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Anatomy of accessory rhynchodeal organs of *Veprecula vepratica* and *Tritonoturris subrissoides*: new types of foregut morphology in Raphitominae (Conoidea)

A. E. FEDOSOV

A.N. Severtzov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky prospect 33, Moscow, 119071, RUSSIA

ABSTRACT. Anatomy of anterior part of digestive system in two representatives of the subfamily Raphitominae, *Veprecula vepratica* and *Tritonoturris subrissoides* has been studied. *V. vepratica* possesses full set of foregut organs while the foregut of *T. subrissoides* is highly reduced — radula, venom apparatus, proboscis and salivary glands are absent. In both species there is an additional foregut organ, lacking in other studied representatives of Raphitominae but having analogues in representatives of other groups of Conoidea. The foregut morphology of *V. vepratica* and *T. subrissoides*, apparently representing new types of foregut organization for Raphitominae is described, and the possible functioning of these organs is discussed in comparison to analogous structures found in other conoideans.

Origin of special foregut complex, consisting of highly modified radula and venom apparatus and underlying the unique feeding mechanism of Conoidea, was a crucial step in evolution of the group. It allowed their rapid radiation, unusual diversity and doubtless evolutional success [Taylor et al., 1993]. High effectiveness of this mechanism, consisting in usage of separate radular teeth held at the tip of the proboscis for stabbing and envenomation of the prey, allowed *Conus* to become one of the most species-rich genera among invertebrates. Moreover, mollusks of this genus are a rare example of invertebrates having developed fish-hunting [Duda, Palundi, 2003]. Nevertheless, in representatives of some groups of Conoidea the foregut complex providing this effective feeding mechanism, undergoes significant transformations.

In some evolutionary advanced lineages of Conoidea a clear tendency to the reduction or complete loss of radula has been noticed [Taylor et al., 1993, Oliverio, 1995; Kantor, Taylor, 2002]. Usually the loss of radula is accompanied by a reduction of proboscis, venom apparatus and, sometimes, salivary gland, i.e. the other foregut organs employed in the classical conoidean mode of feeding.

The opposite tendency of foregut transformation is the origin of specialised accessory organs, usually constituting outgrowths of rhynchodaeum. Formation of these organs has been observed in mollusks possessing a full set of foregut organs as well as in mollusks demonstrating full loss of foregut complex [Taylor, 1990].

Loss of radula in representatives of Turridae is an extraordinary event and in both known cases a complete reduction of foregut organs is accompanied by appearance of special rhynchodeal structures. These organs are pyriform gland of *Zemacies excelsa* [Medinskaya, Sysoev, 2003] and distinct tongue-shape muscular outgrowth in some species of *Horaiclavus* [Fedosov, Kantor, in press]. These organs have developed in representatives of two subfamilies, Zemaciinae and Crassispirinae, independently.

Some representatives of the family Terebridae also possess a special rhynchodeal organ [Taylor, Miller, 1990]. The presence of this organ, named APS (accessory proboscis structure), does not correlate with the state of reduction of other foregut organs. It sporadically appears in both radulate and radula-less terebrids.

Family Conidae, particularly the subfamily Raphitominae, is characterized by unusually high diversity of foregut morphology exceeding that in other groups of Conoidea [Kantor, Taylor, 2002]. Raphitominae include most of described radula-less representatives of Conoidea [Kantor, Sysoev, 1989; Kantor, Taylor, 2002, our unpublished data]. Despite this great morphological diversity, additional foregut structures have never been found in representatives of Raphitominae, as well as in other Conidae.

While studying anatomy of anterior part of digestive system in representatives of the subfamily Raphitominae, two new types of the foregut which include different rhynchodeal outgrowths, were found in *Veprecula vepratica* Hedley, 1903 and *Tritonoturris subrissoides* Hervier, 1897. They are described below together with the discussion of possible functioning of these organs.

