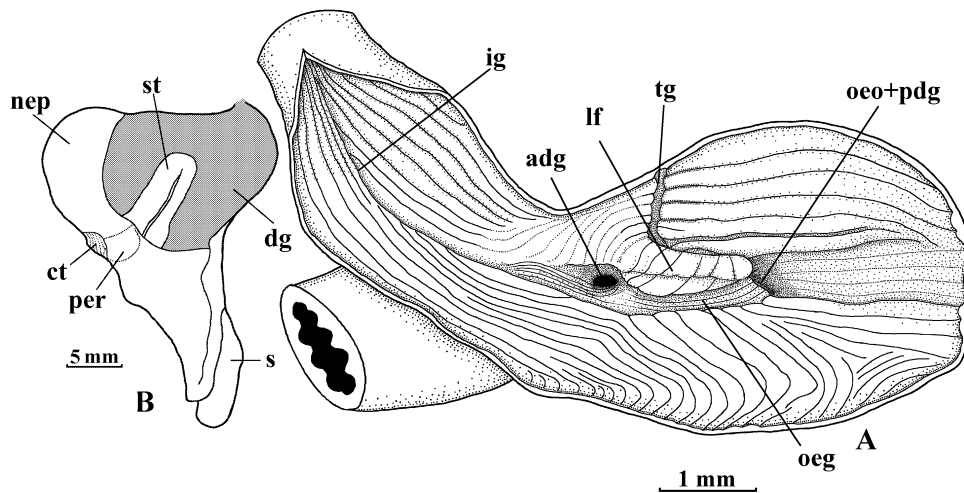


Figure 7. *Puzosia puzosia*. **A.** Stomach opened along mid-dorsal line and external wall reflected. **B.** Schematic view of whorls of the visceral mass to show position of stomach in relation to digestive gland, gonad and nephridium. See Fig. 1 legend for explanation of abbreviations.

was inserted into the barnacle through the mid-opening of the opercular plates. By contrast, the same species in India preys on various bivalves (Benny, Venmathiamaran & Ayyakkannu, 1996).

Busycon carica (Gmelin, 1791) (Fig. 8)

Material examined: One preserved male specimen, Lewes, Delaware, coll. M. G. Harasewych.

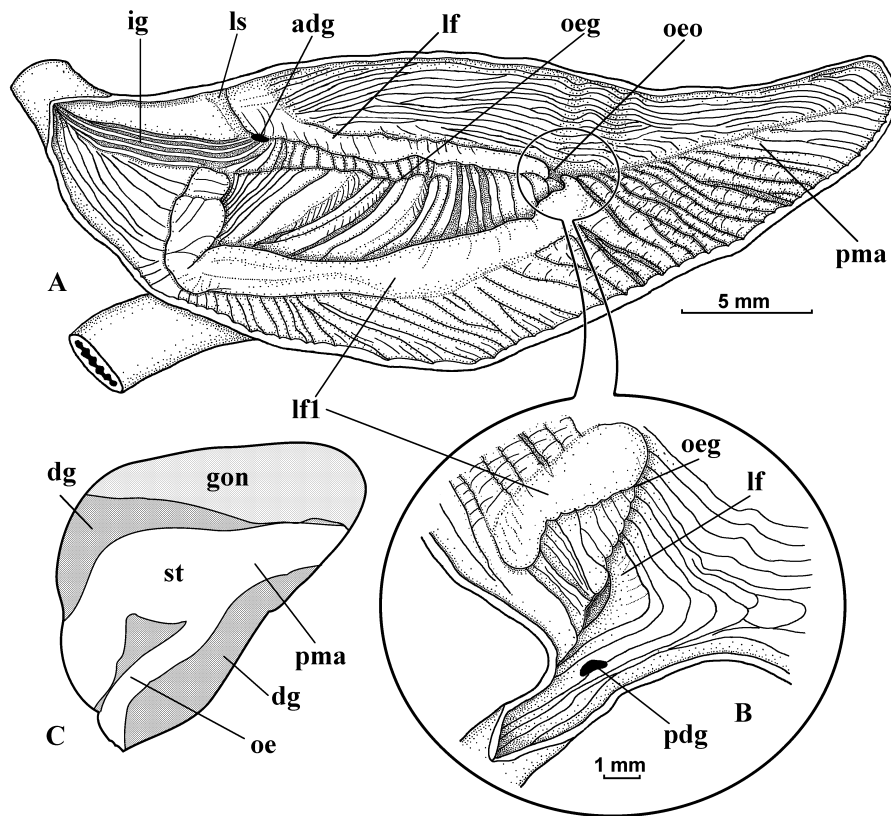


Figure 8. *Busycon carica*. **A.** Stomach opened along mid-dorsal line and external wall reflected. **B.** Enlarged part of stomach, showing opening of oesophagus into gastric chamber. Oesophagus partially opened along ventral line and outer stomach wall reflected. **C.** Schematic view of whorls of the visceral mass to show position of the stomach.

Description: The stomach occupies the central part of the whorl bordering the testis. It is rather large and broad, and extends for about half the whorl behind the posterior nephridial border (Fig. 8C). The oesophagus is broad and opens ventrally, midway along the length of the stomach. The posterior mixing area is large.

The posterior oesophagus is lined with low, longitudinal folds. These folds are continuous with the oblique, longitudinal folds on the outer stomach wall, which lead into the posterior mixing area. In contrast, the folds on the inner walls of the oesophagus and the posterior mixing area are curved and directed anteriorly (Fig. 8B).

The gastric chamber is clearly divided into the dorsal and rather broad ventral chambers by two distinct folds, one on the inner stomach wall (Fig. 8A: lf) and the other on the outer stomach wall (Fig. 8A: lf1). The most dorsal part of the ventral chamber is formed by the oesophageal groove (Fig. 8A: oeg), occupying a mid-ventral position. The outer wall of the ventral chamber is lined with partially transverse, partially oblique, well-developed folds. The dorsal channel is lined with longitudinal folds that are larger and more prominent on the outer stomach wall. The lateral sulcus is very shallow, connecting dorsal and ventral channels.

The ducts of the digestive glands are small and oval, with the anterior duct being slightly larger than the posterior. The anterior duct is located at the base of the lateral sulcus, while the posterior lies at the entrance of the oesophagus into the stomach.

The typhlosoles are not well defined. The intestinal groove is distinct and lined with narrow, raised, longitudinal folds.

Busycon carica, like other species of the genus, feeds on species of bivalves, penetrating the closed shells by wedging the outer lip between the valves (Warren, 1916; Carriker, 1951).

Fasciolariidae
***Fasciolaria lillium* (G. Fischer, 1807)**
(Fig. 9)

Material examined: Indian River in the vicinity of Fort Pierce, Florida, coll. Y. I. Kantor, April 1993; two specimens dissected (one live).

