# Morphology and development of the valve of Leiblein: Possible evidence for paraphyly of the Neogastropoda

**Yuri I. Kantor**
**Alexander Fedosov**

A.N. Severtsov Institute of Ecology and Evolution
Russian Academy of Sciences
33 Leninski Prospekt
Moscow 119071
RUSSIA
kantor@malaco-sevin.msk.ru
fedosov_zool@mail.ru

## ABSTRACT

Neogastropoda are generally considered to be monophyletic, although their monophyly is usually challenged in molecular phylogenies. Such results suggest that serious reconsideration of the synapomorphies and autapomorphies defining the group is needed. One of the uncontroversial monophyletic groupings within the neogastropods is the superfamily Buccinoidea. This taxonomically rich clade lacks two out of three characters that are considered to be key autapomorphies of Neogastropoda, namely accessory salivary glands and the rectal gland. The only other autapomorphy that unites Buccinoidea with the rest of Neogastropoda is the valve of Leiblein. This study of the morphology of the valve of Leiblein of different neogastropods (two species of Raphitominae, Conidae, one of Muricidae, one of Nassariidae, one of Buccinidae, one of Cancellariidae, and one of Olividae) revealed its strong morphological heterogeneity. Published and original data on the embryonic development of the valve in Buccinidae and Muricidae demonstrate that the valve originates from different sections of the anterior foregut. Preliminary data indicate that the homology of the valve of Leiblein within Neogastropoda is, at best, questionable. This casts further doubts on the monophyly of the Neogastropoda, which probably include at least two stems.

*Additional keywords:* Gastropoda, phylogeny, monophyly, alimentary system, development

## INTRODUCTION

The origin and phylogeny of the Neogastropoda were the subjects of many publications over the past decades. Several hypotheses on the sister groups were also proposed, including higher "mesogastropods" of the order Tonnoidea (Amaudrut, 1898; Graham, 1941, and more recently Riedel, 1994, 2000), and an "archaeogastropod" or primitive "mesogastropod" (Ponder, 1974). Morphological analyses of Strong (2003) suggested other possible affinities for the group, with the nearest relatives of

Neogastropoda being Epitoniidae, Cypraeidae and Naticidae (Tonnoidea were not represented in these analyses). The molecular analysis of Colgan et al. (2007) found relationships between neogastropod families (either individually or as groups) and Turritellidae, Tonnoidea, Stromboidea, or Cypraeidae.

Since the publication of Golikov and Starobogatov (1988), mostly overlooked by western malacologists, the monophyly of the Neogastropoda was not contested. These authors suggested that Bucciniformii (to which they attributed majority of neogastropods, but also include Triphoridae) and Coniformii (in which they included Conoidea, Mitridae, Cancellariidae, and Pyrenoidea) originated independently, the former ones from Amberleyoidei while the latter from Turbinoidei. The idea that Conoidea (= Toxoglossa) stands well apart from the rest of the neogastropods was also supported by Sheridan, Van Mol, and Bouillon (1973) and Shimek and Kohn (1981).

Kantor (2002) summarized the major apomorphies of the Neogastropoda and concluded that they are monophyletic. Among recent morphology-based phylogenetic analyses, Strong (2003) and Ponder et al. (2008) supported the monophyly of the Neogastropoda. In Ponder et al. (2008) a Bayesian analysis of a combined morphological dataset and the molecular data also supported the monophyly of the Neogastropoda.

The monophyly of Neogastropoda has usually been challenged, albeit weakly, in molecular analyses (Harasewych et al., 1997; Colgan et al., 2000, 2003, 2007; Riedel, 2000; McArthur and Harasewych, 2003). More details of different molecular data analyses can be found in Colgan et al. (2007). It should be specifically noted that in a number of analyses the Tonnoidea were nested within the Neogastropoda.

A survey of existing theories and suggestions reveals that nearly every possible evolutionary scenario for the Neogastropoda, and nearly all possible relationships have already been proposed. A consensus has not yet been

achieved, and the situation is not becoming clearer with addition of more morphological and/or molecular data.

A major current problem is the incongruence between molecular and morphological analyses both in terms of the monophyly of Neogastropoda and the composition of the clade. The answer may lie in the erroneous interpretations of the synapomorphies and autapomorphies defining Neogastropoda. Taylor and Morris (1988) and, more recently, Kantor (2002) summarized and discussed in detail the autapomorphies of Neogastropoda. Three autapomorphies of neogastropods have been found so far: the presence of a second pair of salivary glands (accessory salivary glands, differing in morphology and histology from the primary salivary glands), the presence of a valve of Leiblein, and the presence of an anal, or rectal gland. It has been unanimously accepted that these three structures are homologous within the Neogastropoda.

One of the uncontroversial monophyletic groups within Neogastropoda is the superfamily Buccinoidea Rafinesque, 1815. This clade was considered as highly advanced by Kantor (1996), or the sister taxon to the rest of the neogastropods (Ponder and Lindberg, 1997). Buccinoidea lack both accessory salivary glands and a rectal gland, leaving the valve of Leiblein as the single remaining autapomorphy that is present in all major branches of the Neogastropoda.

The valve or pharynx of Leiblein is usually described as pear-shaped organ, consisting of a posteriorly directed cone-shaped protuberance that is enclosed in a chamber formed by the expanded walls of the anterior portion of the mid-esophagus (Brown, 1969). The protuberance, or flaps (sensu Fretter and Graham, 1962) are fringed with extremely long cilia that beat very languidly.

The major function of the structure is to prevent regurgitation of food from the more posterior part of the gut during the elongation of the proboscis. It reacts partially mechanically but also chemically—exposure to secretions of the digestive gland or stomach contents caused the flaps to close (Brock, 1936).

Surprisingly, the anatomy of the valve has not been studied extensively. In addition to the description of the valve of Ilyanassa obsoleta (Say, 1822) (Nassariidae) by Brown (1969), the valve was described in detail only for Nucella lapillus (Linnaeus, 1758) (Graham, 1941; Andrews and Thorogood, 2005). Despite these very limited data, the homology of the valve was never questioned. In light of the need to re-evaluate the phylogenetic value of autapomorphies for Neogastropoda, we undertook a comparative study of the valve in different branches of the Neogastropoda.

## MATERIALS AND METHODS

Material for this study was collected in a number of localities; details are given in the corresponding descriptions for each species. For most species, the valve together with parts of anterior and mid-esophagus were dissected out from the body prior to fixation, then fixed in 4% formalin or 75% alcohol. In the laboratory, the valves were dehydrated and embedded in Paraplast; serial sections were cut at 7 μm thickness and stained with Masson's trichrome.

