J. Moll. Stud. (1989), **55**, 537–549.

THE MORPHOLOGY OF TOXOGLOSSAN GASTROPODS LACKING A RADULA, WITH A DESCRIPTION OF NEW SPECIES AND GENUS OF TURRIDAE.

YU. I. KANTOR and A. V. SYSOEV
A.N. Severtzov Institute of Animal Evolutionary Morphology and Ecology of the USSR Academy of Sciences, Moscow, USSR.

(Received 8 August 1988, accepted 20 December 1988)

ABSTRACT

The morphology of some deep-sea Turridae lacking radulae was studied. The main features of their digestive system are the absence of a radula sac, venom and salivary glands and the reduction or absence of a proboscis. A new genus *Teretiopsis* including 3 new species and *T. thaumastopsis* (Dautzenberg and Fischer, 1896) is described. On the basis of differences of the digestive system when compared with other turrids lacking radulae the monotypical subfamily Taraninae Casey, 1904 new status (type genus *Taranis* Jeffreys, 1870) is considered. It is shown that the process of radula reduction has occurred independently in different phylogenetic lines of Toxoglossa—the subfamilies Daphnellinae and Taraninae among Turridae and the family Terebridae.

INTRODUCTION

The marine gastropod order Toxoglossa is large and very variable in the morphology of both the shell and soft anatomy. Available data suggest that the evolutionary radiation of the Toxoglossa is connected to a considerable extent with changes in the radular apparatus and associated features of the anterior digestive system. In this regard, loss of the radula in some representatives of the order is of special importance. Evaluation of the loss of such a functionally significant organ is not only essential for understanding general evolutionary pattern of the group but it is also interesting in respect of their general feeding biology.

The morphology of toxoglossan digestive system has been insufficiently studied and this hampers the understanding of functional anatomy of the feeding process. The aims of our work were, thus: 1) to obtain new data on the anatomy of some toxoglossan representatives lacking a radula, 2) to evaluate the general occurrence of radula loss based on original observations and published descriptions, 3) to study the distribution of this phenomenon among different phylogenetic branches of the order, and 4) to understand concomitant functional transformation of the entire digestive system.

During the study, three new species of a new genus were found. According to Bouchet & Waren (1980) *Taranis moerchi* (Malm, 1861) lacks a radula and the anatomy was studied as a comparison with these species.

MATERIALS AND METHODS

Material for this study was collected by Soviet expeditions on the research vessels *Akademik Kurchatov*, *Vityaz*, *Professor Shtockman*. The type specimens are deposited in the Zoological Museum of Moscow State University. Four preserved specimens of *Taranis moerchi* were kindly provided by Dr. Anders Warén of Naturhistoriska Ricksmuseet, Stockholm, Sweden.

Examination of the external morphology and the mantle complex of organs were carried out with a stereomicroscope. After removing the visceral mass and mantle, the anterior parts of the molluscan body were dehydrated and embedded in paraffin wax and sections 7-10 μm thick were cut and stained with Mallory's triple stain.

Key to abbreviations in figures
bm—buccal mass; c—heart; clm—columellar muscle; cm—circular muscles; ct—ctenidium; dd—ducts of digestive gland; dg—digestive gland; ep—epithelium of the body; epr—epithelium of the rhynchodaeum; f—flagellae of the mantle fold; gon—gonad; h—head; hg—hypobranchial gland; lm—longitudinal muscles; mf—mantle fold; mn—mantle notch; n—nephridium; nr—nervous ring; oe—oesophagus; os—osphradium; ov—ovary ; p—penis; po—pallial oviduct; prp—propodium of the foot; rhc—rhynchocoel; rhd—rhynchodaeum; rns—rhynchostome; rnl—rhynchostomal lips; rpr—rudiment of the proboscis; rsp—rhynchostomal sphincter; rt—rectum; s—siphon; st—stomach; t—tentacle; vs—vesicula seminalis.

SYSTEMATIC DESCRIPTIONS

Order Toxoglossa Gray, 1853
Family Turridae Swainson, 1840
Subfamily Daphnellinae Casey, 1904

Teretiopsis new genus

Type-species—*Teretiopsis levicarinatus* new species

Diagnosis. The shell is small, 5-15 mm high, paucispiral, broad, with a low spire, thin, white, and glossy. The protoconch consists of 4-4.5 whorls, sculptured with diagonally cancellated riblets. Teleoconch whorls are angular, with a nearly flat shoulder. The body whorl is very large and comprises 0.75-0.85 of the shell height. No axial sculpture. The spiral sculpture consists of strong, narrow and widely spaced ribs (1-2 on the spire whorls and 6-15 on the body whorl). Ribs are somewhat waved, at least on the early whorls. The aperture is wide, with no callus on its inner lip. The anal sinus is subsutural, rather shallow and wide. The siphonal canal is rather long. Operculum absent.

The digestive system is characterized by the absence of the radula, venom and salivary glands, and proboscis. The rhynchocoel (rhynchodeal cavity, or proboscis sheath) is vast, with thick muscular walls. The rhynchodaeum (walls of the rhynchocoel) is connected with the body wall by numerous thin muscles. The rhynchostome is either wide and slit-like or rounded and narrow, with small lips and a large sphincter. The buccal mass is rather small, with very narrow cavity. The anal gland is absent.

Differential diagnosis. The new genus is conchologically closest to *Teretia* Norman, 1888, which is also characterized by the absence of a radula, but differs from it by having a broader shell with a much lower spire, by the shallower anal sinus, and by the less numerous, widely-spaced, spiral ribs.

Striking spiral sculpture is also found in *Eucyclotoma* Boettger, 1895 and *Austrocarina* Laseron, 1954. However, the broad shell with low spire, the completely different sculpture of the protoconch and the absence of numerous, thin, axial or spiral riblets, differentiates *Teretiopsis* from these genera.