Description: The stomach is large, extending more than one-third of the whorl from the nephridial border and lacking a posterior mixing area. The epithelium of the posterior oesophagus is dark brown and changes sharply in coloration to cream at the transition to the stomach. The oesophageal groove is narrow and covered with uniform low folds that become indistinct near the anterior duct of the digestive gland. The strong, curved folds, continuous with the longitudinal folds of the oesophagus, line the posterodorsal part of the inner wall of the stomach. A low, transversely striated, longitudinal fold originates from the oesophageal opening, becoming obsolete at the level of the anterior duct of the digestive gland. The inner stomach wall anterior to the anterior duct is finely striated longitudinally. There is a weak transverse fold, marking the transition to the style sac, which may represent the remains of the lateral sulcus seen in other Buccinoidea.

The outer wall of the stomach is lined by strong and complex transverse folds (Fig. 9B). These folds alternate in strength and height, and the lateral sides of the larger folds are covered by oblique grooves that run along the folds. In addition to these grooves there is a secondary, thinner striation covering the folds. Typhlosoles are absent and the intestine walls are lined with subequal longitudinal folds.

The ducts of the digestive gland are paired. The opening of

STOMACHS OF BUCCINOIDEA

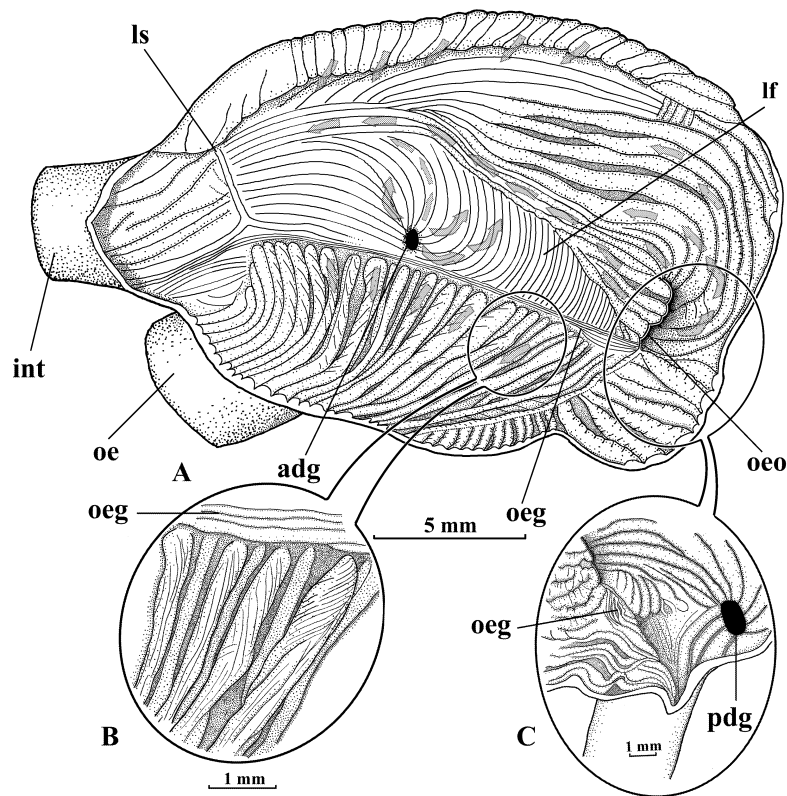


Figure 9. *Fasciolaria lilium*. **A.** Stomach opened along mid-dorsal line and external wall reflected. Arrows indicate major ciliary currents; mucus string not shown. **B.** Enlarged fragment of folds of sorting area. **C.** Posterior oesophagus opened along ventral line to show position of posterior duct of digestive gland. **A.** From living specimen. **B,C.** From preserved specimen.

the posterior duct is oval in outline in preserved specimens (Fig. 9C: pdg), while the anterior duct is larger and more rounded (Fig. 9A: adg). The openings are not recessed into the stomach wall.

The main ciliary currents run along the major folds on the inner stomach wall and ventrodorsally along the folds of the outer wall. On the roof of the stomach the currents lead particles toward the inner stomach wall. There is a permanent outflow of the mucous string from the anterior duct of the digestive gland, which is brought by the main ciliary currents into the intestine.

Fasciolaria filamentosa (Röding, 1798)

Material examined: Krusadai Island, flat reef, off Rameswaram, Southern India, Tamil-Nadu, coll. Y. I. Kantor, September 2000; one live specimen dissected.

Description: The outer morphology and anatomy of the stomach are in major details similar to those of *F. tulipa*. Minor differences include: the small folds on the inner wall of the stomach are much less curved and mainly transverse along most of their length, only in the most dorsal part are they curved and directed anteriorly. The lateral sulcus is distinct on outer and inner walls, although very shallow. The typhlosoles are developed, the major one runs along the median part of the inner wall of the intestine, while the minor occupies a ventral position. The intestinal groove is broad and shallow.

The directions of the ciliary currents were similar to those of *F. tulipa* and the mucous string from the anterior opening of the digestive gland was present. One difference was the presence of the ciliary currents, draining the intestinal groove.

Fusinus nicobaricus (Röding, 1798)

(Fig. 10)

Material examined: Fishing village near Tuticorin, Southern India, Tamil-Nadu, coll. Y. I. Kantor, September 2000; one preserved specimen (male) dissected.

Description: The digestive glands extend through 11/2 whorls (Fig. 10C) and are dark green. The glands are fused without an obvious border.

The stomach is narrowly tubular, long, spanning about 1/3 of the whorl from the nephridial border and lacking a posterior mixing area. The epithelium of the posterior oesophagus is dark orange and is arranged in sharp and tall longitudinal folds (Fig. 10B). There is a sharp change in coloration to cream-greyish at the transition to the stomach. The oesophageal groove is narrow and covered with prominent, closely spaced, transverse folds (Fig. 10A,B: oeg). The posterior-most part of the inner wall of the stomach is recessed into the digestive gland and this is the broadest (in transverse section) part of the stomach. The posterior part of the inner stomach wall near the oesophageal opening is covered with indistinct tile-like folds (Fig. 10A,B: tfl). Most of the posterior part of the outer stomach wall is covered with tall transverse folds. Near the oesophageal groove there are low, but distinct, oblique striae. The middle part of the outer stomach wall is covered with similar thin striations, directed transversely in the dorsal part of the wall and obliquely in the ventral part. Originating at the oesophageal entrance there is low longitudinal fold on the inner wall (Fig. 10A,B: lf), which runs the entire length of the gastric chamber. The fold is wide, low and clearly transversely striated. Dorsal to the fold there are

