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ANATOMICAL BASIS FOR THE ORIGIN AND EVOLUTION OF THE TOXOGLOSSAN MODE OF FEEDING

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ABSTRACT

Five types of feeding mechanism can be recognized in the Toxoglossa. The mechanism by which separate marginal teeth are used at the proboscis tip for stabbing and poisoning the prey with secretions from the venom gland originated in "lower" turrids possessing a radular membrane, solid marginal teeth, a central tooth and sometimes lateral teeth. The morphological prerequisite of the appearance of toxoglossan mode of feeding was firstly the appearance of the venom gland, which initiated the formation of the specialized intraembolic type of proboscis with the buccal mass situated at its base. Hollow marginal teeth originated repeatedly and independently in different phylogenetic lineages of Toxoglossa. It is supposed that the ancestors of Toxoglossa were primitive mesogastropods with a short acrembolic proboscis and taenioglossan radula. The separation of Toxoglossa from the Rachiglossa occurred at an early evolutionary stage, when the common ancestor had seven radular teeth in each transverse row.

Key words: Toxoglossa, evolution, feeding, radula.

INTRODUCTION

The order Toxoglossa is large, diverse, and well differentiated from the other prosobranch gastropods. It includes four Recent families: Turridae, Conidae, Pervicaciidae, and Terebridae. One of the most outstanding and well-known features of the order is the specialized feeding mechanism of its higher representatives. That is the use of separate hollow marginal teeth at the proboscis tip for stabbing and subsequent poisoning the prey, with the venom produced by a usually well-developed, tubular venom gland. Most representatives of the order (the "higher" Turridae, Conidae and part of the Terebridae) lack the radula membrane, and the radula itself consists of only hollow marginal teeth. The teeth being formed in the radula sheath are finally stored in the short arm of the radula sac, which is probably a homologue of the sublingual pouch.

At the same time, many toxoglossans (mainly "lower" turrids) have a normally developed radular membrane with two to five radular teeth per transverse row. Information on feeding mechanisms and the morphology of these "lower" toxoglossans is very limited, although the functional analysis of their digestive system and feeding mechanism may elucidate the pathways of origin and evolution of "toxoglossan" mode of feeding.

One of the most interesting problems is the origin of "toxoglossan" feeding mechanism. Does it have a single or repeated origin in evolution, and what are the morphological prerequisites for its appearance? The main aim of this study was to clarify these problems.

MATERIALS AND METHODS

Materials for the study were obtained mainly from the collections of the Zoological Museum of Moscow State University and Institute of Oceanology of the USSR Academy of Sciences (Moscow). Other material was kindly provided by Dr. James H. McLean (Los Angeles County Museum of Natural History, USA); the late Dr. Virginia O. Maes (Academy of Natural Sciences, Philadelphia, USA); Dr. Anders Warén (Naturhistoriska Riksmuseet, Sweden); and Dr. R. N. Kilburn (Natal Museum, South Africa).

The morphology of the digestive tract was studied using sections 8–10 μm thick, which were cut after dehydration and embedding in paraffin wax. The sections were usually stained with Masson's triple stain. Its second solution, which contains orange-G and aniline blue, was used for staining the radula. Large specimens were also dissected under the stereomicroscope. In total, the morphology of 18 species of Turridae belonging to six subfamilies was studied.

RESULTS AND DISCUSSION

Within the Toxoglossa there is significant variability both in the morphology of the radular teeth and their number in a transverse row (the radular formulae: 1-1-1-1-1, 1-0-1-0-1, 1-1-0-1-1, 1-0-0-0-1). The morphological changes in the radular apparatus and associated structures of the anterior digestive system form the main evolutionary trends of the order. Several authors have tried to classify the radular types of Toxoglossa according to both the morphology and probable mechanism of function (Thiele, 1929; Powell, 1966; Morrison, 1966; McLean, 1971). The most complex classification was proposed by Shimek & Kohn (1981), who isolated six functional types of toxoglossan radula, four of which are found in lower "non-toxoglossate" turrids (those with solid marginal teeth). However, one can say that only two general feeding mechanisms include all the isolated types: "toxoglossate" for those gastropods which have only hollow marginal teeth and lack a radular membrane, and "non-toxoglossate" for lower turrids. In the first feeding type, separate, hollow marginal teeth are used at the proboscis tip for stabbing and poisoning the prey; in the second type, the radula is used as a whole organ only within the buccal cavity. In their analysis, Shimek & Kohn (1981) used mainly isolated radulae, without taking into account the morphology of the digestive tract, and this led to some misinterpretation (Sysoev & Kantor, 1987).

A functional morphological analysis of the digestive system of the species studied suggests that there are at least four different types of feeding mechanism for toxoglossans possessing a radula and one type for radulaless species.

General Anatomy of Toxoglossa

Before a more detailed analysis of the feeding mechanism, a brief description of the anterior part of the digestive system of the Toxoglossa is necessary. One of the outstanding features of the order is the specialized intraembolic type of proboscis (Smith, 1967), which is characterized by the position of the buccal mass at the base of the proboscis or even behind it. This precludes the use of the radula as a whole organ for rasping and grazing, as in other gastropods. The second feature is the presence of the well-developed tubular venom gland entering the anterior oesophagus behind the buccal cavity. It has been shown that the venom gland produces a venom that immobilizes or kills prey animals (Kline, 1956; Pearce, 1966; Miller, 1980; Shimek & Kohn, 1981; Kohn, 1956, 1959, 1968, many others). The buccal tube leads from the buccal cavity to the mouth, which opens at the proboscis tip. The buccal tube has thick muscular walls in "lower" toxoglossans, but is thin-walled and practically lacking muscular fibres in higher representatives.

It should be noted that the functional analysis was carried out mainly using the anatomical evidence, because data on feeding behaviour and diet are scarce and chiefly concern species of Conidae, Terebridae and some higher Turridae. As our knowledge of the morphology of turrids becomes more precise, the proposed classification may change.

Feeding Mechanism Type 1

The first functional type of digestive system and feeding mechanism, that in which the radula is used as a whole organ only within the buccal cavity, was found among species of Pseudomelatominae (Turridae). This is an endemic subfamily from central west America, which includes three genera and several species (McLean, in Keen, 1971). The anatomy of two species—*Pseudomelatoma penicillata* (Carpenter, 1864) and *Hormospira maculosa* (Sowerby, 1834)—indicates the isolated position of the group among the Toxoglossa (Kantor, 1988). This is obvious, in particular, from the presence of long curve of the anterior part of the digestive tract, a rarely found and undoubtedly secondary feature in turrids. The curve is formed either by elongation of the part of the oesophagus between the nerve ring and the buccal mass (in *Pseudomelatoma penicillata* (Fig. 1), the buccal mass is situated at the proboscis base and far ahead of the nerve ring) or by the elongation of the posterior part of the buccal tube (in *Hormospira maculosa*, the buccal mass is situated in front of the nerve ring, distant from the proboscis base).

Both species have a well-developed venom gland, longer in *H. maculosa* (its length comprises 0.5 of the shell height). Although the diet of Pseudomelatominae is unknown, the presence of the large venom gland testifies to predatory mode of feeding. The gastropods have a muscular proboscis with a wide oral opening in the form of triangular or transverse slit and lack an oral sphincter. The radula of

