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Morphology, taxonomic status and relationships of Melongenidae (Gastropoda: Neogastropoda)

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ABSTRACT. External morphology, mantle complex and digestive system of four species of Melongeninae (*Melongena corona, Pugilina pugilina, Hemifusus ternatanus, Volema pyrum)*, three species of Busyconinae (*Busycon carica, B. sinistrum, Busycotypus spiratum)* and one of Buccinidae (*Pisania tincta*) are described. Both subfamilies of Melongenidae differ significantly in morphology: head shape and size; morphology and anatomy of proboscis, including anatomy of its walls; mechanism of proboscis invertion and arrangement of proboscis retractors; the presence of valve and gland of Leiblein (absent in Melongeninae); stomach anatomy. Digestive system of Busyconinae is closer to that of Buccinidae than to Melongeninae. A cladistic analysis of 15 species of Buccinoidea and two outgroups suggested that Busyconinae should be excluded from Melongenidae and transferred to Buccinidae as a subfamily. Melongenidae s.s. are supported by several autapomorphies and significantly differ from the rest of Buccinoidea, undoubtedly deserving a familial status. Busyconinae as a clade are supported by several apomorphies, presence of a proboscis septum with separate holes for salivary ducts being the most important.

Introduction

The Buccinoidea is one of the generally accepted monophyletic groups within neogastropods [Harasewych et al., 1997]. It is abundant and diverse group of carnivorous marine gastropods, which encompasses about 1000 species [Taylor et al., 1980].

The Buccinoidea are one of the most geographically widespread and ecologically diverse clade within the Neogastropoda, surpassed only by Conoidea. Having first appeared during the Early Cretaceous (Valanginian) [Tracey et al., 1993], buccinoideans have radiated to occupy most benthic marine habitats ranging from the tropics to the poles and from the intertidal zone to hadal depths. Several members of the family Nassariidae have even invaded fresh water [Brandt, Temcharoen, 1971; Kantor, Kilburn, 2001].

Up to seven families are usually included in this superfamily: Buccinidae, Fasciolariidae, Nassariidae, Melongenidae, Buccinulidae, Collumbellidae and Colubrariidae. Buccinidae is the most diverse family and its taxonomy on subfamilial level is far from being generally accepted. To encompass the variability of Buccinidae in the northern Pacific, Habe and Sato [1973] recognised 6 subfamilies.

A contrary viewpoint on Buccinoidean taxonomy was expressed by Ponder and Warén [1988], who reduced Nassariidae, Melongenidae and Fasciolariidae to subfamilies of Buccinidae, retained Columbellidae as a separate family and considered Buccinulidae, Colubrariidae and all subfamilial names as mere synonyms of Buccinidae.

Kantor [2003] concluded that one of the reasons for the different views on taxonomy of the group is that their foregut (including radula) is rather uniform and rather poor in taxonomic characters. At the same time, characters of the foregut have been generally used for familial discrimination of neogastropods. He demonstrated that stomach anatomy provides an important set of additional characters, very useful for taxonomic discriminations at generic and familial levels.

The family Melongenidae is a small family of Buccinoidea, encompassing slightly more than 20 species, and divided into two subfamilies, the Melongeninae, which have a global, primarily tropical distribution, and the Busyconinae, which have always been restricted to the temperate waters of the Northwestern Atlantic [Harasewych, 1998]. The subfamily Melongeninae Gill, 1871 includes the following Recent genera: *Melongena* Schumacher, 1817 (New World tropics); *Hemifusus* Swainson, 1840; *Volema* Röding, 1788 (both from Indo-West Pacific); *Pugilina* Schumacher, 1817 (one amphiatlantic species, one Indian Ocean species).

The genus *Taphon* H. & A. Adams, 1853, which has been assigned to the Melongenidae by Wenz [1943], is of uncertain affinities [Harasewych, 1998].

Taxonomy of subfamily Busyconinae Wade, 1917 is still under reconsideration. In a more conservative version [Edwards, Harasewych, 1988], two Recent genera with several subgenera are included: *Busycon* Röding, 1798 (with subgenera *Busycon* s.s., *Sinistrofulgur* Hollister, 1958 and *Busycoarctum* Hollister, 1958) and *Busycotypus* Wenz, 1943 (with subgenera *Busycotypus* s.s. and *Fulguropsis* Marks, 1950). Petuch [1994] described a separate subfamily Busycotypinae and considered busyconids as a separate family.

Traditional inclusion of Busyconinae into Me-

Table 1. List of taxa, included in phylogenetic analysis and sources of anatomical data

Taxa	Source of anatomical data
MELONGENINAE	
Melongena corona (Gmelin, 1791)	Herein
Pugilina pugilina (Born, 1778)	Herein
Hemifusus ternatanus (Gmelin, 1791)	Herein
Volema pyrum (Gmelin, 1791)	Herein
BUSYCONINAE	
Busycon (Busycon) carica (Gmelin, 1791)	Herein
Busycotypus (Fulguropsis) spiratum (Lamarck, 1816)	Herein
Busycon (Sinistrofulgur) sinistrum (Hollister, 1958)	Herein
BUCCINIDAE	
Pisania tincta (Conrad, 1846)	Herein
Buccinum undatum Linnaeus, 1758	Dakin, 1912 + Kantor, 2003
Buccinum thermophilum Harasewych et Kantor, 2002	Harasewych, Kantor, 2002a
Neptunea antiqua Linnaeus, 1758	Goryachev, Kantor, 1983 + Smith, 1967
NASSARIIDAE	
Ilyanassa obsoleta (Say, 1822)	Brown, 1969
Nassarius vibex (Say, 1822)	Kantor, 2003 + unpublished
COLUMBELLIDAE	
Mitrella burchardi (Dunker, 1877)	Kantor, Medinskaya, 1991
Columbella mercatoria (Linnaeus, 1758)	Marcus, Marcus, 1962
OUTGROUPS	
Babylonia areolata (Link, 1807)	Harasewych, Kantor, 2002b
Alcithoe arabica (Gmelin, 1791)	Ponder, 1970

longenidae was based primarily on the conchological similarities. Both Busyconinae and most Melongeninae have pyriform to fusiform shells, usually covered with thick periostracum, with broad, medium long to long siphonal canal.

Anatomy of some of Busyconinae was examined, and species were used for student courses of molluscan anatomy [e.g., Pierce, 1950]. On the contrary, little is known about the anatomy of melongenines. Stomach anatomy of two species [*Melongena corona* (Gmelin, 1791) and *Pugilina pugilina* (Born, 1778)] has been recently described [Kantor, 2003], and, based on the differences of stomachs of *Busycon* and Melongeninae, it was supposed that Busyconinae are more closely related to Buccinidae than to Melongeninae.

The present study was undertaken for detailed examination of melongenid anatomy to clarify the status and relationships of the group.

Material and methods

Seven species of Melongenidae (4 from Melongeninae and 3 from Busyconinae) were examined. For comparative purposes, *Pisania tincta* (Conrad, 1846) and foregut of *Ancistrolepis okhotensis* Dall, 1925 (Buccinidae) have also been studied. Material was partially collected by the junior author in Vietnam and Florida, and also provided to us by Dr. J. D. Taylor, Dr. K.S. Tan, Dr. M.G. Harasewych, and Dr. A. Oleinik. For specimens collected by us, shells were usually cracked (sometimes removed) prior to fixation.

The head size and proportions appeared to be important character, discriminating Melongeninae and Busyconinae. The length of the head was measured from the base of the neck to anterior margin, while the width — between the outer corners of head tentacles.

Radulae were removed by gross dissection, cleaned using diluted bleach (NaOCl), air-dried, coated with carbon and gold and examined by Hitachi 400-A scanning electron microscope.

Parts of the anterior foregut of six species were serially sectioned at 8 μm after embedding in paraffin wax, and stained with Masson triple stain.

Stomach of *Melongena corona* and *Pisania tincta* were examined by dissecting live molluscs, and the ciliary currents were traced with carmine particles. All the stomachs were opened in a standard way by a dorsal longitudinal cut along the upper border with the digestive gland. Terminology for stomach description follows Kantor [2003]. Drawings of stomachs of *Melongena corona, Pugilina pugilina, Busycon carica*, and *Pisania tincta* are after Kantor [2003].

Cladistic analysis was performed using PAUP version 4.0b10 for Microsoft Windows. In addition to the species described in this paper, we included several species, for which sufficient anatomical data are available. The list of taxa is presented in Table 1.

Abbreviations: adg, opening of anterior duct of digestive gland; **agl**, ampule of gland of Leiblein; **AL**, aperture length; **anp**, anal papilla; **ao**, anterior aorta; **aoe**, anterior oesophagus; **ba**, buccal artery; **bm**, buccal mass; **bv**, blood vessel; **cep.t**, cephalic tentacles; **cm**, columella muscle; **cml**, circular muscle layer; **cnt**, connective tissue; **ct**, ctenidium; **dg**, digestive gland; **dgl**, duct of gland of Leiblein; **el**, epithelium of proboscis; **eye**, eye; **ft**, foot; **hd**, head; **hg**, hypobranchial gland; **ig**, intestinal groove; **gl**, gland of Leiblein; **gon**, gonad;

int, intestine; **iprr**, internal proboscis retractors; **lf**, longitudinal fold on the inner stomach wall; **lfl**, longitudinal fold on the outer stomach wall; **lm**, longitudinal muscles; **ls**, lateral sulcus; **m**, mantle edge; **mntph**, minor typhlosole; **mo**, mouth opening; **mtph**, major typhlosole; **nep**, nephridium; **ng**, nephridial gland; **nr**, nerve ring; **od**, odontophore; **odc**, odontophoral cartilage; **odm**, odontophoral muscles; **odr**, odontophoral retractors; **oe**, oesophagus; **oef**, oesophageal folds; **oeg**, oesophageal groove; **oel**, oesophageal lumen; **oeo**, oesophageal opening; **oep**, oesophageal pouch; **op**, operculum; **os**, osphradium; **p**, penis; **pc**, pericardium; **pdg**, opening of posterior duct of digestive gland; **pg**, pallial gonoduct; **pma**, posterior mixing area; **poe**, posterior oesophagus; **pr**, proboscis; **prp**, propodium; **prpg**, propodial cleft; **prr**, proboscis retractors; **pw**, proboscis wall; **r**, radula; **rd**, rhynchodaeum; **re**, rectum; **rs**, radular sac; **rsw**, radular sac wall; **s**, siphon; **sd**, salivary duct; **sf**, striated fold; **sg**, salivary gland; **SL**, shell length; **sm**, spiral muscles; **spt**, septum; **src**, subradular cartilage; **st**, stomach; **tg**, transverse groove; **tm**, transverse muscles; **tph**, typhlosole; **vf**, ventral folds of oesophagus; **vl**, valve of Leiblein.

Morphological descriptions

Melongenidae Gill, 1871
Melongeninae
Melongena corona (Gmelin, 1791)

(Figs. 1; 2; 3, A, B)

Material examined: Indian River, Florida, coll. Yu. Kantor, M.G. Harasewych, 3 preserved specimens dissected for gross morphology, stomach studied on 3 live and 2 preserved specimens.

Morphology. Body strongly contracted. Soft tissues comprise about 2.5 whorls (Fig. 1A — visceral mass removed). Mantle spans about 1/2 whorl, nephridium 1/3 whorl, digestive gland 1 1/3 whorls. Columellar muscle very thick, simple, spans about whorl from attachment to operculum. Head small, cylindrical, very long, with pronounced neck, slightly tapering anteriorwards (Fig. 1A — **hd**), its length about three times exceeds width. Tentacles short, contracted, very small black eyes situated at their bases on head. Foot short in contracted state (length ca. equal width), broadly oval. Propodium thickened, strongly pigmented, delimited by broad and shallow furrow. Operculum large, oval, slightly narrowing towards terminal nucleus, yellowish, semitransparent, with numerous, rather distinct growth lines. Body yellowish; head, tentacles, foot, mantle edge, siphon, and penis strongly pigmented with black speckles.

Mantle (Fig. 1B) strongly contracted, its length slightly exceeds width. It is thick, with muscular and thickened edge, slightly pigmented on inner side. Siphon thick-walled, medium-short, slightly extending beyond the mantle edge. Osphradium bipectinate, of same yellowish colour as ctenidium, symmetrical, with broad axis, about 1/3 of mantle length. Width of osphradium is 2/3 of that of ctenidium. Ctenidium wide and long, occupying 3/4 of mantle length. Ctenidial lamellae are taller in posterior part (closer to heart) and having the shape close to right-angled triangle, while in central and anterior parts becoming broader, close to isosceles triangle. Hypobranchial gland narrower than ctenidium, 2/3 of ctenidium width, formed of numerous ramifying folds. Rectum spanning 2/3 of mantle length, terminating in a small anal papilla.

Digestive system. Proboscis long, lies within very thin-walled, transparent rhynchodaeum, and in retracted position is folded together with rhynchodaeum within body haemocoel. Proboscis 22 mm long (0.85 of AL). Proboscis medium thick-walled, the wall being about 0.2 of proboscis diameter and consisting of several muscle layers. Proboscis lined with columnar epithelium. Epithelium (Fig. 2C — **el**) underlined by an inconspicuous thin layer of unstructured connective tissue. Below there is a thick layer of circular muscles with separate transverse fibers (Fig. 2C — **cml**). It is followed by two rather thin layers of spiral muscles (Fig. 2B, C — **sm**), oriented in opposite directions. The innermost layer is composed of longitudinal muscles (Fig. 2 C — **lm**). Rhynchodaeum wall formed of two thin layers — outer layer of longitudinal muscle fibers and inner (facing proboscis wall) layer of circular ones. Due to its morphology, rhynchodaeum is unable to eversion even in its posteriormost part.

Powerful paired proboscis retractors are attached to the floor of body haemocoel and inserted into posterior part of proboscis walls (Fig. 1C — **prr**). Within the proboscis there is pair of thin retractors, running on both sides of odontophore (Fig. 1C — **iprr**). Anteriorly they ramify forming thin muscle fibers to be inserted into proboscis wall. Along most of the length these retractors are free, they leave proboscis posteriorly and run along anterior oesophagus. These retractors are probably attached to the floor of body haemocoel near the nerve ring (we were unable to trace the exact place of attachment, but they do not pass through the nerve ring). These retractors are referred below as inner proboscis retractors.

Odontophore is longer than radular sac, although short compared to proboscis, formed of paired cartilages (Fig. 2B — **odc**) fused anteriorly. In its posterior part cartilages are replaced by paired muscles, running mid-ventrally and probably functioning as odontophore retractors (Fig. 1C — **odr**). These muscles run together with inner proboscis retractors along oesophagus to be attached to the floor of body haemocoel close to nerve ring. Posteriorly the radular sac adjoins large blood vessel, probably a branch of buccal artery, which is running longitudinally between cartilages and, later, odontophoral retractors.