For the studies of the embryonic development of *Buccinum undatum* Linnaeus, 1758, the egg cases were collected by SCUBA diving in the vicinity of the Biological Station of Moscow State University in Kandalaksha Bay, on the White Sea. The egg cases were maintained in the laboratory in a running seawater aquarium. Capsules were dissected periodically, and embryos preserved in phosphate-buffered 2.5% glutaraldehyde (pH 7.6).

Fixed embryos were dehydrated in graded ethanol series and embedded in epone-araldite medium. Sections were cut at 2–2.5 μm thickness and were stained with methylene blue and toluidine blue in borax. Sections were examined using a Carl Zeiss Axioplan 2 microscope and photographed with an Axio-Cam digital camera.

## RESULTS

### Nassariidae

*Nassarius luteostoma* Broderip and Sowerby, 1829
(Figure 1)

**Material Examined:** Two specimens sectioned, Panama, Pacific Ocean: Venado Island, at low tide on sandy bar, 08°52'48.6" N, 79°35'36.9" W, coll. Yu. Kantor, 2006. The valve of Leiblein is large, pear-shaped, about twice as broad as the anterior esophagus, situated immediately in front of the circumoesophageal nerve ring. Its histology is very similar to that described by Brown (1969) for *Ilyanassa obsoleta*. The cone-shaped papilla (Figure 1, **csp**) is lined by columnar ciliated epithelium which is continuous with that of the anterior esophagus. The cells on the top of the papilla bear extremely long cilia of about 400 μm in length and that span most of the valve length. At the base of the papilla there is a ring of tall, ciliated, light-staining cells confluent with the papilla. In longitudinal section, this ring of cells looks like a triangle (Figure 1, **lsc**). This ring is usually called a mucous pad (Fretter and Graham, 1962; Andrews and Thorogood, 2005), and it is thought that its main function is to produce mucus that binds the particles. This ring of cells is seen as a whitish circle through the valve walls.

The thickened part of the valve is composed of pseudostratified columnar ciliated epithelium (Figure 1, **pse**). The cells are stained dark blue. No traces of the dorsal folds of the anterior esophagus were found.

The outer surface of the valve has an extremely thin layer of muscle fibers (in contrast to the relatively thick layers of longitudinal and circular muscles that form the wall of the anterior esophagus) and a rather thick layer of connective tissue (Figure 1, **ct**).

### Buccinidae

*Triumphis distorta* (Wood, 1828)
(Figure 2)

**Material Examined:** Two specimens sectioned, Panama, Pacific Ocean: Playa Bique, in rock crevices, high in intertidal zone, 08°52'42.3" N, 79°39'18.8" W, coll. Yu. Kantor, 2006.

The valve is large, subcylindrical, about 1.5 times as broad as the anterior esophagus, situated at some distance in front of the nerve ring. Histology of the valve is rather similar to that of *N. luteostoma*, although due to the fixation conditions it seems slightly distorted. The cilia of the cells of the cone-shaped papilla reach at least 1100 μm in length. The ring of the light-staining cells confluent with the papilla is less pronounced (Figure 2, **lsc**). The pseudostratified epithelium lining the valve forms two different zones. The anterior zone, rather narrow and adjoining the cone-shaped papilla is stained very dark blue (Figure 2, **pse**) and similar in histology and staining properties to that of *Nassarius luteostoma*. This type of epithelium is sharply replaced by light staining columnar epithelium, composed of two types of cells. The first one extends from basement membrane to the lumen (Figure 2, **lpsc**), bears cilia, and has small nuclei that are located close to the apical tip. The second type of cells extends to approximately 2/3 the height of the tissue layer, and does not reach the lumen. Their nuclei are situated in the basal 1/3 of the cytoplasm. This type of epithelium occupies a much longer zone of the valve and adjoining part of the mid-esophagus, so that in total it is three times as long as the expanded part of the valve proper.

The outer surface of the valve has an extremely thin layer of muscle fibers and no connective tissue.

Muricidae

*Muricanthus radix* (Gmelin 1798)
(Figures 3–5)

**Material Examined:** Two specimens sectioned, Panama, Pacific Ocean: Venado Island, on rocks at low tide, 08°52'48.6" N, 79°35'36.9" W, coll. Yu. Kantor, 2006.

The valve is large, pear-shaped, 3.5 times as broad as the anterior esophagus, situated immediately in front of the nerve ring. The columnar ciliated epithelium, lining the anterior esophagus, is sharply replaced by very tall columnar epithelium at the entrance to the valve. These tall epithelial cells form the large cone-shaped papilla with broad lumen. The cells on the top and external wall of the papilla bear long cilia (Figure 5, **cil**), around 750 μm in length. The mucous pad at the base of papilla is absent. The thickened part of the valve is composed of tall, columnar, folded ciliated epithelium (Figure 3, **cle**). Due to the staining properties, the nuclei were not seen.

The location of torsion is seen from the exterior, lies in the middle of the valve. The dorsal groove of the anterior esophagus interrupts the cone-shaped papilla and can be traced along the entire valve length (Figure 4, **dg**).

The outer surface of the valve has a very thin layer of muscle fibers (in contrast to the relatively thick layers of longitudinal and circular muscles that form the wall of the anterior esophagus) and no connective tissue.

Conidae, Raphitominae

*Paramontana rufozonata* (Angas, 1877)
(Figures 6–8)

**Material Examined:** One specimen sectioned, Western Australia, Rottnest Island, Cape Vlamingh, intertidal rocks, coll. J.D. Taylor, 1996.

The valve of Leiblein is very small, funnel-shaped, situated immediately posterior to the buccal mass and in front of the nerve ring. It is about twice as broad as the esophagus. The wall of the valve consists of a single layer of ciliated epithelial cells, slightly taller cells form the cone-shaped papilla. These cells bear long cilia (around 120 μm in length). No other structures can be recognized within the valve.

Cancellariidae

*Plesiotriton vivus* Habe and Okutani, 1981
(Figures 9–10)

**Material Examined:** Two specimens sectioned, Philippines, Bohol/Sulu seas, R/V DA-BFAR, PANGLAO 2005 Deep-Sea Cruise, st. CP 2359, 8°49.9' N, 123°34.9' E, 437–476 m.

The enlargement of the esophagus (Figure 9, **vl**), which was recognized as the valve of Leiblein by Graham (1966), lies immediately posterior to the buccal mass in the anterior part of the extremely long, coiled proboscis, and is partially covered by the tubular salivary glands. The structure is coiled, forming at least two complete whorls, meaning that this is not a site of torsion (where the rotation of the esophagus would not exceed 180°). Through the semi-transparent walls of the valve, the narrow strip of opaque white tissue running along the entire length of the valve is clearly seen. On external view, it looks similar to the ring of tall, ciliated light-staining cells (= the mucous pad) in the valve of other neogastropods.