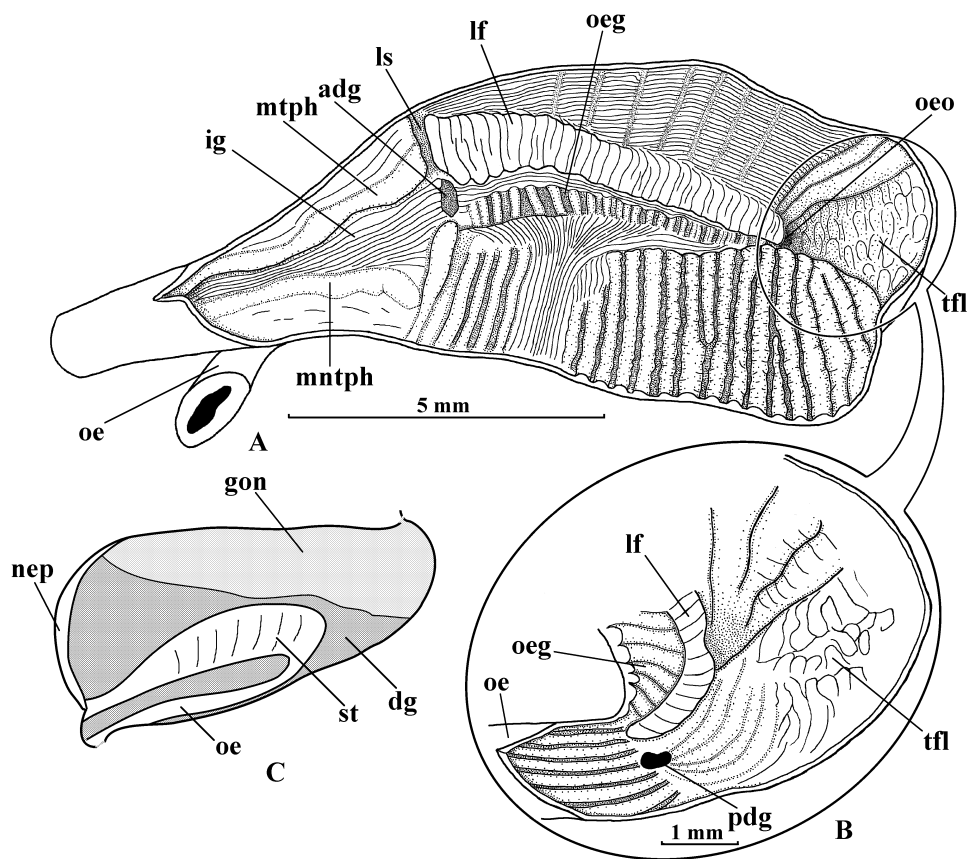


Figure 10. *Fusinus nicobaricus*. **A.** Stomach opened along mid-dorsal line and external wall reflected. **B.** Enlarged part of stomach, showing opening of oesophagus into gastric chamber. Oesophagus partially opened along ventral line and outer stomach wall removed. **C.** Schematic view of whorls of visceral mass to show position of the stomach.

numerous thin, mostly longitudinal striae. The lateral sulcus is narrow and short, although deep. On the outer stomach wall there is a transverse fold, corresponding to the lateral sulcus. The anterior duct of the digestive gland is located at the base of the sulcus. The typhlosoles are distinct, although low, with the major typhlosole (Fig. 10A: mtp) situated in the central portion of the inner wall. The intestinal groove is lined with low longitudinal folds.

The ducts of the digestive gland are paired, narrowly oval in the preserved specimen and not recessed into the stomach wall. The opening of the posterior duct is smaller than the anterior.

The single examined stomach was empty, but in the rectum of the specimen were faeces containing undetermined finely dispersed remains.

***Leucozonia nassa* (Gmelin, 1791)**
(Fig. 11)

Material examined: Florida Keys, at low tide on stones, coll. Y. I. Kantor, 1999; three specimens dissected (two live).

Description: The stomach is long, spanning about one-third of the whorl from the nephridial border (Fig. 11A) and lacks a posterior mixing area. At the opening of the oesophagus into the stomach the low longitudinal fold originates on the ventral part of inner stomach wall and runs the entire length of the gastric chamber. The fold is whitish in live specimens, very low, although clearly transversely striated (Fig. 11B,C: lf). The upper part of the inner stomach wall is smooth. The oesophageal groove is lined with a low epithelium, forming inconspicuous longitudinal striations. It is dark grey in live specimens, since the

epithelium that lines the groove is transparent and the digestive gland is visible through it. The outer stomach wall lacks strong folds, although it has a thin transverse striation. The lateral sulcus on the inner stomach wall (Fig. 11B: ls) is shallow. The ducts of the digestive glands are small. The opening of the anterior duct is situated in the oesophageal groove significantly posterior to the lateral sulcus. The opening of the posterior duct is situated near the oesophageal opening into the stomach. Typhlosoles are well-marked, bordering the intestinal groove. The major typhlosole has a narrow cuticularized zone, facing the lateral sulcus (Fig. 11B: cz).

Strong ciliary currents lead from the oesophageal opening along the oesophageal groove and dorsally along the outer stomach wall. Around the anterior duct there is a strong circular current, as well as currents leading from the duct. Weak, posteriorly directed currents were observed in the uppermost part of the inner stomach wall. There are rather strong currents along and out of the intestinal groove, as well as currents along the outer side of the major typhlosole, leading from the style sac into the intestine. A remarkable feature was a mucous string containing small particles. This string (Fig. 11B,C: ms) originated at the posterior opening of the digestive gland duct and followed the mid-dorsal line on the inner wall of stomach, bypassing the oesophageal and intestine grooves and entering the intestine along the outer side of the major typhlosole.

The stomach anatomy (without much detail) and feeding of this species were studied by Marcus & Marcus (1962). Their description is similar in its main features. They also mentioned the presence of a mucous string ('food-string'), but did not specify its origin from the posterior duct of the digestive gland. The intestines contained 'bristles and teeth of polychaetes'.

