



# Morphological prerequisites for understanding neogastropod phylogeny

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**ABSTRACT** Analysis of anatomy confirms that the neogastropods are a clade, for which monophyly is supported by several apomorphies and common characters, nearly all of which confined to the anterior foregut. The most primitive neogastropods are characterised by short proboscis with the basal buccal mass and with odontophoral and radular muscles passing through the nerve ring and joining the columellar muscle. None of the existing theories on neogastropod evolution (Amaudrut, 1898; Ponder, 1974; Golikov & Starobogatov, 1988; Ponder & Lindberg, 1997; Riedel, 2000) adequately describes the origin and radiation of the group. The potential sister group of Neogastropoda should be found among carnivorous groups of Sorbeoconcha with underived foregut. The Tonnoidea are unlikely a sister group of the neogastropods.

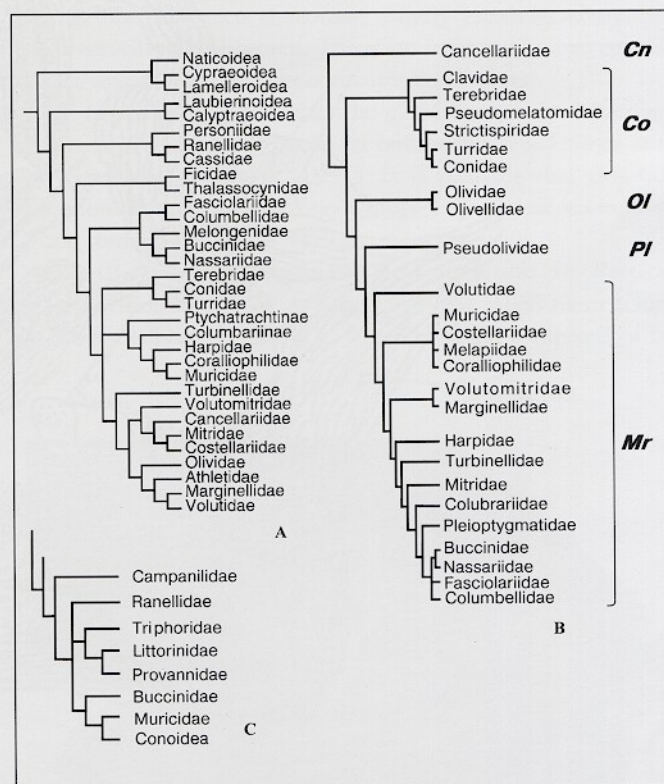
**RIASSUNTO** L'analisi dei dati anatomici disponibili conferma che i neogasteropodi sono un clado, la cui monofilia è supportata da diverse apomorfie e caratteri comuni, principalmente riguardanti la porzione anteriore del canale digerente. I neogasteropodi più primitivi sono caratterizzati da una proboscide corta con la massa boccale basale e con i muscoli odontoforale e radulare uniti al muscolo columellare e passanti attraverso l'anello nervoso. Nessuna delle teorie sinora proposte per l'evoluzione dei neogasteropodi (Amaudrut, 1898; Ponder, 1974; Golikov & Starobogatov, 1988; Ponder & Lindberg, 1997; Riedel, 2000) descrivono adeguatamente l'origine e la radiazione del gruppo. Il potenziale sister-group dei Neogastropoda dovrebbe essere ricercato tra i gruppi carnivori dei Sorbeoconcha con un apparato alimentare anteriore relativamente non modificato. I Tonnoidea sono probabilmente poco plausibili come sister-group dei neogasteropodi.

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## INTRODUCTION

The past decade witnessed significant progress in studies of the Neogastropoda, including the anatomy of various groups, ultrastructure, ontogeny and molecular phylogeny. Among most important, can be mentioned the publications of BALL *et al.* (1997, 1997a) on the ontogeny of different structures of the digestive system in the postveliger stages of *Nucella*, the publication of HARASEWYCH *et al.* (1997) on the molecular phylogeny of neogastropods, the series of studies of different groups of Conoidea (KANTOR & TAYLOR, 1991; TAYLOR, KANTOR & SYSOEV, 1993) and many others. Nevertheless, the phylogenetic hypotheses of the radiation of the Neogastropoda as well as the relationships with other prosobranchs are still the subject of different speculations. Although there are few published comparable phylogenetic schemes for Neogastropoda, we can see major differences in these recently proposed hypotheses of neogastropod evolution, namely those of KANTOR (1996), PONDER & LINDBERG (1997) and RIEDEL (2000) (Figure 1). There are major differences in opinions on the position of most families, as well as in the treatment of characters and character states.

The differing opinions on the neogastropod evolution are likely the result of high rate of homoplasy within the neogastropods. Numerous lineages (20+ families) proliferated rapidly during the Cretaceous, with tendencies to modify organ systems in parallel fashions in many of them (HARASEWYCH *et al.*, 1997). As a consequence, relatively few morphological characters originating during the initial radiation can be identified. Therefore, cladistic analysis of the families and major groupings relationships is often unsatisfactory, with very poor resolution (eg. KANTOR, 1996).



**Figure 1.** Phylogenetic hypothesis of the Neogastropod relationships. A — after RIEDEL (2000) (combined by M.G.Harasewyh). B — after KANTOR (1996). CN — suborder Cancellarioidae, CO — suborder Conoidei, OL — suborder Olivelloidei, PL — suborder Pseudolivoidae, MR — suborder Muri-coidei. C — after Ponder & Lindberg (1997) (modified).



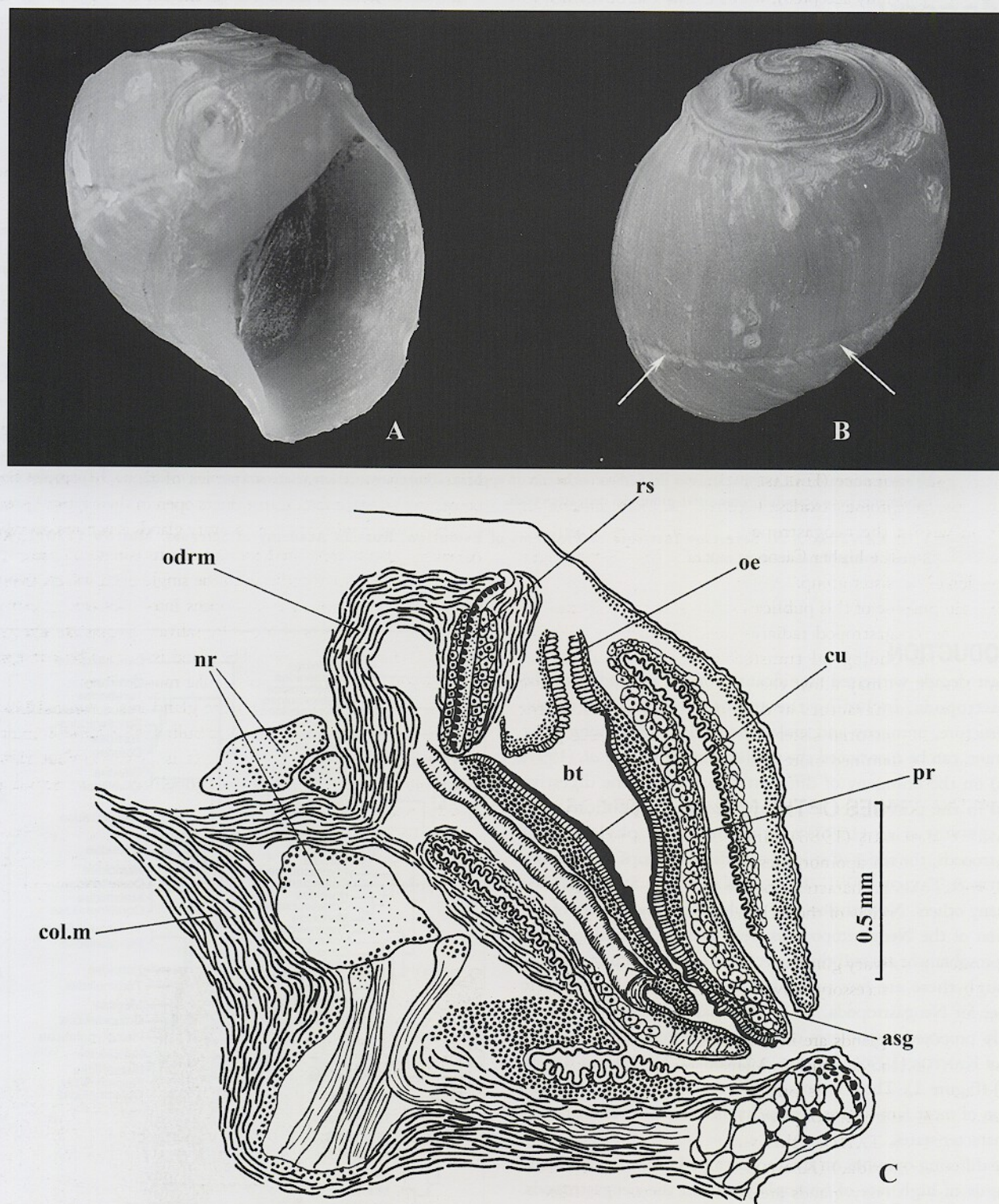


Figure 2. *Benthobia tryoni* Dall, 1889 (Pseudolividae). Eastern Atlantic, 19°45'N, 18°21'E, 2850 m [after KANTOR, 1991]. A, B — apertural and dorso-lateral views of the shell, shell length 8.6 mm. Arrows on B shows the spiral sulcus. C — semidiagrammatic longitudinal section through the anterior foregut. Abbreviations: asg — accessory salivary gland; bt — buccal tube; col.m — columellar muscle; cu — cuticular lining of the buccal tube; nr — nerve ring; odrn — odontophoral retractor; oe — oesophagus; pr — proboscis; rs — radular sac.