In histological sections, this strip is represented by light-staining, low, non-ciliated, large epithelial cells with large, oval nuclei. The remaining wall of the valve is lined with very tall pseudostratified ciliated epithelium, composed of two cells types. Cells of the first type extend from the basement membrane to the lumen, bear cilia, and have small, narrow, elongated nuclei that are located in the upper 1/3 of the cytoplasm. Cells of the second type do not reach the lumen and have rounded nuclei that are situated in the basal most part of the cytoplasm. The cone-shaped papilla is absent. The dorsal groove and folds were clearly seen within the valve. The relatively broad lumen of the valve was filled with blue-staining secretion.

The outer surface of the valve has a very thin layer of muscle fibers (in contrast to the relatively thick layers of longitudinal and circular muscles that form the wall of the anterior esophagus) and hardly any connective tissue.

Olividae

*Oliva bulbosa* (Röding, 1798)
(Figures 11–12)
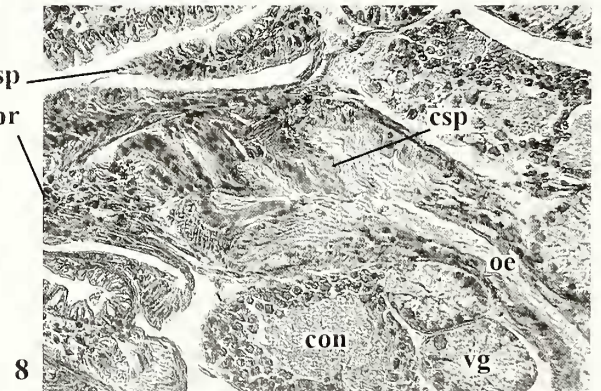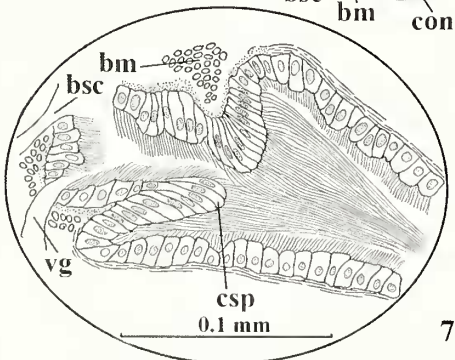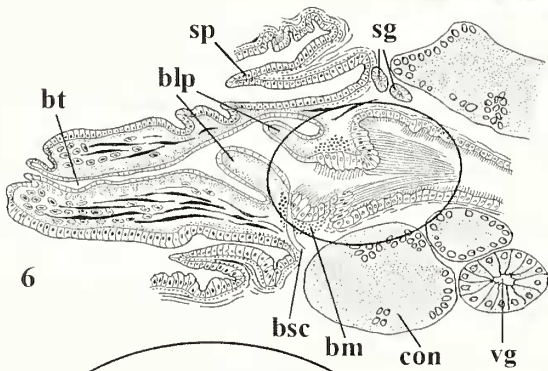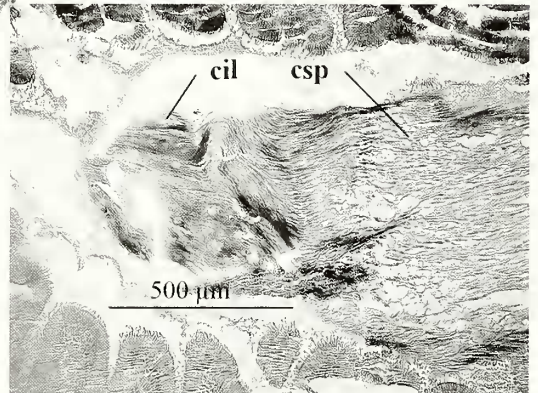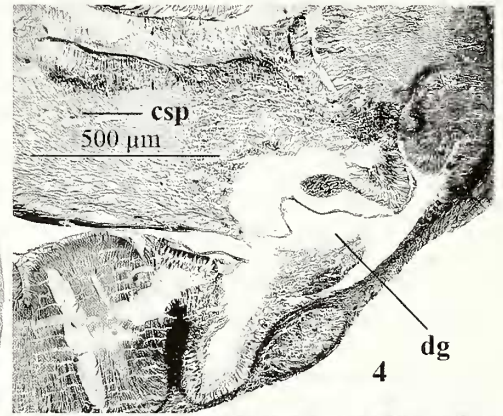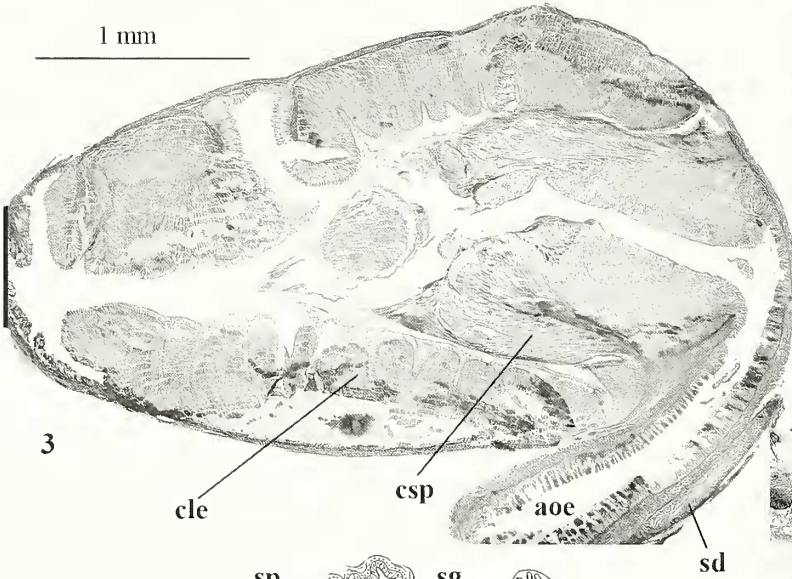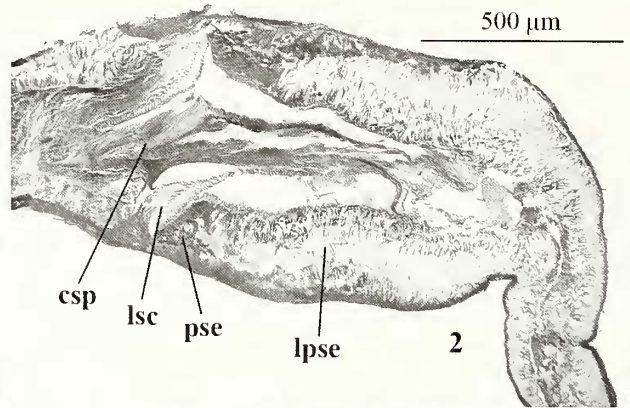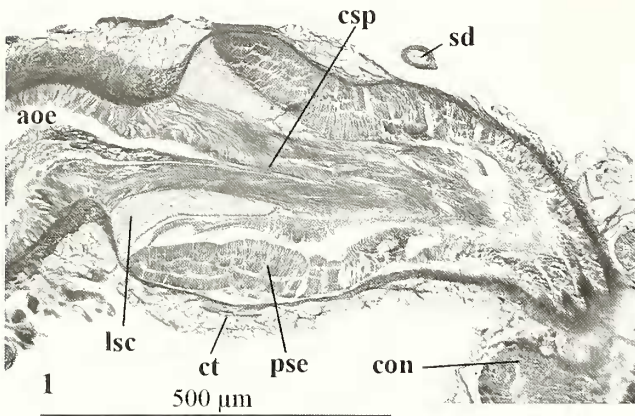
**Material Examined:** One specimen sectioned, Aden Bay, sandy beach 6 km west of Aden; Red Sea, coll. D. Ivanov.