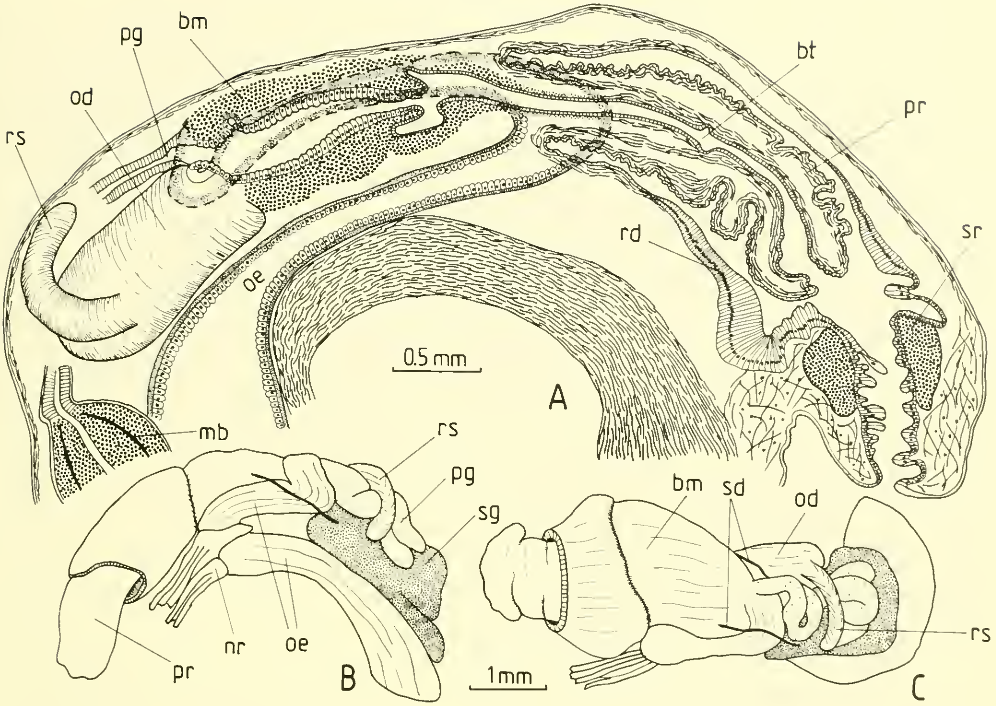

FIG. 1. Anatomy of *Pseudomelatoma penicillata* (Carpenter). A—semidiagrammatic longitudinal section of the anterior part of the molluscan body. Salivary glands with the duct and convolutions of the venom gland together with the nerve ring are not shown. B, C—organs of the body haemocoel (B: from the left, C: from above).

Pseudomelatominae consists of a large and well-developed central tooth, flanked by large, sharply pointed, scythe-like marginal teeth. Thus, although the morphology of the marginal teeth is primitive, the absence of lateral teeth indicates that the group has deviated greatly from the toxoglossan ancestor.

From the morphology of the digestive tract, one can suggest that prey capture probably occurs with the aid of the proboscis tip and is facilitated by the presence of a wide and highly extensible oral opening. The envenomation of the prey probably occurs in the anterior part of the proboscis, and this facilitates the transportation of the prey through the buccal tube into the buccal cavity by the peristaltic movements of well-developed circular muscles in walls of the buccal tube. The presence of a very large odontophore (the largest of all the turrids studied) suggests that the radula tears the prey in the buccal cavity. Thus, the radula of Pseudomelatominae is of the slicing-rasping type as determined by Shimek & Kohn (1981). The large inner volume of the buccal cavity and the curve of the anterior part of the digestive tract suggests that the prey is partially digested in the anterior part of the digestive tract.

In summary, the main features of this feeding mechanism are: prey capture with the aid of the proboscis tip, without using marginal teeth (since the oral opening lacks a sphincter and the shape of the marginal teeth prevents their being held at the proboscis tip); use of the large and powerful radula for slicing and rasping the prey; and, what is probably a secondary feature, at least partial digestion of the prey in the anterior part of the digestive tract. This feeding mechanism is the true "non-toxoglossate" and was probably characteristic of ancestors of the Toxoglossa. In my opinion, it is widespread among turrids, and occurs probably in the Clavinae and other taxa lacking an oral sphincter (for example, *Clavatula diadema*), although digestion of the prey in the anterior part of the digestive system is uncertain.

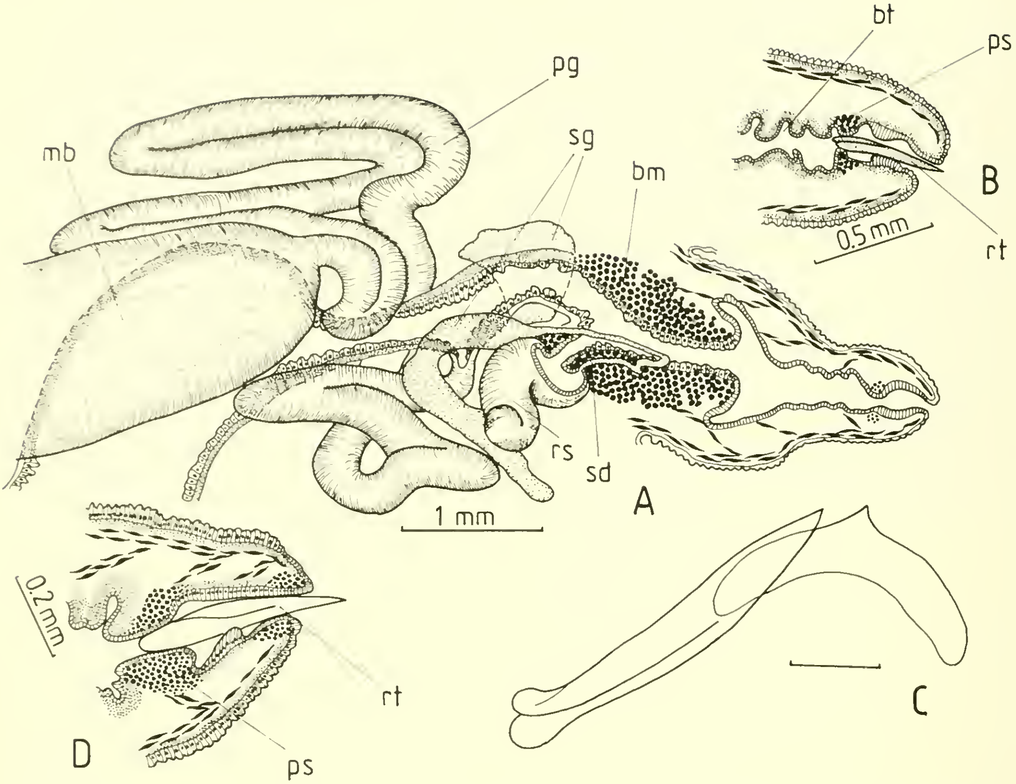

FIG. 2. Morphology of the digestive system of *Aforia* spp. A—C: *Aforia abyssalis* Sysoev et Kantor (A—semidiagrammatic section of the anterior part of the digestive system; B—magnified tip of the proboscis; C—radula); D—magnified tip of the proboscis of *Aforia kupriyanovi* Sysoev et Kantor.

Feeding Mechanism Type 2

The second functional type of digestive system is found in some turrids with a well-developed radular membrane (subfamilies Turriculinae, Clavinae) (Sysoev & Kantor, 1987, 1989). Its typical feature is the use of marginal teeth, which become detached from the radular membrane during its degeneration (in the sublingual pouch), at the proboscis tip for stabbing the prey. Meanwhile, the radula as a whole organ has a different function in the buccal cavity. This type of feeding mechanism can be probably found amongst species of almost all subfamilies of Turridae, except the Pseudomelatominae, Zonulispirinae and probably the Clavatulinae.

Since turrids belonging to this type have varied anatomies, it is difficult to distinguish morphological features common to all representatives of the group. For the species studied (*Aforia* spp., *Antiplanes* spp., *Splendrillia chathamensis* Sysoev & Kantor, 1989) the following features can be noted: a large or medium-sized odontophore, with well-developed radular muscles; a sac-like enlargement of the anterior part of the buccal tube; and a well-developed oral sphincter.

Individual solid marginal teeth were found at the proboscis tip, either held by the oral sphincter as in *Aforia* (Fig. 2 B,D), or attached by their bases to the "mat" of epithelial cells in the enlargement of the buccal tube as in *Splendrillia chathamensis* (Fig. 3B). It should be noted that separate teeth were not found in the sublingual pouch. This seems to indicate that the marginal teeth are not used at the proboscis tip of *Aforia* in every feeding act. On the contrary, the mechanism of tooth fixation in *Splendrillia* testifies to the long-term occurrence of the tooth at the proboscis tip, i.e. the enlargement of the anterior part of the buccal tube may be considered as a functional analogue of the short arm of the radular sac.