Finally, there are certain families of Neogastropoda (although sometimes not generally accepted), which hardly can be defined in cladistic terms, since they lack autapomorphies, e.g. family Pseudolividae. This family is still often considered as subfamily of Olividae (e.g. SMITH, 1998), but in my opinion definitely deserves familial status and is not closely related to any Olividae (KANTOR, 1991). This family is readily distinguished by a combination of some anatomical characters — short proboscis with the buccal mass situated at its base, the passage of the odontophoral retractors through the nerve ring, the presence of an accessory salivary gland (Figure 2C) together with the presence of the spiral sulcus on the body whorl (Figure 2 B, arrows indicate the spiral sulcus). None of these characters are autapomorphies of Pseudolividae and are found in other neogastropods. For example the spiral sulcus is also present in genus *Ceratoxancus* Kuroda, 1952 (subfamily Ptychatractinae, Turbinellidae) (KANTOR & BOUCHET, 1997).

The molecular phylogeny encounters the similar problems. Thus, the analysis of the 18s rDNA cannot resolve the Neogastropoda as a clade, since the rapid adaptive radiation of the neogastropods is probably below the limits of resolution even of the entire gene sequence (HARASEWYCH *et al.*, 1997). On the contrary, the cytochrome *c* oxidase I seem to be more suitable for resolution within the neogastropods, but not very useful for general analysis of the higher Caenogastropoda, thus leaving open the question of the sister group.

The main purpose of this publication is to summarise existing hypotheses on neogastropod radiation and to show the possible sequence of morphological transformations of the digestive system. The latter may allow the definition of plesiomorphic states for some characters and thus may give a clue for determining the potential sister groups of the Neogastropoda, which should be examined more carefully.

## SYNAPOMORPHIES OF THE NEOGASTROPODA

TAYLOR and MORRIS (1988) summarised and provided an analysis of the main apomorphies of the neogastropods. They listed the following characters (below I will provide the brief morphological overview of these characters):

### 1) Two pairs of salivary glands.

Both primary and accessory salivary glands have rather variable morphology.

Primary salivary glands are in most cases acinous, but may be tubular in some Conoidea, such as Mangeliinae and Raphitomininae (family Conidae — in this publication the classification of Conoidea, proposed by TAYLOR *et al.*, 1993 is used) (TAYLOR *et al.*, 1993; KANTOR & TAYLOR, this volume) and few species of Crassispirinae (Turridae) (KANTOR, MEDINSKAYA & TAYLOR, 1997). Primary salivary glands are absent in some Conoidea, in which the venom and radular apparatus are absent (TAYLOR *et al.*, 1993; TAYLOR, 1990). In most cases the glands are paired. In some Buccinidae and Buccinulidae the glands are fused without a visible border, but still retain the paired ducts, e.g. *Habevolutopsius* (KANTOR, 1990), *Chlanidota* (HARASEWYCH & KANTOR, 1999). The ducts of the glands (when present) enter the buccal cavity near the entrance of the radular diverticulum into the buccal cavity and

are always lined with ciliated epithelium.

In radular-less Coralliophilidae the initially paired ducts fuse together and the unified duct passes dorsally to the anterior oesophagus towards its opening into the buccal tube (WARD, 1965; KANTOR, 1995). In some groups, e.g. all Conoidea and Cancellariidae the ducts are short, free along their length (TAYLOR *et al.*, 1993; GRAHAM, 1966). On the contrary, in the majority of Muricoidea (sensu PONDER, 1974) the ducts, after leaving the glands soon become “embedded” into the walls of the anterior oesophagus (usually just in front of the valve of Leiblein), which they follow towards their opening. In Buccinoidea (which usually possess long or very long proboscis) there is an intermediate situation — the ducts are free along most of their length (although usually are attached to the oesophagus by numerous connective tissue fibres) and enter the walls of the anterior oesophagus close to their opening.

Finally, in Mitridae the ducts enter epiproboscis and open at its tip (PONDER, 1972). The epiproboscis (an autapomorphy of the family) is a muscular rod, situated in its own sheath and able to protrude through the mouth opening. In at least one species of Mitridae (a still unnamed species of *Eumitra*, unpublished), possessing an epiproboscis, the ducts open in their typical position.

The situation with accessory salivary glands is not less complicated. Accessory glands are paired tubular organs (single in some species) with ducts that fuse together into the single duct, which then passes ventrally to the oesophagus and opens into anteriormost part of the buccal tube. The ducts of accessory salivary glands are always lined with non-ciliated epithelium. The gland is formed by two epithelial layers, separated by thin layer of circular muscle fibres.

In *Benthobia* (Pseudolividae) the gland has a normal histology, but possesses a very large muscular bulb with a broad lumen at the proximal end (KANTOR, 1991). It is possible that this bulb functions as a propulsive organ propelling the secretion of the gland through the mouth opening.

Finally a most unusual gland is found in *Persicula* (Marginellidae). COVERT & COVERT (1995) called them acinous accessory salivary glands. The gland is large, composed of two



Figure 3. Longitudinal section through the posterior part of the accessory salivary gland of *Persicula persicula* (L., 1758) (Marginellidae). Abbreviations: iel — layer of internal epithelium; ml — layer of muscle fibers; oel — outer epithelial layer





histologically very distinct layers of tissue (Figure 3). The outer layer is of large oval cells with a granulated cytoplasm. The inner one is formed of strongly staining epithelium forming numerous partitions, and underlined by the layer of muscle fibres. The duct of this gland is lined with non-ciliated epithelium and opens into the buccal tube, as in other neogastropods.

## 2) Dorsal midgut gland.

The midgut gland is most often called the gland of Leiblein in Muricoidea, and venom gland in Conoidea. The homology of both structures, as well as the transformation of the gland of Leiblein and associated with it glandular dorsal folds of mid-oesophagus are discussed in details by PONDER (1970, 1974).