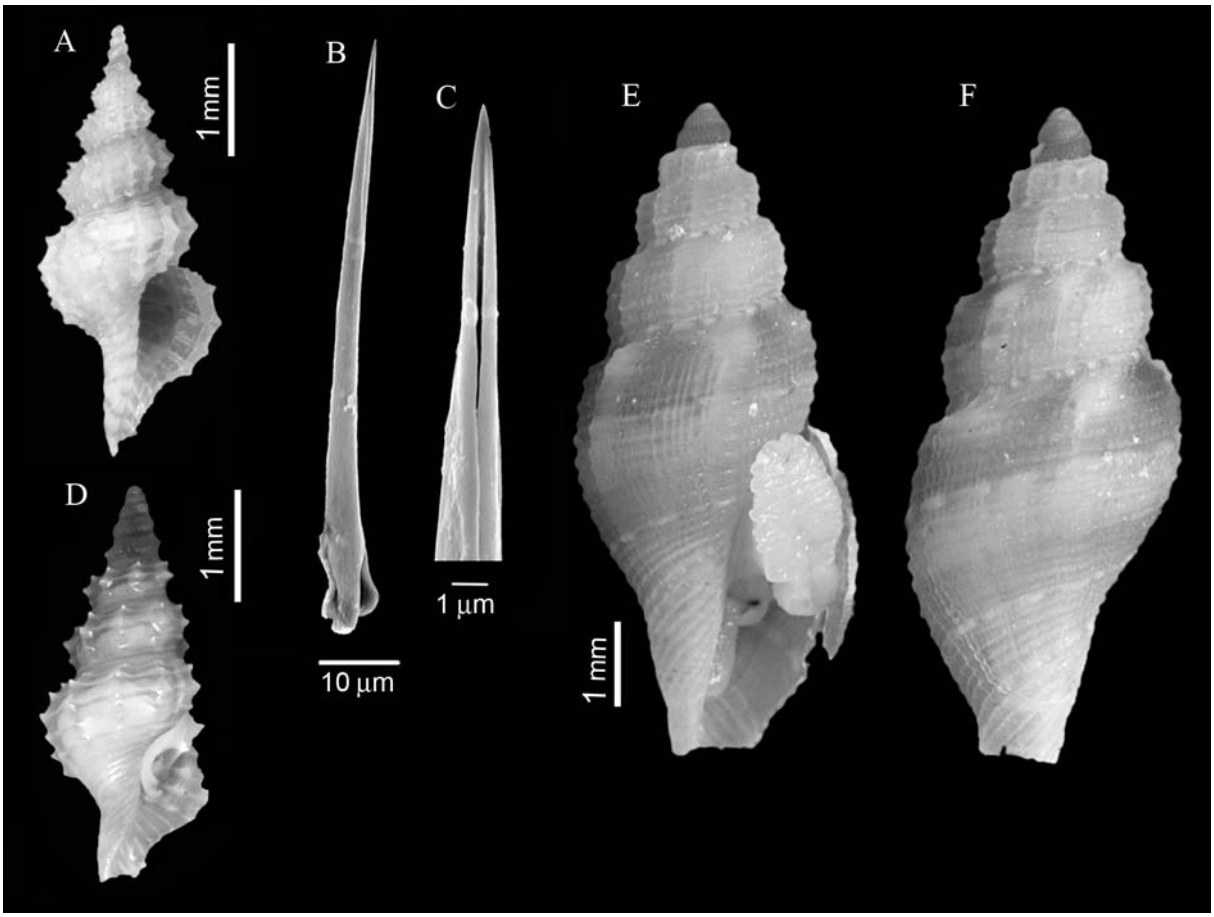

FIG. 1. Studied specimens of *Veprecula* and *Tritonoturris subrissoides*. A–C *Veprecula vepratica*, A — shell, B, C — radular tooth: B — general view, C — tip, D — still undescribed species *Veprecula* n.sp. cf. *spanionema*, E, F — *Tritonoturris subrissoides*.

РИС. 1. Исследованные представители *Veprecula* и *Tritonoturris subrissoides*. A — C *Veprecula vepratica*, A — раковина, B, C — зуб радулы: B — общий вид, C — вершина зуба, D — новый, остающийся неописанным вид *Veprecula* n.sp. cf. *spanionema*, E, F — *Tritonoturris subrissoides*.

Materials and methods

Material for this study was collected from subtidal depths off the southern coast of Vanuatu during Santo'06 expedition of Museum National d' Histoire Naturelle, France. One specimen of *Veprecula vepratica* (Santo'06 st. DS4, 15°31'S, 167°14'E, 20 m, 11.09.2006) (Fig. 1 A), and one specimen of *Tritonoturris subrissoides* (Santo'06, st. DB8, 15°34'S, 167°13'E, 12 m, 12.09.2006) (Fig. 1 E-F) were examined anatomically. Due to the small size of the specimens, especially of *Veprecula* species, their foregut anatomy was studied by serial longitudinal sections of the anterior part of the soft body.

For histological preparations the bodies were extracted from shells, dehydrated and embedded in paraplast; subsequently, serial sections were cut at 5-7 µm thickness and stained with Masson's trichrome.

Abbreviations used on anatomical figures:

bm — buccal mass
bts — sphincter of buccal tube
bw — body wall
cc — central channel of rhynchodeal outgrowth
cm — columellar muscle
co — opening of the central channel
con — circumoesophageal nerve ring
int — rhynchodeal introvert
mb — muscular bulb
oc — opening of the central channel of rhynchodeal outgrowth
oe — oesophagus
pr — proboscis
rns — rhynchostom
ro — rhynchodeal outgrowth
rs — radular suc
rsp — rhynchostomal sphincter
sp — septum
tp — terminal papilla of rhynchodeal outgrowth
vg — venom gland