Included species. At present time, the four following species from bathyal and abyssal (750-5500 m) depths are included in the new genus: *T. levicarinatus* n.sp. (central Atlantic), *T. thaumastopsis* (Dautzenberg & Fischer, 1896) (north-eastern Atlantic), *T. abyssalis* n.sp. (north-western Pacific) and *T. nodicarinatus* n.sp. (south-eastern Pacific).

Teretiopsis levicarinatus new species

(Figs 1A, B; 2; 3)

Material. R/V *Akademik Kurchatov*, station 1157, 05°02,2′N, 20°50,5′W (westward from Liberia), depth 2800 m, Sigsbee trawl, 10.07. 1972, 1 specimen (Holotype), N Lc 5679.

Description. The shell is broadly-fusiform, thin, white, and consists of 2.5 teleoconch whorls and the protoconch. The protoconch consists of 4 whorls, the first one is eroded; the surface of others is covered in their lower part with diagonally cancellated riblets and in their upper part—with curved axial ribs. The teleoconch whorls expand rather rapidly, are angulated at the periphery, with the whorl shoulder almost flat. Below the shoulder, the whorl wall is almost parallel to the shell axis. The suture is shallow. Growth lines are thin and unclear, with some of them slightly thickened in the subsutural zone. Strong spiral ribs are high and rounded, more or less smooth on two last whorls, but somewhat serrated in the earliest definitive part of the shell. The ribs are separated by wide interspaces. On the penultimate whorl, there is one strong rib on the whorl bend and another narrow rib just near the lower suture. On the body whorl, one rib lies on the suture bend, a group of four ribs is situated at the whorl periphery, with one weak rib on the upper part of the shell base. Additionally, there are three narrow but distinct ribs on the siphonal canal. The aperture is wide, rounded, with a weakly and evenly curved inner lip. The canal is slightly curved. The anal sinus is shallow, rounded and broad; its apex is placed in the upper quarter of the whorl shoulder.

Dimensions. Shell height 10.7 mm; body whorl height 8.9 mm; aperture height 7.8 mm; shell diameter (the outer edge of the aperture is broken) 6.4 mm.

Anatomy. The body (Fig. 2A, B) is unpigmented. The last whorl is very large. The mantle extends up to 2/3 of the whorl and covers the head and the part of the foot. It is thin and the ctenidium, osphradium and the rectum (as a greyish band) are clearly seen through it. The foot is large with a broad oval sole and narrow propodium. The operculum is absent.

The head is very large and poorly distinguished from the body (Fig. 2C, D). It is flattened at the front, forming a slightly raised disc, with in the middle a small rounded rhynchostome. The tentacles are very long, thin, cylindrical and rounded at their tips. Eyes are absent. The nephridium is very narrow and the intestine and very large vesicula seminalis are seen through it.

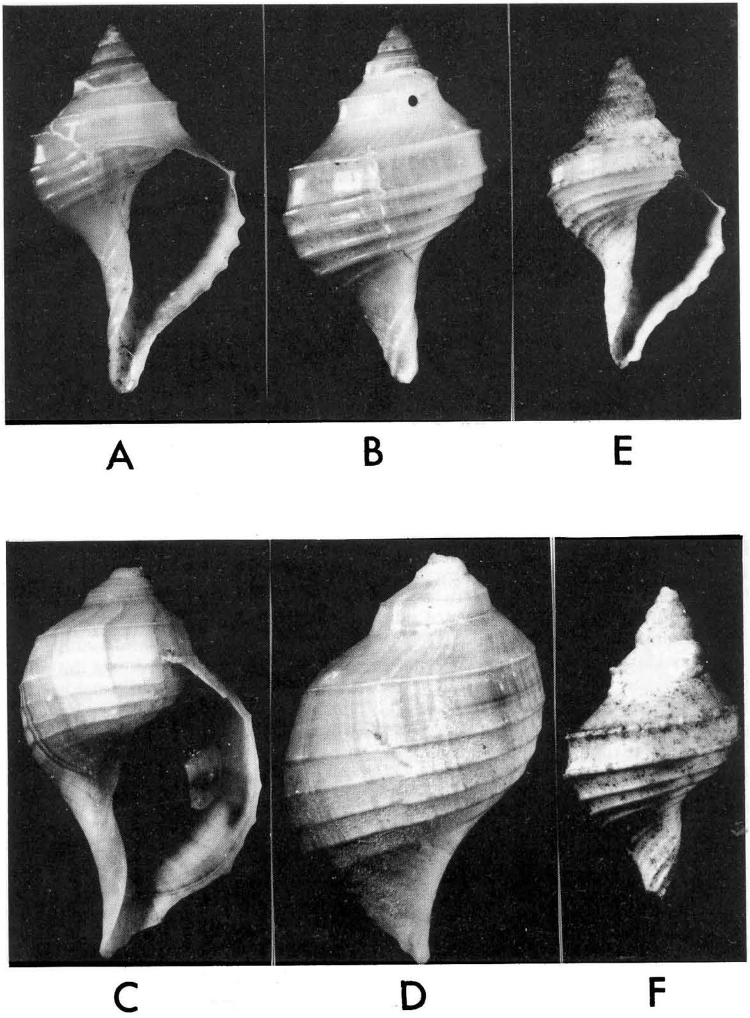

Fig. 1. Shells of *Teretiopsis* new species. A, B—*T. levicarinatus*, Holotype; C, D—*T. abyssalis*, Holotype; E, F—*T. nodicarinatus*, Holotype.