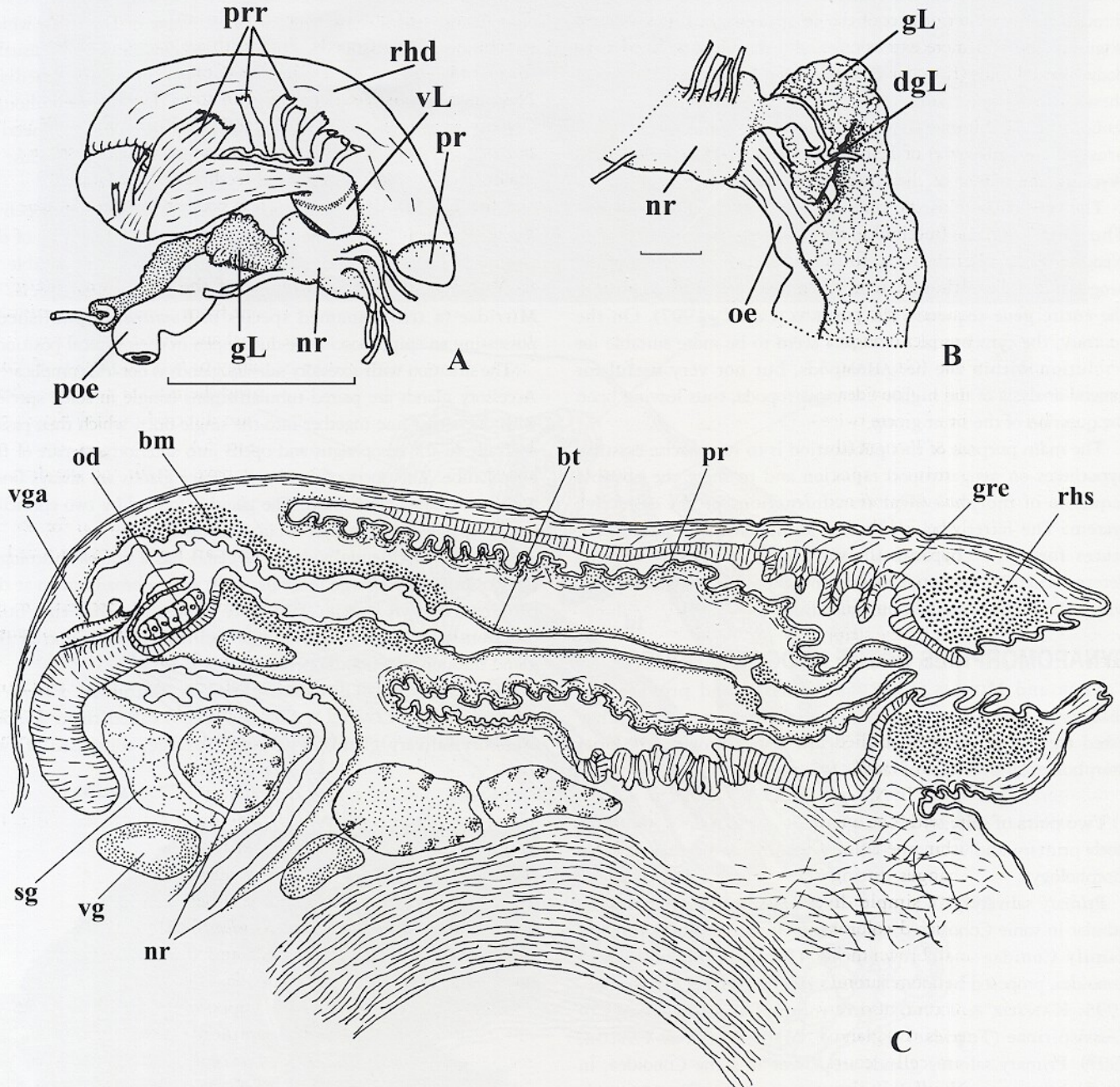


Figure 4. A,B — *Chlanidota (Pfefferia) palliata* (Strebel, 1908) (Buccinulidae) [after HARASEWYCH & KANTOR, 1999, modified from fig. 19]. A — right lateral view of anterior digestive system, salivary gland removed to show the valve of Leiblein. Scale 5 mm. B — Junctionure of gland of Leiblein and oesophagus. Scale 2 mm. C — Semidiagrammatic longitudinal section through the anterior foregut of *Nquma scalpta* Kilburn, 1988 (Conoidea, Turridae, Crassispirinae) [after KANTOR, MEDINSKAYA & TAYLOR, 1997, modified from fig. 16]. Abbreviations: bm — buccal mass; bt — buccal tube; dgl — duct of the gland of Leiblein; gL — gland of Leiblein; gre — glandular epithelium of rhynchodaeum; nr — nerve ring; od — odontophore; oe — oesophagus; poe — posterior oesophagus; pr — proboscis; prr — proboscis retractors; rhd — rhynchodaeum (=proboscis sheath); rhs — rhynchostomal sphincter; sg — salivary gland; vg — venom gland; vga — duct of the venom gland; vL — valve of Leiblein.





The gland of Leiblein is very reduced or absent in many families — some Buccinidae (Volutopsiinae), all Melongenidae, Harpidae, Colubrariidae. When present it opens by a constricted duct either laterally or dorso-laterally in mid-oesophagus (Figure 4, A-B, dgL). The venom gland in Conoidea and midgut gland in some Marginellidae opens ventrally in the posterior part of the buccal cavity (TAYLOR *et al.*, 1993; PONDER, 1970; PONDER & TAYLOR, 1992) (Figure 4C, vga).

In the Tonnoidea there is the oesophageal gland, which is situated in the posterior part of the oesophagus, but it is situated ventrally and is a mere extension of the oesophagus, lined with dorso-ventral folds (KANTOR & HARASEWYCH, 2000).

### 3) Valve of Leiblein.

The valve (or pharynx) of Leiblein is the pear-shaped structure, marking the border of the anterior and mid-oesophagus. In the typical case it contains the cone valve of long cilia, although in some cases (e.g. some Buccinidae) the ciliary cone is absent.

A valve of Leiblein is found in all major groups of Neogastropoda, although it is often very reduced or absent. PONDER (1974) considered the position of the valve just posterior to the buccal cavity as plesiomorphic. It is situated in this position in the Cancellariidae (GRAHAM, 1966). The valve had never previously been found in Conoidea and this led KANTOR (1996) to suppose that it might originate twice in Neogastropod evolution.

Recently KANTOR & TAYLOR (this volume) found a very similar structure in two minute species of Conidae (subfamily Raphitomininae) (*Kermia barnardi* and *Paramontana rufozonata*). It is situated immediately behind the buccal cavity, as in Cancellariidae. The venom gland bypasses the valve and opens anterior to the valve. The same situation is found in some Marginellidae, in which a long coiled gland, similar in general appearance to the conoidean venom gland is formed by the stripping off of glandular folds from the oesophagus (PONDER, 1970).

### 4) Anal gland.

The anal gland has been studied in detail for only a very few species, in particular in *Nucella lapillus* (FRETTER & GRAHAM, 1962; ANDREWS, 1992). In *N. lapillus* it "has the form of a group of caeca which unite with one another to form a duct leading to the rectum just within the anus" (FRETTER & GRAHAM, 1962: 233). The gland changes during the ontogeny and in young *Nucella* the gland is a simple diverticulum from the rectum, lined with simple ciliated columnar epithelium. Later the cells begin to develop small brown melanin granules.

In *Hormospira* (Pseudomelatomidae, Conoidea) the anal gland opens outside the rectum, also very close to the anus (KANTOR, 1988a). In this species the gland in the posterior part is lined with tall epithelium cells, containing the melanin granules (similar to that in *Nucella*). In the anterior part the epithelium is lower, although still having granules. In *Babylonia areolata* (Babyloniidae) there is a simple tubular gland, passing along the rectum and histologically similar to the anterior part of the anal gland in *Hormospira* (HARASEWYCH & KANTOR, this volume).

In some species of *Oliva* the anal gland has a dark coloration, indicating the presence of melanin granules, while in other it is

very light and probably lacking the melanin (KANTOR & TURSCH, unpublished). An anal gland is absent in Buccinoidea.

Detailed examination of the structure of anal gland in a number of Neogastropodan families is still necessary.

Besides these generally accepted synapomorphies of Neogastropoda, two important apomorphies of the radula should be added:

### 5) Five or less teeth in a transverse row of the radula.

The number of the radular teeth in a transverse row is very variable in Neogastropoda. Five teeth are found in at least three unrelated families — Drilliidae (Conoidea), Olivellidae and Nassariidae. Four teeth are found in some Turridae (subfamilies Crassispirinae — KANTOR *et al.*, 1997; Cochlespirinae — KANTOR & SYSOEV, 1991). Three teeth in a row are characteristic for the majority of the Neogastropods, 2 teeth — for the family Conidae, and finally a single central tooth is present in Cancellariidae and majority of Volutidae.

### 6) Morphology and orientation of the lateral and marginal teeth in the radular sac, different from taenioglossan radula.

In taenioglossan radula the marginal and lateral teeth have a long "stalk" (according to the terminology of BANDEL, 1984) which is directed anteriorly, that is towards the radular bending plane, with the cusps on the tip, that are directed posteriorly, to the blind end of the radular sac (Figure 5A). In Neogastropoda the marginal and lateral teeth do not have a stalk and are directed posteriorly (Figure 5B-C).

There are two more characters, that are common for all the Neogastropoda, although they can not be considered as autapomorphies:

a. Proboscis with separate retractor muscles, inserted into the proboscis wall at the distal part. This character opposes Neogastropoda to some probosciferous Tonnoidea (Tonniidae and Ranellidae), in which proboscis is retracted due to the contraction of its muscular walls. In Pisanianuridae and Laubierinidae WARÉN & BOUCHET (1990) recorded long proboscis retractor muscles that pass through the nerve ring.

b. Position of the primary salivary glands "in front" of the circumoesophageal nerve ring (the ducts lie outside the nerve ring). This character is often used to oppose the probosciferous Tonnoidea, in which the salivary ducts pass through the nerve ring, to Neogastropoda. In some other "mesogastropods", e.g. some Littorinidae (*Bembicium*, *Risselopsis*) (REID, 1988), the ducts also lie outside the nerve ring and this character is not an autapomorphy of the Neogastropoda.

Thus Neogastropoda are well supported as a clade by at least 6 autapomorphies and some common characteristics and its monophyly is generally accepted, except by SHERIDAN, VAN MOL & BOUILLON (1973); SHIMEK & KOHN (1981) and GOLIKOV & STAROBOGATOV (1988).

