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COMPARATIVE MORPHOLOGY AND PHYLOGENY OF REPRESENTATIVES OF THE SUPERFAMILIES OF ARCHITAENIOGLOSSANS AND THE ANNULARIIDAE (MOLLUSCA, CAENOGASTROPODA) [1]

(With 354 figures)

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ABSTRACT: As part of a larger project on the phylogeny of the Caenogastropoda superfamilies, a detailed morphological study of 19 non-marine species is provided, of the following taxa: a) Family Ampullariidae: 1} *Pomacea crosseana* (Hidalgo) (from Pantanal, Brazil); 2) P. *curumim* new species (from Xingu River, Amazon Basin, Brazil); 3) P. *scalaris* (Orbigny) (from Pantanal, Brazil); 4) P. *canaliculata* (Lamarck) (same); 5) *P. lineata* (Spix) (several coastal places of Brazil); 6) *P. sordida* Swainson (Rio de Janeiro, Brazil); 7) *P. bridgesi* (Reeve) (Para, Brazil) (most published elsewhere); 8) *Asolene megastoma* (Sowerby) (Rio Grande do Sul, Brazil); 9) *Felipponea neritiniformis* (Dall) (Parana, Brazil); 10) *Marisa planogyra* Pilsbry (Pantanal, Brazil); b) Family Cyclophoridae: 11) *Neocyclotus prominulus* (Orbigny) (Sao Paulo, Brazil); 12) *Incidostoma tupy* new species (Rondonia, Brazil); 13) *Aperostoma branchetiana* (Moricand) (Minas Gerais, Brazil); c) Family Viviparidae: 14) *Viviparus acerosus* (Bourguignat) (Hungary); 15) *V. contectus* (Millet) (same); 16) *Notopala ampuilaroides* (Reeve) (Australia); 17) *N. essingtonensis* (Frauenfeld) (same); 18) *Larina* cf. *stangei* (Adams) (same); d) Family Annulariidae: 19) *Annularia* sp. (Yucatan, Mexico). Based on this study, 143 characters (192 states) were searched, polarized, and a phylogenetic analysis is performed. The single obtained cladogram is the following: ((*Neocyclotusprominulus (Aperostoma blanchetiana* - *Incidostoma tupy*)) (((*Annularia*sp. - Cerithioidea) ((*Viviparus* acerosus - *V. contectus)* ((*Notopala ampuilaroides - N. essingtonensis) Larina* cf *strangei)))* (Marisa *planogyra (Pomacea crosseana (Felipponea neritiniformis(P.scalaris* (*P.curumum*(P. *lineata* ((*P.canaliculata*–*Asolene megastoma)(P. bridgesi*– *P.sordida*))))))))), length 251; ci 77; ri 91. A pool of archaeogastropod characters, the rissooideans-littorinoidean *Annularia*, and the Cerithioidea ground plan were used as main outgroups, however the two latter taxa are operationally included as part of the ingroup. The analysis of obtained cladogram revealed that the taxon Architaenioglossa is paraphyletic, grouping 3 branches of basal caenogastropods successively distributed on the tree as follows: Cyclophoroidea (Cyclophoridae), Ampullarioidea (Ampullariidae), and Viviparioidea (Viviparidae), since the representatives of the remainder the caenogastropods (*Annularia* and Cerithioidea) were terminal in the ingroup. The current concept ot Ampullarioidea (Ampullariidae plus Viviparidae) was also paraphyletic.

Key words: Ampullarioidea, Viviparioidea, Cyclophoroidea, Phylogeny, Morphology

RESUMO: Morfologia Comparativa e Filogenia de representantes das superfamílias de arquitenioglossos e Annulariidae (Mollusca, Caenogastropoda).

Como parte de um projeto sobre fllogenia das superfamilias de Caenogastropoda um estudo morfológico detalhado de 19 espécies nao marinhas e desenvolvido dos seguintes taxons: a) Família Ampullariidae: 1) *Pomacea crosseana* (Hidalgo) (Pantanal, Brasil); 2) P. curumim nova especie (Xingu River, Amazonia, Brasil); 3) P. *scalaris* (Orbigny) (Pantanal, Brasil); 4) P. *canaliculata* (Lamarck) (mesmo); 5) P. *lineata* (Spix) (vários locais costeiros do Brasil); 6) P. *sordida* Swainson (Rio de Janeiro, Brasil); 7) P. *bridgesi* (Reeve) (Para, Brasil) (maioria dos dados publicados em outro tranbalho); 8) *Asolene megastoma* (Sowerby) (Rio Grande do Sul, Brasil); 9) *Felipponea neritiniformis* (Dall) (Parana, Brasil); 10) Marisa *planogyra* Pilsbry (Pantanal, Brasil); b) Familia Cyclophoridae: 11) *Neocyclotus prominulus* (Orbigny) (Sao Paulo, Brasil); 12) *Incidostoma tupy* especie nova (Rondonia, Brasil); 13) Aperostoma branchetiana (Moricand) (Minas Gerais, Brasil); c) Familia Viviparidae: 14) Viuiparus acerosus (Biurguignat) (Hungria); 15) *V. contectus* (Millet) (mesmo); 16) *Notopala ampuilaroides* (Reeve) (Australia); 17) *N. essingtonensis* (Fauenfeld) (mesmo); 18) *Larina* cf. stangei (Adams) (mesmo); d) Familia Annulariidae: 19) *Annularia* sp. (Yucatan, Mexico). Baseando-se neste estudo, 143 caracteres (192 estados) foram levantados, polarizados, e uma analise filogenetica e realizada. O cladograma único e o seguinte: ((*Neocyclotusprominulus (Aperostoma blanchetiana* - *Incidostoma* *tupy*)) (((*Annularia* sp. - Cerithioidea) ((*Viviparus* acerosus - V. contectus) ((*Notopala* ampuilaroides - *N. essingtonensis) Larina* cf *strangei*))) (Marisa *planogyra (Pomacea crosseana (Felipponea neritiniformis* (P. *scalaris (P*. curumim (P. lineata ((*P. canaliculata – Asolene megastoma*) (P. *bridgesi – P. sordida*))))))))), passos: 251; IC 77; IR 91. Um conjunto de caracteres de archaeogastrópodes, o Rissooidea *Annularia*, e o piano básico de Cerithioidea foram usados como principais grupos externos, entretanto, os 2 últimos taxons foram incluídos operacionalmente como parte do grupo interno. A analise do cladograma obtido revelou que o taxon Architaenioglossa e parafiletico, agrupando 3 ramos de cenogastropodes basais sucessivamente distribuídos na arvore como segue: Cyclophoroidea (Cyclophoridae), Ampullarioidea (Ampullariidae), e Viviparioidea (Viviparidae), uma vez que os representantes dos demais cenogastropodes (*Annularia* e Cerithioidea) resultaram como parte terminal do grupo interno. O senso prévio de Ampullarioidea (Ampullariidae mais Viviparidae) também resultou parafiletico.

Palavras-chave: Ampullarioidea, Viviparioidea, Cyclophoroidea, Filogenia, Morfologia.

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INTRODUCTION

Architaenioglossa is an enigmatic taxon that encompasses non-marine mesogastropod prosobranchs, corresponding to three families: Ampullariidae (=Pilidae), Viviparidae and Cyclophoridae (*s.l.*). HASZPRUNAR (1988) presented the more accurate sense of this taxon, regarded as the sister taxon of the branch Caenogastropoda plus Heterobranchia, in the archaeogastropod grade. PONDER AND LINDBERG (1996, 1997), in their phylogenetic analysis of the Gastropoda, advocated that the architaenioglossans were basal members of the caenogastropod branch. Despite those studies, the validity of the formal taxon Architaenioglossa is still unclear, because it is not defined by any synapomorphy, other than the non-marine habitat. It is possible that this taxon actually represents a paraphyletic or even a polyphyletic group. Besides, their relationship with other gastropods is still controversial.

The literature on some architaenioglossans is relatively rich, mainly on the ampullariids, which have species with medical, sanitary, and gastronomic importance. However, despite of this, the taxonomy remains unclear.

The Ampullariidae are medium to large freshwater snails, with representatives in all tropical areas of the Americas, Africa and Asia. There are some papers describing their morphology, such as, *e.g.*, SCOTT (1957) with particular attention to South American representatives. BERTHOLD (1991) made an extensive study with representatives of all genera, and included aspects on morphology, phylogeny and evolution. BERTHOLD (1991), however, did not make a formal phylogenetic analysis of the group, but this, in part, was provided by BIELER (1993). PAIN (1972) referred on the family history. DEMIAN & YOUSIF (1973) provided embryological data. CASTELLANOS & FERNÁNDEZ (1976) provide biologic and biogeographic information. COWIE (1997) addressed the nomenclatural problems with the name Ampullariidae and the genera *Pomacea* and *Ampullaria*. Revisions of South American ampullariids include studies at the Instituto Oswaldo Cruz (*e.g.*, THIENGO, 1987, 1989, 1995).

Viviparidae are freshwater, filter-feeders found in most part of Europe, southern Asia, north and east Australia, and the central-east region of North America. Analysis of the history and distribution of the viviparids can be found in PRASHAD (1928). As its name suggests, they are viviparous or ovoviviparous, with females brooding the young in the pallial oviduct.

The Ampullariidae and the Viviparidae have been normally referred to the same superfamily in recent literature, sometimes as Ampullarioidea (*e.g.*, BOSS, 1982; PONDER & WARÉN, 1988), other times as Viviparioidea (*e.g.*, VAUGHT, 1989). This hypothesis is also investigated herein.

The Cyclophoridae are terrestrial, distributed worldwide, lacking gill. They are, sometimes, divided into several families (*e.g.*, six families in VAUGHT, 1989). They are, also, the subject of several monographic papers, which include taxonomical and some anatomical data. TIELECKE (1940), for example, introduced a classification based mainly on the characters of the shell and pallial oviduct. MORRISON (1955) established a taxonomy based mainly on the male reproductive organ of the American species. Some papers also provide further modifications and further critical analysis of unstable cyclophorid classification is profuse in the literature (*e.g.*, SOLEM, 1956; THOMPSON, 1963, 1967).

The Annulariidae are terrestrial snails from Central and North America, with known relationships with putative basal caenogastropods such as Littorinidae. THOMPSON (1978), pointed out the unusual radula and genital system and explored the concept of the family.

As part of a larger project on the phylogeny of the Caenogastropoda, representatives of each family of all superfamilies of this taxon have been studied in a detailed morphological and comparative scenario. For each caenogastropod superfamily, the following attributes have been tested: 1) the monophyly; 2) taxonomic status; and 3) the ground plan, i.e., the attributes of their hypothetical ancestral. These three parameters can only be tested by means of a phylogenetic analysis. The Architaenioglossa is the focus of the present paper. As the group in general, and the South American members in particular, have a very confused taxonomy, this paper also provides a basis for future more detailed studies on each sub-group. Some previously published phylogenies are part of the project (SIMONE, 1999, 2000, on Terebridae; SIMONE 2001, on Cerithioidea and SIMONE in press, on Stromboidea, Cypraeoidea and Calyptraeoidea) as well as other smaller papers, serving as outgroups. The terrestrial Annulariidae, which has a representative studied herein, are undoubtedly a non-architaenioglossan caenogastropod (see THOMPSON, 1978; PONDER & WARREN, 1988). Its inclusion has as main objective to test how adaptation to a non-marine environment can influence this kind of analysis.

MATERIAL AND METHODS

Although some living species of *Pomacea* were examined in the laboratories of the Museu de Zoologia da USP (MZSP), most of the specimens studied were fixed in 70% ethanol. The extraction of the specimens from their shells were mostly easy, in some specimens the shell was broken. The dissections were performed under a stereomicroscope following traditional techniques, with the specimens immersed in fixative. All drawings were made with aid of a camera lucida. The hard parts, such as shells (of small specimens), jaws and radulae, were also examined in SEM, in the Laboratório de Microscopia Eletrônica of MZSP.

In the descriptions, a more detailed one is presented for the first species, P. *crosseana*, (it was the first species studied in the project). In the remaining species, and when possible, the description is basically comparative to *P. crosseana*, without any description of similar characters. A similar approach is given in the figures.

A part of the cladistic analysis was performed with the aid of the computer programs and "Tree Gardner 2.2" (RAMOS, 1997). The last basically works as an interface of the program "Hennig86" (FARRIS, 1988), the algorithm used was mh*, bb* and ie. For the polarization of the character states the outgroup method was used.

The section of comparative morphology is organized as a phylogenetic analysis, the presentation of each character begins with abbreviated descriptive sentence followed by plesiomorphic and derived conditions(s); also included are CI and RI (consistency and retention indices, respectively), values for the character under the most parsimonious hypotheses. Following the apomorphic state(s), a list of terminal taxa with the apomorphic condition is presented. In the next section, all character states are presented in the table 1.

The remaining Caenogastropoda studied in this project were selected as outgroups, despite sometimes they are not directly included in the data matrix. They are mainly the following: Cerithioidea (SIMONE, 2001); Littorinoidea (SIMONE, 1998); Rissooidea-Littorinoidea (SIMONE & MORACCHIOLI, 1994; SIMONE 1995a, *Annularia* sp. - this study); Stromboidea (SIMONE in press c); Calyptraeoidea (SIMONE, submitted); Tonnoidea (SIMONE, 1995b); Muricoidea (SIMONE, 1995c on *Thala crassa*; SIMONE, 1996b on *Buccinanops* spp); Conoidea (SIMONE, 1999, 2000, on Terebridae). As more distant outgroups, some archaeogastropods were also analyzed (*e.g.*, SIMONE, 1996A; 1997; LEAL & SIMONE, 1998; 2000). However, in the analysis of the matrix in the computer programs, only three outgroups are included: 1) A pool of archaeogastropods, mainly based on SASAKI (1998). 2) The *Annularia* sp., studied herein, representing the Risooidea-Littorinoidea branch, with a species adapted to the non-aquatic environment. 3) The Cerithioidea ground plan, *i.e.*, the node # 1 of the cerithioidean cladogram, obtained in a previous study (SIMONE, 2001). Operationally, only the archaeogastropod set of characters was utilized as the outgroup, with *Annularia* sp. and Cerithioidea ground plan analyzed as part of the ingroup. So that, the monophyly of the "Architaenioglossa" could be tested.

Characters were polarized separately, and the polarization is justified, if necessary, in the discussion that follows each character. In that discussion, the final cladogram obtained is considered (*i.e.*, the allocation and optimization of some character states are discussed) although, the cladogram is only formally presented in the following section.

Three parameters considered here are known as polemic, and sometimes there are authors who do not accept them. The FIRST is the use of the ingroup synapomorphies (those that support node 1, or the ingroup "autapomorphies" in this case). They are used herein because they are the main goal of this study, since the Architaenioglossa is still lacking a phylogenetic definition. This definition, as referred in the Introduction, is essential for the larger project on caenogastropod phylogeny. Besides, there are authors who advocate this approach (*e.g.*, YEATES, 1992). The SECOND is to consider some multistate characters as additive (ordered). In those character states, the ordering has support from ontogeny or by comparison (*i.e.*, each state is clearly a modification of the preceding one). For additive characters, an extra explanation is presented in the discussion of each character. Furthermore, a parallel analysis in which the character is considered unordered was performed and any change of the result is reported. The THIRD is the arbitrary choice of an optimization in the presented cladogram (Fig. 353) in those few cases where more than one optimization is equally parsimonious. It is possible to apply the heuristic options ACCTRAN (assuming convergence is more likely than reversion) or DELTRAN (vice-versa), which would produce two trees with same the topology, a duality that is avoided here. In those cases where more than one optimization is possible, they are all reported, though only one is presented in figure 353.

Abbreviations in the figures: (aa) anterior aorta, (ad) adrectal sinus, (af) afferent gill vessel, (ag) albumen gland, (am) ampulla of anterior aorta, (an) anus, (ap) apical gland of penis shield, (ar) male pore, (as) aperture of seminal receptacle into pallial cavity, (au) auricle, (bb) bulged region of br, (bg) buccal ganglion, (bm) buccal mass, (bp) brood pouch, (br) subradular membrane, (bv) blood vessel, (ce) cerebral ganglion, (cg) capsule gland, (cm) columellar muscle, (co) collar vessel, (cp) capsules, (cv) ctenidial vein, (dc) dorsal chamber of buccal mass, (dd) duct to digestive gland, (df) dorsal fold of buccal mass, (dg) digestive gland, (di) diaphragm-like septum of haemocoel, (dp) dorsal-basal gland of penis shield, (dq) dorsal-basal gland of penis shield aperture, (ec) esophageal crop, (ed) ejaculatory duct immerse in integument, (ef) esophageal folds, (en) endostyle, (ep) esophageal pouch, (es) esophagus, (ey) eye, (fg) food groove, (fp) female pore, (fs) foot sole, (ft) foot, (ga) gastric ventral chamber, (gb) gastric dorsal chamber, (gf) gastric fold, (gi) gill, (gm) gastric muscle, (go) gonad, (gp) pleural ganglion, (gs) gastric shield, (gt) gastric transversal septum, (ha) haemocoel, (ic) intestinal chamber, (il) intestinal loop(s) into kidney chamber, (in) intestine, (ip) intestinal loop close to pericardium, (ir) insertion of m4 in tissue on radula (to), (is) insertion of m5 in radular sac, (jw) jaw, (ka) kidney anterior chamber (kc) kidney connection between anterior and posterior chambers, (kd) kidney dorsal lobe (ki) kidney (kp) kidney posterior chamber (11) left head-foot lobe (lp) lung pneumostome, (lr) right head-foot lobe, (lu) lung, (m1 to m14) extrinsic and intrinsic odontophore muscles, (ma) mouth abductor muscle, (mb) mantle border, (mc) buccal sphincter and circular muscles of oral tube, (me) mesentery, (mj) jaws, buccal, and oral tube muscles, (mo) mouth, (ne) nephrostome, (nr) nerve ring, (nv) nerve, (oa) odontophore secondary cartilage, (oc) odontophore cartilage, (od) odontophore, (om) ommatophore, (op) operculum, (os) osphradium, (ot) oral tube, (ov) pallial oviduct, (oy) ovary, (pa) posterior aorta, (pc) pericardium, (pd) penis duct, (pe) penis, (pf) penis furrow, (pg) pedal glands anterior furrow, (ph) penis shield notch, (pi) penis sac, (pl) penis shield longitudinal furrow, (pm) penis shield middle gland, (po) solid portion of penis sac (penis base), (pp) penis papilla, (pr) penis sac connection with penis shield, (ps) penis shield, (pt) prostate, (pu) pedal ganglion, (py) pallial cavity, (ra) radula, (rm) retractor muscle of snout, (rn) radular nucleus, (rp) reno-pericardial aperture, (rs), radular sac, (rt) rectum, (sa) salivary gland aperture, (sc) subradular cartilage, (sd) salivary duct, (se) septum between esophagus and odontophore in buccal mass, (sg) salivary gland, (sl) snout tentacle, (sn) snout, (sr) seminal receptacle, (st) stomach, (su) supra-esophageal ganglion, (sv) seminal vesicle, (sy) statocyst, (te) cephalic tentacle, (tg) integument, (to) tissue on middle region of radula preceding its exposure, (tp) distal chamber of copulatory right cephalic tentacle, (ts) testis, (ug) urinary gutter, (up) ureter pore, (ur) ureter, (vd) vas deferens, (ve) ventricle, (vf) vas deferens pallial furrow, (vg) vaginal duct, (vo) visceral oviduct.

Abbreviations of institutions: (AMS) Australian Museum, Sydney; (BMNH) The Natural History Museum, London; (MNHN) Museum National d'Histoire Narurelle, Paris; (MZSP) Museu de Zoologia da Universidade de Sao Paulo; (ZSM) Zoologische Staatssammlung Müchen, Germany.

Some terms used in discussion merit some explanation. The word "archaeogastropod" is used in traditional sense, but it is recognized as a paraphyletic taxon. The term "basal" caenogastropods refers to those taxa which generally are in the beginning of the mesogastropods in most catalogues (*e.g.*, Abbott, 1974; Rios, 1994), in particular the Cerithioidea, Littorinoidea and Hydrobioidea. The term "higher" caenogastropods in general refers to Tonnoidea and Neogastropoda. Where mentioned "examined species" only the ingroup species are included.

SYSTEMATICS

Family Ampullariidae
Genus *Pomacea* Perry, 1810
Type-species *Pomacea maculata* Perry, 1810)

Ampullaria Lamarck, 1799:76 (Case 2996, ICZN, see Cowie, 1997).
Pomacea Perry, 1810:28.
Ampullarius Montfort, 1810:242.

Pomacea crosseana (Hidalgo, 1871)
(Figs. 1-2, 97- 98, 115-116, 150-173)

Ampullaria crosseana Hidalgo, 1871:206-207; 1872:142-143 (pl.7, fig.1); Sowerby, 1909:348.

Ampullarius crosseanus - MORRETES, 1949:66.

Type-locality: Brazil, Amazon River.

Description

Shell (Figs. 1-2). Medium to large (up to 45mm), globose. Color homogeneous pale brown, sometimes successive spiral bands pale and dark brown. Periostracum thin, velvet-like. Spire small. Suture somewhat deep. Aperture elongated antero-posteriorly.

Head-foot (Figs. 151-152, 158). Color beige, with irregular brown spots. Head broad, protruded. Cephalic tentacles stubby, slender and long, tip pointed. Ommatophore long, about ¼ of tentacle length, tip rounded, base at outer surface of tentacles, their base slightly overlapping. Eyes dark, at tip of ommatophores. Snout somewhat cylindrical, broad, anterior surface flattened; mouth longitudinal, in middle region of anterior surface. Two slender snout tentacles, originating laterally at anterior end of snout, about as long as cephalic tentacles, base broad gradually narrowing distally, tip somewhat pointed. Two nuchal lobes, or siphons, flap-like, projecting forward, located on both sides of head, origin at posterior region of head, between head and adjacent region of connection between head-foot and mantle. Left siphon long and broad, with secondary low fold connecting its right edge with right attachment between mantle and head-foot. Right siphon shorter and narrower than left siphon. Foot large, ample, dorso-ventrally flattened. Opercular pad large on dorsal posterior surface of foot. Anterior furrow of pedal glands narrow, borders thin, occupying almost entire anterior half of pedal margin. Columellar muscle broad, with lateral muscular expansions supporting connection of mantle border; very short (about 1/6 whorl), slightly longer at right.

Operculum (Figs.97-98, 151). Occupying entire aperture. Corneous, semi-circular, thick, flexible. Margins thin, sharp, almost circular, short expansion on inner-superior region. Nucleus almost central, slightly dislocated towards inner margin. From nucleus concentric growth lines. Inner surface smooth. Scar circular, large, close to inner margin.

Mantle organs (Figs. 153-156). Mantle border thick, generally smooth, sometimes with series of small undulations at right; color homogeneous beige. Pallial cavity occupying about half whorl. Osphradium broad, elliptical, high, located in left region just posterior and parallel to mantle border. Osphradium base a high, thick fold (stalk), elliptical in section. Osphradium filaments on tip of this basal fold; two series of thin, slightly triangular, septum-like filaments situated alternately in each side of tall, thin, fold-like, longitudinal, central axis (Figs. 155-156). Lung large (about 1/3 of pallial cavity volume and area), outline approximately elliptical, dorso-ventrally flattened, walls thick, richly vascular, scarcely muscular. Lung vessels mostly transverse (from left to right), high, close to each other. Lung vessels connect anterior marginal vessel (from afferent gill vessel) with ctenidial vein (Fig. 155). Pneumostome slit-like, margins muscular, located in anterior-left-ventral lung region, just posterior to left siphon. Gill long and narrow, slightly broader anteriorly, surrounding right and posterior lung margins from mantle border to left posterior end of pallial cavity, close to pericardium. Gill filaments triangular, slightly low, tips slightly right-central, somewhat displaced to right; right and left margins straight (Fig. 156). Gill anterior end broadly pointed. Ctenidial vein narrow in anterior region, becomes broader short distance from its anterior end, where lung vessels connect (see below for more details). Pericardium, kidney and rectum (respectively) running along right margin of gill (Figs. 153-154), with only anterior gill region free of these structures in females; in males this region occupied by penis shield. Gonoducts lying between rectum and right margin of pallial cavity; oviduct, when mature, dislocated ventrally. Pallial gonoducts described below.

Visceral mass (Fig. 153). Globose, of about 4 whorls. Pericardium and kidney as anterior structures, bulge into pallial cavity. Stomach about 1/3 whorl posterior to pallial cavity. Digestive gland dark brown, almost black, surrounds stomach except for some ventral and dorsal areas. Gonad beige, located on digestive gland in superior and peri-columellar regions.

Circulatory and excretory systems (Figs. 154, 157). Pericardium relatively large, located just posterior to left-posterior limit of pallial cavity, partly connected to pallial floor. Afferent gill vessel with branch crossing from right to left in anterior region of gill, running dorsal to gill and short distance beyond gill in pallial roof (Fig. 155), and then as anterior border of lung. All lung drainage runs towards ctenidial vein, edging along left gill margin and right lung margin. Ctenidial vein connects with auricle just posterior to gill posterior end. Auricle somewhat short. Ventricle massive, almost spherical, posterior to auricle. Aortas located posterior to ventricle; posterior aorta narrow; anterior aorta runs anteriorly on opposite side from posterior aorta. Just after separation of posterior aorta, lies anterior aorta bulb (ampulla), massive, walls muscular and thick, narrows after distance equivalent to ventricle length. Anterior aorta runs along haemocoel, with special branches in buccal mass region (see below). Kidney broad and ample (about half whorl), divided into 2 chambers. Posterior chamber most hollow, filled by intestinal loops (described below) connected to right surface by mesentery (Fig. 157). Dorsal glandular lobe of kidney dorso-ventrally flattened, cream colored, surface almost uniform, covering dorsal wall of posterior chamber (disconnected from intestine). Anterior renal chamber ("ureter") slender and long, connected to posterior chamber by orifice at left; runs towards right attached to anterior edge of posterior kidney lobe and adjacent pallial roof, gradually narrows to pointed blind-sac. Inner surface of anterior renal chamber filled by two series of transverse septa, cream colored. Anterior series of septa larger and broader than posterior series and start between anterior and posterior renal chambers; posterior series of septa edging nephrostome. Both series of septa connected to central, longitudinal, dorsal fold. Nephrostome slit-like located in middle region between anterior and posterior renal chambers, separated from anterior renal chamber by posterior series of septa. Urinary gutter beginning ventral and at some distance from nephrostome as a tall fold, runs towards right; anteriorly attached to structures of right margin of pallial cavity, as oviduct-prostate and rectum, finishing close to right siphon.

Digestive system (Figs. 158-169) - Buccal mass (Figs. 159-161) large, occupies entire inner space of snout and about 1/3 remainder of haemocoel (Fig. 158). Buccal sphincter (mc) ventrally thick and dorsally thin. Jaw muscles (mj) thick, origin in odontophore dorsal surface, insertion around mouth inside mc. Pair of jaw plates large and thick (Figs. 150-160), outline elliptical, cutting-edge broad, composing anterior and median margins; small, broad projection in anterior region of median margin towards anterior. Pair of dorsal inner folds of buccal mass (Fig. 160) broad and tall, surface with several superficial transverse furrows. Dorsal folds cover posterior margin of jaws, running towards posterior turning medially, covering a somewhat deep dorsal chamber. Dorsal chamber with several, longitudinal, low folds. Peri-buccal and odontophoral muscles (Figs. 159, 161-167): ml) jugal muscles, several small muscular fibers connecting buccal mass with adjacent region of haemocoel inner surface, more concentrated around mouth; m1a) dorsal protractor muscle of buccal mass, somewhat thin, origin in dorsal region of mouth runs posteriorly close to median line attached to surface of buccal mass, insertion in middle level of dorsal surface of buccal mass; m1b) two pairs of lateral protractor muscles of buccal mass, origin in lateral-dorsal region of mouth, run posteriorly edging latero-dorsal surface of buccal mass, insertion in posterior region of buccal mass, close to buccal ganglia; ma) pair of jaw abductor muscles, origin in several points of outer surface of jaw, runs immersed in mc and mj dorsally in 3 or 4 branches, after mc and mj, they unite as single pair, with insertion in adjacent region of dorsal-lateral surface of haemocoel; m2) pair of retractor muscles of buccal mass, origin in ventral-lateral surface of haemocoel adjacent to middle level of odontophore, run dorsally, by short distance to penetrate mj fibers, insertion in inner layer of longitudinal fibers of mj in three different and somewhat equidistant, small points, located in ventral and lateral region of jaw plates; m3) superficial, thin muscle immersed in membrane covering posterior region of odontophore, with transverse fibers just anterior to radular sac; m4) large pair of ventral tensor muscles of subradular membrane, origin in inner-posterior surface of odontophore cartilages (oc), most fibers of this muscle surrounding ventral and lateral surface of cartilages, connecting with cartilage on opposite side than their origin, some fibers surrounding posterior margin of cartilages, running from posterior to anterior region edging dorsal surface of cartilages, insertion along subradular membrane (br) and in posterior-inner surface of accessory cartilages; m5) pair of dorsal tensor muscles of radula, origin wide in m4 posterior-median outer surface, surrounding m4, running towards median and anterior, gradually narrowing, insertion in middle-dorsal region of radular sac preceding its exposed (in use) area in buccal cavity; m6) horizontal muscle, with transverse fibers, connecting dorsal surface of both cartilages, insertion at some distance from dorsal edge of cartilages (Figs. 164, 166); m7) pair of very slender muscles, origin in posterior region of dorsal edge of cartilages, running posteriorly and ventrally, penetrating radular sac in region preceding its entrance in odontophore, insertion in ventral surface of radular sac like fan; m9) two pairs of medial dorsal tensor muscles, anterior pair broad, flattened and thin, posterior pair narrower, origin in tissue (to) on middle region of radula (preceding buccal cavity), close to median line, running antero-laterally short distance to insert in posterior-dorsal edge of subradular membrane, also partly connected to adjacent outer surface of m4; m10) pair of ventral protractor muscles of buccal mass, narrow and thin, origin in ventral inner surface of mouth, run towards posterior lying ventral surface of buccal mass, insertion in postero-ventral region of odontophore close to median line, in both sides of radular sac; m11) pair of thin and long dorsal tensor muscles of subradular membrane, origin in ventral inner surface of haemocoel in region adjacent to middle level of odontophore, runs dorsally short distance, penetrate odontophore just anterior to radular sac, crossing dorsal to m7, insertion along ventral surface of subradular membrane close to median line (Figs. 162, 166); m12) pair of narrow, short muscles annexed to m6 (Fig. 167), origin in medial-anterior region of odontophore cartilages, just anterior to m6, running antero-laterally short distance, insertion in transition between subradular membrane and accessory cartilage just anterior to insertion of m4. Pair of odontophore cartilages large, flattened, outline elliptical. Pair of accessory cartilages thin, small, outline elliptical, in anterior-dorsal region of subradular membrane, just inside more protruded region of exposed part of radula. Subradular membrane (br) thin, strong and semi-transparent, covering inner surface of subradular cartilage, radular ribbon and adjacent areas. Subradular membrane margin mostly connected to dorsal surface of m4 pair, this pair working as tensor. Subradular cartilage forming expanded transparent projections of radula in buccal cavity, covering part of odontophore inside buccal mass. Radular sac short, little longer than odontophore. Radular nucleus broad, with pair of conspicuous blood vessels inserted in it, one terminal posterior and other ventro-anterior, this latter vessel running anteriorly along ventral surface of odontophore on median line. Radular teeth (Figs. 115, 116): rachidian tooth short and broad, 7 stubby cusps, central cusps 2-3 times larger than neighboring cusps; pair of low and broad basal cusps; lateral tooth about 1.5 times broader than rachidian, curved inwards, with about 5 broad cusps, third cusp terminal and about 3 times larger than neighbor; inner marginal tooth tall, broad and flat, about same length as lateral tooth; tip bluntly pointed, inner edge with conspicuous sub-terminal cusp, outer edge smooth or with up to 3 small, sub-terminal cusps; basal region with longitudinal concavity in outer edge where outer marginal tooth encased; outer marginal tooth tall, somewhat triangular, shorter and slender than inner marginal tooth, somewhat thick-longitudinal reinforcement along outer edge; tip sharp pointed and abruptly curved inwards, cusp small, sub-terminal on inner edge. Pair of esophageal pouches long, cylindrical, tip rounded, walls thin, located just posterior to buccal mass (Figs. 159-161). Pair of inner dorsal folds of buccal mass abruptly narrowing in level of pouches and curving externally, penetrating into dorsal wall of pouches, at about half of pouches length, tapering gradually. Remainder of pouches inner surface smooth (Fig. 160), apparently without glands. Anterior esophagus (posterior to pouches) narrow, short, inner surface with pair of broad longitudinal folds (originating from pouches folds) and some lower, narrower secondary folds. Middle esophagus very broad, bulging, walls thin, inner surface without folds. Pair of salivary glands massive, separated from each other, located just posterior to pouches. Salivary ducts in anterior region of glands, attached to dorsal surface of buccal mass, close to median line, passing through nerve ring, penetrating buccal mass wall in about middle level; to open lateral surface of anterior region of dorsal folds. Posterior esophagus long (about half of esophagus length), narrow, inner surface smooth. Stomach (Figs. 168-169) large, spherical, with two chambers. Ventral chamber small, ventral wall thin, about five narrow ducts to digestive gland irregularly disposed in ventral surface. Dorsal chamber larger, walls thick, muscular, inner surface folded by muscle bundles. Ventral and dorsal gastric chambers separated from each other by tall, transverse, muscular septum (part of dorsal chamber walls); esophagus and intestine connected to both cambers. Columellar-gastric muscle well-developed, thick, origin in columellar surface of mantle in level adjacent to stomach (separated and posterior from columellar muscle), running anterio-dorsally, penetrating between esophagus insertion and intestine origin, insertion spread in gastric dorsal muscular wall, more concentrated towards posterior. Esophagus insertion and intestine origin side by side in anterior-left stomach region. Intestine wide, inner surface smooth, running anteriorly and left to renal chamber, becoming exposed inside left-posterior region of renal chamber. Intestine abruptly turning towards posterior-right, running parallel to preceding portion, surrounding posterior and right inner surface of renal chamber. Intestine bearing chamber occupying most of outer-left inner surface of this twisted portion, where it touches pericardium; intestine having constriction, in form of transverse fold (taller right), preceding this chamber; chamber forming blind sac positioned contrary to flow, bearing 5-6 secondary smaller, blind-sacs on outer surface. Intestine with three loops, connected to renal wall by mesentery, in middle level of right surface of renal chamber (Fig. 157). Schematic representation (in ventral view) shown in figure 154. Anterior to loops, intestine running towards anterior, exiting to pallial cavity. Anus siphoned (*i.e.*, preceded by short unattached stalk of rectum), broad, with two inner successive edges covered by narrow longitudinal folds, located close to right siphon (Figs. 153, 168, 170).

Genital system - ♂ (Figs. 170-171): Testis lies on columellar surface of visceral mass, on digestive gland, at about three whorls since visceral apex. Visceral vas deferens narrow, runs in left (inferior) edge of testis last whorl. Vas deferens becomes thicker walled in pallial cavity, running at right of and close to rectum. Posterior to anus, vas deferens crossing over rectum, staying to left side of base of anus; where its abruptly expands as ejaculatory tube. Ejaculatory tube with loop along right wall of penis sac. Penis sac relatively large, located at left of anus; walls thin, aperture located anteriorly, turned to base of penis shield, this aperture preceded by long tubular region. From ejaculatory tube, vas deferens exits to penis sac T-shaped; anterior branch of this structure solid fold attached to dorsal wall of penis sac, preceding its aperture; Penis is posterior branch of that structure. Penis long, slender, intensely coiled, narrowing gradually; distal third very slender, about 10 times narrower than its base. Penis duct entirely closed (tubular), very coiled in penis base, gradually less coiled towards distal region. Penis duct aperture very small, in penis tip. Penis shield large (about 1/3 of pallial cavity volume), slightly triangular, located in superior (right) half of inner edge of mantle border, generally inside pallial cavity. Penis shield base very broad, thick, bulging due to basal gland. Basal gland aperture small, located in left-outer region of penis shield base. Penis shield gradually narrows, distal tip flat, with slightly rounded borders and central concavity. Penis shield furrow runs along central region of inner surface of shield, somewhat deep, small notch in right-basal region; distal end of furrow Y-shaped, close to shield tip. No other penis shield gland detectable. 9 (Figs. 172-173): Visceral structures in similar location to corresponding structures of male (Fig. 153). Ovary beige in color. Pallial structures not seen in details due to poor fixation. Relatively broad oviduct running at right of rectum for short distance and opening to large pallial oviduct. Pallial oviduct about ¼ of pallial cavity volume when mature; located at right and ventral to rectum, partly connected to pallial floor. Visceral oviduct inserts in right region of pallial oviduct. From this insertion broad, flat and coiled inner lumen starts, running towards anterior. Lumen immersed in capsule gland tissue. Albumen gland widely connected anteriorly to left side of posterior capsule gland, its lumen flat and broad, closed as blind-sac posteriorly. Pallial oviduct abruptly narrows in approximate anterior third level of pallial cavity as vaginal tube. Vaginal tube long, thick walled, circular in section, at right edge of rectum. Female pore small, papilla-like, at right of, and close to anus.

Nervous system - Nerve ring very similar to those described by SCOTT (1957) and BERTHOLD (1991) for other ampullariids. Hypoathroid, located in middle level of buccal mass. Both cerebral ganglia separated by long, thick comissure. Buccal ganglia large, located relatively close to median line in dorsal-posterior region of buccal mass, near bases of esophageal pouches. Statocysts with several small, iridescent, statoconia, located deeply in foot musculature, just ventral and slightly outside pedal ganglia.