Mantle complex (Fig. 2F). The mantle is short and broad. On the right side, the mantle edge forms a small but distinct notch, corresponding to the anal sinus of the shell. The siphon is very short with thick walls. A moderately broad transverse fold passes the anterior part of the mantle. It lies parallel to the mantle edge and has a few rather short flagellae on its right side. These flagellae are morphologically similar to the lamellae of the ctenidium. The ctenidium is narrow but very long, occupies nearly all the length of the mantle, and is divided into two distinct zones. The posterior zone, near the nephridium, is formed of tall triangular lamellae which bear long flagellae (Fig. 2F.a), which adhere to the inner side of the lamellae. In the anterior zone of the ctenidium, lamellae are absent, while flagellae are free in their outer half (Fig. 2 F.b). The osphradium is very large, relatively broader than the ctenidium and occupies up to 3/4 of its length. The osphradial axis is broad and is formed of three length set at obtuse angles to each other. The osphradium is asymmetrical, the right side much broader with 34 lamellae and the left side with 20 lamellae. The rectum is narrow. The anal opening is placed at the middle of the mantle length. Both an anal gland and distinct anal papilla are absent.

Digestive system (Fig. 3) is characterized by considerable simplification. The radular sac, poison and salivary glands, and proboscis are absent. The rhynchocoel is short and broad; it has thick, muscular, walls consisting of tall, blackish, epithelium and thick layers of circular and longitudinal muscles. The rhynchodaeum is connected with the body walls by numerous thin muscles, which pass through the layers of longitudinal muscles of the rhynchodaeum and the body wall. The rhynchostome is rounded, with small, weakly-developed lips and a large sphincter. The small buccal mass, with thick walls consisting of circular muscles, is situated near the large circumoral nerve ring. The lumen of the mass (the buccal cavity) is very narrow. The oesophagus leaves the buccal cavity to the posterior and has a similar type of epithelium to the rhynchodaeum. The oesophagus gradually widens and passes toward the U-shaped stomach, which contains 2 ducts of the digestive gland (Fig. 2E), the anterior wider than the posterior. After the posterior duct the stomach gradually narrows and passes toward the intestine.

Food remains were found in the intestine, and consisted of a homogeneous whitish mass, with short setae, possibly from annelids.

Reproductive system. The vesicula seminalis (Fig. 2G) is very large and formed by only three loops of very thick seminal duct. The penis (Fig. 2D) is moderately short, smooth and narrows toward its tip. The male gonopore is situated at the apical part of the penis and is not surrounded by the fold. The vas deferens is slightly coiled and is seen through the penis walls.

Teretiopsis abyssalis new species

(Figs 1C, D; 4; 5)

Material. R/V *Vityaz*, st. 3156, 39°57′N, 165°07′8″E (east of Japan), depth 5510 m, Sigsbee trawl, 1 specimen (Holotype) N Lc 5680.

Description. The shell is broad, rounded, thin, glossy, yellowish-white, consisting of two teleoconch whorls and a portion of the last whorl of the broken protoconch. The preserved part of the protoconch is sculptured with diagonally cancellated riblets in the lower part of the whorl, and with curved axial riblets in the upper part. The teleoconch whorls expand very rapidly, are angulated at the smooth shoulder, and are separated by distinct, rather shallow sutures. Growth lines are very thin and indistinct. The spiral sculpture consists of strong, rounded, more or less smooth, cord-like ribs separated from each other by wide, uneven, interspaces. On the penultimate whorl, there is a single rib situated on the whorl shoulder. On the body whorl, there is one similar rib, which is separated by a wide space from four other ribs, one of them very weak. Ribs are absent on the shell base and present only on the siphonal canal. The aperture is wide, and rounded, with the inner lip concave at the lower part of the columellar side. The siphonal canal is curved. The anal sinus is shallow and occupies the whole whorl shoulder. Below the whorl shoulder, the growth lines are disposed almost parallel to the shell axis. The sinus apex is situated in the upper third of the whorl shoulder.

Dimensions. Shell height 14.3 mm; body whorl height 13.1 mm; aperture height 10.7 mm; shell diameter 9.2 mm.

Remarks. The new species can be distinguished from other species of the genus by its rounded shell, relatively narrow and low spiral ribs of equal prominence, the presence of a single keel on the spire whorls, by the concave lower part of the aperture inner lip, and by the strongly curved siphonal canal.

Anatomy. The rounded body (Fig. 4A, B) consists of only 2.5 whorls, with the last whorl very large. The mantle extends up to 2/3 of the whorl and covers the head and part of the foot. It is thin, nearly translucent and the osphradium,

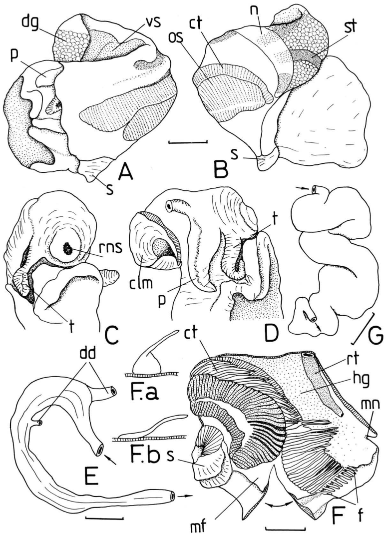

Fig. 2. Morphology of the soft body of *Teretiopsis levicarinatus* n.sp., Holotype. A, B—body, removed from the shell; C—anterior view of the head; D—anterior part of the body (view from the right, mantle removed); E—stomach; F—mantle; F. a—lamella of the posterior zone of the ctenidium; F. b—flagellum of the anterior zone of the ctenidium; G—vesicula seminalis. Scales—A-D, F—1 mm; E, G—0.5 mm.