## FUNCTIONAL MORPHOLOGY AND MAIN EVOLUTIONARY TRENDS IN NEOGASTROPODA

All the above mentioned synapomorphies of neogastropods except one are confined to the digestive system, and to be more specific, to



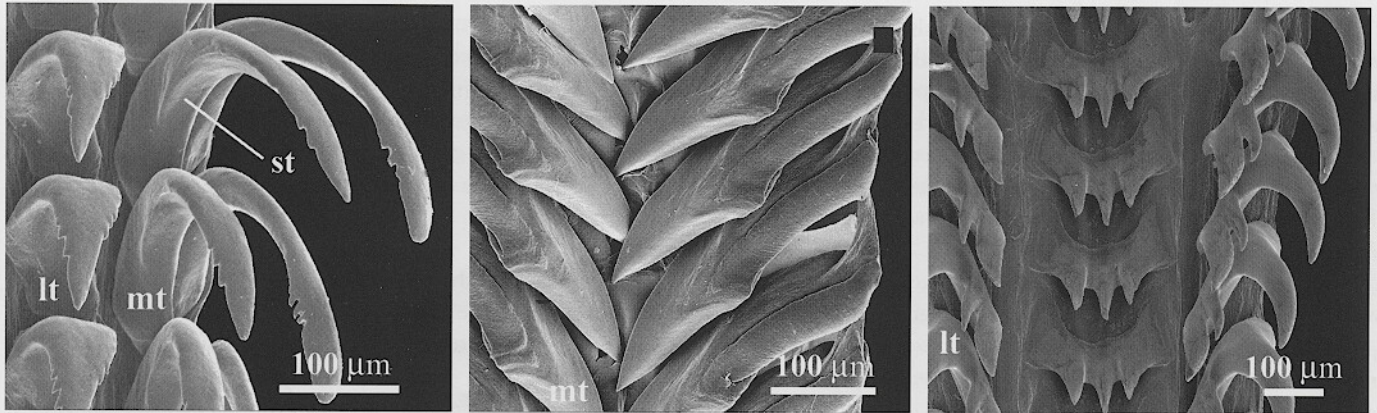


Figure 5. Lateral and marginal teeth of: A — Tonnoidea [*Obscuranella papyrodes* KANTOR & HARASEWYCH, 2000 — after KANTOR & HARASEWYCH, 2000, figure 22]. B — Conoidea [*Clionella sinuata* (Born, 1778)]. C — Buccinoidea [*Cblanidota* (*Cblanidota*) *densesculpta* (Martens, 1875) — after HARASEWYCH & KANTOR (1999), fig. 6A]. Abbreviations: lt — lateral tooth; mt — marginal tooth; st — “stalk” of the marginal tooth.

its anterior section. This is an important proof that origin and radiation of neogastropods was closely related to the main morphological transformations in the anterior foregut.

One of the most prominent characters that cause general morphological reorganisations of the foregut is the proboscis. Several different types and subtypes of proboscis have been described, two major — intraembolic (Conoidea) and pleurembolic (rest of neogastropods). [For the current review of proboscis morphology see BALL, ANDREWS & TAYLOR, 1997].

SHERIDAN, VAN MOL & BOUILLON (1973) as well as SHIMEK & KOHN (1981) considered the Conoidea with its characteristic intraembolic proboscis to have separate origin from the rest of the Neogastropoda due to major differences of the proboscis. Recently the questions of the homology of intraembolic proboscis of Conoidea and the pleurembolic proboscis were discussed by SIMONE (1999), who suggested the homology of both types.

The major difference between pleurembolic and intraembolic proboscis is the position of the buccal mass. In the former it is terminal, situated near the proboscis tip, while in the latter it is basal, situated at the proboscis base and in number of Conoidea even posterior to it. TAYLOR & MORRIS (1988), supposed, based on the anatomy of the proboscis of *Turricula nelli* (Turridae) (in which the buccal mass is situated at the mid-length of proboscis), that the conoidean proboscis might originate from the pleurembolic by the shift of the buccal mass backwards. At the same time they did not give any explanation for the possible reasons of backwards shifting of the buccal mass (with radula and normally developed odontophore, armed with the regular set of the muscles), which would prevent the radular protraction through the mouth and the contact with the prey. Failure to explain basal position of the buccal mass in Conoidea led KANTOR & SYSOEV (1990) to suggest an independent origin of intraembolic proboscis from the apleurembolic one.

Later, additional neogastropods with the “intraembolic” proboscis were found, e.g. a representative of the family Pseudolividae, *Benthobia tryoni* (Figure 2C) (KANTOR, 1991). Finally, it appears that the basal position of the buccal mass is not unique for these mentioned groups, but is found in unrelated families — in Olivellidae (*Olivella*) (KANTOR, 1991), in all genera of the subfamily Ptychatractinae

(usually attributed to Turbinellidae, but probably being the separate family) (Figure 7A) (KANTOR & BOUCHET, 1997; BOUCHET & KANTOR, 2000), in Mitridae (still unnamed species of *Eumitra*) (unpublished). In many neogastropods, the buccal mass occupies a mid-proboscis position, e.g. in Costellariidae (PONDER, 1972) and Marginellidae (GRAHAM, 1966). In Cancellariidae the buccal mass is situated at a significant distance from the mouth and only the tips of the very elongated radular teeth can be protruded through the mouth (HARASEWYCH & PETT, 1984; 1986) (Figure 8A,C).

In my opinion the shift of the radular apparatus backward (as supposed for Conoidea by TAYLOR & MORRIS, 1988) does not have any reasonable functional explanation. In this case the radula, the main organ of prey capture, is moved from the mouth opening thus preventing its main functions. There is an opposite possibility that the basal position of the radular apparatus is a primitive state, inherited from the ancestor, while the terminal position of the buccal mass at the proboscis tip appeared in result of the secondary shift of the buccal mass.

Important evidence, that the basal position of the buccal mass is plesiomorphic for the neogastropods, is found in the arrangement of the radular musculature. In at least some Caenogastropoda lacking a proboscis and with the radula and buccal mass situated near the mouth, the radular sac is protruded backwards through the nerve ring (e.g. in Littorinidae — FRETTER & GRAHAM, 1962, fig. 17). Correspondingly, some radular muscles are situated posterior to the nerve ring and are attached to the floor of the body haemocoel. In Neogastropoda, with the formation of the proboscis, the radular sac was pulled anterior to lie in front of the ring. One may expect, that at least on initial stages of this transformation the muscles should pass through the ring to join the floor of body haemocoel. This condition is found in some Neogastropods, particularly in Drilliidae (Conoidea) (Figure 6, odrn) (SYSOEV & KANTOR, 1989), Pseudolividae and Olivellidae (KANTOR, 1991), as well as in Ptychatractinae (KANTOR & BOUCHET, 1997; BOUCHET & KANTOR, 2000) (Figure 7B, vodr). All these groups are characterised by short proboscis and basal buccal mass.

An intermediate stage is found in *Amalda* (Olividae) (KANTOR, 1991) and *Strictispira* (Strictispiridae, Conoidea)





(KANTOR & TAYLOR, 1994), where the radular muscles join the columellar muscle, but do not pass through the ring. In *Olivella*, some muscle branches are passing through the ring and some are bypassing it (KANTOR, 1996).

Finally in families which have a more or less long proboscis (apomorphic condition) and terminal buccal mass (e.g. in Buccinidae), the radular muscles in adults never pass through the nerve ring and are attached to the walls of the proboscis (WILLSMAN, 1943, fig. 2). Therefore we can observe the clearly directed sequence of morphological transformations — from short proboscis with basal buccal mass and radular muscles passing through the nerve ring to long proboscis with terminal buccal mass and muscles attached to the proboscis walls.

In the ontogeny of *Nucella* the embryo passes through stages, which are characterised by very short proboscis with a basal buccal mass and some radular muscles passing through the nerve ring (BALL *et al.*, 1997). Later these muscles are resorbed. Thus, despite striking differences in adult morphology between a proboscis with the basal buccal mass and a proboscis with a terminal

buccal mass, the latter can be easily derived from the former.

Even so the initial basal position of the buccal mass, when radula could not be used for prey capture should be explained functionally. KANTOR (1996) proposed the following evolutionary scenario. The establishment of the Neogastropoda as a clade was most probably connected with the development of the predatory mode of feeding. Active predation requires a shift of the mouth opening from the ventral position on the head (like in grazing gastropods) to a terminal position. This can be achieved by the formation of a proboscis or a snout as its first stage.

In all known predatory gastropods there is proboscis (introvert) of one of two basic types. Some of the predatory "mesogastropods" (Naticidae and Triphoridae) developed an acembolic proboscis, which in the everted position brings the radula to the tip. In tonnoidean "mesogastropods" and neogastropods the elongation of the snout, which became retractable in its posterior part, formed the proboscis. The walls of the posterior part of the snout formed the rhynchodaeum, or proboscis sheath.