Radula (Fig. 3A, B) short, 5.2 mm long (0.24 proboscis length), consists of 57 rows of teeth, 4 nascending. Radular width 360 μm. Lateral teeth bicuspidate, claw-like, with strongly curved outer cusps (their length about 120 μm). Width of lateral tooth base about 110 μm, or 0.30 of radular width. Central tooth about 120 μm wide, tricuspid or bicuspid (Fig. 3A) with central cusp missing, with

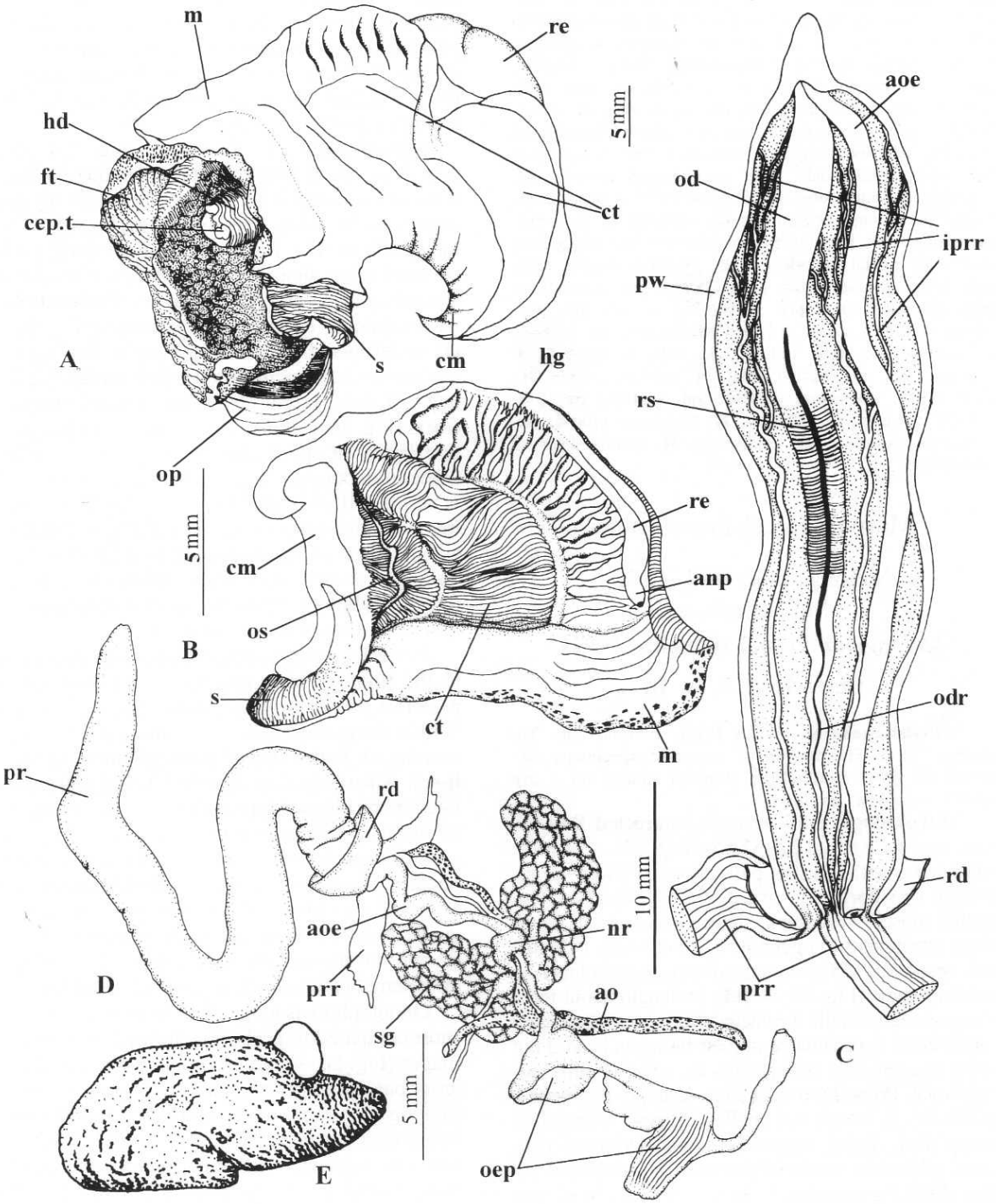


FIG. 1. *Melongena corona* (Gmelin, 1791). A — external view of the soft body, upper whorls of visceral mass removed. B — mantle. C — proboscis opened on dorsal side. D — dorsal view of the anterior part of digestive system. E — penis.

РИС. 1. *Melongena corona* (Gmelin, 1791). A — внешний вид мягкого тела, верхние обороты туловищного мешка удалены. B — мантия. C — хобот, вскрытый дорзально. D — передний отдел пищеварительной системы, вид с дорзальной стороны. E — пенис.

РИС. 2. (на противоположной странице) *Melongena corona* (Gmelin, 1791). A — поперечный срез пищевода в области нервного кольца. B — поперечный срез средней части хобота. C — последовательность мускульных слоев в стенке хобота. D — поперечный срез заднего пищевода и передней аорты. E — внешний вид желудка. F — желудок, вскрытый с дорсальной стороны. G — увеличенный участок желудка в месте перехода гастрической камеры в мешок кристаллического стебелька. Стрелки показывают основные токи, производимые ресничным эпителием. E-G — по Kantor [2003], с изменениями.

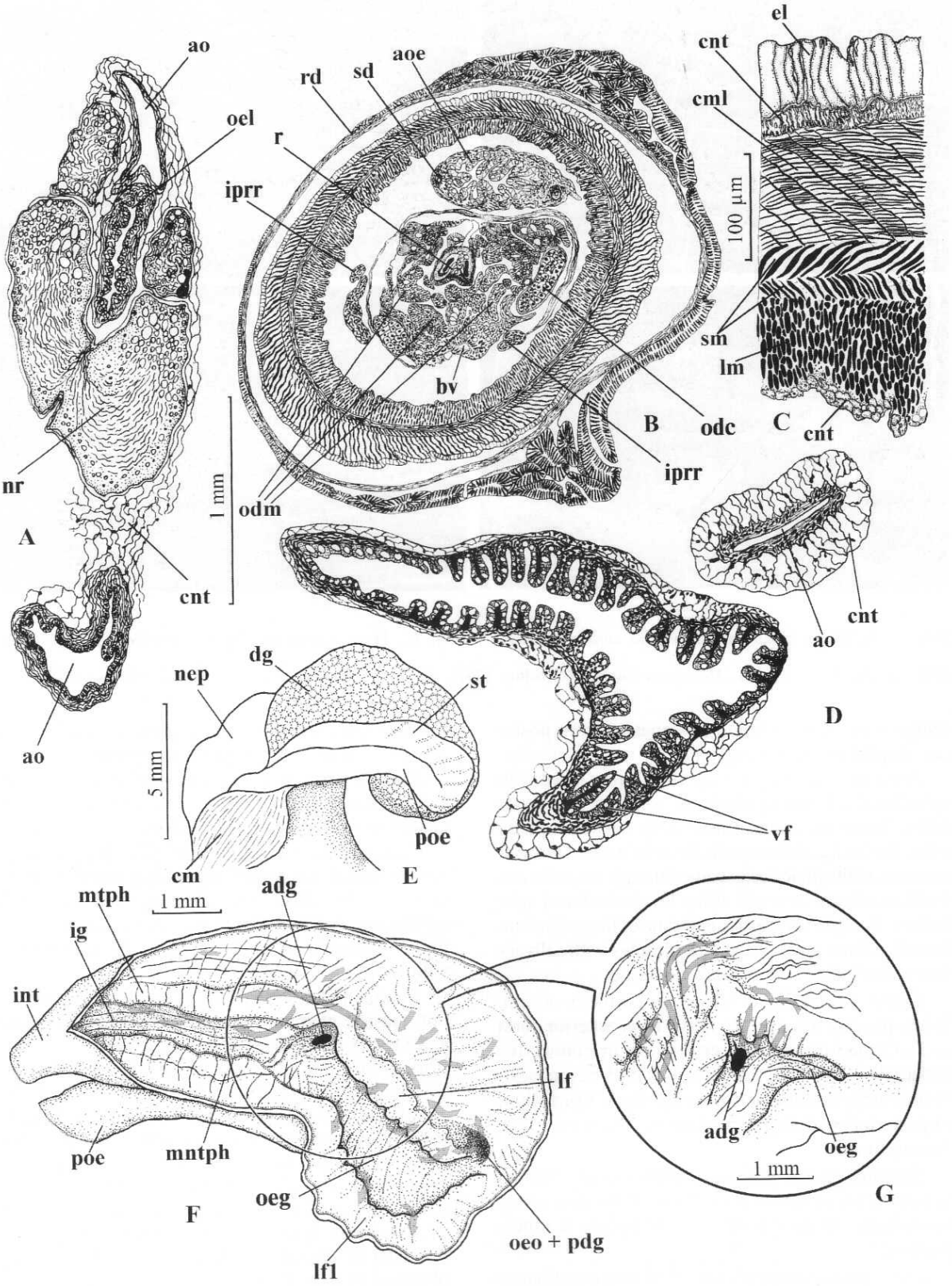


FIG. 2. *Melongena corona* (Gmelin, 1791). A — transverse section of oesophagus in the region of the nerve ring. B — transverse section in the middle part of proboscis. C — sequence of the muscle layers in the proboscis wall. D — transverse section of the posterior oesophagus and anterior aorta. E — latero-ventral external view of the stomach. F — stomach, opened on dorsal side. G — enlarged part of the stomach, showing transition of the gastric chamber into the style sac. Arrows indicate main ciliary currents. E-G — after Kantor [2003], modified.

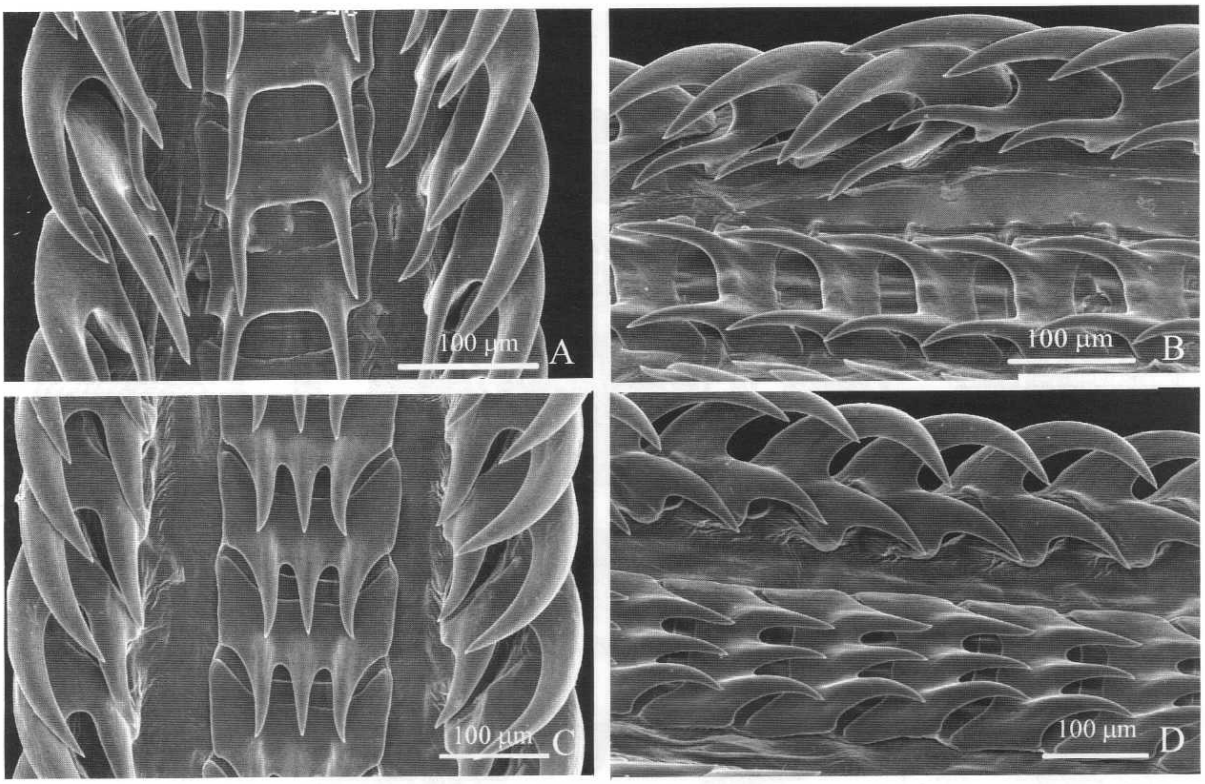


FIG. 3. A, B — radula of *Melongena corona* (Gmelin, 1791). C, D — radula of *Pugilina pugilina* (Born, 1778).

РИС. 3. A, B — радула *Melongena corona* (Gmelin, 1791). C, D — радула *Pugilina pugilina* (Born, 1778).

sharp cusps equal in length, emanating from posterior margin of tooth base. Anterior margin arcuate.

Anterior oesophagus (Fig. 1D — **aoe**) lined with cylindrical ciliated epithelium, forming numerous folds. There are some mucus cells between ciliary ones. The bodies of these cells lie in the mass of circular muscles, while their necks come through muscles and basal membrane and end at the level of ciliated epithelium. Beneath the basal membrane of the epithelium there is a thick layer of circular muscles with salivary ducts attached to it by connective tissue.

Gland and defined valve of Leiblein absent. While passing through the nerve ring, anterior aorta and mid-oesophagus are enveloped in connective tissue (Fig. 2A — **cnt**). Structure of mid-oesophagus is similar to that of anterior oesophagus. Epithelium of posterior oesophagus contains pyriform cells producing mucus.

Salivary glands acinous, medium-sized, situated at both sides of nerve ring. Their ducts pass along oesophagus to fuse with its wall before it enters proboscis.

After passing through the nerve ring oesophagus sharply widens to form a large lateral irregular-shaped blind pouch. As is seen on transverse section through it (Fig. 2D — **oep**), its columnar epithelium forms on lateral walls numerous folds subequal in size, two ventral of them being slightly better expressed and bordering a groove (Fig. 2D — **vf**). Circular muscles underlying epithelium are less expressed than in anterior and mid-oesophagus.

Parallel to the posterior oesophagus a thick-walled anterior aorta is passing, enveloped in whitish connective tissue (Fig. 1D — **ao**).

Stomach narrow and tubular (Fig. 2E), occupies dorsal part of the whorl, extending from about 1/3 to 1/2 of the whorl. Oesophagus lined with pink epithelium that is replaced by yellow one at transition to stomach. Stomach epithelium is uniformly yellowish.

Stomach is simple, with poorly pronounced relief. Gastric chamber is clearly divided into dorsal and ventral channels (oesophageal groove) by two distinct and tall folds (**lf+lf1** in Fig. 2F) that are continuous with typhlosoles. Ducts of digestive gland paired, the posterior very narrow and situated at the oesophagus entrance to stomach. Anterior duct is much broader and located in a rather deep pouch (Fig. 2G — **adg**, shown shallower on the drawing). Lateral sulcus not pronounced. Typhlosoles poorly developed. A mucous string, emerging out of anterior duct of digestive gland into the intestine, was observed in live specimens.

Ciliary currents from oesophagus lead to dorsal channel and then anteriorward along longitudinal fold towards compacting area. There are ciliary currents leading from oesophageal groove into dorsal channel. Currents carry fluids out of anterior duct back into the oesophageal groove, from which they

are moved to the dorsal channel. Marking the currents with carmine particles did not reveal any current leading from dorsal channel or oesophagus into oesophageal groove.

Penis (Fig. 1 E) medium-short, contracted, pigmented with black speckles. It bears a large dorsal seminal papilla without speckles.

Pugilina pugilina (Born, 1778)

(Figs. 3, C, D; 4; 5)

Material examined. Vietnam, Haiphong market, 1988, Yu. Kantor. Three specimens were dissected for gross anatomy, two for stomach anatomy.

Morphology. Soft tissues comprise 3 whorls; mantle cavity spans one whorl, nephridium 1/3 whorl, digestive gland two whorls.

Head small, cylindrical, very long, with pronounced neck, slightly tapering anteriorward (Fig. 4A — **hd**). Its length about three times exceeds the width. Tentacles short, contracted. Small black eyes situated on head at tentacles bases. Foot large and powerful, bears elongated leaf-shaped operculum with terminal nucleus. Body colour tan, dorsal surfaces of head, foot, external mantle edge, siphon, and penis (Fig. 4A, B, C) strongly pigmented with black speckles.

Mantle long, length being 1.5 width (Fig. 4B). Mantle edge thickened and muscular. Siphon thick-walled, medium-short, slightly extended beyond mantle edge. Osphradium bipectinate, symmetrical, with broad axis, occupies 1/3 of mantle length. Ctenidium occupies 5/6 of mantle length. Hypobranchial gland is as wide as ctenidium and occupies 2/3 of mantle length, formed of numerous oblique folds. Rectum spanning 3/4 of mantle length, terminating in small anal papilla.

Digestive system. Proboscis smooth, long, folded twice with rhynchodaeum within body haemocoel, 35 mm long (0.81 of AL). Proboscis thick-walled, wall being about 0.15 of proboscis diameter. Anatomy of. proboscis wall is similar to that of *Melongena*. Proboscis is lined with tall columnar epithelium (Fig. 5B — **el**). Epithelium is underlined by a thin layer of connective tissue. Below is thick layer of circular muscles with separate transverse fibers (Fig. 5B — **cml**). It is followed by two rather thin layers of spiral muscles (Fig. 5B — **sm**), oriented in opposite directions. Innermost layer is composed by longitudinal muscles (Fig. 5B — **lm**). Rhynchodaeum very thin-walled, nearly transparent, evertable part absent.

Powerful paired proboscis retractors are attached to the floor of body haemocoel and inserted into posterior part of proboscis walls (Fig. 4F). Inner proboscis retractors similar to that of *Melongena*.

Odontophore longer than radular sac, although short compared to proboscis, formed of paired cartilages (Fig. 5, B — **odc**), fused anteriorly. In its posterior part cartilages replaced by paired muscles running mid-ventrally and probably functioning as odontophore retractors (Fig. 4F). Posterior to radular sac a large blood vessel, probably branch of buccal artery, is running longitudinally between cartilages and, later, odontophoral retractors (Fig 5B — **ba**).

Radula (Fig. 3C, D) short, 6.1 mm long (0.17 proboscis length), consists of 56 rows of teeth, three nascending. Radular width 540 μm. Lateral teeth bicuspidate, claw-like, with strongly curved outer cusps. Width of lateral tooth base about 120 μm, or 0.22 of radular width. Central tooth about 170 μm wide, tricuspid, with closely spaced sharp cusps equal in length, emanating from the posterior margin of the tooth base. Anterior margin arcuate.