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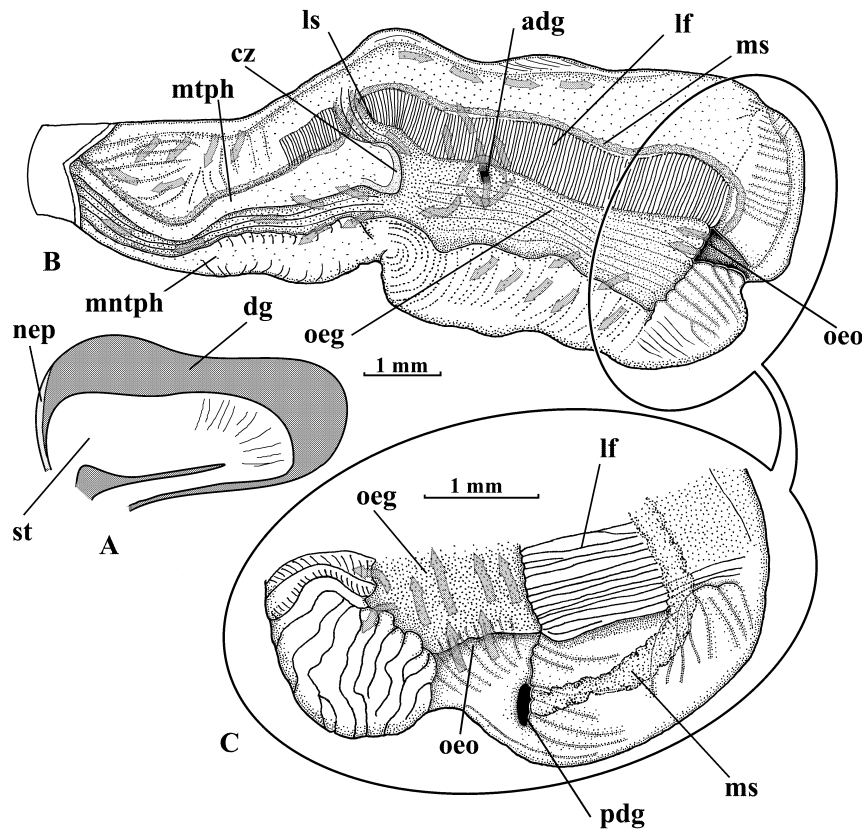


Figure 11. *Leucozonia nassa*. **A.** Schematic view of whorls of visceral mass to show position of the stomach in relation to digestive gland. **B.** Stomach opened along mid-dorsal line and external wall reflected. Arrows indicate major ciliary currents. **C.** Enlarged posterior part of stomach, showing opening of oesophagus into stomach and origination of mucus string from posterior duct of digestive gland.

Columbellidae

Anachis floridana (Rehder, 1939)

(Figs 12 and 13)

Material examined: Florida Keys, on a sea grass, coll. Y. I. Kantor, 1999; two specimens dissected, one stomach examined on SEM.

Description: The stomach is large relative to the visceral mass and long, spanning nearly two-thirds of the whorl, broadly tubular and occupies the mid-dorsal side of the whorl. A posterior mixing area is absent (Fig. 12A). The gastric chamber is rather short compared with the style sac. The posterior duct is rounded, rather large and situated close to the entrance of the oesophagus into the stomach (Fig. 12A: pdg). The anterior duct is smaller and opens at the base of the major typhlosole, close to the intestinal groove (Fig. 12A: adg). The lateral sulcus is not pronounced.

The outer stomach wall near the entrance of the oesophagus is lined with numerous distinct, although low and narrow folds that are morphologically similar to the sorting area. The ventral parts of the folds are lined with a ciliated epithelium (Fig. 13D: ci), while the dorsal parts seem to be cuticularized (Fig. 13D: cu). At the base of the minor typhlosole there is a large pad-shaped fold, lined with a ciliated epithelium (Fig. 12A–B: psf, 13D: ci). The inner wall is lined with oblique, strong folds, that are also lined with ciliated epithelium (Fig. 13F: ci). On the inner wall between the openings of the digestive gland ducts there is a medium-sized, cuticularized, gastric shield (Fig. 12A: gs). The typhlosoles are well-marked and large, although interrupted at the transition to the intestine.

Ciliary currents were difficult to observe due to the small size of the stomach. There were strong currents along the intestinal

groove and weaker dorsal and ventral currents in the ‘sorting area’. Also, currents leading from the oesophageal opening along the inner stomach wall passed dorsally in the posterior part of the gastric chamber, but were ventrally directed in the anterior part of the chamber.

In captivity, *Anachis floridana* consumed green algae and preyed on a minute species of Marginellidae.

Buccinulinae Unnamed species (Fig. 14)

Material examination: Elephant Island, 60°53' S, 55°32' W, 120–178 m, R/V *Polarstern*, station 42/079, 07.12.1996.

Description: Stomach small, tubular, U-shaped, without posterior mixing area (Fig. 14A,B). The posterior oesophagus (Fig. 14B, C: poe) is lined with epithelium that is somewhat darker than that of the stomach, and forms very tall and distinct folds. The epithelium changes in coloration at the transition to the stomach. The folds of the stomach epithelium are rather low (over-emphasized on the drawing). The opening of the posterior duct of the digestive gland (Fig. 14: pdg) lies at the entrance of the oesophagus, and is small and situated in the oesophageal groove (Fig. 14: oeg). The groove is bordered by a low longitudinal fold (lf) and lined with minute longitudinally directed folds. The anterior duct (Fig. 14C: adg) is much larger and situated at the base of a shallow lateral sulcus (ls). Ducts lie in shallow duct pouches that are slightly recessed into the digestive glands. At the right side of the anterior duct of the digestive gland there is a medium-sized, subtriangular, cuticularized gastric shield (Fig. 14C: gs), only slightly raised above the stomach wall. The

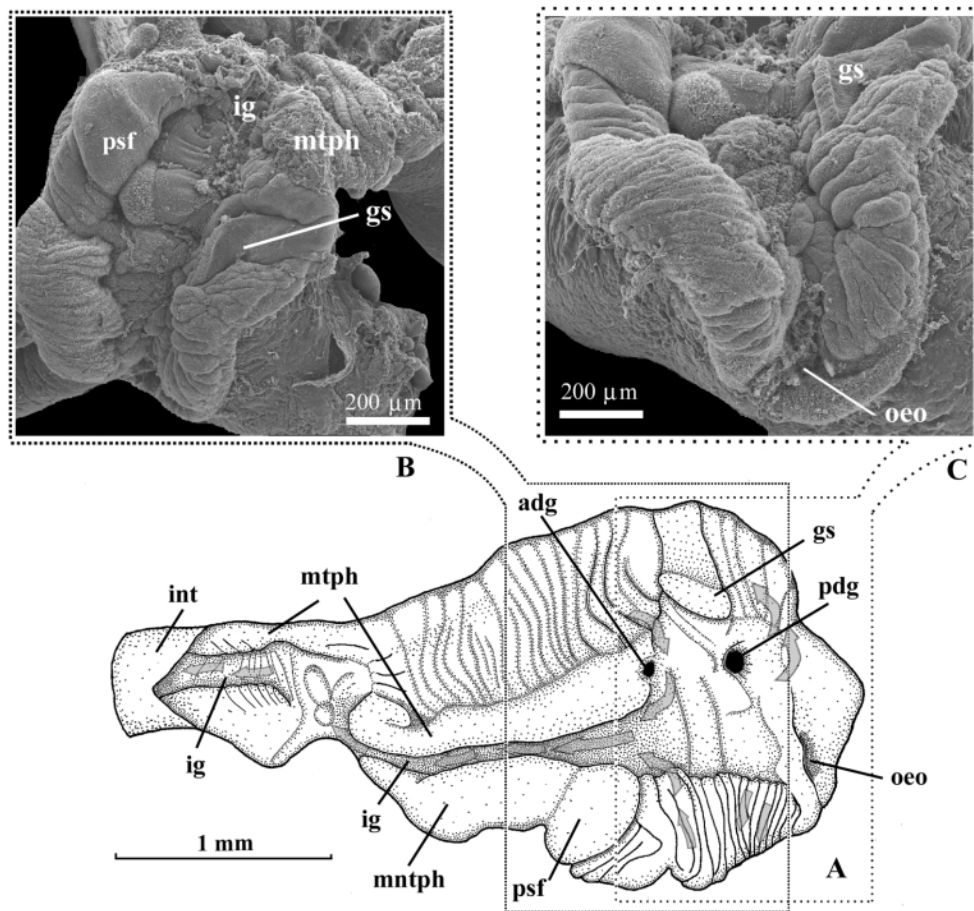


Figure 12. *Anachis floridana*. **A.** Stomach opened along mid-dorsal line and external wall reflected. Arrows indicate major ciliary currents. **B, C.** SEM photomicrographs of opened stomach.