The fixation of the buccal mass in neogastropods at the proboscis

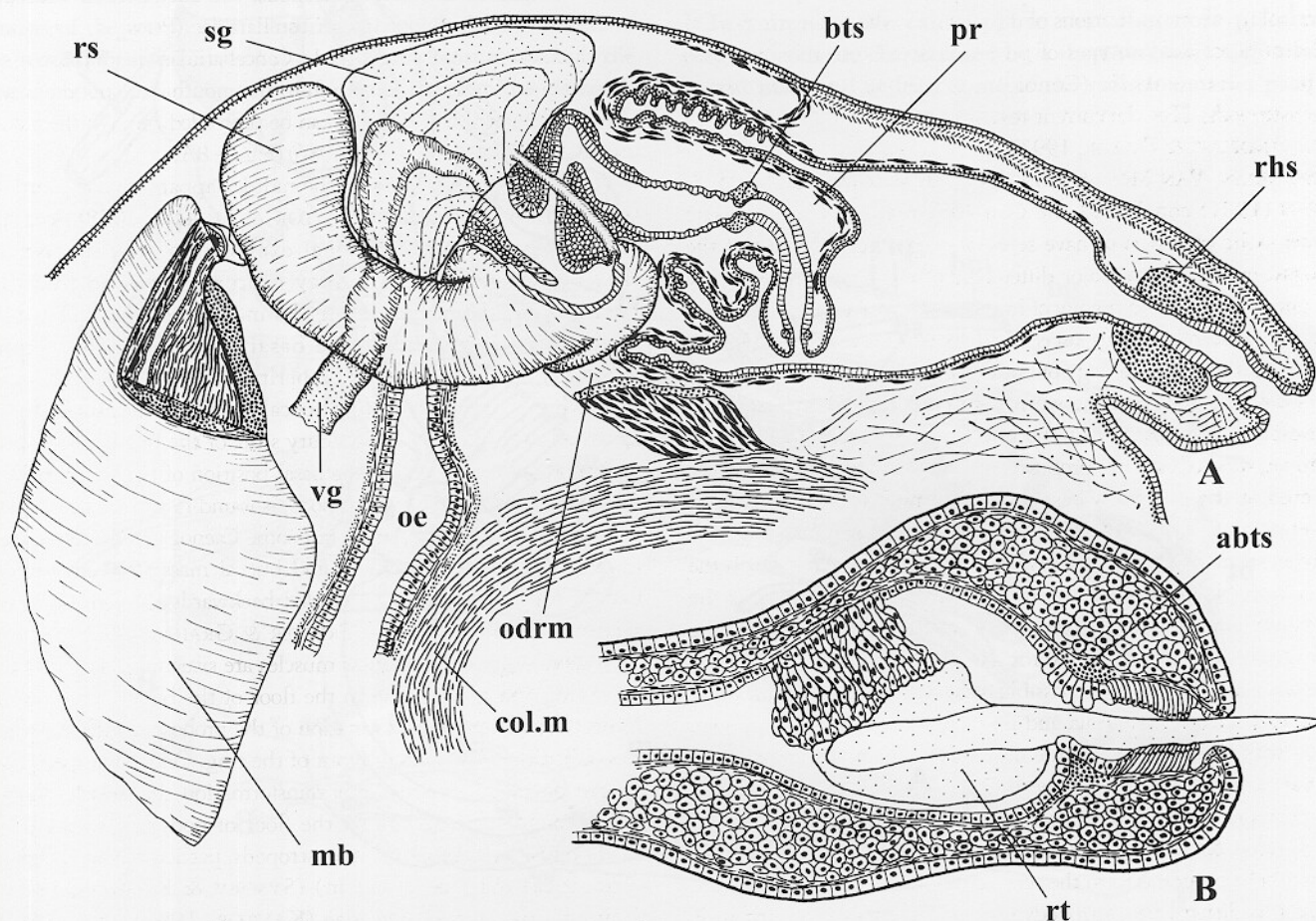


Figure 6. A — Semidiagrammatic longitudinal section through the anterior foregut of *Splendrillia chatamensis* Sysoev et Kantor, 1989 (Conoidea, Drilliidae). Nerve ring and large part of the venom gland are not shown; B — enlarged proboscis tip. [A, B — after SYSOEV & KANTOR, 1989]. Abbreviations: abts — anterior sphincter of the buccal tube; bts — intermediate sphincter of the buccal tube; col.m — columellar muscle; mb — muscular bulb of the venom gland; odr.m — odontophoral retractor muscle; oe — oesophagus; poe — posterior oesophagus; pr — proboscis; prr — proboscis retractors; rhd — rhynchodaeum (=proboscis sheath); rhs — rhynchostomal sphincter; rs — radular sac; rt — radular tooth; sg — salivary gland; vg — venom gland.



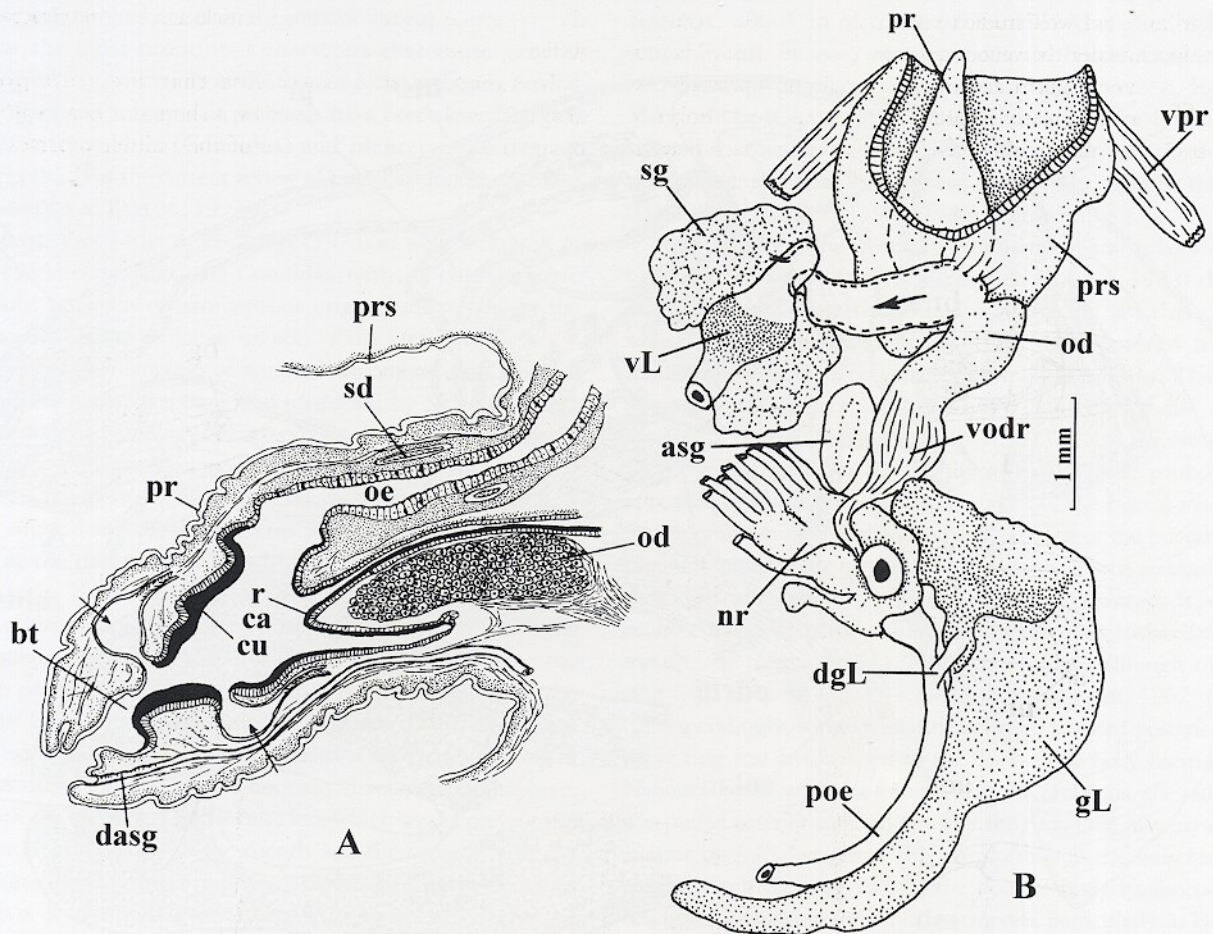
base can be explained by a less complex transformation of the radular muscles, passing through the nerve ring, as well as by the possibility of capturing prey without using radula, if it is slow-moving (like some benthic worms) and swallowed whole, without tearing or rasping. Some Recent neogastropods, that can capture prey without using the radula are found among predatory Conoidea (genera *Caenodagreautes* — SMITH, 1967a, *Teretiopsis* — KANTOR & SYSOEV, 1989; many Terebridae — TAYLOR, 1990; and others), in which the radula and venom apparatus have completely disappeared (KANTOR & TAYLOR, this volume, figs. 15-16).

One of the ways of increasing the effectiveness of prey capture was further elongation of the proboscis. This allowed feeding on organisms, living in crevices and other shelters. The basal position of the buccal mass and initial arrangement of the radular and odontophoral muscles precluded further elongation of the proboscis, while disappearance of those branches of the muscles that passed through the ring allowed the anterior shift of the radular apparatus. Finally, the radula muscles become attached to the proboscis walls,

thus eliminating any limitations for the elongation of the proboscis. Indeed, the neogastropod families with longest proboscis (Buccinidae, Vasiidae, etc.) all have a terminal buccal mass. Among Recent neogastropods we can find different intermediate stages of the process of anterior shift of buccal mass and re-arrangement of radular musculature.

Prey capture, especially while the basal radular apparatus has reduced mobility, can be significantly facilitated with some kind of the mechanism of prey immobilisation. The use of a toxic secretion became such a mechanism and this explains the origin of the second pair of salivary glands (accessory salivary glands). In the ontogeny of *Nucella* the glands form as paired invaginations on ventral proboscis lip (BALL *et al.*, 1997). Thus, they are not connected with the anterior gut and open into anterior buccal tube despite any transformation of the foregut.