Anterior oesophagus (Fig. 5B — **oe**) lined with cylindrical ciliated epithelium, forming numerous folds. Beneath basal membrane of epithelium there is a thick layer of circular muscles, with salivary ducts being attached to it by connective tissue.

Gland and valve of Leiblein absent. While passing through nerve ring, anterior aorta and mid-oesophagus are enveloped in connective tissue. Structure of mid-oesophagus is similar to that of anterior oesophagus. Salivary glands acinous, medium-sized, situated at both sides of nerve ring. Their ducts are free for short distance, then run along oesophagus, tightly connected to it by connective tissue (Fig. 4E — **sd**).

After passing through nerve ring, oesophagus sharply widens to form a lateral blind pouch (Fig. 4E — **oep**). As is seen on transverse section of enlarged region of posterior oesophagus, its columnar epithelium is forming several folds subequal in size, with two ventral of them being especially well expressed and bordering a groove (Fig. 5A — **vf**). Circular muscles underlying epithelium are less expressed than in anterior and mid-oesophagus. Beneath basal membrane of the epithelium, folds are filled with connective tissue.

Parallel to posterior oesophagus thick-walled anterior aorta is passing, enveloped in whitish connective tissue. On dissection, aorta has rough walls, impregnated with white rounded particles.

Stomach is very small, tubular, simple, U-shaped, with long axis directed at about 50° to the whorl (Fig. 5D). Oesophagus is broad compared to stomach, opening ventrally into posterior part of stomach. Posterior mixing area absent.

Posterior oesophagus lined with well developed longitudinal folds. Folds on the dorsal side of oesophagus are continuous with longitudinal folds on outer stomach wall. Gastric chamber subdivided into dorsal and ventral channels by distinct and tall (although short) longitudinal fold on inner stomach wall (Fig. 5C — **lf**). Ventral channel is represented by oesophageal groove, occupying mid-ventral position (Fig. 5C — **oeg**) which is continuous with rather deep intestinal groove, lined with tall longitudinal, but narrow folds (not seen on the drawing). Dorsal channel of gastric chamber lined with oblique, longitudinal folds, that are much larger and more raised on outer stomach wall.

In one of the two studied specimens there was a very narrow and shallow transverse groove (Fig. 5C — **tg**) absent in second specimen.

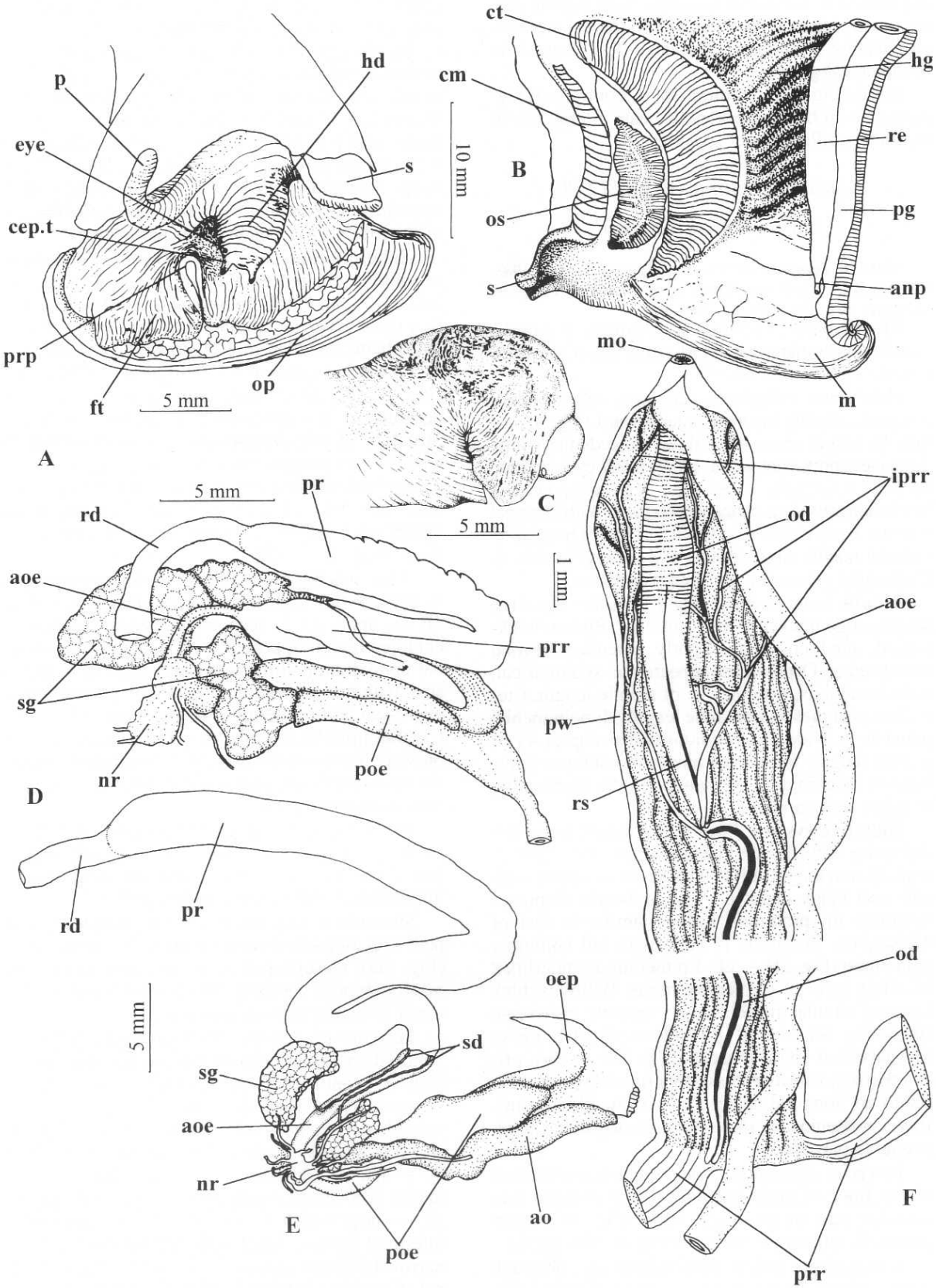


FIG. 4. *Pugilina pugilina* (Born, 1778). A — external front view of the body, upper whorls removed. B — mantle. C — penis. D — organs of anterior part of digestive system, left lateral view. E — anterior part of digestive system of another specimen, extended, proboscis retractors not shown. F — proboscis dissected dorsally.

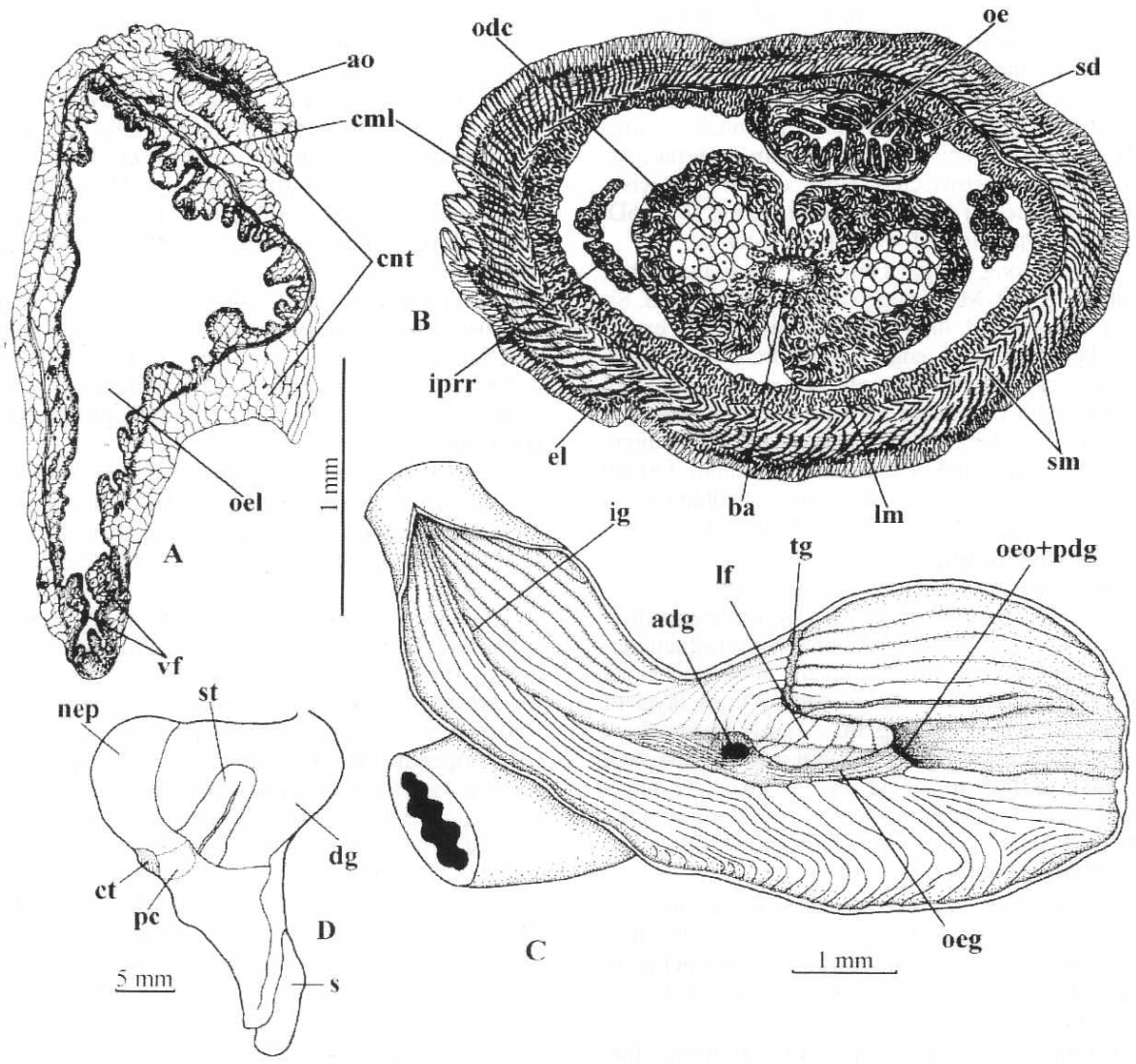


FIG. 5. *Pugilina pugilina* (Born, 1778). A — transverse section of the posterior oesophagus. B — transverse section of the middle part of proboscis, rhynchodaeum removed. C — stomach opened dorsally. D — schematic view of the whorls of visceral mass to show the position of the stomach in relation to the digestive gland, gonad, and nephridium. C-D — after Kantor [2003].

РИС. 5. *Pugilina pugilina* (Born, 1778). A — поперечный срез заднего пищевода. B — поперечный срез средней части хобота, ринходеум удален. C — желудок. D — схема строения висцерального мешка, показывающая положение желудка по отношению к пищеварительной железе, гонаде и нефридиуму. C-D — по Kantor [2003].

Openings of digestive glands ducts are large and oval. Anterior opening is located just anterior and ventral to the transverse fold, while posterior one — at the entrance of oesophagus into stomach. Duct pouches are not pronounced. Typhlosoles are poorly pronounced.

Penis (Fig. 4C) is wider than in *Melongena*, medium-short, contracted, pigmented with black speckles. It bears large antero-dorsal seminal papilla without speckles.

Hemifusus ternatanus (Gmelin, 1791)

(Fig. 6; 7, A, B, C)

Material examined: Mins Bay, Hong-Kong, 10-20 m, coll. J. D. Taylor, April 1986, one immature female (SL 71.2 mm) examined.

Morphology. Soft tissues comprise 2.5 whorls (Fig. 6D); mantle cavity spans one whorl, nephridium 1/3 whorl, digestive gland and gonad 1.5 whorls.

Head small, cylindrical, very long, with pronounced neck (Fig. 6E). Its length is about three times

РИС. 4. (на предыдущей странице) *Pugilina pugilina* (Born, 1778). A — внешний вид спереди, верхние обороты удалены. B — мантия. C — пенис. D — органы переднего отдела пищеварительной системы в исходном положении, вид слева. E — расправленный передний отдел пищеварительной системы другого экземпляра, ретракторы хобота не изображены. F — хобот, вскрытый дорсально.

width. Tentacles short, comparatively thick (about 1/4 of head width), contracted, with large black eyes situated on head at their bases. Foot large and powerful, folded transversely, bears large, elongated leaf-shaped operculum with terminal nucleus, slightly longer than aperture. Propodium very narrow, delimited by narrow cleft. Body colour yellowish, dorsal surfaces of head, foot, and siphon (Fig. 6D, E) strongly pigmented with black speckles.

Mantle long, length being 1.5 times more than width (Fig. 6F). Mantle edge thickened, indented. Siphon thick-walled, medium-short, moderately extending beyond mantle edge. Osphradium bipectinate, symmetrical, with narrow axis, occupies about 1/3 of mantle length. Ctenidium occupies 5/6 of mantle length, 1.5 times broader and twice longer than osphradium. Hypobranchial gland broader than ctenidium, formed of tall curved folds. Rectum narrow, spanning 2/3 of mantle length, terminating in small anal papilla.

Digestive system. Proboscis smooth, very long, folded twice with rhynchodaeum within body haemocoel, 40 mm long (1.57 of AL). Proboscis thin-walled, wall being about 0.12 of proboscis diameter, consists of several muscle layers. Proboscis lined with cubic epithelium underlined by thick layer of circular muscle fibers (Fig. 6C — **sml**). Below there are two rather thin layers of spiral muscles, oriented in opposite directions (Fig. 6C — **sm**). The innermost thickest layer composed of longitudinal muscles (Fig. 6B, C — **lm**). Rhynchodaeum thin-walled, evertable part absent.

Powerful paired proboscis retractors are inserted into posteriormost part of proboscis walls and fuse before entering the floor of body haemocoel (Fig. 6A — **prr**). Inner proboscis retractors (Fig. 6A — **iprr**) are similar to those of *Melongena* and *Pugilina*.

Odontophore short compared to proboscis, formed of paired cartilages, not fusing anteriorly (Fig. 6B — **odc**). In its posterior part cartilages are replaced by paired muscles (Fig. 6A, C — **odr**), gradually thinning and attached to proboscis base. They probably function as odontophoral retractors. Posterior to radular sac a large blood vessel, probably branch of buccal artery, is running longitudinally between cartilages and, later, odontophoral retractors (Fig. 6 — **ba**).

Radula (Fig. 7A, B, C) short, 3.2 mm long (0.08 proboscis length), consists of 42 rows of teeth, 3-4 nascending. Radular width about 310 μm. Lateral teeth bicuspidate, claw-like, with strongly curved outer cusps (their length about 55 μm). The width of lateral tooth base is about 85 μm, or 0.26 of radular width. Central tooth about 90 μm wide, tricuspid, with broadly spaced sharp cusps, emanating from the posterior margin of the tooth base, central one twice shorter than laterals. Anterior margin arcuate.

Anterior oesophagus (Fig. 6B — **oe**) lined with cylindrical ciliated epithelium forming numerous folds. Beneath basal membrane of epithelium there is thick layer of circular muscles with salivary ducts attached by connective tissue.

Gland and valve of Leiblein absent. Structure of mid-oesophagus similar to that of anterior oesophagus. Salivary glands medium-sized, acinous, situated at both sides of nerve ring. Their ducts are free for short distance, then run along oesophagus, tightly connected to it by connective tissue.

After passing through large nerve ring, oesophagus sharply widens to form large lateral blind pouch.

Parallel to posterior oesophagus thick-walled anterior aorta is passing, enveloped in whitish connective tissue.

Stomach is U-shaped, very small, and tubular. It spans less than 1/2 whorl (Fig. 6H). Stomach morphology (Fig. 6I) resembles that of *Pugilina*, except for presence of very short posterior mixing area. Posterior oesophagus is broad, gradually narrowing before opening ventrally into stomach. Longitudinal folds of the oesophagus continue into posterior mixing area (Fig. 6I — **pma**). Gastric chamber is subdivided into ventral and dorsal parts by low, although well pronounced longitudinal fold (Fig. 6I — **lf**), running on inner stomach wall. Longitudinal fold is lined with distinct oblique folds and becomes obsolete at level of anterior opening of duct of digestive gland. Oesophageal groove (Fig. 6I — **oeg**) is midventral and lined with thin longitudinal folds. Posterior opening of digestive gland duct is very large, funnel-shaped, situated close to oesophagus entrance into stomach. Anterior opening is not large and opens in anterior ventral part of the gastric chamber. Inner wall of dorsal part of stomach is lined with long narrow longitudinal folds. Outer wall in its most dorsal part has oblique folds. Style sac is lined with transverse folds. Lateral sulcus absent, typhlosoles not pronounced.