The valve is large, at least 3.5 times as broad as the esophagus, pear-shaped, and situated immediately in front of the nerve ring. The cone-shaped papilla (Figure 11, **csp**) is lined by columnar ciliated epithelium which is continuous with that of the anterior esophagus. The cells on the top of the papilla bear long cilia about 200 μm in length (Figure 12, **cil**). Probably due to the contraction of the papilla, its inner lumen was not observed. At the base of the papilla there is a ring of tall extremely light-staining cells confluent with the papilla (Figure11, **lsc**). The thickened part of the valve is composed of pseudostratified columnar ciliated epithelium (Figure 11, **pse**). The cells are stained dark blue. No traces of the dorsal folds of the anterior esophagus were found inside the valve. The outer surface of the valve has an extremely thin layer of muscle fibers.

## DISCUSSION

Morphological Comparisons of the Valve of Leiblein Among Different Lineages of Neogastropoda: Graham (1941) described the significant differences in the foreguts of *Nucella* and *Buccinum*, and suggested their independent origins from different groups because they exhibit different positions of torsion in the mid-esophagus. In *Nucella*, torsion occurs within the valve, while in *Buccinum* the position of torsion is posterior to the nerve ring. Ponder (1974) did not consider the position of torsion to be of great importance, and did not dispute the homology of the valve. At the same time he pointed out the significant differences among taxa in the position of the valve relative to the buccal mass. While in most of the Neogastropoda the valve lies immediately in front of the nerve ring, in Cancellarioidea it is situated just behind the buccal cavity, with the mid-esophagus positioned in front of the nerve ring (Graham, 1966).

The data presented confirm the significant morphological variability of the "valve of Leiblein" found in different lineages of the Neogastropoda. The most-divergent "valve" from the few described in literature was found in *Plesiotriton* (Cancellariidae), in which it is coiled and forms at least two complete whorls. The cone-shaped papilla and the ciliary valve are completely absent (Figures 9–10). The way in which it functions is unclear. The position of the valve itself in the most-anterior part of

the proboscis is unusual for the Neogastropoda, but its position in relation to the buccal mass is similar to that in Conoidea.

In the remaining families studied, the valve of Leiblein demonstrates a higher degree of similarity, being pear-shaped and possessing the cone-shaped papilla either formed by or lined with epithelium with very long cilia, varying from 120 μm (*Paramontana rufozonata*) to 1100 μm (*Triumphis distorta*) in length. In relation to the circumoesophageal nerve ring the valve in adults is always positioned in front of the ring. The other character common to all the studied species is that the walls of the valve lack any substantial muscle layer, unlike the walls of the adjoining part of the esophagus.

Within Conoidea presence of a valve was recorded only in two species, *Paramontana rufozonata* and *Kermia barnardi* (Brazier, 1878) (Kantor and Taylor, 2002). Both species have a valve of very similar structure, which is formed by only a single layer of cells. It should be noted that these species are characterized by a very small shell (less then 5 mm). Therefore the valve seems to be very much simplified due to the minute size of the mollusks.

Some significant differences can be found among the valves studied to date, mostly in the presence/absence of the dorsal groove of the anterior esophagus within the valve. It can be clearly observed in nearly all families studied—Muricidae, Cancellariidae, Volutidae (Ponder, 1970), Costellariidae (Ponder, 1972), and Volutomitridae (Kantor and Harasewych, 1992). It is absent in studied Buccinoidea, including Fasciolariidae (Marcus and Marcus, 1962), as well as in Olividae and Conidae (our data). Another difference among valves has to do with the position of the valve in relation to the site of the torsion. Torsion is situated posterior to the valve in all taxa except Muricidae. We were not able to trace the torsion site in Conidae due to the minute size of the animal.

Another difference observed was the presence/absence of the ring of the ciliated light-staining cells (mucous pad). It was mentioned for every studied species possessing the valve of Leiblein, but surprisingly it was absent in *Muricanthus* (although present in *Nucella*). It was similarly absent in two species of Conidae.

Development of the Valve in Ontogeny: These differences observed in the histology of the valve of Leiblein prompted us to check whether its development is identical in the embryogenesis of different neogastropod lineages.