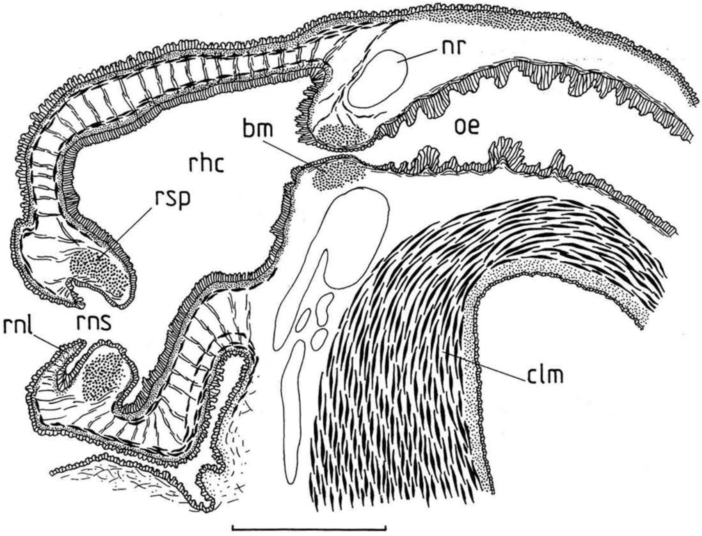

Fig. 3. Semidiagrammatic longitudinal section of the anterior part of the digestive system of *Teretiopsis levicarinatus* n.sp. Scale—0.5 mm.

the ctenidium and the pallial oviduct are seen through it. The body lacks pigmentation. The foot is long, with a very narrow propodium and a broad but shallow marginal cleft. An operculum is absent.

The head is long and broad, poorly distinguished from the body, with moderately long tentacles (Fig. 4C, D). Eyes are absent. The rhynchostome is a broad narrow slit with moderately developed lips.

Mantle complex. The mantle is short, broad, and convex (Fig. 4E). On the right side, the mantle edge forms a distinct notch, corresponding to the anal sinus of the shell. The siphon is short, with thick walls and without a distributive valve at the base. The broad transverse fold passes parallel to the mantle edge, and becomes broader as approaching the right side of the mantle. To the right the fold bears the small flagellae which are morphologically similar to those of the ctenidium lamellae. The ctenidial morphology is similar to that of *T. levicarinatus* n.sp. It is long and narrow and occupies nearly all mantle length. The osphradium is very large, much broader than the ctenidium and occupies up to 3/4 of its length. The osphradium is asymmetrical and with the right side broader than the left and consisting of 45 lamellae, while the left one has only 30 lamellae. The outer side of each lamella is taller, than the inner. The osphradial axis is formed of three lengths set at obtuse angles to each other.

Digestive system (Fig. 5) is similar to that of *T. levicarinatus* n.sp. The radular sac, proboscis, poison and salivary glands are absent. The rhynchodaeum consists of tall epithelium and layers of circular and longitudinal muscles (Fig. 5B). The rhynchodaeum is connected to the body walls by numerous muscles. The rhynchostomal sphincter is large. The small buccal mass with thick walls and a very narrow buccal cavity is situated in front of the nerve ring. The broad oesophagus leaves the buccal cavity and passes toward a U-shaped stomach. The epithelium of oesophagus and rhynchocoel has a dark-brown coloration. The stomach is typical for Turridae and contains two ducts of the digestive gland; the anterior one is broader than the posterior. The stomach gradually narrows and passes toward the intestine. The rectum is narrow and