Measurements of shells (in mm). MZSP 29522: 9 #1, 42.0 by 35.8; 9 #2, 38.6 by 31.1; ♂ #3, 37.9 by 33.1.

Distribution - Brazil, upper Amazon and upper Parana basins.

Habitat - On *Eichornia* and other aquatic plants of lakes and low flow rivers.

Material examined - BRAZIL - MATO GROSSO DO SUL: Passo do Lontra, MZSP 29522, 2♂, 39 , 8 young specimens, MZSP 30758, 9 (Figs. 1-2) (Simone and Lipparelli cols., V/1993).

Discussion – The shell of *P. crosseana* is very similar to the sympatric and more abundant *P. canaliculata*. The two species are difficult to separate on shell characters alone. P. crosseana, however, is distinguishable by its elongates shell and generally uniform and paler color; although some exceptions occur. On the other hand, there are considerable anatomical differences, as discussed in the comparison below. The simplest way for differentiate *P. crosseana* from P. *canaliculata* is by the penis shield features, which P. crosseana having flattened concave tip (Fig. 170), while P. *canaliculata* has longer broad tip with an apical gland (Fig.205).

Pomacea *curumim* new species
(Figs.3-4, 57-60, 107-108, 117-118, 174-188)

Types - Holotype MZSP 30760. Paratypes - BRAZIL - PARA: Xingu River, Between Senador Jose Porfiro and Porto de Moz; 2°00'22.9-42.6"S 52°12'59-8"-13'04.6"W, MZSP 29844, 12 specimens (sta. AMZ94-52, Zanata and others, 08/XI/1994); 2°03'40.7"-04'15.4"S 52°14'43.5-47.4"W, MZSP 29845, 29 specimens (sta. LRP94-44, Rapp Py-Daniel and other cols., 08/XI/1994); 2°02'45.1"-03'24.8"S 52°14'56.2"-15'03.8"W, MZSP 29846 12 specimens (sta. LRP94-45, Rapp Py-Daniel and others cols., 08/XI/1994).

Type-locality - BRAZIL - PARA: Xingu River, Between Senador Jose Porfiro and Porto de Moz; 2°04'15"S 52°14'43.5"W (Rapp Py-Danieland other cols., 08/XI/1994).

Diagnosis - Very small, globose shell, with large aperture. Lung reduced. Penis shield with single basal gland on right, an apical folded region, and notch in middle level.

Description

Shell (Figs.3-4, 57-60). Size small (up to 12mm), globose, outline almost circular but broader near to upper suture, color pale greenish beige. Periostracum thick, smooth or sometimes with axial or spiral striae in some areas. Spire small and low, eroded, about four low, convex whorls. Last whorl large, slightly long anteriorly and somewhat conical. Aperture elliptical, slightly long antero-posteriorly. Outer lip rounded, with cut edge. Inner lip concave in superior half, without callus; convex in inferior half, with cut edge. Siphonal region bluntly angular, shortly projected anteriorly. Umbilicus deep, narrow, simple.

Head-foot (Fig. 174). Similar characters to those of preceding species but shorter antero-ventrally and broader laterally. Head very broad, tentacles lateral located. Columellar muscle very short and thick.

Operculum (Figs. 107-108, 174). Similar attributes as those of preceding species, but slightly longer antero-posteriorly. Outer surface with uniform concentric striae. Nucleus at short distance from middle level of inner edge. Inner scar occupying about 2/3 of inner surface, lie at short distance inner edge, and at some distance from remainder edges.

Mantle organs (Figs. 175-178, 187). Characters also similar to those of *P. crosseana*, distinctive or notable features following. Pallial cavity very short, less than half whorl. Penis shield occupies most of inner pallial space in males. Osphradium almost sessile, its base (stalk) in same level of mantle (Figs. 175-177). Lung reduced, pneumostome very small pore. Gill proportionally large and straight; anterior end on mantle border or penis shield base (of males), just posterior to anterior end becomes broad, narrowing gradually. Gill filaments slightly low, curved to right, tip rounded. Ctenidial vein narrow. Between gill and right pallial structures narrow space.

Circulatory and excretory systems (Figs. 178-179). Similar attributes as those of preceding species, with following distinctive features. Heart ampulla (of anterior aorta) almost spherical and short. Kidney dorsal lobe low, separated from intestinal loops, presenting 2 regions; posterior region narrow, transverse, with several transverse furrows, edges first intestinal loop; anterior region larger (about 4/5), covered by net of vessels intensely anastomosed, large vessel covers left side of connection with anterior lobe. Kidney anterior lobe short, broad, turned forwards, inner glandular folds similar to those of P. crosseana, but with an outstanding bulged portion preceding nephrostome. Intestinal loops inside kidney chamber described below.

Digestive system - Buccal mass and odontophore characters (Figs. 180-183) similar to those of preceding species, with following differences and notes: outline shorter and circular; buccal mass in general dislocated slightly anterior to mouth; jaws with circular outline (Fig. 182); (mj) thick, short, conic, (ma) pair thinner and simple, (m4) pair with wider portion free from odontophore cartilages in their median surface, (m6) with outer surface attached to adjacent inner surface of br, (m7) pair also connected to posterior-median extremity of odontophore cartilages, (m12) pair present. Radular teeth features similar to those of P. crosseana with following notable attributes (Figs. 117-118): rachidian tooth proportionally larger, 5-7 cusps, central cusps about 1.5 times larger than neighbor cusps, pair of basal cusps oblique; lateral tooth as broad as rachidian, 3-4 cusps, second cusps terminal and about double than neighbor cusps; inner and outer marginal teeth with larger sub-terminal cusp in inner edge and no cusps in outer edge. Esophageal characters, pouches and inner folds (Fig. 182) similar to those of P. *crosseana,* except for continuous fashion of esophageal main folds in region of pouches aperture (without notch). Esophageal pouches with narrow dorsal inner fold each, connected to adjacent dorsal surface of esophageal main folds. Salivary glands fashion also similar to those of preceding species, except for aperture located in middle region of dorsal folds of buccal mass and with form of deep slit projected towards anterior. Stomach characters (Figs. 186, 188) also similar to those of P. *crosseana,* including thick muscular walls, columellar-gastric muscle and inner transverse muscular septum. Stomach differs by smaller ventral chamber (with thin walls), and fewer ducts to digestive gland. Intestine initially very broad. Region adjacent to pericardium narrow, preceded by tall fold in its dorsal surface, fold posterior portion arched, transverse, lies ventral surface, finishes towards posterior protected by posterior portion (Fig. 188). Remainder intestine runs somewhat similar to that of preceding species. In region of kidney broad and complex loop as shown in figure 179. Rectum broad and slightly short. Anus simpler, without double layer of papillate folds.

Genital system - ♂ (Figs. 175, 187): Testis color cream, situated in upper region of digestive gland coils. Visceral and pallial vas deferens attributes similar to those of preceding species, except for broad expansion in region just at right from anus. Penis sac spherical, thin walled at left and thick muscular at right (penis base or ejaculatory tube). Penis sac amply opened in left edge towards penis shield base. Penis very shorter than that of P. *crosseana,* with relative uniform width along its length. Penis tip abruptly pointed. Penis shield very large (occupies most of pallial cavity inner space) and conic. Pair of penis shield glands, basal, dorsal gland massive, with location and aperture similar to those of P. *crosseana.* Other gland smaller, semi-spherical, located in right side just over base. Penis shield ventral groove deep, runs about along its center; notch in right side in middle region, where penis projects. Penis shield apical region slightly broad, most folded by transverse, successive, irregular furrows (mainly in ventral and right surfaces). Penis shield ventral groove runs very narrow and shallow at left side of apical folded region. F (Figs. 184-185): Visceral structures fashion similar to those of P. *crosseana.* Pallial oviduct massive, also of somewhat similar features of preceding species. Visceral oviduct ends sub-terminally in sac-like bursa copulatrix, partially separated from remainder pallial oviduct by furrow. Bursa copulatrix flattened, broad, located along left side of pallial oviduct, connected to it in middle level. Capsule gland massive, its lumen irregularly coiled as shown in figure 185. Capsule gland lumen with 2 short coils anterior to bursa connection. Vaginal tube with about same length than capsule gland. Vaginal tube broad, walls relatively thin, inner surface with some longitudinal folds. Female pore small, at right and close to anus.

Measurements of shells (in mm) - MZSP 29845: ♂ 1, 8.9 by 9.1; ♂2, 8.8 by 7.8; 9 3, 9.2 by 8.2.

Distribution - For moment known in Xingu River (Above Amazon tributary), in region between Senador Jose Porfirio and Porto de Moz cities, Para, Brazil.

Habitat - In clear, planar river, from 12.5 to 20m depth, 300 to 4000m distant from shore. Substrate sandy, rocky and forest.

Material examined - Types.

Etymology - The specific epithet refers to Tupy language, meaning small children (*curumim*). A reference to the small size in relation to normal large fashion of the other species.

Discussion - The species was initially interpreted as young samples of other species, after serial sections and exam of several specimens, the adult nature of the specimens was cleared. Complex pallial genital structures and full-developed gonad are present in most specimens, exceptionally larger than 10mm. The size and the less developed lung suggest a process of paedomorphosis. P. curumim is certainly the smaller known species of ampulariid. On the other hand, reduction of lung has been found in ampullariids from Lake Malawi (Africa) (BERTHOLD, 1990) with the explanation that the animals habitat is deep (1.5 to 90m) for they reach the surface.

Pomacea scalaris (Orbigny, 1835)
(Figs.5-9, 85-87, 119, 189-198)

Synonymy see CASTELLANOS & FERNANDEZ (1976: 14). Complement:

Ampullaria scalaris - ORBIGNY, 1835:31; 1843:369-371 (pl.50, figs. 1-3) (see present figs.85-87); SCOTT, 1957:305-307 (pls.1, 3; pl.4, fig.5; pl.5; pl.6, fig.10; pl.7. figs. 15-16; pls. 10, 12; pl. 13, fig.32; pl.22, fig.1); FIGUEIRAS, 1964:171; CASTELLANOS & FERNANDEZ,

1976:14-15 (pl.1, figs.l, 4, pl.2, fig.1; pl.3, fig.3); MARTÍN, 1980:47-50 (fig.4).
Ampullarius scalari - OLIVEIRA *et al.*, 1981:76.
Pomacea scalari: - QUINTANA, 1982:111

Description

Shell (Figs.5-9, 85-87). Characteristic by a conspicuous shoulder in spire and last whorl. Color purple-brown, pale (almost white) between carina and suture. Other details in SCOTT (1957:305, pl.22, fig.1), CASTELLANOS & FERNÁNDEZ (1976:14).

Head-foot and operculum - Characters similar to those of P. crosseana. Other details in SCOTT (1957, pl.1).

Mantle organs (Figs. 189-190, 193). Organization and features similar to those of P. crosseana with remarks following. Osphradium on a stalk tall in right side and low in left side. Gill filaments narrow, pointed.

Circulatory and excretory systems (Fig. 192) - Heart attributes like those of P. *crosseana*. Kidney features also similar to those of P. crosseana, except for following characters. Dorsal renal lobe tall, pale brown, covered by several vessels, strongly arched (edging intestinal loops mesentery). Anterior renal chamber relatively short (less than half of posterior renal chamber length). Inner organization of septa and folds similar to those of P. *crosseana*, except for longitudinal fold not connected to nephrostome edge.

Digestive system (Figs. 191, 194-196) - Buccal mass characters similar to those of P. crosseana, remarkable features following. Jaw plates smaller, with circular outline (Fig. 195). Dorsal folds with smooth surface; aperture of salivary glands located between their middle and posterior thirds. Dorsal chamber (between both dorsal folds) relatively deep. Odontophore muscles: ma, 2 narrow pairs; m4 pair with smaller area attached to inner surface of cartilages; m6 narrower; m10 pair narrow; m10a, a pair of broad muscles, origin in ventral surface of mouth, runs dorsal to m10, insertion in middle-ventral region of odontophore. Other details of odontophore in Scott (1957, pls.3-5, 7). Radular teeth characters similar to those of P. crosseana, with following distinctions (Fig. 119): rachidian shorter, base somewhat triangular, 3-5 broad cusps, central cusps about 1.5 times larger than neighbor cusps, basal cusp narrow and oblique; lateral tooth little broader than rachidian, weakly curved inwards, 3-4 cusps, second cusps terminal and about 1.5 times larger than neighbor cusps; inner and outer marginal teeth slender and tall, longer than lateral tooth, inner marginal somewhat broader than outer marginal tooth, tip narrowly rounded, sub-terminal cusp conspicuous, in inner edge [other details in Scott (1957, fig. 10)]. Esophageal pouches and inner folds with characters similar to those of P. *crosseana*, except for broader pouches, with larger inner fold each (Fig. 195). Stomach features also similar to those of P. crosseana, other details in Scott (1957, pl. 10). Digestive gland brown in color. Intestinal loops inside renal chamber as shown in Fig. 192. Anus with single layer of papillae.

Genital system - ♂ (Fig. 198): Visceral and pallial structures with characters similar to those of P. crosseana, distinctive or notable features following. Testis beige in color. No bulged portion of vas deferens preceding anus. Penis sac with only 1/3 of its (posterior) walls thick. Penis sac aperture long tube, only opened in anterior end, close to penis shield groove base. Penis relatively short, uniform width along its length, apex pointed. Penis shield slightly conic, tip long, narrow, curved towards right. Other details in MARTIN (1980, fig.4). 9 (Fig. 197): Visceral and pallial organs characters similar to those of P. *crosseana*, with following remarkable features. Visceral oviduct connects with pallial oviduct about in middle region of its ventral side. Bursa copulatrix immerse in capsule gland, insertion of visceral oviduct in its posterior-ventral region, connection with capsule gland lumen in its anterior-ventral region. Capsule gland lumen flat, irregular, connection with bursa narrow, abruptly expands and contours bursa dorsally, after certain distance from bursa connects in middle region of broad dorsal branch of capsule gland lumen. Ventral branch of capsule gland lumen connects with vaginal tube. Vaginal tube long, narrow, walls thick. Female pore small, at right from anus.

Central nervous system - Described in SCOTT (1957, pl.12).

Measurements of shells (in mm) - MZSP 29590 (Figs 5-6): 33.0 by 29.0; (Figs.7-9): 48.6 by 47.7.

Distribution - Amazon and Parana Macrobasins.

Habitat - In freshwater courses of low flow, under aquatic plants.

Material examined - Types - BOLIVIA: MNHN, 3 shells, syntypes. Ordinary material: BRAZIL - MATO GROSSO DO SUL: Passo do Lontra, MZSP 29590, 55 specimens (Simone and Lippareli cols., V/1993).

Pomacea canaliculata (Lamarck, 1801)
(Figs. 11-12, 88-89, 120-121, 199-205)

Synonymy see SCOTT (1957:299); CASTELLANOS & FERNÁNDEZ (1976:13). Complement:

Ampullaria insularum Orbigny, 1835:32; 1843:374-375 (pl.51, figs. 1-2) (see present figs.88-89); MARTÍN, 1980:47-51 (figs.2, 6).

Ampullaria canaliculata - SCOTT, 1957:299-303 (pl.22, fig.3; pl. 14, figs.34-35; pl. 16, fig.42; pls. 17-21); FIGUEIRAS, 1964:170; CASTELLANOS & FERNÁNDEZ, 1976:13 (pl.1, figs.3, 6; pl.3, fig.2); MARTÍN, 1980:47-52 (figs.1, 5).

Ampullarius canaliculat - OLIVEIRA *et al.*, 1981:78.

Pomacea canaliculata - ANDREWS, 1965b:71-91 (figs. 1-5, 6b, 7b); QUINTANA, 1982:109; CAZZANIGA & ESTEBENET, 1984:213-222 (fig.1-6); BERTHOLD, 1989:143, 151, 153 (figs.2, 6e); CAZZANIGA, 1990:384-387 (figs. 1-4); THIENGO *et al.*, 1993:68-70 (figs.1-6); THIENGO, 1995:66-68 (figs.2, 8-9, 14).

Types - See MERMOD (1952:88-89, fig. 149).

Description

Shell (Figs.11-12, 88-89). Large, some specimens with about 100mm. Color pale to dark brown, with some spiral dark bands. Spire slightly short, suture deep. Other details in SCOTT (1957: 299) THIENGO et al. (1993, fig.1).

Head-foot and operculum. Characters similar to those of P. crosseana.

Mantle organs (Figs. 199, 205). Features like those of P. crosseana, with succeeding distinctive or notable attributions. Osphradium similar to that of P. *scalaris*, but with taller filaments. Gill filaments narrower and pointed. Ctenidial-pulmonary vein separated into 2 parallel vessels in anterior $^2/_3$ of its length, close with each other, pulmonary branch dorsal and broader. These 2 vessels unite with each other and run as those of preceding species. Narrow ad-rectal sinus distinguishable. Other details in ANDREWS (1965b:figs.1-3).

Circulatory and excretory systems (Figs.202, 204) - Heart characters similar to those of P. crosseana, ampulla of anterior aorta broad. Kidney organization also similar to that of P. crosseana, distinguishing or remarkable features following. Dorsal renal lobe relatively small, surface most smooth, with deep notch adjacent to intestine loops; few and broad vessels present close to aperture to anterior renal chamber. Intestinal loops attributes inside renal chamber described below. Anterior renal chamber longer, with more septa, longitudinal fold not directly attached to nephrostome wall. Urinary gutter of ordinary fashion. Other details in ANDREWS (1965b:figs.1b, 4-6)

Digestive system (Figs.200-204) - Buccal mass characters (Figs.200) comparable to those of *P. crosseana*, remarkable features succeeding. Size proportionally larger. Annex cartilages thinner and smaller. Jaw plates very large and thick, with small median-anterior projection. Dorsal folds broad, smooth, with long portion covering jaws. Odontophore muscles (Fig.200): m1a thinner; m1b as several thin pairs; ma as multiple, relatively narrower pairs; m3a pair of thin muscles with dorso-ventral fibers covering posterior surface of odontophore; m4 pair not so attached to inner surface of odontophore cartilages; m6 very thick; m7, m11 and m12 with insertions more anterior; m10 pair thick; m10c absent. Esophageal characters also similar to those of preceding species, including inner folds and pouches. Differs in taller esophageal folds posterior to pouches. Radular teeth attributes similar to those of P. crosseana, distinctions following (Figs. 120-121): rachidian tooth broad and shorter, 5-7 cusps, central cusps about double than neighbor cusps, basal cusps weak; lateral tooth about as broad as rachidian, 3-4 cusps, second cusp terminal, broad, and several times larger than neighbor cusps; inner marginal tooth with about half weight and same length of lateral tooth, tip bluntly pointed, sub-terminal cusp in inner edge very small; outer marginal tooth about 3-4 times slender than inner marginal and encased in special concavity of outer edge of this tooth, tip sharp pointed, sub-terminal cusp small, in inner edge. Stomach features (Figs.201, 203) similar to those of P. crosseana including gastric-columellar muscle, remarks following. Ventral chamber (with thin walls) very smaller, about 6 ducts to digestive gland. Gastric walls most thick muscular. Inner transverse muscular septum thick, with edges turned inwards. Intestine proximal portion relatively narrow. Digestive gland dark, almost black. Intestinal region adjacent to pericardium preceded by mosaic of several folds and chambers (Fig.201). Intestinal loops inside renal chamber complex, as shown in situ in figure 204. Anus with layer of papillae.

Genital system – ♂ (Fig.205): Testis beige, occupies last visceral whorls up to stomach. Pallial structures similar to those if P. crosseana, with following remarks. No bulged portion of vas deferens preceding anus. Penis sac with about $^2/_3$ thick; its posterior $^1/_3$ with thin walls. Penis sac aperture long tube edging thick penis sac portion, ending in penis shield groove base; this tube with aperture all along its dorsal surface. Penis very long, narrows abruptly in its middle level, distal half very slender. Penis shield large (about half of mantle border width), almost cylindrical. Penis shield groove deep, notch in before distal third, evolved by apical gland. Apical gland only in ventral surface, with mosaic of irregular furrows and folds (Fig.205). Other details in LOPES (1956b, figs.30-46), SCOTT (1957, fig.42), THIENGO *et al.* (1993, flgs.3-5), MARTÍN (1980, flgs.l, 2, 5, 6), BERTHOLD (1989, fig.6e). $: Adequate description in SCOTT (1957, figs.34-35); THIENGO *et al.* (1993, flg.6).

Measurements of shell - MZSP 29633: 54.7 by 50.5 (Figs. 11-12).

Distribution - Amazon and Parana Basins.

Habitat - In freshwater curses of low energy, under aquatic plants.

Material examined - Types - ARGENTINA: Rio de La Plata, MNHN, 2 shells, syntypes of *Ampullaria insularum* Orbigny. Ordinary material: BRAZIL - MATO GROSSO DO SUL: Passo do Lontra, MZSP 29633, 45 specimens (Simone and Lippareli cols., V/1993).

Pomacea lineata (Spix, 1827)

(Figs. 13-15, 64-65, 74-84,
95-96, 122, 125-126, 206-214)

Synonymy see CASTELLANOS & FERNANDEZ (1976). Complement:

Ampullaria fasciata - SWAINSON, 1822:21 (pl. 103) (*non* ROISSY, 1805 *nec* LAMARCK, 1819); SPIX (1827:3, pl.5, flg.2) (see present figs.81-82).

Helix lineata Spix, 1827:3-4 (pl.4, fig.4; pl.5, fig.2) (see present figs.79-80).

Ampullaria fingulina Spix, 1827:2 (pl.4, fig.4) (see present fig.83-84).

Ampullaria physis Hupé, 1857:67 (pl. 12, fig.2) (see present fig.78).

Ampullarius lineatus - OLIVEIRA *et al.*, 1981:77.

Ampullaria testudinea Reeve, 1856 (pl.24, fig. 114) (see present figs.74-75); SOWERBY, 1909:358; BAKER, 1913:660.

Ampullarius (Ampullarius) testudineus - MORRETES, 1949:68.

Pomacea lineata - THIENGO, 1987:564-568 (figs.1-21); 1995:66-68 (flgs.l, 4-7, 11-13, 16-17).

Description

Shell (Figs. 13-15, 64-65, 74-84). Medium size (up to 45mm). Outline globose. Color of spire dark brown, almost black; last whorl greenish brown with about 8 spiral, dark brown bands. Spire moderately tall (about half of body whorl length), slightly pointed; about 5 convex whorls. Last whorl almost spherical or weakly broader in superior region. Protoconch of 2.5 smooth whorls. Border between protoconch and teleoconch gradual and inconspicuous. Sculpture almost absent, only series of spiral lines uniformly distributed, after 5-6 lines slightly taller line with hair. Aperture elliptical. Outer lip and siphonal region rounded. Umbilicus deep and narrow. Other details in THIENGO (1987, fig. 1).

Head-foot and operculum (Figs.95-96). Features similar to those of *P. crosseana*. Head-foot color beige, with dark brown spots thorough exposed areas (except sole). Pedal gland furrow restrict to anterior sole edge.

Mantle organs (Figs.206, 210, 212). Similar features to those of *P. crosseana*, with following notable or differentiable characters. Osphradium on low stalk, relatively small, stalk slightly taller at right; osphradium base without edges covering filaments. Ctenidial and pulmonary veins separated from each other in anterior half (similar to those of P. *canaliculata*). Gill broader, shorter, and not so curved; its posterior end almost in middle region of pallial cavity posterior border. Gill filaments narrow, tall, tip slender and rounded, strongly curved towards right, tip blunt. Other details in THIENGO (1987, fig. 17).

Circulatory and excretory systems (Figs.208, 211) - Heart and kidney characters similar to those of P. *crosseana*, remarks following. Heart proportionally smaller, ampulla about as large as ventricle. Anterior renal chamber broad and slightly short; internally 2 series of transverse septa separated by narrow longitudinal fold, all them restrict to dorsal surface. Nephrostome located in middle-posterior edge of this chamber. Posterior renal chamber broad and flat; dorsal renal lobe with circular outline, not attached to intestine, ventral surface covered by several anastomozed vessels. Connection between anterior and posterior renal chambers simple, protected at right by relatively broad vessel. Intestinal loops inside kidney chamber described below. Other details in THIENGO (1987, figs 6-8).

Digestive system (Figs.207-209, 211) - Buccal mass feature (Fig.207) similar to those described for P. *crosseana*, with following distinctive or remarkable attributes. Jaw plates very large. Aperture of salivary glands located about in middle region of dorsal folds, edged by several small folds. Dorsal folds with strong transverse furrows. Dorsal chamber between these both folds relatively deep, 2 to 4 longitudinal, somewhat tall folds running up to anterior esophagus, where faint. Odontophore muscles (Fig.207): m3 as transverse cover edging radular sac entrance in odontophore, covers also m10 insertion; m10 pair very narrow; m11 pair inserted anterior, m12 pair broad. Radular teeth attributes similar to those of *P. crosseana*, notable as follows (Figs. 122, 125-126): rachidian broad and shorter, 5-7 cusps, central cusps 3-4 times broader than neighbor cusps; lateral tooth about as broad as rachidian, 3-4 cusps, second cusps terminal and several times larger than remainder cusps, tip bluntly pointed; inner marginal tooth with about half of rachidian width and about same lateral tooth length, basal concavity (where outer marginal encases) conspicuous and lying about $^2/_3$ of tooth's length, tip sharp pointed, sub-terminal cusp small and at some distance from tip; outer marginal tooth with about half of inner marginal width and about its same length, slender, weakly sigmoid, tip sharp pointed, secondary cusp at short distance from tip. Accessory pair of cartilages very thin. Branch of anterior aorta irrigating odontophore (running with m11) presents muscular fibers in its walls. Esophageal inner folds and pouches characters similar to those of P. crosseana, except for presence of 3-4 tall folds between both longitudinal folds of each pouch. Stomach features (Figs.208-209, 211) also similar to those of P. crosseana, including strong gastric-columellar muscle, remarks following. Ventral gastric chamber (with thin walls) small, about 4 ducts to digestive gland. Transverse muscular septum tall, with edge turned inwards. Intestinal origin preceded by small dorsal diverticulum. Digestive gland almost black. Intestine initially broad, its region adjacent to pericardium preceded by pair of sac-like, thick walled chambers. Ventral chamber simple, small; dorsal chamber larger, with other 3 inner sub-chambers (Figs.209, 211). Intestinal loops inside renal chamber shown in Fig.208. Anus with simple layer of papillae.

Genital system - ♂ (Figs.210, 213): Visceral structures similar to those of P. crosseana, and described by Lopes (1956a) Thiengo (1987, figs.5, 9-10, 12-13). Testis pale beige. Seminal vesicle single, sac-like, small, located in posterior region of pallial vas deferens. Pallial vas deferens broad, wall thick glandular; anterior region narrower, connected to penis sac crossing ventral to rectum. Bulged short portion of vas deferens preceding anus present. Penis sac antero-posteriorly long; anterior half solid, posterior half thin walled, its left edge bears tubular projection united to penis shield right base; this tubular projections presents longitudinal dorsal aperture. Penis very long and coiled, base broad, gradually narrows up to very slender end long distal region. Penis duct broad and highly coiled at penis base, becomes less coiled and narrower between basal and middle penis thirds. Penis shield very large, occupying more than half of mantle edge (free portion) length, and about half of pallial cavity volume. Gill finishes on penis shield left base. Penis shield form almost conical, basal half broad, basal gland large, with normal fashion of aperture at dorsal surface. Distal half marked by abrupt reduction between it and basal half, curved towards right. Middle gland small, elliptical, located in right edge close to central furrow, in middle shield level. Apical gland long, narrow, ventral surface transversally furrowed (more details in THIENGO, 1987). Notch between apical and middle glands, restrict to right edge. ♀ (Fig.214): General organizations similar to that described for P. crosseana, and well described by Thiengo (1987: figs. 11, 15-16, 18-20). Remarks following. Ovary beige, relatively small, restricts to columellar surface of visceral whorls; ovary acina narrow, successively ramified, somewhat separated from each other. Pallial oviduct very large (more than half of pallial cavity volume when mature). Visceral oviduct very narrow, inserting in anterior end of seminal receptacle in middle level of pallial oviduct ventral surface. Seminal receptacle large and flat, with about half of pallial oviduct width and length, located in its ventral region immerse in glandular tissue. Seminal receptacle walls iridescent muscular, outline elliptical. Narrow projection of seminal receptacle runs from its posterior end, curving abruptly towards anterior, running at left from it at about its same length; this projection wall also iridescent muscular, finishes as blind-sac. Remainder lumen of pallial oviduct bearing several loops and flattened and arched chambers obeying a shape as represented in figure 214; origin narrow, sub-terminal, in anterior end of seminal receptacle projection. Albumen gland as first loop, located along left surface of pallial oviduct. Capsule gland occupying remainder regions of pallial oviduct, without clear separation of albumen gland. Vaginal tube originating in middle region of pallial oviduct right surface, running towards anterior separated from it. Vaginal tube broad, inner lumen also broad, its posterior region with transverse, tall, thick folds situated alternately. Its anterior region (about 2/3 of its length) with longitudinal, tall and thick folds; lateral-right fold larger, its walls curves positioned with its free edge touching its base, forming secondary inner tube. Genital pore broad and low papilla, located at short distance and slightly anterior to anus.

Measurements of shells (in mm) - MZSP 27996: #1, 35.8 by 31.2; #2, 36.6 by 30.7. MZSP 31147: ♂ 1) 33.3 by 28.2; ♂2) 34.7 by 29.6; 9 3) 32.1 by 28.5; 9 4) 32.0 by 27.1; 9 5) 32.5 by 27.5 (photo); MZSP 32197, 9 2) 44.8 by 37.5 (larger specimen).

Distribution - Central America, Amazon and Parana Macrobasins. Coastal basins of Paraiba to Alagoas; Fernando de Noronha oceanic island.

Habitat - Similar to those of preceding species. On streams of low flow, close to margins and under aquatic plants.

Measurement of shells (in mm) - MZSP 26684: #1: 41.8 by 37.2; #2: 35.5 by 31.2.

Material examined - Types: without locality, BMNH, 1 shell, holotype of*Ampullaria testudinea* Reeve. BRASIL; MNHN, 2 shells, syntypes (?) of *A. lineata* Spix of collection Ferussac (1837). PARAGUAY; NMHN, 2 shells, syntypes of *Ampullaria physis* Hupé. Remainder photos of Spix's types are courtesy of Dr. Silvana Thiengo, Fundação Oswaldo Cruz (Figs.79-84). Ordinary material: BRAZIL - PERNAMBUCO: Fernando de Noronha Archipelago; Atalaia Beach, MZSP 31147, 23 specimens (Simone, Souza Jr. and Martins cols., 18/VII/1999). PARAÍBA: Cabedelo, MZSP 27108, 1♂, 29 (A.C.C. Almeida col., IV/1989). ALAGOAS: Ponta Verde, Sonho Verde Beach, MZSP 32197, 23 specimens (Simone col., 16/VII/1989). BAHIA: Ilheus, Almada river, MZSP 26684, 2♂, 29 , 6 shells (S.Thiengo col., 4/II/1984). SÃO PAULO: Guarapiranga Dam, near to OSEC, MZSP 27996, 11 specimens (P.Auricchio col., 21/V/1990).

Pomacea sordida (Swainson, 1823)

(Figs. 16-17, 72-73, 99-100, 123-124, 215-222)

Ampullaria sordida Swainson, 1823 (pl. 143) (no locality); PHILIPPI, 1851:38 (pl. 10, fig.3); REEVE, 1856 (pl.3, fig. 14); COUSIN, 1887:278; SOWERBY, 1909:357; TILLIER, 1980:24 (pl.2, flg.l).

Ampullaria intermedia Ferussac, 1824 (pl.68, figs.1-2); 1827:135; ORBIGNY, 1835:31; 1837:371; HUPÉ, 1857:66.

Ampullaria autumnalis Reeve, 1856 (pl.4, fig. 16).

Ampullaria melanicheila Reeve, 1856 (pl.5, fig.24) (see present figs.72-73).

Ampullarius (Ampullarius) sordidus - MORRETES, 1949:67; OLIVEIRA *et al.*, 1981:76.

Pomacea *sordida* – LOPES, 1955:208-210 (figs. 17-23); QUINTANA, 1982:111; THIENGO (1989:351-355, figs. 1-9).

Description

Shell (Figs. 16-17, 72-73). Adequate description in Thiengo (1989, 352, fig. 1), characteristic by flatter fashion and an ampler umbilicus.

Head-foot and operculum (Figs.99-100). Similar features as those of *P. crosseana*.

Mantle organs (Figs.215-216, 218). Organization similar to that described for P. crosseana, with following remarks. Osphradium proportionally smaller, its basal, stalk-like portion low, lacking marginal fold covering base of filaments. Lung ampler, occupying about half of pallial roof area. Ctenidial vein separated into 2 in its posterior $^1/_3$, bearing pulmonary vein (although this vein apparently also receives gill blood flow). Gill weakly curved. Gill filaments tall; rod narrow, extending beyond filament; tip rounded.

Circulatory and excretory systems (Fig.217) - Both with similar fashion than that described for *P. crosseana*, with following remarkable features. Heart large, about half of kidney volume. Auricle with secondary connection to anterior-inner surface of pericardium, at right from ctenidial vein insertion. Aortas and ampulla connected to adjacent dorsal surface of pericardium. Anterior renal chamber broad and slightly short; internally 2 series of transverse septa separated by narrow longitudinal fold, all them main connected to dorsal surface and also reaching ventral surface. Nephrostome located in middle-posterior edge of this chamber. Connection between anterior and posterior renal chambers simple, protected at right by relatively broad vessel. Posterior renal chamber with tall renal dorsal lobe, this lobe covered by conspicuous, branched, anastomozed vessels. Intestine free from renal lobe.

Digestive system - Foregut characters similar to those of *P. crosseana*, remarks following. Dorsal chamber (between both longitudinal dorsal folds of buccal mass) with 4 longitudinal secondary folds that faint along anterior esophagus. Odontophore muscles (Figs.219, 221): m1b, generally composed by 3 narrow pairs; m1d, pair parallel to m1b, but insertion more posteriorly, in lateral-posterior region of buccal mass dorsal surface; m3 transverse, slightly thick, covering radular sac; m6 short and broad. Pair of pouches with dorsal inner fold having highly irregular surface, and lacking any longitudinal fold. Radular sac short, extending little beyond odontophore. Radular teeth of similar attributes as those of P. *crosseana*, notable features following (Figs. 123-124): rachidian tooth with rectangular outline, 7 cusps, central cusp with about twice neighbor cusps size; lateral tooth with about 1.5 times rachidian width, 3 cusps, middle cusps terminal and several times larger than remainder cusps. Mid and hindgut features (Figs.215, 220) also similar to those of P. *crosseana*, distinctions following. Posterior region of esophagus smooth internally. Stomach ventral chamber very small (about $^{1}/_{10}$ of dorsal chamber). Transversal septum low and restrict to ventral surface. Gastric walls slightly thinner muscular. Gastric muscle narrower. Digestive gland very dark, almost black. Intestine origin with smooth inner surface. Intestinal chambers in its region crossing pericardium double (Fig.220), proximal chamber transverse and ventral, its blind-sac, narrow distal end located inside aperture of distal chamber; distal chamber longitudinal and dorsal. Remainder intestine inner surface with several transverse, low folds. Intestinal loops inside renal chamber particularly complex, obeying pattern showed in situ in figure 215.

Genital system - ♂ (Figs.215, 222): Visceral and pallial structures organized similarly to those of P. *crosseana*, differing by following features. Testis pale beige lying along superior and columellar surfaces of visceral whorls, finishing half whorl posterior to pallial cavity. Pallial vas deferens thick walled (prostate) and somewhat conical; in its anterior end abruptly narrows and connects with penis sac crossing dorsal to rectum. Penis sac almost circular, its projection connected to penis shield almost as broad as penis sac. Penis sac anterior $^{1}/_{3}$ solid, posterior $^{2}/_{3}$ thin walled. Penis sac projection opened longitudinally along its dorsal surface; this aperture protected posteriorly by low fold originated from penis base. Penis of moderate length and coil degree, base broader, narrows gradually up to very slender apical region. Penis duct also with moderate degree of coiling. Penis shield broad; tip blunt, thick, curved towards right. Basal penis shield gland with aperture located in its dorsal-left side and presents normally 3 closely located slits. Secondary small gland located ventrally in right edge of penis shield base. Notch of penis shield furrow located in its middle level. Apical gland very large, composed by 5-7 successive broad folds lying along left edge of shield. Groove, coming from penis shield longitudinal furrow, surrounds basal edge of this apical gland, runs along dorsal surface of this gland and finishes broadly opened in middle region penis shield apex. More details in LOPES (1955, figs.19-23) and THIENGO (1989, figs.4-7). ♀: See description of Thiengo (1989, figs.8-9). Ovary, like digestive gland, almost black. Vaginal tube somewhat narrow, inner surface with some longitudinal, irregular, tall folds. Female pore a sub-terminal, ventral, transverse slit, located at right from anus.

Central nervous system - Features similar to those described for preceding ampullariids, except for lateral position of buccal ganglia.

Measurements of shells (in mm) - MZSP 32195: ♀ 1) 44.8 by 38.6; ♂ 2) 32.8 by 31.9.

Distribution - Bolivia, Brazil (RJ, SP, PR, SC), Paraguay, La Plata River (Argentina).

Habitat - Among aquatic plants of low-flow streams.

Material examined - Type: without locality, BMNH, 1 shell, holotype of *Ampullaria melanocheila* Reeve. Ordinary material: BRAZIL - RIO DE JANEIRO: Silva Jardim, MZSP 32195, 1♂, 2♀ (S.Thiengo col. and leg, X/1999).