**Figures 1–8.** The valve of Leiblein. **1.** *Nassarius luteostoma* Broderip and Sowerby, 1829, longitudinal section through the valve. **2.** *Triumphis distorta* (Wood, 1828), longitudinal section through the valve. **3–5.** *Muricanthus radix* (Gmelin, 1791). **3.** Longitudinal section through anterior esophagus and valve. **4.** Enlarged fragment of the longitudinal section showing the dorsal groove of the anterior esophagus interrupting the cone-shaped papilla. **5.** The tip of the cone-shaped papilla showing the long cilia. **6–8.** *Paramontana rufozonata* (Angas, 1877). **6.** Semi-diagrammatic longitudinal section through proboscis, buccal mass, and valve. **7.** Enlarged semi-diagrammatic section through the valve. **8.** Histological section through the valve. Abbreviations: **aoe,** anterior esophagus; **blp,** buccal lips; **bm,** buccal mass; **bsc,** buccal sac; **bt,** buccal tube; **cil,** cilia; **cle,** columnar folded ciliated epithelium; **con,** circumoesophageal nerve ring; **csp,** cone-shaped papilla; **ct,** connective tissue; **dg,** dorsal groove; **lpse,** light staining columnar epithelium; **lsc,** light-staining cells; **pse,** pseudostratified epithelium; **sd,** salivary duct; **sg,** salivary gland; **sp,** septum of the rhynchocoel; **vg,** venom gland.
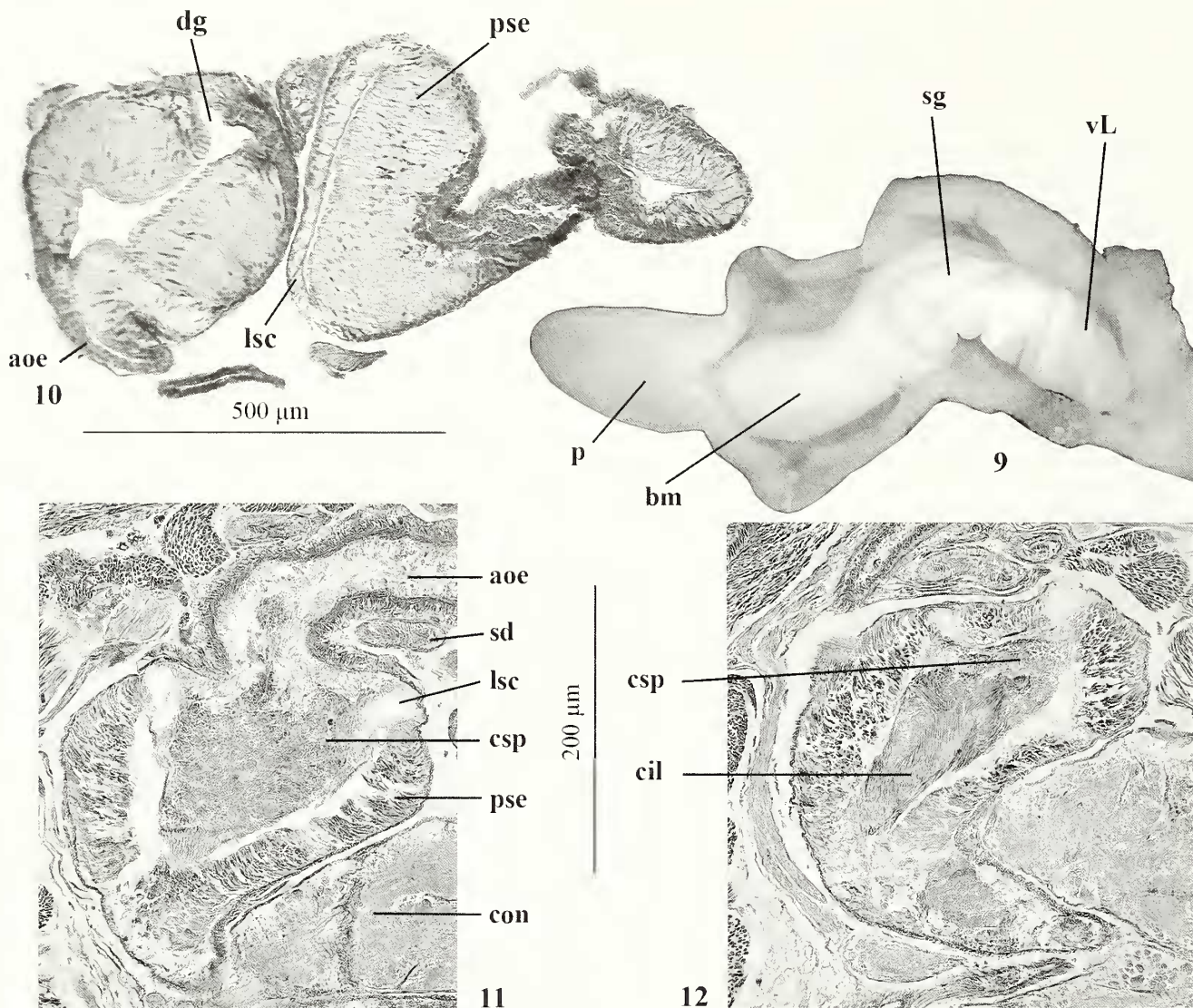
**Figures 9–12.** Valve of Leiblein. **9–10.** *Plesiotriton vivus* Habe et Okutani, 1981. **9.** Anterior part of the proboscis dissected to show the position of the valve in relation to the buccal mass. **10.** Longitudinal section through the anterior esophagus and the coils of the valve. **11–12.** *Oliva bulbosa* (Röding, 1798). **11.** Longitudinal section through anterior esophagus and valve. **12.** Longitudinal section through valve and mid-esophagus, showing the long cilia of the cone-shaped papilla. Abbreviations: **p,** proboscis; **vL,** valve of Leiblein. Other abbreviations see in captions to Figures 1–8.

There is very little published data on the development of the valve of Leiblein in ontogeny. Ball et al. (1997a, b) examined the ontogeny of the foregut in *Nucella lapillus* (Figures 13–15).

Abro (1969) (summarized by Fretter, 1969) examined the embryology of *Nassarius incrassatus* (Ström, 1768) and *N. reticulatus* (Linnaeus, 1758) (Nassariidae). Page (2005) re-examined the development of the foregut and proboscis in a different nassariid species, *Nassarius mendicus* (Gould, 1850) with planktotrophic larvae and illustrated it by a series of outstanding photographs. We complemented the data on the Nassariidae by observations of direct developing embryos of *Buccinum undatum*.