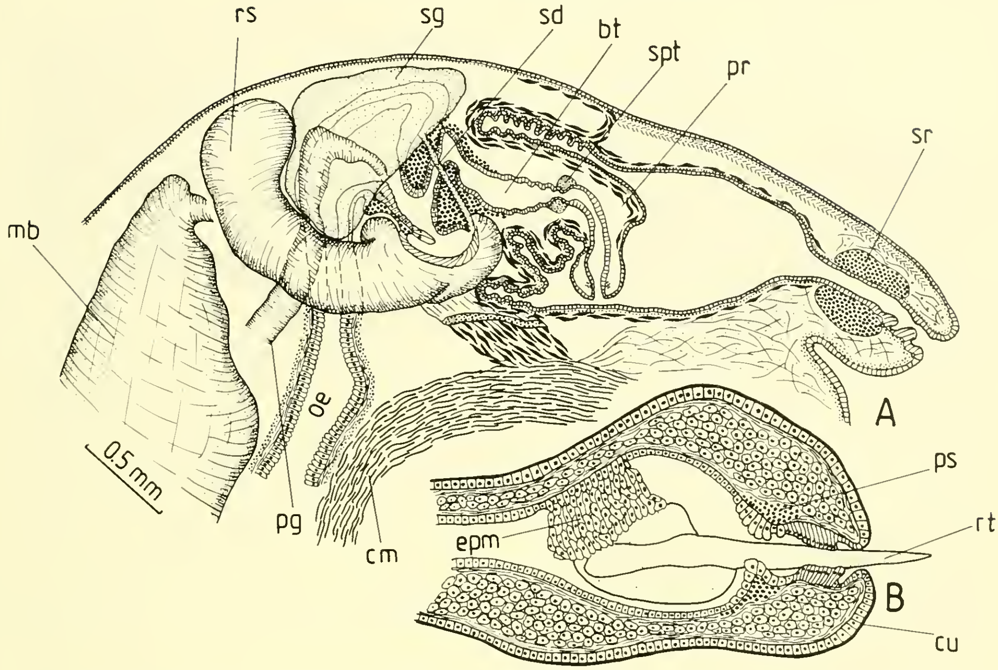

FIG. 3. Anatomy of *Splendrillia chatamensis* Sysoev & Kantor. A—semidiagrammatic longitudinal section of the anterior part of molluscan body; B—magnified tip of the proboscis.

Transportation of teeth to the proboscis tip in *Aforia* may occur with the flow of venom during contraction of the muscular bulb or also by peristaltic movements of circular muscle fibres of the buccal tube. *Splendrillia chathamensis* has an additional, well-developed sphincter in the middle part of the buccal tube (Fig. 3A, spt), which probably takes part in the transportation of the tooth. The marginal tooth is detached from the membrane and is pushed into the buccal cavity by the contracting walls of the buccal sac. The tooth length is about 1/3–1/4 of the contracted proboscis length. During the contraction of the proximal part of the proboscis, the tooth becomes held by the additional sphincter. When the distal part of the proboscis contracts, the tooth is passed into the oral sphincter.

The function of the radula as a whole organ within the buccal cavity is most probably for the transport of food from the cavity to the oesophagus. This may be confirmed, in particular, by the observations of Maes (1981), who noted the presence of intact sipunculans in the posterior part of the oesophagus of *Drillia cydia* (Bartsch, 1943) (Clavinae), although the large, pectinate lateral teeth might at first sight be thought to serve for tearing or rasping the prey.

The use of marginal teeth at the proboscis tip in turrids with a well-developed radular membrane is probably a widespread phenomenon amongst the Turridae. This may explain the origin of hollow marginal teeth in different groups possessing the radular membrane and odontophore. For example, *Imaclava* (Clavinae), most probably also uses the teeth at the proboscis tip for stabbing the prey in a way similar to higher toxoglossans.

In summary, the main features of this feeding mechanism are: the detachment of marginal teeth from the radular membrane during its degeneration; transportation of the teeth to the proboscis tip; and their use for damaging and poisoning the prey with the venom. A feature of the proboscis is the sac-like enlargement of the anterior part of the buccal tube, with the sphincter holding the base or the middle part of the tooth. The function of the radula as a whole organ is mainly for the transport of the food from the buccal cavity to the oesophagus, although in some turrids it may be used also for tearing and rasping. This could be confirmed by the investigation of the prey ob-

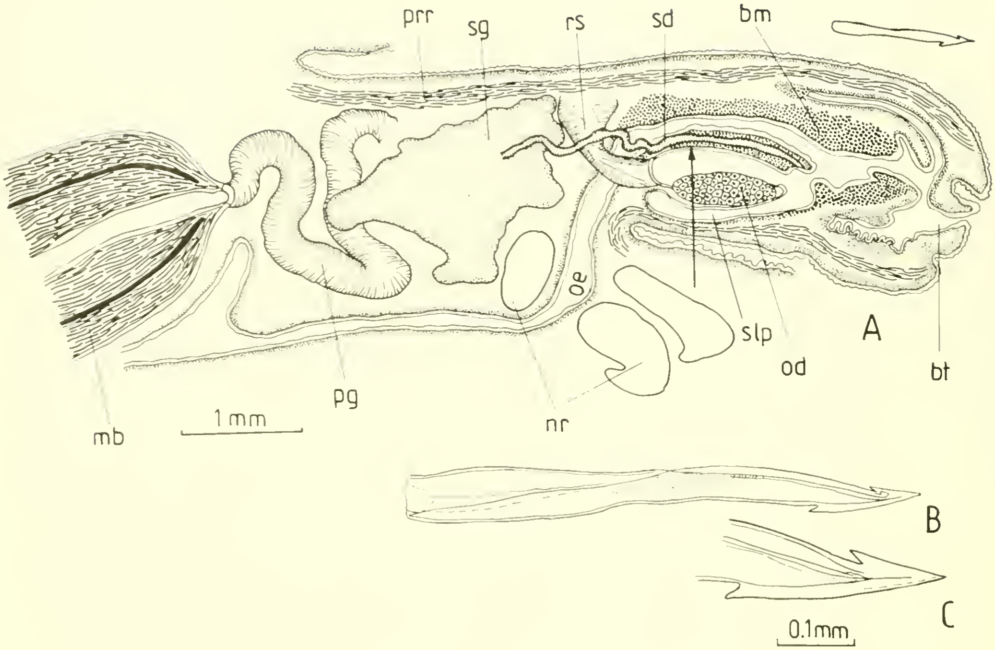

FIG. 4. Morphology of the digestive system of *Toxiclionella tumida* (Sowerby). A—semidiagrammatic longitudinal section of the anterior part of the digestive system. The convolution of the venom gland and posterior part of the radular sac are not shown, the arrow indicates the entrance of the venom gland in the oesophagus; B—marginal tooth; C—the tip of the tooth, enlarged.

tained from the buccal cavity and anterior oesophagus. Thus, the slicing, slicing-rasping, and slicing-stabbing types of radula described by Shimek & Kohn (1981) belong principally to the same functional type, which may be named "stabbing–transporting" type.

Feeding Mechanism Type 3

The third feeding mechanism has been found so far only in a single species of Turridae, *Toxiclionella tumida* (Sowerby, 1870) (Clavatulinae), although it probably exists in other species of this endemic south African genus. A feature of the morphology of the digestive system is the position of the buccal mass, with the odontophore near the proboscis tip (Fig. 4A). The oral sphincter is absent. The gastropod has a well-developed, long venom gland and an unpaired salivary gland with paired ducts, which is situated in the posterior part of the proboscis. The radula consists only of hollow, marginal teeth which are morphologically similar to the teeth of higher turrids (Fig. 4B,C); a radular membrane is present. The teeth are sufficiently long (the tooth, at the same scale, is figured above the proboscis on Fig. 4) that during protraction of the odontophore the tips would protrude through the oral opening. This leads to the conclusion that the mollusc uses the radula as a whole organ for stabbing the prey.

The main difference of this mechanism from all others in which a marginal tooth is used for stabbing and poisoning the prey, is that the radula is used as a whole organ, not as separate teeth. It is possible that a similar mechanism occurs in *Turricula nelliae spurius* (Hedley, 1922) (Taylor, 1985), which has a similar proboscis morphology.