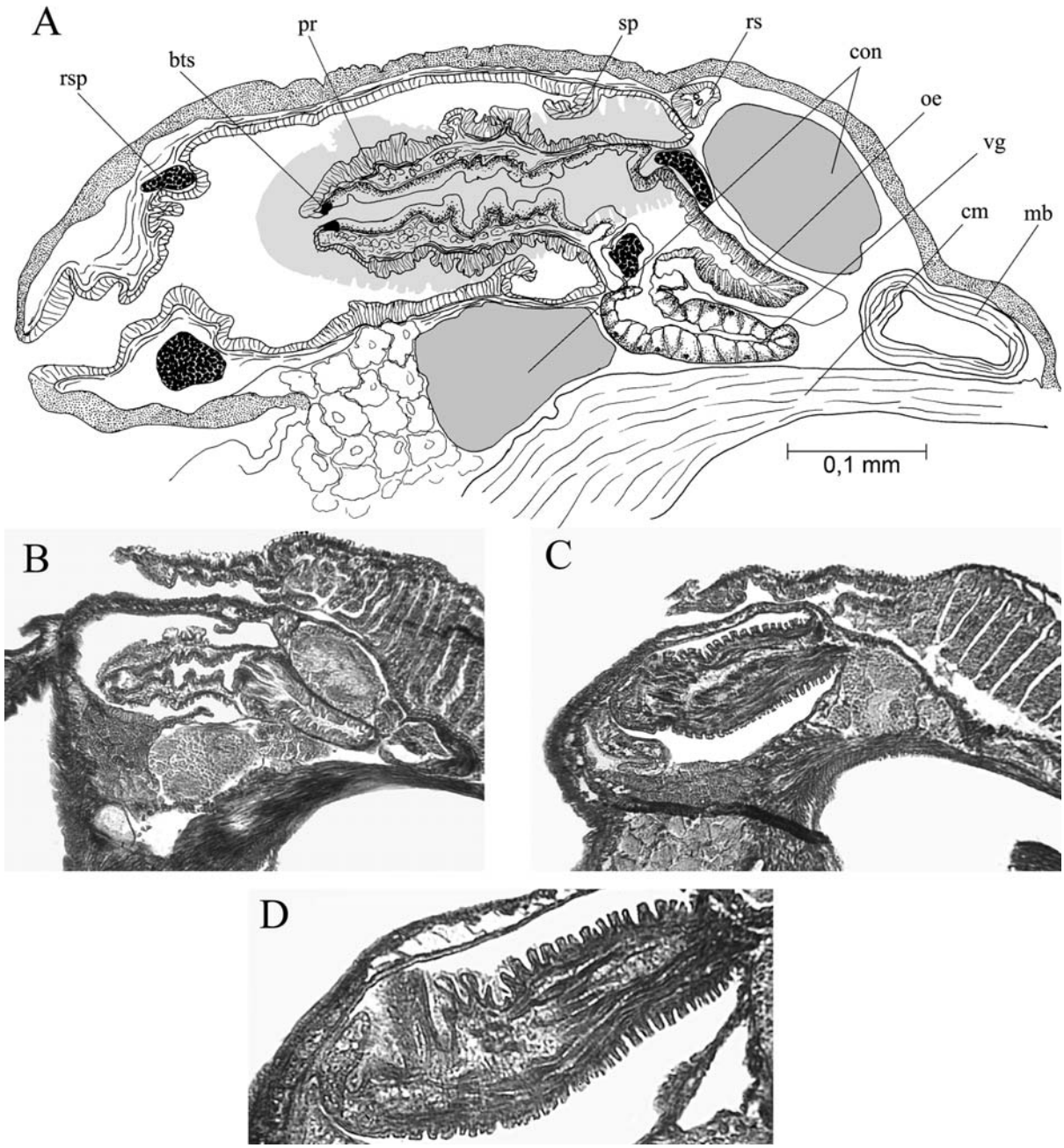

FIG. 2. Foregut anatomy of *Veprecula vepratica*. A — semidiagramatic longitudinal section of the foregut. Position of rhynchodeal outgrowth is shown by gray colour, B — histological section through the buccal mass and proboscis, C, D — histological sections through the rhynchodeal outgrowth.

РИС. 2. Анатомия переднего отдела пищеварительной системы *Veprecula vepratica*. A — схематизированный продольный срез переднего отдела пищеварительной системы. Положение выроста ринходеума показано серым цветом, B — срез через буккальную массу и хобот, C, D — срезы через вырост ринходеума.

Results

Foregut anatomy of *Veprecula vepratica* Hedley, 1903

The rhynchostomal introvert is absent (Fig. 2 A). Rhynchostomal sphincter is medium-sized. There is a rhynchodeal septum, located rather posteriorly in the rhynchocoel. Epithelium lining rhynchocoel anterior to the septum is tall and columnar, while posterior to the septum it becomes significantly lower. Rhynchodeum is underlined by very thin muscular layer.