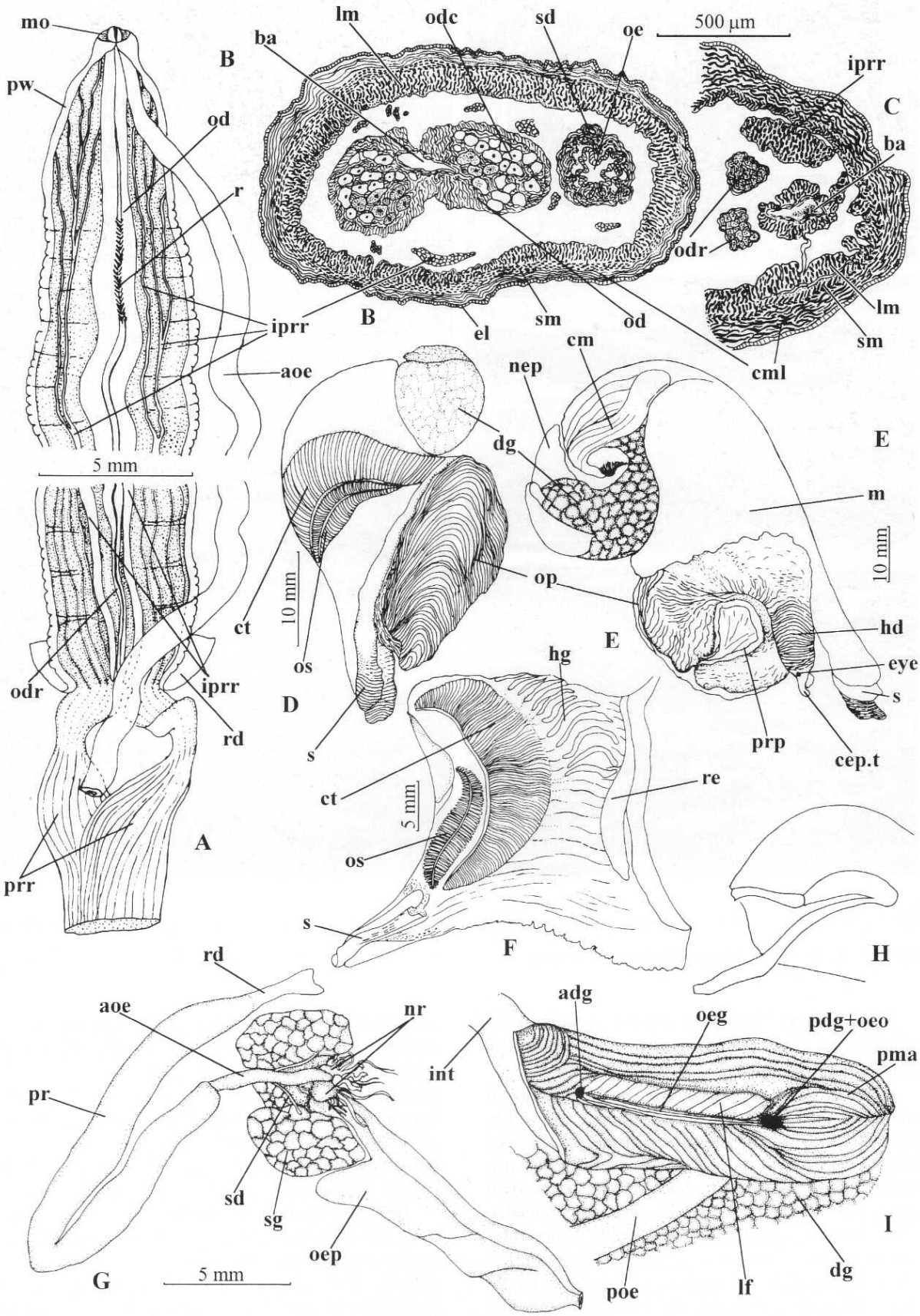
Volema pyrum (Gmelin, 1791)

(Fig. 7, D, E; 8)

Material examined: Mida Creek, Kenya, 1969, two females dissected.

FIG. 6. (opposite page) *Hemifusus ternatanus* (Gmelin, 1791). A — proboscis dissected dorsally. B — transverse section in the anterior third of proboscis, rhynchodaeum removed. C — transverse section in the posterior third of proboscis, rhynchodaeum removed. D — external ventral view of the soft body, upper whorls removed. E — external dorsal-right view of the soft body. F — mantle. G — anterior part of digestive system, proboscis retractors not shown. H — external stomach view. I — stomach dissected dorsally.

РИС. 6. (на противоположной стороне) *Hemifusus ternatanus* (Gmelin, 1791). A — хобот, вскрытый дорсально. B — поперечный срез передней трети хобота, ринходеум удален. C — поперечный срез задней трети хобота, ринходеум удален. D — внешний вид мягкого тела с вентральной стороны, верхние обороты удалены. E — внешний вид мягкого тела дорсально и сбоку. F — мантия. G — передний отдел пищеварительной системы с дорсальной стороны, ретракторы хоботы не показаны. H — внешний вид желудка. I — желудок, вскрытый с дорсальной стороны.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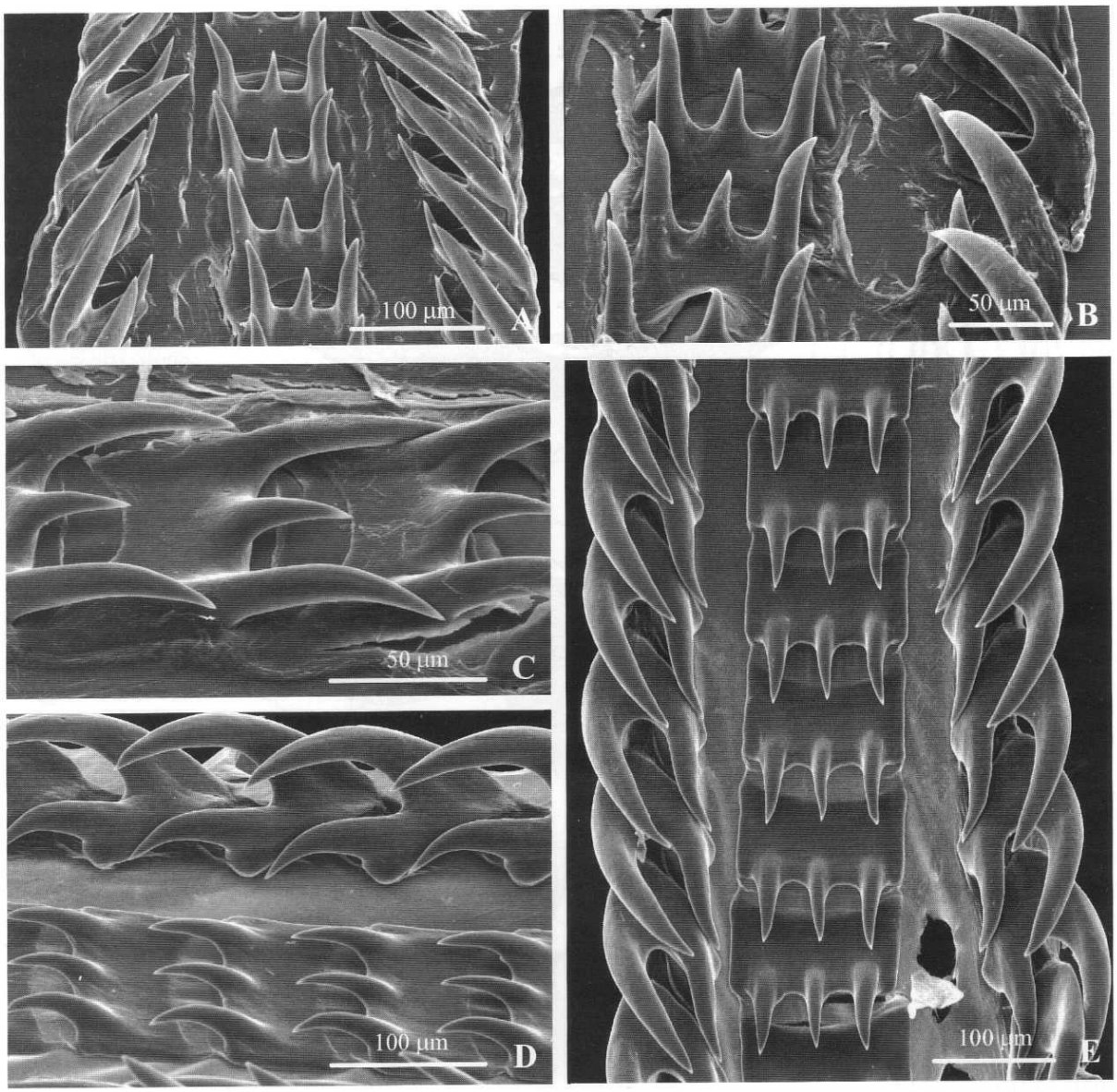

FIG. 7. A, B, C — radula of *Hemifusus ternatanus* (Gmelin, 1791). D, E — radula of *Volema pyrum* (Gmelin, 1791).

РИС. 7. A, B, C — радула *Hemifusus ternatanus* (Gmelin, 1791). D, E — радула *Volema pyrum* (Gmelin, 1791).

Morphology. The soft tissues comprise 2.5 whorls (Fig. 8A), mantle cavity spans about 0.5 whorl, digestive gland and gonad 1.5 whorls.

Head small, cylindrical, long, with pronounced neck (Fig. 8C — **hd**). Its length is twice the width. Tentacles very short, contracted, small black eyes situated on head at their bases. Foot large and powerful, folded transversely, bears large, narrow, oval operculum tapering towards terminal nucleus, whose length exceeds aperture length. Propodium narrow, delimited by narrow cleft. Body colour pink-yellowish; head, dorsal surface of foot, outer mantle edge, and siphon (Fig. 8A, B) strongly pigmented with black speckles.

Mantle short, width 1.5 times exceeding length (Fig. 8B). Mantle edge thickened, smooth. Siphon thick-walled, medium-short, moderately extending beyond mantle edge. Osphradium bipectinate, nearly symmetrical, with broad axis, occupies about 1/3 of mantle length. Ctenidium occupies 5/6 of mantle length, 1.5 times broader and twice longer than osphradium. Hypobranchial gland is formed of thin ramifying folds. Rectum narrow, spanning 3/4 of mantle length, terminating in large anal papilla.

Digestive system. Proboscis with folded walls, long, folded twice with rhynchodaeum within body haemocoel, 14 mm long (0.64 of AL in specimen with SL 27.0 mm, AL 15.0 mm). In second, larger specimen (SL 53.0 mm, AL 26 mm) proboscis was about 70 mm long (2.69 of AL).

Powerful paired proboscis retractors inserted into posteriormost part of proboscis walls and fuse before

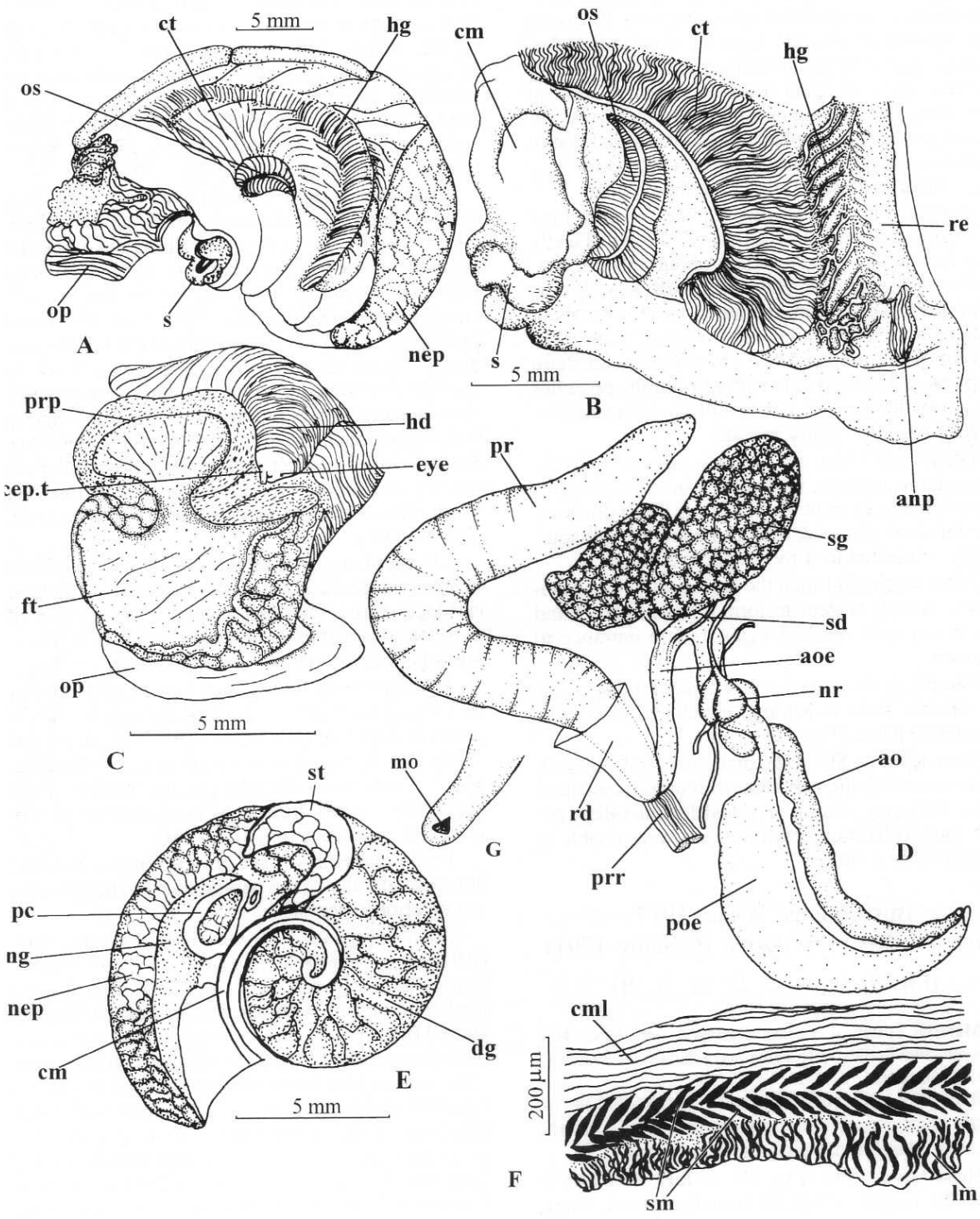

FIG. 8. *Volema pyrum* (Gmelin, 1791). A — external view of the body from left dorsal side, upper whorls of visceral mass removed. B — mantle. C — external front-ventral view of the body, upper whorls removed. D — right lateral view of anterior part of digestive system. E — outer view of the stomach and visceral mass from ventral side. F — transverse section of proboscis wall, epithelium dislodged during fixation. G — ventral view of proboscis tip.

РИС. 8. *Volema pyrum* (Gmelin, 1791). A — внешний вид тела с левой дорсальной стороны, верхние обороты туловищного мешка удалены. B — мантия. C — внешний вид тела спереди и снизу, верхние обороты удалены. D — передний отдел пищеварительной системы, вид сбоку. E — внешний вид желудка с вентральной стороны. F — поперечный срез стенки хобота, эпителий отслоился при фиксации. G — вершина хобота с вентральной стороны.

entering floor of body haemocoel. Subradular cartilages fused in anterior third of odontophore. Proboscis wall consists of external layer of circular muscles, internal layer of longitudinal fibers and two oppositely directed layers of spiral muscles, situating between them (Fig. 8F). Epithelium of proboscis wall was not present on sections, probably being dislodged due to fixation conditions. Inner proboscis retractors very thin, similar to those of other described species.

Radula (Fig. 7D, E) rather long, 5.5 mm long (0.39 proboscis length), consists of 61 rows of teeth, 3-4 nascending. Radular width about 310 μm. Lateral teeth bicuspidate, claw-like, with strongly curved outer cusps. Width of lateral tooth base about 120 μm, or 0.29 of radular width. Central tooth about 130 μm wide, tricuspid, with broadly spaced sharp cusps equal in length, emanating from the posterior margin of the tooth base. Tooth base rectangular, anterior margin slightly arcuate.

Gland and valve of Leiblein absent. Salivary glands large, acinous, separate, situated at both sides of oesophagus in front of nerve ring. Their ducts are free for short distance, then run along oesophagus, tightly connected to it by connective tissue.

After passing through the large nerve ring, oesophagus sharply widens to form a large lateral blind pouch and then narrows again before entrance to stomach.

Parallel to the posterior oesophagus a thick-walled anterior aorta is passing, enveloped in whitish connective tissue (Fig. 8D — **ao**).

Stomach (Fig. 8E — **st**) small, tubular, U-shaped, borders nephridium, very thin, with semi-transparent walls. Posterior mixing area and lateral sulcus absent. Due to fixation conditions we were unable to examine it in details.