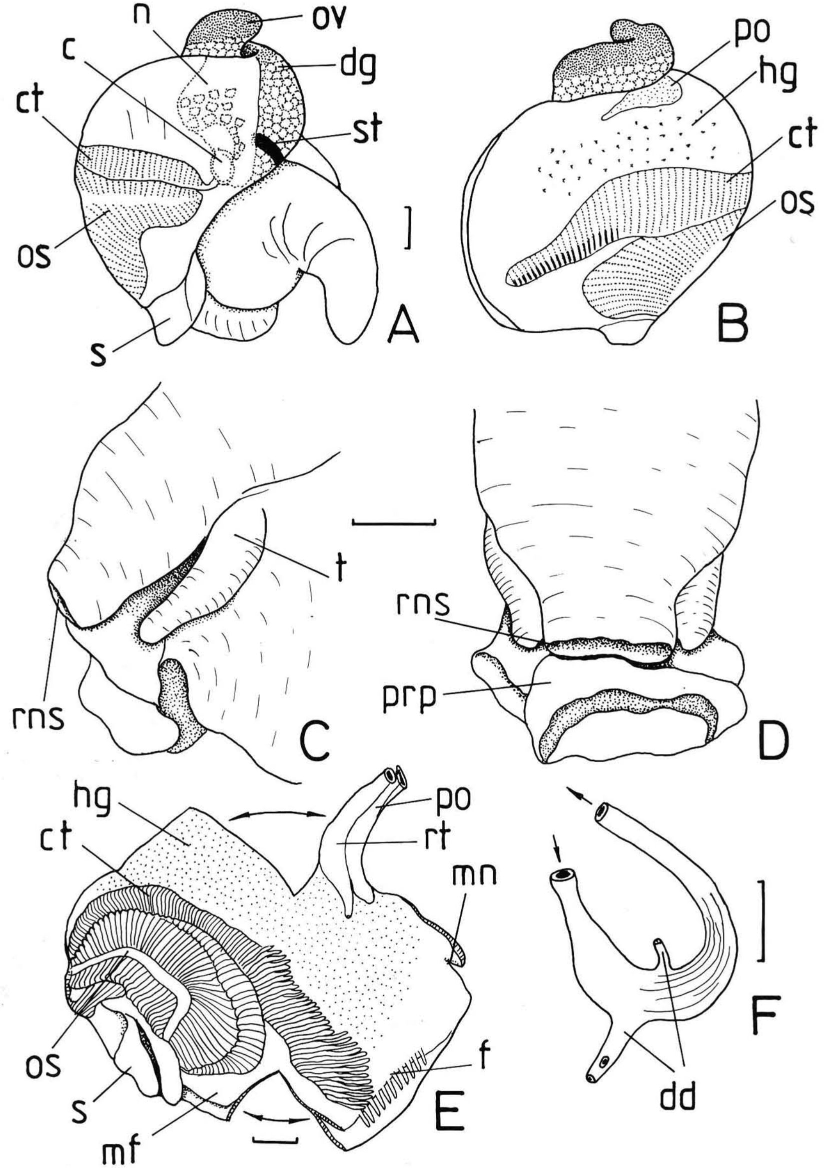

Fig. 4. Morphology of the soft body of *Teretiopsis abyssalis* n.sp., Holotype. A,B—body, removed from the shell; C—head (view from the left, mantle removed); D—anterior view of the head; E—mantle; F—stomach. Scales—1 mm.

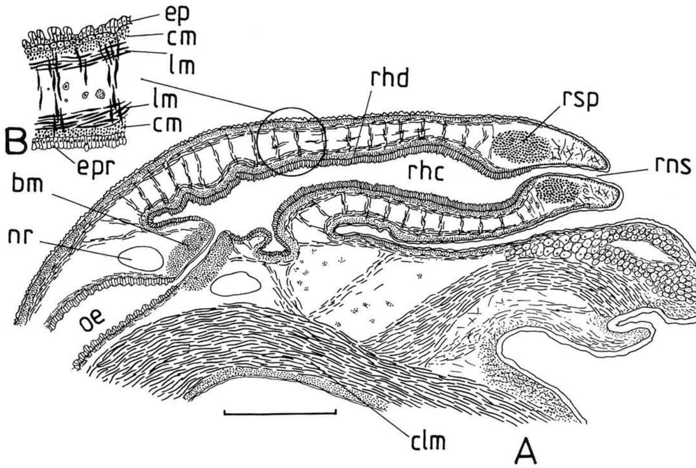

Fig. 5. *Teretiopsis abyssalis* n.sp. A—semidiagrammatic longitudinal section of the anterior part of the digestive system; B—enlarged part of the section through the body wall and rhynchodaeum. Scales—1 mm.

short, opens at the middle of the mantle length. *Reproductive system*. The studied holotype is an immature female. The pallial oviduct has the view of thin, flattened, whitish tube.

Teretiopsis nodicarinatus new species

(Fig. 1E, F)

Material. R/V *Professor Shtokman*, st. 2019, 25°06′ S, 99°28′ W (Sale y Gomez Ridge), depth 750 m, 7.05. 1987, Galathea trawl, 1 specimen (Holotype), N Lc 5681.

Description. The shell is small, consists of four preserved whorls of the protoconch (earliest 1-1.5 whorls missing) and 1.5 teleoconch whorls. The preserved part of the protoconch is dark brown, and the sculpture consists of curved axial riblets on the upper part of the whorl and of diagonally cancellated ones on the rest of the whorl. Teleoconch whorls are grey, thin, with a shining surface, angulated at the periphery, with an almost flat subsutural zone. Growth lines are generally very thin and indistinct, but some of them are very prominent and form rounded folds in the subsutural zone close to the suture. Spiral sculpture consists of two keels on the spire whorls, one on the whorl shoulder and the other on the whorl periphery. On the body whorl, besides these keels, there are wide and rounded ribs (5 on the shell base and 7 on the canal). In the subsutural zone the sculpture consists only of poorly visible hair-like riblets. A small grove passes along the crest of the upper keel. The keels are ornamented with weak and widely spaced nodules which are more visible on the upper keel. The whorl surface between the keels is flat. The siphonal canal is rather long. The anal sinus is subsutural and shallow, with its apex situated in the upper half of the subsutural zone.

Dimensions. Shell height 4.9 mm; shell diameter 2.9 mm.

Remarks. This species is conchologically very similar to the north-eastern Atlantic species *T. thaumastopsis* (Dautzenberg and Fischer, 1896), differing in its stronger second keel which is absent on the spire whorls of the latter species, and in more slowly expanding whorls of the protoconch. The new species differs from *T. levicarinatus* n.sp. in having noded keels and sculpture on the base of the keel.

Taranis moerchi (Malm, 1861)

(Fig. 6)

Material. Sixten Bocks Skagerrakexpedition, Skagerrak, 58°14′N, 9°52′E, depth 275–300 m, 24.07. 1937, 1 specimen, shell height 5.7 mm;

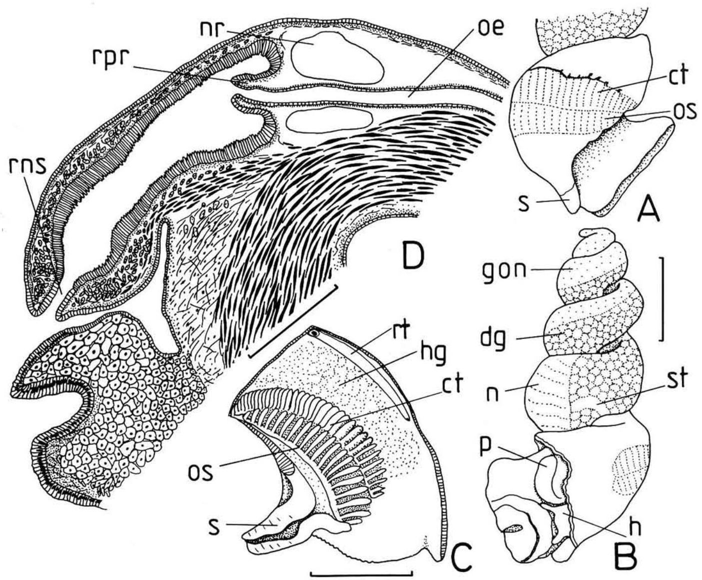

Fig. 6. Morphology of the soft body of *Taranis moerchi* (Malm). A,B—body, removed from the shell; C—mantle; D—semidiagrammatic section of the anterior part of the digestive system. Scales—A-C—1 mm; D—0.25 mm.

western coast of Sweden, Lindo, Bohuslän, depth 110-130 m (type locality), 3 specimens.