lateral sulcus is lined with an orange epithelium arranged into sharp, low folds, and bordered anteriorly by a tall and thick transverse fold. The style sac is longer than the gastric chamber, with low typhlosoles bordering a shallow intestinal groove (Fig. 14C: ig), lined with a very low epithelium. The intestinal groove is seen through the stomach walls as a dark band (Fig. 14B: ig).

DISCUSSION

Taxonomic discrimination of buccinoidean families is usually based on shell and radular characters and is clear only in some cases. There are some genera for which the familial position is arbitrary. A recent example is the erroneous allocation of the genus *Babylonia* Schlüter, 1838, which has been traditionally placed in the Buccinidae (Altena & Gittenberger, 1983[Q3]). Examination of the anatomy (including the stomach) has demonstrated that it should be excluded not only from the Buccinidae, but also from the Buccinoidea (Harasewych & Kantor, 2002).

The stomach is the most complex organ of the digestive system and thus may provide an array of characters for taxonomic analysis, but difficulties of examination and the necessity of specially preserved specimens have precluded the common use of stomach anatomy for this purpose.

Examination by the author of a number of species revealed the important fact that stomach morphology does not depend on diet. Indeed, species with a similar diet may have very different stomachs (e.g. *Busycon* and *Melongena*, both preying on

bivalves), while related species with dissimilar diet (e.g. carnivorous and herbivorous Columbellidae) have rather similar stomachs (see below). Therefore, similarities in stomach anatomy more likely reflect phylogenetic relationships, rather than similarities in diet.

The following is an attempt to evaluate the applicability of the use of stomach anatomy in buccinoidean taxonomy. Presently, only a minor fraction of this very diverse group has been examined so the conclusions are necessarily preliminary.

Comparison of stomach anatomy

A summary of stomach characters within the different families is shown in Table 1.

Among the studied Buccinoidea, members of the Buccinidae have the most variable stomach morphology. Although the stomach of a number of species has been described in the literature, only a few species were dissected and drawn in a similar way that allows comparison. These are: *Neptunea antiqua* and *Colus gracilis* (Smith, 1967), *Buccinum middendorffii*, *N. bulbacea* (Medinskaya, 1993), *Siphonorbis danielsseni*, *Tacita arnoldi* (Lus, 1981a,b). Despite many variations, Buccinidae have the following general characters: broadly spaced ducts of the digestive glands (anterior one usually placed at the base of the lateral sulcus); a well-developed longitudinal fold, isolating the ventral part of the gastric chamber; a deep lateral sulcus (in some species present on the outer stomach wall as well as on the inner) and transverse folds in the posterior part of the dorsal channel of the style sac [Smith (1967) called them the 'sorting area'].

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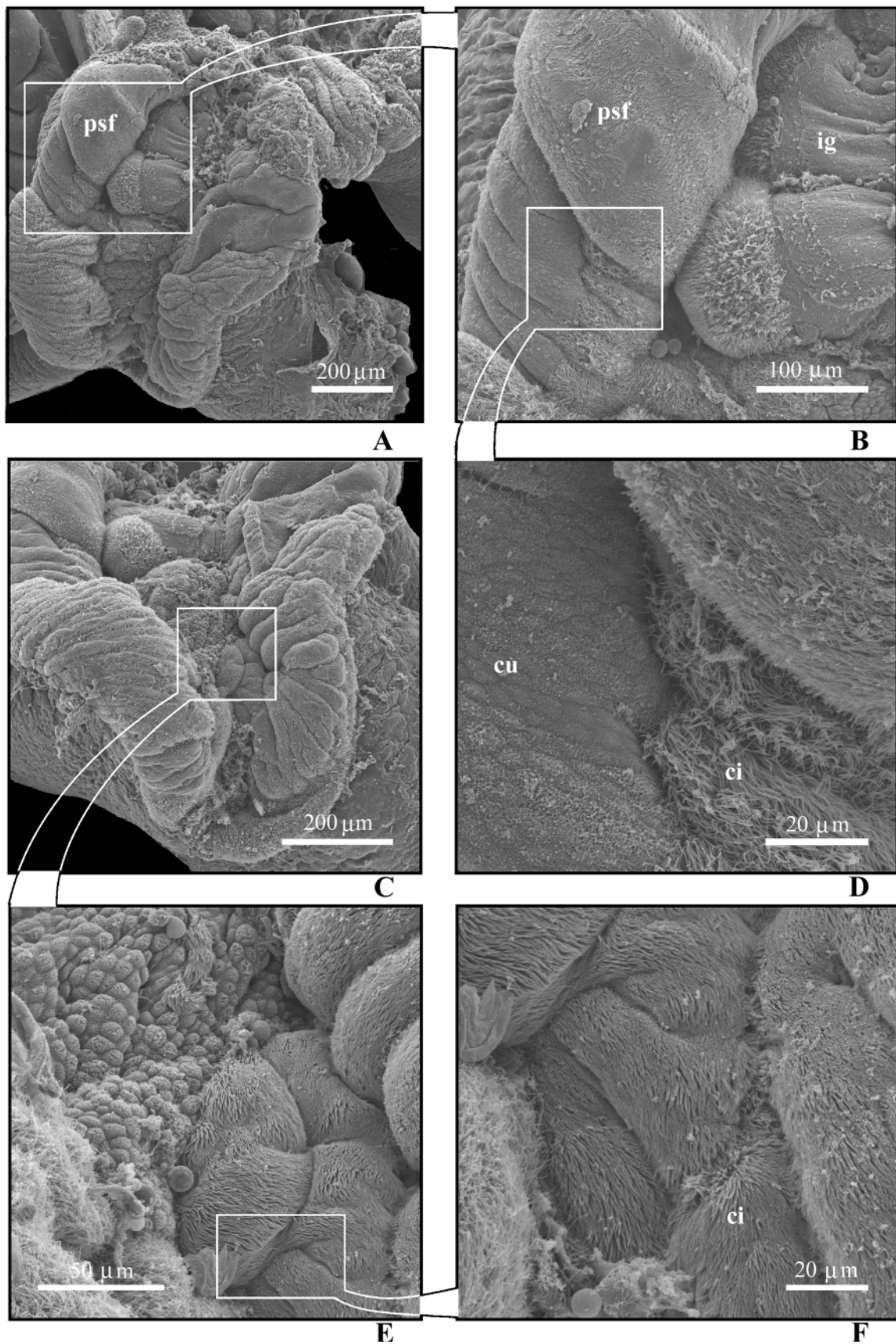


Figure 13. *Anachis floridana*, 1939. SEM photomicrographs of details of opened stomach. **A, B, D.** Pad-shaped fold at base of minor typhlosole. **C, E, F.** Lining of bottom of gastric chamber.