Pomacea bridgesi (Reeve, 1856)
(Figs. 18-21, 67-71, 127-128)

The study on this species has been published in a separated paper: THIENGO & SIMONE, in press. However, the data on P. bridgesi have been included in the present analysis. Some shells are shown in the present paper (Figs. 18-21, 67-71) including some type specimens, and radular SEM pictures (Figs. 127-128).

Genus *Asolene* Orbigny, 1837
Type-species - *Helix platae* Maton, 1809

Asolene megastoma (Sowerby, 1825)
(Figs.23-24, 90, 129, 223-229)

Synonymy see CASTELLANOS & FERNANDEZ (1976:18). Complement:

Ampullaria neritoides Orbigny, 1835:31; 1843:368-369 (pl.49, figs. 1-2) (see present fig.90).

Asolene (Pomella) megastoma - SCOTT, 1957 (pl.2; pl.4, fig.6; pl.7, figs.17-18; pls.8-9; pl.11, fig.29; pl. 13, fig.33; pl. 14, fig.36-37; pl. 15; pl.23, fig.9); CASTELLANOS & FERNANDEZ, 1976:18(pl.1, fig.2; pl.4, fig.5); OLIVEIRA *et al.*, 1981:76.

Pomella megastoma - FIGUEIRAS, 1964:173.

Description

Shell (Figs.23-24, 90): very large (about 100mm). Spire short, almost plane. Aperture very ample. Umbilicus lacking. Other details in Scott (1957:314-315, pl.23, fig.9), CASTELLANOS & FERNÁNDEZ (1976:18).

Head-foot and operculum (Fig.223). Characters similar to those described for *P. crosseana*. Distinctive features following. Form very broad, head relatively small. Snout somewhat an inverted cone, base narrow. Lobes (siphons) relatively short. Tentacles broader in base.

Pallial organs (Figs.224-225). Similar features to those of P. crosseana. Except for osphradium peduncled; osphradium base short and smaller (about half of osphradium area). Gill filaments narrower. Other details in SCOTT (1957, fig.20).

Circulatory and excretory systems - Heart attributes similar to those of P. *crosseana*, but with auricle connected to anterior wall of pericardium. Kidney closely similar to that described for *P. canaliculata*. Dorsal renal lobe thick, brown, surface with irregular folds, most converging to aperture of anterior lobe; no connection with intestine. Anterior lobe long, broad, with 2 series of thick septa, pale beige, separated by longitudinal, tall fold. This longitudinal fold ventral edge free, connects only with nephrostome anterior edge. Intestinal loops inside kidney described below.

Digestive system - Buccal mass and odontophore muscles characters (Fig.226) similar to those of P. crosseana, but with most structures thicker and proportionally larger, including jaw plates. Some distinctive and notable features follow. Odontophore muscles: m1a thick; ma pair multiple; m3a pair, transverse portion anterior to radular sac covers m9; m7 pair origin located in postero-median margin of odontophore cartilages; m10 pair insertion part in m4 and part in m5, on their anterior surface (other details of odontophore in Scott, 1957, pls.7-9). Dorsal folds with very irregular-folded surface. Radular tooth similar to those of P. crosseana, with following remarks (Fig. 129): rachidian broad and shorter, smooth cut-edge lacking cusps except broad, blunt central projection, basal cusps long and oblique; marginal tooth about as broad as rachidian, slightly sigmoid, broadly pointed tip lacking secondary cusps; inner marginal tooth 2-3 times broader than inner marginal tooth, both with very small, sub-terminal cusps in inner edge. Pair of pouches longer, inner surface with pair of opposite located longitudinal folds, being dorsal folds broader. Esophagus characters (Fig.226) also similar to those of P. crosseana, except for thicker muscular walls. Stomach features (Figs.227-228) also similar to those of that species, including columellar-gastric muscle and transverse muscular septum. Differs by smaller ventral chamber (with thin walls), bearing 4-5 ducts to digestive gland close with each other; and by transverse muscular septum presenting taller edge turned inwards. Intestine initially broad, inner surface smooth. Intestinal portion adjacent to pericardium preceded by 2 chambers with aperture turned towards stomach; dorsal chamber as small, simple blind sac; ventral chamber larger and more complex, located just proximal to dorsal chamber, bears 3 distal flat ramifications (Fig.227). Digestive gland dark brown, with about 3 whorls posterior to stomach. Intestinal loops inside of kidney chamber as shown in situ in figure 227, complex, wholly connected by mesentery. Rectum narrow. Anus small, with simple borders.

Genital system - ♂ (Fig.224): Visceral and pallial structures with characters similar to those of P. *crosseana*. Distinctive or notable features following. Gonad pale cream, in columellar side of first visceral whorl. No broad region of pallial vas deferens by side of anus. Penis very slender and convolute, basal half folded by successive transverse furrows. Penis distal half narrowing gradually. Penis tip very slender. Penis sac anterior half very thick walled, posterior half very thin walled. In this posterior half dorsal fold runs from penis base to aperture of this chamber. This aperture broad, edged ventrally by thick fold with coiled distal border. Penis shield conic, very large (occupies most of pallial cavity and about half of mantle border length). Basal penis shield gland and aperture similar to those of P. crosseana, no other detectable basal glands. Penis shield ventral groove narrow, deep, running approximately along central region; secondary, smaller, oblique groove present at left. Penis distal region with irregular folded, massive, elliptical gland restrict to ventral side; main and secondary penis shield grooves converge in proximal margin of this distal gland and edge it in its left-proximal border. Other details in SCOTT (1957, pl. 15). $ (Fig.229): Visceral and pallial organs similar in characters to those of P. crosseana. Pallial oviduct very massive, greatly bulging inside pallial cavity. Visceral oviduct connects with bursa copulatrix in middle level of left pallial oviduct side. Bursa copulatrix, just after visceral oviduct insertion, elliptical and circular in section; bears flat, posterior, somewhat same lengthened expansion towards posterior, at some distance from visceral oviduct insertion. Capsule gland lumen flat, sinuous, complex; coils as shown in figure 229. Insertion of bursa narrow, located approximately between middle and posterior thirds of capsule gland region. Capsule gland connection with vaginal tube located approximately between middle and anterior thirds of capsule gland, towards ventral. Vaginal tube broad, walls thick, inner surface smooth, length about half of that capsule gland. Female pore small, papilla-like, located close to and at right from anus. Other details in SCOTT (1957, pl.14, figs.36-37).

Measurements of shell (Figs.23-24) - 83.0 by 87.0.

Distribution - Uruguay River (RS, Brazil; Argentina, Uruguay).

Habitat - In rivers with some degree of flow energy.

Material examined - Types - URUGUAY: Uruguay River, MNHN, 1 shell, probable holotype of *Ampullaria neritoides* Orbigny. Ordinary material: BRAZIL: Uruguay River; RIO GRANDE DO SUL: Itaqui, MZSP 250, 2♂, 8♀ (E.Garbe col., 1915).

Genus *Felipponea* Dall, 1919

Type-species:
Ampullaria (Felipponea) neritiniformis Dall
Felipponea neritiniformis (Dall, 1919)
(Figs. 130, 230-231)

Synonymy see CASTELLANOS & FERNÁNDEZ (1976:19). Complement:

Felipponea neritiniformis - SCOTT, 1957:317-318 (pl.6, fig.14; pl.23, fig.10); FIGUEIRAS, 1964:173; CASTELLANOS & FERNANDEZ, 1976:19 (pl.2, fig.5; pl.5, fig.15).

Asolene neritiniformis - OLIVEIRA *et al.*, 1981:76.

N.B.: VAZ & MARTINS (in press) have provided a whole description of this species in a submitted paper. The present description is greatly reduced, restrict to some aspects only. Complementary data must be reported to that paper.

Shell. Relatively small (about 30mm). Color pale greenish beige to brown, frequently with spiral dark bands. Spire tall, eroded. Umbilicus very narrow. Other details in DALL (1919:10-11), SCOTT (1957:317-318), CASTELLANOS & FERNÁNDEZ (1976:19).

Head-foot. Similar to *A. megastoma*, but not so broad. Head narrower. Siphons (nuchal lobes) formed by low folds (not so tall as those of *Pomacea* spp).

Pallial cavity (Fig.231). Osphradium elliptical, almost sessile (stalk very short and broad).

Circulatory and excretory systems - Heart with anterior aorta ampulla similar to those of preceding species.

Digestive system - Buccal mass and odontophore muscles characters very similar to those of *A. megastoma*, including m3a as fold covering radular sac, m10 pair long and narrow; differs by ma as single pair and by narrower m1 pairs. Jaw plates, dorsal folds, esophageal pouches and folds similar in features as those of *A. megastoma*. Radular teeth features similar to those of *P. crosseana*, with following remarks (Fig. 130): rachidian longer, outline almost square, 5-7 small cusps, central cusp about 1.5 times larger than neighbor cusps, basal cusp weak, somewhat longitudinal; lateral tooth about as broad as rachidian, 3-4 small cusps, first cusp terminal, second cusp about 3-times larger than neighbor cusps; inner marginal tooth with about double of outer marginal tooth width, both with tip sharp pointed and sub-terminal cusps in inner edge somewhat long (other details in SCOTT, 1957, pl.23, fig.10). Stomach characters similar to those of *A. megastoma*, except for thinner muscular gastric walls and by transverse muscular septum lacking long edge turned inwards. Intestinal region adjacent to pericardium preceded by pair of small, dorsal, sac-like chambers with aperture towards posterior. Intestinal loops inside renal chamber shown in figure 230.

Genital system - ♂: Penis shield somewhat similar to that of *P. lineata*, but with shorter tip lacking glands. Pair of glands in base of penis shield, being right gland smaller and more superficial. Penis shield furrow relatively deep, running almost all along its length. ♀ : Pallial oviduct proportionally large, with features similar to those of *A. megastoma*. Vaginal tube broad, walls glandular, origin about in half level on capsule gland.

Material examined - BRAZIL - PARANA: Ivai River, Floresta, MZSP 29713, 5 specimens, MZSP 30759, 5 specimens (A.L.Falavigna col.).

Genus *Marisa* Gray, 1824

Type-species: *Helix cornuarietis* Linné, 1758
Marisa planogyra Pilsbry, 1933
(Figs.22, 25-28, 101-102, 131-132, 232-241)

Synonymy see SCOTT (1957:321). Complement:

Marisa planogyra - SCOTT, 1957:321-322 (pl.23, fig.8); CASTELLANOS & FERNÁNDEZ, 1976:21

(pl.2, fig.6; pl.5, fig. 16-17); MARTÍN, 1980:47-50 (fig.3). OLIVEIRA *et al.*, 1981:78; MELLO, 1988:7-13 (figs.1, 3a-e); MELLO & MARINI, 1995:70-71 (fig.1).

Description

Shell (Figs.22, 25-28). Practically planispiral, with apex slightly dislocated to left. Aperture relatively small, elliptical. Other details in SCOTT (1957:321-322), CASTELLANOS & FERNANDEZ (1976:21). Color usually pale beige, with dark brown spiral bands, however, some uniform colored specimens occur (Figs.22, 25-27).

Head-foot (Figs.234, 237). Characters somewhat similar to those of P. *crosseana*, distinctive features following. Form relatively narrower laterally and longer antero-posteriorly. Anterior furrow of pedal gland restricted to anterior foot edge. Lobes (siphons) also long; right siphon with longer longitudinal fold running along floor of pallial cavity. Columellar muscle very longer, thinner and flattened, about 1 whorl length.

Operculum (Figs. 101-102, 234). Also of similar characters than that of P. *crosseana*, except for more rounded outline.

Pallial cavity (Figs.232-233, 235). Narrow and deep (about % whorl). Organs arrangement somewhat similar to that of P. crosseana, with following distinctive or notable features. Osphradium small, elliptical, on short stalk. Lung narrow and very long, almost as long as pallial cavity. Inner lung surface with transverse vessels like those of P. crosseana. Pneumostome an oblique, muscular edged slit located close to anterior-left region of lung ventral surface. Gill narrow and long, edges entire lung right margin. Gill filaments short, relatively broad, right margin slightly straight, left margin convex, apex rounded. Between gill and rectum a relatively narrow space, but broader as those of preceding species.

Circulatory and excretory systems (Fig.236) - Heart relatively small and narrow. Auricle just posterior to pallial cavity posterior end. Ventricle posterior to auricle. Anterior aorta ampulla broad and long. Kidney features somewhat similar to those of P. crosseana, with following distinctive or interesting attributes. Renal dorsal lobe slightly thin, dark brown, surface with some irregular-sized vessels; one of this vessels broader, connected to right edge of aperture to anterior renal chamber. Renal dorsal lobe free from intestine. Anterior renal chamber conic, narrow and short (about half of remainder kidney length). Anterior renal chamber with 2 same-sized dorsal series of transverse septa, separated by a tall, dorsal, longitudinal fold; this longitudinal fold not connected to nephrostome edges. Urinary gutter also similar of those of preceding species but longer; at some distance from mantle border abruptly twist and run in floor of pallial cavity (Figs.232-233).

Visceral mass (Figs.233, 236) - Length about same than that of pallial cavity, about 2.5 planispiral whorls. Stomach and adjacent digestive tubes occupy last half whorl. Gonad located in first half whorl, extending little beyond this by outer surface. Remainder visceral space occupied by dark brown digestive gland.

Digestive system - Buccal mass, odontophore muscles and esophageal characters similar to those of *P. crosseana*, distinctive or remarkable features following (Figs.237-238). Jaw plates thinner. Odontophore muscles (Fig.238): ma in 2 narrow pairs; m4 pair not attached to inner surface of odontophore cartilages (only covering them) and constituted by 2 thick layers (fused with each other laterally), also connects with tissue preceding exposed part of radula (to) via m9; m5 pair thicker and shorter; m10 pair narrower; m12 pair broader. Accessory pair of cartilages softer and thinner. Radular teeth attributes similar to those of *P. crosseana*, with following remarkable notes (Figs. 131-132): rachidian shorter, 7-9 tall and broad cusps, central cusp larger (about double than neighbor), remainder cusps decreasing towards lateral, pair of basal cusps narrow, low and oblique; marginal tooth strongly curved inwards and distally, 3-4 large and tall cusps, second cusp terminal and about double sized than neighbor cusps, conspicuous longitudinal, middle reinforcement in basal half; inner and outer marginal teeth tall slender, terminally curved, similar with each other (inner slightly broader than outer marginal tooth), both several times narrower than marginal tooth, tip pointed, sub-terminal cusp with about half of tip size. Esophagus uniformly narrow (without bulged posterior portion). Esophagus inner surface with about 6 longitudinal, slightly tall folds all along its length. Stomach with similar attributes as those of P. crosseana, including gastric-columellar muscle, distinctive features following (Figs.239-240): gastric muscular wall very thinner; transverse muscular septum absent; low longitudinal fold separates gastric chamber into esophageal and intestinal portions, inserts in posterior region of gastric-columellar muscle. Single duct to digestive gland bifurcating at short distance from its origin, running towards opposite side. Intestine initially broad, inner surface smooth except for pair of shallow, dorsal diverticles in its limit with stomach. Intestinal portion adjacent to pericardium preceded by pair of small, sac-like chambers with apertures towards posterior; each chamber aperture edged by thick border, left chamber encased inside aperture of right chamber (Fig.239). Remainder intestine slightly narrow, running somewhat similar to that of P. *crosseana*. Intestinal loops inside renal chamber showed in situ in Fig.240. Rectum narrow and very long. Anus simple, small.

Genital system - ♂ (Figs.232-233): Testis cream in color, located in posterior end of visceral mass first whorl. Visceral vas deferens very narrow, lying in columellar surface of visceral whorls. Pallial vas deferens also narrow and very long, lies at right from rectum. Genital organs close to mantle border, with organization somewhat similar to those preceding species. Pallial vas deferens crosses dorsal to pre-anal region of rectum without bulged portion. Penis sac most with thin walls, very short portion with thicker walls in penis base. Penis relatively short, width uniform along its length, narrows at short distance from pointed apex. Penis sac amply opened in left region, in penis shield base. Penis shield conic, large (about half of mantle border width). Basal gland situation and aperture similar to those of preceding species. Pair of small glands in each side of basal half of penis shield, being right gland smaller and more superficial. Penis shield groove relatively shallow, runs about in central region of shield ventral surface. Penis shield groove with secondary fold in its basal-right region coming from penis sac aperture. Penis shield groove runs almost entire shield length, finishes at some distance from shield tip. Penis shield distal half narrowing gradually, conspicuous notch at right located approximately in middle shield level. Penis shield slightly pointed, lacking glands. Other details in Mello (1988: 8-12, fig. 1), Martin (1980, fig.3). *9* (Fig.241): Pallial oviduct somewhat similar to those of preceding species, but smaller and narrower. Visceral oviduct inserts sub-terminally in bursa copulatrix, inside pallial oviduct mass. Bursa copulatrix conic, long, inserts in capsule gland lumen between its middle and posterior third parts. Bursa immersed in capsule gland. Capsule gland lumen flat and as blind-sac in posterior third, remainder intensely coiled (Fig.241). Vaginal tube narrow and very long (about twice capsule gland length), runs at right from urinary gutter and rectum. Female genital pore small, at right and close to anus. Other details in MELLO (1988:12, figs.1a-e).

Measurements of shells (in mm) - MZSP 29673: ♂ 1, 11.7 by 32.0; ♂, 12.0 by 30.0; ♀ 2, 11.0 by 28.8.

Distribution - Parana Macrobasin, central South America.

Habitat - Between *Eichornia* and other aquatic plants.

Material examined - BRAZIL - MATO GROSSO: Poconé, MZSP 29674, 15 specimens (L.S.Rocha col., 28/III/1997). MATO GROSSO DO SUL: Passo do Lontra, MZSP 29673, *2(3* , 2$, 1 shell (Simone and Lipparelli cols., V/1993).

Discussion - M. *planogyra* is very close related to *M, cornuarietis* (Linné, 1758), from which is very difficult separated conchologically. The anatomical differences between both species are neither well explored, except for study on their genital system (MELLO, 1988). That paper convincingly provides data for specific separation in the penis shield glands (M. *planogyra* has 2 glands, while *M. cornuarietis* 4 glands) and length (M. cornuarietis longer). Based on that paper, the specimens studied herein are all *M. planogyra*. Sexual dimorphism has been found in shell and foot color in *M. cornuarietis* specimens (Demian & Ibrahim, 1972).

Superfamily Cyclophoroidea
Family Cyclophoridae (=Potieridae, Amphicyclotidae)
Genus *Neocyclotus* Fischer & Crosse, 1886
Type-species: *Cyclostoma dysoni* L.Pfeiffer
Neocyclotus prominulus (Orbigny, 1840)
(Figs.29-31, 91-94, 109-111, 133-134, 242-258)

Synonymy see KOBELT (1902:238). Complement:
Cyclostoma prominula - ORBIGNY, 1846:362-363 (see present figs.91-94).
Neocyclotus prominulus - KOBELT, 1902:238; MORRETES, 1949:65.
Incerticyclus prominulus - TORRE *et al*, 1942:277 (pl.39, fig.7-9).
Aperostoma (?) prominula - MORRETES, 1953:47.

Description

Shell (Figs.29-31, 91-94). Size small (up to 15mm), discoid and flattened. Spire small, low. Suture deep, each whorl circular in section. Sculpture successive, uniform axial threads. Other details in KOBELT (1902:238), TORRE *et al.* (1942:277).

Head-foot (Figs.242, 245). Head little projected (almost inlaid). Snout stubby, most sessile, low. Mouth longitudinal, in anterior-dorsal snout surface. Pentacles shorter than snout, base at side and posterior to snout base. Ommatophore short, located about in middle level of outer tentacle surface. Eyes small, dark. Foot thick, relatively small. Furrow of pedal gland edging entire foot sole, deeper anteriorly. Columellar muscle very thick and short (about $^1/_3$ whorl). Columellar muscle distal end somewhat bifid, with right branch flatter and taller. Males with exophalic penis located just posterior to right tentacle (described below).

Operculum (Figs. 109-111, 242). Outline circular, calcareous, thick, edge double (Fig.111). Nucleus central, smooth; multispiral shallow furrow originated from nucleus. Outer surface opaque. Inner surface glossy, low projection central, from which scar turns around in growth (seen by previous scars). Inner scar rounded, with about ¼ of opercular area.

Mantle organs (Figs.243-244, 246-247). Pallial cavity of about half whorl, relatively narrow. Mantle border thick, simple. Osphradium and gill lacking. Broad vessel (probably homologous to ctenidial vein) edges left margin of pallial cavity, anterior region with 2 branches (being collar vessel one of them), becomes broader towards posterior, inserts in left extremity of pericardium. Pericardium and kidney as left-posterior limits of pallial cavity. Between left vessel-kidney and rectum a broad smooth area without large transverse vessels (between kidney and rectum a narrower area). Rectum very broad (about ½ of pallial cavity width), edging pallial cavity right border, abruptly narrows, Anus small, shortly siphoned, close to right end of mantle border. Pallial oviduct and prostate located between rectum and right border of pallial cavity, displacing it towards left (both described below).

Visceral mass (Figs.246-247). About 2.5 whorls in length. Kidney and pericardium as left-anterior limit; pallial gonoducts and rectum as right-anterior limit. Gonad located in first whorl outer surface, covering small portion of digestive gland. Stomach large and long, with about half whorl in length, half whorl posterior to pallial cavity. Stomach separates almost completely digestive gland into posterior and anterior branches, being connected with each other by thin and narrow ventral portion. Last half whorl of visceral mass filled by digestive gland (posteriorly) and intestinal loops (anteriorly). Other details below.

Circulatory and excretory systems (Figs.244, 247-248) - Heart relatively small, located behind to left-posterior corner of pallial cavity. Narrow vessel edges anterior surface of kidney, entrance into pericardium and inserts in auricle. Auricle and ventricle small, connected with each other by narrow and short tube, Auricle at right and slightly anterior to ventricle. Aortas bifurcate shortly after ventricle origin of common aorta, anterior aorta with about double width than posterior aorta. Broad vessel of left margin of pallial cavity runs dorsal-left to pericardium; just before this region smaller branch which edges pericardium inserts. After pericardium contoured, this vessel connects with other vessel coming from visceral mass and runs towards kidney. Kidney with 2 chambers. Anterior renal chamber totally filled by glandular tissue, somewhat triangular in section, connects with pericardium by small and narrow slit. This glandular tissue almost solid, formed by several branched, transverse, glandular septa. Posterior renal chamber simple hollow sac mostly filled by intestinal loops (described below). Nephrostome a small slit located in ventral surface of anterior renal chamber, close to posterior limit of pallial cavity. Urinary gutter starts just ventral to nephrostome, runs as shallow groove in pallial floor towards left and by left side of head-foot.

Digestive system - Buccal mass (Figs.249-251) relatively large (about $^1/_3$ of haemocoel volume) (Fig.245). Oral tube short, walls thick, circular muscle (mouth sphincter - mc) broad. Buccal mass dorsal wall (Fig.251) thin, anterior half covered by jaws. Jaw plates very large, slightly triangular, connected with each other in median line. Surface constituted by several oblique striae. Jaws anterior cut-edge thin, sharp, arched. Dorsal folds tall, narrow in region just posterior to jaws, gradually become broader and newly narrow after buccal mass end. Odontophore muscles (Figs.249-250, 252-253): ml, several small and narrow muscle fibers connecting buccal mass with adjacent inner surface of haemocoel; m1a, pair of narrow dorsal jugal muscles, origin in dorsal inner surface of haemocoel, in approximate middle level of odontophore, runs towards ventral and anterior, insertion in anterior region of buccal mass dorsal surface; m1b, pair of narrow and thin jugal muscles, origin close to m1a origin, runs towards ventral and posterior, insertion in each side of odontophore posterior region; mj, jaws and peribuccal muscles, relatively thick, origin in odontophore lateral-ventral surface, insertion in dorsal wall of buccal mass around jaws; ma, pair of thick and short muscles, origin in lateral-anterior inner surface of haemocoel, runs towards medial through mj fibers, insertion along outer surface of jaws; m3d, pair of thin and narrow muscles, origin in posterior-dorsal-lateral region of buccal mass, run in surface towards ventral and anterior, insertion along ventral surface of odontophore close to median line; m4, broad pair of radular tensors, possessing some branches: m4 main body surrounding inner, ventral and lateral surfaces of cartilages, connected to cartilages only in ventral and lateral surfaces and in some sparse branches to inner surface; m4v, ventral branches, pair covering outer-lateral surface of cartilages, origin in m4 main branches posterior region, runs towards anterior, insertion along subradular membrane inner surface from median line to lateral; m4a, thinner pair covering ventrally m4 main branch, origin along their lateral surface, insertion with tissue on radular ribbon (to) in region preceding its exposure; m5, pair of dorsal tensor muscles of radula, relatively thin, origin broad on m4a, run towards medial and anterior covering m4, insertion relatively narrow in dorsal surface of radular sac preceding exposed region of radula; m6, horizontal muscle, connects dorsal surface of both cartilages along and at some distance from their medial edge; m7, pair very thin and narrow, origin in posterior end of cartilages, each runs towards medial connecting with its pair, penetrate and insert in inner surface of radular sac; m10, pair of protractor muscles of buccal mass, origin in ventral-inner surface of mouth, runs towards posterior, insertion in ventral-anterior surface of odontophore, close to median line; m10c, similar to m10 but running dorsal to it, insertion more anterior and dorsal to those of m10; m11 pair of narrow, thin and long muscles, origin in ventral surface of haemocoel close to median line at middle level of odontophore, run dorsal, penetrate in odontophore in medial line, after run attached to subradular membrane, insertion along median line. Other non-muscular buccal mass structures: oc odontophore cartilages, single, large, flat pair, outline oval; ih, inner ligaments between radular sac and inner surface of m6; br, subradular membrane similar to those of ampullariids. Pair of buccal ganglia located laterally in posterior-ventral region of buccal mass (Fig. 249), their comissure relatively broad. Pair of nerves penetrates in odontophore just anterior to m11 penetration. Radular sac long (about 3 times longer than buccal mass length), not coiled, only twisted posteriorly. Radular nucleus thick. Radular teeth (Figs. 133-134): rachidian long and narrow, 3 stubby cusps, central cusp about double than neighbor cusps; lateral tooth with about double of rachidian width, situated obliquely (lateral end in level of rachidian distal roll), 3 cusps, middle cusp terminal, 3-4 times larger than neighbor cusps, base long and narrow; inner marginal tooth tall, slender, somewhat flat, 3 terminal and broad cusps, central cusp about 1.5 times larger than neighbor cusps; outer marginal tooth sigmoid, about same length than inner marginal tooth, base broad and flat, with broad projection, middle region slender and curved, distal region slightly broader, pointed, secondary cusps small, sub-terminal, on inner edge. Salivary glands somewhat triangular, separated from each other, located posterior to esophageal pouches. Salivary gland ducts long and convolute, runs on dorsal surface of anterior esophagus and buccal mass, penetrate in dorsal wall of buccal mass close to their apertures.

Anterior esophagus with pair of tall dorsal folds (continuation from those of buccal mass), which gradually faint in middle esophagus (Figs. 249, 251). Pair of large, lateral pouches located just posterior to buccal mass, both connect with esophagus by narrow aperture, after aperture abruptly expand and become reniform sac. Pouches inner surface covered by several papillae. Dorsal esophageal folds cover each pouch aperture. Especial branches of anterior aorta irrigate each esophageal pouch, connected with them close to their connection with esophagus. Middle esophagus broad, inner surface with sparse, oblique, low folds. Posterior esophagus narrow, inner surface smooth.

Stomach (Figs. 247, 254) long and broad. Esophagus inserts in stomach in middle level of its ventral surface, but retains separation from gastric chamber by longitudinal, tall fold. Stomach mostly a simple sac, without inner especial structures, inner surface most smooth. Duct to digestive gland single, located in ventral-right region of anterior third part of stomach. Transverse groove present in anterior third of stomach, begins in aperture of duct to digestive gland, runs in ventral surface up to opposite side where faint, just in beginning of longitudinal, low fold of intestine. Digestive gland beige, with small brown spots (other details above). Intestine broad, with several loops inside posterior renal chamber as shown in Fig. 247. Fecal pellets elliptical, large, fill intestine after its first loop in renal chamber. Rectum and anus described above.

Genital system - ♂: Testis (Fig. 246) (described above) cream in color. Visceral vas deferens very narrow, runs along ventral surface of stomach up to median-ventral-posterior edge of pallial cavity. Prostate large, located in right side of pallial cavity, part attached to pallial floor; visceral vas deferens inserts in middle region of prostate left side. Prostate elliptical in section, inner lumen flat (Fig.246). Prostate aperture a small, anterior papilla, opens towards pallial cavity floor where groove begins. Pallial sperm groove runs short distance up to penis base. Penis relatively small (little longer than tentacle), located just posterior to right tentacle (Fig.242). Penis base broad, gradually narrows, in its middle region newly expands and curves towards right (Figs.242, 255). Penis tip broad, asymmetrical. Penis sperm groove runs all along penis length, approximately in middle of its ventral surface. Penis sperm groove distal end on small papilla. 9 (Figs.247, 256-258): Ovary small, occupies only columellar side of visceral first whorl (Fig.247). Visceral oviduct very slender, thin and long, runs along ventral surface of stomach up to middle region of pallial cavity posterior edge. In this region abruptly curves towards posterior and runs obliquely to right, augmenting very gradually. After distance equivalent to about ¼ whorl suddenly curves towards posterior, running parallel to its preceding portion. Close and anterior to its first curve inserts in seminal receptacle base. Seminal receptacle very long, increase gradually, rounded distal tip. Seminal receptacle aperture small slit in middle region of pallial oviduct vaginal groove. Capsule gland as remainder, massive region of pallial oviduct; possesses 2 flat, thick-glandular walled chambers. Right chamber a blind-sac connected to left chamber posteriorly. Left chamber with pair of tall, oblique folds preceding its connection with right chamber, and several other low, narrow folds along posterior half of its left wall. Left chamber opens anteriorly in female pore as simple, thick-walled slit.

Central nervous system (Figs.245, 249) - Nerve ring located anterior to buccal mass, just posterior to mouth. Hypoathroid type, with long comissure between both cerebral ganglia. Statocyst with several statoliths.

Measurements of shells (in mm) - MZSP 24542: 9 l,8.6by 13.6;9 2, 7.7 by 12.8; ♂ 4, 7.4 by 12.7; MZSP 24538, 9 : 10.4 by 15.7.

Distribution - South Rio de Janeiro and Sao Paulo Atlantic Rain Forest.

Habitat - Terrestrial, under plants.

Material examined - Types - BRAZIL; MNHN, 2 shells, probable syntypes of *Cyclostoma prominula* Fer. in Orbigny. Ordinary material: BRAZIL - SAO PAULO: Sao Vicente (O.Schubart col.), MZSP 24547, 19 (27/I/1960), MZSP 24545, 1 specimen (27/I/1960), Prainha, MZSP 24542, 11 specimens, 8 shells, (27/I/1958), MZSP 24539, 3 specimens (15/II/1953), MZSP 24543, 3 specimens (27/I/1959), MZSP 24540, 1 specimen (15/II/1953), Paranapoã, MZSP 24548, 1 shell (1/II/1960), Porchat Island, MZSP 24544, 3 specimens (29/I/1959), Itararé, MZSP 24546, 8 specimens (29/I/1960); Itanhaém, Viuva Conde Farm, MZSP 24535, 1 shell (O.Schubart col., 9/IX/1941); Iporanga, MZSP 15615, 7 specimens (Leme and Papavero cols., 1/XI/1983), MZSP 24538, 19 (O.Schubart col., 30/XI/1952); Iguape, MZSP 24532, 2 shells (Leme and Biasi cols., 1-5/XI/1968); PARANA: Serrada Graciosa, MZSP 29575, 1 shell (AVC Dutra col., X/1979).

The anatomy of *Neocyclotus inca* (Orbigny, 1835) has been provided by SALGADO *et al.* (1989), reporting a similar organization to *N. prominulus*. These species are different mainly in the penis fashion.

Genus *Incidostoma* Morrison, 1942

Type-species:
Aperostoma (Incidostoma malleatum Morrison, 1942)

fricidostoma tupy new species

(Figs.32-36, 135-136, 259-270)

Types - Holotype: MZSP 29560, 19 from type-locality. Paratypes - BRAZIL - RONDÔNIA: Nova Esperança, MZSP 29578, 2♂ (MZ polonoroeste sta. 831888, 6-9/XII/1983), MZSP 29561, 2 specimens (sta.831874, 6-7/XII/1983); Nova Brasilia, 11°09'S 61°34'W, MZSP 29561, 2 specimens (PNW 840566, 6-11/XI/1984); Jaru, MZSP 24553, 19 (K.Okushigue col., 10/IX/1976).

Type-locality - BRAZIL - RONDÔNIA: Santa Cruz da Serra [MZSP 29560, Vanzolini col., (MZ poloeste sta. 840169)].

Diagnosis - Malleated surface weakly developed. Aperture ample, separated from preceding whorl. Outer lip free.

Description

Shell (Figs.32-36). Size about 30mm, discoid, flat, about 4.5 whorls. Color uniform brown. Outer surface rich of undulated and delicate growth lines; malleated surface (*i.e.*, several low, small concavities sprayed by surface) almost absent, seen in some area in outer surface preceding aperture. Walls thin. Protoconch dome-shaped, small, of 1 whorl, surface smooth and opaque, suture well-marked, transition with teleoconch unclear. Teleoconch with convex whorls, almost planispiral. Spire very low, approximate angle of 170°. Each whorl covers small area of preceding whorl. Umbilicus very ample end deep. Peristome white, somewhat thick, weakly prosocline, oval. Notch deep in superior corner, close to suture; its lips surround small orifice, anterior-left edge touches adjacent virtual suture; satellite growth lines contours notch in preceding area, gradually becoming perpendicular to suture at short distance from aperture.

Head-foot (Figs.259-260). Characters similar to those of *N. prominulus,* with following remarkable features. Snout slightly taller, with mouth turned ventrally. Pedal gland furrow restrict to anterior edge of foot sole. Urinary gutter at right of head deeper. Penis of males proportionally larger.

Operculum (Figs.259-260): Somewhat similar in characters to those of preceding species, except for simple (not double) outer edge, and broader last whorls of outer sculpture.

Mantle organs (Figs.261-262). Features somewhat similar to those of *N. prominulus,* with following distinctive or notable attributes. Lung with net of vessels more clear, with 6-7 branched vessels alternating drainage to left (ctenidial?) vessel and to ad-rectal sinus. Probable hypobranchial gland present as lobe bulging at right from kidney, part covered dorsally by rectum [normally connected to excretory features, commented below (excretory system and discussion)].

Circulatory and excretory systems (Figs. 161-162) - Heart and pericardium characters similar to those of N. *prominulus,* differ only in having left (ctenidial) vessel plus vessel edging kidney inserted directly to auricle. Kidney also with similar attributes as those of *N. prominulus,* including anterior (solid-glandular) and posterior (hollow, filled by intestinal loops) renal chambers. Differs only by more protruded nephrostome and presence of solid excretory hypobranchial gland (as described in mantle organs). Urinary gutter deeper.

Digestive system (Figs.263-264) - Buccal mass attributes similar to those of *N. prominulus,* with following remarks. Dorsal folds with tall middle region as stalk for aperture of salivary glands. Odontophore muscles: m1b pair thinner, closer to median line; m3 pair similar but with an additional branch connecting with each other running on posterior odontophore surface, dorsal to radular sac; m11 pair thicker. Radular teeth features similar to those of *N. prominulus,* with following remarkable notes (Figs. 135-136): rachidian slender, almost triangular, 3 cusps, central cusp several times larger than neighbor cusps, distal edge concave; marginal tooth with about twice rachidian length, 3 cusps, central cusp terminal and several times larger than remainder cusps, basal region long, narrow and oblique; inner and outer marginal teeth slightly broader. Esophageal pouches, folds and regions similar in features to those of *N. prominulus,* except for taller folds edging pouches aperture and more developed irrigation of blood vessel in region of these tall folds. Large blood sinus located in ventral region between esophagus and buccal mass, this sinus evolves radular sac and possesses thick branches to salivary glands, to esophageal pouches and to odontophore. Middle esophagus with 4-5 narrow, longitudinal folds. Salivary gland cluster as single mass located posterior to pouches. Stomach attributes also similar to those of*N. prominulus,* except for: 1) more anterior insertion of esophagus; 2) posterior region of stomach (as blind sac) longer, its inner surface covered by transverse folds (sorting area?); 3) fold continuation from esophagus taller; 4) groove running from duct to digestive gland aperture deeper. Intestinal loops, characters and digestive gland features like those described fop *N. prominulus.*

Genital system - ♂ (Figs.259, 265-266): Visceral and pallial organs with characters similar to those of *N. prominulus,* with remarkable features following. Prostate circular in section. Sperm groove between prostate and penis base longer. Penis very larger (about same length than that of entire head-foot). Penis base broad, gradually narrows, middle third part of uniform width. Penis distal third broad, flat, slightly triangular. Penis sperm groove runs along lateral edge of penis and also superior edge of penis tip. Penis groove ends in pointed, small papilla (Fig.266). Penis papilla stay turned inwards, bulged, semispherical structure precedes it. Immature penis simpler, with tip coiled (Figs.267-268). ♀ (Figs.261, 269-270): Visceral and pallial structures with characters similar to those of N. *prominulus,* with following remarks. Albumen gland more differentiated, as thicker region of visceral oviduct last loop. Seminal receptacle similar located, but possessing aperture direct to pallial cavity (and not inside pallial oviduct). Seminal receptacle aperture a small papilla located in posterior edge of pallial cavity close to pallial oviduct. Capsule gland similar to that of *N. prominulus,* with same components. Genital pore a thick edged slit.