The SEM photographs of the shell of *T. moerchi* are represented in Bouchet and Waren (1980).

The morphology of 2 specimens (shell height 5.7 mm, male and 3.7 mm, female) was studied.

Anatomy. The body of the 5.7 mm specimen consists of nearly 5 whorls (Fig. 6A, B), and lacks pigmentation. The mantle extends up to 2/3 of the whorl and does not cover the head and penis. The mantle edge is thickened and serrated. The ctenidium and osphradium are seen through the mantle. The head is small with short tentacles, and well distinguished from the body. Eyes are absent. The foot is large, with an oval sole, narrow propodium and shallow marginal cleft. The operculum is absent.

Mantle complex (Fig. 6C). The length of the mantle equals 1.5 of its width. At the right side of the mantle forms a small notch, corresponding to the anal sinus of the shell. The siphon is moderately long with thin walls and a small distributive valve at its base. The ctenidium is very long and narrow, occupies 2/3 of the mantle length and consists of about 30 tall, triangular, lamellae. The osphradium is large and monopectinate, equal in length but broader than the ctenidium and consists of only 20 lamellae. The rectum is narrow, and an anal gland absent.

Digestive system (Fig. 6D). The radular sac, poison and salivary glands are absent. The proboscis is nearly completely reduced and only a small papilla is seen in the posterior part of the rhynchocoel. The rhynchostome is small, and rounded, without distinct lips or sphincter. The rhynchodaeum is formed by thin layers of circular muscles and tall epithelium. The space between rhynchodaeum and the body walls is filled with parenchyma. The buccal mass is absent. There are separate muscle fibres which connect the rhynchodaeum with the body wall and penetrate the parenchyma. The oesophagus is narrow and lined with low epithelium. The stomach is U-shaped (we were unable to prepare it).

The penis of the mature male specimen is smooth and short.

Remarks. This description shows that the morphology of the digestive system and mantle of *Taranis* differs sufficiently from that of all other turrids lacking radula. These latter are, however, sufficiently similar to each other to comprise a single group, obviously belonging to the subfamily Daphnellinae.

The taxonomic position of *Taranis* is still uncertain. On the basis of shell morphology, Powell (1966) noted the difficulty of referring this genus to any subfamily and provisionally included it in the subfamily Turrinae on account of the position of the sinus at the whorl periphery. However, there is no reason for including *Taranis* in Turrinae, for all other representatives have both radula and operculum, but also differ in shell characters. Moreover, the peripheral position of a very shallow anal sinus of *Taranis*, postulated by Powell can also be questioned. Position of the sinus on the whorl shoulder seems to describe the actual situation more adequately (see Bouchet & Waren, 1980, figs 162-166). Casey (1904) isolated a tribe Taranini basing on the conchological peculiarities of the genus *Taranis*. However, this taxon was not recognized or used by subsequent authors. Considering the peculiarities of shell and soft body morphology, one can see that this genus cannot be referred to any known subfamily of Turridae. This situation has caused us to revaluate Casey's taxon as a subfamily of Turridae.

Subfamily **Taraninae** Casey, 1904 new status
Type genus—*Taranis* Jeffreys, 1870.

Diagnosis. The shell is very small, 2-6 mm high. The protoconch consists of 1.5-2 whorls sculptured with spiral rows of minute granules. Spiral and axial sculpture is moderately developed. The aperture is smooth within. The siphonal canal is short. The anal sinus is shallow, wide and situated on the whorl shoulder. The operculum, radula, venom and salivary glands are absent. The head is small. The rhynchocoel is vast and long, and without a rhynchostomal sphincter. The buccal mass is absent. The proboscis is almost absent. The osphradium is monopectinate.

Differential diagnosis. The new subfamily differs from most subfamilies of Turridae by the absence of a radula. From species of Daphnellinae without radulae, it differs in the character of the protoconch, the very small shell with a wide and shallow anal sinus, and in characters of the digestive system, that is, the absence of the buccal mass, sphincter of the rhynchostome, and the cavity between the rhynchodaeum and body walls. Additionally, taranids have only a rudimentary proboscis and a monopectinate osphradium.

Composition of the subfamily. At present, we can include in the subfamily only the genus *Taranis*, species of which are widely distributed in the North Atlantic and Indo-Pacific including the Australian-New Zealand region (Powell, 1966, 1967).

DISCUSSION

Transformations of the radula and associated structures of the digestive system are of extreme importance for the understanding of evolutionary trends within the Toxoglossa. The probable evolutionarily very early mode of feeding, using individual marginal teeth at the proboscis tip to inject the venom secretion into the prey body, is specific only to the Toxoglossa. The morphological prerequisites of the development of such a feeding mode were both the intraembolic proboscis and the venom gland, which seemed to appear at the earliest stages of evolution. The intraembolic proboscis which is characterized by the fixation of the buccal mass at its base, prevents the functioning of the radula as a whole outside the buccal cavity (Sysoev & Kantor, 1987). The evolution of the venom gland and the mechanism of killing the prey with its secretion, induced the change in the radula function. Use of the radular ribbon steadily decreased, while the use of individual teeth at the proboscis tip assumed greater importance.