Feeding Mechanism Type 4

The fourth feeding mechanism was found in higher toxoglossans that lack a radular membrane, i.e. higher Turridae, Conidae and some Terebridae. The main feature of the mechanism is the use of individual, hollow marginal teeth at the proboscis tip for stabbing the prey, and the completely reduced function of the radula as a whole organ within the buccal cavity. The feeding and the diet of

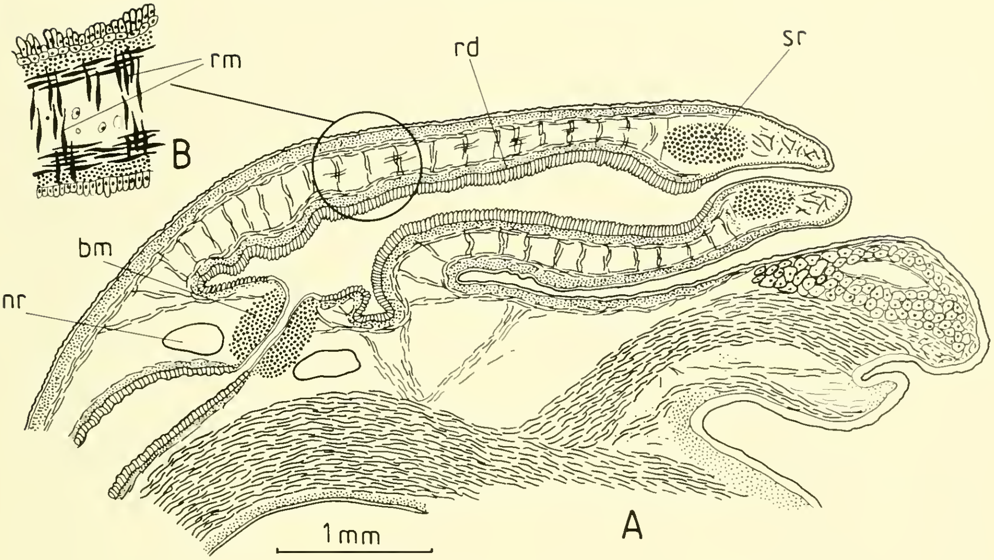

FIG. 5. Anatomy of *Teretiopsis abyssalis* Kantor & Sysoev. A—semidiagrammatic longitudinal section of the anterior part of the molluscan body; B—enlarged part of the section through the body wall and rhynchodaeum.

species with this functional type is well known, and it is unnecessary to describe it in detail. Only the most important morphological features should be noted. These are the vestigial, or completely reduced, radular membrane; the absence of an odontophore; the presence of the short arm of the radular sac, where the fully formed marginal teeth are stored; and a well-developed, oral sphincter for tooth fixation. The radula is represented only by hollow marginal teeth, with the most specialized and complex morphology found within the prosobranchs. The tooth ligament (long flexible stalk attached to the tooth base) is probably the rudiment of the radular membrane. Amongst molluscs of this functional group, the enlarged rhynchostomal lips appeared. In some species, the lips are able to invert (i.e. to form a pseudoproboscis) and this is used in prey capture. It should be noted that in some representatives of the group—some vermivorous species of *Conus* (Marsh, 1970) and *C. geographus* L., 1758 (Johnson & Stablum, 1971)—stabbing is not a necessary part of each feeding act.

Judging from the morphology of the digestive system, Zonulispirinae occupy an intermediate position between the gastropods of the second and the fourth functional groups. They have hollow marginal teeth, attached to a rather strong radular membrane. This may indicate that separate teeth are used at the proboscis tip. Moreover, the gastropods have very small odontophore (Maes, 1983); this indicates that the function of the radula as a whole organ within the buccal cavity is probably rudimentary.

Feeding Mechanism Type 5

The fifth and last functional type is found among those Toxoglossa lacking a radula. Gastropods of this group belong to higher Turridae (according to the shell morphology) and some Terebridae. The most important features are: a reduced or completely absent proboscis; and absence of a radular sac, and venom and salivary glands. Most representatives of this group have either well-developed rhynchostomal lips or a large pseudoproboscis (Terebridae—Miller, 1975; *Philbertia linearis* (Montagu), Turridae—Sheridan et al., 1973). Some turrids (*Cenodagreutes* spp.—Smith, 1967; *Abyssobella atoxica* Kantor & Sysoev—Kantor & Sysoev, 1986; *Teretiopsis* spp.—Kantor & Sysoev, 1989), lacking a pseudoproboscis, have a vast rhynchocoel and have developed a cavity between the rhynchodaeum and body walls, which are connected by numerous muscles in the cavity

(Fig. 5). Species of the genus *Taranis* lack both a pseudoproboscis and a cavity.

The feeding mechanism is known for terebrids (Miller, 1970, 1975). Thus, species with a relatively short pseudoproboscis feed on the enteropneust *Ptychodera flava*, and species with a long pseudoproboscis feed on polychaetes. The capture and engulfment of the prey occurs with the aid of the pseudoproboscis. Turrids lacking a pseudoproboscis, but with a cavity between the rhynchodaeum and the body walls, probably engulf the prey with the aid of negative pressure, which arises in the rhynchocoel during contraction of the radial muscle fibres (at that moment the inner volume of the rhynchocoel increases). It is difficult at present to say anything certain about the feeding mechanism of *Taranis*.

The feeding of such aberrant groups as Strictispirinae (Turridae) is unclear. These gastropods lack a venom gland and have a very large odontophore. According to the figure of Maes (1983), *Strictispira paxillus* (Reeve, 1845) has a short buccal tube. Thus, there is a possibility that it can protrude the radula through the mouth opening and use it pincer-like, tearing off small pieces of food.

Origin of the Toxoglossan Mode of Feeding

In my opinion, the development of the unique "toxoglossan" mode of feeding is connected with certain morphological prerequisites. These were the appearance of the venom gland and the intraembolic type of the proboscis.

The mobile proboscis, which in the contracted state is situated in the special cavity of the body haemocoel, or proboscis-like structures (for exampie, the extrovert formed by the walls of the buccal cavity in Janthinidae—Graham, 1965) appeared independently in different groups of marine predatory gastropods. The presence of the proboscis allows an increase in the mobility of the buccal mass, and this is achieved by its shift from the ventral side of the head (as in herbivorous gastropods) in the terminal (axial) position. This also allows "distant" feeding, i.e. to feed on prey hidden in burrows, crevices, etc., and also on animals with external skeletons, for example on bivalves (inserting the proboscis between the open valves or through a drilled hole).

Usually three types of proboscis are defined: acrembolic, pleurembolic, and intraembolic, these are differentiated by the position of the buccal mass and the mode of eversion. Only the latter two types are found among Neogastropoda. In gastropods with the pleurembolic proboscis, the buccal mass with radular sac is situated near the proboscis tip, and proboscis eversion occurs with the aid of the posterior invaginable part of the rhynchodaeum (wall of the proboscis sheath or rhynchocoel). In many neogastropods with this proboscis type, the entire or nearly entire rhynchodaeum takes part in proboscis eversion. On the contrary, in gastropods with the intraembolic proboscis, the buccal mass is situated at the proboscis base or even behind it (*Pseudomelatoma penicillata*, Turridae—Fig. 1), the invaginable part of the rhynchodaeum is absent, and the proboscis eversion results only from its stretching. Recently, a proboscis somewhat intermediate between the typical pleurembolic and intraembolic types was described in *Turricula nelliae spurius* (Taylor, 1985) and *Toxiclionella tumida* (herein). In these gastropods, the buccal mass is situated near the proboscis tip, and the rhynchodaeum is capable of partial eversion.

Usually, the Neogastropoda are considered as a monophyletic group (Ponder, 1973; Taylor & Morris, 1988). On the other hand, doubts on the monophyletic origin of neogastropods were expressed by Golikov & Starobogatov (1975), with moreover the Toxoglossa (*sensu* Golikov & Starobogatov who included Mitroidea along with Conoidea and Terebroidea in the order) were separated from the rest. The problem of the ancestral group is also essential to the argument. Ponder (1973) considered that the Neogastropoda originated from archaeogastropods or primitive mesogastropods. Thus, the proboscis of neogastropods in general and of Toxoglossa in particular should be considered as *de novo* structure. Taylor & Morris (1988), on the contrary, suggested the possibility of the origin of Neogastropoda from higher, advanced Mesogastropoda and their proboscides thus should be homologous with the pleurembolic proboscis of predatory Mesogastropoda. Finally, Sheridan et al. (1973) stated that the intraembolic type of the proboscis originated from the acrembolic type.

For more careful consideration of the question some comments on the morphology of the buccal muscles are necessary.