The proboscis is of medium size, when retracted it occupies more than half the length of the rhync-

hodeum (Fig. 2 A, B). Due to the strongly folded walls of the proboscis, we suggest that in studied specimen the proboscis was sectioned in contracted state. Defined proboscis retractor muscles are absent. The buccal tube is relatively wide, with thick and slightly folded walls due to contracted state of the proboscis. There is a distinct buccal tube sphincter, located near the tip of the proboscis.

The buccal mass is of moderate size, with thick walls formed of circular muscle fibers, lies within relatively very large circum-oesophageal nerve ring. The buccal cavity is lined by medium-tall epithelial cells, possessing long cilia.

The salivary gland is single, tubular, and relatively short, with a wide lumen, and adjoins the middle part of the radular sac.

The venom gland is relatively very thick, short and weakly convoluted. It has uniform histology along the entire length; its inner secretory layer is formed by large rounded cells with granulated cytoplasm. Venom gland opens into the buccal cavity ventrally, posterior to the muscular sphincter of buccal mass. The muscular bulb is small, approximately of the same diameter as the venom gland, composed of single thin layer of muscular fibers and has a wide lumen (that is typical structure for Raphitominae).

The radula sac opens into the buccal cavity ventrally just anterior to the muscular sphincter of the buccal mass. It is long, narrow and curved. Radular teeth are relatively short (Fig. 1 B-C), simple, with unbarbed tip and large base. Radula consists of about 10-12 transversal rows of marginal teeth.

Left half of the rhynchocoel is occupied by a large outgrowth of the rhynchodaeum attached to its posterior part (Fig. 2 C, D). This outgrowth is sausage-shaped and bears several lobes on the tip. Walls of the outgrowth are strongly folded, suggesting ability of its strong extension, and generally resemble proboscis wall. Apical lobes are covered by non-folded epithelium, the cells of which bear long cilia (Fig. 2 D). Below the epithelium there are numerous separate ribbon-like, longitudinal closely spaced muscles, running for entire length of the outgrowth and forming dense muscular layer under the epithelium. These muscles obviously act as retractors, contracting and widening rhynchodeal outgrowth. After leaving the outgrowth, retractors fuse with the muscle layer of the rhynchodaeum. Due to the strongly folded epithelium of the rhynchodeal outgrowth, we suggest that it has been sectioned in contracted condition.

There is a cavity inside the outgrowth, which is confluent with cephalic haemocoel of the mollusk. This cavity has no epithelial lining and is partially filled by loose matrix with few embedded cells. Apical lobes have no such powerful muscle layer as the rest of the outgrowth and have no cavity inside.

Foregut anatomy of *Tritonoturris subrissoides* Hervier, 1897

There is a large rhynchodeal introvert, which in retracted state occupies more than two thirds of the length of the rhynchodeum with very large rhynchostomal sphincter (Figs. 3, 5 E). There is no rhynchodeal septum. Epithelium, lining rhynchocoel, is composed of cubic cells underlined by very thin layer of muscular fibers.

The proboscis is absent, buccal cavity opens directly into the rhynchocoel (Figs. 3, 5 E). There are no folds or any other structures which could represent remains of the proboscis. The buccal mass is short, with thick muscular walls. Oesophagus is delimited from the buccal mass by two circular folds of epithelium.

Radular apparatus, venom and salivary glands are absent.

The most striking feature in the foregut of *Tritonoturris subrissoides* is an enigmatic outgrowth, arising into the cavity of rhynchocoel from its left-dorsal wall (Fig. 4, 5 A-G). It has massive base, occupying almost all left part of rhynchocoel. It gradually narrows towards the tip and bears a long papilla, attached to the outgrowth laterally, slightly posterior to the tip. Papilla in studied specimen entered the buccal cavity. Generally rhynchodeal outgrowth is directed obliquely and posteriorly from upper-left to right part of rhynchocoel.

The outgrowth is covered by the unfolded epithelium composed of uniform non-ciliated cells. Epithelium of the outgrowth is underlined by thin layer of circular muscular fibers. Most of the inner volume of the outgrowth is occupied by complex and well-developed muscles. They are attached to the left side of the roof of the body (Fig. 5 B), forming here a thick layer. At the base of the outgrowth the longitudinal muscles are non-differentiated (Fig. 5 B), more distally they are differentiated into separate bundles (Fig. 5 C-F).

In the center of the outgrowth there is a peculiar channel formed by invagination of the left-dorsal surface of the body wall within mantle cavity (Figs. 4, 5 A-G). The channel runs for nearly entire length of the outgrowth and terminates just under the outgrowth apical surface. The channel is surrounded by thick layer of longitudinal muscles that fuse with the muscle bundles of the outgrowth wall approximately at mid-length of the outgrowth. There is rather spacious cavity between the muscle layers and bundles inside the outgrowth, penetrated by radial muscle fibers connecting muscular layers.

Papilla of the outgrowth (Figs. 4, 5 F) has thin muscular wall, no ducts present.