Busyconinae Wade, 1917

Busycon (Busycon) carica (Gmelin, 1791)

(Fig. 9; 10, A-C, E; 11, A, B)

Material examined: Lewes, Delaware, coll. M.G. Harasewych, two bodies were examined (shells were removed prior to fixation).

Morphology. Soft tissues comprise 3 whorls; mantle cavity spans 2/3 whorl, nephridium 1/5 whorl, digestive gland and the gonad two whorls.

Head large, short (Fig. 9B — **hd**), its width is twice the length. Tentacles broadly spaced, short, tapering towards the tip, bearing small black eyes on the lobes in basal part of tentacles (Fig. 9B — **eye**). Foot large, rounded, folded transversely during fixation, bears large oval operculum with terminal nucleus. Propodium narrow, delimited by deep propodial cleft. Body colour tan, dorsal surfaces of head, tentacles, foot, siphon, and penis pigmented with black spots.

Mantle short, width 1.6 times exceeds length (Fig. 9E). Mantle edge thickened, completely covering head and penis. Siphon long and muscular, extending substantially beyond mantle edge. Osphradium bipectinate, narrow, symmetrical, with narrow axis, greenish-brown, occupies about third of mantle length. Ctenidium occupies 3/4 of mantle length, twice longer and four times wider than osphradium. Hypobranchial gland poorly pronounced, with nearly indistinguishable folds. Rectum wide, spanning *ca.* half of mantle length, sharply narrowing towards small anal papilla.

Digestive system. Proboscis 55 mm long (Fig. 9C, D), thick, length/diameter ratio *ca.* 3.8. Rhynchodaeum thin anteriorly and thick and muscular posteriorly, forming an evertable part. In inverted proboscis the buccal mass (Fig. 9C — **bm**) significantly protrudes behind rear of proboscis. In everted proboscis buccal mass lies completely within proboscis. Proboscis wall forms septum, that is able to occlude proboscis lumen, when latter is protracted, thus isolating inner proboscis space from that of body haemocoel. Septum penetrated by large hole, through which oesophagus passes, and smaller separate holes for salivary ducts (for more details and illustrations see description of *Busycotypus spiratum* (Fig. 13 D-F).

Odontophore very large, longer than proboscis in inverted position, consists of paired subradular cartilages fused anteriorly, and complex system of muscles, attached to the proboscis walls (Fig. 9F — **odr**). Posteriorly odontophore bifurcates.

Proboscis wall rather thick (about 0.65 mm, or *ca.*13% of proboscis diameter). Proboscis wall is covered with tall cylindrical epithelium (Fig. 10E — **el**). Below is thick layer of connective tissue (Fig. 10E — **cnt**) with separate circular muscle fibers (Fig. 10E — **cml**). Innermost layer consists of longitudinal muscles (Fig. 10E — **lm**).

Proboscis retractors are grouped in two bundles, attached laterally to the central part of rhynchodaeum anterior to septum.

Radula (Fig. 11 A-B) very long, 53.4 mm long (0.97 proboscis length), consists of 117 rows of teeth, four nascending. Radular width 2500 μm. Lateral teeth multicuspid, with outer cusps longest, slightly curved (their length about 850 μm). Width of lateral tooth base about 850 μm, or 0.34 of radular width. Inner side of base forms distinct rounded projection (marked by arrow on Fig. 11B). Innermost cusps triangular in shape, with nearly straight edges. Intermediate cusps (2 or 4) vary significantly in size from row to row and on right and left lateral teeth. Central tooth about 650 μm wide, forming wing-like projections on anterior arcuate margin, with 5 cusps subequal in length, two central ones fused. Cusps emanate from posterior margin of tooth base. Outermost cusps twice wider, that inner ones.

After leaving proboscis, anterior oesophagus forms a loop and runs forward along half of proboscis length to pass through nerve ring. Just before nerve ring there is small valve of Leiblein, poorly differentiated from oesophagus (Fig. 9 D — **vl**; on the drawing posterior oesophagus is bent outward).

Gland of Leiblein narrowly tubular (Fig. 9D — **gl**), light-brownish, passes along anterior aorta to

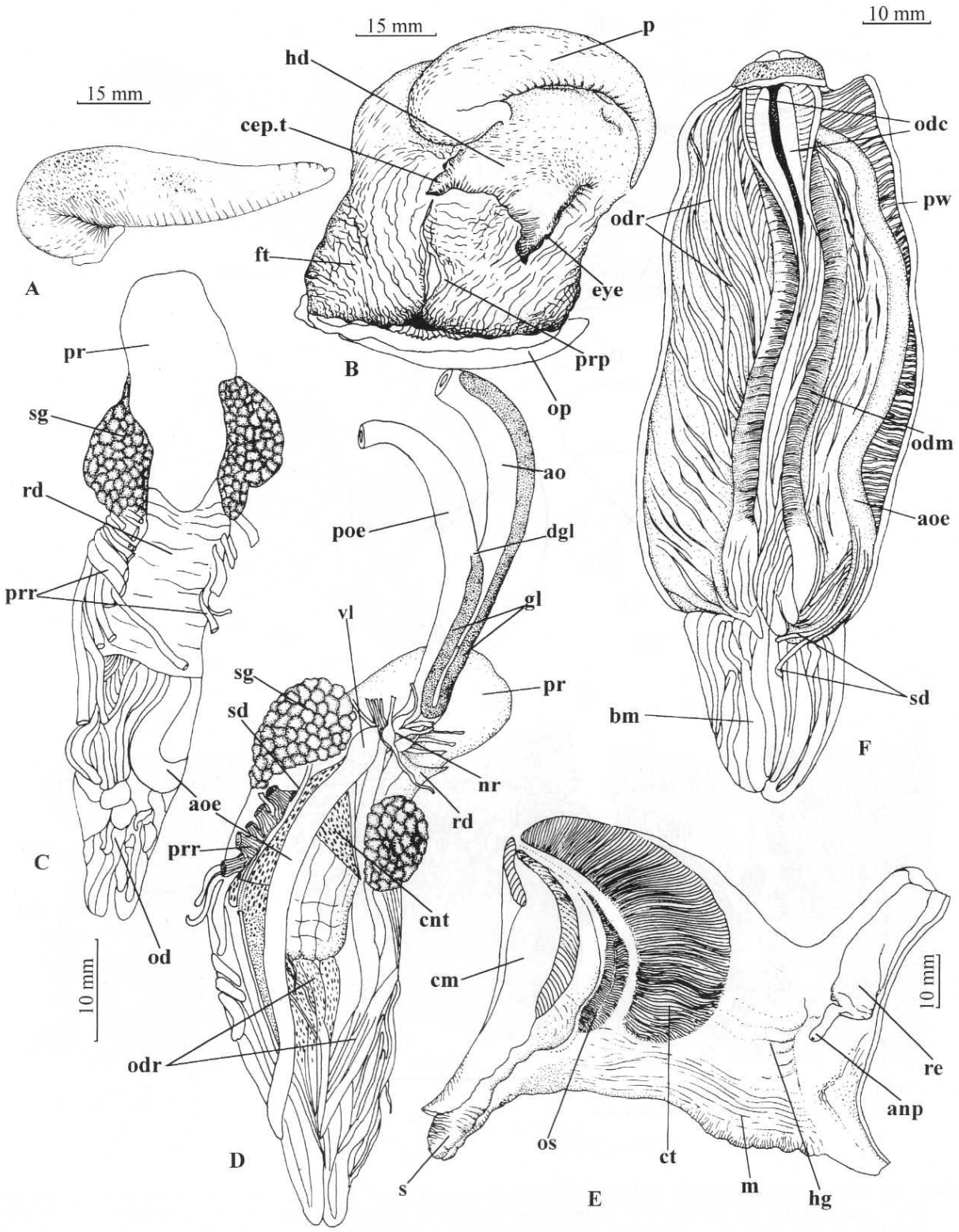

FIG. 9. *Busycon carica* (Gmelin, 1791). A — penis. B — external front view of the soft body, upper whorls removed. C — organs of the body haemocoel, dorsal view. D — organs of the body haemocoel, ventral view. E — mantle. F — proboscis, dissected ventrally.

РИС. 9. *Busycon carica* (Gmelin, 1791). A — пенис. B — внешний вид мягкого тела спереди, верхние обороты удалены. C — передний отдел пищеварительной системы в компактном состоянии, вид с дорсальной стороны. D — то же, вид с вентральной стороны. E — мантия. F — хобот, вскрытый с вентральной стороны.

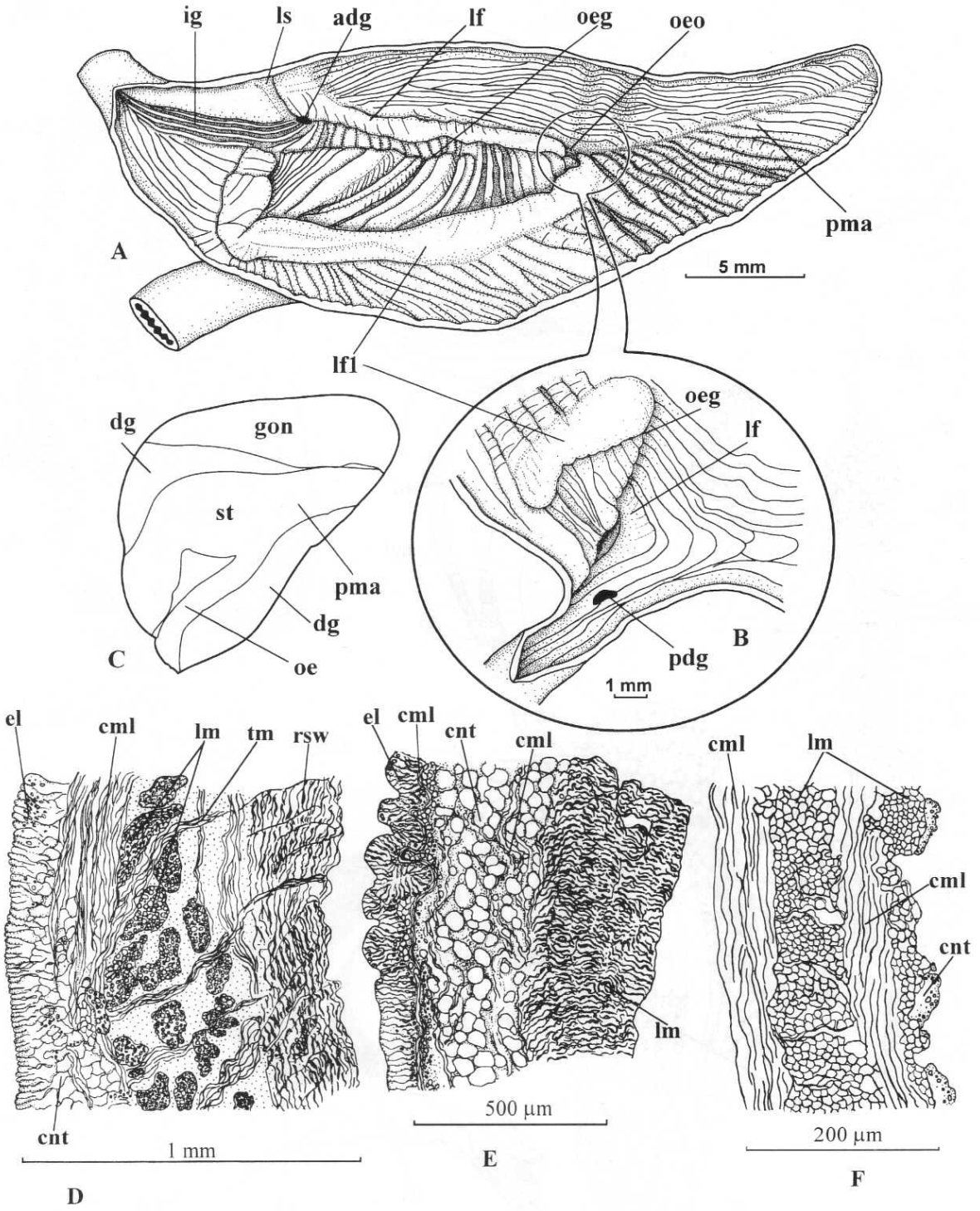

FIG. 10. *Busycon carica* (Gmelin, 1791): A — stomach opened along mid-dorsal line and external wall reflected. B — enlarged part of the stomach, showing the opening of oesophagus into the gastric chamber. Oesophagus partially opened along the ventral line and outer stomach wall reflected. C — schematic view of the whorls of the visceral mass to show the position of the stomach. D — transverse section of proboscis wall of *Busycotypus spiratum* (Lamarck, 1816), E — transverse section of proboscis wall of *B. carica*, F — transverse section of proboscis wall of *Ancistrolepis okhotensis* Dall, 1925. A-C — after Kantor [2003].

РИС. 10. *Busycon carica* (Gmelin, 1791): A — желудок, вскрытый по дорсальной стороны, наружная стенка отогнута. B — увеличенный участок желудка в месте впадения пищевода. Пищевод частично вскрыт по вентральной стороне, внешняя стенка желудка отогнута. C — схема оборотов висцерального мешка, показывающая внешний вид желудка. D — поперечный срез стенки хобота *Busycotypus spiratum* (Lamarck, 1816), E — поперечный срез стенки хобота *B. carica*, F — поперечный срез стенки хобота *Ancistrolepis okhotensis* Dall, 1925. A-C — по Kantor [2003].

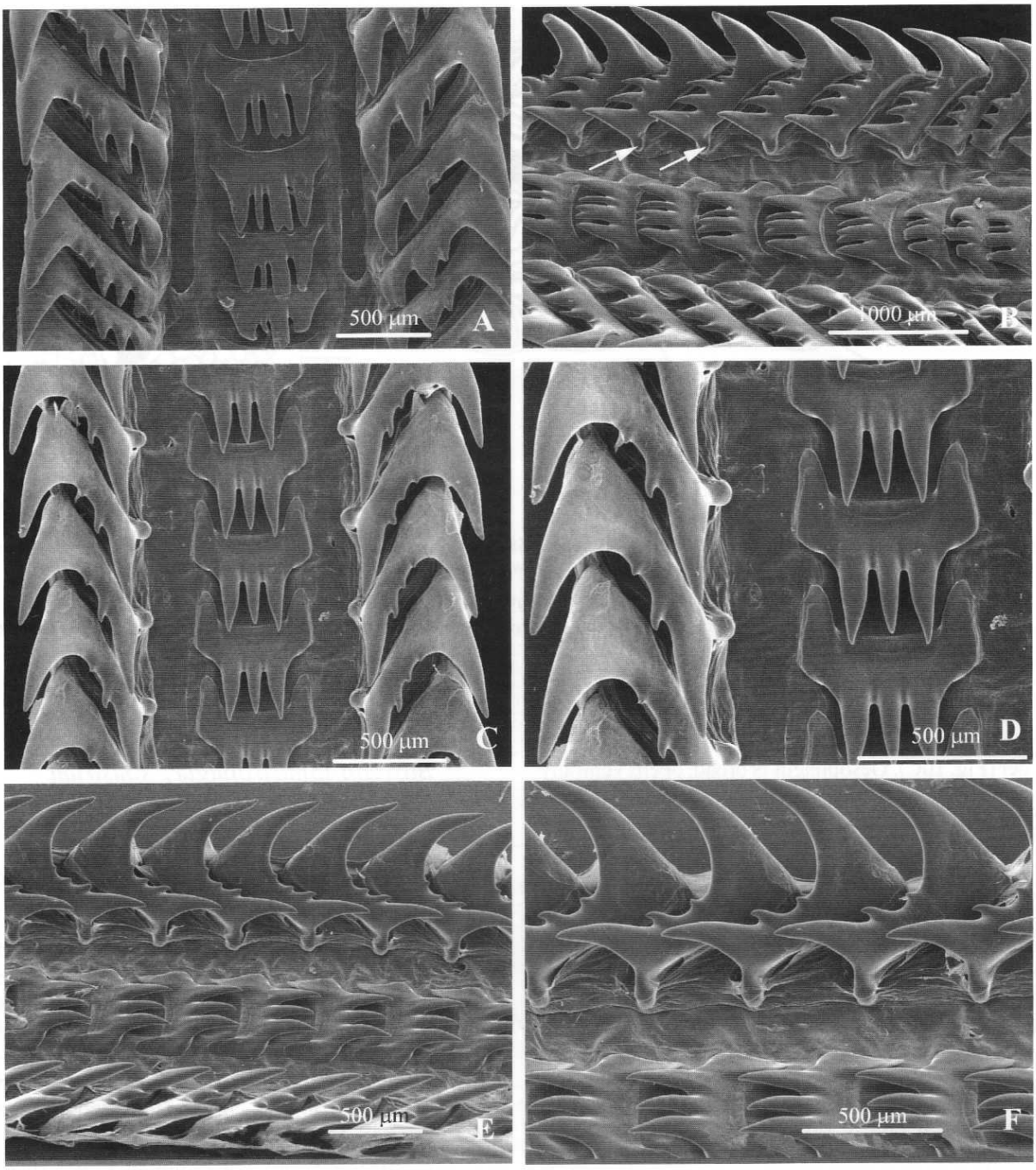

FIG. 11. A, B — radula of *Busycon carica* (Gmelin, 1791). C-F — radula of *Busycotypus spiratum* (Lamarck, 1816).