In archaeogastropods and primitive mesogastropods lacking a proboscis, there are numerous buccal muscles that are connected to the columellar and pedal muscles. On the contrary, in Mesogastropoda and Neogastropoda with a developed pleurembolic proboscis, the buccal muscles have lost such a connection and are attached to the proboscis walls (Graham, 1973; herein). In a species of Clavinae, which are considered to be the least-derived Toxoglossans, there is such a connection of supramedian, radular tensor and columellar muscles (Fig. 3A). In my opinion, this undoubtedly confirms the original basal position of the buccal mass in Clavinae. In the opposite case, the connection of the buccal and columellar muscles would be lost. Thus, one can state that the intraembolic proboscis has evolved independently from the pleurembolic type and not from the latter (by the shift of the buccal mass to the proboscis base) and that the origin of Toxoglossa and all Neogastropoda in general (if they are considered as a monophyletic group) from higher probosciferous mesogastropods is improbable. Proboscides of different groups of Neogastropoda probably appeared independently, and the detailed morphological studies of some poorly known groups would corroborate this supposition.

The appearance of the intraembolic proboscis in Toxoglossa may be connected with appearance and development of the venom gland. It is very likely that toxoglossan ancestors were carnivorous gastropods with a short acrembolic proboscis. The acrembolic proboscis is found among various primitive gastropods (for example, Naticidae, Triphoridae, Cerithiopsidae) and principally may be considered as an elongated buccal tube that has an ability to evert through the mouth opening as a glove finger. In the inverted position, the buccal mass is situated at the base of the proboscis, while in an everted position it is located at the proboscis tip (Fig. 6 A). During proboscis eversion the oesophagus is pulled through the nerve ring.

The elongation of the acrembolic proboscis allows gastropods to feed on animals hidden in deep burrows, crevices or tubes, for example on polychaetes. At the same time, the elongation of the proboscis limits the size of the oesophageal glands, which have to be pulled through the nerve ring during eversion.

It could be suggested that at early evolutionary stages, these gastropods started to use the secretion produced by the dorsal glandular folds of the oesophagus and squirted through the mouth for immobilization of the prey. This simplified the capture and swallowing of actively moving prey. After the appearance of such feeding mechanism, the proboscis may have elongated by the development of a tube in front of the mouth opening, which was situated in the sheath formed by the walls of introvert of the acrembolic proboscis (Fig. 7B). The main function of the proboscis was not to move the buccal mass forward, but to form the tube through which the venom reaches the prey.

Such elongation of the proboscis appears closely related to the enlargement of the dorsal oesophageal folds; as the inner volume of the proboscis grew, more venom was necessary to fill it. Gradually the glandular folds stripped off from the oesophagus and formed a tube, i.e. the venom gland. In the initial stages of the formation of the new proboscis type, the introvert was probably able to evert, but the enlarged size of the venom gland prevented its being pulled through the nerve ring. Finally, this caused fixation of the buccal mass in front of the nerve ring at the proboscis base, and the introvert ceased to evert. At that moment, the newly formed proboscis possessed all features of the intraembolic type (Fig. 6C). The functions of the radula were the same as in other gastropods (tearing and rasping the prey and its transportation to the oesophagus), but it acted only within the buccal cavity.

If this proposed scheme of origin of the intraembolic proboscis is accepted, then one can suppose that the rhynchodaeum is a homologue of the introvert wall of the acrembolic proboscis and the proboscis itself is *de novo* structure that is not homologous with the pleurembolic proboscis of other neogastropods.

The discovery of a mechanism by which individual solid marginal teeth are used at the proboscis tip in turrids with a well-developed radular membrane, allows us to reconstruct the development of the typical "toxoglossan" mode of feeding. In the process of radula growth, anterior (the oldest) rows of teeth are detached from the radular membrane, which in turn degenerates in the sublingual pouch. It is reasonable to suppose that some detached teeth are not removed through the digestive tract (as usually occurs in gastropods) but are somehow transported to the proboscis tip where they are used for damaging the prey integument. This intensifies the efficiency of venom action. Fixation of such a mechanism in evolution created the prerequisites and necessity of the appearance of hollow marginal teeth. This was an important stage in toxo-

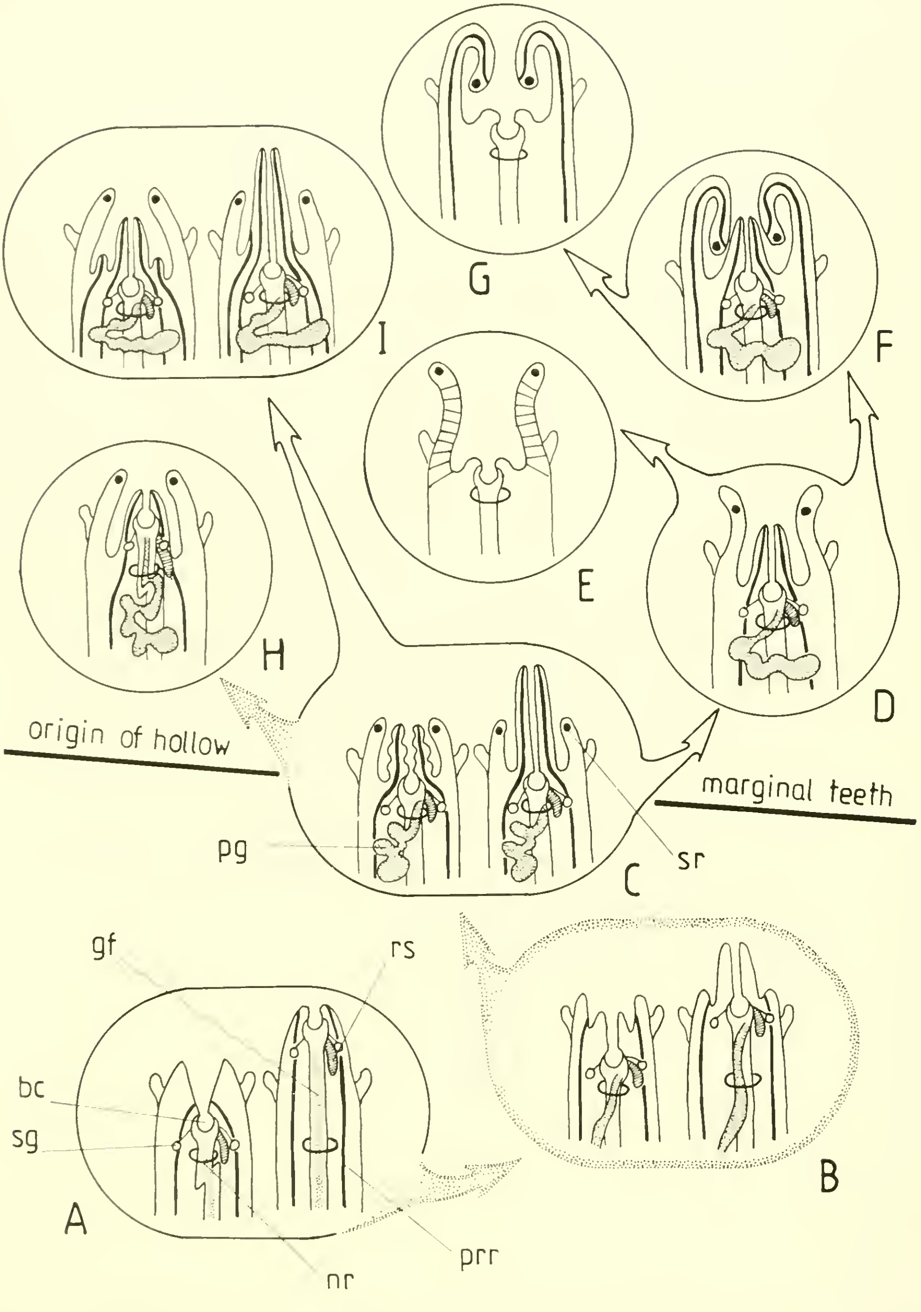

FIG. 6. A scheme for the origin and evolution of the proboscis of Toxoglossa. The dotted arrows indicate hypothetical connections. The hypothetical morphological stage is given on the dotted background. A—acrembolic proboscis of the ancestral group; B—intermediate morphological stage between the acrembolic and intraembolic proboscis types; C—the basal type of the intraembolic proboscis; D—origin of rhynchostomal lips; E—reduction of the proboscis, radula and venom and salivary glands; F—origin of pseudoproboscis; G—reduction of the proboscis, radula and venom and salivary glands; H—displacement of the buccal mass toward the proboscis tip and formation of the curve of the digestive tract; I—formation of the radial folds at the proboscis base.