Central nervous system (Fig.263) - Similar characters to those of *N. prominulus.*

Measurements of shells (in mm) - Holotype: 17.4 by 31.3; MZSP 29561: 17.0 by 29.2; 19.3 by 30.9.

Distribution - Known in some points of Rondonia State, Brazil, Amazon Forest.

Habitat - No data.

Material examined - Types.

Etymology - The specific epithet refers to the ancient indigenous people living in region.

Discussion - The superior notch of outer lip clearly allows the generic attribution of the new species, also with the aid of generic key of TORRE *et al.* (1942:187). *I. tupy* differs from */. malleatum* (Morrison, 1942) (without locality), */. pergrandis* (Kobelt, 1912) from Colombia and *I. kobelti* (Morrison, 1942)(from Colombia) by less developed malleated surface, ampler aperture more separated from preceding whorl, and by more developed axial sculpture. MORRISON (in TORRE *et al,* 1942) presented the distribution of the genus for Colombia, Ecuador and Peru, (Andes localities). The present description expands the geographic distribution towards east, for Brazilian territory (Rondonia) relatively away from Andes. However, *I. malleatum,* just the type species of the genus, remains lacking a more precise locality.

The presence of the hypobranchial gland in cyclophorids has been related to the excretion (ANDREWS & LITTLE, 1972), but a clear gland is found only in */. tupy* (Fig.262 in middle-superiorregion).

Genus *Aperostoma* Troschel, 1847
Type-species: *A. blanchetianum* Moricand

Aperostoma blanchetiana (Moricand, 1826)
(Figs.37-39, 112, 137-138, 271-275)

Synonymy see TORRE *et al* (1942:244-245). Complement:

Neocyclotus (Neocyclotus) inca - (part) KOBELT, 1902:236 (in synonymy) (non ORBIGNY, 1835).

Aperostoma (Aperostoma) blanchetianum: TORRE *et al,* 1942:244-245 (pl.35, figs.7-9).

Description

Shell (Figs.37-39). Discoid and flat. Color brown with paler spiral bands variable in localization and number in specimens. Spire somewhat tall. Umbilicus slightly narrow. Aperture rounded, slightly prosocline, very weak notch in superior corner in form perpendicular. Other details in TORRE *et al.* (1942:245)

Head-foot and operculum (Figs. 112). Characters similar to those of */. tupy.*

Mantle organs (Fig.271). Features similar to those of /. tupy. Narrow fold of hypobranchial (?) gland present edging rectum.

Circulatory and excretory systems (Fig.271) - Characters similar to those of preceding cyclophorids, remarkable features following. Lung vessels preceding auricle somewhat similar to those of *I. tupy,* but left (ctenidial) vessel strongly curved preceding its connection, and secondary vessel running along border between kidney and pericardium (not running on pallial surface). Kidney also with 2 chambers, anterior (solid-glandular) chamber longer antero-posteriorly. Nephrostome a slit preceded by short stalk.

Digestive system (Fig.272) - Morphological attributes in general similar to those of */. tupy,* distinctive or notable features following. Jaw plates separated from each other, outline somewhat circular, with small projection in median-anterior edge. Buccal mass dorsal chamber (between both dorsal folds) with taller longitudinal folds. Odontophore muscles: m1, several pairs in ventral region connecting odontophore outer surface with mouth; m1b absent. Radular teeth with similar attributes as those of preceding cyclophorids, remarkable features following (Figs. 137, 138): Rachidian slender and long, 3 cusps, central cusp about 3 times larger than remainder cusps, distal edge concave, with an additional central concavity; marginal tooth with 3-4 cusps, penultimate cusp terminal and several times larger than remainder cusps; inner and outer marginal teeth broader, outer marginal strongly sigmoid. Large sinus around radular sac with branches to both pouches and salivary glands present. Stomach with groove adjacent to duct to digestive gland longer, surrounds transversally entire gastric circumference with short portion parallel to its initial region. Gastric inner surface with an additional longitudinal, low, flattened fold located between esophagus aperture and duct to digestive gland.

Genital system - ♂ (Figs.274, 275): Similar characters to those of *I. tupy,* with following remarkable features. Prostate longer, broader and curved, walls transversally folded. Sperm groove between prostate and penis base longer. Penis large, curve, middle third part narrower than basal and distal regions. Penis apex broad, flat, asymmetrical, expanded, thick. Penis sperm groove runs along inner edge and superior edge of penis tip; finishes in penis right side. Final part of penis groove with pair of small papillae; left papilla broader, tip rounded, more basal located; right papilla slender, pointed and more distal. 9 (Figs.273): Visceral and pallial structures with characters closely similar to those of *I. tupy*, including albumen gland developed and seminal receptacle opened directly into pallial cavity. Differs by narrower genital pore.

Measurements of shells - MZSP 16534♂: 14.4 by 20.8; MZSP 16534: 14.3 by 21.5.

Distribution - Bahia and Minas Gerais states.

Habitat - No data.

Material examined - BRAZIL - MINAS GERAIS: Buritis, Jaboticaba stream, MZSP 16534, 3♂, 2$ (sta. 642152, Vanzolini col.).

Discussion - The shell attributes of the examined specimens are closely similar to those described by TORRE *et al.* (1942:245) for A. *blanchetiana*, allowing the specific identification. However, there is another very similar species, *A. merrilli* Morrison, 1942 (from Braganga Railway, Amazon valley, Brazil).

Superfamily Viviparioidea
Family Viviparidae
Genus *Viviparus* Montfort, 1810

Type-species:
Helix fluviorum Montfort = *viviparus* Linné

Viviparus acerosus (Bourguignat, 1862)
(Figs.40-41, 103-104, 139-140, 276-295)

Viviparus acerosus - FECHTER & FALKNER, 1993:119 (fig.5); FALNIOWSKI *et al.*, 1996.

Description

Shell (Figs.40-41). Globose, color greenish-brown. Spire tall, apex slightly rounded. Suture deep, each whorl circular in section and scarcely attached to neighboring whorls. Body whorl harmoniously sized with spire. Umbilicus wide. Periostracum heavy, smooth. Sculpture lacking except growth lines and axial undulations. Aperture circular, lips somewhat projected. Young specimens (from brood pouch) with up to 4 whorls; protoconch smooth, of 1 whorl; remaining whorls sculptured with several narrow, spiral lines uniformly distributed, 2 or 3 of them markedly larger and equidistant from each other, bearing periostracal hair.

Head-foot (Figs.276, 279-280, 291, 293). Head slightly protruded, relatively small (about $^1/_3$ of head-foot width). Snout cylindrical, anterior margin flat. Tentacles long (about 1.5 times longer than snout), stubby, base at side of snout base. Ommatophore short, located between basal and middle third of outer surface of each tentacles. Pair of siphons (lobes) similar to those of ampullariids, but shorter. Food groove edged by thick, low borders; running slightly to right of middle region of pallial floor. Food groove with posterior end fainting; anterior end in right siphon (nuchal lobe), dividing it into two projections, anterior (dorsal) projection with medial limit close to base of snout (Fig.293: lr). Foot large (about $^2/_3$ of head-foot volume), sole simple. Opercular pad larger than its base in dorsal foot surface, with edges projecting beyond it. Anterior furrow of pedal glands restricted to anterior foot, edged by thick borders. Columellar muscle thick, length about $^3/_4$ whorl. Head-foot connection with mantle border very thick and richly vascular. Male genital structures described below.

Operculum (Figs. 103-104, 276). Occupying entire shell aperture. Horny, somewhat similar in characters to those of ampullariids. Outline slightly circular, with low projection in inner-superior region. Nucleus sub-central, located closer to inner margin. Sculptured with concentric growth lines. Inner surface glossy; scar sub-circular, close to inner margin, occupying about $^2/_3$ of opercular area.

Mantle organs (Figs.277-278, 281). Pallial cavity of about 1 whorl. Mantle border simple, thick. Osphradium ridge-like, oblique, almost parallel to mantle border, length about $^1/_2$ of that mantle border, very close to gill. Ctenidial vein narrow, uniform in width throughout. Gill long and narrow, about same length as pallial cavity; anterior end at mantle border. Gill filaments very tall and narrow, arched towards right; apex slightly pointed, close to food groove. Gill filaments with short, low, glandular portion preceding afferent gill vessel, forming glandular ridge along left gill margin (endostyle) (Figs.277, 281). Glandular tissue (hypobranchial gland?) covering afferent gill vessel; but broad space apparently lacking hypobranchial gland between gill base and rectum. Right margin of pallial cavity filled by oviduct in females. Ad-rectal sinus modified in ureter, broad, running all along pallial cavity right margin in males or edging oviduct in females. Rectum on dorsal and left sides of ad-rectal sinus. At right end of mantle border, in females, presenting three openings, most posterior and smaller is ureter pore, anus most anterior, and female pore larger, located between anus and ureter pore.

Visceral mass (Figs.277-278). Long, with about 4 whorls, approximately smaller than pallial cavity. Kidney anterior, with stomach and adjacent intestine just posterior to it. Gonad and digestive gland occupying about 2.5 whorls posterior to stomach. Gonad brown, located in columellar surface of each whorl. Digestive gland pale green. Details of each structure below.

Circulatory and excretory systems (Figs.278, 282) - Heart relatively small, located behind posterior-left region of pallial cavity, partly posterior to anterior lobe of kidney. Auricle connection with ctenidial vein just posterior to gill; possessing portion protruding anterior to this connection. Ventricle posterior to auricle, narrow connection between both. Kidney with two chambers and ureter. Anterior kidney chamber small, triangular in section, entirely filled by glandular tissue (having only small inner hollow portion close to nephrostome). Anterior kidney chamber with four almost plane surfaces: 1) posterior surface towards pericardium, with ventral, small, middle slit as reno-pericardial pore; 2) left with pallial cavity; 3) ventral right with ureter; 4) dorsal with mantle. Nephrostome an elliptical, small pore, without muscular edges, located in middle-posterior region of ventral-anterior surface of anterior renal chamber. Posterior renal chamber simple hollow sac filled by anterior region of stomach and intestinal loops. Ureter apparently specialization of broad adrectal sinus (Figs.278, 281), runs between rectum and oviduct (in females) or right pallial cavity edge (in males). Posterior end of ureter ventral to anterior renal chamber; anterior end in muscular, papilla-like ureter pore just posterior to anus (or just posterior to female pore). No special inner glands in ureter. No urinary gutter.

Digestive system - Buccal mass just posterior to mouth, extends slightly posterior to snout inside haemocoel (Fig.280). Mouth longitudinal, ventral. Jaw plates small, thin, outline elliptical (Fig.283). Dorsal folds broad, smooth and simple. Deep dorsal chamber between both dorsal folds, inner surface smooth. Odontophore and peribuccal muscles (Figs.284-288): mc, circulatory fibers of buccal sphincter, thick and broad; m1, several pairs of small muscular fibers connecting buccal mass outer surface with adjacent regions of haemocoel, no differentiated pair; mj, pair of jaw and peribuccal muscles, origin in odontophore cartilage lateral-anterior surface, insertion along dorsal wall of buccal mass just dorsal to jaws; m2, pair of retractor muscles of buccal mass (retractor of pharynx), origin in lateral inner surface of haemocoel posterior to buccal mass, run towards anterior, insertion in posterior-lateral surface of odontophore (Figs.284, 286), most part on membrane which covers odontophore and small part in m4; m4, pair of large ventral tensor muscle of radula and subradular membrane, origin in odontophore cartilages around mj, cover cartilages almost completely (only dorsal edge free), insertion in small lateral region of tissue on radular ribbon preceding buccal cavity (to), subradular membrane also connecting along lateral and anterior edges of m4, part of dorsal branch m4 of with weak fibers along it; m5, pair of dorsal tensor muscles of radula, originating on m4 posterior-lateral region, running medially covering m4, insertion along radular sac in region opposed to m4 insertion (each m5 does not connect with its pair); m6, horizontal muscle, similar to those of ampullariids, little shorter in length than cartilages; m7, narrow, long pair, origin in m4 dorsal branch at medial-posterior edge, run posteriorly on subradular membrane (br) inner surface fusing with each other, penetrating in radular sac, insertion along radular sac and radular nucleus (Figs.287, 288); m7a, pair of thick muscles, originating in ventral surface of haemocoel close to median line and in level just posterior to odontophore, run dorsally and, after, anteriorly attached to radular sac ventral surface, insertion in m5 anterior edge (Figs.285, 288); m9 absent; m10, pair of ventral protractor muscles of buccal mass, origin in ventral inner surface of mouth, run posteriorly on mc, insertion in ventral-anterior region of odontophore; m10a, paired continuation of m10, running close to median line and attached to membrane covering odontophore, insertion along this membrane in its medial-ventral-posterior region; m11, pair of long and relatively broad muscles, originating on haemocoel inner ventral surface in region posterior to odontophore, close to origin of m7a, running dorsally, penetrating in odontophore just anterior to radular sac, insertion along subradular membrane close to median line reducing anteriorly; m12, small pair of muscles similar to those of ampullariids, origin in lateral-anterior inner surface of m4 and br, running towards medial and dorsal, insertion shortly on cartilages anterior-outer surface close to m6 (Fig.287). Other odontophore structures: br, subradular membrane, similar to those of preceding species, cover inner surface of (and probably secretes) subradular cartilage, most inserted in lateral and anterior edges of m4, but also connects with radular sac (via m5 pair) and peribuccal epithelium (via mj); reinforcement of subradular membrane in its dorsal-middle region with posterior, "W"-shaped edge; oc, pair of odontophore cartilages, similar to those of preceding species, flat, outline elliptical; om, odontophore outer membrane, transparent, covering outer surfaces of odontophore, except narrow portion close to median line where is penetrated by radular sac, some muscles (m7, m7a, ml 1) and some nerves; to, tissue on radular ribbon preceding buccal cavity, length more or less equivalent to portion of radula passing through odontophore. Buccal ganglia located laterally, on each side of border of odontophore and dorsal wall of buccal mass, close and dorsal to m2 insertion. Salivary glands (Figs.280, 283, 284) clustering as single mass posterior to nerve ring (localized posterior to buccal mass) and as two narrow glandular masses through it. Salivary ducts as continuation from these two masses, run on dorsal wall of buccal mass outer surface, penetrating into wall just close to their apertures, in anterior extremities of dorsal folds, close to median line.

Radular sac about as long as buccal mass (Figs.284-286), radular sac surrounded by large blood sinus. Radular teeth (Figs. 139, 140): all teeth with similar shape, tall, as flat rod, tip rounded, curved inwards, bearing several small, sharp cusps. Rachidian shorterst tooth, with 7-9 cusps, central cusp about three times broader than neighboring cusps (but same length); lateral tooth with 7-9 cusps, central cusp terminal, about three times width of remaining cusps (but same length); inner marginal tooth similar to lateral tooth, slightly longer; outer marginal tooth similar to inner marginal tooth, differing only in uniformity of cusps (lack central differentiated cusp).

Esophagus relatively narrow and long. Anterior esophagus with pair of dorsal, broad, longitudinal folds (as continuation from dorsal folds of buccal mass), without pouches (Figs.283, 284). Middle esophagus with several (about 10) inner, narrow, low, longitudinal folds. Posterior esophagus with smooth inner surface. No detectable esophageal glands.

Stomach (Figs.278, 289-290) large, about half whorl in length, located half whorl posterior to pallial cavity; posterior half immersed in digestive gland. Esophagus insertion in posterior-left gastric extremity, as gradual enlargement, curved towards left. In this curve very small duct to digestive gland. Stomach, after this fist curve, abruptly expands becoming almost as wide as whorl; posteriorly narrowing, without clear separation with intestine. Main duct to digestive gland located in posterior-left-ventral surface of stomach. Stomach inner surface most smooth; pair of low, narrow folds runs on its dorsal surface (as continuation from esophagus), and curve towards posterior and run along gastric dorsal wall. Another tall and complex fold, as small chamber, located in posterior extremity of stomach, at some distance from esophageal insertion and close to smaller duct to digestive gland (Fig. 189). This tall fold with outer surface possessing 4-5 secondary folds, and smooth inner surface. Narrow fold, also initiated in esophageal insertion, running further posteriorly, lying anteriorly to posterior taller fold. No clear style sac. Intestine narrowing after leaving stomach, and abruptly curving towards right and runs parallel to gastric anterior wall. This curve located adjacent to pericardium, not possessing any special inner structure (like those of ampullariids). Intestine, then, curving towards anterior in middle gastric region, and lies parallel to its preceding loop on dorsal wall of posterior renal chamber (Figs.278, 290); then exiting to pallial cavity. Rectum narrow, running along ureter outer-dorsal wall. Anus described above.

Genital systeqa - ♂ (Figs.291-293): Testis pale green, lies on superior and columellar surface of visceral whorls, from first whorl to pallial cavity. Visceral vas deferens very narrow, running on columella and inferior-ventral margin of testis, with successive, very narrow branches from different portions of testis. In pallial cavity, vas deferens opening to large prostate gland (Fig.292), running along pallial cavity floor for about 1/3 of its length. Pallial vas deferens, after this distance, narrowing abruptly, becoming duct, curving towards left, penetrating into haemocoel integument. Remaining $^2/_3$ of vas deferens lies immersed in integument, surrounded by very thick, muscular walls in several layers, forming an ejaculatory duct. Ejaculatory duct bulging into haemocoel, displacing inner structures (as esophagus) towards left; its lumen small, closer to left side. Ejaculatory tube anteriorly with broader lumen and thinner muscular walls, abruptly narrowing, penetrating through right cephalic tentacle. Vas deferens runs all along right tentacle, its inner surface relatively broad, with some inner, longitudinal, low folds. Vas deferens opens in tentacle tip as broad papilla with rounded tip. Right tentacle possesses deep concavity located at right from genital papilla (Figs.291, 293). Papilla can retract into this concavity. 9 (Figs.294-295). Ovary greenish brown, located in same position as testis (Fig.277). Visceral oviduct very narrow, runs along columella. Pallial oviduct very large, occupying about half of pallial cavity space and also bulges posteriorly to last whorl of visceral mass, displacing kidney and intestine to left. Visceral oviduct making large loop and penetrating pallial oviduct dorsally, between posterior and middle third; connecting subterminally, forming small papilla inside narrow dorsal chamber. This dorsal chamber running posteriorly, continuous with ventral chamber. This dorsal chamber running to posterior end of pallial oviduct, abruptly curving ventrally and greatly increasing in size. Ventral chamber of pallial oviduct functioning as large brood pouch (although possessing some small capsules in final portion of dorsal chamber), walls thin, semi-transparent, smooth. Low and very thin fold running along dorsal-left side of entire ventral chamber, curved to right, starting close to dorsal chamber aperture, tapering posterior to genital pore. Ventral chamber (brood pouch) filled by about 20 capsules, size varying. Each capsule covered by transparent, heavy, horny membrane, filled by hyaline, yellow, jelly mass and young specimens of about 4 whorls. Vaginal tube with thick, muscular walls and some inner transverse folds, located as continuation from brood pouch. Female genital pore small, close to mantle border, with several inner folds.

Central nervous system (Figs.284) - Unlike preceding species, but similar to remainder caenogastropods, of epiathroid type, and located posterior to buccal mass. Statocysts with several statoliths. More details in *Viviparuscontectus.*

Distribution - Europe.

Habitat - No data beyond freshwater environment. Filterfeeding.

Material examined - HUNGARY - ALFÖLD: Canal Tápió, (circa 60km SE of Budapest), MZSP 29403, 1♂, 2$ (J.Hemmen leg).

Vwiparus contectus (Millet, 1813)

(Figs. 10, 42-43, 61-62, 141-142, 296-301, 348)

Vwiparus contectus – FALNIOWSKI, 1989:59 (key); FECHTER & FALKNER, 1993:119-119 (fig.7); ELEUTHERIADIS & DIMITRIADOU, 1995:41-52; FALNIOWSKI *et al.*, 1996; KATOH & RIBI, 1996:67-82.

Description

Shell (Figs. 10, 42-43, 61-62). Characters similar to those of *Viviparus acerosus*, differing in being broader, whorls shorter and more convex, and by paler color. Young specimens (from brood pouch) similar to those of preceding species (Figs.61-62).

Head-foot and operculum. Similar to *V. acerosus,* differing only in darker pigment.

Mantle organs (Fig.296). As *V. acerosus.*

Visceral mass. Closely similar to those of *V. acerosus,* except gonad and digestive gland almost same color (pale beige) and testis shorter (restricted to last visceral whorl posterior to stomach).

Circulatory and excretory systems - Similar to *Vwiparus acerosus.*

Digestive system (Fig.297) - Similar to *V. acerosus,* except for following features. Odontophore muscles: m2 pair with small portion of insertion also connected to lateral side of anterior esophagus; m7a, m10a pairs also present. Radular teeth similar to *V.* acerosus (Figs. 141-142), but differing in: rachidian slightly longer, with 9-11 cusps; lateral tooth with 8-11 cusps. Stomach with same folds (including tall posterior complex fold) and ducts to digestive gland.

Genital system - ♂ : Visceral and pallial structures similar to those of V. acerosus, including ejaculatory tube running in integument and modified right tentacle as penis. Differing only by shape of papilla of right tentacle tip (where vas deferens opens), being pointed and more elongated (Figs.298-299), with concavity at side of papilla deeper. ♀ : Visceral and pallial organs similar to those of *V. acerosus,* but with final region of visceral oviduct and dorsal chamber of pallial oviduct (Fig.301) shorter, and connection between both simpler. Also presenting papilla separating visceral oviduct from dorsal chamber of brood pouch. Additionally, dorsal chamber running directly towards posterior, increasing gradually. More capsules, about 30, in ventral chamber of pallial oviduct (brood pouch), chaotically organized.

Central nervous system (Fig.300, 348) - As in *V. acerosus.* But commissure between both cerebral ganglia relatively long. Supra and subesophageal ganglia located far from nerve ring. Each pair of connectives uniting cerebral-pleural ganglia with pedal ganglia "V"-shaped, with dorsal portion of each connective far from each other. Cerebral ganglia separated from each other, connected by a relatively long and wide commissure, form triangular, dorso-ventrally flat; lateral edge possessing ophthalmic nerve in anterior region and tentacular nerve in posterior region. Right pleural ganglion with about half of cerebral ganglion size, located at short distance ventral from it, right cerebro-pleural connective narrow, with length equivalent to half of pleural ganglion length; form elliptical. Left pleural ganglion somewhat diffuse, with borders not so clear; left cerebro-pleural connective length equivalent to that of right one, but wider. Pedal ganglia antero-posteriorly long, located deeply inside pedal musculature, close to each other and to median line; dorsal region long and narrow, middle region wider, with a projection directed to its pair, becoming unclear if this is ganglion or commissure (both pedal ganglia separated by a shallow transversal furrow), anterior possessing a median nerve and a lateral, broad anterior projection. Cerebro-pedal connective (cl) narrow and long, connecting anterior corner of cerebral ganglia (just ventral and anterior to ophthalmic nerve) with dorsal end of pedal ganglia. Pleuro-pedal connective (pn) about twice wider that cerebro-pleural connective, boundary with pleural ganglia unclear, looking like their continuation. Cerebro-pedal connectives ventrally close to pleuro-pedal connectives, gradually becoming far from them towards dorsal, inserting respectively in cerebral and pleural ganglia far from each other, with a distance equivalent to that of cerebral ganglia.

Measurements of shells (in mm) - MZSP 29402: 9 1, 32.7 by 26.2; ♂ 2, 34.5 by 25.7.

Distribution - Central Europe.

Material examined - HUNGARY - ALFÖLD: Canal Tápió (circa 60km SE of Budapest), MZSP 29402, 1♂, 49 (J.Hemmen col.)

Genus *Notopala* Cotton, 1935
Type: *Paludina hanleyi* Frauenfeld, 1864:339 OD

Notopala ampullaroides (Reeve, 1863)
(Figs.44-46, 63, 105-106, 143-144, 302-319, 349-352)

Synonymy see SMITH (1992).

Description

Shell (Figs.44-46, 63). Somewhat similar, but shorter than those of *Viviparus*, of about 5.5 whorls. Color pale brown. Adult with eroded apex. Sculpture series of spiral, somewhat uniform striae, disappearing on last whorl. Aperture rounded, prosocline, peristome white. Umbilicus narrow, located at middle of inner lip. Young specimen (found in brood pouch) (Fig.63) with up to 3.5 whorls; first whorl smooth, concave, dome-shaped; remainder of whorls almost smooth, with 3 equidistant spiral cords formed by successive small nodes, third cord located on periphery forming low carina.

Head-foot (Figs.302, 306, 315). Features similar to those of *Viviparus*, remarks following. Color dark grey, with some pale grey spots, sometimes coalescent. Food groove forming tall fold (Figs.302-303), appearing abruptly in posterior end of pallial cavity; left edge taller and curved inwards; right edge low and broad. Pedal furrow wider, occupying anterior half of foot edge.

Operculum (Fig.302). Characters similar to those of *Viviparus*, except for nucleus being almost central, slightly towards inner edge; sculpture concentric.

Mantle organs (Figs.304, 307). Organization and components similar to Viuiparus; distinctive features noted below. Mantle edge thick, smooth, color dark grey. Osphradium long and broad, located on ctenidial vein. Osphradium right edge with series of small and well-spaced projections. Ctenidial vein broad throughout. Gill filaments tall and slender, tip sharp pointed. Endostyle broad, also at right of gill.

Visceral mass (Figs.304-305). Similar to other viviparids, but slightly lower, about 2.5 whorls. Gonad occupying superior and columellar regions of each whorl. Color of both gonad and digestive gland greenish beige.

Circulatory and excretory systems (Figs.305) - Similar to *Viviparus*, remarks following. Heart large (about ¼ of posterior renal chamber volume); auricle broad, connected to ctenidial vein posteriorly. Anterior aorta about 3-times broader than posterior aorta. Heart and posterior kidney chambers connected with each other, pericardium membrane separating them lacking (Fig.305). Posterior kidney chamber without apparent glandular tissue, greatly compressed by intestinal loop and by posterior region of pallial oviduct in females. Anterior kidney chamber solid, somewhat long and flat; posterior surface (with posterior kidney chamber) concave, triangular, with small, tight pore located in anterior-right region; its surface with pallial cavity (left) concave and broad, anterior end rounded; its surface with ureter (right) convex, with similar form of surface with pallial cavity; nephrostome located in middle region of latter part, papilla-like, with muscular, slightly tall edges. Ureter (Figs.304-305, 307) and renal aperture as in *Viviparus*.

Digestive system - Most features similar to of for preceding viviparids; distinctive or remarkable characters following. Jaw plates thin, laterally located (Fig.310). Buccal mass dorsal folds tall and narrow, located close to median line. Aperture of salivary glands very small, close to median line, located in anterior end of dorsal folds. Odontophore muscles (Figs.308-309, 311-314): ma pair single, slightly thick; m2 pair with double insertion surrounding buccal ganglion; m4 insertion in tissue on radular ribbon preceding buccal cavity (to) by means of short and thin muscles; m7 pair very narrow; m7a pair well-developed, insertion with 2 branches running in opposite direction; m10 broad and thin; ml 1 pair thick and broad. Salivary glands long, slender and intensely convolute (Figs.308-309); located posterior to nerve ring; both narrowing and crossing through nerve ring dorsally. Radular features similar to those of preceding viviparids (Figs. 143-144). Salivary ducts immersed in dorsal wall of buccal mass in posterior-lateral region (just dorsal to buccal ganglia) and run immersed in dorsal folds. Anterior esophagus with pair of inner folds continuous with dorsal folds of buccal mass; gradually these folds unite with each other and run as single, broad fold, from distance equivalent to buccal mass length, abruptly disappearing. Posterior esophagus with irregular, narrow inner folds; posterior region slender. Middle and hindgut with characters similar to those of Viuiparus (Figs.305), notable features following. Esophageal insertion in stomach sub-terminal, on its lateral-ventral surface. Stomach broad and long, somewhat conic. Stomach inner surface mostly smooth; narrow and low transverse fold running in dorsal surface, at level of esophageal aperture; pair of narrow, low folds (origin in dorsal surface) at level of digestive gland duct; folds running opposed to each other, surrounding at some distance duct to digestive gland; both folds approach one another in ventral surface, running parallel along intestinal surface, disappearing gradually. Duct to digestive gland single, small, located in middle region of anterior half of ventral surface of stomach. Stomach-intestinal border unclear, stomach narrowing gradually up to right region of pericardium. Digestive gland greenish beige, of 1.5 whorls posterior to stomach, and about half whorl surrounding it. Intestine, rectum and anus as in Viuiparus.

Genital system - ♂: Similar to that of Viuiparus, remarkable features following. Testis large (Fig.317: pt), located in pallial cavity instead of visceral mass; lying along right edge of pallial cavity, bordering ureter; color beige, thick glandular walls. Pallial vas deferens originating short distance from posterior end of testis, in its ventral-left surface. Ejaculatory duct similar to those of preceding viviparids, immersed in integument (Fig.315), walls thick, with concentric muscles, bulging into haemocoel. Ejaculatory duct abruptly narrowing in base of right cephalic tentacle, walls becoming thinly muscular; it running along tentacle to its apex. Right (copulatory) cephalic tentacle base broad (Figs.315, 316), inner duct also broad; in middle level, both tentacle and inner duct abruptly narrows. Distal half of right tentacle strongly and irregularly curved towards left (Fig.316). 9 (Figs.318-319): Characters similar to those of Viuiparus, with following distinctive or notable features. Ovary greenish beige, located in columellar and superior regions of visceral whorls, from apex to posterior end of stomach (Fig.304). Visceral oviduct very narrow, running in middle region of columellar surface of visceral mass. Pallial oviduct very large, its posterior third encroaching into renal chamber. Albumen gland solid, running in left-posterior region of posterior third of pallial oviduct, surrounding rectum. Albumen gland narrowing anteriorly, becoming duct; with visceral oviduct inserting in this region. Albumen gland narrow, with walls thick, inner surface longitudinal folded; zigzagging just within posterior edge of pallial cavity, then running towards posterior. Short distance from albumen gland posterior end, abruptly becoming broader, running anteriorly. Capsule gland posterior third of pallial oviduct, dorsal to kidney, walls thickly-glandular, inner surface longitudinally folded; special broader furrow running in ventral-left inner surface. Brood pouch anterior 2/3 of last portion of pallial oviduct, walls thin, semi-transparent inner surface smooth. About 20-30 capsules, containing specimens from 1 to 4 whorls, larger specimens located anteriorly. Anterior end of pallial oviduct with narrow duct and muscular walls; finishing in low papilla. Female pore small, sub-terminal, ventral.

Central nervous system (Figs.306, 309, 349-352) - Located posterior to buccal mass. Cerebral ganglia flat and triangular; commissure between both cerebral ganglia (cc) with about $^1/_3$ of ganglia length, located in anterior region of ganglia medial edge; a pair of small nerves located in this commissure (Figs.350-351), running towards anterior; two pairs of broad nerves (lateral pair broader) running towards anterior, innervating dorsal-lateral surface of buccal mass (bn), these nerves as anterior vertex of ganglia; ophthalmic nerves (of) originating dorsally to these buccal mass nerves, running short distance, penetrating in ommatophores base orifice in haemocoelic surface; tentacular nerves (tn) about half-wide than ophthalmic nerves, originating in cerebral ganglia posteriorly and separated to them, running a short distance, penetrating into tentacles base. Pleural ganglia with about a third of cerebral ganglia size; both asymmetric, right ganglion (re) smaller than left (le) and possessing three nerves in anterior end, two running posteriorly (broader one as connective with visceral ganglion), and one running anteriorly; equivalent nerves inserted in left pleural ganglia in opposed side, close to connective with pedal ganglion. Connective between both cerebral and pleural ganglia (cn) very short, marked only by a single and abrupt curve in posterior vertex of cerebral ganglia. Connective between cerebral and pedal ganglia (cl) broad, separated from cerebro-pleural connectives, originated in anterior vertex, ventral to buccal mass nerves, length little shorter than cerebral ganglion length, inserting in posterior third of pedal ganglia. Pedal ganglia antero-posteriorly very long (about twice cerebral ganglia length), no clear border with pleural connective, running towards anterior penetrating in pedal musculature; pedal ganglia form similar to those of *Viviparus*, but shorter. Pedal commissure (uc) relatively long (about half of pedal ganglion width) and well discernible. Statocysts with about half size of pedal ganglia, located ventral and lateral to them, inside pedal musculature; internally several sand-like statoconia. Pair of visceral connectives (vc) very long (same length of haemocoel), relatively thick close to their insertion on pleural ganglia, narrowing gradually, becoming very narrow. Visceral ganglion (Fig.349: vi) relatively small, located in anterior edge of pericardium.

Measurements of shells (in mm) - AMS 202766 9 1: 26.7 by 23.2 (Figs.44-46); 9 2: 20.7 by 17.2; ♂3: 18.6 by 17.5.

Material examined - AUSTRALIA: North Australia; Northern Territory, Douglas R. crossing, 13°40.0'S 130°39.54'E, 1.5m depth, AMS 202766, 19 specimens (sta. 21437B; W.F.Ponder, C.Miller, D.L.Beechey and V.Kessner cols., 25/VI/1996).

Notopala essingtonensis (Frauenfeld, 1862)
(Figs.47-48, 51, 66, 145, 320-321)

Synonymy see STODDART (1982:169); SMITH (1992).

Description

Shell (Figs.47-48, 51, 66). Characters very similar to those of *N. ampullaroides*, distinctions following. Outline more elongated. Color pale green. Sculpture of 3 low, spiral, equidistant, dark threads per whorl; series of low, narrow spiral striae between threads. Umbilicus very narrow. Aperture almost circular slightly prosocline. Young specimen similar to that of preceding species (Fig.66). Other details in STODDART (1982).

Head-foot and operculum. Features similar to those described by *N. ampullaroides*, except for darker grey color.

Mantle organs (Fig.321). Similar to those of *N. ampullaroides*, except for somewhat broader gill filaments. Osphradium slightly longer and narrower, bearing more small projections along right edge.

Circulatory and excretory systems - As those described for *N. ampullaroides.*

Digestive system (Figs. 145) - Most features closely similar to those of *N. ampullaroides*. Although, m6 is slightly shorter (about 2/3 of cartilage length).

Genital system - cf (Fig.320): Posterior structures as described for *N. ampullaroides*, except for form of copulatory right cephalic tentacle, longer, narrowing gradually (slightly longer than left tentacle), with broad and low projection located in its middle-ventral surface. Copulatory tentacle inner duct broad in its base, abruptly narrowing, very slender along tentacle's length. 9 : No available female with well-preserved visceral region was available, precluding analysis of visceral and posterior pallial structures. All other structures apparently closely similar to those described for *N. ampullaroides.*

Central nervous system - Similar to that of *N. ampullaroides.*

Measurements of shells (in mm) - AMS 1535779 1: 27.1 by 20.8; cf 2: 22.9 by 18.6; ♂ 3: 23.6 by 18.5.

Distribution - Australia: Queensland, NT (SMITH, 1992).

Habitat - Lentic freshwater, lotic freshwater.

Material examined - AUSTRALIA - QUEENSLAND: Walkers Ck., 35 km south of Normanton, on Normanton-Karuba Rd., AMS 153577, 3♂, 39 (sta. 21169, D.F.McMichael col., 14/XII/1963).

Genus *Larina* A. Adams, 1854
Type: *L. strangei* A. Adams, M)

Larina cf strangei A. Adams, 1854
(Figs.50, 52-54, 146, 322-329

Possible synonymy - *Larina strangei* A.Adams, 1854:41 (pl.27, fig.3); PRASHAD, 1928:179; WENZ, 1938:705 (fig.2032).

Description

Shell (Figs.50, 52-54). Similar to those of *Notopala*. Distinctions following. Outline shorter and broader, somewhat discoid. Spire shorter, of 3 whorls; suture slightly deep. Color dark brown. Sculpture of irregular, spiral, low, narrow striae. Periostracum thick, smooth, except for 8 lines of periostracal hairs, each along spiral threads, clearer in young shells (Fig.50). Aperture rounded, prosocline (about 30° of longitudinal axis).

Head-foot (Fig.322). Similar to those of *Notopala*, except: foot slightly larger; color pale grey; pedal gland furrow lying along anterior half of foot edge.

Operculum (Figs.323-324). Almost circular. Outer sculpture concentric, low. Nucleus almost central, slightly towards middle level of inner edge. Inner scar occupying about ¼ of inner surface area, closer to inner edge.

Mantle organs (Fig. 325). Generally like those of *N. ampullaroides*, remarks including following. Osphradium slightly longer, also on ctenidial vein and possessing series of small projections along its right edge. Gill filaments with broader base, narrowing abruptly; their distal 2/3 long and filiform; apex narrow and rounded. Endostyle ridge-like, running along entire gill right margin. Ad-rectal sinus conspicuous.

Circulatory and excretory systems (Fig.326) - Morphological attributes similar to those of *Notopala* species, with similar absence of separation between pericardium and posterior renal chamber. Anterior renal lobe broader laterally, both pores, including muscular, papilla-like pore to ureter, similar to *Notopala*.

Visceral mass (Fig. 236) - Organization similar to preceding viviparids, but shorter, having only 1 whorl posterior to stomach. Gonad and digestive gland pale greenish beige.

Digestive system (Figs.326-327) - Foregut characters generally similar to those of *Notopala*. Jaw plates somewhat thicker. Aperture of salivary gland larger, disposed longitudinally in anterior half of buccal mass dorsal folds. Odontophore muscles: m2 pair also with double insertion surrounding buccal ganglia; m7 pair very narrow; m7a pair similar, with double branches (one running towards posterior and other anterior) in radular sac; m11 pair also broad. Radular teeth shown in Fig. 146. Salivary gland smaller, also convolute. Anterior esophagus slender; anterior region with pair of longitudinal folds (continuation from buccal mass dorsal folds), which gradually weaken and disappear. Middle and posterior esophagus also slender, inner surface covered by oblique, irregular, low, narrow folds. Middle and hindgut with similar features as those of *Notopala*, except for stomach having strong constriction in middle level of right surface, internally corresponding to thin gastric shield. Pair of ducts to digestive gland, located close together in ventral-anterior surface. Digestive gland with 2 incompletely separated lobes, one posterior and other ventral to stomach, each connected to duct from stomach. Rectum with elliptical fecal pellets, lacking any apparent organization.