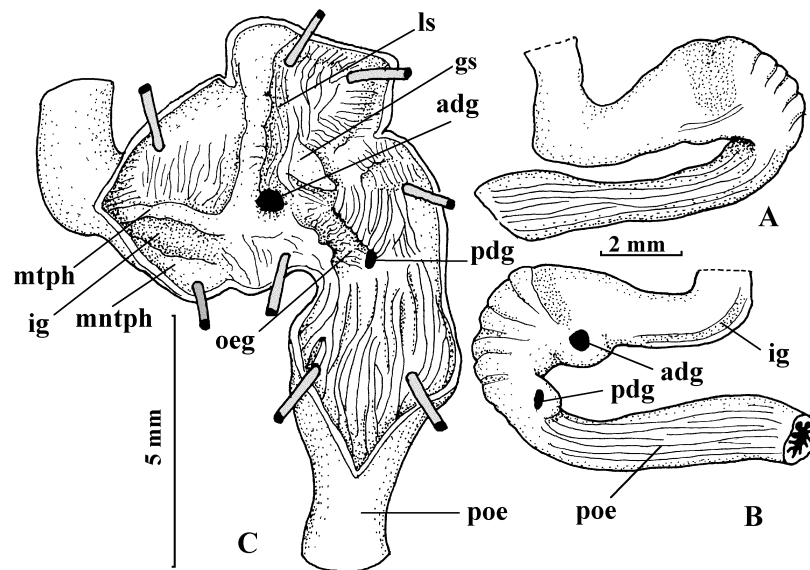


Figure 14. Unnamed species of Antarctic Buccinulidae. **A.** Stomach from outer side. **B.** Stomach from inner side. **C.** Stomach opened along mid-dorsal line and external wall reflected.

Two basic types of stomach can be recognized within Buccinidae. In the first type, the posterior mixing area is present and ranges from short (*Tacita arnoldi*, *Lussivolutoipsius* spp.; Kantor, 1990) to long (*Buccinum* spp., *Neptunea* spp.). The second type is characterized by the complete absence of the posterior mixing area and such stomachs were found in both northern and southern species. Among the northern ones are *Colus gracilis* and *Siphonorbis danielsseni*, while among southern species are representatives of the genus *Chlanidota* (Harasewych & Kantor, 1999), '*Tromina*' *abyssorum* Lus, 1993 and still unnamed new species (Y. I. Kantor & M. G. Harasewych, unpublished). The southern genera and species are usually attributed to family Buccinulidae, which is undoubtedly closely related, if separate from Buccinidae. Related to the absence of the posterior mixing area is the widening of the posterior oesophagus, which is lined with an obviously glandular epithelium. In at least two species of the second type (*Colus gracilis* and the unnamed new species from the Antarctic) the cuticularized gastric shield was present (Fig. 14: gs).

Nassariidae have a rather similar stomach to that of the first type of Buccinidae, but have a much longer and narrower posterior mixing area, and very closely spaced ducts of the digestive glands, situated near the oesophageal entrance. For *Nassarius reticulatus* Graham (1949) illustrated only a single duct, although it is more likely that the duct openings are very close to each other (Morton, 1958). The other character, found in most species of Nassariidae is the presence of a gastric shield. In *Ilyanassa obsoleta*, a shield was present in almost all specimens recently collected from the field, but then absent from the majority of animals maintained in the laboratory for any extensive length of time on a diet of frozen shrimp (Brown, 1969). It was not found in any specimens of *Nassarius vibex*, even if preserved immediately after collection. In some species of Nassariidae, a crystalline style has been recorded (Morton, 1958; Brown, 1969) that in *I. obsoleta* is present only when the animals feed on detritus and disappears with transfer to a carnivorous diet. The species that possess a crystalline style otherwise have a stomach anatomy typical for the family. In *Nassarius vibex*, as well as probably in *Ilyanassa obsoleta* (according to fig. 18 of Brown, 1969) the ducts lie in a common pouch, surrounded by a muscular edge that is able to contract and occlude the ducts. There are some minor variations of the stomach anatomy (e.g. the length of the longitudinal fold, which is much longer

in *Nassarius incrassatus* than in any other species; Smith, 1967), but the general form in all species studied is characteristic and similar to each other.

In this respect the taxonomic position of *Clea* is of special interest. Traditionally, this freshwater genus has been attributed to the Buccinidae (e.g. Thiele, 1929). However, its stomach has many more features in common with Nassariidae than any Buccinidae. In particular, it has an extremely long posterior mixing area, a short gastric chamber and very closely spaced ducts of the digestive glands. It might be necessary to reconsider the familial position of *Clea*, but this will need additional investigation. In the genus *Nassaria* (*N. pusilla*, *N. coromandelica*; unpublished), also attributed to Buccinidae (Cernohorsky, 1981) the outer stomach morphology is very similar to *Clea*. Unfortunately, due to the lack of adequately preserved material it has not been possible to examine the stomach anatomy of these 'buccinid' species in the present study and, therefore, the taxonomic position of this genus remains uncertain.

Species of Fasciolariidae have a rather distinctive stomach morphology, similar in all the studied species. Distinctive characters are: the low relief of the folds on the inner stomach wall; presence of transverse striations on the low longitudinal fold (which also differs in coloration from surrounding tissues in living snails); absence of clear differentiation of the gastric chamber into dorsal and ventral parts; absence of a posterior mixing area and a shallow lateral sulcus. Since representatives of three subfamilies (Fasciolariinae: *Fasciolaria lilium*, *F. filamentosa*; Fusiniinae: *Fusinus nicobaricus*; Peristerniinae: *Leucozonina nassa*), it may be concluded that the listed characters define Fasciolariidae as a family.