РИС. 11. A, B — радула *Busycon carica* (Gmelin, 1791).C-F — радула *Busycotypus spiratum* (Lamarck, 1816).

which it is attached by thick although loose connective tissue. Gland of Leiblein forming a loop and, gradually narrowing, follows to its opening into oesophagus, which is situated far behind nerve ring. Posterior oesophagus (Fig. 9D — **poe**) flattened. Anterior aorta (Fig. 9D — **ao**), passing along oesophagus is thick-walled, with diameter exceeding that of oesophagus. Gland of Leiblein, oesophagus and anterior aorta are packed in thick, although loose whitish connective tissue, thus forming a compact structure.

Paired acinous salivary glands situated at both sides of rhynchodaeum, to which they are tightly connected by connective tissue. Salivary ducts thick, run ventrally along anterior oesophagus, pass through holes in septum, follow to dorsal side between odontophoral retractors, and enter oesophageal wall at the rear of proboscis (Fig. 9F — **sd**).

Stomach occupies central part of whorl, dorsally bordering testis. It is rather large, broad, and extends for about ½ whorl behind posterior nephridium bor-

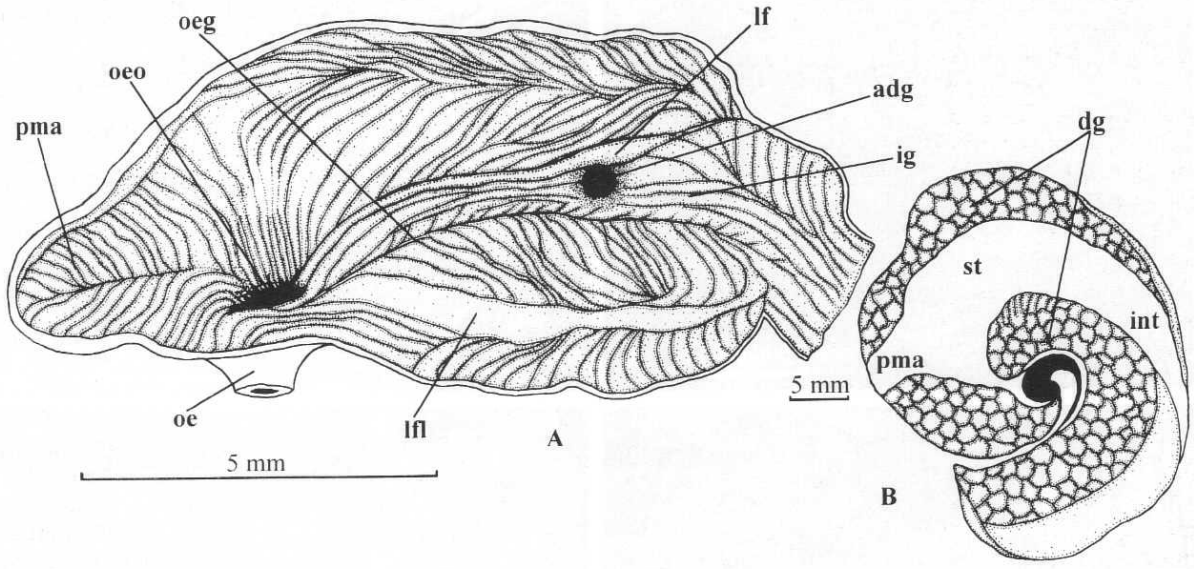

FIG. 12. *Busycon (Sinistrofulgur) sinistrum* (Hollister, 1958): A — stomach opened along mid-dorsal line (external wall reflected). B — schematic ventral view of the whorls of visceral mass to show the stomach position.

РИС. 12. *Busycon (Sinistrofulgur) sinistrum* (Hollister, 1958): A — желудок, вскрытый по дорсальной стороне, наружная стенка отогнута. B — схема оборотов висцерального мешка (вид снизу), показывающая расположение желудка.

der (Fig. 10C). Oesophagus is broad, opens ventrally midway along the length of stomach. Posterior mixing area is large.

Posterior oesophagus lined with low, longitudinal folds. These folds are continuous with oblique, longitudinal folds on outer stomach wall, which lead to posterior mixing area. On the contrary, folds on inner walls of oesophagus and posterior mixing area are curved and directed anteriorward (Fig. 10B).

Gastric chamber is clearly divided into dorsal and rather broad ventral chambers by two distinct folds, one on inner stomach wall (Fig. 10A — **lf**) and the other on outer stomach wall (Fig. 10A — **lf1**). The most dorsal part of ventral chamber is formed by oesophageal groove (Fig. 10A — **oeg**), occupying mid-ventral position. Outer wall of ventral channel lined with partially transverse, partially oblique, well developed folds. Dorsal channel lined with longitudinal folds, that are much larger and more prominent on outer stomach wall. Lateral sulcus is very shallow, connecting dorsal and ventral channels.

Ducts of digestive glands small and oval, with anterior duct being slightly larger than the posterior one. Anterior duct is located at the base of lateral sulcus, while posterior one — at the entrance of oesophagus to stomach.

Typhlosoles are not well pronounced. Intestinal groove distinct, lined with narrow and raised longitudinal folds.

Reproductive system. Penis long (Fig. 9A), laterally compressed, tapers gradually towards its tip. Seminal papilla very small, surrounded by a circular fold.

Busycon (Sinistrofulgur) sinistrum (Hollister, 1958)

(Fig. 12)

Material examined: west coast of Florida, Sanibel Island, in 20-25 cm, on sand, 1996, coll. A. Oleinik, one specimen (female) examined.

Morphology. External body morphology and mantle complex are very similar to those of *B. carica* (except that since *B. sinistrum* has sinistral shell its body is mirror arranged). Soft tissues comprise 3 whorls: mantle cavity spans 2/3 whorl, kidney — 1/5, digestive gland and gonad two whorls. Siphon is twice longer than in *B. carica*. Head, foot, siphon and proboscis are strongly pigmented with black.

The structure of foregut is similar to that of *B. carica*. The minor differences are: better development of valve and gland of Leiblein, and smaller salivary glands.

Radula is almost twice longer than proboscis in inverted position, 35 mm in length (0.72 AL). It is very similar to radula of *B. carica* and differs in presence of 5 equal in length cusps on the rachidian. Radula consists of 106 rows of teeth, 8 nascending. Radular width 1880 μm (3.87% of AL). Width of lateral tooth base about 600 μm, or 0.32 of radular width. Central tooth about 600 μm wide.

Stomach occupies central part of the whorl. It is rather large, broad, and extends for about 1/2 whorl behind posterior nephridium border (Fig. 12B). Oesophagus narrow, opens ventrally . Posterior mix-

ing area distinct, although narrow, and significantly shorter than in *B. carica*.

Posterior oesophagus lined with low longitudinal folds. These folds are continuous with oblique folds of stomach wall, leading into posterior mixing area. Gastric chamber is divided into dorsal and ventral parts by two distinct folds, one on inner and one on outer stomach wall (Fig. 12A — **lfl**, **lf1**). Most ventral part of the ventral chamber is formed by oesophageal groove (Fig. 12A — **oeg**), occupying median position. Stomach walls of dorsal chamber are lined with low oblique folds, crossing at sharp angle on inner stomach wall. Outer wall of ventral channel lined with partially oblique, partially curved, rather well developed folds. Lateral sulcus not pronounced.

Rather large rounded opening of anterior duct of digestive gland is located in the intestinal groove on inner stomach wall near intestine opening. Posterior opening has not been identified due to fixation conditions. Typhlosoles are not well pronounced.

Busycotypus (Fulguropsis) spiratum (Lamarck, 1816)

(Figs. 10, D; 11, C-F; 13)

Material examined: Yucatan, Mexico, one female specimen examined for outer and anterior foregut morphology; west coast of Florida, Sanibel Island, in 20-25 cm, on sand, 1996, coll. A. Oleinik, one specimen (female) examined.

Morphology. External morphology and mantle are very similar to those of *Busycon carica*.

Digestive system. Proboscis everted in one specimen (Fig. 13D), 62 mm long (0.67 of aperture length), gradually narrowing towards its tip. Length/diameter (in the central part) ratio *ca.* 4.8. In second specimen proboscis inverted (Fig. 13E), 16 mm long (0.39 of AL).

Proboscis wall medium thick (about 0.6 mm, or *ca.* 11% of proboscis diameter) (Fig. 10D). It is lined with tall columnar epithelium (Fig. 10D,E — **el**). Below there is a layer of connective tissue (Fig. 10E — **cnt**) with separate circular muscle fibers (Fig. 10E — **cml**). Innermost is a layer of longitudinal muscles with separate transverse muscle fibers (Fig. 10E — **tm**). Wall of radular sac is tightly attached to this layer (Fig. 10D — **rsw**).

Base of inverted proboscis is occluded with septum (Fig. 13D — **spt**, it is partially cut off proboscis wall while opening proboscis). Septum has separate highly contractible hole for oesophagus and separate holes for each salivary duct. During proboscis retraction, odontophore is passing through the same hole as oesophagus. In inverted position of proboscis (Fig. 13E) septum transforms into circular fold of rhynchodaeum. Salivary duct, after leaving salivary gland on its way to rear of proboscis passes behind septum (Fig. 13E — **sd**) and then through hole in septum (schematic transverse section of rhycnhodaeum and septum is presented on Fig. 13F).

Numerous proboscis retractors are attached immediately anterior to septum (in retracted proboscis, Fig. 13E — **prr**) and protruding from the rear of everted proboscis.

Odontophore consists of paired subradular cartilages fused anteriorly and numerous muscles, attached to the proboscis walls (Fig. 13D — **odr**). Posteriorly odontophore is bifurcating.

Radula (Fig. 11 C-F) very long, 55.3 mm in length (0.89 proboscis length), consists of 146 rows of teeth, eight nascending. Radular width 1780 μm (*ca.* 3.3% of AL). Lateral teeth multicuspid, with outer cusps longest, slightly curved (their length about 1200 μm). Width of lateral tooth base about 700 μm, or 0.39 of radular width. Inner side of base forms distinct rounded projection. Innermost cusps slightly curved, nearly twice shorter than outermost. Intermediate cusps (2 or 3) very small in comparison with marginal cusps. Central tooth about 530 μm wide, forming wing-like projections on anterior arcuate margin, with 3 sharp cusps, central one slightly shorter. Cusps emanate from posterior margin of the tooth base.

Valve of Leiblein better pronounced than in *B. carica* (Fig. 13D — **vl**). Gland of Leiblein well developed, narrowly tubular, dark-brownish. Posteriorly gland is gradually tapering and terminates with ampulla (Fig. 13B — **agl**). It opens into oesophagus far behind the nerve ring.

Stomach (Fig. 13G) occupies central part of whorl, medium-sized, extends for half of whorl. Posterior oesophagus broad, opens mid-ventrally into stomach. Posterior mixing area very short, practically absent. Posterior oesophagus lined with low longitudinal folds, that are continuous with oblique folds on inner stomach wall, strongly ramifying into small posterior mixing area. Gastric chamber is divided into dorsal and ventral channels by two distinct folds, one on inner (Fig. 13G — **lf**) and one on outer stomach wall (**lfl**). Stomach walls are lined with oblique folds oriented in opposite directions.

Stomach walls of dorsal chamber are lined with low folds, mostly longitudinal on inner stomach wall and mostly transverse on outer wall. Outer wall of ventral channel lined with partially oblique, partially curved rather well developed folds. Lateral sulcus is not pronounced.

The medium-sized oval opening of anterior duct of digestive gland is located in the intestinal groove on the inner stomach wall near the intestine opening. The posterior opening has not been identified due to fixation conditions. The typhlosoles are not pronounced.

Buccinidae Rafinesque, 1815
Pisaniinae Gray, 1857
Pisania tincta (Conrad, 1846)

(Fig. 14)

Material examined: Sebastian Inlet, Brevard County, Florida; coll. Yu. Kantor, 1999, gross anatomy studied in two females, stomach examined in 5 specimens (2 live).

Morphology. Soft tissues comprise about 3 whorls; mantle cavity spans ½ whorl, nephridium ¼ whorl, digestive gland and gonad two whorls.

Head large, short (Fig. 14A — **hd**), its width 1.5

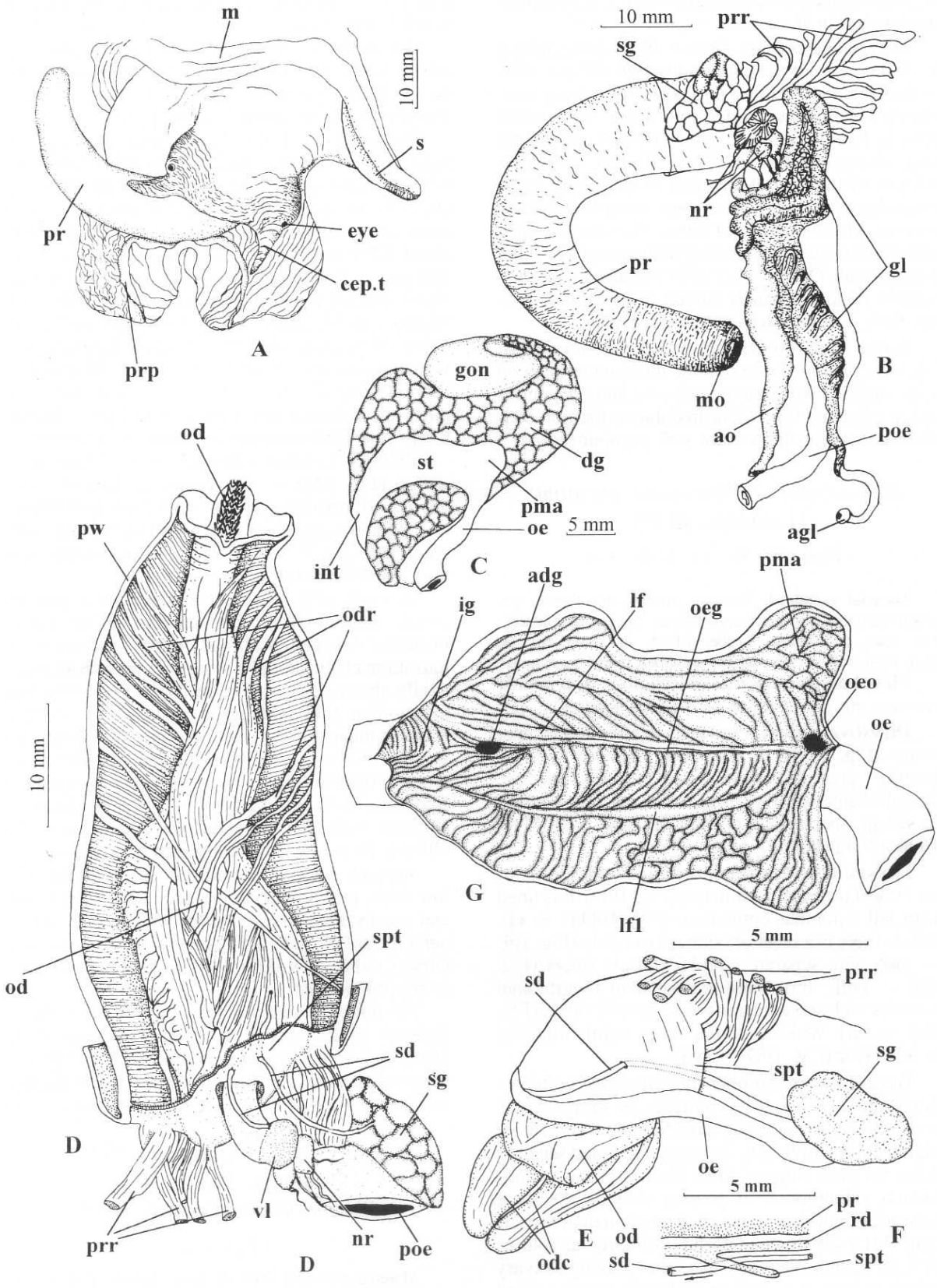

FIG. 13. *Busycotypus spiratum* (Lamarck, 1816). A — external front view of the soft body, upper whorls removed. B — anterior part of digestive system, left lateral view, proboscis everted. C — external view of the stomach. D — everted proboscis, dissected ventrally. E — posterior inverted proboscis. F — schematic transverse section through septum and rhynchodaeum in inverted proboscis to show the passage of salivary duct. G — stomach opened along mid-dorsal line (external wall reflected).

times exceeds length. Tentacles broadly spaced, short in contracted state, tapering towards tips, bearing very small eyes on lobes in basal part of tentacles (Fig. 14A — **eye**). Foot large, oval, folded transversely during fixation, bears large leaf-shaped operculum (substantially corroded on Fig. 13B) with terminal nucleus. Propodium medium narrow, delimited by deep propodial cleft. Columellar muscle with broad lumen, spans 1.3 whorls. Body colour tan, dorsal surfaces of head, tentacles, foot, and siphon pigmented with black spots.