Genital system - ♂ (Fig.322): Organization of posterior structures similar to those of *Notopala*, remarks following. Testis also pallial, lying on right of rectum. Ejaculatory tube also muscular, immersed in integument. Right cephalic copulatory tentacle about double left tentacle length, base twisted, narrowing gradually along its length; tip somewhat rounded and slightly broader than preceding region. Vas deferens very narrow throughout right tentacle. ♀ (Figs.326, 328-329): Visceral and pallial structures with similar features to those of *Notopala*. Albumen gland surrounding rectum behind pallial cavity. Albumen gland duct anterior and somewhat broad and thick. Visceral oviduct anterior end very narrow (Fig.328:vo), joining albumen gland duct as it exiting pallial cavity. Subsequently, albumen gland duct having long loop dorsal to ureter (about ¼ of brood pouch length), lies towards posterior, running close and at right from albumen gland and ventral to rectum. Capsule gland thick glandular walled, running about ¼ whorl in dorsal region of posterior renal chamber, twisting and lying towards anterior. Capsule gland inner surface with about 10 longitudinal, tall folds, its connection with brood pouch slightly narrow, at level of posterior region of pallial cavity. Brood pouch as for *Notopala*.

Central nervous system - Nerve ring similar to *Notopala*. Buccal ganglia large, located laterally to posterior region of buccal mass

Measurements of shells (in mm) - AMS 338590:

♀ 1: 16.0 by 16.0 (photo); ♀ 2: 16.4 by 16.2; ♂ 4: 8.7 by 9.1.

Distribution - Mid coastal Queensland.

Habitat - Under rocks and wood, in small to medium rivers (Ponder, person. communic.).

Material examined - AUSTRALIA - QUEENSLAND: Dawson R. nr. Theodore, on Taroom-Theodore Rd., 24°56.49'S 150°4.18'E, 0.01-0.1m depth. AMS 338590, 2♂, 139 (sta. 28911A; W.F.Ponder and D.Lindberg cols., 05/VII/1997).

Discussion – The present studied sample of *Larina* is not attributed with certainty to the species of the genus, with which it is very similar, pending a review of the taxonomy of the group (PONDER, personal communication). PRASHAD (1928) suggested that *Larina* is the only viviparid living in an estuarine environment, the others being freshwater, and had doubts about the familial placement of the genus, since the anatomy was unknown. Despite the imprecision of the identification of the present sample must be considered, *Larina* appears to be clearly similar to *Notopala*, and may belong to the same viviparid subgroup as that genus. See additional discussion on differences in the central nervous system in the character discussion section.

Superfamily Littorinoidea
Family Annulariidae
Genus *Annularia* Schumacher, 1817
Type-species: Turbo *lincina* Linné

Annularia sp.
(Figs.49, 55-56, 113-114, 147-149; 330-347)

Description

Shell (Figs.49, 55-56). Of small size (up to 15mm), tall, long, apex lost. Spire of about 3 whorls convex of somewhat same size. Sculpture successive axial threads, orthocline. Aperture rounded, with projected lips. Umbilicus narrow.

Head-foot (Figs.330-332, 336). Head broad, outstanding, color beige. Snout long and broad, slightly dorso-ventrally flattened; anterior margin plane, flat, with short lateral pointed expansions. Tentacles stubby and long (about same snout length). Ommatophores small, in outer side of their bases. Tentacles tip broad, rounded, brown pigmented. Foot relatively short, borders thick. Anterior furrow of pedal glands short. Another furrow runs in pedal sole along median line, from middle-ventral region of anterior furrow to posterior third of foot sole. Opercular pad large, lateral margins extending little beyond foot edges. Males with long penis located posterior removed and at right from head (described below). Columellar muscle thick, of $^2/_3$ whorl, with apparently 2 regions separated by low fold. Haemocoel narrow and long, anterior half with walls thick muscular, posterior half walls thin. Pair of narrow and thin ventral retractor muscles of snout, passing through nerve ring. Some secondary thin and narrow ventral pairs of retractor muscles present, attached to haemocoel inner surface. Diaphragm-like septum in limit between head-foot haemocoel and visceral mass, thin, scarcely muscular.

Operculum (Figs. 113-114). Sub-circular, thick, calcareous, palcispiral. Pale brown basal plate connected to opercular pad. White hard fold on spiral suture, protruded outside, margins irregularly broken.

Mantle organs (Figs.333, 337). Mantle border simple, smooth slightly thick. Some specimens (about 50%) with tall septa posterior to mantle border restricting pallial cavity aperture. Pallial cavity of about 1.5 whorls. Osphradium a small, low and long fold located in anterior-left corner of cavity. Similar sized glandular fold present at left of osphradium. Gill absent. Vessel net of lung somewhat sparse, intercalated branches of adrectal and left collar main vessels (circulation described below). Rectum very broad, sometimes occupying about half of cavity volume, replete of elliptical fecal pellets. Anus siphoned, small, located close to right margin of cavity posterior removed from mantle border. Pallial gonoducts run at right and dorsal to rectum (described below). Posterior limit of pallial cavity with pericardium (left) and kidney (right).

Visceral mass (Figs.243, 333). Of about 3 whorls, 2 first whorls most filled by digestive gland. Last whorl most occupied by stomach. Gonad relatively narrow, running in columellar surface.

Circulatory and excretory systems (Figs.335, 337) - Heart relatively small, located longitudinally in left limit of pallial cavity, part connected to columellar muscle. Auricle anterior, directly connected to left collar vessel. Adrectal vessel draining to kidney. Ventricle elliptical, posterior. Kidney divided into 2 regions. Posterior region a hollow chamber mostly filled by intestinal loops, loops connected to dorsal wall by mesentery. Posterior renal region with about half whorl. Anterior kidney region with about half of posterior region size, triangular, flat; entirely filled by folded renal tissue and separated from neighbor structure by membrane. Anterior renal region limited posteriorly by its posterior chamber, anteriorly by pallial cavity and at left by pericardium. Nephrostome a small slit in middle-dorsal region of membrane between kidney and pallial cavity. Renal lobe(s) and nephridial gland not distinguishable, probably mixed in that single folded mass. Renal tissue not connected to intestine, attached to dorsal wall of anterior kidney region and detached from ventral walls, this narrow space nephrostome connects with pallial cavity. Shallow and narrow urinary furrow starts ventral to nephrostome, in pallial cavity floor, runs edging left pallial structures, contours right insertion of mantle in head-foot and gradually faints towards ventral in short distance.

Digestive system - Mouth in center of anterior snout surface (Fig.336). Buccal mass large, half inside snout and half protruded in remainder haemocoel (Fig.336). Odontophore about $^2/_3$ of buccal mass volume. Jaw plates missing. Dorsal wall of buccal mass inner surface with pair of dorsal folds low and narrow. Aperture of salivary glands small longitudinal slits, located in median and anterior region of dorsal folds (Fig. 342). Between both dorsal folds shallow and smooth surface. Buccal mass and odontophore muscles (Figs.334, 338-341): ml) several small muscular fibers of jugal muscles, particularly more concentrated around posterior region of buccal mass, no pair outstanding; mj) peribuccal muscles with some layers of circular, oblique and longitudinal fibers mostly originated from outer surface of cartilages; m2) absent; m3) single thin and flat muscle in posterior-dorsal region of odontophore, insertion in both lateral ends; m4) pair similar to those of preceding species but constituted by single muscular mass (and not several pairs), origin in dorsal, ventral and ventral surfaces of odontophore cartilages, surround most of these cartilages tensioning subradular membrane (br) contour mj, insertion in tissue on radula preceding its exposed area (to); m5) thick and short, origin on m4 median-posterior outer surface, runs towards dorsal, insertion in radular sac dorsal surface; m6) horizontal muscle, short, thin, restrict to anterior, subterminal region of cartilages; m7) pair narrow, thin and long, origin in m4 ventral branch, runs towards posterior attached to subradular membrane on median line, in posterior level of odontophore connect with each other, insertion in single bundle inside radular sac region just posterior to odontophore; m9) pairs of narrow, superficial and flat muscles in dorsal-posterior region of odontophore just anterior to m3, origin lateral in superficial membrane of odontophore, run towards posterior and medial slightly perpendicular to m4 fibers, insertion on "to" just posterior to m4 insertion; m10) pair broad, slightly thin, origin in ventral region of mouth, run towards posterior, insertion in odontophore ventral and lateral surfaces; m11) absent; m14) pair of superficial ventral protractor muscles of odontophore, thin and flat, origin in ventral-anterior surface of snout inner wall, run towards posterior lying odontophore ventral surface, insertion in posterior-ventral end of odontophore. Odontophore cartilages (Fig.341) long, flat and slightly arched, anterior end somewhat bifid. Septum between esophagus and odontophore tall; in this region dorsal inner folds bifurcate, outer branch very short, inner branches run along esophagus. Radular teeth (Figs. 147-149): rachidian tooth tall and slightly barrow, outline triangular, cut-edge curved, cusps lacking, bluntly pointed tip, base broad and flat; lateral tooth tall, slender, outline slightly triangular, about as broad as rachidian, curved inwards, tip bluntly pointed, cusps lacking; inner marginal tooth narrow, tall, width about half of that of rachidian, uniform width along its length, base with longitudinal concavity where outer marginal tooth encases, tip broad, 4 stubby cusps in cut-edge of almost same size; outer marginal tooth broad, about twice rachidian width, base narrower than distal region, thicker reinforcement along inner edge, remainder middle and basal regions thin and flat, distal (cut) edge ample, about 50 long, slender, curved cusps which decrease gradually towards lateral. Salivary glands as 2 separated, slightly triangular masses (Fig.338) just posterior to nerve ring; their ducts somewhat broad and sinuous, run on dorsal surface of buccal mass through nerve ring, in short distance after nerve ring penetrate in dorsal wall, aperture above described. Esophagus long, broad, thin walled. Anterior esophagus with pair of low, longitudinal folds in a side (Fig.342). Posterior esophagus narrower, inner surface smooth. Stomach (Fig.343) very large and long (about 1 whorl length). Esophagus insertion in middle level of ventral-left (inferior) surface, single duct to digestive gland at right (superior) to esophagus insertion, relatively small. Gastric shield thin, elliptical, small, located dorsal and slightly anterior to esophagus insertion. Stomach inner surface most smooth, single longitudinal fold in left (inferior) surface, from esophagus insertion (slightly dorsal to it) to posterior gastric end. Stomach gradually narrows anteriorly, without clear separation with intestine and style sac. No style found. Digestive gland beige, covers some portions around stomach and about 1.5 whorls posterior to it. Intestine broad, with 3 loops anterior to stomach inside renal posterior chamber (Fig. 337). Fecal pellets formed in first intestinal loop. Rectum and anus above described.

Genital system - ♂ : Testis pale beige, long and very small, located in columellar surface of digestive gland first 1.5 whorls. Vas deferens very narrow, runs along ventral surface of stomach. Seminal vesicle intensely coiled (Fig. 344), starts about 1 whorl posterior to pallial cavity. Seminal vesicle abruptly finishes at some distance from pallial cavity, vas deferens becomes very narrow and runs towards right and anterior, at right from rectum. Prostate long and broad (Fig. 344), walls thick glandular, entirely closed (tubular). Prostate posterior end just in pallial cavity posterior limit. Prostate anterior end just posterior to anus, abruptly narrows and crosses to pallial cavity floor, runs short distance and penetrates in penis base. Penis (Figs.330, 331, 345) long, large, curved in base and apex, slightly flattened, length about same than that of pallial cavity. Muscular tissue present in anterior region of penis base connecting it with adjacent integument. Penis tip pointed. Penis duct very narrow, slightly coiled in basal half, simple in distal half, runs closer to lateral penis margin. $: Visceral organs Fig.343) similar located than respective structures of males, including very small and narrow gonad. Ovary color pale cream. Visceral oviduct (Figs.333, 347) with bulged portion of about ¼ whorl followed by another portion of ¼ whorl narrow and coiled, just posterior to pallial cavity. Albumen gland small, cylindrical, as thick pallial continuation of visceral oviduct. Capsule gland large, elliptical, broad, dorso-ventrally flattened, located dorsal to rectum, connected with middle level of pallial oviduct by narrow, subterminal duct. Vaginal tube, after capsule gland duct, gradually expands, part dorsal to rectum. Aperture a longitudinal slit turned to right, posterior to anus. Inner surface of vaginal tube thick, with pair of longitudinal folds.

Nervous system (Figs.346) - Of typical epiathroid fashion, supra esophageal ganglion far from nerve ring. Anterior pedal nerve very broad. Statocysts with single and large statolyth (Figs.334, 346).

N.B. - All examined specimens possess several small pearls along visceral mass, irregular in size, iridescent, most in larger blood sinus as renal chamber.

Measurements of shells (in mm) - MZSP 28273: 9 , 14.8 by 7.6; MZSP 28281, ♂ 1, 10.6 by 6.1; ♂ 2, 9.1 by 5.6.

Distribution - Full range unknown, but includes at least NE Mexico.

Habitat - Terrestrial, on dry vegetation.

Material examined - (R.Pinto-da-Rocha and S.Casari cols.) MEXICO - YUCATAN: Uxmal, MZSP 28266, 12 specimens, MZSP 28273, 3 specimens, MZSP 28275, 5 shells (25/IX/1996); near Blankanché Cave, MZSP 28281, 7 specimens (24/IX/1996).

Discussion - This unnamed species is very characteristic of the genus, however, a more precise identification was not possible because of the large number of species and the taxonomic confusion in the group. The generic placement of this species is based on the key to genera of HENDERSON & BARTSCH (1921:54). Although, it looks similar to *Choanopoma terecostatum* Thompson, 1966 (from Chiapas, Mexico) in shell and operculum characters, but differs in its shallower suture. Despite there being relatively comprehensive revisions of the Annulariidae (*e.g.*, BARTSCH, 1946), the anatomical knowledge of the group is still poor.

DISCySSION OF THE CHARACTERS

SHELL

1. Spire: 0= high (about 2 times aperture length); 1= low (ampullariids, cyclophorids, *Larina*); 2= planispiral (*Marisa*) (CI: 50; RI: 66; additive).

This character can be considered additive due to ontogeny, since *Marisa* presents a low spire during early development, as seen in protoconch. But when treated as non-additive nothing changes, neither in result or indices.

2. Periostracum: 0= thin; 1=thick/(viviparids) (CI: 100; RI: 100).

3. Suture: 0= deep; 1= shallow (plane) (*F. neritiniformis*, *A. megastoma*) (CI: 50; RI: 0)

4. Sculpture: 0= absent (smooth); 1= axial ridges (cyclophorids, *Annularia*) (CI: 50; RI: 66).

5. Determinate growth: 0= absent; 1= present (*Annularia*, cerithioideans) (CI: 100; RI: 100).

The shell characters (1-5) are little more than 3.5% of the characters. The shell is the main structure analyzed in most literature, and is the most accessible structure that the malacologist has for analysis. With this in mind, special attention was paid to searching for conchological characters, but most were deleted as autapomorphies. Of the 5 shell characters used, only 2 (characters 2 and 5) are non-homoplastic in this analysis.

The determinate growth (character 5), which became a non-architaenioglossan caenogastropods synapomorphy (node 7), was explored in detail by VERMEIJ & SIGNOR (1992). It consists of the formation of a differentiated peristome in the shell when the animal reaches the adult phase. Determinate growth is, however, also known in some Cyclophoroidea not included in this study.

OPERCULUM

6. Outline: 0= circular; 1= with an upper-inner projection(sub-pyriform) (ampullariids, viviparids) (CI: 50; RI: 80).

The plesiomorphic condition is that normally found in the vetigastropods, with rounded outline and multi- or paucispiral. Although somewhat circular, the ampullariids and viviparids have a modified outline, a projection in upper-inner quadrant. This is an apparent adaptation for fitting it tightly into the aperture, occluding this completely and hermetically.

7. Outer surface: 0= spiral; 1=concentric (ampullariids, viviparids, cyclophorids) (CI: 50; RI: 50).

The members of the three architaenioglossan families in the analysis modified the outer surface of the operculum from a spiral to a concentric growth pattern. This condition was apparently reverted in the remainder basal caenogastropods, in which the paucispiral operculum is the rule.

The concentric outer sculpture is also found, by convergence, in some other caenogastropods, such as some families of Cerithioidea, in Stromboidea and in all "higher" superfamilies.

8. Type: 0= corneus; 1= calcareous (cyclophorids, *Annularia*) (CI: 50; RI: 66).

The calcareous operculum is herein considered derived from the corneus one. This type resulted as a convergence between both terrestrial forms (cyclophorids and annulariids). However, calcareous opercula are known to occur in several outgroups, such as, *e.g.*, the vetigastropod Trochoidea (Trochidae = corneus; Turbinidae, Phasianellidae = calcareous). Moreover, the ampullariids have representatives (not included here) with calcareous operculum, as in genus *Pila* Röding, 1798.

HEAD-FOOT

9. Food groove: 0= absent; 1= present (viviparids) (CI: 100; RI: 100).

The food groove running on the head-foot, in the floor of the pallial cavity, is an adaptation for filter feeding. The groove runs close to the apex of the gill filaments and conducts mucus with particles towards the mouth, by means of cilia (COOK, 1949).

Amazingly similar food grooves are found convergently in other filter-feeding caenogastropods, such as struthiolariids (Stromboidea), vermetids (Cerithioidea) and calyptraeids (Calyptraeoidea). These taxa apparently lacking any close relationship. The viviparid food groove differs from those of the other filter-feeding groups in being taller, forming almost a carina, and in having a relation with the right siphon (or nuchal lobe). This latter structure conducts the food to the mouth.

10. Right siphon: 0= absent; 1= present (ampullariids); 2= with a fold to mouth (viviparids) (CI: 66; RI: 88; additive).

The additive optimization of this character is because of ontogeny, as very young viviparids (state 2), found inside the brood pouch, lack the fold to mouth. If this character is considered non-additive, the result is the same, but both indices change to 100.

11. Left siphon: 0= absent; 1= present (ampullariids, viviparids); 2= very long (*Marisa*, *P. crosseana*, *P. scalaris*, *P. curumim*, *P. lineata*, *P. bridgesi*, *P. sordida*, *P. canaliculata*) (CI: 40; RI: 75; additive).

The right and left siphons, also called nuchal lobes (PRASHAD, 1925; SCOTT, 1957) and pseudo-epipodia (PRASHAD, 1925), are prominent muscular flaps with the apparent function of controlling the water flow inside the pallial cavity. The left siphon is longer and works in the incurrent, and the right siphon in the excurrent flow (ANDREWS, 1965b).

In some ampullariids, the left siphon is very extensive, becoming sometimes twice as long as the shell. Its tip may be extended from the water surface, capturing air (PRASHAD, 1925:120; DEMIAN, 1965; pers.obs.). Their presence and length have also been considered by BERTHOLD (1991) and BIELER (1993, characters 37-38), and have been utilized for separating genera long ago (BINNEY, 1867:2).

Due to their similarity, the head-foot siphons of the ampullariids and viviparids were tentatively considered homologues. However, the siphons of both groups differ in some details of their bases, with the viviparids having the base divided by a median, tall fold (clearer in the right siphon). This fold is maybe an adaptation for conducting the food to the mouth, and is lacking or inconspicuous in the ampullariids. Considering the cladogram obtained in this analysis, the siphons should have arisen in node 4 and reverted in node 7. However, another equally parsimonious optimization exists, convergence between nodes 6 and 10 (viviparids and ampullariids respectively). The first hypothesis is shown in the cladogram.

The ampullariid and viviparid siphons are clearly a modification of the head-foot, which differentiates them from the siphons of the "higher" caenogastropods. In these groups, the siphons are clearly a modification of the pallial edge (ANDREWS, 1965b:86).

The character 11 was considered additive because the state 2 is potentially a state 1 modification. The tree is the same if the character was considered non-additive, the indices, however, change to CI: 50 and RI: 81.

12. Ommatophore in tentacles; 0= absent; 1= present (all species) (CI: 100; RI: 100).

The ommatophore is here defined as a secondary stalk for the eyes, positioning them away from the main axis of the cephalic tentacles. In the archaeogastropods, the ommatophore, when present, is normally located close to, but separated from the tentacle. In the architaenioglossans, as well as in the other caenogastropods that possess this structure, the ommatophore is part of the cephalic tentacle. Although, in the 2 basal branches (cyclophorids and ampullariids) the ommatophore is located on the tentacle base, while in the other caenogastropods it is located more distally.

13. Pedal furrow of pedal glands: 0= anterior margin only; 1= entire foot margin (*Neocyclotus prominulus*); 2= also along sole, on median line (*Annularia*) (CI: 100; RI: 100; non-additive).

Pedal glands are expected to be found in all gastropods. In the caenogastropods, beyond this, possess an additional furrow lying at anterior margin of the foot, into which the anterior mucus glands open. This furrow probably is used for spreading the mucus along the foot sole. Beyond this adaptation, 2 additional modifications to the foot furrow were detected, as noted above, resulting as autapomorphies.

14. Columellar muscle: 0= 1.5 whorls; 1= ¾ whorl (cyclophorids); 2= 1/3 whorl (ampullariids except *Marisa*) (CI: 100; RI: 100; non-additive).

See comments after character 17.

15. Columellar muscle number: 0= 2; 1=1 (all species) (CI: 100; RI: 100).

The single columellar muscle is a derived condition from the double one found in archaeogastropods. However, it is known that the state 1 is shared with a few members of the caenogastropod sister-taxon, the Heterobranchia.

16. Pair of snout tentacles: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

The snout tentacles are long projections of the lateral edges of the structure anterior surface, being almost as long as the cephalic tentacles. PRASHAD (1925) described them for *Pila*, calling them labial palps or anterior tentacles. These tentacles are a notable ampullariid synapomorphy, and have also been considered by BERTHOLD (1991) and BIELER (1993, character 1). Analogous structures are also found in some heterobranchs, such as the nudibranchs.

PALLIAL CAVITY

17. Pallial cavity length: 0= 1 whorl; 1= 1.5 whorls (viviparids); 2= less than ½ whorl (ampullariids except *Marisa*) (CI: 100; RI: 100; non-additive).

The viviparids, because of their filter-feeding adaptations, developed a very long pallial cavity (state 1). Most ampullariids (node 12), on the other hand, presents a very short cavity (state 2), maybe a consequence of the spherical shell. This shortness is also reflected in the columellar muscle length (character 14).

18. Osphradium form and type: 0= small, circular; 1= long, ridge-like (viviparids, *Annularia*, cerithioideans); 2= elliptical (ampullariids); ?= cyclophorids (CI: 100; RI: 100; non-additive).

The osphradium commonly found in the archaeogastropods and in the heterobranchs (which have it) is in form of a small node. This state was modified in the ingroup: the cyclophorids lost it; the ampullariids developed an elliptical, bipectinate fashion (state 2); while the viviparids, as well as the remaining caenogastropods, have a long, ridge-like osphradium (state 1).

19. Osphradium leaflets: 0= absent; 1= present (ampullariids); 2= small projections on right side only (*Notopala* spp, *Larina*) (CI: 100; RI: 100; non-additive).

20. Osphradium: 0= sessile; 1= on a stalk (*P. crosseana*, *P. bridgesi*, *P. sordida*, *P. canaliculata*, *A. megastoma*); 2= on ctenidial vein (*Notopala* spp, *Larina*) (CI: 66; RI: 85; non-additive).

The osphradium is a sensory organ of olfaction, important in aquatic species. In caenogastropods, particularly, this structure is normally complex and large if compared to those of other molluscs. In terrestrial forms, the osphradium is generally reduced *(e.g.*, annulariids), or missing *(e.g.*, cyclophorids). The vestigial osphradium of *Annularia* sp., despite its small proportions, is long, which suggests the tentative attribution to the state 1 in the character 18.

The osphradium of the ampullariids has been classified as bipectinate. Bipectinate osphradia are also found in other caenogastropods, such as, *e.g.*, cerithiids (Cerithioidea), strombids (Stromboidea), and "higher" caenogastropods (Calyptraeoidea, Naticoidea, Cypraeoidea, Tonnoidea, Neogastropoda), as I have observed. However, the ampullariid bipectinate osphradium is *a* quite different from these other caenogastropods in being located on a stalk, and in having a conspicuous longitudinal fold uniting both sides of the filaments. Those differences suggest that the bipectinate condition of the ampullariid osphradium may be due to convergence, and that this kind of modification, for increasing the surface of this sensory organ, may be a common feature among caenogastropods. Only the osphradium short length have been considered by BERTHOLD (1991) and BIELER (1993, character 2). PRASHAD (1925:95, 143) has described the osphradium of *Pila* and is a quite similar to the South American species studied here.

No vestige of an osphradium was found in the examined cyclophorids. This is the reason for putting question marks on the matrix in all osphradial characters of the cyclophorids. However, it is expected that additional studies on ontogeny, and on more species, will bring new revelations.

21. Gill: 0= present; 1= absent (cyclophorids, *Annularia*) (CI: 50; RI: 66).

The terrestrial, air-breading species, lost the gill. However, a vestige of its original blood supply, with an afferent vessel on the right and an efferent (homologue to the ctenidial) vessel on the left, is found in annulariids and cyclophorids. The collateral circulation between these 2 vessels is markedly increased, to form a lung.

22. Gill anterior end: 0= posterior from mantle border; 1= on mantle border (viviparids); ?= no gill (CI: 100; RI: 100).

23. Gill outline: 0= elliptical; 1= narrow and curved (ampullariids except *P.* curumtm) (CI: 50; RI: 85).

24. Gill filaments: 0= triangular; 1= rounded (P. *curumim*) (CI: 100; RI: 100).

25. Gill filament tip: 0= central; 1= at right (F. *neritiniformis*, P. *scalaris*. *P.* curumtm, P. lineata, *P. canaliculata, A. megastoma, Viviparus* spp., cerithioideans) (CI: 25; RI: 57).

The gill of the viviparids has an additional function beyond respiration, as it is also used for filter feeding. For this task, the viviparid gill obviously presents modifications, manly an enlargement of the total length and of the filaments. The ampullariid gill, on the other hand, due to the compression of the lung (which additionally helps in the respiration), is narrow, and normally curves around the lung sac. The unusual fashion of the ampullariid gill have been considered by BERTHOLD (1991) and BIELER (1993, character 4), and was described in more detail by PRASHAD (1925:96-98) for *Pila* and by LUTFY & DEMIAN (1965) for *Marisa cornuarietis*.

Once more, because of the absence of the structure in the terrestrial forms, the gill characters have been coded with a question mark on the matrix for the cyclophorids and annulariid.

26. Ctenidial vein: 0= single; 1= double (P. *lineata, P. sordida, P. canaliculata*) (CI: 33; RI: 0).

Beyond the development of the lung (see comments after character 29), the ctenidial vein of the above *Pomacea*, species is double in its middle and anterior parts.

27. Distance gill-rectum: 0= broad; 1= very close (*Pomacea spp, A. megastoma, F. neritiniformis*) (CI: 100; RI: 100).

28. Endostyle: 0= absent; 1= present at right of gill (viviparids) (CI: 100; RI: 100).

The name "endostyle" is used as an analogy to the structure in the Cephalochordata, and has been used in the literature on filter-feeding gastropods. The endostyle is an additional glandular ridge parallel to the gill, normally present in filter-feeding caenogastropods, such as struthiolariids (Stromboidea), turitellids-vermetids (Cerithioidea) and calyptraeids (Calyptraeoidea). In these taxa, the endostyle is different in being located along the left edge of the gill, and is apparently developed from a modification of the local mucus cells of the mantle. As the viviparids are filter-feeding animals, they also developed a glandular ridge, here called an endostyle (Fig.304: en). However, the viviparid endostyle is unlike those of above mentioned taxa in being located along the right edge of the gill (instead of in left side), and in being apparently developed from a modification of the gill filaments. This is suggested because of the location of the structure between the filaments and the afferent gill vessel, as well as the presence of successive septa in the endostyle, each one corresponding to a gill filament.

29. Lung sac: 0= absent; 1= present and short (ampullariids); 2= present and very long (*Marisa*) (CI: 100; RI: 100; additive).

It is intuitive to deduce the evolution of the gill-less pallial cavity of air-breading snails such as the cyclophorids and annulariids *(e.g.,* CEI, 1942). In fact the lung vessel present in both groups running on the left margin of the pallial cavity is probably homologous to the ctenidial vein, since it is located in a similar position and is connected to the auricle. However, the derivation of the net of lung vessels from the vessels and sinuses of the gill is still not clear. The pallial cavity of *Cyclophorus* (TIELECKE, 1940) is similar to the cyclophorids examined herein. Some studies on the pallial blood vessel circulation *(e.g.,* TIELECKE, 1940) shows that the circulation pattern in /. *tupy* and A. *blanchetiana* is normal for the family, and *N. prominulus* could present a derived condition. This species has the vessel homologous to the ctenidial vein running along the left edge of the lung inserting in the kidney, instead of the auricle.

The ampullariid lung differs from that in any other terrestrial gastropod, normally formed in the pallial cavity by the loss of the gill and an enlargement of the mantle vessels (see comments after character 21). The ampullariid lung is surrounded on the right by the gill and is restricted to the left region of the pallial cavity, posterior to the osphradium.

The ampullariid lung is a sac with muscular walls, its inner surface has a net of transverse brood vessels, protruding inside it. A pneumostome, with muscular edges, is the aperture of the lung sac, and is located in its anterior-left region, turned to the base of the left siphon. BERTHROLD (1991) noted that some ampullariids lack musculature surrounding the pneumostome, which may be the plesiomorphic condition, and this was considered by BIELER (1993) as character 36. The lung sac is a conspicuous synapomorphy present in all species of the family, and has also been considered by BERTHOLD (1991) and BIELER (1993, character 3).

The analysis of the morphology of the lung sac reveals that the blood inside its vessels came from the marginal vessel located along the anterior and left edges of the organ. The origin of this vessel is almost in the anterior end of the afferent ctenidial vessel, and afterwards, it crosses above the anterior region of the gill. This arrangement suggests that the lung sac afferent vessel may be derived from the afferent ctenidial vessel. Details of the histology of the lung are found in LUTFY & DEMIAN (1965). The blood situated in the lung sac vessels flows to the ctenidial vein, which supplies both, the gill and the lung (ANDREWS & LITTLE, 1972: fig.1d; this study). In some species (character 26), the ctenidial vein is duplicated in its anterior and middle regions, differentiating a lung efferent vessel. However, PRASHAD (1925) has described for *Pila* a totally duplicated vessel, *i.e.*, a pulmonary and ctenidial vein, wholly separated from the anterior region until they reach the auricle (see his figs. 10, 12, and fig. 1 of pl. 18). This condition is assumed to be the more derived state. The additional afferent vein of *Pomacea canaliculata* has been advocated as a development of a horizontal division of the efferent ctenidial vein (ANDREWS, 1965b). A study on the respiratory mechanism of an ampullariid (Marisa *cornuarietis*) was provided by DEMIAN (1965). BROOKS (1907) and BROOKS & MCGLONE (1908, pls. 1-7) have reported the embryological appearance of the ampullariid lung, and suggested an origin from the gill.

The long lung sac of *Marisa* is perhaps an adaptation to the planispiral shell, and is suggested that it has been derived from the short lung sac, present in other ampullariids. For this reason, the 3 states of character 29 are considered additive. However, nothing changes if the character is not considered additive. The lung of *Pomacea* has been regarded as more highly organized than that of other genera (ANDREWS, 1965b: 88), this is true in relation to *Marisa*, but this does not differentiate the genus from *Felipponea*, *Pomella* and *Asolene*; anyway, this character could be another basing the node 12.

30. Hypobranchial gland: 0= thick; 1= thin, inconspicuous (ampullariids, *Notopala spp.*, *Larina*, *Annularia*, cyclophorids) (CI: 33; RI: 33).

The hypobranchial gland is normally well developed in caenogastropods, particularly in aquatic taxa. However, most ingroup species have a thin, inconspicuous hypobranchial gland, practically represented only by the mantle mucosa. ANDREWS (1965b) demonstrated that hypobranchial gland is present in *Pomacea canaliculata*, but only distinguishable in sections, and is unusual in covering the rectum and genital ducts. Further studies are necessary to determine, though, if the caenogastropod hypobranchial gland is actually homologous to the hypobranchial gland of the archaeogastropods.

Cyclophorids have modified the hypobranchial gland for an accessory excretory gland (ANDREWS & LITTLE, 1972, 1982). This feature is commented in the character 44.

The basal gland, present in the base of the male penis shield of the ampullariids, has been referred to as hypobranchial gland. This nomenclature is not followed here because the gland is only present in the males. Additionally, nothing else suggests a homology of this gland with the ordinary hypobranchial gland, normally located between the gill and the rectum.

CIRCULATORY SYSTEM

31. Pericardium: 0= visceral and pallial; 1= also connected to pallial floor (ampullariids) (CI: 100; RI: 100).

32. Ampulla in anterior aorta: 0= absent; 1=present (ampullariids) (CI: 100; RI: 100).

The ampullariids have the two modifications in the heart explored in the characters 31 and 32. The ampulla at the origin of the anterior aorta (Figs. 154, 179:am) is of particular interest for future physiological studies. This structure is almost as large as the ventricle, differing by its thinner walls, and by its location just after the origin of the posterior aorta. The ampulla is a long known ampullariid feature *(e.g.,* PRASHAD, 1925: fig.10), and has also been taken into consideration by BERTHOLD (1991) and BIELER (1993, characters 5, 40).

The development of an ampulla have been advocated as an adaptation to accommodating the blood forced into the heart during the retraction of the animal into its shell (ANDREWS, 1965b).

33. Intestinal loop inside pericardium: 0= absent; 1= present (*Larina, Notopala spp.)* (CI: 100; RI: 100).

Normally there is a structural correlation between the pericardial cavity and the kidney cavity, particularly with the posterior renal chamber (when 2 chambers are present). The Australian viviparids *Notopala* and *Larina* are derived in have lost the membrane that separates both the pericardium and the posterior renal chamber. This state forms a wide cavity in which the heart and intestinal loops stay together.

EXCRETORY SYSTEM

34. Number of kidneys: 0=2; 1=1 (all species) (CI: 100; RI: 100).

Most archaeogastropods possess a pair of kidneys, as well as a pair of pericardial structures and pallial organs. The caenogastropods, on the other hand, lost totally the (post-torsional) right structures, including the kidney. However, it is known that the loss of the right structures is a derived condition shared with the heterobranchs, the caenogastropods sister-taxon, and also some sparse archaeogastropod taxa.

35. Renal tissue: 0= solid glandular mass in pallial cavity roof; 1 = solid glandular mass confined in a separated chamber (ampullariids); 2= a thin layer of gland and vessels (viviparids) (CI: 100; RI: 100; non-additive).

36. Renal lobes: 0= single: 1= 2 (all species) (CI: 100; RI: 100).

37. Intestinal loops in kidney chamber connected by a mesentery: 0= absent; 1= present (ampullariids, *Annularia*) (CI: 100; RI: 100).

The clear mesentery present in some ingroup species, connecting the intestinal loops inside the posterior renal chamber to its dorsal-right surface, is an interesting feature, mainly relative to the discussion of the coelomatic condition of molluscs, as it suggests a true coelom. BERTHOLD (1991) and BIELER (1993, character 18) have considered a "repeatedly coiled" intestine as an ampullariid feature, however, but did not mention an association with the kidney. On the other hand, BOUVIER (1888, figs.2, 7) BURNE (1898) and PRASHAD (1925) have reported the coiled intestine inside the renal chamber. The ampullariid kidney function has been investigated by LITTLE (1968), but no information on the function of the intestinal loops was reported.

38. Anterior septate chamber: 0= absent; 1=present, with two equal-sized series of septa (*Marisa*); 2= present, with two asymmetrical series of septa (remainder ampullariids) (CI: 100; RI: 100; additive).

The anterior chamber has been reported by BOUVIER (1888, fig.3) and PRASHAD (1925, fig.13), and was also considered by BERTHOLD (1991) and BIELER (1993, character 6). Some histological features of this kidney region are found in PRASHAD (1925:124).

The anterior chamber has been referred as "ureter" by some authors *(e.g.* THIENGO, 1987, fig.8). This terminology can suggest any homology with the ureter of the viviparids, however, based on investigations on the structure of viviparids (JOHANSSON, 1950), ANDREWS (1965b:88) have suggested that this hypothesis is not upheld. Another current name for the anterior renal chamber is "lamellar renal organ" (BURNE, 1898).

The additive optimization is based on ontogeny, since very young specimens of all ampullariids possesses state 1. However, nothing changes if the character was considered non-additive.

39. Connection between longitudinal fold of renal anterior chamber with nephrostome edge: 0= absent, 1= present (ampullariids, except *Marisa*) (CI: 100; RI: 100).

40. Nephrostome: 0= in middle region of membrane between kidney and pallial cavity; 1=close to posterior end of pallial cavity (cyclophorids); 2= inside ureter (viviparids); 3= connected by an anterior chamber (ampullariids) (CI: 100; RI: 100; non-additive).

The position of the nephrostome of the ampullariids has been shown and discussed by BURNE (1898).

41. Closed ureter: 0= absent; 1= present (viviparids) (CI: 100; RI: 100).

42. Communication between kidney and ureter; 0= absent; 1= an open pore (viviparids); 2= a muscular papilla (*Notopalaspp, Larina*) (CI: 100; RI: 100; additive).