Three species of Melongenidae were studied. The stomachs of *Melongena* and *Pugilina* are rather similar, both being narrowly tubular and simplified. A posterior mixing area is absent; the gastric chamber is very distinctly separated into dorsal and ventral parts by strong longitudinal fold(s), which are continuous with poorly developed typhlosoles, and a lateral sulcus is absent. The stomach of *Busycon* is strikingly different in possessing a large posterior mixing area and in the presence of a lateral sulcus. In addition, Melongenidae have a characteristic, disproportionately small, cylindrical head with narrow tentacles. In *Busycon* the head is large, broad, with long tentacles, similar in morphology to species of Buccinidae. It is possible that *Busycon*

Table 1. Summary of the stomach anatomical characters of Buccinoidea

Character	Buccinidae (except <i>Clea</i>)	Buccinulidae	Genus <i>Clea</i>	Nassariidae	Melongenidae (except <i>Busycon</i>)	Genus <i>Busycon</i>	Fascioliariidae	Columbellidae
Broadened glandular posterior oesophagus	Present or absent	Present	Absent	Absent	Absent	Absent	Absent	Absent
Posterior mixing area	Present (medium long) or absent	Absent	Present (very long)	Present (very long)	Absent	Present (long)	Absent	Absent
Longitudinal fold(s) separating gastric chamber into ventral and dorsal channels	Present, well developed, may be paired	Present, single on the inner wall	Present, very short, on the inner wall	Present, short, on the inner wall	Present, well developed, may be paired	Present, well developed, paired	Present, very low, transversely striated	Absent
Lateral sulcus	Present, well marked	Present, well marked	Present, well marked	Present, well marked	Absent	Present, well marked	Present, poorly marked	Absent
Transverse folds in posterior part of style sac	Present	Present	Present	Present	Absent	Absent	Absent	Absent
Ducts of the digestive gland	Broadly spaced	Broadly spaced	Very closely spaced	Very closely spaced	Broadly spaced	Broadly spaced	Broadly spaced	Closely spaced
Gastric shield	Absent or present	Absent or present	Absent	Absent or present	Absent	Absent	Absent	Present in herbivorous species
Crystalline style	Absent	Absent	Absent	May be present	Absent	Absent	Absent	May be present

should be transferred to the Buccinidae, but careful examination of foregut anatomy is needed.

Species of Columbellidae seem to be better studied among Buccinoidea. The stomach was examined in eight species by Marcus & Marcus (1962b), including both herbivorous and carnivorous species, but they illustrated only the stomach of *Anachis valeda*. Medinskaya (1993) illustrated the stomach of the carnivorous *Mitrella burchardi*. *Anachis floridana* described here feeds both on algae and minute gastropods. In general, features of the stomach of Columbellidae are rather uniform between species. It is characterized by a short gastric chamber and a long style sac, the absence of the posterior mixing area, and lack of a longitudinal fold separating the gastric chamber into dorsal and ventral parts. The lateral sulcus is not clearly demarcated, although there is a depression anterior to the usually present gastric shield, which may represent the vestige of the sulcus. A gastric shield was reported by Marcus & Marcus (1962b) for all species, but is absent in *Mitrella burchardi*.

The Colubrariidae remain practically unstudied. Only one species [*Ratifusus mestayerae* (Iredale, 1915)] has been examined (Ponder, 1968). Its stomach is of fundamentally different morphology compared with any other buccinoidean. It is long, thin-walled, not U-shaped, since the opening of the oesophagus is situated in the morphologically anterior part of the stomach, while the intestine leaves it posteriorly and forms a curve along the upper edge of the stomach running to the mantle cavity. Little is known about the feeding and biology of Colubrariidae. The single record concerns *Colubraria obscura* (Reeve, 1844), which was observed sucking blood from parrotfish (Bouchet & Perrine, 1996). For *Ratifusus mestayerae* Ponder supposed that its muscular proboscis can be used as a pump. It cannot be excluded that this species also sucks liquid food and that the very simplified sac-like stomach is an adaptation for the consumption of large quantities of fluids.

This preliminary analysis suggests that most families of Buccinoidea can be differentiated by stomach characters. The stomach of the southern Buccinulidae is rather similar to that of some boreal genera and cannot be separated. The present systematic position of some genera of Buccinoidea (*Clea*, *Nassaria* and *Busycon*) needs reconsideration.

Functioning of the stomach

Studies of molluscan functional morphology, reviewed by Morton (1958), Fretter & Graham (1962, with minor additions in 1994) and Brown (1969) suggested that the first gastropods fed on small particles. The particles were non-selectively scraped from the substratum by the radula and bound by mucus into a 'food string'. The particles were then transported along the alimentary canal by ciliary activity, and eventually subjected to phagocytosis and intracellular digestion within the blind tubules of the digestive gland. Intracellular digestion required size-sorting of the food particles, so that particles within certain size limits were available for phagocytosis. This sorting in gastropods was accomplished almost solely by means of ciliary sorting fields within the stomach.

With the shift to carnivory in gastropods, especially in the Neogastropoda, the mode of feeding and digestion greatly changed. First, the food in carnivorous gastropods consists not of small particles, but of large pieces of flesh, torn off by the radula, or the prey may be swallowed whole (in Conoidea). Rather few species still feed on particulate food, such as sediments (Nassariidae). Secondly, intracellular digestion was replaced by extracellular (and, therefore, the necessity for sorting mechanisms disappeared). Finally, a different set of enzymes is used for digestion of plant and animal food.

Graham (1949) considered the stomach of neogastropods as merely a sac, in which food is mixed with enzymes from the

digestive glands, and is digested and absorbed in the tubules of the gland. For *Nassarius reticulatus*, he mentioned that 'in the immediate vicinity of the duct from the digestive gland the folding is more elaborate and the ciliation in this region is more complex, so that it perhaps represents part of the posterior sorting area' (p. 749). Smith (1967), on the contrary, considered the stomach of the Neogastropoda a much more complex structure, and recognized in stomachs of Buccinoidea a posterior sorting area connected to the oesophageal groove and sorting area in the style sac. Actually, he did not take into account that the food of neogastropods generally consists of large fragments (that is confirmed by our observations on the stomach content of many Buccinoidea) and identified the ciliary currents with the 'moving of the food particles'. This view was followed by Medinskaya (1993) in her analysis of the neogastropod stomach. Brown (1969) especially studied the presence of sorting mechanisms in *Ilyanassa obsoleta* and concluded that there was no actual sorting of particles by size, or the presence of two currents perpendicular to each other to effect such a separation.

Our observations on the ciliary currents by the addition of finely dispersed particles of carmine did not reveal any sorting activities either. At the same time, in some species there are, indeed, vast areas covered by similarly orientated folds, with an especially complicated arrangement on the outer stomach wall of Fascioliariidae (particularly in *Fasciolaria lilium*). Unfortunately, food was not observed in any of the fascioliariid stomachs examined here. Taylor & Lewis (1995) [Q5] listed the diet of a number of Indo-Pacific *Peristernia* and *Latirolagena*. The range of prey is wide, including polychaetes, gastropods, crustaceans and ascidians. The presence of gastropod radulae suggests that the consumed food consists of large pieces, as in other Buccinoidea. Therefore, there is no clear evidence for the presence of sorting mechanisms, but the question in Fascioliariidae should be clarified with more detailed studies using particles of different sizes.