Published and original data on the embryonic development of the valve in Buccinidae and Muricidae demonstrated that it originates from different sections of the anterior foregut. From the diagrams of Ball et al. (1997a, b), it is obvious that in *Nucella*, the buccal mass with the radula originated from the ventral outpocketing of the esophagus during the early stages of proboscis formation (Figure 13). The valve of Leiblein appeared in the next stage (Figure 14), as development of the esophagus posterior to the nerve ring. Later, the progressive elongation of the proboscis pulls the salivary glands, radular sac, and the valve through the nerve ring into their final positions (Figure 15). Thus, the valve is formed as part of the anterior larval esophagus.
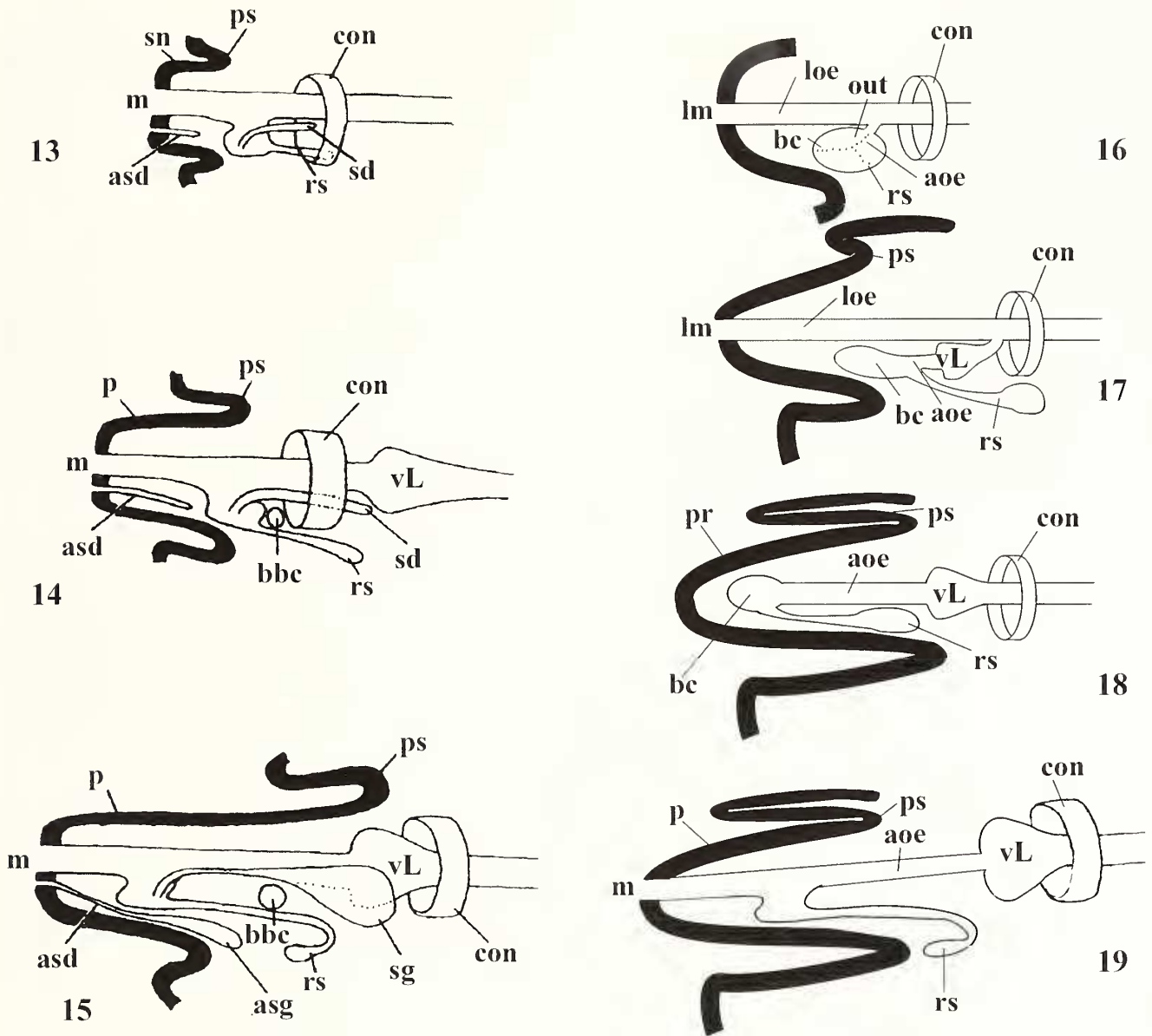
**Figures 13–19.** Diagrammatic lateral view of the development of the foregut and proboscis. **13–15.** *Nucella lapillus* (after Ball et al., 1997a, b, modified). **13.** Stage 6, the buccal mass has developed. **14.** Stage 7, the valve of Leiblein lies posterior to the cerebral commissure. **15.** Stage 8, the valve of Leiblein, acinous salivary glands, and the radular sac lie anterior to the nerve ring. **16–19.** Selected stages of the foregut development in Buccinoidea (based on Page, 2005, on *Nassarius mendicus* (Gould, 1850) and observations on *Buccinum undatum*). Salivary glands are omitted for simplicity. **16.** Formation of the ventral outpocketing. **17.** Formation of buccal cavity, anterior esophagus, valve of Leiblein, and radular sac. Larval esophagus still open. **18.** Larval esophagus resorbed, larval mouth opening is sealed. **19.** Postmetamorphic new mouth is formed. Abbreviations: **asd,** duct of accessory salivary gland; **asg,** accessory salivary gland; **bbc,** buccal commissure; **bc,** buccal cavity; **lm,** larval mouth; **loe,** larval esophagus; **m.** mouth; **out,** outpocketing; **ps,** proboscis sheath; **sn,** snout. Other abbreviations as in captions to Figures 1–12.