Mantle medium long, width being equal to length (Fig. 14C). Mantle edge thickened, even. Siphon short and muscular, extending substantially beyond mantle edge. Osphradium bipectinate, narrow, symmetrical, with narrow axis, greenish-brown, occupies about third of mantle length. Ctenidium occupies 4/5 of mantle length, slightly longer and wider than osphradium. Hypobranchial gland well pronounced, the same width as ctenidium, with poorly developed folds. Rectum wide, spanning nearly entire mantle length, gradually narrowing towards small anal papilla.

Digestive system. Proboscis is 13 mm long, medium thick. Rhynchodaeum thin anteriorly and thick and muscular posteriorly, forming an evertable part. In inverted proboscis buccal mass lies within the proboscis. Proboscis retractors form two lateral bundles, attached to middle part of rhynchodaeum. Besides, there are paired large retractors, attached laterally and more posterior (Fig. 14D — **prr**). Mouth opening triangular, odontophore was partially protruded through it.

Proboscis wall thin (about 0.15 mm), lined with cylindrical epithelium, underlined by thick layer of unstructured connective tissue, layer of circular muscles, two layers of spiral muscles, and layer of longitudinal muscles (Fig. 14H).

Odontophore large, about 2/3 of proboscis length (Fig. 14E — **od**), consists of paired subradular cartilages fused anteriorly, and complex system of muscles, attached to proboscis walls.

Radula in a specimen with the SL 29.5 mm, AL 17.2 mm, very long, 13.5 mm long, exceeds proboscis length, consists of 161 rows of teeth, nine nascending. Radular width 410 μm. Lateral teeth tricuspid, with outermost cusp longest, slightly curved. Intermediate cusp situated closer to innermost and is the smallest. Central tooth subsquare, with 3 subequal in length short cusps, bordered by small denticle on both sides of outer cusps. Cusps emanate from posterior margin of the tooth base. Anterior margin of the tooth base is slightly arcuate.

After leaving proboscis, anterior oesophagus forms loop and runs unattached to rhynchodaeum forward along most of proboscis length to pass through nerve ring. Just in front of nerve ring there is small valve of Leiblein, poorly differentiated from oesophagus (Fig. 14D — **vl**). Gland of Leiblein is not large, flaccid, nearly devoid of glandular tissues, opens through short duct into oesophagus slightly posterior from the nerve ring.

Stomach long and extends for slightly more than half whorl from the nephridium border. Dorsal side of stomach nearly borders gonad. Integuments of visceral mass covering digestive gland, strongly pigmented in black. Oesophagus opens into stomach near its posterior end. Posterior mixing area short, and lined with strong transverse folds, visible through outer stomach wall (Fig. 14 F, G — **pma**). Posterior opening of digestive gland duct small and situated at the entrance of oesophagus (Fig. 14G — **pdg**). Narrow, distinct, longitudinal fold (Figure 14 F — **lf**), originates at the level of posterior opening and runs the length of stomach bordering oesophageal groove. It is white in contrast to rest of stomach, which is lined with dark grey epithelium. Inner and part of outer walls are covered with very low and narrow parallel oblique folds. In some specimens mucus string was observed running along mid-portion of inner wall into intestine. This string envelops food remains in intestinal groove and forms faecal string. The oesophageal groove (Fig. 14G — **oeg**) is dark grey and in some specimens is nearly smooth, while in others it is covered with oblique folds. Outer stomach wall has oblique, very distinct fold that is transversely striated (Fig. 14F, G — **sf**). It is directed ventro-dorsally and disappears at border with the style sac. In some specimens the fold originates near entrance of oesophagus, while in others at the level of anterior opening of the digestive gland duct. Ventral to this fold there is a rather broad zone of thick epithelium, covered with mucus and forming irregularly spaced transverse folds. Lateral sulcus (Fig. 14F — **ls**) is very shallow and seen on the inner and outer stomach walls. It is also visible through outer wall of the stomach. Style sac area very short and partially covered by nephridium. Opening of anterior duct of digestive gland very small and situated in oesophageal groove. Diameter of anterior duct itself, as it passes inside digestive gland, is large and similar to that of the stomach. Typhlosoles low and indistinct. Inner wall of posterior part of dorsal channel of style sac lined with low transverse folds, while anterior part has distinct longitudinal folds.

Strong ciliary currents absent. Weak flow from oesophagus into posterior mixing area and dorsally along stomach inner wall was observed. In oesophageal groove there were stronger turbulent currents, as well as dorsally directed currents along striated fold, draining the groove.

РИС. 13. (на противоположной странице) *Busycotypus spiratum* (Lamarck, 1816). A — внешний вид мягкого тела спереди, верхние обороты удалены. B — передний отдел пищеварительной системы, вид слева, хобот вывернут. C — внешний вид желудка. D — вывернутый хобот, вскрытый с вентральной стороны. E — задняя часть ввернутого хобота. F — схематичный поперечный срез через септу и ринходеум, показывающий прохождение слюнного протока. G —желудок, вскрытый по дорсальной стороне, наружная стенка отогнута.

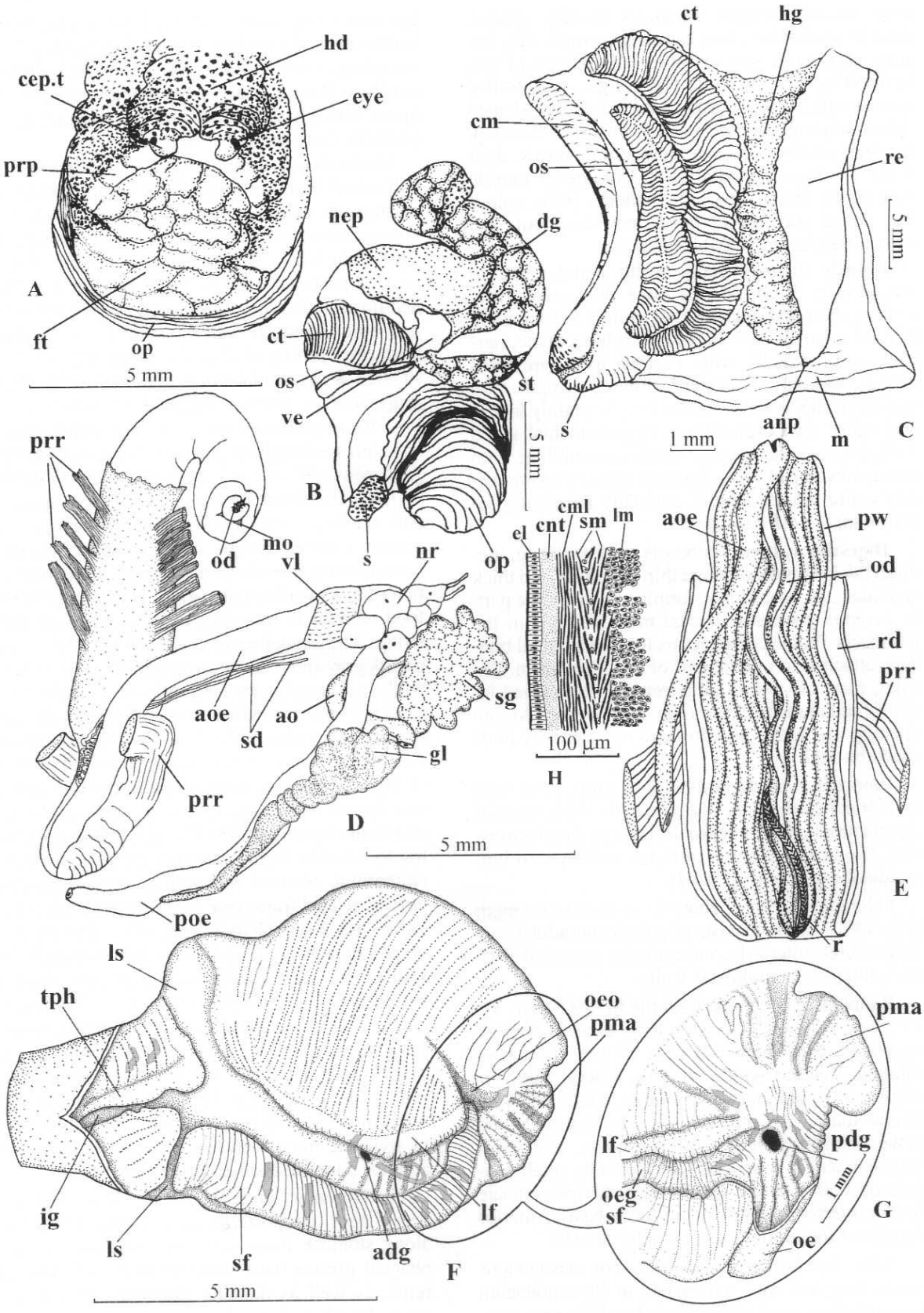

FIG. 14. *Pisania tincta* (Conrad, 1846). A — external front view of the soft body, upper whorls removed. B — external lateral view of the soft body, upper whorls removed. C — mantle. D — ventral view of anterior part of digestive system. E — proboscis, dissected dorsally. F — stomach opened along the dorso-lateral line. G — enlarged part of the stomach, showing the opening of the oesophagus into the gastric chamber. Oesophagus partially opened along the ventral line. Arrows indicate the main ciliary currents in the stomach. H — transverse section of proboscis wall. F-G after Kantor [2003], modified.

Discussion

Buccinoidea are relatively well studied anatomically, although very unevenly. While there is a number of publications, devoted to anatomy of boreal, tropical, and deep-water Buccinidae [Dakin, 1912; Lus, 1981, 1989, etc.; Kantor, 1990; Ponder, 1973, etc.], some to Antarctic and subantarctic Buccinulidae [Harasewych, Kantor, 1999; Harasewych, Kantor, *in press*], very few papers describe the anatomy of other families of Buccinoidea. We can mention publications of Ponder [1968] on Colubrariinae, Marcus and Marcus [1962] on Columbellidae.

Anatomy of representatives of Melongeninae has not been described in any details, although Ponder [1974] mentioned that *Melongena* lacks gland and valve of Leiblein, and Harasewych [1988] described characteristic head morphology and very long proboscis in Melongeninae.

The head morphology of Melongeninae is unique for Buccinoidea and can be considered as an autapomorphy of the subfamily. In all studied species the head is very long, narrow, cylindrical, with rhynchostome in a shape of narrow slit on ventral side of the head shifted anteriorly. Tentacles in preserved specimens are very narrow and small, while eyes are situated antero-laterally on the head rather than at tentacles.

The rest of Buccinoidea (and the majority of other Neogastropoda, except Conoidea) have broad and short head with ventral rhynchostome shifted to the base of the head. Tentacles are large, usually conic and with eyes situated at the base of tentacles (on small lobes, at least in Buccinidae and Busyconinae).

Our data demonstrate that Melongeninae and Busyconinae differ markedly in several characters of the digestive system: proboscis morphology, anatomy of proboscis walls, morphology of odontophore, radular morphology, structure of posterior oesophagus, and in stomach anatomy (Table 2).

Anatomy of all studied Melongeninae is rather uniform and varies in minor details.

In all Melongeninae proboscis is very long and narrow in inverted position, its length exceeds diameter by at least 8 times (subadult specimen of *Volema pyrum*), but usually much more, up to 25 times (adult *Volema pyrum*). Very characteristic is that in inverted position the proboscis is folded together with thin rhynchodaeum within the body haemocoel.

In Busyconinae proboscis is short, length of retracted proboscis exceeds diameter by 4 times, and proboscis is never folded. In retracted proboscis the buccal mass always significantly (sometimes nearly twice) exceeds the proboscis length and is protruded posteriorly. In all studied species odontophore is characteristically bifurcated posteriorly.

Folding of the proboscis in retracted position is not unique for Melongeninae. It was recorded in the genus *Ancistrolepis* Dall, 1895 (*A. eucosmius* Dall, 1891; *A. okhotensis* Dall, 1925; *A. vietnamensis* Goryachev et Sirenko, 1990 [Kantor, 1988; unpublished observations]) among Buccinidae, in *Ratifusus mestayerae* (Iredale, 1915) (Colubrariidae) [Ponder, 1968], in *Vasum muricatum* (Born, 1778) [Medinskaya et al., 1996] and other Turbinellidae, different Conoidea [Taylor et al., 1993].

Proboscis may be folded within rhynchodaeum (*Ancistrolepis,* Conoidea, Colubrariidae) or together with the rhynchodaeum within body haemocoel (Melongeninae, Turbinellidae). The mechanism of the proboscis folding remains still unclear.

In three species of Busyconinae we found a highly contractible septum, outgrowth of proboscis wall, that can isolate the proboscis inner cavity from the rest of the body haemocoel when proboscis is protracted. This septum was not recorded in any other neogastropods, although it is not impossible that it will be found in future. Majority of preserved specimens of neogastropods have proboscis in inverted position. In inverted proboscis, the septum looks like a circular fold on outer surface of rhynchodaeum and can be easily overlooked. In Busyconinae this septum is penetrated by separate holes for salivary ducts and unusual passage of salivary ducts (Fig. 13E), initially under the fold (septum) and then through the hole, allows easy determination of septum presence even in retracted position. The presence of the septum is most probably explained by the mechanism of proboscis evertion.

In general, neogastropod proboscises function as a muscular hydrostat [Greene, Kohn, 1989]. Proboscis wall normally contains at least two muscle layers — circular and longitudinal. Contraction of longitudinal muscles results in proboscis shortening, while that of circular muscles — in reduction of proboscis diameter and, since the inner volume of proboscis remains constant, its elongation. The proboscis and body haemocoel are confluent, and the increase of pressure of blood that is filling the latter, together with contraction of circular muscles causes strong elongation and evertion of proboscis through rhynchostome. Usually in neogastropods the posterior part of rhynchodaeum is invaginable and during proboscis evertion adds to proboscis length. The border between invaginable and non-invaginable parts of rhynchodaeum is marked by changes in its histology. The former part has the same thickness and muscular arrangement as proboscis wall, while

РИС. 14. (на противоположной странице) *Pisania tincta* (Conrad, 1846). A — внешний вид мягкого тела спереди, верхние обороты удалены. B — внешний вид мягкого тела с вентральной стороны, верхние обороты удалены. C — мантия. D — передний отдел пищеварительной системы с вентральной стороны. E — хобот, вскрытый с дорсальной стороны. F — желудок вскрытый с дорсальной стороны. G — увеличенный участок желудка в месте впадения пищевода. Пищевод частично вскрыт по вентральной стороне. Стрелки показывают основные ресничные токи, создаваемые ресничным эпителием. H — поперечный срез стенки хобота. F-G по Kantor [2003], с изменениями.

Table 2. Summary of morphological characters of studied species.

	Busyconinae			Melongeninae				Buccinidae
	Busycon carica	*Busycon spiratum*	*Busycotypus spiratum*	*Pugilina pugilina*	*Melongena corona*	*Hemifusus ternatanus*	*Volema pyrum*	*Pisania tincta*
Head (length/ width ratio)	1:2	1:2	1:2	3:1	3:1	3:1	2:1	1:2
Proboscis length/ AL ratio	—	0.36	0.39-0.67 (everted proboscis)	0.81	0.85	1.57	0.64-2.69	1.0
Radula length/ proboscis length ratio	0.97	2	0.89	0.17	0.24	0.08	0.39	1.1
Number of rows of teeth	117	106	146	56	57	42	61	100
Number of cusps on lateral teeth	4-6	5	4-5	2	2	2	2	3
Proboscis retractors	Attached to central part of rhyncho-daeum	Attached to central part of rhyncho-daeum	Attached to central part of rhyncho-daeum	Attached to proboscis base	Attached to proboscis base	Attached to proboscis base	Attached to proboscis base	Attached to central part of rhyncho-daeum
Inner proboscis retractors	Absent	Absent	Absent	Present	Present	Present	Present	Absent
Valve of Leiblein	Present	Present	Present	Absent	Absent	Absent	Absent	Present
Gland of Leiblein	Present	Present	Present	Absent	Absent	Absent	Absent	Present
Posterior mixing area of stomach	Present, long	Present, medium long	Very short, practically absent	Present, short	Absent	Present, short	Absent	Present

non-invaginable part is usually thinner and has different epithelial lining.