Stomach walls are mostly lined with ciliated epithelium, providing sometimes rather strong ciliary currents. The directions of these ciliary currents are rather complex. In general, they are directed from the oesophagus into the posterior mixing area (when present) or to the dorsal chamber of the stomach and then anteriorly towards the intestine. There are usually clockwise-directed currents along the outer and inner stomach walls, and in all species studied there was a rather strong, ventrally directed current along the lateral sulcus. There were no strong currents, or no currents at all, that lead from the oesophagus into the oesophageal groove (except in *Leucozonia nassa*). Finally, there are always strong outgoing currents from the ducts of the digestive glands. In many cases, strong ciliary currents were directed not along but even across strong folds. Thus functional conclusions, based on the morphology of preserved specimens alone should be avoided (e.g. Medinskaya, 1999). Since food usually consists of large fragments that cannot be moved by ciliary action, the function of these currents is probably the distribution of enzymes produced by the digestive glands.

The functioning of the stomach is intimately connected with that of the digestive gland and therefore cannot be discussed separately. The digestive gland (or mid-gut gland) is actually paired glands that are usually fused without a distinct border. The anterior gland is usually small and compact, and is situated near the style sac. The posterior gland is much larger, adjoining the ventro-posterior side of the stomach and extending to the tip of the visceral mass. The glands consist of tubules lined with two basic cell types, digestive and secretory cells. The latter undergo cyclic activity, as has been demonstrated for Nassariidae and *Littorina* (Martoja, 1964; Merdsoy & Farley, 1973; Bogen & Farley, 1974).

There is strong controversy about the site of food absorption in Neogastropoda. Martoja (1964) in numerous experiments with different substances (China ink; different stains—trypan blue, neutral red, indigo-carmin, sudan; $^{35}\text{SO}_4$) demonstrated

that in *Nassarius reticulatus* digested food is not absorbed within the tubules of the digestive gland, but in the stomach and intestine. At the same time, the isotope was finally concentrated in the epithelial cells of the digestive gland through the activity of cells, moving in intertubular spaces ('cellules basophiles intertubulaires'). Her conclusion was that the digestive gland is not an absorptive organ. Similar results were obtained by Brown (1969), with the absence of absorption of carborundum and carmine particles by the cells of the digestive gland.

More controversial are the results of the experiments of McLean (1971) with three species of Nassariidae, namely *Nassarius fossatus*, *N. tegula* and *Ilyanassa obsoleta*. He added colloidal graphite, carmine, rice starch grains and titanium dioxide powder, identifiable under light microscope, to the food of nassariids and registered the presence of the substances within the tubules of the digestive gland, as well as their accumulation in the apices of epithelial cells. He concluded that, at least in these three species, absorption of food takes place within the tubules of the digestive gland. Thus, the question of where absorption of the food takes place remains unanswered.

The present observations on the ciliary currents in living species conform with the conclusions of Martoja and Brown. In none of the species studied here were the currents leading particles and fluids into the ducts. On the contrary, there were strong currents carrying particles and mucus from the ducts into the stomach lumen. This was also recorded for *Ilyanassa obsoleta* (Nassariidae) by Brown (1969). Smith (1967) did not specifically mention ciliary currents leading from the stomach into the digestive gland tubules, although he indirectly considered that entry of digested material into the ducts was possible. For *Nassarius incrassatus* he mentioned (p. 86) that 'large amount of secretions flow into the stomach and that the major part of the digestive process takes part in the posterior mixing area. It is possible, however, that material could enter the ducts by the muscular compression of the lumen of the stomach'. The latter supposition seems rather improbable, especially for nassariids. Ducts in most species (including *N. incrassatus*) are isolated from the dorsal part of the gastric chamber by a longitudinal fold and, in some species, can be completely closed by contraction of the muscular edge of the duct pouch. Moreover, in many species there is an outflow of mucus from the opening of the digestive gland ducts (thus blocking the entering of the stomach content into the ducts). This outflow is very conspicuous in Fascioliariidae. In *Leucozonia nassa* mucus leaving the posterior duct forms a swiftly moving string leading to the intestine. When cut, this string is soon restored. Most probably the function of these mucous strings is the entanglement of indigestible food fragments and their transport to the intestine.

The question of how digested food can enter the ducts of the digestive gland (and therefore whether absorption occurs in the tubules of the gland) remains open. One may suppose that there are periodic currents, leading from the duct and carrying enzymes, when food is present in the stomach lumen, but flowing in the opposite direction when there is an 'absorption' phase, but dissection of the stomach, either filled with food or empty, never revealed any incoming currents.

It could be supposed that the presence of the ciliary currents leading into the ducts depends on the degree of food digestion before it enters the stomach. Thus, in species in which food is predigested, it should enter the ducts of the digestive gland. Gastropods of the genus *Oliva* are characterized by a peculiar feeding mechanism, where the food item is placed into a pouch, which is formed by the posterior part of the very broad and thin foot. In experiments it was shown that the epithelium of the sole produces proteolytic enzymes. Thus, food entering the *Oliva* stomach, is already digested. Examination of ciliary currents, nevertheless, revealed a very strong outgoing current from the ducts of the digestive glands (Kantor & Tursch, 2001).

Another question concerns the origin and composition of the particles that were observed flowing out of the ducts of the digestive gland. The digestive gland does not have excretory functions, but the amount of this material can be very large, for example in *Nassarius vibex*.

The only species of neogastropod for which a ciliary current leading into the duct of the digestive gland has been found is *Alcithoe arabica* (Volutidae; Ponder, 1970). It is interesting that in *Alcithoe* there is a single opening of the duct, situated at the transition of the oesophagus to the stomach. Thus, the food particles that may enter the duct are not yet digested. It is also strange, that in this species a complicated sorting area consisting of complex arrangement of tall folds is present anterior to the duct.

A division of the stomach into ventral and dorsal chambers connected by a lateral sulcus is present in most Buccinoidea. Nevertheless, the functional significance of this remains poorly understood. Smith (1967) supposed that predigested food enters the oesophageal groove and passes to the ducts of the digestive glands. Nevertheless, in most cases strong currents have not been seen leading from the oesophagus into the groove. Moreover, as shown above, there are no ciliary currents leading into the ducts.

CONCLUSIONS

In conclusion, the presence of vast sorting areas, as suggested by Smith (1967), is improbable, since no actual size sorting has been observed in the studied species. It is still unclear where absorption of digested food occurs, since the strong ciliary currents leading from the ducts prevent the entry of ingested food into the tubules of the digestive gland. Finally, the functional significance of the separation of the stomach into ventral and dorsal chambers, as found in most Buccinoidea, is unclear.

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