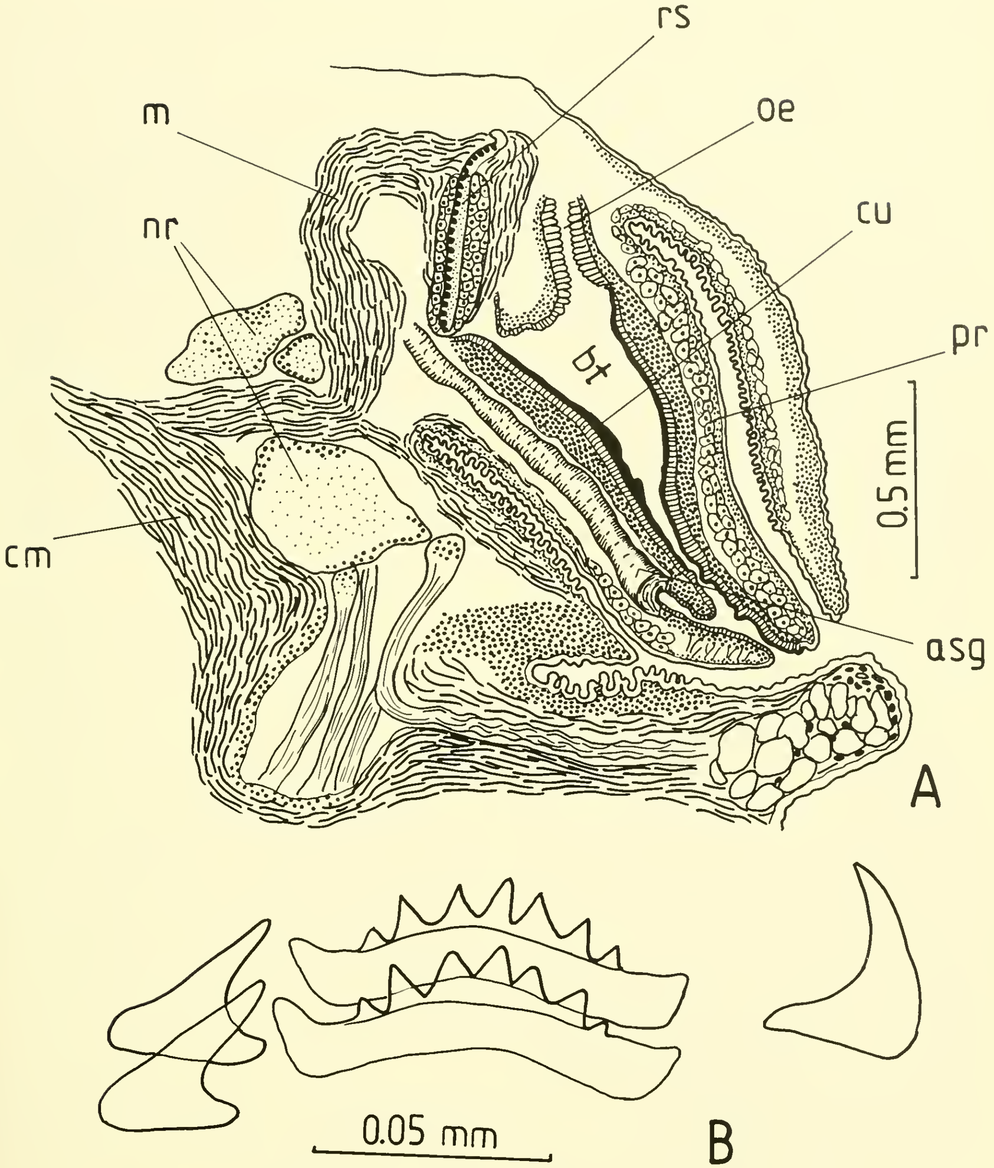

FIG. 7. The anatomy of *Benthobia* n.sp. A—semidiagrammatic longitudinal section of the anterior part of the molluscan body; B—radula.

glossan evolution. As the mechanism of prey stabbing and poisoning by the teeth at the proboscis tip improved, the functions of the radula as a whole organ within the buccal cavity became less and less important. This finally led to reduction of the odontophore, central and lateral teeth, and as a final stage, the radular membrane.

Up until now the intraembolic proboscis has been found only amongst Toxoglossa. However, a similar proboscis type was found by the author in a species of the family Pseudolividae (Fig. 7), *Benthobia* n.sp. The buccal mass in this species is situated at the proboscis base; moreover, there is a connection of the buccal muscles with the columellar muscle (this confirms the primary position of the buccal mass, see above). This gastropod also has a very large gland of Leiblein. According to Ponder (1973), the venom gland of the Toxoglossa and the gland of Leiblein were formed independently, but in similar way, by the stripping off of the glandular folds from the oesophagus. Thus, one can state that Pseudolividae and Toxoglossa are not related groups, and the similar proboscis type appeared independently. The radular morphology of *Benthobia* (Fig. 7B) (very similar to Olividae), as well as details of the morphology of the anterior part of the digestive tract, indicates that the marginal teeth are not used at the proboscis tip by *Benthobia*. Thus, the development of the venom gland rather than the position of the buccal mass at the proboscis base, was the main factor conditioning the appearance of "toxoglossan" mode of feeding in evolution.

The origin of hollow marginal teeth took place repeatedly and independently in different phylogenetic lineages of Toxoglossa. Hollow marginal teeth appeared at least twice among turrids, simultaneously with the retention of the radular membrane and the central and sometimes lateral teeth. Radulae of this type are found among *Imaclava unimaculata* (Sowerby, 1843) (Clavinae) (Shimek & Kohn, 1981) and *Toxiclionella elstoni* (Barnard, 1962) (Clavatulinae) (Kilburn, 1985).

The main trends of subsequent evolution of the Toxoglossa are variable and characterized by morphological changes in the anterior part of the digestive system. Thus, three main pathways of the morphological evolution of the proboscis may be defined. Some Toxoglossa have circular folds formed by the proboscis in the contracted state (Fig. 6I). This reduces the length of the contracted proboscis, and probably simplifies the transportation of the individual marginal teeth from the radular sac to the proboscis tip.

The second lineage is connected with origin and development of the mobile rhynchostomal lips, which take part in the prey capture (Fig. 6D). The progressive development of lips into an introvert results in the pseudoproboscis (Fig. 6F) of some turrids and most Terebridae. The action of prey capture gradually transferred from the proboscis to the rhynchostomal lips or pseudoproboscis, and this finally led to the complete reduction of the true proboscis (Fig. 6E, G). The process is evolutionarily connected with the complete reduction of the radula, venom and salivary glands, a process that occurred independently in different phylogenetic lineages.

Finally, the third, less studied trend is connected with the shift of the buccal mass toward the proboscis tip. Also the rhynchodaeum secondarily evolved the capability of partial eversion (this was made possible by the elongation of the oesophagus between the buccal mass and the nerve ring and formation of the curve of the oesophagus, as it takes place in Rachiglossa). The tendency is best seen in *Turricula nelliae spurius* (Turriculinae) and *Toxiclionella tumida* (Clavatulinae). An intermediate morphological stage is found in *Clavatula diadema* (Kiener, 1840) (Fig. 8), in which the buccal mass is situated inside the proboscis nearer to its base, and the rhynchodaeum is capable of partial eversion. The presence of two consecutive morphological stages in the same subfamily confirms the secondary character of this evolutionary lineage.

In conclusion, one more question should be discussed, the resolution of which may shed light on the ancestral group of Neogastropoda and Toxoglossa. Usually, the radula of Clavinae (Turridae), with a central tooth, flanked by pairs of lateral and marginal teeth, is considered as a plesiomorphic condition in neogastropods (Taylor & Morris, 1988). In pectinibranchiate gastropods, the radula is folded lengthways in the radular sac. The folds in the gastropods with differentiated groups of teeth are situated between the marginal and lateral teeth and between the lateral and central teeth. Thus, in gastropods with marginal and lateral teeth, there are two pairs of folds. A similar condition is observed in *Olivella*, except for the Clavinae, the only genus of neogastropods which has five teeth in a transverse row (Fig. 9A). Nevertheless, the clavine radula has only one pair of folds, which are situated between the central and lateral teeth (Fig. 9B). Species of the genus *Antiplanes* have the central formations which were considered as a reduced central tooth. Investigations of the radula indicate that it has only one fold (Fig. 9C). This may indicate that traditional interpretation of the radular teeth of Clavinae is wrong and their radula is formed by central and two pairs of marginal teeth, which have become greatly differentiated in evolution. In *Antiplanes*, the central tooth is possibly completely reduced, and the central formations are the rudiments of the inner pair of the marginal teeth.