Hollow marginal teeth which are adapted to administering the venom secretion into the prey have developed, most likely independently in different phylogenetic lineages. The most specialized and morphologically complex teeth are found in the Conidae. Characteristic of the toxoglossan general pattern (a rolled sheet which forms a hollow tube), they have developed additional external and internal spurs, barbs, large ligaments. Similar features have developed in some higher Turridae. This radular apparatus is highly specialized and perhaps lacks the adaptability to cope with novel types of food. Obviously, one of the possible ways out of this situation may be a change in the feeding mechanism. In particular, this may be the loss of the radular apparatus adapted to *previous* feeding mechanism.

Such a phenomenon may be observed in different toxoglossan groups. Known cases of *facultative* use of radular teeth in the feeding process and deviations from the typical use of the teeth for primary immobilization of prey may be considered as an intermediate stage of the radula loss. For instance, it has been shown in laboratory investigations that stinging of the prey with the tooth is not necessary for feeding in some vermivorous *Conus* species (Kohn, 1959; Saunders & Wolfson, 1961; Marsh, 1970). Piscivorous *C. geographus* at first releases narcotizing liquid and then engulfs the fish by the extended rostrum (funnel-shaped anterior part of the rhynchodaeum). Only after the mollusc has embraced most part of the prey with its rostrum does the stinging actually take place (Johnson & Stablum, 1971). This species probably uses its radula for defence rather than for feeding, since the mollusc extends its proboscis holding the tooth without extending the rostrum when the shell is touched (Johnson & Stablum, 1971).

Some higher Turridae (for instance, *Oenopota harpularia* and *O. turricula*, see Bogdanov, 1985) have very small and simplified teeth which are unlikely to be held at the proboscis tip and used for damaging the prey body.

It should be emphasized that, in the above cases, the reduction of marginal teeth and their function is not accompanied by a decrease in the function of the venom gland. Thus, the venom gland appears to be an evolutionarily more persistent feature than the radula and is probably lost later.

The phenomenon of radula loss is quite widespread within the Toxoglossa. The lack of a radula has been recorded in some species of *Terebra* (Terebridae) (Rudman, 1969; Miller, 1975) and at present, six genera of Turridae are known (*Taranis* Jeffreys, 1870; *Teretia* Norman, 1888; *Conorbela* Powell, 1951; *Cenodagreutes* Smith, 1967; *Abyssobela* Kantor & Sysoev, 1986; *Teretiopsis* gen.n.) without a radula (Powell, 1966; Smith, 1967 a, b; Bouchet & Warén, 1980; Kantor & Sysoev, 1986). Additionally, the radula is absent in *Philbertia linearis* (Montagu) (Sheridan, Van Mol & Bouillon, 1973) whose systematic position is uncertain.

Thus, the absence of a radula has been shown for representatives of two families out of the four (Conidae, Terebridae, Turridae, Pervicaciidae) recognized at present time. Among the Turridae, most of the genera can be referred, judging from the morphology of shell, and in particular the protoconch, to the Daphnellinae, one of the most derived subfamilies. The genus *Taranis* is referred to the subfamily Taraninae (discussed above). The monotypic genus *Conorbela* cannot be confidently referred to any subfamily and, moreover, probably is not toxoglossan at all. Powell (1951, 1966) has indicated superficial conchological resemblance to the Admetidae. However, the radula-less Admetidae have also lost the operculum which is present in *Conorbela*. Thus the taxonomic position of this genus remains uncertain until the anatomy is studied.

These data indicate that the loss of radula has occurred independently in different evolutionary branches of the Toxoglossa. One may predict that the number of species known without a radula will grow as our knowledge of toxoglossan anatomy increases.

It is interesting to consider the morphological diversity of the digestive system in Toxoglossa lacking a radula. These have been derived from the relatively uniform digestive apparatus of all Toxoglossa.

In many Toxoglossa, a progressive development of rhynchostomal lips can be observed, which play an important and often a primary role in the prey capture. This feature was a morphological prerequisite to the decreasing importance of radular teeth in prey capture.

In some species with a well-developed radula, the development of lips and elongation of the anterior part of the snout resulted in formation of the 'polyembolic' (Smith, 1967 b) type of proboscis (pseudoproboscis *fide* Rudman, 1969). The anterior part of rhynchodaeum develops the ability to be inverted, which facilitates capture and engulfment of the prey. This feature is characteristic, in particular, for the turrids *Philbertia leufroyi boothi* and *P. purpurea* (Smith, 1967 b), and the terebrids *Hastula inconstans* and *H. cinerea* (Marcus & Marcus, 1969; Miller, 1980).

As the pseudoproboscis develops and its function are intensified, the true proboscis is reduced. This process can be demonstrated in a group of related species. For instance, *Philbertia purpurea* has both a pseudoproboscis and a well-developed proboscis; in *P. leufroyi boothi*, the proboscis is almost completely absent but the radula is present and *P. linearis* has a pseudoproboscis, but the proboscis and radula are absent (Smith, 1967 b; Sheridan *et al.*, 1973).

It seems very likely that, as the significance of rhynchostomal lips and their derivative, pseudoproboscis, for prey capture increases, the necessity of the radula for prey immobilization decreases. This resulted in the loss of the radular apparatus, venom and salivary glands.

In some species, the pseudoproboscis may be undeveloped, and a significant morphological and, as shown below, functional feature of most of such species is the presence of a cavity developed between the rhynchodaeum and body walls which are connected by numerous muscles in the cavity.