There is only one investigation of the chemical composition of the secretions from accessory salivary glands in Neogastropoda (ANDREWS, ELPHICK & THORNDYKE, 1991). It was demonstrated



**Figure 7.** Anatomy of the anterior digestive system of Ptychactractidae. A — longitudinal semidiagrammatic section of the proboscis of *Latiromitra barthelemyi* (Bartsch, 1942) [after BOUCHET & KANTOR, 2000, modified from fig. 2]. Arrows mark the enlargement of the salivary ducts ("ampullas"). B — anterior digestive system of *Exilia*. Anterior oesophagus cut in front of the nerve ring to show the passage of ventral odontophoral retractor through the ring. Abbreviations: asg — accessory salivary gland; bt — buccal tube; ca — buccal cavity; cu — cuticular lining of the buccal cavity; dasg — duct of accessory salivary gland; dgL — duct of gland of Leiblein; gL — gland of Leiblein; nr — nerve ring; od — odontophore; oe — oesophagus; poe — posterior oesophagus; pr — proboscis; prs — rhynchodaeum (=proboscis sheath); r — radula; sd — salivary duct; sg — salivary gland; vL — valve of Leiblein; vodr — ventral odontophoral retractor; vpr — ventral proboscis retractor.





that the secretion in *Nucella lapillus* causes flaccid paralysis in prey. As it was said above, the ducts of the gland are lined with non-ciliated epithelium, while the wall of the gland contains the circular layer of muscle fibres. It seems likely, that contraction of the muscle fibres causes the propulsion of the secretion through the duct.

Although even with a basal buccal mass feeding is possible (as is demonstrated by presence of different Recent neogastropods with basal buccal mass), we have no data on the feeding mechanisms of many of them. Nevertheless, we can observe different ways of morphological and functional transformations among recent neogastropods, that allow the use of the radula for feeding, that "overcome" the plesiomorphic basal position of the buccal mass.

In Cancellariidae, the lateral and marginal teeth are lost, while the central teeth are greatly elongated so that their tips can protrude through the mouth opening (Figure 8). For some Recent representatives of Cancellariidae, parasitism on fishes and echinoderms has been demonstrated (O'SULLIVAN, McCONNAUGHEY & HUBER, 1987; BUCK, 1991). Thus, the radula is probably used for penetration of the prey skin, and only the tips of the teeth are in contact with the prey (PETIT & HARASEWYCH, 1986).

Most striking and well studied are the feeding mechanisms of Conoidea. In Conoidea the venom apparatus was developed, which consists of the venom gland and muscular bulb. The evolution of the venom apparatus greatly improved prey capture through the envenomation, and allowed the retention of the primitive proboscis

type with the basal buccal mass in most groups of Conoidea. At a very early stage of evolution of the group, the specialised mechanism of using the detached marginal teeth at the proboscis tip for stabbing the prey appeared (SYSOEV & KANTOR, 1987; KANTOR & TAYLOR, 1991). Nevertheless, even within Conoidea, different ways of overcoming the basal position of the buccal mass can be found. In some non-related genera, the buccal mass is shifted forward and the radula can be protruded through the mouth opening (e.g. *Turricula*, *Toxicionella*, *Strictispira* — KANTOR & TAYLOR, 1994). In several conoidean taxa the buccal mass itself is able to evert through the mouth, which allows the direct use of the radula for prey capture (TAYLOR *et al.*, 1993) (Figure 9 — *Funa jeffreysii*). In some Clavatulinae (Turridae) with an anteriorly shifted buccal mass the posterior part of the rhynchodaeum can evert and this makes the proboscis similar in many respects to that of pleurembolic type (including a secondary elongation of the oesophagus between buccal mass and nerve ring).

Finally, in the majority of Neogastropoda the buccal mass was shifted to the proboscis tip and the radula became the primary organ for prey capture. In these molluscs, the radular muscles mostly lost the connection to the columellar muscle and became attached to the walls of the proboscis.

In summary we can suppose that the most primitive neogastropods are characterised by a short proboscis with a basal buccal mass and at least some of the radular muscles passing

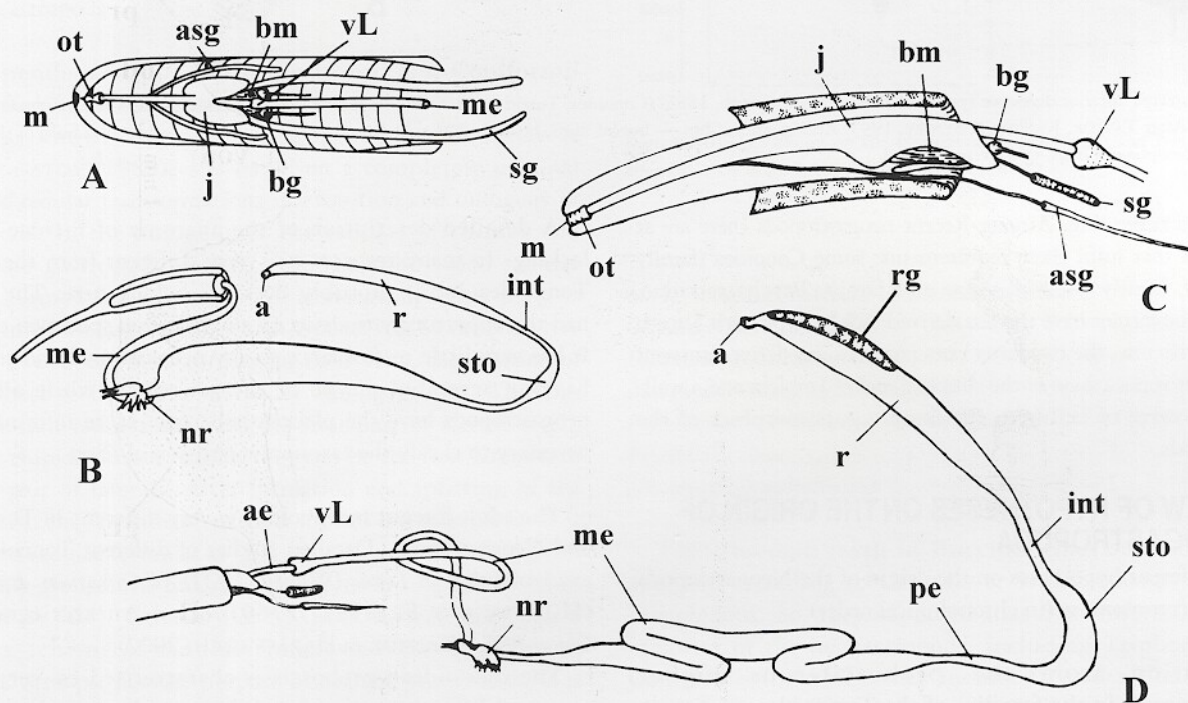


Figure 8. Digestive system of Cancellariidae: A, B — *Admete viridula* (Fabricius, 1780) [after HARASEWYCH & PETIT, 1986, modified]. C, D — *Olsonella smithi* (Dall, 1888) [after HARASEWYCH & PETIT, 1984, modified]. A — dissection of anterior portion of proboscis, opened mid-dorsally. B — diagrammatic representation of the digestive system. C — dissection of retracted proboscis, viewed from left side. D — diagrammatic representation of the digestive system. Abbreviations: a — anus; ae — anterior oesophagus; asg — accessory salivary gland; bg — buccal ganglia; bm — buccal mass; int — intestine; j — jaw; m — mouth; me — mid-oesophagus; nr — nerve ring; or — oral tube; pe — posterior oesophagus; rg — anal (rectal) gland; sto — stomach; vL — valve of Leiblein.



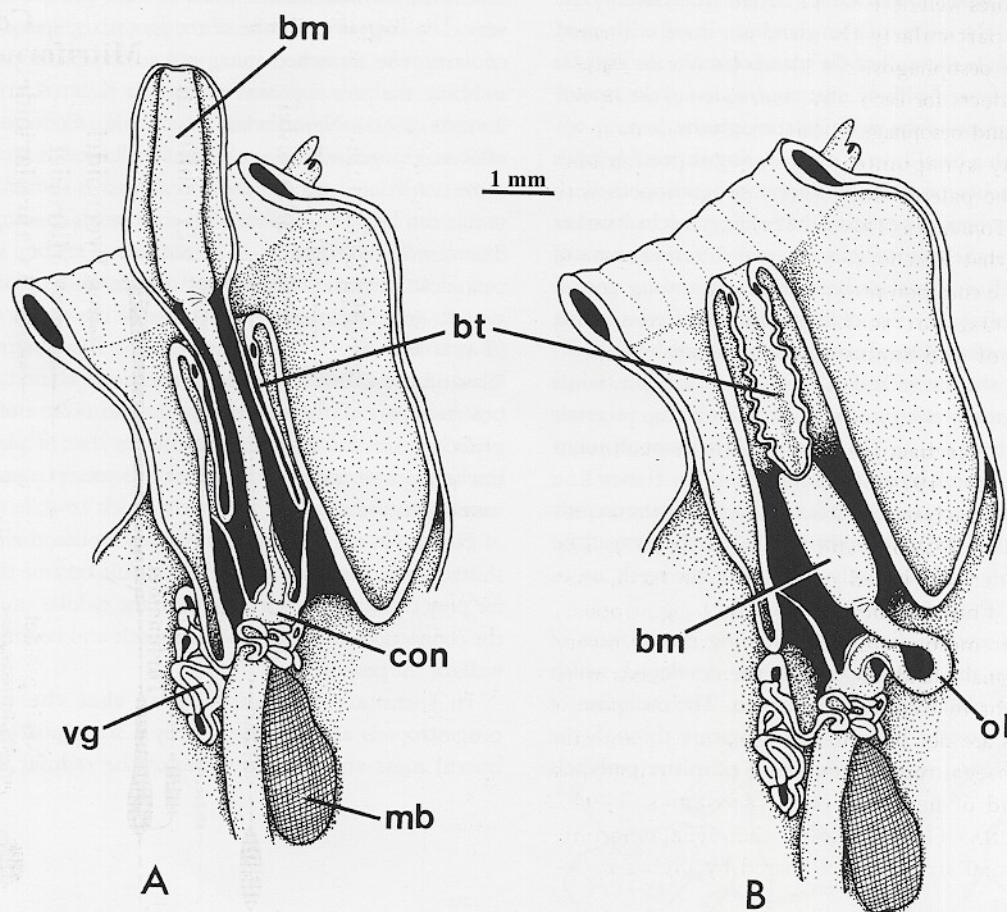


Figure 9. Dissected anterior digestive system of *Funa jeffreysii* (Smith, 1885) (Conoidea, Turridae). A — buccal mass in everted position; B — buccal mass in retracted position. After TAYLOR, KANTOR & SYSOEV, 1993. Abbreviations: bm — buccal mass; bt — buccal tube; con — nerve ring; mb — muscular bulb of the venom gland; ol — oesophageal loop; vg — venom gland.