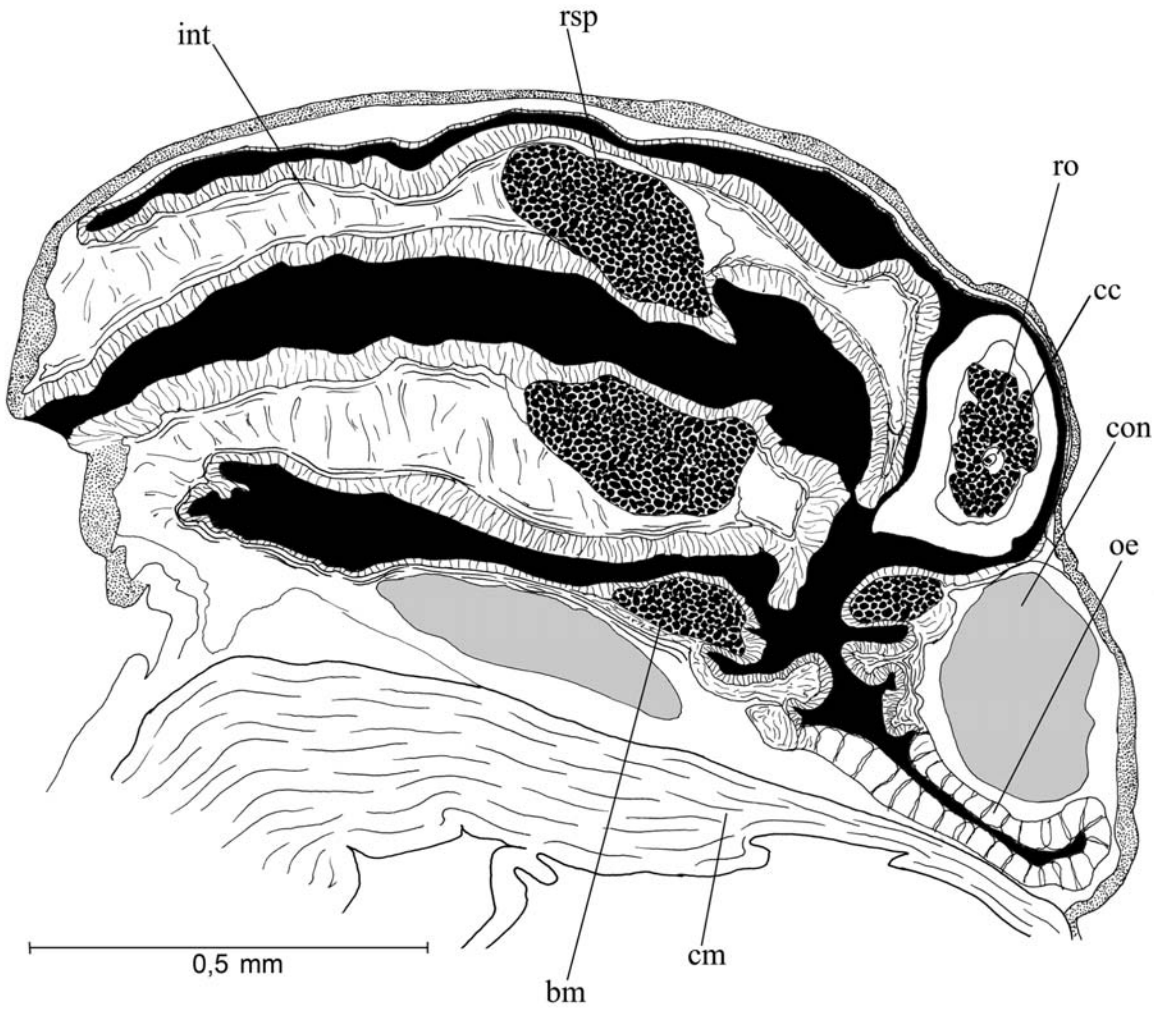

FIG. 3. Semidiagramatic longitudinal section through the foregut of *Tritonoturris subrissoides*.

РИС. 3. Схематизированный продольный срез переднего отдела пищеварительной системы *Tritonoturris subrissoides*.

Discussion

Rhynchodeal outgrowth of *Veprecula vepratica* is characterized by strongly folded walls and presence of a well developed complex of longitudinal muscles that obviously act as retractors. These features are characteristic for organs capable to strong extension, like proboscis. Judging by strongly folded wall of the outgrowth, we suggest that it was contracted in studied specimen. When extended, it perhaps becomes much longer, so most likely it might be protruded through the rhynchostome. But functioning of this structure is unclear. In the position (to the left from the proboscis) and external morphology, the rhynchodeal outgrowth of *V. vepratica* is similar to APS of *Hastula bacillis* and *Terebra affinis* [Taylor, Miller, 1990; Taylor, 1990]. Moreover, the foregut morphology of *V. vepratica* and *H. bacillis* is very similar, in both species there is a rhynchodeal outgrowth together with well developed proboscis, venom gland and radula, i.e. organs providing the classical conoidean mode of feeding. The only difference is the presence of rhynchostomal introvert in *H. bacillis*.