The situation with Nassariidae and *Buccinum* differs significantly. In these groups, the larval esophagus is initially a ciliated tube that extends from the mouth to the stomach. A patch of enlarged, non-ciliated cells is embedded within the ventral wall of the distal larval esophagus and forms an outpocketing (Figure 16, 20–21). Eventually, the outpocketing will enlarge and become extensively elaborated to form the entire post-metamorphic foregut. At first, the future buccal cavity, radular sac, and valve of Leiblein form from different chambers of the original outpocketing (Figures 17, 22–23). With the enlargement of these structures as well as elongation of the proboscis, dramatic changes take place. Most notable among these events are the complete occlusion of the larval mouth and the degeneration and loss of the distal larval esophagus between the larval mouth and the point
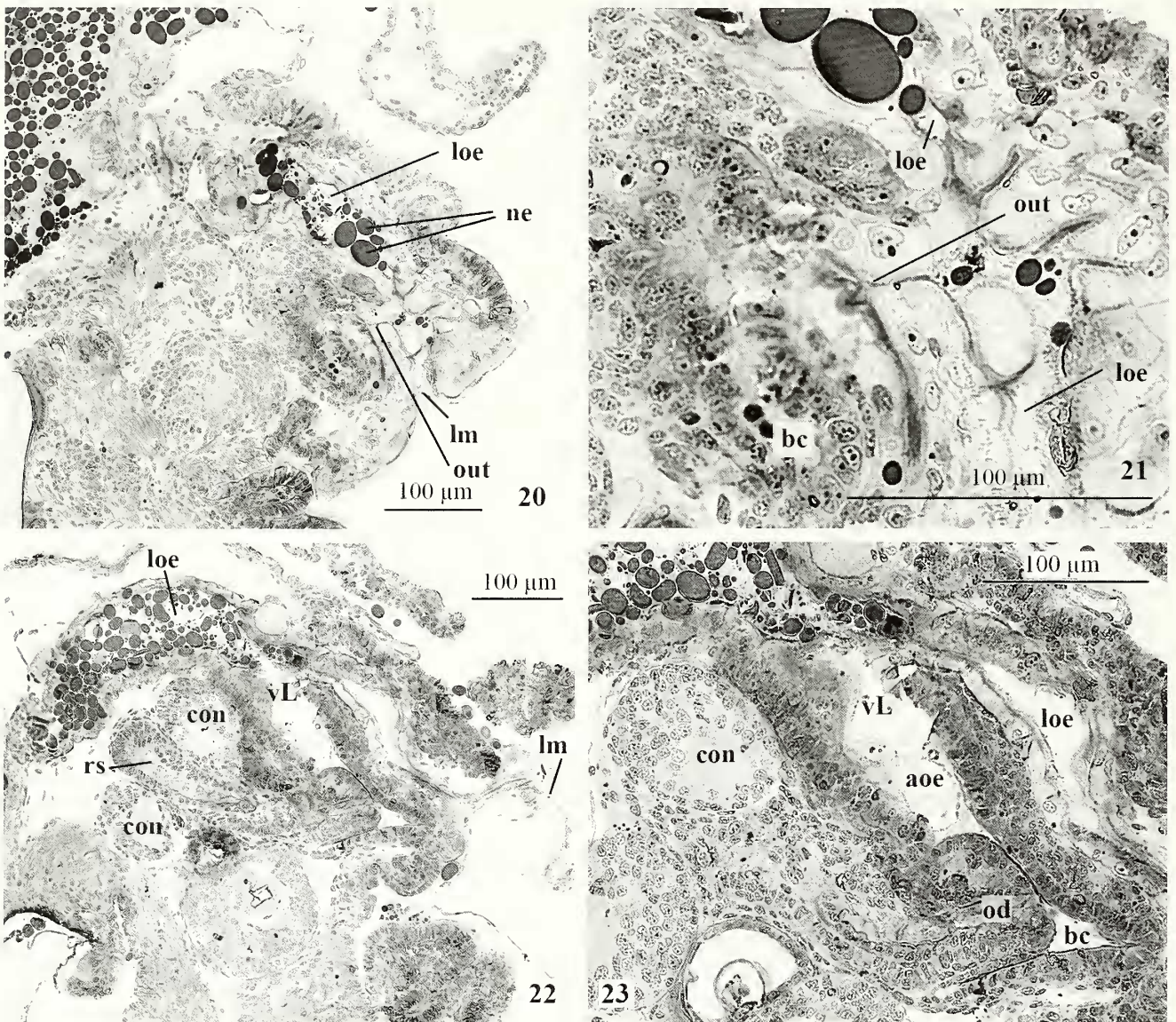
**Figures 20–23.** Selected stages of development of *Buccinum undatum*. **20.** Mid-sagittal section through a larva. Ventral outpocketing formed. The stage corresponds to Figure 16. **21.** Enlarged region of Figure 20. **22–23.** Formation of buccal cavity, anterior esophagus, valve of Leiblein, and radular sac. Larval esophagus still open. The stage corresponding to Figure 17. **23.** Enlarged regiont of Figure 22. Abbreviations: **ne,** nurse eggs; **od,** odontophore. Other abbreviations see in captions to Figures 1–19.

where the post-metamorphic foregut extends from the ventral side of the larval esophagus (Figure 18). Later, the new definitive mouth ruptures through the transient epithelial seal that formed over the larval mouth (Figure 19) (Page, 2005, figs. 2 B, C). Thus the overall similarity of adult foreguts of Buccinoidea and Muricidae in fact is achieved through very different processes. We want to emphasize that the radular apparatus in both stems originates from homologous structures—the ventral outpocketings of the esophagus. In contrast, the "valve" originated from different parts of the foregut—from the posterior chamber of ventral outpocketing in Buccinidae and part of the anterior larval esophagus in Muricidae.

Our attempts to examine the entire development of the foregut in embryos of *Buccinum undatum* failed due to asynchronous development of the embryos even within the same egg cluster and egg capsules. Therefore it was not possible to obtain the embryos on consequent developmental stages with any reliable timing. Nevertheless, we were able to observe the early stages which roughly corresponded to approximate halfway point of obligatory larval development (21 days post-hatching) in *Nassarius mendicus* (Page, 2005).

The major difference between studied nassariids and *Buccinum* is that the nassariids are characterized by feeding planktonic larvae, while *Buccinum* has direct development, feeding on nurse eggs inside the egg capsule and

hatching in the crawling stage. The nurse eggs are consumed in rather early stages, and are clearly seen in the larval esophagus (Figures 20–2, ne). We have not observed the stage with the degenerated larval esophagus, but have seen an example of the strongly differentiated initial outpocketing giving rise to the radular sac, in which the radular teeth were seen, and the buccal mass with odontophore and future anterior esophagus with valve of Leiblein was situated in exactly the same position as in *N. mendicus* (Figures 22–23). Therefore, it is presumed that the development of the valve in *Buccium undatum* is analogous to that in *Nassarius*.

It should be emphasized that the development of the valve seems to be unrelated to the mode of embryogenesis. Similar developmental patterns were found in related species with planktotrophic (*Nassarius*) and lecitotrophic larvae (*Buccinum*), while unrelated species with lecitotrophic larvae (*Buccinum* and *Nucella*) differed in the development of the valve. Both *Buccinum* and *Nucella* feed on the nurse eggs during the first stages of the development (Fretter and Graham, 1962).

Our preliminary data demonstrated significant differences in the morphology of the valve of Leiblein in different groupings of Neogastropoda, and different origins of the valve during embryogenesis, at least in Muricidae and Buccinidae. This suggests that, despite the superficial similarity, the homology of the valve of Leiblein within Neogastropoda is at best questionable.

If this supposition is correct, then Buccinoidea do not share any of the previously hypothesized autapomorphies with the rest of neogastropods. This raises the prospect of a paraphyletic Neogastropoda that includes two stems, one including the Buccinoidea, the other containing the remaining neogastropod families.

## ACKNOWLEDGMENTS

## LITERATURE CITED

Abro, A.M. 1969. Studies in the functional anatomy of some British monotocardian veligers, with observations on the musculature of the buccal mass of *Littorina littorea* (L.). Ph.D. dissertation, University of Reading, Berkshire, UK.

Amaudrut, A. 1898. La partie antérieure de tube digestif et le torsion chez les mollusques gastéropodes. Annales des Sciences naturelles, 8ᵉ series, Zoologie 7: 1–291, pls. 1–10.