Three principal types of structure in the anterior part of the digestive system of Toxoglossa lacking a radula can be defined.

1. Toxoglossa with a well-developed pseudoproboscis. The following species are referred to this type: *Philbertia linearis* and all studied Terebridae (*Terebra gouldi, T. thaanumi, T. dimidiata, T. areolata, T. crenulata*) (Sheridan *et al.*, 1973; Miller, 1975).
2. Toxoglossa without a pesudoproboscis but with a developed cavity between the rhynchodaeum and body walls. This type is represented by *Cenodagreutes* spp., *Abyssobela atoxica, Teretiopsis* spp. (Smith, 1967 b; Kantor & Sysoev, 1986; herein).
3. Toxoglossa lacking both a pseudoproboscis and the cavity between the rhynchodaeum and body walls. Only the genus *Taranis* can be referred to this type.

Taxonomic analysis of individual groups indicates an obvious correlation between some evolutionary lineages and certain changes in the digestive system. All Terebridae which have lost the radula belong to the first type, most Daphnellinae—to the second one and Taraninae—to the third type. At the same time, some convergence is seen, for one daphnellinid species also belongs to the first type.

These differences in the digestive system are likely to reflect differences in feeding mechanisms and diet. Unfortunately, observations on feeding behaviour are available only for Type 1 structure. The feeding behaviour of the first group of gastropods has been studied for *Terebra gouldi* (Miller, 1975). This feeds on the enteropneust *Ptychodera flava*. The mollusc catches the prey with its everted pseudoproboscis and then, inverting it, pulls the prey to the 'buccal tube' (*fide* Miller, 1975) i.e. to the anterior part of the buccal mass. The end of the worm is held by contraction of circular muscles of the buccal mass and then the worm is gradually pushed into the oesophagus. All other terebrids studied with the same proboscis type (type 1A, *fide* Miller, 1975) feed also on *P. flava*. One can suggest that *P. linearis* catches and engulfs prey in a similar way.

The feeding of molluscs from the second group can be judged only from gut contents and the morphology of the anterior part of digestive system. An important feature appears to be the presence of more or less vast cavity between the rhynchodaeum and body walls, connected with numerous thin muscles. The functional significance of the muscles is probably in their ability to increase the volume of the rhynchocoel cavity during contraction. The pressure of the body cavity liquid is an antagonist of the muscles. Thus, when muscles contract, a negative pressure arises in the rhynchocoel which allows mollusc to suck food through the rhynchostome.

The food of gastropods of this group is practically unknown. Shells of diatoms, infusoria and foraminifers were found in the intestine of *Abyssobela atoxica,* and in the intestine of *Teretiopsis levicarinatus*, there was a rather homogeneous mass with small setae (probably Annelida).

As for representatives of the third group, it is difficult at present to say anything certain about their feeding mechanism. The absence of prominent muscles connecting the rhynchodaeum with the body walls and the cavity between them indicates the lack of an active mechanism of sucking the food. Taking into consideration the very small sizes of the molluscs, one can suggest that *Taranis* spp. are microphages.

Thus, analyzing the evolution of Toxoglossa, one can note the regular reduction and loss of the radula, which although functionally a very significant organ, has lost its evolutionary plasticity as a result of striking specialization.

ACKNOWLEDGEMENTS

The authors wish to express their thanks to Dr. Anders Warén for providing the material to study and also Dr. Lev I. Moscalev from Institute of Oceanology of the USSR Academy of Sciences for providing material.

REFERENCES

BOGDANOV, I.P. 1985. Morphological and functional analysis of the structure of the frontal section of the digestive system in molluscs of the genus *Oenopota* (Gastropoda, Turridae). *Zoologichesky Zhurnal*, **64**, 1632-1639. (In Russian).

BOUCHET, T. & WARÉN, A. 1980. Revision of the

North-East Atlantic bathyal and abyssal Turridae (Mollusca, Gastropoda). *Journal of Molluscan Studies, Supplement* **8**, 1-119.

CASEY, T.L. 1904. Notes on the Pleurotomidae with description of some new genera and species. *Transactions of the Academy of Sciences of St. Louis*, **14**, 123-170.

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

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

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

MARCUS, E. & MARCUS, E. 1960. On *Hastula cinerea*. *Boletin da Facultade de Filosofia, Ciências et Letias. Universidad de São Paulo,* **260**, Zoologia **23**, 25-66.

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

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 the life history similarities among other hastulas of similar proboscis type. *Pacific Science*, **33**, 289-306.

POWELL, A.W.B. 1951. Antarctic and subantarctic Mollusca: Pelecypoda and Gastropoda. *Discovery Reports*, **26**, 47-196.

POWELL, A.W.B. 1966. The molluscan families Speightiidae and Turridae. *Bulletin of the Auckland Institute and Museum*, **2**, 1-188.

POWELL, A.W.B. 1967. The family Turridae in the Indo-Pacific. Part 1a. The subfamily Turrinae concluded. *Indo-Pacific Mollusca,* **7**, 409-431.

RUDMAN, W.B. 1969. Observations on *Pervicacia tristis* (Deshayes) and a comparison with other toxoglossan gastropods. *Veliger,* **12**, 53-64.

SAUNDERS, P.R. & WOLFSON, F. 1961. Food and feeding behaviour in *Conus californicus* Hinds. *Veliger*, **3**, 73-76.

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

SMITH, E.H. 1967a. Two new species of British turrids. *Veliger*, **10**, 1-4.

SMITH, E.H. 1967b. The proboscis and oesophagus of some British turrids. *Transactions of the Royal Society of Edinburgh*, **67**, 1-22.

SYSOEV, A.V. & KANTOR, Yu. I. 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.