Taylor and Miller [1990] suggested that APS in some Terebridae most likely functions as chemosensory organ recognizing most preferable prey. Despite strong affinities in foregut between *V. vepratica* and some species of Terebridae, functioning of the rhynchodeal outgrowth of *V. vepratica* is unclear. Based on the outgrowth morphology, we suggest that it (1) can be protruded through the rhynchostome, (2) acts rather as chemical or mechanic receptor, judging from ciliated lobes on the apical surface of the outgrowth. Unfortunately there is no data about diet and feeding biology of *V. vepratica*, which could confirm or refute this proposal.

The presence of morphologically similar organs in the foregut of *V. vepratica* and some terebrids

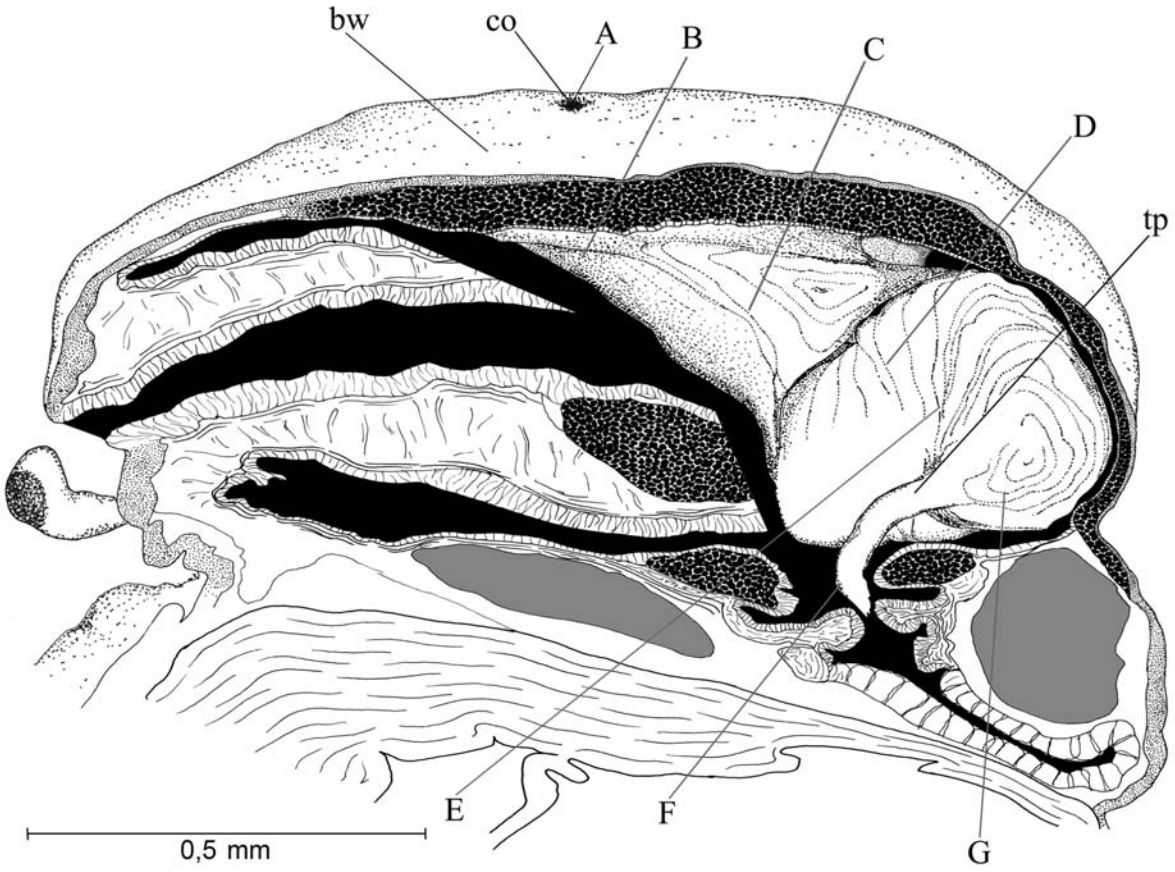

FIG. 4. Reconstruction of the foregut of *Tritonoturris subrissoides*. Capital letters on the three-dimensional drawing of rhynchodeal outgrowth indicate position of sections, photos of the sections are given on the next figure.

РИС. 4. Реконструкция переднего отдела пищеварительной системы *Tritonoturris subrissoides*. Прописные буквы на трёхмерном рисунке выроста ринходеума соответствуют продольным срезам, фотографии которых приводятся на следующем рисунке.

apparently does not suggest close relations of these clades. Most likely APS originated several times in different lineages of Terebridae. It was found in both very primitive and some clearly advanced representatives, so obviously APS can not be regarded as a plesiomorphic character of Terebridae. As well, rhynchodeal outgrowth found in *V. vepratica* has not been observed in another representative of this genus, still undescribed species *Veprecula* cf. *spanionema*, which is conchologically close to *V. vepratica* (Fig 1 D).