Andrews, E.B. and K.E. Thorogood. 2005. An ultrastructural study of the gland of Leiblein of muricid and nassariid Neogastropods in relation to function, with a discussion on its homologies in other Caenogastropods. Journal of Molluscan Studies 71: 269–300.

Ball, A.D., E.B. Andrews, and J.D. Taylor. 1997a. The ontogeny of the pleurembolic proboscis: *Nucella lapillus* (Gastropoda: Muricoidea). Journal of Molluscan Studies 63: 87–95.

Ball, A.D., J.D. Taylor, and E.B. Andrews. 1997b. Development of the acinous and accessory salivary glands in *Nucella lapillus* (Gastropoda: Muricoidea). Journal of Molluscan Studies 63: 245–260.

Brock, F. 1936. Suche, Aufnahme und enzymatische Spaltung der Nahrung durch die Wellhornschnecke *Buccinum undatum* L. Zoologica, Stuttgart 34(92): 1–136 (not seen).

Brown, S.C. 1969. The structure and function of the digestive system of the mud snail *Nassarius obsoletus* (Say). Malacologia 9: 447–500.

Colgan, D.J., W.F. Ponder, and P.E. Eggler. 2000. Gastropod evolutionary rates and phylogenetic relationships assessed using partial 28S rDNA and histone H3 sequences. Zoologica Scripta 29: 29–63.

Colgan, D.J., W.F. Ponder, E. Beacham, and J.M. Macaranas. 2003. Molecular phylogenetic studies of Gastropoda based on six gene segments representing coding or noncoding and mitochondrial or nuclear DNA. Molluscan Research 23: 123–148.

Colgan, D.J., W.F. Ponder, E. Beacham, and J.M. Macaranas. 2007. Molecular phylogenetics of Caenogastropoda (Gastropoda: Mollusca). Molecular Phylogenetics and Evolution 42: 717–737.

Fretter, V. 1969. Aspects of metamorphosis in prosobranch gastropods. Proceedings of the Malacological Society of London, 38: 375–385.

Fretter, V. and A. Graham. 1962. British Prosobranch Molluscs. Ray Society, London, xvi + 755 pp.

Golikov, A.N. and Ya.I. Starobogatov. 1988. Problems of phylogeny and system of the prosobranchiate gastropods. Proceedings of the Zoological Institute, Leningrad 187: 4–77 [In Russian].

Graham, A. 1941. The oesophagus of the stenoglossan prosobranchs. Proceedings of the Royal Society of Edinburgh, series B, 61: 1–23.

Graham, A. 1966. The fore-gut of some marginellid and cancellariid prosobranchs. Studies in Tropical Oceanography, Miami, 4: 134–151.

Harasewych, M.G., S.L. Adamkewicz, J.A. Blake, D. Saudek, T. Spriggs, and C.J. Bult. 1997. Neogastropod phylogeny: A molecular perspective. Journal of Molluscan Studies 63: 327–351.

Kantor, Yu. I. 2002. Morphological prerequisites for understanding Neogastropod phylogeny. In: M. Oliverio and R. Chemello (eds). Systematics, Phylogeny and Biology of the Neogastropoda. Bollettino Malacologico, Supplement 5: 2–15.

Kantor, Yu.I. and M.G. Harasewych. 1992a. Morphology of the digestive system of *Volutomitra alaskana* Dall, 1902 (Gastropoda, Pectinibranchia, Volutomitridae), with notes on the possible mechanism of feeding. Ruthenica, Russian Malacological Journal 2(1): 27–35.

Kantor, Yu.I. and J.D. Taylor. 2002. Foregut anatomy and relationships of raphitomine gastropods (Gastropoda:

Conoidea: Raphitominae). In: M. Oliverio and R. Chemello (eds). Systematics, Phylogeny and Biology of the Neogastropoda. Bollettino Malacologico, Supplement 5: 161–174.

Marcus, E. and E. Marcus. 1962. On *Leucozonia nassa*. Boletim da Facultade de Filosofia, Ciências e Letras, Universidade de São Paulo, 261, Zoology 24: 11–30.

McArthur, A.C. and M.G. Harasewych. 2003. Molecular systematics of the major lineages of the Gastropoda. In: C. Lydeard and D.R. Lindberg (eds.). Molecular Systematics and Phylogeography of Mollusks. Smithsonian Books, Washington, pp. 140–160.

Page, L.R. 2005. Development of foregut and proboscis in the buccinid neogastropod *Nassarius mendicus*: evolutionary opportunity exploited by a developmental module. Journal of Morphology 264: 327–338.

Ponder, W.F. 1970. The morphology of *Alcithoe arabica* (Mollusca: Volutidae). Malacological Review 3: 127–165.

Ponder, W.F. 1972. The morphology of some mitriform gastropods with special reference to their alimentary and reproductive systems (Neogastropoda). Malacologia 11: 295–342.

Ponder, W.F. 1974. Origin and evolution of the Neogastropoda. Malacologia 12: 295–338.

Ponder, W.F., D.J. Colgan, J.M. Healy, A. Nützel, L.R.L. Simone, and E.E. Strong. 2008. Caenogastropoda. In: W. F. Ponder and D.R. Lindberg (eds.). Phylogeny and Evolution of the Mollusca. University of California Press, Berkeley: 331–383.

Ponder, W.F. and D.R. Lindberg. 1997. Towards a phylogeny of gastropod molluscs — an analysis using morphological characters. Zoological Journal of the Linnean Society 119: 83–265.

Riedel, F. 1994. Recognition of the superfamily Ficoidea Meek 1864 and definition of the Thalassocynidae fam. nov. (Gastropoda). Zoologische Jahrbucher, Abteilung für Systematik, Geographie und Biologie der Tiere 121: 457–474.

Riedel, F. 2000. Ursprung und Evolution der "höheren" Caenogastropoda. Berliner Geowissenschaftliche Abhandlungen E 32: 1–240, 21 Tafeln.

Sheridan, R., J.J. Van Mol, and J. Bouillon. 1973. Étude mophologique du tube digestif de quelques Turridae (Mollusca-Gastropoda-Prosobranchia-Toxoglossa) de la région de Roscoff. Cahiers de Biologie Marine 14: 159–188.

Shimek, R.L. and A.J. Kohn. 1981. Functional morphology and evolution of the toxoglossan radula. Malacologia 20: 423–438.

Strong, E.E. 2003. Refining molluscan characters: morphology, character coding and a phylogeny of the Caenogastropoda. Zoological Journal of the Linnean Society 137: 447–554.

Taylor, J.D. and N.J. Morris. 1988. Relationships of Neogastropoda. Malacological Review, Supplement 4: 167–179.