Thus, one can suppose that the toxoglossan

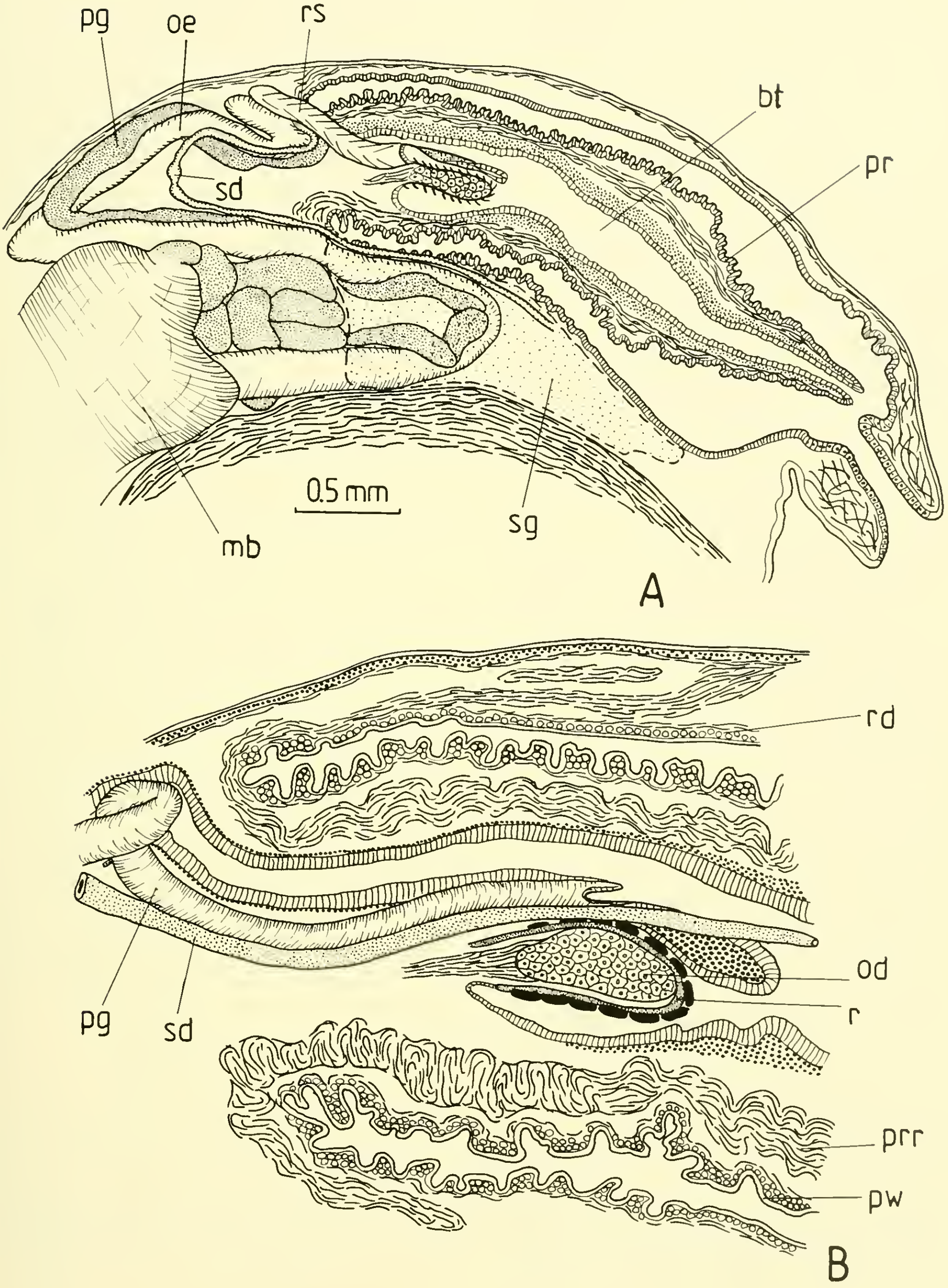

FIG. 8. The anatomy of *Clavatula diadema* (Kiener). A—semidiagrammatic longitudinal section of the anterior part of the molluscan body; B—magnified base part of the proboscis.

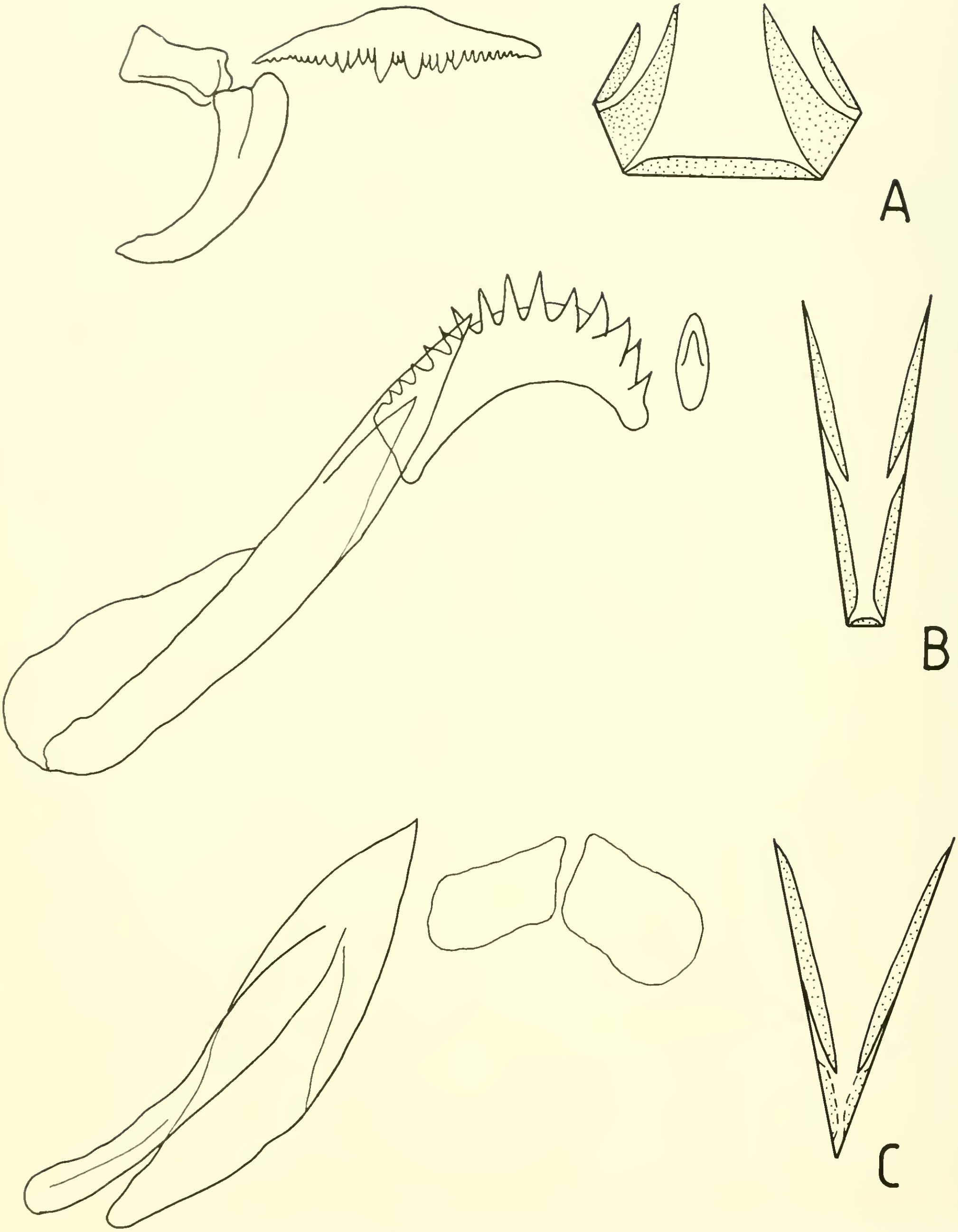

FIG. 9. The radular folding in different Neogastropoda. At the left—the shape of radular teeth, at the right—diagrammatic transverse section of the radula sheath. A—*Olivella*; B—*Splendrillia* (Clavinae); C—*Antiplanes* (Turriculinae).

radula originated from the taenioglossan (2-1-1-1-2) by the reduction of true lateral teeth and differentiation of the marginals. (The radular formula of Clavinae should be 2-0-1-0-2, of *Antiplanes*, 2-0-0-0-2.) On the contrary, in *Olivella* the radula is formed by the rudiments of the marginal teeth, by a pair of laterals and a central, i.e. it originated from the taenioglossan by a reduction of the pair of marginal teeth (formula: 1-1-1-1-1). The present hypothesis supposes that if the Neogastropoda is a monophyletic group, their ancestor had the taenioglossan radula, and the derivation of Rachiglossa and Toxoglossa occurred at an early stage, when the ancestor had seven teeth per transverse row.