through the nerve ring. Among Recent neogastropods there are at least 3 taxa that fulfil these requirements: some Conoidea (family Drilliidae), family Pseudolividae and family Ptychatractidae. Although the former have the less derived radular type with 5 teeth in a transverse row, the two latter ones possess a less derived anterior foregut, that is possession of the simple gland of Leiblein and a well-developed valve of Leiblein, the main autapomorphies of the neogastropods.

## OVERVIEW OF HYPOTHESES ON THE ORIGIN OF THE NEOGASTROPODA

Among different hypotheses on the origin of the Neogastropoda four are in common use (in chronological order).

### 1. Derivation from the probosciferous higher mesogastropods in the families of the Tonnoidea.

This hypothesis was proposed by AMAUDRUT (1898) and supported by GRAHAM (1941). Currently BANDEL and RIEDEL support this point of view. RIEDEL (1994, 2000) actually included Ficidae in neogastropods, considering the Tonnoidea their sister group.

A detailed description of the anatomy of Ficidae is still lacking. In many respects it is very different from the rest of Tonnoidea and it probably does not belong here. The author had the opportunity to dissect a single frozen specimen of *Ficus*. It has very little resemblance to any neogastropod and seems to have an acrembolic type of the proboscis, while all other neogastropods have the pleurembolic one. More information is necessary to clarify the taxonomic position of *Ficus*.

The adult foregut morphology is very different in Tonnoidea and Neogastropoda. Detailed studies of different Tonnoidea are available: that of *Tonna* (WEBER, 1927), of *Cymatium* and *Bursa* (HOUBRICK & FRETTER, 1969), of an Antarctic ranellid *Obscuranella* (KANTOR & HARASEWYCH, 2000).

The tonnoidean proboscis is characterised by very small terminal buccal mass and radular muscles attached to the proboscis wall. Therefore the plesiomorphic proboscis of the neogastropods with the basal buccal mass can not be derived from that of Tonnoidea. Moreover most Tonnoidea do not have proboscis retractors (see above). Instead, the contraction of the proboscis is achieved by the contraction of the proboscis walls.





There are some structures well developed in Tonnoidea, but absent in Neogastropoda, particularly the presence of the lateral longitudinal folds in oesophagus; the bilobed salivary glands, which have separate ducts for each lobe, that fuse together; the well developed jaws and oesophageal gland. So, for the moment we do not have any synapomorphies for Tonnoidea and neogastropods. In the paleontological record Neogastropoda appeared earlier than Tonnoidea (TRACEY, TODD & ERWIN, 1993).

One can suppose that Recent Tonnoidea and neogastropods may have some remote common predatory ancestor, possessing a very short proboscis, but so far we do not have any morphological proof and such an assumption is a mere speculation.

## 2. Derivation from an archaeogastropod or primitive lower mesogastropod (Ponder, 1974).

This hypothesis was analysed and rejected by TAYLOR and MORRIS (1988) and by PONDER and LINDBERG (1997). The supposition of Ponder was based mainly on the facts, that neogastropods share similar structures with archaeogastropods, but not with higher mesogastropods; namely the accessory salivary glands and anal gland. Accessory salivary glands were thought to be present in Acmaeidae, but later it was proven that these structures are not homologous. Similarly, the rectal pouches of some archaeogastropods appear not to be homologous with the anal gland of neogastropods (ANDREWS, 1992). Moreover, HASZPRUNAR (1985) showed that synapomorphic characters of osphradial structure are shared by higher meso- and neogastropods.

## 3. Independent origin of Bucciniformii and Coniformii from different archaeogastropod ancestors.

This less-known hypothesis, proposed by GOLIKOV & STAROBOGATOV (1988), was based on a completely original theory of radular transformations in evolution and ontogeny of gastropods. In the ontogeny of the radulae of chitons and pulmonate gastropods (KERTH, 1983) a subdivided radular plate is formed initially. Later in some groups this plate is divided into two large teeth, which GOLIKOV & STAROBOGATOV named "initial" teeth. According to their view, the position of these initial teeth differs markedly among groups: Thus, in taenioglossan radulas they are the first pair of lateral teeth, while in rhipidoglossan radulas they can be the first laterals, or the 6th pair of laterals. After formation and splitting of the initial teeth the "rachidian" tooth is formed between them. It is marked in radulae formulas as "R".

In other groups, the initial teeth fuse to form a central tooth (marked as "C"). GOLIKOV & STAROBOGATOV provided a complex scheme of radulae transformation in different gastropod groups. For the purpose of current presentation it is important, that they distinguish two types of median tooth — central and rachidian. GOLIKOV & STAROBOGATOV provided several neogastropod radulae formulae:

*Cyclope* (Nassariidae): M — : — (L) — C — (L) — : — M,

where M — marginal; L — lateral (position in brackets indicate the reduction of the tooth); C — central; : — position

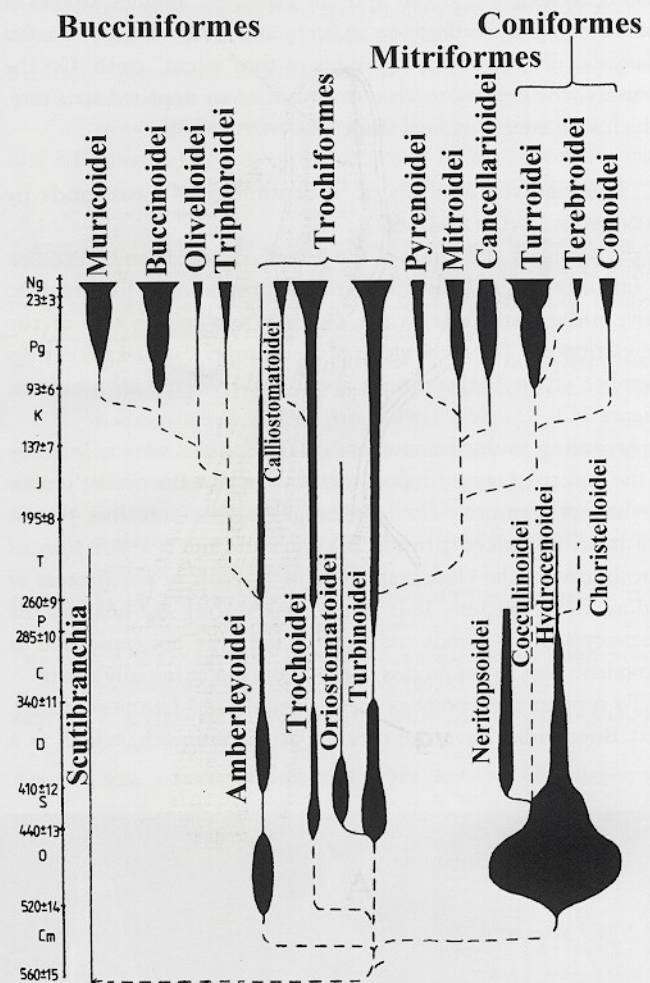


Figure 10. Hypothesis on the phylogenetic relationships of Neogastropoda, after GOLIKOV & STAROBOGATOV, 1988 (modified).

of the longitudinal bent of radular membrane.

*Olivella* (Olivellidae): (M) — M — : — C — : — M — (M)

*Buccinum* (Buccinidae): M — : — C — : — M

*Marginella* (Marginellidae): C

*Pseudomelatomia* (Pseudomelatomidae): M — : — R — : — M

*Fasciolaria* (Fascioliidae): I — : — R — : — I

*Anachis* (Columbellidae): I — : — (R) — : — I

Thus, median teeth in Bucciniformes and Coniformes appeared according to GOLIKOV & STAROBOGATOV not to be homologous. So, they supposed that Bucciniformii (that are majority of the neogastropods, including Triphoridae) and Coniformii (in which they included besides Conoidea also Mitridae, Cancellariidae and Pyrenoidae) originated independently, the former ones from Amberleyoidei while the latter from Turbinoidei (Figure 10).