The presence of the septum at the base of everted proboscis allows its stretching by mere contraction of circular muscles without changing the blood pressure in body haemocoel. We may suppose that septum presence may be connected with the large size of *Busycon* species and that it may be found in other large neogastropods with long in protracted state proboscis.

Invertion of the proboscis is a complex combination of both muscular action and changes in hydrostatic pressure in body/proboscis haemocoel. To facilitate proboscis invertion in neogastropods, proboscis retractors are always present. In most studied Buccinoidea (including species of *Ancistrolepis* and Busyconinae), numerous separate proboscis retractors are arranged in symmetrical groups, attached to outer rhynchodaeum wall in its central part or shifted more anteriorly (when proboscis is inverted). In *Pisania,* besides these lateral retractors, there are paired large retractors, attached to the posterior of the evertable part of rhynchodaeum wall. On the distal ends retractors are attached to walls and floor of body haemocoel. During proboscis extension, place of attachments of retractors to rhynchodaeum is shifted forward together with invaginable part. As a result, in everted proboscis, retractors are attached to inner proboscis walls. During proboscis retraction, the contraction of proboscis retractors causes invagination of the posterior part of proboscis wall and, associated with contraction of longitudinal muscles in the proboscis wall, the shortening of proboscis.

In Melongeninae the proboscis retractors are arranged differently. They are represented by paired thick and large muscles (fused at their bases in *Hemifusus* and *Volema*), inserted into posterior part of proboscis walls and attached to the bottom of the body haemocoel. The evertable part of rhynchodaeum is absent. Besides, there are additional inner proboscis retractors (autapomorphy of the subfamily), attached to the anterior proboscis walls, free along proboscis length, leaving proboscis posteriorly and attached to the bottom of the body haemocoel. Paired proboscis retractors function as an "anchor" fixing the proboscis base and are also responsible for contraction of proboscis length. Folding of proboscis together with rhynchodaeum within body haemocoel probably occurs due to unilateral contraction of proboscis wall (which may be facilitated by contraction of inner proboscis retractors).

Thus the mechanism of proboscis retraction in Melongeninae differs significantly from that in other

Buccinoidea (including Busyconinae), except probably Colubrariidae which also have paired "basal" proboscis retractors and non-evertable very thin rhynchodaeum [Ponder, 1968].

Proboscis wall has similar anatomy in all studied Melongeninae and is comprised of 4 muscular layers. Columnar or cubic epithelium of proboscis is underlined by a more or less thick layer of unstructured connective tissue, under which there is a thick layer of circular muscle fibers, comprising more than third of the thickness of proboscis wall. Within the circular layer there are few muscle fibers, oriented mostly in radial direction. Below the circular muscle layer there are two much thinner subequal in thickness layers of spiral muscles, oriented in opposite directions. Finally the innermost layer is composed of thick longitudinal muscle fibers. The spiral muscles allow rotation of proboscis along its long axis [Kier, 1988; Greene, Kohn, 1989] and therefore increases proboscis mobility.

In both studied species of Busyconinae the proboscis wall lacks spiral muscles, but is rather complexly arranged (Fig. 10 D-E), having a thick layer of connective tissue (*Busycon carica*) or well developed transverse muscles, penetrating the layer of longitudinal muscle fibers (*Busycotypus spiratum*).

Proboscis wall anatomy of very few Buccinoidea has been examined. Medinskaya [1992] described *Buccinum middendorffi* Verkrüzen, 1882, *Neptunea bulbacea* (Valenciennes, 1858) (both Buccinidae), and *Tritia fratercula* (Dunker, 1860), while Kantor and Medinskaya [1991] studied of *Mitrella burchardi* (Dunker, 1877). In the former two species, proboscis wall is basically comprised of circular and longitudinal muscle layers, while in *Mitrella* the layers of spiral muscles are distinct and well developed. Wilsman [1943] in her fundamental publication on the pharynx of *Buccinum undatum* L., 1758 did not describe the anatomy of proboscis wall in any details, but her fig. 9 (transverse section of the proboscis) shows a layer very similar to spiral (although only single one). Thus the presence of spiral muscles in the proboscis wall sporadically occurs among Buccinoidea. At the same time, the proboscis wall in Busyconinae has distinct similarity to *B. middendorffii* and *N. bulbacea*.

One may suggest that the folding of proboscis together with rhynchodaeum (or within it) correlates with the presence of spiral muscles in the proboscis wall. This is disproved by the anatomy of proboscis of *Ancistrolepis okhotensis* (Fig. 10F), which lacks spiral muscles (although there are additional inner layers of circular and longitudinal muscles). At the same time, the proboscis is folded within rhynchodaeum during retraction.

The arrangement of odontophoral muscles in Busyconinae is similar to that of *Buccinum* [Wilsman, 1943], although in specimens of *Busycon* spp. with inverted proboscis, odontophore is large and protrudes significantly beyond the rear of the proboscis. Odontophoral muscles are numerous, complex and attached to the proboscis walls.

On the contrary, in all studied Melongeninae the odontophore is rather compact and narrow, although muscular in its anterior part (Fig. 2B). Posteriorly, odontophore terminates in relatively thin paired muscles, running along proboscis length, leaving it from behind and attached to the floor of body haemocoel together with inner proboscis retractors. Subradular cartilages are longer than the radular sac (Fig. 5B). Posteriorly, the place of the radular sac is occupied by a large blood vessel (Fig. 5B — **ba**) that probably ramifies from the buccal artery.

Radula in all Melongeninae species is rather uniform and characterised by bicuspid lateral teeth with strongly curved cusps and subrectangular rachidians, bearing usually 3 cusps (Figs. 3, 7). It is short, consisting of 42-61 rows of teeth and comprising from 0.08 (in *Hemifusus*) to 0.39 (*Volema*) of proboscis length. It is also narrow, being 310-540 μm wide, that is 0.012-0.020 of AL.

Radula of Busyconinae (Fig. 11) has similar morphology of rachidians, while laterals differ markedly, being much broader and multicuspid, with 3-4 intermediate smaller cusps. It is much longer than in melongenines, consisting of 117-146 rows of teeth and comprising 0.89 (in *B. spiratum* with everted proboscis) to 0.97 of proboscis length. It is also much broader, being 1780-2500 μm wide, that is 0.32-0.33 of AL.

Radulae of both Melongeninae and Busyconinae do not possess any unique characters and are generally buccinoidean.

Structure of oesophagus also differs markedly in both subfamilies. In Melongeninae, valve and gland of Leiblein are absent, while oesophagus after passing through the nerve ring significantly broadens and forms lateral oesophageal pouch of irregular shape. In Busyconinae, oesophagus lacks such pouch, while possesses valve and gland of Leiblein.

Stomach of Melongeninae has several characteristic features: it lacks pronounced posterior mixing area and lateral sulcus. Gastric chamber is distinctly separated into dorsal and ventral parts by strong longitudinal fold(s), which are continuous with poorly developed typhlosoles. Stomach of Busyconinae is relatively much larger than in melongenins, although varies significantly between studied species, and while in *B. carica* and *B. sinistrum* it has a large or medium-sized posterior mixing area, in *B. spiratum* the posterior mixing area is very short. In all three species there was a longitudinal fold on the outer stomach wall.

Phylogenetic analysis

As was demonstrated above, representatives of Busyconinae differ from Melongeninae in many characters of the digestive system having more affinities to Buccinidae. In order to clarify relationships between subfamilies we conducted a phylogenetic analysis. The list of taxa is presented in Table 1. *Babylonia* (Babyloniidae) and *Alcithoe* (Volutidae) were selected as outgoups.

Twenty five characters (Table 3) coded as 59

Table 3. Description of morphological characters and data matrix of character states used in cladistic analysis.

1. Head: 0 — broad (length/width <1); 1 — narrow (length/width >1.5)
2. Eyes: 0 — on the tentacle base; 1 — on lateral sides of the head at tentacle bases
3. Proboscis: 0 — not folded during contraction; 1 — folded during contraction
4. Buccal mass: 0 — significantly protrudes backward from rear of inverted proboscis; 1 — contained within inverted proboscis
5. Proboscis retractors: 0 — numerous, attached to middle part of rhynchodaeum; 1 — paired, separate, attached to proboscis base; 2 — paired, fusing, attached to proboscis base
6. Inner proboscis retractors: 0 — absent; 1 — present
7. Layer of spiral muscles in proboscis wall: 0 — absent; 1 — present
8. Paired odontophoral retractors, continuing subradular cartillages and attached to walls of body haemocoel: 0 — absent; 1 — present
9. Lateral teeth: 0 — bicuspid; 1 — multicuspid; 2 — columbellid type, 3 — absent
10. Radular length/proboscis length: 0 — long (>0.9); 1 — short (<0.4)
11. Number of rows of radular teeth: 0 — more than 90; 1 — less than 60.
12. Number of cusps on rachidian tooth: 0 — absent; 1 — 1 to 5; 2 — 7 and more
13. Valve of Leiblein: 0 — present; 1 — absent
14. Gland of Leiblein: 0 — present; 1 — absent
15. Evertable part of rhynchodaeum: 0 — present; 1 — absent
16. Accessory salivary glands: 0 — present; 1 — absent
17. Posterior oesophagus: 0 — narrow, without a pouch; 1 — broadened without a pouch; 2 — broadened, with a pouch; 3 — narrow, with a pouch
18. Posterior mixing area of the stomach: 0 — present, long; 1 — present, short; 2 — absent
19. Lateral sulcus: 0 — present; 1 — absent
20. Ducts of the digestive glands: 0 — closely spaced; 1 — broadly spaced; 2 — single.
21. Gastric shield: 0 — present; 1 — absent
22. Longitudinal fold on the outer stomach wall: 0 — present; 1 — absent
23. Anal gland: 0 — present; 1 — absent
24. Salivary glands: 0 — acinous; 1 — ramified tubular
25. Operculum: 0 — terminal nucleus; 1 — subcentral nucleus

Melongena	1111111101111111221111100
Pugilina	1111111101111111221111100
Hemifusus	1111211101111111211111100
Volema	111121110111111122?11?100
Busycon carica	0000000010010001000110100
B. sinistrum	000000?010010001001110100
Busycotypus spiratum	0000000010010001011110100
Pisania	0001001010010001010110100
Buccinum undatum	0001001010010001300111101
B. thermophilum	000100101001000130?111101
Neptunea	0001000010010001000110100
Ilyanassa	000100?01?020001000001100
Nassarius	000100?010020001000011100
Mitrella	001100102000000102111100
Columbella	000100?020000001021101100
Babylonia	000000?000111100121211000
Alcithoe	010100?030?10000021211010

states were used in analysis. Majority of characters are described above. Characters 9, 23 and 24 need short explanations.

Representatives of Columbellidae possess unique lateral radular teeth (character 9, state 2). They have a very narrow base attached to membrane, and 3-4 cusps on the inner side of the tooth [Marcus, Marcus, 1962].

Anal (rectal gland) (character 23) is one of the few synapomorphies of Neogastropoda [Kantor, 2002], secondarily lost in Buccinoidea and some other families. It is present in the outgroups.

Histology of salivary glands (character 24) is rather variable in Neogastropoda [Kantor et al., 1997]. The most common are acinous salivary glands, characteristic of all but one analysed species. In *Alcithoe* salivary glands are ramified tubular.

The analysis (with all characters treated as unordered) produced 4 equally parsimonious trees at length 45 steps [consistency index (CI) = 0.7333; homoplasy index (HI) = 0.2667], differing only in relative postion of genera of Melongeninae. The resulting strict consensus and 50% majority rule trees are shown in Fig. 15.

The analysis clearly demonstrates that Melongeninae constitute a well supported clade, which in our trees appeared to be a sister taxon to the remaining Buccinoidea included in the analysis.

Busyconinae also comprise a clade (supported by several autapomorphies, such as bifurcating posteriorly buccal mass and the presence of the septum), most close to Buccinidae of the subfamilies Colinae and Pisaniinae.

Results of the analysis suggest that Melongenidae in its currently adopted volume are a paraphyletic group. Busyconinae should be excluded and transferred to Buccinidae as a separate subfamily. Neither anatomy nor phylogenetic analysis support isolation of Busycotypinae. On the contrary, *Busycon sinistrum* constitutes a clade with *Busycotypus spiratus*, rather than with *Busycon carica*.

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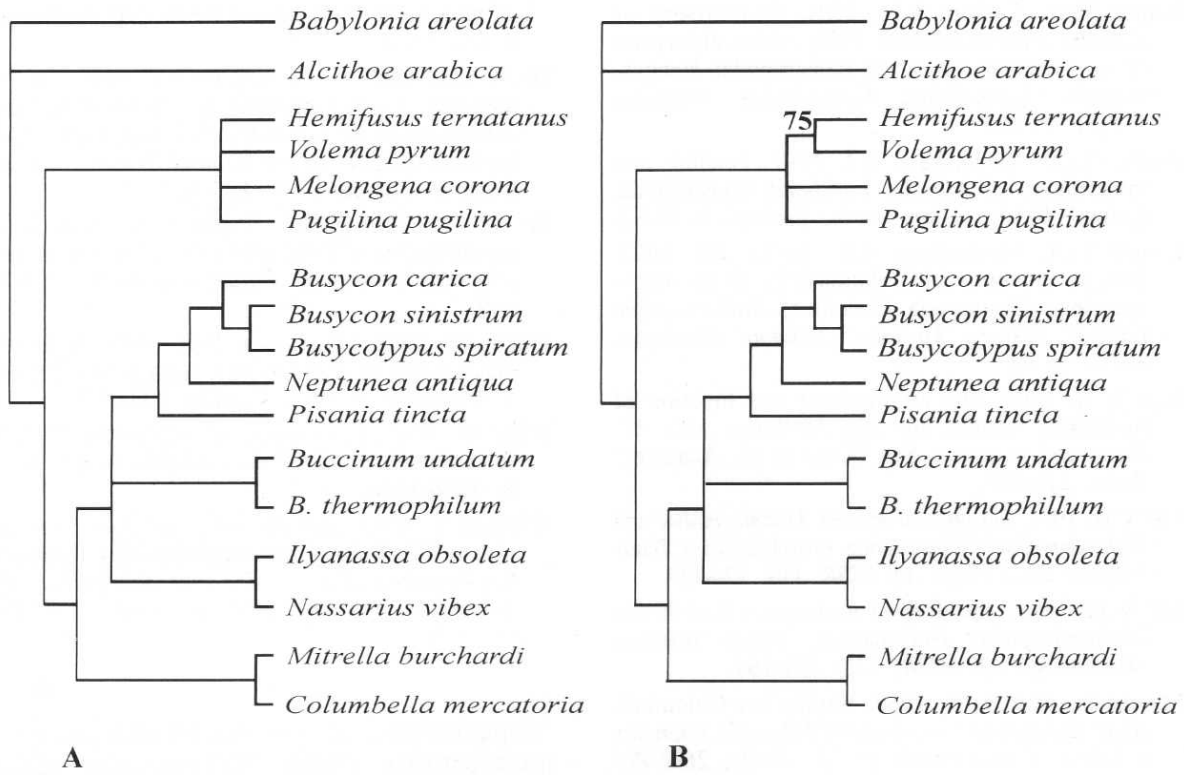

FIG. 15. Strict consensus (A) and majority rule (B) trees derived from 4 equally parsimonious trees 45 steps long.

РИС. 15. Строго консенсусное дерево (A) и консенсусное дерево, полученное по правилу большинства (B), полученные из 4 равно парсимониевых деревьев длиной 45 шагов.

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Морфология, таксономический статус и родственные связи Melongenidae (Gastropoda: Neogastropoda)

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РЕЗЮМЕ. Описаны внешняя морфология, строение мантийной полости и пищеварительной системы четырех видов Melongeninae (*Melongena corona, Pugilina pugilina, Hemifusus ternatanus, Volema pyrum)*, трех видов Busyconinae (*Busycon carica, B. sinistrum, Busycotypus spiratum)* и одного вида Buccinidae (*Pisania tincta*). Оба подсемейства Melongenidae существенно различаются между собой внешней морфологией и анатомией пищеварительной системы: строением головы, морфологией и анатомией хобота, включая строение его стенок, механизмом вворачивания хобота, морфологией и размерами радулы, наличием клапана и железы Лейблейна (отсутствуют у Melongeninae), морфологией желудка. Пищеварительная система Busyconinae оказывается более близкой к представителям семейства Buccinidae, чем к Melongeninae. Проведенный кладистический анализ с привлечением 15 видов Buccinoidea и двух аутгрупп показал, что Busyconinae должны быть исключены из состава Melongenidae и переведены в Buccinidae в ранге подсемейства. Busyconinae как клад поддерживаются несколькими аутапоморфиями, среди которых наиболее важной является наличие септы (пронзенной отверстиями для протоков слюнных желез), изолирующей полость вывернутого хобота от туловищного гемоцеля.