While the foregut morphology of *V. vepratica* has analogues within Conoidea, the structure of foregut of *Tritonoturris subrissoides* appears to be unique. The strange muscular organ in the rhynchocoel of *T. subrissoides* evidently plays some role in feeding, but it is difficult to propose any exact mechanism. Judging by well developed and highly differentiated muscular system, the outgrowth is capable to complex and well coordinated movements. Contraction of one or several adjacent muscular fascicles of the outgrowth leads to its bending. Longitudinal muscles of the outgrowth most likely act as its retractor, while the layer of circular muscles together with intramuscular cavity function as a muscular hydrostat, causing elongation of the outgrowth. The channel formed by body wall and lying inside the outgrowth, most likely provides an additional extension of the outgrowth. Typical organ acting as muscular hydrostat is characterized by constant volume, so its capability to extension is limited. The central channel in outgrowth of *T. subrissoides* opens outside and probably mollusk can manage its volume, pumping water into this channel or discharging it. As a result the general volume of the outgrowth changes depending of occupancy of its central channel. This mechanism allows mollusk to adjust the size of the outgrowth, while muscular hydrostat slaves to change its proportions.

The role of terminal papilla is obscure, probably it facilitates operations with food prior to swallowing.

In general combination of (1) large rhyncodeal sphincter, (2) muscular rhyncodeal outgrowth, and

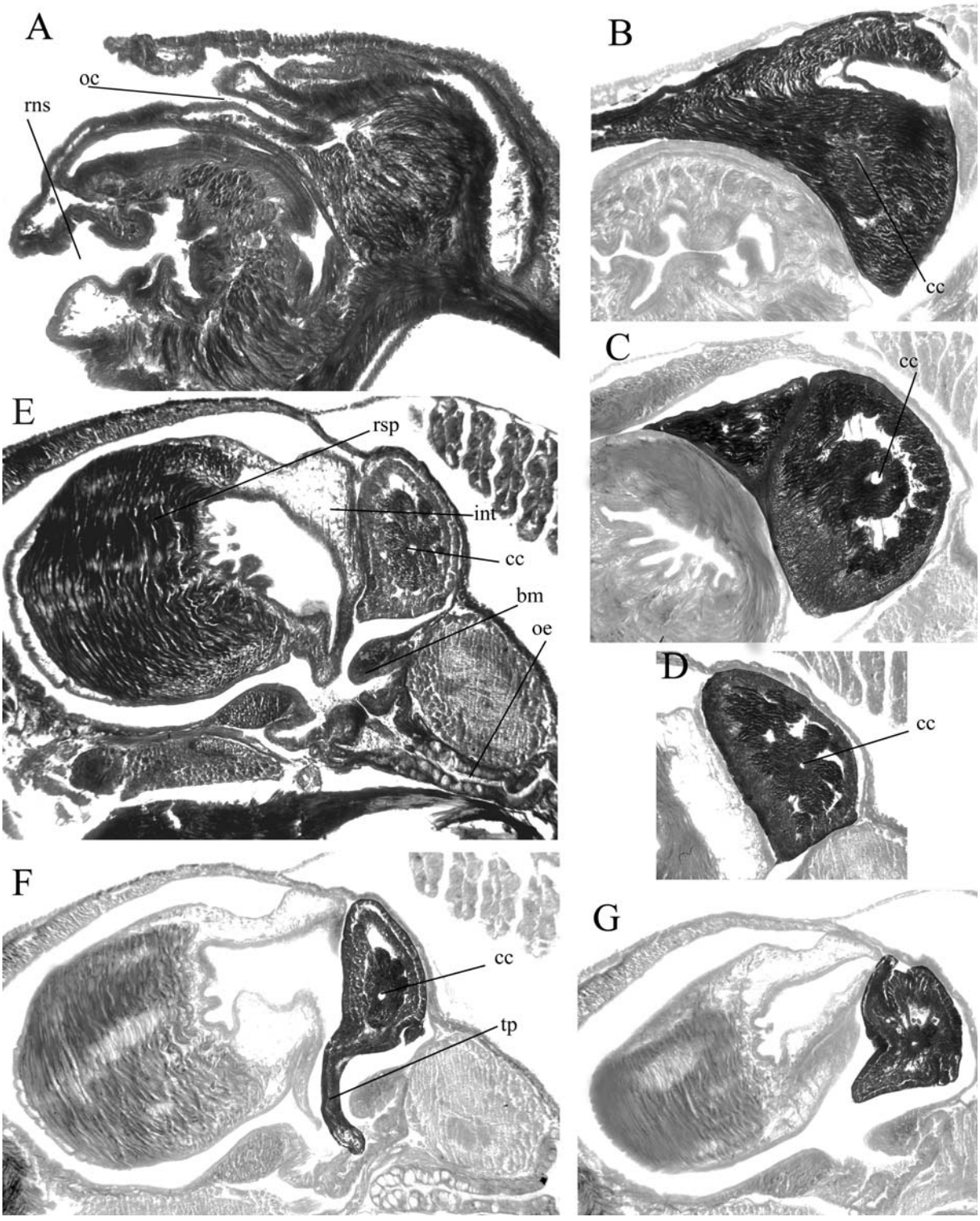

FIG. 5. Histological sections of the anterior part of the digestive system of *Tritonoturris subrissoides.* Position of the sections are indicated on previous figure. On sections B, C, D, F and G brightness of rhynchodeal outgrowth was increased in relation to other foregut structures.