This hypothesis ignores the large number of synapomorphies of both groups recognised by GOLIKOV & STAROBOGATOV and therefore supposes the independent origin of accessory salivary



glands, rectal gland, dorsal mid-gut gland, etc. Besides, studies of radular ontogeny in *Buccinum undatum* and *Volutomitra groenlandica alaskana* did not reveal any signs of the "initial" teeth. On the contrary, the median tooth was formed as an unpaired structure, which soon attains its final shape (KANTOR, 1988b).

#### 4. The cladistic analysis of morphology of gastropods by PONDER & LINDBERG (1997).

In the summary cladogram of the gastropods, obtained by PONDER & LINDBERG (1997) on the basis of morphological characters, Buccinidae came out as the sister taxon to the rest of the neogastropods. The sister group of Neogastropoda itself is a certain member of the Sorbeoconcha above the level of cerithioideans (Figure 1C).

According to discussion above concerning the foregut anatomy of the underived neogastropod, it is obvious that Buccinidae cannot be the most primitive family of neogastropods, since they possess the most advanced proboscis structure. Such a position of Buccinidae in the cladogram may be a result of the process of coding the characters. It is stated, that during the analysis the accessory salivary glands and rectal gland were not considered as secondarily lost in the process of evolution, but as initially absent.

To support their point of view, PONDER and LINDBERG stated, that Buccinidae have the caecum of the stomach, which is a

plesiomorphic character, absent in many neogastropods. This statement is incorrect. First, in many of the neogastropods the stomach caecum (usually referred to as *posterior mixing area*) is present. It is well developed and large, e.g. in *Oliva*, *Olivella*, Muricidae and many others. It is also absent in some Buccinidae (e.g. *Colus gracilis* — SMITH, 1967b) and closely related Buccinulidae (HARASEWYCH & KANTOR, 1999) and Fascioliariidae (unpublished). Secondly, there is no proof, that the posterior mixing area in neogastropods is homologous with the caecum of mesogastropods.

A serious problem in understanding neogastropod origin and radiation is the incongruence between morphological data and palaeontological records. From the morphological standpoint, Buccinoidea should be the most derived neogastropods, possessing long proboscis with terminal buccal mass and lacking the accessory salivary and rectal glands (obviously secondary loss). At the same time, Buccinidae and Fascioliariidae are the first families of the neogastropods, found in fossil record (TAYLOR, MORRIS & TAYLOR, 1980; TRACEY, TODD & ERWIN, 1993).

Nevertheless, there is high uncertainty in attributing early Cretaceous fossil neogastropods to current families. Unfortunately the mentioned oldest records are based on unpublished materials of

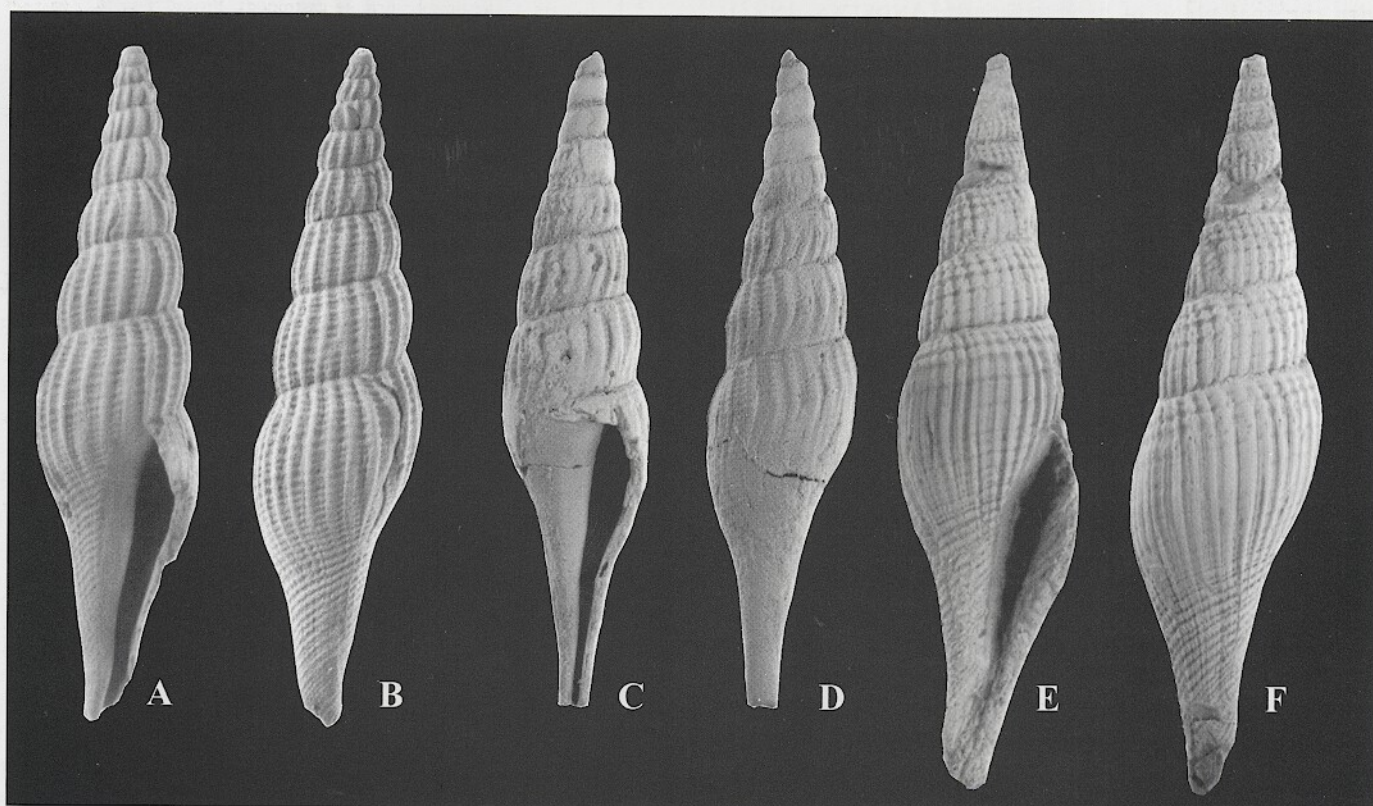


Figure 11. Fossil members of the genus *Exilia* (Ptychotractidae), erroneously attributed to Fascioliariidae. A-B — *Exilia pergracilis* Conrad, 1860. Lower Eocene, Midway Group, near Oak Hill, Alabama, specimen illustrated by Bentson, 1940: pl. 1, figs 9-10 (Museum of Paleontology, University of California, Berkeley, UCBMP 11623), 14.8 mm. C-D — *Exilia lincolnensis* Weaver, 1916. Upper Eocene, Lincoln Creek Formation, Porter Bluff, Washington, (The Burke Museum, University of Washington, UWBMP 19936), 30.5 mm. *Exilia terebriformis* Stephenson, 1941, type-species of *Graphidula*, Maastrichtian, Nacatoch Sand, near Chatfield, Navarro County, Texas, holotype (National Museum of Natural History, Smithsonian Institution, Washington, DC, USNM 77085), 46.0 mm. All photos — courtesy of Dr. Anton Oleinik.





Noel Morris and therefore can not be checked. In the discussion of the oldest fasciolarid species ("*Fusus*" *valangiensis* Pictet & Campiche, 1872) TRACEY *et al.* (1993) cited the personal communication of N. Morris: "Such early fusiform gastropods may belong to a stem group of the paraphyletic Fasciariidae and the Turridae". As it is known from morphological data these are totally unrelated groups.

The other example of erroneous allocations to the family Fasciariidae is the fossil genus *Exilia* Conrad, 1860 (Figure 11). CONRAD (1860) originally did not assign *Exilia* to any family, but later placed it in the Pleurotomidae [= Turridae] (CONRAD, 1865). Several authors followed this view, e.g. WENZ (1943), and with doubts also POWELL (1966). Alternatively, the genus has been classified in various buccinoid families: Fasciariidae (HICKMAN, 1980), Fusinidae (BENTSON, 1940), Buccinidae (THIELE, 1929). Finally MAXWELL (1988) correctly placed *Exilia*, together with *Graphidula*, in the subfamily Ptychactinidae of the Turbinellidae, which as was mentioned already, have most primitive foregut anatomy.

Therefore, many of the fossil Cretaceous Neogastropoda still await for critical reassessment of their taxonomic position and there is still no certainty, which representatives of which families are the oldest in paleontological records.

## CONCLUSIONS

The most primitive neogastropods were characterised by a short proboscis with a basal buccal mass and radular retractors passing through the nerve ring and joining the columellar muscle, possessing a valve of Leiblein, the anal and accessory salivary glands. There are several groups, that fulfil these requirements, particularly Conoidea (families Drilliidae and Turridae), Pseudolividae and Ptychactinidae. The Pseudolividae and the anatomically close Ptychactinidae have less modified mid-gut glands than Conoidea.

We should seek for a sister group of Neogastropoda among carnivorous groups of Caenogastropoda, or more specific Sorbeoconcha, with an underived foregut. More studies of the anatomy of primitive Tonnoidea are necessary before we can either support or disprove the possibility of them being the sister group of the Neogastropoda.

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