43. Urinary gutter: 0= absent; 1= a furrow along right margin of pallial cavity and head (cyclophorids); 2= a fold along rectum and pallial gonoducts (ampullariids) (CI: 100; RI: 100; non-additive).

PRASHAD (1925), DEMIAN (1965) and LUTFY & DEMIAN (1965) have called the urinary gutter of ampullariids as "epitaenia".

44. Collar vessel: 0= inserted in kidney; 1 = inserted in auricle (*A. blanchetiana, I. inca*) (CI: 100; RI: 100).

The ingroup taxa are all non-marine gastropods. Adaptations to freshwater (ampullariids, viviparids) or terrestrial (cyclophorids, annulariids) environments certainly demand modifications of the kidney, because this organ must conserve electrolytes (freshwater forms) and water (terrestrial forms). These extra efforts, if compared with marine groups, certainly brings effects in the morphology. This has presumably resulted in the complexity of the ingroup kidneys, outlined in characters 35-44. Although the members of each ingroup family have similar kidney modifications, each family is very different from each other. All taxa have two chambers, a posterior, with intestinal loops and usually connected to pericardium, and another anterior, in pallial cavity. The cyclophorids differs in having the posterior chamber lacking visible glands, and an almost solid anterior chamber. The ampullariids have a dorsal renal lobe in the posterior chamber and the anterior chamber has two series of transverse glandular septae. The viviparids resemble the cyclophorid arrangement, but the anterior chamber is solid.

The urine transportation from the nephrostome to the exterior also involves further modifications. The ampullariids and the cyclophorids have a urinary gutter, formed by a fold running along the right edge of the pallial cavity, from the nephrostome to the region behind the head (character 43). The viviparids, on the other hand, developed a tubular ureter (character 41), which conducts the urine from the nephrostome to the region close to the mantle border; this ureter runs attached to the rectum and its pore is close to the anus.

Most of the ingroup kidney structures have obscure functions, and are an interesting area for further investigation. ANDREWS & LITTLE (1972) performed a discussion on of the excretory system of architaenioglossans, comparing their anatomy and physiology (their fig.6, p.410). The authors described a large hypobranchial gland in all examined species (no one from South America), composed by subepithelial tubular glands, secreting purines, phospholipids and mucus. Such a gland is absent, at least as a clear organ, in the examined species, except *Incidostoma tupy*, in which it is small and lies covered ventrally by posterior portion of rectum [Fig.262, middle-superior region, between rectum (rt)]. Further and wider discussion on the excretory strategies, in a comparative scenario, is provided by ANDREWS (*e.g.*, 1979, 1981).

DIGESTIVE SYSTEM

BUCCAL MASS

45. Jaws: 0= pair of small plates; 1= very large (ampullariids); 2= plated fused in median line (cyclophorids); 3= absent (*Annularia*) (CI: 100; RI: 100; non-additive).

The enlargement of the ampullariid jaws has been also considered by BERTHOLD (1991) and BIELER (1993, character 11).

46. Dorsal chamber of buccal mass: 0= deep; 1= shallow (*Annularia*, cerithioideans) (CI: 100; RI: 100).

47. Dorsal folds of buccal mass: 0= low, inconspicuous; 1= broad, tall (all species); 2= with transverse furrows (ampullariids) (CI: 100; RI: 100; additive).

anterior, and female pore larger, located between anus and ureter pore.

Visceral mass (Figs.277-278). Long, with about 4 whorls, approximately smaller than pallial cavity. Kidney anterior, with stomach and adjacent intestine just posterior to it. Gonad and digestive gland occupying about 2.5 whorls posterior to stomach. Gonad brown, located in columellar surface of each whorl. Digestive gland pale green. Details of each structure below.

Circulatory and excretory systems (Figs.278, 282) - Heart relatively small, located behind posterior-left region of pallial cavity, partly posterior to anterior lobe of kidney. Auricle connection with ctenidial vein just posterior to gill; possessing portion protruding anterior to this connection. Ventricle posterior to auricle, narrow connection between both. Kidney with two chambers and ureter. Anterior kidney chamber small, triangular in section, entirely filled by glandular tissue (having only small inner hollow portion close to nephrostome). Anterior kidney chamber with four almost plane surfaces: 1) posterior surface towards pericardium, with ventral, small, middle slit as reno-pericardial pore; 2) left with pallial cavity; 3) ventral right with ureter; 4) dorsal with mantle. Nephrostome an elliptical, small pore, without muscular edges, located in middle-posterior region of ventral-anterior surface of anterior renal chamber. Posterior renal chamber simple hollow sac filled by anterior region of stomach and intestinal loops. Ureter apparently specialization of broad adrectal sinus (Figs.278, 281), runs between rectum and oviduct (in females) or right pallial cavity edge (in males). Posterior end of ureter ventral to anterior renal chamber; anterior end in muscular, papilla-like ureter pore just posterior to anus (or just posterior to female pore). No special inner glands in ureter. No urinary gutter.

Digestive system - Buccal mass just posterior to mouth, extends slightly posterior to snout inside haemocoel (Fig.280). Mouth longitudinal, ventral. Jaw plates small, thin, outline elliptical (Fig.283). Dorsal folds broad, smooth and simple. Deep dorsal chamber between both dorsal folds, inner surface smooth. Odontophore and peribuccal muscles (Figs.284-288): mc, circulatory fibers of buccal sphincter, thick and broad; m1, several pairs of small muscular fibers connecting buccal mass outer surface with adjacent regions of haemocoel, no differentiated pair; mj, pair of jaw and peribuccal muscles, origin in odontophore cartilage lateral-anterior surface, insertion along dorsal wall of buccal mass just dorsal to jaws; m2, pair of retractor muscles of buccal mass (retractor of pharynx), origin in lateral inner surface of haemocoel posterior to buccal mass, run towards anterior, insertion in posterior-lateral surface of odontophore (Figs.284, 286), most part on membrane which covers odontophore and small part in m4; m4, pair of large ventral tensor muscle of radula and subradular membrane, origin in odontophore cartilages around mj, cover cartilages almost completely (only dorsal edge free), insertion in small lateral region of tissue on radular ribbon preceding buccal cavity (to), subradular membrane also connecting along lateral and anterior edges of m4, part of dorsal branch m4 of with weak fibers along it; m5, pair of dorsal tensor muscles of radula, originating on m4 posterior-lateral region, running medially covering m4, insertion along radular sac in region opposed to m4 insertion (each m5 does not connect with its pair); m6, horizontal muscle, similar to those of ampullariids, little shorter in length than cartilages; m7, narrow, long pair, origin in m4 dorsal branch at medial-posterior edge, run posteriorly on subradular membrane (br) inner surface fusing with each other, penetrating in radular sac, insertion along radular sac and radular nucleus (Figs.287, 288); m7a, pair of thick muscles, originating in ventral surface of haemocoel close to median line and in level just posterior to odontophore, run dorsally and, after, anteriorly attached to radular sac ventral surface, insertion in m5 anterior edge (Figs.285, 288); m9 absent; m10, pair of ventral protractor muscles of buccal mass, origin in ventral inner surface of mouth, run posteriorly on mc, insertion in ventral-anterior region of odontophore; m10a, paired continuation of m10, running close to median line and attached to membrane covering odontophore, insertion along this membrane in its medial-ventral-posterior region; m11, pair of long and relatively broad muscles, originating on haemocoel inner ventral surface in region posterior to odontophore, close to origin of m7a, running dorsally, penetrating in odontophore just anterior to radular sac, insertion along subradular membrane close to median line reducing anteriorly; m12, small pair of muscles similar to those of ampullariids, origin in lateral-anterior inner surface of m4 and br, running towards medial and dorsal, insertion shortly on cartilages anterior-outer surface close to m6 (Fig.287). Other odontophore structures: br, subradular membrane, similar to those of preceding species, cover inner surface of (and probably secretes) subradular cartilage, most inserted in lateral and anterior edges of m4, but also connects with radular sac (via m5 pair) and peribuccal epithelium (via mj); reinforcement of subradular membrane in its dorsal-middle region with posterior, "W"-shaped edge; oc, pair of odontophore cartilages, similar to those of preceding species, flat, outline elliptical; om, odontophore outer membrane, transparent, covering outer surfaces of odontophore, except narrow portion close to median line where is penetrated by radular sac, some muscles (m7, m7a, m11) and some nerves; to, tissue on radular ribbon preceding buccal cavity, length more or less equivalent to portion of radula passing through odontophore. Buccal ganglia located laterally, on each side of border of odontophore and dorsal wall of buccal mass, close and dorsal to m2 insertion. Salivary glands (Figs.280, 283, 284) clustering as single mass posterior to nerve ring (localized posterior to buccal mass) and as two narrow glandular masses through it. Salivary ducts as continuation from these two masses, run on dorsal wall of buccal mass outer surface, penetrating into wall just close to their apertures, in anterior extremities of dorsal folds, close to median line.

Radular sac about as long as buccal mass (Figs.284-286), radular sac surrounded by large blood sinus. Radular teeth (Figs. 139, 140): all teeth with similar shape, tall, as flat rod, tip rounded, curved inwards, bearing several small, sharp cusps. Rachidian shorterst tooth, with 7-9 cusps, central cusp about three times broader than neighboring cusps (but same length); lateral tooth with 7-9 cusps, central cusp terminal, about three times width of remaining cusps (but same length); inner marginal tooth similar to lateral tooth, slightly longer; outer marginal tooth similar to inner marginal tooth, differing only in uniformity of cusps (lack central differentiated cusp).

Esophagus relatively narrow and long. Anterior esophagus with pair of dorsal, broad, longitudinal folds (as continuation from dorsal folds of buccal mass), without pouches (Figs.283, 284). Middle esophagus with several (about 10) inner, narrow, low, longitudinal folds. Posterior esophagus with smooth inner surface. No detectable esophageal glands.

Stomach (Figs.278, 289-290) large, about half whorl in length, located half whorl posterior to pallial cavity; posterior half immersed in digestive gland. Esophagus insertion in posterior-left gastric extremity, as gradual enlargement, curved towards left. In this curve very small duct to digestive gland. Stomach, after this fist curve, abruptly expands becoming almost as wide as whorl; posteriorly narrowing, without clear separation with intestine. Main duct to digestive gland located in posterior-left-ventral surface of stomach. Stomach inner surface most smooth; pair of low, narrow folds runs on its dorsal surface (as continuation from esophagus), and curve towards posterior and run along gastric dorsal wall. Another tall and complex fold, as small chamber, located in posterior extremity of stomach, at some distance from esophageal insertion and close to smaller duct to digestive gland (Fig. 189). This tall fold with outer surface possessing 4-5 secondary folds, and smooth inner surface. Narrow fold, also initiated in esophageal insertion, running further posteriorly, lying anteriorly to posterior taller fold. No clear style sac. Intestine narrowing after leaving stomach, and abruptly curving towards right and runs parallel to gastric anterior wall. This curve located adjacent to pericardium, not possessing any special inner structure (like those of ampullariids). Intestine, then, curving towards anterior in middle gastric region, and lies parallel to its preceding loop on dorsal wall of posterior renal chamber (Figs.278, 290); then exiting to pallial cavity. Rectum narrow, running along ureter outer-dorsal wall. Anus described above.

Genital system - (Figs.291-293): Testis pale green, lies on superior and columellar surface of visceral whorls, from first whorl to pallial cavity. Visceral vas deferens very narrow, running on columella and inferior-ventral margin of testis, with successive, very narrow branches from different portions of testis. In pallial cavity, vas deferens opening to large prostate gland (Fig.292), running along pallial cavity floor for about 1/3 of its length. Pallial vas deferens, after this distance, narrowing abruptly, becoming duct, curving towards left, penetrating into haemocoel integument. Remaining $^{2}/_{3}$ of vas deferens lies immersed in integument, surrounded by very thick, muscular walls in several layers, forming an ejaculatory duct. Ejaculatory duct bulging into haemocoel, displacing inner structures (as esophagus) towards left; its lumen small, closer to left side. Ejaculatory tube anteriorly with broader lumen and thinner muscular walls, abruptly narrowing, penetrating through right cephalic tentacle. Vas deferens runs all along right tentacle, its inner surface relatively broad, with some inner, longitudinal, low folds. Vas deferens opens in tentacle tip as broad papilla with rounded tip. Right tentacle possesses deep concavity located at right from genital papilla (Figs.291, 293). Papilla can retract into this concavity. (Figs.294-295). Ovary greenish brown, located in same position as testis (Fig.277). Visceral oviduct very narrow, runs along columella. Pallial oviduct very large, occupying about half of pallial cavity space and also bulges posteriorly to last whorl of visceral mass, displacing kidney and intestine to left. Visceral oviduct making large loop and penetrating pallial oviduct dorsally, between posterior and middle third; connecting subterminally, forming small papilla inside narrow dorsal chamber. This dorsal chamber running posteriorly, continuous with ventral chamber. This dorsal chamber running to posterior end of pallial oviduct, abruptly curving ventrally and greatly increasing in size. Ventral chamber of pallial oviduct functioning as large brood pouch (although possessing some small capsules in final portion of dorsal chamber), walls thin, semi-transparent, smooth. Low and very thin fold running along dorsal-left side of entire ventral chamber, curved to right, starting close to dorsal chamber aperture, tapering posterior to genital pore. Ventral chamber (brood pouch) filled by about 20 capsules, size varying. Each capsule covered by transparent, heavy, horny membrane, filled by hyaline, yellow, jelly mass and young specimens of about 4 whorls. Vaginal tube with thick, muscular walls and some inner transverse folds, located as continuation from brood pouch. Female genital pore small, close to mantle border, with several inner folds.

Central nervous system (Figs.284) - Unlike preceding species, but similar to remainder caenogastropods, of epiathroid type, and located posterior to buccal mass. Statocysts with several statoliths. More details in *Viviparus contectus*.

Distribution - Europe.

Habitat - No data beyond freshwater environment. Filter feeding.

Material examined - HUNGARY - ALFÖLD: Canal Tápió, (circa 60km SE of Budapest), MZSP 29403, 1 , 2 (J.Hemmen leg).

Viviparus contectus (Millet, 1813)

(Figs. 10, 42-43, 61-62, 141-142, 296-301, 348)

Viviparus contectus - FALNIOWSKI, 1989:59 (key); FECHTER & FALKNER, 1993:119-119 (fig.7); ELEUTHERIADIS & DIMITRIADOU, 1995:41-52; FALNIOWSKI *et al.*, 1996; KATOH & RIBI, 1996:67-82.

Description

Shell (Figs. 10, 42-43, 61-62). Characters similar to those of *Viviparus acerosus*, differing in being broader, whorls shorter and more convex, and by paler color. Young specimens (from brood pouch) similar to those of preceding species (Figs.61-62).

Head-foot and operculum. Similar to V. acerosus, differing only in darker pigment.

Mantle organs (Fig.296). As *V. acerosus*.

Visceral mass. Closely similar to those of *V. acerosus*, except gonad and digestive gland almost same color (pale beige) and testis shorter (restricted to last visceral whorl posterior to stomach).

Circulatory and excretory systems - Similar to *Viviparus acerosus*.

Digestive system (Fig. 297) - Similar to *V. acerosus*, except for following features. Odontophore muscles: m2 pair with small portion of insertion also connected to lateral side of anterior esophagus; m7a, m10a pairs also present. Radular teeth similar to V. acerosus (Figs. 141-142), but differing in: rachidian slightly longer, with 9-11 cusps; lateral tooth with 8-11 cusps. Stomach with same folds (including tall posterior complex fold) and ducts to digestive gland.

Genital system - : Visceral and pallial structures similar to those of V. *acerosus*, including ejaculatory tube running in integument and modified right tentacle as penis. Differing only by shape of papilla of right tentacle tip (where vas deferens opens), being pointed and more elongated (Figs.298-299), with concavity at side of papilla deeper. $: Visceral and pallial organs similar to those of *V. acerosus*, but with final region of visceral oviduct and dorsal chamber of pallial oviduct (Fig.301) shorter, and connection between both simpler. Also presenting papilla separating visceral oviduct from dorsal chamber of brood pouch. Additionally, dorsal chamber running directly towards posterior, increasing gradually. More capsules, about 30, in ventral chamber of pallial oviduct (brood pouch), chaotically organized.

Central nervous system (Fig.300, 348) - As in *V. acerosus*. But commissure between both cerebral ganglia relatively long. Supra and subesophageal ganglia located far from nerve ring. Each pair of connectives uniting cerebral-pleural ganglia with pedal ganglia "V"-shaped, with dorsal portion of each connective far from each other. Cerebral ganglia separated from each other, connected by a relatively long and wide commissure, form triangular, dorso-ventrally flat; lateral edge possessing ophthalmic nerve in anterior region and tentacular nerve in posterior region. Right pleural ganglion with about half of cerebral ganglion size, located at short distance ventral from it, right cerebro-pleural connective narrow, with length equivalent to half of pleural ganglion length; form elliptical. Left pleural ganglion somewhat diffuse, with borders not so clear; left cerebro-pleural connective length equivalent to that of right one, but wider. Pedal ganglia antero-posteriorly long, located deeply inside pedal musculature, close to each other and to median line; dorsal region long and narrow, middle region wider, with a projection directed to its pair, becoming unclear if this is ganglion or commissure (both pedal ganglia separated by a shallow transversal furrow), anterior possessing a median nerve and a lateral, broad anterior projection. Cerebro-pedal connective (cl) narrow and long, connecting anterior corner of cerebral ganglia (just ventral and anterior to ophthalmic nerve) with dorsal end of pedal ganglia. Pleuro-pedal connective (pn) about twice wider that cerebro-pleural connective, boundary with pleural ganglia unclear, looking like their continuation. Cerebro-pedal connectives ventrally close to pleuro-pedal connectives, gradually becoming far from them towards dorsal, inserting respectively in cerebral and pleural ganglia far from each other, with a distance equivalent to that of cerebral ganglia.

Measurements of shells (in mm) - MZSP 29402: 1, 32.7 by 26.2; 2, 34.5 by 25.7.

Distribution - Central Europe.

Material examined - HUNGARY - ALFOLD: Canal Tápió (circa 60km SE of Budapest), MZSP 29402, 1 , 4 (J.Hemmen col.)

Genus *Notopala* Cotton, 1935

Type: *Paludina hanleyi* Frauenfeld, 1864:339 OD

Notopala ampullaroides (Reeve, 1863)

(Figs.44-46, 63, 105-106, 143-144, 302-319, 349-352)

Synonymy see SMITH (1992).

Description

Shell (Figs.44-46, 63). Somewhat similar, but shorter than those of *Viviparus*, of about 5.5 whorls. Color pale brown. Adult with eroded apex. Sculpture series of spiral, somewhat uniform striae, disappearing on last whorl. Aperture rounded, prosocline, peristome white. Umbilicus narrow, located at middle of inner lip. Young specimen (found in brood pouch) (Fig.63) with up to 3.5 whorls; first whorl smooth, concave, dome-shaped; remainder of whorls almost smooth, with 3 equidistant spiral cords formed by successive small nodes, third cord located on periphery forming low carina.

Head-foot (Figs.302, 306, 315). Features similar to those of Viuiparus, remarks following. Color dark grey, with some pale grey spots, sometimes coalescent. Food groove forming tall fold (Figs.302-303), appearing abruptly in posterior end of pallial cavity; left edge taller and curved inwards; right edge low and broad. Pedal furrow wider, occupying anterior half of foot edge.

Operculum (Fig.302). Characters similar to those of Viuiparus, except for nucleus being almost central, slightly towards inner edge; sculpture concentric.

Mantle organs (Figs.304, 307). Organization and components similar to Viuiparus; distinctive features noted below. Mantle edge thick, smooth, color dark grey. Osphradium long and broad, located on ctenidial vein. Osphradium right edge with series of small and well-spaced projections. Ctenidial vein broad throughout. Gill filaments tall and slender, tip sharp pointed. Endostyle broad, also at right of gill.

Visceral mass (Figs.304-305). Similar to other viviparids, but slightly lower, about 2.5 whorls. Gonad occupying superior and columellar regions of each whorl. Color of both gonad and digestive gland greenish beige.

Circulatory and excretory systems (Figs.305) - Similar to Viuiparus, remarks following. Heart large (about 1/4 of posterior renal chamber volume); auricle broad, connected to ctenidial vein posteriorly. Anterior aorta about 3-times broader than posterior aorta. Heart and posterior kidney chambers connected with each other, pericardium membrane separating them lacking (Fig.305). Posterior kidney chamber without apparent glandular tissue, greatly compressed by intestinal loop and by posterior region of pallial oviduct in females. Anterior kidney chamber solid, somewhat long and flat; posterior surface (with posterior kidney chamber) concave, triangular, with small, tight pore located in anterior-right region; its surface with pallial cavity (left) concave and broad, anterior end rounded; its surface with ureter (right) convex, with similar form of surface with pallial cavity; nephrostome located in middle region of latter part, papilla-like, with muscular, slightly tall edges. Ureter (Figs.304-305, 307) and renal aperture as in *Viviparus*.

Digestive system - Most features similar to of for preceding viviparids; distinctive or remarkable characters following. Jaw plates thin, laterally located (Fig.310). Buccal mass dorsal folds tall and narrow, located close to median line. Aperture of salivary glands very small, close to median line, located in anterior end of dorsal folds. Odontophore muscles (Figs.308-309, 311-314): ma pair single, slightly thick; m2 pair with double insertion surrounding buccal ganglion; m4 insertion in tissue on radular ribbon preceding buccal cavity (to) by means of short and thin muscles; m7 pair very narrow; m7a pair well-developed, insertion with 2 branches running in opposite direction; m10 broad and thin; m11 pair thick and broad. Salivary glands long, slender and intensely convolute (Figs.308-309); located posterior to nerve ring; both narrowing and crossing through nerve ring dorsally. Radular features similar to those of preceding viviparids (Figs. 143-144). Salivary ducts immersed in dorsal wall of buccal mass in posterior-lateral region (just dorsal to buccal ganglia) and run immersed in dorsal folds. Anterior esophagus with pair of inner folds continuous with dorsal folds of buccal mass; gradually these folds unite with each other and run as single, broad fold, from distance equivalent to buccal mass length, abruptly disappearing. Posterior esophagus with irregular, narrow inner folds; posterior region slender. Middle and hindgut with characters similar to those of *Viviparus* (Figs.305), notable features following. Esophageal insertion in stomach sub-terminal, on its lateral-ventral surface. Stomach broad and long, somewhat conic. Stomach inner surface mostly smooth; narrow and low transverse fold running in dorsal surface, at level of esophageal aperture; pair of narrow, low folds (origin in dorsal surface) at level of digestive gland duct; folds running opposed to each other, surrounding at some distance duct to digestive gland; both folds approach one another in ventral surface, running parallel along intestinal surface, disappearing gradually. Duct to digestive gland single, small, located in middle region of anterior half of ventral surface of stomach. Stomach-intestinal border unclear, stomach narrowing gradually up to right region of pericardium. Digestive gland greenish beige, of 1.5 whorls posterior to stomach, and about half whorl surrounding it. Intestine, rectum and anus as in *Viviparus*.

Genital system -   : Similar to that of Viuiparus, remarkable features following. Testis large (Fig.317: pt), located in pallial cavity instead of visceral mass; lying along right edge of pallial cavity, bordering ureter; color beige, thick glandular walls. Pallial vas deferens originating short distance from posterior end of testis, in its ventral-left surface. Ejaculatory duct similar to those of preceding viviparids, immersed in integument (Fig.315), walls thick, with concentric muscles, bulging into haemocoel. Ejaculatory duct abruptly narrowing in base of right cephalic tentacle, walls becoming thinly muscular; it running along tentacle to its apex. Right (copulatory) cephalic tentacle base broad (Figs.315, 316), inner duct also broad; in middle level, both tentacle and inner duct abruptly narrows. Distal half of right tentacle strongly and irregularly curved towards left (Fig.316).

(Figs.318-319): Characters similar to those of Viuiparus, with following distinctive or notable features. Ovary greenish beige, located in columellar and superior regions of visceral whorls, from apex to posterior end of stomach (Fig.304). Visceral oviduct very narrow, running in middle region of columellar surface of visceral mass. Pallial oviduct very large, its posterior third encroaching into renal chamber. Albumen gland solid, running in left-posterior region of posterior third of pallial oviduct, surrounding rectum. Albumen gland narrowing anteriorly, becoming duct; with visceral oviduct inserting in this region. Albumen gland narrow, with walls thick, inner surface longitudinal folded; zigzagging just within posterior edge of pallial cavity, then running towards posterior. Short distance from albumen gland posterior end, abruptly becoming broader, running anteriorly. Capsule gland posterior third of pallial oviduct, dorsal to kidney, walls thickly-glandular, inner surface longitudinally folded; special broader furrow running in ventral-left inner surface. Brood pouch anterior 2/3 of last portion of pallial oviduct, walls thin, semi-transparent inner surface smooth. About 20-30 capsules, containing specimens from 1 to 4 whorls, larger specimens located anteriorly. Anterior end of pallial oviduct with narrow duct and muscular walls; finishing in low papilla. Female pore small, sub-terminal, ventral.

Central nervous system (Figs.306, 309, 349-352) - Located posterior to buccal mass. Cerebral ganglia flat and triangular; commissure between both cerebral ganglia (cc) with about $^1/_3$ of ganglia length, located in anterior region of ganglia medial edge; a pair of small nerves located in this commissure (Figs.350-351), running towards anterior; two pairs of broad nerves (lateral pair broader) running towards anterior, innervating dorsal-lateral surface of buccal mass (bn), these nerves as anterior vertex of ganglia; ophthalmic nerves (of) originating dorsally to these buccal mass nerves, running short distance, penetrating in ommatophores base orifice in haemocoelic surface; tentacular nerves (tn) about half-wide than ophthalmic nerves, originating in cerebral ganglia posteriorly and separated to them, running a short distance, penetrating into tentacles base. Pleural ganglia with about a third of cerebral ganglia size; both asymmetric, right ganglion (re) smaller than left (le) and possessing three nerves in anterior end, two running posteriorly (broader one as connective with visceral ganglion), and one running anteriorly; equivalent nerves inserted in left pleural ganglia in opposed side, close to connective with pedal ganglion. Connective between both cerebral and pleural ganglia (cn) very short, marked only by a single and abrupt curve in posterior vertex of cerebral ganglia. Connective between cerebral and pedal ganglia (cl) broad, separated from cerebro-pleural connectives, originated in anterior vertex, ventral to buccal mass nerves, length little shorter than cerebral ganglion length, inserting in posterior third of pedal ganglia. Pedal ganglia antero-posteriorly very long (about twice cerebral ganglia length), no clear border with pleural connective, running towards anterior penetrating in pedal musculature; pedal ganglia form similar to those of *Viviparus*, but shorter. Pedal commissure (uc) relatively long (about half of pedal ganglion width) and well discernible. Statocysts with about half size of pedal ganglia, located ventral and lateral to them, inside pedal musculature; internally several sand-like statoconia. Pair of visceral connectives (vc) very long (same length of haemocoel), relatively thick close to their insertion on pleural ganglia, narrowing gradually, becoming very narrow. Visceral ganglion (Fig.349: vi) relatively small, located in anterior edge of pericardium.

Measurements of shells (in mm) - AMS 202766 9 1: 26.7 by 23.2 (Figs.44-46); 2: 20.7 by 17.2; ♂ 3: 18.6 by 17.5.

Material examined - AUSTRALIA: North Australia; Northern Territory, Douglas R. crossing, 13°40.0'S 130°39.54'E, 1.5m depth, AMS 202766, 19 specimens (sta. 21437B; W.F.Ponder, C.Miller, D.L.Beechey and V.Kessner cols., 25/VI/1996).

Notopala essingtonensis (Frauenfeld, 1862)
(Figs.47-48, 51, 66, 145, 320-321)

Synonymy see STODDART (1982:169); SMITH (1992).

Description

Shell (Figs.47-48, 51, 66). Characters very similar to those of *N. ampullaroides*, distinctions following. Outline more elongated. Color pale green. Sculpture of 3 low, spiral, equidistant, dark threads per whorl; series of low, narrow spiral striae between threads. Umbilicus very narrow. Aperture almost circular slightly prosocline. Young specimen similar to that of preceding species (Fig.66). Other details in STODDART (1982).

Head-foot and operculum. Features similar to those described by *N. ampullaroides*, except for darker grey color.

Mantle organs (Fig.321). Similar to those of *N. ampullaroides*, except for somewhat broader gill filaments. Osphradium slightly longer and narrower, bearing more small projections along right edge.

Circulatory and excretory systems - As those described for *N. ampullaroides*.

Digestive system (Figs. 145) - Most features closely similar to those of *N. ampullaroides*. Although, m6 is slightly shorter (about 2/3 of cartilage length).

Genital system - ♂ (Fig.320): Posterior structures as described for *N. ampullaroides*, except for form of copulatory right cephalic tentacle, longer, narrowing gradually (slightly longer than left tentacle), with broad and low projection located in its middle-ventral surface. Copulatory tentacle inner duct broad in its base, abruptly narrowing, very slender along tentacle's length. 9 : No available female with well-preserved visceral region was available, precluding analysis of visceral and posterior pallial structures. All other structures apparently closely similar to those described for *N. ampullaroides*.

Central nervous system - Similar to that of *N. ampullaroides*,

Measurements of shells (in mm) - AMS 1535779 1: 27.1 by 20.8; 2: 22.9 by 18.6; 3: 23.6 by 18.5.

Distribution - Australia: Queensland, NT (SMITH, 1992).

Habitat - Lentic freshwater, lotic freshwater.

Material examined - AUSTRALIA - QUEENSLAND: Walkers Ck., 35 km south of Normanton, on Normanton-Karuba Rd., AMS 153577, *3d*, 39 (sta. 21169, D.F.McMichael col., 14/XII/1963).

Genus *Larina* A. Adams, 1854
Type: *L. strangei* A. Adams, M)
Larina cf *strangei* A. Adams, 1854
(Figs.50, 52-54, 146, 322-329

Possible synonymy - *Larina strangei* A.Adams, 1854:41 (pl.27,fig.3); PRASHAD, 1928:179; WENZ, 1938:705 (fig.2032).

Description

Shell (Figs. 50, 52-54). Similar to those of *Notopala*. Distinctions following. Outline shorter and broader, somewhat discoid. Spire shorter, of 3 whorls; suture slightly deep. Color dark brown. Sculpture of irregular, spiral, low, narrow striae. Periostracum thick, smooth, except for 8 lines of periostracal hairs, each along spiral threads, clearer in young shells (Fig.50). Aperture rounded, prosocline (about 30° of longitudinal axis).

Head-foot (Fig.322). Similar to those of *Notopala*, except: foot slightly larger; color pale grey; pedal gland furrow lying along anterior half of foot edge.

Operculum (Figs.323-324). Almost circular. Outer sculpture concentric, low. Nucleus almost central, slightly towards middle level of inner edge. Inner scar occupying about ¼ of inner surface area, closer to inner edge.

Mantle organs (Fig.325). Generally like those of *N. ampullaroides*, remarks including following. Osphradium slightly longer, also on ctenidial vein and possessing series of small projections along its right edge. Gill filaments with broader base, narrowing abruptly; their distal 2/3 long and filiform; apex narrow and rounded. Endostyle ridge-like, running along entire gill right margin. Ad-rectal sinus conspicuous.

Circulatory and excretory systems (Fig.326) - Morphological attributes similar to those of *Notopala species*, with similar absence of separation between pericardium and posterior renal chamber. Anterior renal lobe broader laterally, both pores, including muscular, papilla-like pore to ureter, similar to *Notopala*.

Visceral mass (Fig.236) - Organization similar to preceding viviparids, but shorter, having only 1 whorl posterior to stomach. Gonad and digestive gland pale greenish beige.

Digestive system (Figs.326-327) - Foregut characters generally similar to those of *Notopala*. Jaw plates somewhat thicker. Aperture of salivary gland larger, disposed longitudinally in anterior half of buccal mass dorsal folds. Odontophore muscles: m2 pair also with double insertion surrounding buccal ganglia; m7 pair very narrow; m7a pair similar, with double branches (one running towards posterior and other anterior) in radular sac; m11 pair also broad. Radular teeth shown in Fig. 146. Salivary gland smaller, also convolute. Anterior esophagus slender; anterior region with pair of longitudinal folds (continuation from buccal mass dorsal folds), which gradually weaken and disappear. Middle and posterior esophagus also slender, inner surface covered by oblique, irregular, low, narrow folds. Middle and hindgut with similar features as those of *Notopala*, except for stomach having strong constriction in middle level of right surface, internally corresponding to thin gastric shield. Pair of ducts to digestive gland, located close together in ventral-anterior surface. Digestive gland with 2 incompletely separated lobes, one posterior and other ventral to stomach, each connected to duct from stomach. Rectum with elliptical fecal pellets, lacking any apparent organization.

Genital system - (Fig.322): Organization of posterior structures similar to those of *Notopala*, remarks following. Testis also pallial, lying on right of rectum. Ejaculatory tube also muscular, immersed in integument. Right cephalic copulatory tentacle about double left tentacle length, base twisted, narrowing gradually along its length; tip somewhat rounded and slightly broader than preceding region. Vas deferens very narrow throughout right tentacle. (Figs.326, 328-329): Visceral and pallial structures with similar features to those of *Notopala*. Albumen gland surrounding rectum behind pallial cavity. Albumen gland duct anterior and somewhat broad and thick. Visceral oviduct anterior end very narrow (Fig.328:vo), joining albumen gland duct as it exiting pallial cavity. Subsequently, albumen gland duct having long loop dorsal to ureter (about ¼ of brood pouch length), lies towards posterior, running close and at right from albumen gland and ventral to rectum. Capsule gland thick glandular walled, running about ¼ whorl in dorsal region of posterior renal chamber, twisting and lying towards anterior. Capsule gland inner surface with about 10 longitudinal, tall folds, its connection with brood pouch slightly narrow, at level of posterior region of pallial cavity. Brood pouch as for *Notopala*.

Central nervous system - Nerve ring similar to *Notopala*. Buccal ganglia large, located laterally to posterior region of buccal mass

Measurements of shells (in mm) - AMS 338590:

1: 16.0 by 16.0 (photo); 9 2: 16.4 by 16.2; 4: 8.7 by 9.1.

Distribution - Mid coastal Queensland.

Habitat - Under rocks and wood, in small to medium rivers (Ponder, person. communic.).

Material examined - AUSTRALIA - QUEENSLAND: Dawson R. nr. Theodore, on Taroom-Theodore Rd., 24°56.49'S 150°4.18'E, 0.01-0.1m depth. AMS 338590, 2 , 13 (sta. 2891 1A; W.F. Ponder and D.Lindberg cols., 05/VII/1997).

Discussion - The present studied sample of *Larina* is not attributed with certainty to the species of the genus, with which it is very similar, pending a review of the taxonomy of the group (PONDER, personal communication). PRASHAD (1928) suggested that *Larina* is the only viviparid living in an estuarine environment, the others being freshwater, and had doubts about the familial placement of the genus, since the anatomy was unknown. Despite the imprecision of the identification of the present sample must be considered, *Larina* appears to be clearly similar to *Notopala*, and may belong to the same viviparid subgroup as that genus. See additional discussion on differences in the central nervous system in the character discussion section.

Superfamily Littorinoidea
Family Annulariidae
Genus *Annularia* Schumacher, 1817

Type-species: Turbo lincina Linné

Annularia sp.

(Figs.49, 55-56, 113-114, 147-149; 330-347)

Description

Shell (Figs.49, 55-56). Of small size (up to 15mm), tall, long, apex lost. Spire of about 3 whorls convex of somewhat same size. Sculpture successive axial threads, orthocline. Aperture rounded, with projected lips. Umbilicus narrow.

Head-foot (Figs.330-332, 336). Head broad, outstanding, color beige. Snout long and broad, slightly dorso-ventrally flattened; anterior margin plane, flat, with short lateral pointed expansions. Tentacles stubby and long (about same snout length). Ommatophores small, in outer side of their bases. Tentacles tip broad, rounded, brown pigmented. Foot relatively short, borders thick. Anterior furrow of pedal glands short. Another furrow runs in pedal sole along median line, from middle-ventral region of anterior furrow to posterior third of foot sole. Opercular pad large, lateral margins extending little beyond foot edges. Males with long penis located posterior removed and at right from head (described below). Columellar muscle thick, of $^2/_3$ whorl, with apparently 2 regions separated by low fold. Haemocoel narrow and long, anterior half with walls thick muscular, posterior half walls thin. Pair of narrow and thin ventral retractor muscles of snout, passing through nerve ring. Some secondary thin and narrow ventral pairs of retractor muscles present, attached to haemocoel inner surface. Diaphragm-like septum in limit between head-foot haemocoel and visceral mass, thin, scarcely muscular.

Operculum (Figs. 113-114). Sub-circular, thick, calcareous, palcispiral. Pale brown basal plate connected to opercular pad. White hard fold on spiral suture, protruded outside, margins irregularly broken.

Mantle organs (Figs.333, 337). Mantle border simple, smooth slightly thick. Some specimens (about 50%) with tall septa posterior to mantle border restricting pallial cavity aperture. Pallial cavity of about 1.5 whorls. Osphradium a small, low and long fold located in anterior-left corner of cavity. Similar sized glandular fold present at left of osphradium. Gill absent. Vessel net of lung somewhat sparse, intercalated branches of adrectal and left collar main vessels (circulation described below). Rectum very broad, sometimes occupying about half of cavity volume, replete of elliptical fecal pellets. Anus siphoned, small, located close to right margin of cavity posterior removed from mantle border. Pallial gonoducts run at right and dorsal to rectum (described below). Posterior limit of pallial cavity with pericardium (left) and kidney (right).