CONCLUSIONS

(1) The evolution of Toxoglossa as a separate taxon was connected with the origin and development of the venom gland. The development of the venom gland determined the appearance of the specialized intraembolic type of proboscis and the specific "toxoglossan" mode of feeding.

(2) The ancestors of Toxoglossa were probably lower mesogastropods with a short acrembolic proboscis and taenioglossan radula.

(3) In higher Toxoglossa, the specific "toxoglossan" mode of feeding, using separate, hollow marginal teeth at the proboscis tip, has originated repeatedly and independently in the Turridae. A similar feeding mechanism with the use of solid marginal teeth at the proboscis tip in some lower turrids with a well-developed radular membrane and odontophore may be considered as the intermediate evolutionary stage.

(4) In "higher" Toxoglossa with well-developed rhynchostomal lips or with a pseudoproboscis, a decrease of the proboscis size usually occurs and this leads finally to the complete reduction of the radula, venom and salivary glands.

ABBREVIATIONS

asg—accessory salivary gland; bc—buccal cavity; bm—buccal mass; bt—buccal tube; cm—columellar muscle; cu—cuticle; epm—"mat" of epithelial cells; gf—glandular folds of the oesophagus; m—buccal muscle, connected to the columellar muscle; mb—muscular bulb of the venom gland; nr—nerve ring; od—odontophore; oe—oesophagus; pg—venom gland; pr—proboscis; prr—proboscis retractor muscles; ps—proboscis sphincter; pw—proboscis wall; r—radula; rd—rhynchodaeum; rm—radial muscles, connecting the rhynchodaeum and the body wall; rs—radular sac; rt—marginal tooth, held at the proboscis tip; sd—salivary duct; sg—salivary gland; slp—sublingual pouch; spt—intermediate sphincter of the buccal tube; sr—rhynchostomal sphincter.

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LITERATURE CITED

GOLIKOV, A.N. & Y.I. STAROBOGATOV. 1975. Systematics of prosobranch gastropods. *Malacologia*, 15: 185–232.

GRAHAM, A., 1965, The buccal mass of janthinid prosobranchs. *Proceedings of the Malacological Society of London*, 36: 323–338.

GRAHAM, A., 1973, The anatomical basis of function in the buccal mass of prosobranch and amphineuran molluscs. *Journal of Zoology, London*, 169: 317–348.

JOHNSON, C. R. & W. STABLUM, 1971, Observations on the feeding behaviour of *Conus geographus* (Gastropoda: Toxoglossa). *Pacific Science*, 25: 109–111.

KANTOR, Yu. I., 1988, On the anatomy of Pseudomelatominae (Gastropoda, Toxoglossa, Turridae) with notes on functional morphology and phylogeny of the subfamily. *Apex*, 3: 1–19.

KANTOR, Yu. I. & A. V. SYSOEV, 1986, A new genus and new species from the family Turridae (Gastropoda, Toxoglossa) in the northern part of the Pacific Ocean. *Zoologicheskij Zhurnal*, 65: 485–498. (In Russian).

KANTOR, Yu. I. & A. V. SYSOEV, 1989, On the morphology of toxoglossan gastropods lacking a radula, with a description of new species and genus of Turridae. *Journal of Molluscan Studies*, 55: 537–549.

KILBURN, R. N., 1985, Turridae (Mollusca: Gastropoda) of southern Africa and Mozambique. Part 2. Subfamily Clavatulinae. *Annals of Natal Museum*, 26: 417–470.

KLINE, P., 1956, Notes on the stinging operation of *Conus*. *Nautilus*, 69: 76–78.

KOHN, A. J., 1956, Piscivorous gastropods of the genus *Conus*. *Proceedings of the National Academy of Sciences*, 42: 168–171.

KOHN, A. J., 1959. The ecology of *Conus* in Hawaii. *Ecological Monographs,* 29: 47–90.

KOHN, A. J., 1968, Microhabitats, abundance and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. *Ecology,* 49: 1046–1061.

MAES, V. O., 1983, Observations on the systematics and biology of a turrid assemblage in the British Virgin Islands. *Bulletin of Marine Sciences,* 33: 305–335.

MARSH, H., 1970, Preliminary studies of the venoms of some vermivorous Conidae. *Toxicon,* 8: 271–277.

McLEAN, J. H., 1971, A revised classification of the family Turridae, with the proposal of new subfamilies, genera, and subgenera from the eastern Pacific. *Veliger,* 14: 114–130.

McLEAN, J. N., 1971, Family Turridae. In KEEN, A. M. *Sea shells of tropical West America; marine molluscs from Baja California to Peru.* Second ed. Stanford: Stanford University Press, pp. 686–766.

MILLER, B. A., 1970, Studies on the biology of some Indo-Pacific Terebridae. Ph. D. thesis, University of New Hampshire, Dover, 213 pp.

MILLER, B. A., 1975, The biology of *Terebra gouldi* Deshayes and a discussion of life history similarities among other terebrids of similar proboscis type. *Pacific Science,* 29: 227–241.

MILLER, B. A., 1980, The biology of *Hastula inconstans* (Hinds, 1844) and a discussion of life history similarities among other hastulas of similar proboscis type. *Pacific Science,* 33: 289–306.

MORRISON, J. P. E., 1966, On the families of Turridae. Annual *Report of the American Malacological Union for 1965*: 1–2.

PEARCE, J. B., 1966, On *Lora treveliana* (Turton) (Gastropoda: Turridae). *Ophelia,* 3: 81–91.

PONDER, W. F., 1973, Origin and evolution of the Neogastropoda. *Malacologia,* 12: 295–338.

POWELL, A. W. B., 1966, The molluscan families Speightiidae and Turridae. An evaluation of the valid taxa, both Recent and fossil, with lists of characteristic species. *Bulletin of the Auckland Institute and Museum,* 5: 184 pp.

SHERIDAN, R., J.-J. VAN MOL & J. BOUILLON, 1973, Etude morphologique du tube digestif de quelques Turridae de la région de Roscoff. *Cahiers de Biologie Marine,* 14: 159–188.

SHIMEK, R. L. & A. J. KOHN, 1981, Functional morphology and evolution of the toxoglossan radula. *Malacologia,* 20: 423–438.

SMITH, E. N., 1967, The proboscis and oesophagus of some British turrids. *Transactions of the Royal Society of Edinburgh,* 67: 1–22.

SYSOEV, A. V. & Yu. I. KANTOR, 1987, Deep-sea gastropods of the genus *Aforia* (Turridae) of the Pacific: species composition, systematics, and functional morphology of the digestive system. *Veliger,* 30: 105–126.

SYSOEV, A. V. & Yu. I. KANTOR, 1989, Anatomy of molluscs of genus *Splendrillia* (Gastropoda: Toxoglossa: Turridae) with description of two new bathyal species of the genus from New Zealand. *New Zealand Journal of Zoology,* 16: 205–214.

TAYLOR, J. D., 1985, The anterior alimentary system and diet of *Turricula nelliae spurius* (Gastropoda: Turridae). In: MORTON, B. & D. DUDGEON, eds., *Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong 1983,* Hong Kong University Press, pp. 175–190.

TAYLOR, J. D. & N. J. MORRIS, 1988, Relationships of neogastropods. *Malacological Review, Supplement 4*: 167–179.

THIELE, J., 1929 [–1931], *Handbuch der systematischen Weichtierkunde.* Jena, Gustav Fischer, 1929–1935: 1154 pp.

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