РИС. 5. Гистологические срезы переднего отдела пищеварительной системы *Tritonoturris subrissoides*. Положение срезов показано на предыдущем рисунке. На срезах B, C, D, F и G яркость выроста ринходеума относительно других органов повышена.

(3) extremely reduced foregut of *Tritonoturris subrissoides* reminds the foregut of radula-less representatives of Turridae (*Zemacies excelsa* and *Horaiclavus* spp.). Loss of radula in all these cases is associated with similar morphological transformations of foregut and apparently linked to feeding specialization. Appearance of specialized rhynchodeal structures in these representatives of Conoidea most likely testifies the simultaneous origination of a principally new mode of feeding, independently in at least three lineages of Conoidea.

At the same time a lot of Raphitominae representatives, demonstrating extremely reduced foregut without any additional rhynchodeal structures have been described [Kantor, Sysoev, 1989; Kantor, Taylor, 2002]. Existence of such species suggests that it is quite possible for at least some Conoidea to feed without radula and venom secretion and without any additional organs as well.

The discovery of rhynchodeal outgrowth in *Zemacies excelsa* and in some terebrids warrants distinguishing of new types of foregut morphology in these species [Taylor, Miller, 1990; Taylor, 1990; Medinskaya, Sysoev, 2003]. Similarly, the foregut morphology of *V. vepratica* should be regarded as representing a principally new type for Raphitominae, though in all other respects it is quite common for Raphitominae. Foregut morphology of *T. subrissoides* undoubtedly represents a new type for Conodea, although in general it resembles radula-less Turridae.

Subfamily Raphitominae appears to be most diverse within Conoidea in respect to their foregut morphology [Kantor, Taylor, 2002]. Newly described representatives of Raphitominae, demonstrating two principally new types of foregut organization, further increase the known morphological diversity of the subfamily. To explain such a great diversity of foregut morphology, additional data concerning diet, feeding and general biology of representatives of Raphitominae as well as investigation of evolutionary pathways within subfamily is necessary.

Conclusions

Summarizing all the above-said, we can confidently maintain that described types of foregut morphology are new for Raphitominae. The structure of rhynchodeal outgrowth and general foregut morphology of *Veprecula vepratica* are close to those in some species of Terebridae, with the outgrowth most likely having a receptor function. The foregut arrangement of *Tritonoturris subrissoides* is undoubtedly unique for Conoidea. Exact mechanisms of functioning of described rhynchodeal organs are unclear and new data on the feeding biology of studied species are necessary to clarify them. Discovering of two new types of foregut arrangement in representatives of Raphitominae once again testifies the unusually high diversity of foregut morphology within the subfamily.

At the moment, similar morphological structures originated independently have been found in representatives of all three species-rich families of Conoidea: Turridae, Conidae and Terebridae. This fact confirms the high level of homoplasy within Conoidea and suggests high morphological and evolutionary plasticity of Conoidea.

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Анатомия *Veprecula vepratica* и *Tritonoturris subrissoides*: новые варианты строения переднего отдела пищеварительной системы в подсемействе Raphitominae (Conoidea)

А.Э. ФЕДОСОВ

Институт проблем экологии и эволюции им. А.Н.Северцова РАН, 119071, Ленинский проспект, 33, Москва, РОССИЯ

РЕЗЮМЕ. Исследовано строение переднего отдела пищеварительной системы двух представителей исключительно разнообразного подсемейства Raphitominae, *Veprecula vepratica* и *Tritonoturris subrissoides*. *V. vepratica* характеризуется наличием полного набора органов переднего отдела пищеварительной системы без каких-либо признаков редукции. Пищеварительная система *T. subrissoides,* напротив, сильно редуцирована: радула, ядовитый аппарат, хобот и слюнные железы полностью отсутствуют. В полости ринхоцеля обоих представителей обнаружены органы, отсутствующие у прочих представителей Raphitominae, но имеющие аналоги у представителей других подсемейств Conoidea. Приводятся описания морфологии переднего отдела пищеварительной системы *V. vepratica* и *T. subrissoides*, очевидно представляющих новый для Raphitominae тип организации пищеварительной системы, и обсуждаются возможные способы функционирования обнаруженных органов.