Visceral mass (Figs.243, 333). Of about 3 whorls, 2 first whorls most filled by digestive gland. Last whorl most occupied by stomach. Gonad relatively narrow, running in columellar surface.

Circulatory and excretory systems (Figs.335, 337) - Heart relatively small, located longitudinally in left limit of pallial cavity, part connected to columellar muscle. Auricle anterior, directly connected to left collar vessel. Adrectal vessel draining to kidney. Ventricle elliptical, posterior. Kidney divided into 2 regions. Posterior region a hollow chamber mostly filled by intestinal loops, loops connected to dorsal wall by mesentery. Posterior renal region with about half whorl. Anterior kidney region with about half of posterior region size, triangular, flat; entirely filled by folded renal tissue and separated from neighbor structure by membrane. Anterior renal region limited posteriorly by its posterior chamber, anteriorly by pallial cavity and at left by pericardium. Nephrostome a small slit in middle-dorsal region of membrane between kidney and pallial cavity. Renal lobe(s) and nephridial gland not distinguishable, probably mixed in that single folded mass. Renal tissue not connected to intestine, attached to dorsal wall of anterior kidney region and detached from ventral walls, this narrow space nephrostome connects with pallial cavity. Shallow and narrow urinary furrow starts ventral to nephrostome, in pallial cavity floor, runs edging left pallial structures, contours right insertion of mantle in head-foot and gradually faints towards ventral in short distance.

Digestive system - Mouth in center of anterior snout surface (Fig.336). Buccal mass large, half inside snout and half protruded in remainder haemocoel (Fig.336). Odontophore about $^2/_3$ of buccal mass volume. Jaw plates missing. Dorsal wall of buccal mass inner surface with pair of dorsal folds low and narrow. Aperture of salivary glands small longitudinal slits, located in median and anterior region of dorsal folds (Fig. 342). Between both dorsal folds shallow and smooth surface. Buccal mass and odontophore muscles (Figs.334, 338-341): ml) several small muscular fibers of jugal muscles, particularly more concentrated around posterior region of buccal mass, no pair outstanding; mj) peribuccal muscles with some layers of circular, oblique and longitudinal fibers mostly originated from outer surface of cartilages; m2) absent; m3) single thin and flat muscle in posterior-dorsal region of odontophore, insertion in both lateral ends; m4) pair similar to those of preceding species but constituted by single muscular mass (and not several pairs), origin in dorsal, ventral and ventral surfaces of odontophore cartilages, surround most of these cartilages tensioning subradular membrane (br) contour mj, insertion in tissue on radula preceding its exposed area (to); m5) thick and short, origin on m4 median-posterior outer surface, runs towards dorsal, insertion in radular sac dorsal surface; m6) horizontal muscle, short, thin, restrict to anterior, subterminal region of cartilages; m7) pair narrow, thin and long, origin in m4 ventral branch, runs towards posterior attached to subradular membrane on median line, in posterior level of odontophore connect with each other, insertion in single bundle inside radular sac region just posterior to odontophore; m9) pairs of narrow, superficial and flat muscles in dorsal-posterior region of odontophore just anterior to m3, origin lateral in superficial membrane of odontophore, run towards posterior and medial slightly perpendicular to m4 fibers, insertion on "to" just posterior to m4 insertion; m10) pair broad, slightly thin, origin in ventral region of mouth, run towards posterior, insertion in odontophore ventral and lateral surfaces; m11) absent; m14) pair of superficial ventral protractor muscles of odontophore, thin and flat, origin in ventral-anterior surface of snout inner wall, run towards posterior lying odontophore ventral surface, insertion in posterior-ventral end of odontophore. Odontophore cartilages (Fig.341) long, flat and slightly arched, anterior end somewhat bifid. Septum between esophagus and odontophore tall; in this region dorsal inner folds bifurcate, outer branch very short, inner branches run along esophagus. Radular teeth (Figs. 147-149): rachidian tooth tall and slightly barrow, outline triangular, cut-edge curved, cusps lacking, bluntly pointed tip, base broad and flat; lateral tooth tall, slender, outline slightly triangular, about as broad as rachidian, curved inwards, tip bluntly pointed, cusps lacking; inner marginal tooth narrow, tall, width about half of that of rachidian, uniform width along its length, base with longitudinal concavity where outer marginal tooth encases, tip broad, 4 stubby cusps in cut-edge of almost same size; outer marginal tooth broad, about twice rachidian width, base narrower than distal region, thicker reinforcement along inner edge, remainder middle and basal regions thin and flat, distal (cut) edge ample, about 50 long, slender, curved cusps which decrease gradually towards lateral. Salivary glands as 2 separated, slightly triangular masses (Fig.338) just posterior to nerve ring; their ducts somewhat broad and sinuous, run on dorsal surface of buccal mass through nerve ring, in short distance after nerve ring penetrate in dorsal wall, aperture above described. Esophagus long, broad, thin walled. Anterior esophagus with pair of low, longitudinal folds in a side (Fig.342). Posterior esophagus narrower, inner surface smooth. Stomach (Fig. 343) very large and long (about 1 whorl length). Esophagus insertion in middle level of ventral-left (inferior) surface, single duct to digestive gland at right (superior) to esophagus insertion, relatively small. Gastric shield thin, elliptical, small, located dorsal and slightly anterior to esophagus insertion. Stomach inner surface most smooth, single longitudinal fold in left (inferior) surface, from esophagus insertion (slightly dorsal to it) to posterior gastric end. Stomach gradually narrows anteriorly, without clear separation with intestine and style sac. No style found. Digestive gland beige, covers some portions around stomach and about 1.5 whorls posterior to it. Intestine broad, with 3 loops anterior to stomach inside renal posterior chamber (Fig. 337). Fecal pellets formed in first intestinal loop. Rectum and anus above described.

Genital system – : Testis pale beige, long and very small, located in columellar surface of digestive gland first 1.5 whorls. Vas deferens very narrow, runs along ventral surface of stomach. Seminal vesicle intensely coiled (Fig. 344), starts about 1 whorl posterior to pallial cavity. Seminal vesicle abruptly finishes at some distance from pallial cavity, vas deferens becomes very narrow and runs towards right and anterior, at right from rectum. Prostate long and broad (Fig. 344), walls thick glandular, entirely closed (tubular). Prostate posterior end just in pallial cavity posterior limit. Prostate anterior end just posterior to anus, abruptly narrows and crosses to pallial cavity floor, runs short distance and penetrates in penis base. Penis (Figs.330, 331, 345) long, large, curved in base and apex, slightly flattened, length about same than that of pallial cavity. Muscular tissue present in anterior region of penis base connecting it with adjacent integument. Penis tip pointed. Penis duct very narrow, slightly coiled in basal half, simple in distal half, runs closer to lateral penis margin. 9 : Visceral organs Fig. 343) similar located than respective structures of males, including very small and narrow gonad. Ovary color pale cream. Visceral oviduct (Figs.333, 347) with bulged portion of about 1/4 whorl followed by another portion of 1/4 whorl narrow and coiled, just posterior to pallial cavity. Albumen gland small, cylindrical, as thick pallial continuation of visceral oviduct. Capsule gland large, elliptical, broad, dorso-ventrally flattened, located dorsal to rectum, connected with middle level of pallial oviduct by narrow, subterminal duct. Vaginal tube, after capsule gland duct, gradually expands, part dorsal to rectum. Aperture a longitudinal slit turned to right, posterior to anus. Inner surface of vaginal tube thick, with pair of longitudinal folds.

Nervous system (Figs.346) - Of typical epiathroid fashion, supra esophageal ganglion far from nerve ring. Anterior pedal nerve very broad. Statocysts with single and large statolyth (Figs.334, 346).

N.B. - All examined specimens possess several small pearls along visceral mass, irregular in size, iridescent, most in larger blood sinus as renal chamber.

Measurements of shells (in mm) - MZSP 28273: 9 , 14.8 by 7.6; MZSP 28281, 1, 10.6 by 6.1; 2, 9.1 by 5.6.

Distribution - Full range unknown, but includes at least NE Mexico.

Habitat - Terrestrial, on dry vegetation.

Material examined - (R.Pinto-da-Rocha and S.Casari cols.) MEXICO - YUCATAN: Uxmal, MZSP 28266, 12 specimens, MZSP 28273, 3 specimens, MZSP 28275, 5 shells (25/IX/1996); near Blankanché Cave, MZSP 28281, 7 specimens (24/IX/1996).

Discussion - This unnamed species is very characteristic of the genus, however, a more precise identification was not possible because of the large number of species and the taxonomic confusion in the group. The generic placement of this species is based on the key to genera of HENDERSON & BARTSCH (1921:54). Although, it looks similar to *Choanopoma terecostatum* Thompson, 1966 (from Chiapas, Mexico) in shell and operculum characters, but differs in its shallower suture. Despite there being relatively comprehensive revisions of the Annulariidae *(e.g.,* BARTSCH, 1946), the anatomical knowledge of the group is still poor.

DISCUSSION OF THE CHARACTERS

SHELL

1. Spire: 0= high (about 2 times aperture length); 1= low (ampullariids, cyclophorids, *Larina*); 2= planispiral (*Marisa*) (CI: 50; RI: 66; additive).

This character can be considered additive due to ontogeny, since *Marisa* presents a low spire during early development, as seen in protoconch. But when treated as non-additive nothing changes, neither in result or indices.

2. Periostracum: 0=thin; 1=thick/(viviparids) (CI: 100; RI: 100).

3. Suture: 0= deep; 1= shallow (plane) *(F. neritiniformis,A. megastoma)* (CI: 50; RI: 0)

4. Sculpture: 0= absent (smooth); 1= axial ridges (cyclophorids, *Annularia*) (CI: 50; RI: 66).

5. Determinate growth: 0= absent; 1= present (*Annularia*, cerithioideans) (CI: 100; RI: 100).

The shell characters (1-5) are little more than 3.5% of the characters. The shell is the main structure analyzed in most literature, and is the most accessible structure that the malacologist has for analysis. With this in mind, special attention was paid to searching for conchological characters, but most were deleted as autapomorphies. Of the 5 shell characters used, only 2 (characters 2 and 5) are non-homoplastic in this analysis.

The determinate growth (character 5), which became a non-architaenioglossan caenogastropods synapomorphy (node 7), was explored in detail by VERMEIJ & SIGNOR (1992). It consists of the formation of a differentiated peristome in the shell when the animal reaches the adult phase. Determinate growth is, however, also known in some Cyclophoroidea not included in this study.

OPERCULUM

6. Outline: 0= circular; 1= with an upper-inner projection(sub-pyriform) (ampullariids, viviparids) (CI: 50; RI: 80).

The plesiomorphic condition is that normally found in the vetigastropods, with rounded outline and multi- or paucispiral. Although somewhat circular, the ampullariids and viviparids have a modified outline, a projection in upper-inner quadrant. This is an apparent adaptation for fitting it tightly into the aperture, occluding this completely and hermetically.

7. Outer surface: 0= spiral; 1=concentric (ampullariids, viviparids, cyclophorids) (CI: 50; RI: 50).

The members of the three architaenioglossan families in the analysis modified the outer surface of the operculum from a spiral to a concentric growth pattern. This condition was apparently reverted in the remainder basal caenogastropods, in which the paucispiral operculum is the rule.

The concentric outer sculpture is also found, by convergence, in some other caenogastropods, such as some families of Cerithioidea, in Stromboidea and in all "higher" superfamilies.

8. Type: 0= corneus; 1= calcareous (cyclophorids, *Annularia*) (CI: 50;RI: 66).

The calcareous operculum is herein considered derived from the corneus one. This type resulted as a convergence between both terrestrial forms (cyclophorids and annulariids). However, calcareous opercula are known to occur in several outgroups, such as, *e.g.*, the vetigastropod Trochoidea (Trochidae = corneus; Turbinidae, Phasianellidae = calcareous). Moreover, the ampullariids have representatives (not included here) with calcareous operculum, as in genus *Pila* Röding, 1798.

HEAD-FOOT

9. Food groove: 0= absent; 1= present (viviparids) (CI: 100; RI: 100).

The food groove running on the head-foot, in the floor of the pallial cavity, is an adaptation for filter feeding. The groove runs close to the apex of the gill filaments and conducts mucus with particles towards the mouth, by means of cilia (COOK, 1949). Amazingly similar food grooves are found convergently in other filter-feeding caenogastropods, such as struthiolariids (Stromboidea), vermetids (Cerithioidea) and calyptraeids (Calyptraeoidea). These taxa apparently lacking any close relationship. The viviparid food groove differs from those of the other filter-feeding groups in being taller, forming almost a carina, and in having a relation with the right siphon (or nuchal lobe). This latter structure conducts the food to the mouth.

10. Right siphon: 0= absent; 1= present (ampullariids); 2= with a fold to mouth (viviparids) (CI: 66; RI: 88; additive).

The additive optimization of this character is because of ontogeny, as very young viviparids (state 2), found inside the brood pouch, lack the fold to mouth. If this character is considered non-additive, the result is the same, but both indices change to 100.

11. Left siphon: 0= absent; 1=present (ampullariids, viviparids); 2= very long (*Marisa, P. crosseana, P. scalaris, P. curumim, P. lineata, P. bridgesi, P. sordida, P. canaliculat* (CI: 40; RI: 75; additive).

The right and left siphons, also called nuchal lobes (PRASHAD, 1925; SCOTT, 1957) and pseudo-epipodia (PRASHAD, 1925), are prominent muscular flaps with the apparent function of controlling the water flow inside the pallial cavity. The left siphon is longer and works in the incurrent, and the right siphon in the excurrent flow (ANDREWS, 1965b).

In some ampullariids, the left siphon is very extensive, becoming sometimes twice as long as the shell. Its tip may be extended from the water surface, capturing air (PRASHAD, 1925:120; DEMIAN, 1965; pers.obs.). Their presence and length have also been considered by BERTHOLD (1991) and BIELER (1993, characters 37-38), and have been utilized for separating genera long ago (BINNEY, 1867:2).

Due to their similarity, the head-foot siphons of the ampullariids and viviparids were tentatively considered homologues. However, the siphons of both groups differ in some details of their bases, with the viviparids having the base divided by a median, tall fold (clearer in the right siphon). This fold is maybe an adaptation for conducting the food to the mouth, and is lacking or inconspicuous in the ampullariids. Considering the cladogram obtained in this analysis, the siphons should have arisen in node 4 and reverted in node 7. However, another equally parsimonious optimization exists, convergence between nodes 6 and 10 (viviparids and ampullariids respectively). The first hypothesis is shown in the cladogram.

The ampullariid and viviparid siphons are clearly a modification of the head-foot, which differentiates them from the siphons of the "higher" caenogastropods. In these groups, the siphons are clearly a modification of the pallial edge (ANDREWS, 1965b:86).

The character 11 was considered additive because the state 2 is potentially a state 1 modification. The tree is the same if the character was considered non-additive, the indices, however, change to CI: 50 and RI: 81.

12. Ommatophore in tentacles; 0= absent; 1= present (all species) (CI: 100; RI: 100).

The ommatophore is here defined as a secondary stalk for the eyes, positioning them away from the main axis of the cephalic tentacles. In the archaeogastropods, the ommatophore, when present, is normally located close to, but separated from the tentacle. In the architaenioglossans, as well as in the other caenogastropods that possess this structure, the ommatophore is part of the cephalic tentacle. Although, in the 2 basal branches (cyclophorids and ampullariids) the ommatophore is located on the tentacle base, while in the other caenogastropods it is located more distally.

13. Pedal furrow of pedal glands: 0= anterior margin only; 1 = entire foot margin (*Neocyclotus prominulus*); 2= also along sole, on median line (*Annularia*)(CI: 100; RI: 100; non-additive).

Pedal glands are expected to be found in all gastropods. In the caenogastropods, beyond this, possess an additional furrow lying at anterior margin of the foot, into which the anterior mucus glands open. This furrow probably is used for spreading the mucus along the foot sole. Beyond this adaptation, 2 additional modifications to the foot furrow were detected, as noted above, resulting as autapomorphies.

14. Columellar muscle: 0= 1.5 whorls; 1= % whorl (cyclophorids); 2= 1/3 whorl (ampullariids except *Marisa*) (CI: 100; RI: 100; non-additive).

See comments after character 17.

15. Columellar muscle number: 0= 2; 1=1 (all species) (CI: 100; RI: 100).

The single columellar muscle is a derived condition from the double one found in archaeogastropods. However, it is known that the state 1 is shared with a few members of the caenogastropod sister-taxon, the Heterobranchia.

16. Pair of snout tentacles: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

The snout tentacles are long projections of the lateral edges of the structure anterior surface, being almost as long as the cephalic tentacles. PRASHAD (1925) described them for *Pila*, calling them labial palps or anterior tentacles. These tentacles are a notable ampullariid synapomorphy, and have also been considered by BERTHOLD (1991) and BIELER (1993, character 1). Analogous structures are also found in some heterobranchs, such as the nudibranchs.

PALLIAL CAVITY

17. Pallial cavity length: 0= 1 whorl; 1= 1.5 whorls (viviparids); 2= less than ½ whorl (ampullariids except *Marisa*) (CI: 100; RI: 100; non-additive).

The viviparids, because of their filter-feeding adaptations, developed a very long pallial cavity (state 1). Most ampullariids (node 12), on the other hand, presents a very short cavity (state 2), maybe a consequence of the spherical shell. This shortness is also reflected in the columellar muscle length (character 14).

18. Osphradium form and type: 0= small, circular; 1= long, ridge-like (viviparids, *Annularia*, cerithioideans); 2= elliptical (ampullariids); ?= cyclophorids (CI: 100; RI: 100; non-additive).

The osphradium commonly found in the archaeogastropods and in the heterobranchs (which have it) is in form of a small node. This state was modified in the ingroup: the cyclophorids lost it; the ampullariids developed an elliptical, bipectinate fashion (state 2); while the viviparids, as well as the remaining caenogastropods, have a long, ridge-like osphradium (state 1).

19. Osphradium leaflets: 0= absent; 1= present (ampullariids); 2= small projections on right side only (*Notopala spp, Larina*) (CI: 100; RI: 100; non-additive).

20. Osphradium: 0= sessile; 1= on a stalk (*P. crosseana, P. bridgesi, P. sordida, P. canaliculata, A. megastoma*); 2= on ctenidial vein (*Notopala spp, Larina*) (CI: 66; RI: 85; non-additive).

The dorsal chamber (character 46) is located in the dorsal wall of the buccal mass, opposite the odontophore, and may be an adaptation to avoid radular auto-injury. It is particularly large in the archaeogastropods. In the caenogastropods, however, there are a pair of broad and somewhat tall folds (character 47), and the dorsal chamber is reduced. These states have been regarded as notable synapomorphies of the ingroup (*e.g.*, Fig. 160: df, dc). Heterobranchs, on the other hand, apparently lack both the folds and chamber, with the dorsal wall of the buccal mass more muscular and with the inner surface simpler. The dorsal folds had been also reported by PRASHAD (1925), and called a "buccal gland on the roof of the buccal cavity".

The additive optimization is based on ontogeny, since young specimens of ampullariids lack transverse furrows, acquiring them early in development. However, the result and indices are the same if the character is considered non-additive.

ODONTOPHORE

48. Mj: 0= diffuse; 1= 2 broad bands (all species) (CI: 100; RI: 100).

49. M1a: 0= absent; 1= present (cyclophorids) (CI: 100; RI: 100).

50. M1b: 0= absent; 1= double *(N. prominulus)*; 2= single mass *(A. blanchetiana, I. inca)* (CI: 100; RI: 100; non-additive).

51. M2 as pair of retractor muscles of buccal mass: 0= absent; 1= present (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

The m2 of the 3 above mentioned groups work as retractors of the buccal mass (retractor of "pharynx"). The pair is dissimilar to that called m2 of ampullariids, which is an abductor of the jaw plates, and is not considered homologous.

52. Ma: 0= absent; 1= present and single (cyclophorids); 2= multiple (ampullariids) (CI: 100; RI: 100; non-additive).

PRASHAD (1925, fig.4) described 3 pairs of here denominate 'ma' for *Pila*, calling them anterior dorsolateral muscles; while BROWN & BERTHOLD (1990), describing *Lanistes neritoides*, called madible adductors.

53. M3: 0= absent; 1= pair with dorso-ventral fibers *(N. prominulus)*; 2= single, with transverse (latero-lateral) fibers (P. *scalaris, P. curumim, P. lineata. P. bridgesi, P. sordida, Annularia)*; 3= both (H-fashion) (*Marisa, P. crosseana. F. neritiniformis, P. canaliculata, A. megastoma*) (CI: 60; RI: 80; non-additive).

An m3 is also present in *Pila*, according to PRASHAD (1925, fig.5), which he called "superficial muscles of the ventral surface of the buccal mass".

54. M4 pair: 0= composed by several muscles; 1= composed by 2 pairs of muscular layers surrounding odontophore cartilages (all species); 2= a single pair of large mass surrounding odontophore cartilages (viviparids; *Annularia*, cerithioideans) (CI: 100; RI: 100; additive).

The additive optimization is a try for testing if the large mass fashioned m4 is a modification (fusion) of the 2 layered m4 of 2 more basal branches. However, the result and indices do not change if the character was optimized as non-additive. This result is compatible with the suggestion, but further studies are surely necessary.

55. M4 connection with tissue on middle region of radula (to): 0= absent; 1= via m9 (ampullariids); 2= present (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100; non-additive).

Although in part of the viviparids (*Larina* and *Notopala*) a pair of m9 muscles is found (divided in some separated fibers), they have a connection between the m4 pair with the above referred tissue. Then, these species are coded in the state 2.

56. Ventral and dorsal branches of m4 pair: 0= not connected anteriorly; 1= connected anteriorly (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

57. Ventral tensor muscle of radula: 0= present; 1= very reduced (m11) (all species) (CI: 100; RI: 100).

58. Dorsal tensor muscle of radula: 0= weak; 1= strong (m4 + m5) (all species) (CI: 100; RI: 100).

59. M5 pair: 0= connected with odontophore cartilages; 1= on m4 (all species) (CI: 100; RI: 100).

60. M5 pair form: 0= short and broad; 1= long and thin (all species) (CI: 100; RI: 100).

61. M6: 0= edging most of medial surface of odontophore cartilages; 1= edging less than 2/3 of this surface (all species) (CI: 100; RI: 100).

62. M6: 0= narrow and thin; 1= broad and thick (all species) (CI: 100; RI: 100).

63. M7: 0= absent; 1= present (all species) (CI: 100; RI: 100).

64. M7a pair (inserted in m5): 0= absent; 1=present (*Viviparus* spp) (CI: 100; RI: 100).

65. M2 as abductor of jaw plates: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).
See comments after character 51.

66. Approximator muscles of cartilages: 0= present; 1= absent or part of m4 (all species) (CI: 100; RI: 100).

67. M9: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

68. M10 insertion in odontophore ventral surface: 0= posterior; 1= anterior (all species) (CI: 100; RI: 100).

69. M10a: 0= absent; 1= present (viviparids) (CI: 100; RI: 100).

70. M10c: 0= absent; 1= present (cyclophorids) (CI: 100; RI: 100).

71. M11: 0= broad, *as* ventral tensor muscle of radula; 1= narrow (all species) (CI: 100; RI: 100).

72. M12: 0= absent; 1= present (ampullariids, *Viviparus* spp, cerithioideans) (CI: 33; RI: 71).

73. M14: 0= absent; 1= present (*Annularia*) (CI: 100; RI: 100).

74. Number of main cartilages: 0= more than 1 pair; 1= single pair (all species) (CI: 100; RI: 100).

75. Pair of accessory cartilages: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

The odontophore muscles and structures are an important source of comparative data (characters 48-75). The architaenioglossans present an interesting link between the archaeogastropod and other caenogastropod odontophores in several characters. An example is the pair of m4 muscles. This muscle is the largest pair from the caenogastropod odontophore, surrounding almost the entire cartilages, and apparently works as the main tensor of the subradular membrane. Analyzing the archaeogastropod odontophore, nothing similar to m4 is found. Apparently, the caenogastropod m4 is a combination of several pairs of archaeogastropod muscles, such as the several pairs that connect the cartilages to the subradular membrane (character 54), and also the pairs that connect the anterior with the posterior cartilages (character 66). The two first branches of the caenogastropods, the Cyclophoroidea and the Ampullarioidea, have the m4, composed by two layers (m4 and m4a). This state is here interpreted as an intermediate step to a single-layered and thick m4, derived from several pairs of muscles.

The odontophore cartilages (character 74) are present, in general, as more than one pair in the archaeogastropods, mostly as two pairs (anterior and posterior pairs). However, all caenogastropods (including the architaenioglossans) have a single pair. This pair is homologue to the anterior pair of archaeogastropod cartilages, according to the analysis of some muscles, such as, *e.g.*, the horizontal muscle (m6).

A possible function of the muscles and odontophore is suggested elsewhere (SIMONE, 2001), the odontophore of the caenogastropods, including those of architaenioglossans, differs from the archaeogastropod and heterobranch odontophore in having no apparent gliding between the radula and the cartilages, provided, in those taxa, by the ventral and dorsal tensor muscles (characters 57, 58) working alternately. In the caenogastropods, the muscles apparently work pulling and stretching the subradular structures (membrane and cartilage) and the entire odontophore works grinding the food.

Most of the comparative analyses and the polarization of the odontophore characters (48-75) are based on comparisons with the archaeogastropods. Although some heterobranchs were examined, their odontophore apparently has other, still unclear, modifications, any comparative analysis is still premature.

The present discussion on odontophore features is still superficial. Further analysis will be done in the final stage of the project, when all caenogastropod superfamilies will be analyzed and each muscle will be discussed.

The ampullariids developed a secondary pair of thin cartilages (Figs.166-167:oa), this pair of cartilages is probably a modification of the subradular membrane. These cartilages connect the ventral and dorsal branches of the pair m4. Analyzing their location, it is clear that the secondary cartilages are new acquisitions. The cyclophorids have nothing uniting both referred branches of the m4, while the remainder caenogastropods (including viviparids) both branches are united with each other (character 55). PRASHAD (1925) performed a detailed study on the odontophore of *Pila globosa* and have described two pairs of cartilages. What he called "superior cartilages" are apparently what is called here subradular cartilage (*e.g.*, figs. 163, 286: sc). This structure is shown as very thick (his figs 6, 8, 9), but he referred to them as very thin in the text (PRASHAD 1925:102). Then, PRASHAD's "superior" cartilages are not related to the accessory cartilages described herein, suggesting that *Pila* lacks this attribute. He called the ordinary odontophore cartilages as "lateral" cartilages.

RADULA

76. Subradular cartilage: 0= narrow; 1= broad (all species) (CI: 100; RI: 100).

The subradular cartilage (sc) is most probably secreted by the subradular membrane (br), and is a transparent, chitinous pair of expansions of the radula, in buccal cavity. The subradular cartilage is a specialization of the cartilage that covers the inferior surface of the radular ribbon, which links the teeth.

The subradular cartilage is present in the archaeogastropods, but is narrow. In caenogastropods, the structure is broad, entirely covering the buccal surface of the subradular membrane that, otherwise, would be exposed directly to the buccal cavity, accessible to injuries. The heterobranchs apparently also have a broad subradular cartilage, but is sill unclear its state in the basal taxa.

77. Radular sac length: 0= long; 1= short (about same length of buccal mass) (ampullariids) (CI: 100; RI: 100).

The short length of the radula in ampullariids has also been considered by BERTHOLD (1991) and BIELER (1993, character 12).

78. Rachidian form: 0= narrow; 1= broad (ampullariids); 2= tall and curved (viviparids) (CI: 100; RI: 100; non-additive).

79. Rachidian cusps: 0= few (0-3); 1= multicuspid (ampullariids, viviparids, cerithioideans) (CI: 50; RI: 75).

80. Rachidian basal broad cusp pair: 0= absent; 1=present (ampullariids) (CI: 100; RI: 100).

81. Rachidian tip: 0= broad; 1= pointed *(A. blanchetiana; I. inca; Annularia)* (CI: 50; RI: 50).

82. Lateral teeth number: 0= several (about 5); 1= 1 (all species) (CI: 100; RI: 100).

83. Lateral teeth tip: 0= multicuspid; 1= 1-2 cusps (*A. megastoma, F. neritiniformis,* cyclophorids, Annularia) (CI: 25; RI: 40).

84. Lateral teeth shape: 0= different from rachidian; 1 = tip tends to be similar shaped to rachidian (all species) (CI: 100; RI: 100).

85. Marginal teeth number: 0= many (more than 10); 1= 2 (all species) (CI: 100; RI: 100).

86. Marginal teeth shape: 0= similar to each other; 1= different (all species) (CI: 100; RI: 100).

In the current literature, radular characters have generally been more important than those of the shell and operculum in comparative analyses. Several radular characters were in fact searched in present study, but they were eliminated because resulted as autapomorphies. Only the characters 77-86 are suitable, and were polarized mainly based on the analysis on the archaeogastropods. In those taxa, the typical radula is rhipidoglossate, with a central (rachidian), about 5 lateral, and many marginal teeth. Nearly all caenogastropods, however, have a taenioglossate radula (or a kind of radula derived from it), including the architaenioglossans. The taenioglossate radula has only 7 teeth per row: a central or rachidian, a pair of lateral, and two pairs of marginal teeth.

SALIVARY GLANDS

87. Aperture in dorsal wall of buccal mass: 0= middle; 1= anterior (viviparids, Annularia, cerithioideans) (CI: 100; RI: 100).

88. Salivary glands: 0= absent; 1= present as 2 separated masses (all species); 2= a single fused mass (ampullariids, *Annularia)* (CI: 66; RI: 88; additive).

The additive optimization of this character is based on ontogeny, since, as well as is known, the ontogeny of the salivary glands starts as 2 separated masses. The apparent fusion is normally due to enlargement. If the character was considered non-additive, nothing changes in the result, only the RI changes to 87.

89. Type: 0=glandular; 1= tubular (*Notopala* spp, *Larina*) (CI: 100; RI: 100).

Salivary glands are present in other classes of the mollusks, but there are several archaeogastropod taxa lacking them (SASAKI, 1998). The polarization of salivary glands characters (87-89) is mainly based on the archaeogastropods that possess them. The salivary glands are particularly well developed in caenogastropods. Additionally, they developed salivary ducts, a character also shared with heterobranchs.

The salivary aperture in the caenogastropods is distinct in opening generally in the anterior region of the dorsal folds of buccal mass (character 47), (character 87) in the taxa allocated after the node 5.

ESOPHAGUS

90. Position of esophagus origin: 0= in lateral-dorsal region of odontophore; 1= in its posterior region (all species) (CI: 100; RI: 100).

The typical shape of the archaeogastropod foregut is a "V", with the mouth at the base, and the arms are the odontophore and the esophagus respectively. This differs from the arrangement typically found in the caenogastropods, where the esophagus is more or less continuous with the buccal mass. In this case, the esophagus is inserted in the posterior-dorsal region of the odontophore. The caenogastropod fashion is considered derived, although appears to be shared with some heterobranchs.

91. Anterior esophagus: 0= with a pair of pouches; 1= a simple tube (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

92. Esophageal pouches: 0= a simple diverticulum; 1= covered with papillae (cyclophorids); 2= with a dorsal fold (ampullariids) (CI: 100; RI: 100; non-additive).

93. Special pair of blood vessels connected to esophageal pouches: 0= absent; 1= present (ampullariids, cyclophorids) (CI: 100; RI: 100).

The cyclophorids and the ampullariids have a pair of prominent pouches connected to the lateral surface of the anterior esophagus. Their inner surface connects with the adjacent esophageal cavity. Important branches of the anterior aorta irrigate both pouches. Something similar, but lacking the distinct blood vessels, is found in vetigastropods and neritimorphs, and other archaeogastropods (SASAKI, 1998: 150; pers.obs.). The presence of esophageal pouches is considered plesiomorphic, however, it is possible that they are not homologous structures, because they differ in several details as referred above. The esophageal pouches with demarcated esophageal gland have been considered by BERTHOLD (1991) and BIELER (1993, character 16). PRASHAD (1925: 109, fig.4) described short and rounded esophageal pouches for *Pila*, which differ from the species studied here. PRASHAD (1925:116, fig. 11) described the arterial system in the foregut in more detail, and showed a small pair of vessels irrigating the pouches.

94. Middle esophagus: 0= narrow; 1= bulging (ampullariids except Marisa); 2= very narrow (*Notopala* spp, *Larina*) (CI: 100; RI: 100; non-additive).

95. Esophageal insertion in stomach: 0= in posterior region; 1=in middle region (cyclophorids, *Annularia*, cerithioideans) (CI: 50; RI: 75).

The insertion of the esophagus in the posterior region of the stomach (state 0) is "U"-shaped, as happens in most archaeogastropods. The esophageal insertion in the middle region of the stomach (state 1) is apparently associated with gastric enlargement, and resulted in convergence between the cyclophorids (first branch) and the remainder of the basal caenogastropods (represented by node 7).

STOMACH

96. Gastric caecum: 0= developed; 1= small, only internal (*Viviparus* spp); 2= absent (remainder species) (CI: 66; RI: 50; additive).

A homologous structure to the archaeogastropod gastric caecum is not found in the ingroup species. However, the viviparids have a septum that surrounds a small chamber, and possesses a folded inner surface. This small chamber was initially interpreted as a caecum vestige (as denoted by the above states).

The gastric caecum was apparently lost in the caenogastropods and, if the small viviparid chamber is homologous to that, it is a reversion. Nevertheless, it is likely that this structure is a new viviparid acquisition. For testing this hypothesis, the character was considered additive. The result is the same if it was considered non-additive. Both indices, however, change to 100. This may be an indication that the *Viviparus* structure may be a new acquisition. PONDER & LINDBERG (1997) argue that gastric caecum is a vetigastropod apomorphy.

97. Stomach walls: 0= thin; 1= dorsal half muscular (Marisa, P. crosseana, P. *scalaris*, *F. neritiniformis*); 2= almost entirely muscular (remainder of ampullariids) (CI: 100; RI: 100; additive).

98. Stomach transverse muscular septum: 0= absent; 1= present (ampullariids); 2= bending inwards (P. *lineata*, *P. bridgesi*, *P. canaliculata*, *A. megastoma*) (CI: 66; RI: 90; additive).

The ampullariid stomach is unusual in being highly muscular (character 97), working as a gizzard. Additionally, the stomach developed a muscular transverse septum (character 98). This septum divides the stomach of most ampullariids into 2 chambers, a larger dorsal chamber with muscular walls, and a ventral chamber with thin walls, bearing the ducts to digestive gland. This septum is also present in the genus *Pila* (PRASHAD, 1925). The characters 97 and 98 are optimized as additive because of the ontogeny, since state 1 precedes 2 during development. The result is the same if both states were considered non-additive, only the RI of the character 98, changes from 90 to 85.

99. Gastric muscle: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

The gastric muscle, an ampullariid synapomorphy, is apparently reported for the first time. Its origin is in the shell columella, just posterior to that of the columellar muscle; and it runs dorsally and anteriorly, and penetrates the stomach wall just anterior to the ventral gastric chamber. After this, the gastric muscle fibers spread like a fan along the gastric muscular walls, and divide the stomach into esophageal and intestinal branches.

The gastric muscle is small in *Marisa*, and broad and thick in the remainder of the studied ampullariids. Nothing is known about its occurrence in other ampullariid genera, as it is not reported in the consulted literature.

The gastric muscle probably works as a base for the musculature of the gastric wall. But, further investigations are necessary to clarify the function of this muscle, as well as the remainder of the complex structures of the ampullariid stomach, some of which are explored in characters 97-99. The ampullariid stomach is a rich source of characters for comparative analysis, but has been poorly explored. BERTHOLD (1991) and BIELER (1993) considered only a single character (17): 2 median stomach grooves.

100. Ducts to digestive gland: 0= 2; 1= 1 (cyclophorids, *Annularia*, *Notopala* spp.); 2= several (ampullariids) (CI: 50; RI: 77; non-additive).

The plesiomorphic number of the ducts to the digestive gland, as shown by most archaeogastropods, is a pair. One of them is in the esophageal insertion, and the other in the stomach ventral surface, close to the intestinal origin. However, the number and location of the ducts are highly variable. A duct may reduce and even disappear (state 1). On the other hand, the duct may multiply, as in the case of the ampullariids (state 2). The analysis of the location of the several ducts to the digestive gland in the ampullariids suggests that they are derived from both original ducts, with both becoming close together on the ventral gastric surface. This is suggested because there are ducts turned both, anteriorly and posteriorly. Notwithstanding, it is possible that the esophageal duct could be missing, and all ducts are a result of the division of the gastric duct only. This could probably be resolved with further studies on ontogeny.

101. Style sac: 0= present; 1= absent (ampullariids, viviparids, cyclophorids) (CI: 50; RI: 50).

Despite the absence of a gastric style sac in the archaeogastropods (the main outgroups), its presence in the caenogastropods is regarded as plesiomorphic. This polarization is based on the presence of style sacs in other classes, notably the bivalves. Thus loss is assumed in the archaeogastropod taxa, as well as the architaenioglossans. Its presence in the remaining caenogastropods is interpreted as a reversion. On the other hand, it is possible that the caenogastropod style sac is an extraordinary convergence with those of bivalves.

INTESTINE

102. Intestinal loop close to kidney-pericardium region, in left part of visceral mass: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

103. Dorsal chamber of intestinal region close to pericardium: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

104. Ventral chamber of intestinal region close to pericardium: 0= absent; 1= simple (ampullariids); 2= complex (*P. lineata*, *P. canaliculata*, *A. megastoma*) (CI: 66; RI: 91; additive).

The ampullariids have an intestinal region near the pericardium, which contain 1 to several small, blind-sacs. Apparently the region is reported for the fist time. These chambers are disposed from longitudinally to transversally, and the aperture of each is normally turned proximally (contrary to the flow). Sometimes, the transverse chamber has its origin in the longitudinal chamber aperture. The term "complex" is used for that state with several small sub-chambers.

The formation and function of the intestinal chambers are unknown and interesting goal for further investigations.

PRASHAD (1925) have reported an intestinal "caecum" for *Pila globosa*, being a short blind sac in which he tried to find a crystalline style. Looking at his fig.2 (p.99) the topology of the caecum is comparable to the topology of the intestinal chambers, however, the aperture of this caecum is close to the stomach in his fig.7 of pl. 17. The homology of these structures remains unclear.

105. Intestinal loops in visceral mass: 0= several; 1= a single "S" (ampullariids, viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

106. Intestinal loops localization: 0= immerse in digestive gland; 1= free from digestive gland (ampullariids, viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

107. Intestinal loop in haemocoel: 0= present; 1= absent (all species) (CI: 100; RI: 100).

Unlike the archaeogastropods and heterobranchs, the caenogastropods tend towards a reduction of the midgut, in favor of the development of the foregut, even in herbivorous groups. Most archaeogastropods and heterobranchs have a several-looped intestine, mostly immersed in the digestive gland, then, in visceral mass. The caenogastropods, on the other hand, including the architaenioglossans, have the midgut "Z"-shaped (an angle is the stomach and the other the pericardial or renal loop. In the cases of several looped caenogastropod intestines, the loops are inside the kidney or in the pallial cavity.

The haemocoel of the caenogastropods is separated from the visceral cavity by a thin septum. This obstructs the passage of visceral structures, what does not happen in other gastropods. In some archaeogastropod groups, such as vetigastropods and neritimorphs, there is an intestinal loop almost touching the buccal mass. Nothing similar is found in the ingroup, however, SASAKI (1998: 151) considered the condition of ampullariids comparable to archaeogastropods.

108. Intestinal region passing through kidney: 0= with single or two loops; 1 = several looped (*P. scalaris, P. curumim, P. lineata, P. bridgesi, P. sordida, P. canaliculata, A. megastoma, Marisa*) (CI: 50; RI: 87).

The intestinal loops inside the renal chamber of the ampullariids are here apparently explored for comparative purposes for the first time. There is uniformity of the loops shape in samples of the same species, and there are conspicuous differences among species. Those differences certainly are useful for species distinction. Same ampullariids have complex renal intestinal loops that, besides their interest in systematics, are an interesting subject for further physiological analyses.

109. Fecal pellets: 0= absent; 1= present (all species) (CI: 100; RI: 100).

Fecal pellets were also explored as phylogenetic character by previous authors (PONDER & LINDBERG, 1997; SASAKI, 1998) and are also the goal of comparative studies (MOORE, 1931). In the present study, fecal pellets resulted as a notable synapomorphy of the Caenogastropoda, differing from the archaeogastropods and heterobranchs that, characteristically, have a single continuous fecal strip. Fecal pellets are also convergently found in some Polyplacophora and in amphibolids (Pulmonata) (PONDER & LINDBERG, 1997).

GENITAL SYSTEM

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110. Testis: 0= along visceral mass; 1= restrict to posterior region of visceral mass (cyclophorids) (CI: 100; RI: 100).

111. Seminal vesicle: 0= absent; 1= present (*Annularia*, cerithioideans) (CI: 100; RI: 100).

The seminal vesicle is a differentiated glandular portion of the anterior region of the visceral vas deferens, in general convolute and iridescent because of presence of spermatozoids. The vesicle is absent in the architaenioglossans, but remarkably present in remainder caenogastropods. PRASHAD (1925:127, fig.15) reported a "vesicula seminalis" for the ampullariid *Pila*, but of different fashion and topology, certainly a new acquisition.

112. Prostate: 0= absent; 1= present in pallial region (all species) (CI: 100; RI: 100).

The prostate is a broad glandular portion of the caenogastropod pallial vas deferens. The gland may be opened (a furrow), as in the cerithioideans, or closed (a tube), as in architaenioglossans and annulariids. The prostate gland most probably secretes the spermatophore. The prostate of the Australian viviparids (*Notopala, Larina*) is difficult to be seen because of the pallial positioned testis. According to the literature (*e.g.*, ANNANDALE & SEWELL, 1921), the prostate lies in the wall below the food groove and is actually difficult to be seen.

113. Pallial vas deferens: 0= a furrow; 1= partially closed (cyclophorids); 2= entirely closed (tubular) (ampullariids, viviparids, *Annularia*) (CI: 50; RI: 60; additive).

The vas deferens is mostly absent in archaeogastropods (except Neritimorpha), and highly modified in the heterobranchs (running free into haemocoel). Those facts in part preclude the analysis of the structure in the ingroup. However, the 3 states are presently aligned in a single ordered evolutionary trend based on the ontogeny, which the 3 states appear successively during the development of the state 3-bearing groups. The result is the same if they were optimized as non-additive, both indices, however, change to 66.

114. Vas deferens aperture: 0= in posterior end of pallial cavity; 1= in dorsal end of right cephalic tentacle (viviparids); 2= in penis tip (ampullariids, *Annularia*); 3= in penis base (cyclophorids) (CI: 75; RI: 85; non-additive).

The character has connection with the degree of closure of the pallial vas deferens, in such the states 0 and 1-2 are extremes (entire open and entire closed respectively), with the state 3 as intermediary.

115. Ejaculatory tube as a long muscular portion

of vas deferens immersed in integument, and protruding into pallial floor and haemocoel: 0= absent; 1= present (viviparids) (CI: 100; RI: 100).

116. Right cephalic tentacle modified as copulatory organ, with vas deferens running along it: 0= absent; 1= present (viviparids) (CI: 100; RI: 100).

117. Special cavity for retraction of right cephalic tentacle tip: 0= absent; 1= present (*Viviparus* spp) (CI: 100; RI: 100).

The characters 115-117 and the state 2 of the character 114 explore the modification of the male pallial genital structures of viviparids, which are very different from any other gastropod. The pallial vas deferens runs in the floor of the pallial cavity, immerse in the integument, mostly surrounded by thick muscular walls disposed concentrically in many layers, protruding into the haemocoel. The right cephalic tentacle is also modified as a copulatory organ, or a penis-like structure. Although this kind of modification of the right tentacle is convergently found in several cocculiniforms and some neritimorphs, the viviparid modification is unique in having a closed duct running along its inner region. Besides, several viviparid species have special features of the copulatory tentacle, which are characteristic of the species and genera, as explored in the character 117 and others that were autapomorphic.

118. Exophalic penis (behind right tentacle): 0= absent; 1= present (cyclophorids, *Annularia*) (CI: 50; RI: 66).

119. Papilla on exophalic penis tip: 0= absent; 1= simple (*N. prominulus*); 2= double (A. *blanchetiana*, *I. inca*) (CI: 100; RI: 100; non-additive).

The cyclophorid exophalic penis (characters 118-119) is extraordinarily similar in shape and location to the exophalic penis found in the higher caenogastropods, such as most mesogastropods and neogastropods. They are here considered homologues. But, according to the tree, the cyclophorid structure is convergent. More complex penises have been describes for other cyclophorids, having even retractile terminal papilla, *e.g.*, in *Murdochia pallidum* (MORTON, 1952).

The penis of annulariids is apparently homologous to those of higher caenogastropods. However, THOMPSON (1978) referred to the penis as of pallial origin and innerved by the left pleural ganglion.

120. Penis sac: 0= absent; 1= present, with abroad and short penis (ampullariids); 2= present, with a very long, convolute penis (P. *crosseana*, P. *canaliculata*, *A. megastoma)* (CI: 66; RI: 90; additive).

The ordered optimization is based on th ontogeny, since young specimens of taxa with state 2 penis have a state 1-like one. The result does not change if the character was considered non-additive, only the RI changes to 87.

121. Penis duct highly convolute: 0= no; 1= yes (P. *crosseana*, *A. megastoma*, P. *sordida*, P. *canaliculata*, P. *lineata*) (CI: 33; RI: 60).

122. Penis shield: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

123. Penis shield tip: 0= absent; 1= simple (ampullariids); 2= glandular (P. *curumim*, P. *lineata*, *P. bridgesi*, *P. sordida*, *P. canaliculata*, *A. megastoma)* (CI: 100; RI: 100; non-additive).

124. Penis shield middle region: 0= simple; 1=with a flap (ampullariids).

125. Penis shield middle-right gland: 0= absent; 1 = present (*Marisa*, F. *neritiniformis*, *P. curumim*, *P. lineata*, *P. bridgesi*, *P. sordida*, *P. canaliculata)* (CI: 25; RI: 57).

126. Penis shield gland in tip: 0= no gland; 1= far from middle flap (P. curumim, P. *lineata)*, 2= close to flap (P. canaliculata, *P. bridgesi*, *P. sordida*, *A. megastoma)* (CI: 100; RI: 100; non-additive).

Despite the fact the 3 states are considered non-additive, the position of the taxa on the tree suggests that they actually may be additive. If considered additive, nothing changes, neither in result or indices.

127. Penis shield base: 0= without gill; 1= with gill (*Marisa*, P. curumim, P. lineata, *P. bridgesi*, *A. megastoma)* (CI: 25; RI: 40).

The ampullariid modifications of the male pallial genital structures (characters 120-127) are unlike those of other gastropods. The pallial vas deferens runs along the right edge of the pallial cavity, along the side rectum, as it is found in other caenogastropods, however this is the only similarity. Close to the anus, the vas deferens crosses to a penis sac (character 120), which is half solid and half hollow. The hollow portion contains a convolute and slender penis. The penis may be shorter and broad, or very long, with a filiform apical region (character 120). The duct of the penis may or not be highly convolute (character 121). The penis is protruded protected by a special structure of the mantle border - the penis shield (characters 122-127). The penis shield is very large, sometimes more than half the volume of the pallial cavity. It is retracted inside this cavity, except during copulation. The penis shield is much more complex than the penis itself, and has several valuable characters for comparative analysis. Although most of the characters are autapomorphies in the present study, some of them are explored in the characters (123-127). Male genital characters have been also considered by BERTHOLD (1989, 1991) and BIELER (1993, characters 7, 48-58).

Maybe due to the invasion of freshwater (ampullariids and viviparids) and the terrestrial (cyclophorids) habitats, the architaenioglossans are highly modified in their male genital system. They possess highly specialized features not found in any other gastropod. On the other hand, no close correlation between these major groups is possible, showing that most probably these structures evolved independently.

BERTHOLD (1991) and BIELER (1993, characters 8-9) also considered two other male features as ampullariid synapomorphies: the presence of eupyrene and atypical sperm anchored by nurse cells, and reduction of the spermatophore.

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128. Pallial oviduct: 0= absent; 1= present and opened (a glandular furrow) (cerithioideans); 2= closed (a glandular tube) (ampullariids, viviparids, cyclophorids, *Annularia*) (CI: 66; RI: 0; additive).

The pallial oviduct is present in neritimorphs amongst the archaeogastropods, in all heterobranchs and all caenogastropods. Possibly it is an indicative of a close relationship among those three groups. Some archaeogastropods, however, have an inconspicuous furrow running from the female genital aperture (*e.g.*, cocculiniformians), which is an analogous the structure. In caenogastropods, the pallial oviduct can be open (as a furrow), this condition is found only in the cerithioideans; or closed (tubular), found in the other groups. It is suggested that the open condition is a step between the inconspicuous furrow and the closed state. Though, according to the tree, the open condition of the cerithioideans is a reversion. If the character was optimized as unordered, nothing changes in the result, but both indices become 100. The indices of the whole cladogram become the following: length: 249 (instead 252), CI: 77 (instead 76), RI: 91 (same).

129. Brood pouch: 0= absent; 1= present as part of oviduct (viviparids) (CI: 100; RI: 100).

The viviparid brood pouch (or uterus), contains capsules with young specimens from 1 to 4 whorls. These young specimens are born already well-formed, justifying the name of the type genus of the family.

130. Pallial oviduct localization: 0= in pallial floor; 1= entirely at right of rectum (all species) (CI: 100; RI: 100).

The position of the pallial oviduct in caenogastropods differentiates it from the pallial oviducts of other groups that possess this structure (the heterobranchs and neritiforms). In these groups, the pallial oviduct runs partially or totally in the pallial floor. Obviously, in several caenogastropods, when the pallial oviduct is mature, acquiring enormous proportions, a part of it also attaches to the floor of the cavity, but it always arises from the pallial roof.

131. Albumen gland: 0= absent; 1= loop of visceral oviduct (cyclophorids); 2: a compact mass (ampullariids); 3= a posterior glandular sac (*Notopala* spp, *Larina*) (CI: 100; RI: 100; non-additive).

The albumen glands of the different architaenioglossan taxa are doubtless not homologous. Most probably they are independent acquisitions from different portions of the pallial oviduct.

132. Bursa copulatrix: 0= absent; 1= present, connected to visceral oviduct (*N. prominulus*); 2= present, opening in pallial cavity (*A. blanchetiana*, *I. inca*) (CI: 100; RI: 100; non-additive).

The bursa copulatrix is unusual in the cyclophorids, in which (state 2) it opens directly to the pallial cavity. The pallial oviduct thus has two apertures: a posterior one (the bursa) and an anterior one (the capsule gland). The plesiomorphic condition of the bursa connected to the pallial oviduct and not directly connected to the pallial cavity is present in some cyclophorids, such as *Cyclophorus* perdue *tuba* (Tielecke, 1940), and *Cyclobrandia beauianus*(Petit) (THOMPSON, 1967). THOMPSON (1969) has reported a more variable condition of the bursa aperture, in a study on Mexican and Central American cyclophorids, which he also called a seminal receptacle.

133. Capsule gland: 0= absent; 1= present (all species); 2= with a complex, sometimes spiral inner duct (ampullariids) (CI: 100; RI: 100; additive).

The additive optimization is based on ontogeny. Young ampullariid specimens possess a very simple capsule gland duct. However, nothing changes if the character was considered unordered.

134. Inner blind-sac glandular chamber in capsule gland: 0= absent; 1=present (cyclophorids) (CI: 100; RI: 100).

Based on the morphological disparity and different localization, the capsule glands (character 133-134) of the different groups are possibly not homologous. The gland of the ampullariids is very large, and surrounds most structures of the pallial oviduct. Its duct is complex, sometimes spiral or with series of blind-sac, flat chambers. The gland of the cyclophorids is U-shaped, with a branch as a blind sac.

135. Female pore: 0= not developed (pallial oviduct absent or opened); 1= a slit (cyclophorids, *Annularia*); 2= a papilla (ampullariids, viviparids) (CI: 50; RI: 50).

The additive optimization is based on comparison, since state 2 appears to be a modification of state 1. The ontogeny also corroborates this optimization as I have observed in young specimens. However, nothing changes in the result or indices if the character was considered non-additive.

136. Vaginal tube: 0= absent; 1=origin in anterior end of pallial oviduct (ampullariids); 2= origin in middle level of pallial oviduct *(F. neritiniformis, P. bridgesi, P. sordida, A. megastoma)* (CI: 50; RI: 83; additive).

The vaginal tube is long and has thick-glandular walls. It runs parallel to the rectum and connects the capsule gland to the female pore. This happens in two different ways as mentioned above. The additive condition is based on the ontogeny as I have observed, because the species, that have state 2 in the mature stage have state 1 in immaturity. The result is the same if the character was considered non-additive, the single change is RI: 75.

The pallial oviduct structures have been referred here by names, based on the nomenclature found in the literature and on topology. However, there is no uniformity of the designations and there is few taxa studied on the function of each portion (ANDREWS, 1964, 1965a; PRINCE, 1967). The nomenclature employed here is thus provisional.

137. Brood strategy: 0= absent (eggs free); 1= inside pallial oviduct (viviparids); 2= a jelly mass laid out of water (ampullariids) (CI: 100; RI: 100; non-additive).

The reproductive strategies of the viviparids and ampullariids are unusual for gastropods. In the former, the viviparous strategy raising the name of the type genus (*Viviparus*) (see FALNIOWSKI et al., 1996). In the latter, the strategy is to fix the capsules out of the water, despite the aquatic condition.

CENTRAL NERVOUS SYSTEM

138. Nerve ring position: 0= surrounding mouth; 1= in middle level of buccal mass (ampullariids, cyclophorids); 2= posterior to buccal mass (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100; additive).

The nerve ring position in the archaeogastropods and heterobranchs is characteristically anterior to the buccal mass*. Notwithstanding, most caenogastropods have the nerve ring posterior to the buccal mass. In the ampullariids and cyclophorids, however, the position of the nerve ring is intermediate, *i.e.*, located in the middle level between the anterior and posterior ends of the buccal mass. According to the tree, the location of these two groups is intermediate between the plesiomorphic condition found in the outgroups (nerve ring anterior to buccal mass) and the apomorphic one of the remainder of the caenogastropods, viviparids included. The result shows the tendency to a posterior positioned nerve ring, present since the basal taxa.

The additive condition of the states is based on ontogeny. In caenogastropods the buccal mass arises posterior to the nerve ring, and gradually passes trough it during the development, positioning anterior to it (BALL *et al.*, 1997). However, if considered non-additive, the result and indices do not change.

139. Position of pleural ganglia: 0= close to pedal ganglia (hypoathroid); 1=close to cerebral ganglia (epiathroid) (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

140. Connective pedal-pleural ganglia: 0= very short; 1= long, separated from pedal-cerebral connective (viviparids); 2= long, running close to pedal-cerebral connective (*Annularia*, cerithioideans) (CI: 100; RI: 100; non-additive).

These characters (139-140) have correlations to the hypo- and epiathroid conditions of the nerve ring, explored by previous authors in comparative and phylogenetic studies (*e.g.*, HASZPRUNAR, 1988, PONDER & LINDBERG, 1997, 1998). HASZPRUNAR (1988:394-398) commented extensively about the subject and referred to the viviparid nerve ring as of dystenoid type, the same designation given by BOUVIER (1888) and ANNANDALE & SEWELL (1921:236). This type is hypoathroid on the left side and epiathroid on the right side (HASZPRUNAR, 1988:395, fig.3c).

The hypoathroid condition of the cyclophorids is a long known feature (TIELECKE, 1940, figs. 19-20). A similar condition is found in the ampullariids (BURNE, 1899; PRASHAD, 1925:fig.17).

The nerve ring of the viviparid species studied here, show that they can be considered as epiathroid, since both pleural ganglia are located close to the cerebral ganglia (Figs.349-352). However, unlike the normal fashion of the epiathroid nerve ring, present in the other caenogastropods, the viviparid pedal connectives to the other two pairs of ganglia are separated from one another in a V-shaped fashion (Figs.300, 348-352). In the normal epiathroid condition both pair of connectives run close and parallel to each another. However, the viviparid pedal ganglia are apparently modified in a long fashion (ANNANDALE & SEWELL, 1921: figs.8-9; FRETTER & GRAHAM, 1962, fig. 161), lacking clear boundaries. The pedal ganglia are apparently diffused along a wide length, becoming unclear where the pleuro-pedal connective and the anterior pedal nerve start. This fashion precludes the exact classification of the viviparid nerve ring.

Additionally, an interesting difference between the two groups of examined viviparids, *i.e.*, the European *Viviparus* and the Australian *Notopala-Larina*, was found. Like the other architaenioglossans, but unlike the higher caenogastropods, the cerebral commissure is distinct and relatively long, but the *Viviparus* fashion is longer than that of the *Notopala*, in such both cerebral ganglia are closer (Figs.348, 350:cc). The viviparid pedal ganglia are distinct in being antero-posteriorly long, but those of *Notopala* have a wider and more distinct pedal commissure than those of *Viviparus*. The connectives between the pedal ganglia with the other two pair of ganglia are shorter and broader in *Notopala* than in *Viviparus* species, but in both cases they are separated from each other dorsally, as referred above. In both viviparid groups the pedal ganglia have a dorsal narrow and long region in such connectives to the other two pairs of ganglia insert, this region is shorter in *Notopala* than in *Viviparus* species; this dorsal region is singular in confusing with the connectives, becoming difficult to interpret where is the division between the connectives and the ganglia.

Interpreting the cladogram obtained in the present study, the epiathroid condition of the nerve ring appeared at node 5, including the viviparids (character 139). However, the connectives apparently evolved in two different ways. These ways can be seen as steps of a single evolutionary trend, as also suggested by HASZPRUNAR (1988:395). This last hypothesis is explored in character 140. This character was optimized both, as additive or non-additive, and nothing changed in the result or in the indices.

BERTHOLD (1991) and BIELER (1993) have considered other nerve ring attributes as ampullariid synapomorphies, such as presence of pleurosupraintestinal zygosis, subintestinal ganglion fused with right pleural ganglion, presence of pleural commissure, and pedal and pleural ganglia fused on both sides (BIELER, 1993, characters 19-22).

141. Statocysts: 0= with several statoconia; 1= with single statolith (*Annularia*)(CI: 100; RI: 100).

Although state 1 resulted as an Annularia autapomorphy, it is a state found in many higher caenogastropods. Thus, the character is maintained and will be used in future comparisons.

142. Buccal ganglia: 0= close to nerve ring; 1= separated, far from nerve ring (all species) (CI: 100; RI: 100).

143. Buccal ganglia position: 0= close to median line; 1= lateral (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

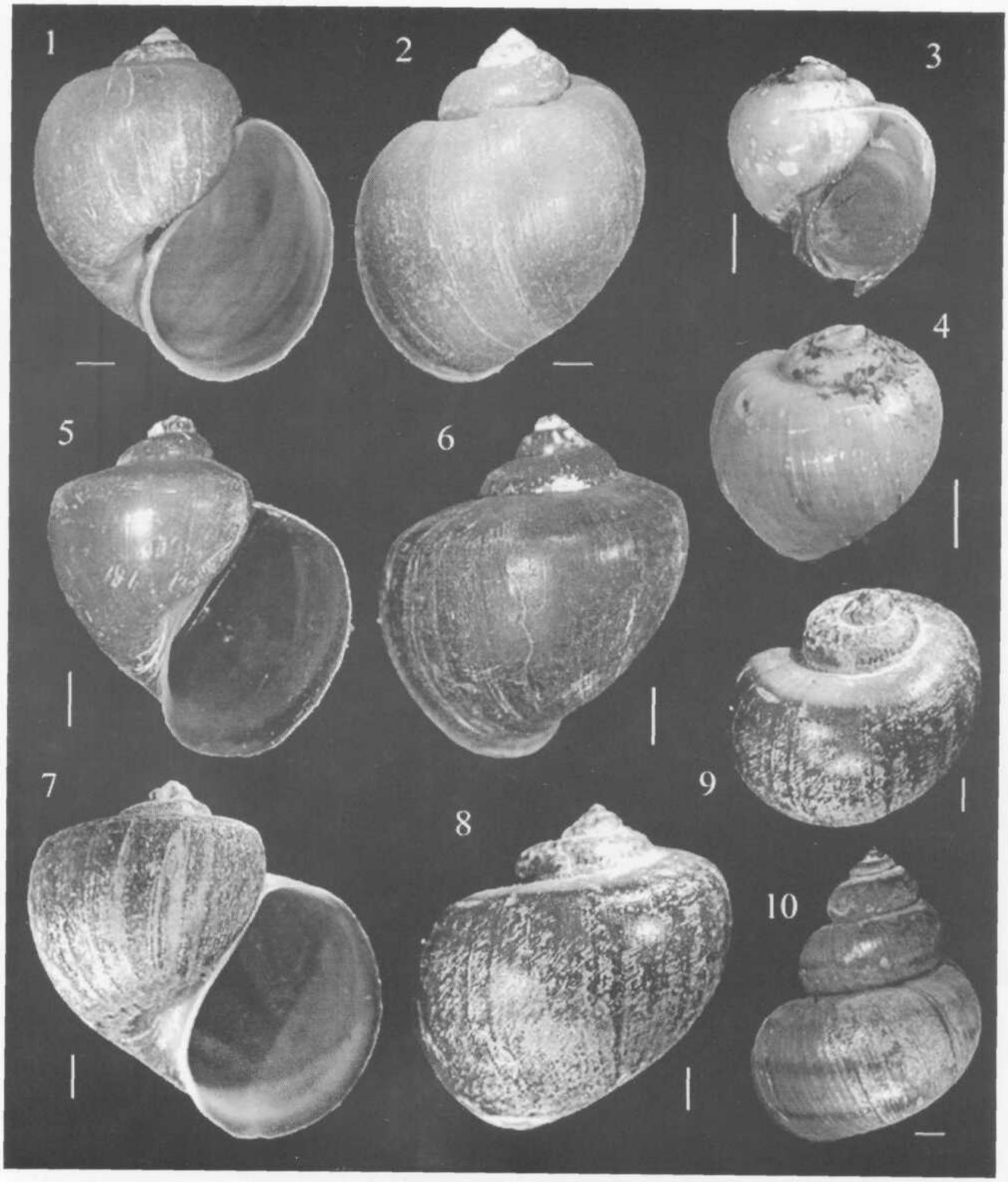
The buccal ganglia, as reported by SASAKI (1998), are not distinct in the archaeogastropods, being represented by a thickening of the buccal nerve, and located close to the nerve ring. In the caenogastropods, the pair of buccal ganglia becomes well delimited, and is located at some distance from the nerve ring, closely attached to the posterior region of buccal mass.

MATRIX OF CHARACTERS

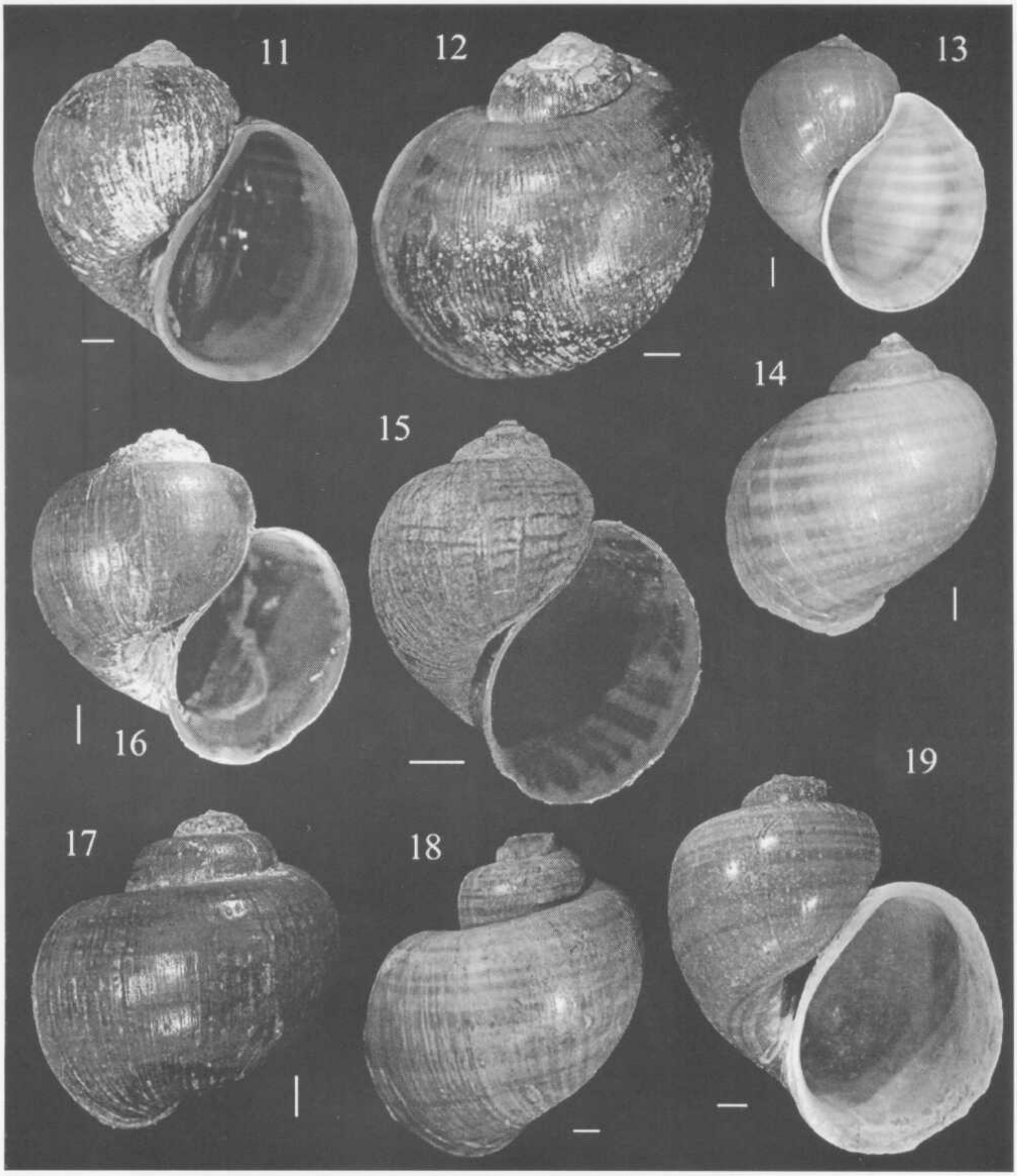
Table 1. Matrix of characters and their states, including 2 outgroups in last lines.

CHARACTER TAXON	1 2 3 4 5 6 7 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12
P.crosseana	10000 11001 21021 12211 00100 01011 11012 11213 00201 02100 02311 01111 11101 11100 11
P.canaliculata	10000 11001 21021 12211 00101 11011 11012 11213 00201 02100 02311 01111 11101 11100 11
P.scalaris	10000 11001 21021 12210 00101 01011 11012 1121300201 0210002211 01111 11101 11100 11
P.lineata	10000 11001 21021 1221000101 11011 11012 11213 00201 02100 02211 01111 11101 11100 11
P.curumim	10000 11001 21021 12210 00011 01011 11012 11213 00201 02100 02211 01111 11101 11100 11
Marisa	20000 11001 21001 10210 00100 00021 11012 11103 00201 0110002311 01111 11101 11100 11
Asolene	10100 11001 11021 12211 00101 01011 11012 11213 00201 02100 02311 01111 11101 11100 11
Felipponea	10100 11001 11021 12210 00101 01011 11012 11213 00201 02100 02311 01111 11101 11100 11
P.bridgesi	10000 11001 21021 12211 00100 01011 11012 11213 00201 02100 02211 01111 11101 11100 11
P.sordida	10000 11001 21021 12211 00100 11011 11012 11213 00201 02100 02211 01111 11101 11100 11
Neocyclotus	10010 01100 01111 00?00 1????00001 00010 100?1 00102 01111 01110 01111 11100 10101 10
Aperostoma	10010 01100 01011 00?00 1???? 00001 00010 100?1 00112 01112 01010 01111 11100 10101 10
Incidostoma	10010 01100 01011 00?00 1????00001 00010 100?1 00112 01112 01010 01111 11100 10101 10
V.contectus	01000 11012 11001 0110001001 0010000011 100?2 1100001100 10022 11111 11110 10110 11
V.acerosus	01000 11012 11001 01100 01001 00100 00011 100?2 11000 01100 10022 11111 11110 10110 11
N.ampullaroid	01000 11012 11001 01122 01000 00101 00111 100?2 12000 01100 10022 11111 11100 10110 10
N.essigntone.	01000 11012 11001 01122 01000 00101 00111 100?2 12000 01100 10022 11111 11100 10110 10
Larina	11000 11012 11001 01122 01000 00101 00111 100?2 12000 01100 10022 11111 11100 10110 10
Annularia	00011 00100 01201 00100 1????00001 00010 110?0 00003 11100 10222 11111 11100 10100 10
Cerithioidea	00001 00000 01001 00100 00001 00000 00010 100?0 00000 11100 10022 11111 11100 10100 11

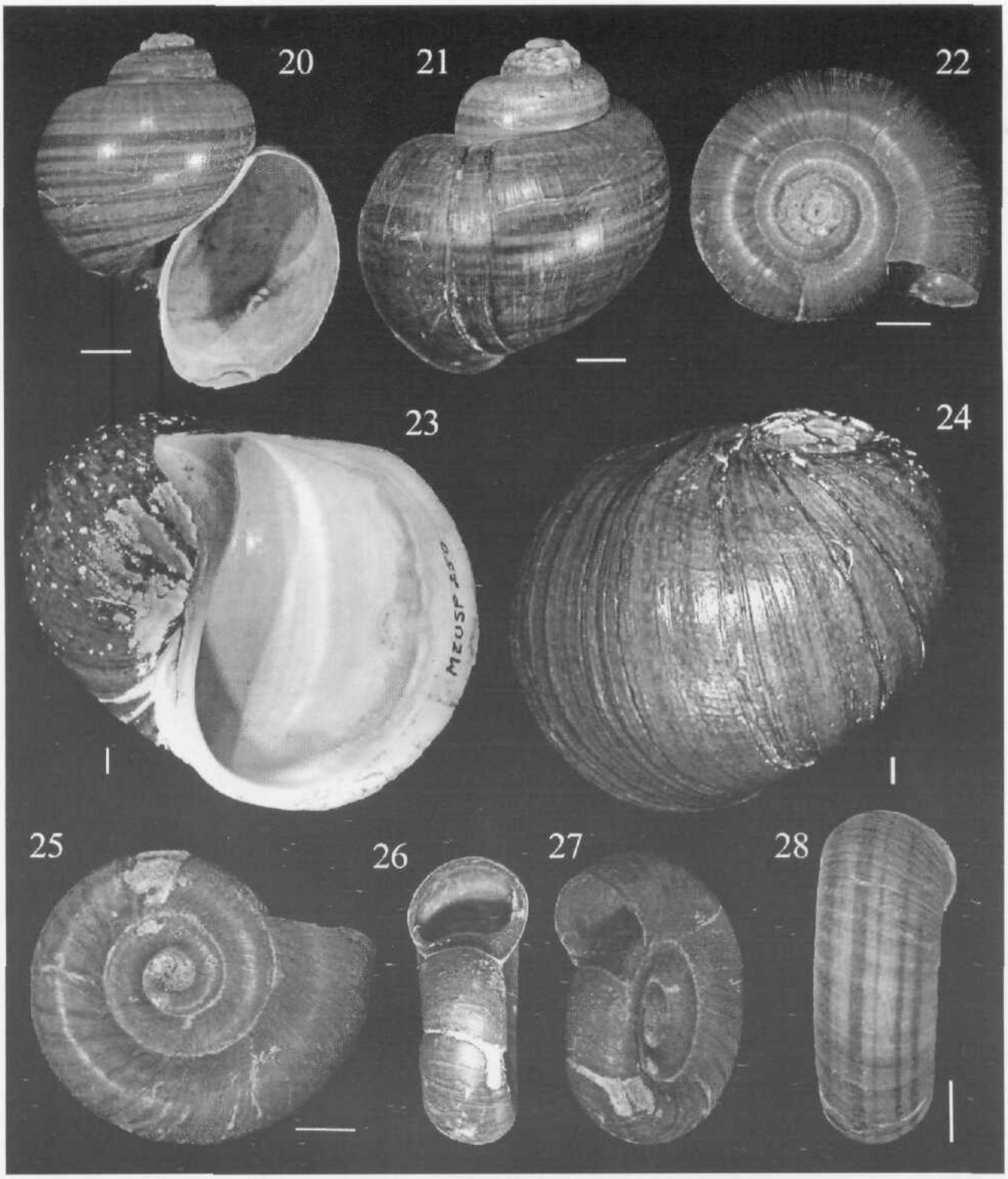
CHARACTER TAXON	7 8 9 10 11 12 13 14 345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 123
P.crosseana	011 11111 01011 10201 02110 21112 11111 11010 00220 00002 11110 00201 20202 12100 010
P.canaliculata	011 11111 01011 10201 02110 22212 11121 11110 00220 00002 11211 20201 20202 12100 010
P.scalaris	011 11111 01011 10201 02110 21112 11111 11110 00220 00001 01110 00201 20202 12100 010
P.lineata	011 11111 01011 10201 0211022212 11121 11110 00220 00001 11211 11201 20202 12100010
P.curumim	011 11111 01011 10201 0211022112 11111 11110 00220 00001 01211 11201 20202 12100 010
Marisa	011 11111 01011 10201 02100 21012 11111 11110 00220 00001 01111 01201 20202 12100 010
Asolene	011 11111 01111 10201 02110 22212 11121 11110 00220 00002 11210 21201 20202 22100 010
Felipponea	011 11111 01111 10201 02110 21112 11111 11010 00220 00001 01111 0?201 20202 22100 010
P.bridgesi	011 11111 01011 10201 02110 22212 11111 11110 00220 00001 01211 21201 20202 22100 010
P.sordida	011 11111 01011 10201 02110 22112 11111 11110 00220 00001 11211 20201 20202 22100 010
Neocyclotus	010 10000 01111 10101 01101 20001 10000 01011 00130 00110 01000 00201 11111 00100 010
Aperostoma	010 10000 11111 10101 01101 20001 10000 01011 00130 00120 01000 00201 12111 00100 010
Incidostoma	010 10000 11111 10101 01101 20001 10000 01011 00130 00120 01000 00201 12111 00100 010
V.contectus	010 10210 01011 11101 1??00 10000 10001 11010 01211 11000 01000 00211 00102 01211 011
V.acerosus	010 10210 01011 11101 1??00 10000 10001 11010 01211 11000 01000 00211 00102 01211 011
N.ampullaroid	010 10210 01011 11111 1??20 20001 10001 1101001211 10000 01000 00211 30102 01211 011
N.essigntone.	010 10210 01011 11111 1??20 20001 10001 1101001211 10000 01000 00211 30102 01211 011
Larina	010 10210 01011 11111 1??20 20000 10001 11010 01211 10000 01000 00211 30102 01211 011
Annularia	110 10000 11111 11201 1??01 20001 00001 11010 11220 00100 01000 00201 00101 00212 111
Cerithioidea	010 10010 01011 11101 1??01 20000 00001 11010 11000 00000 01000 00101 00100 00212 011



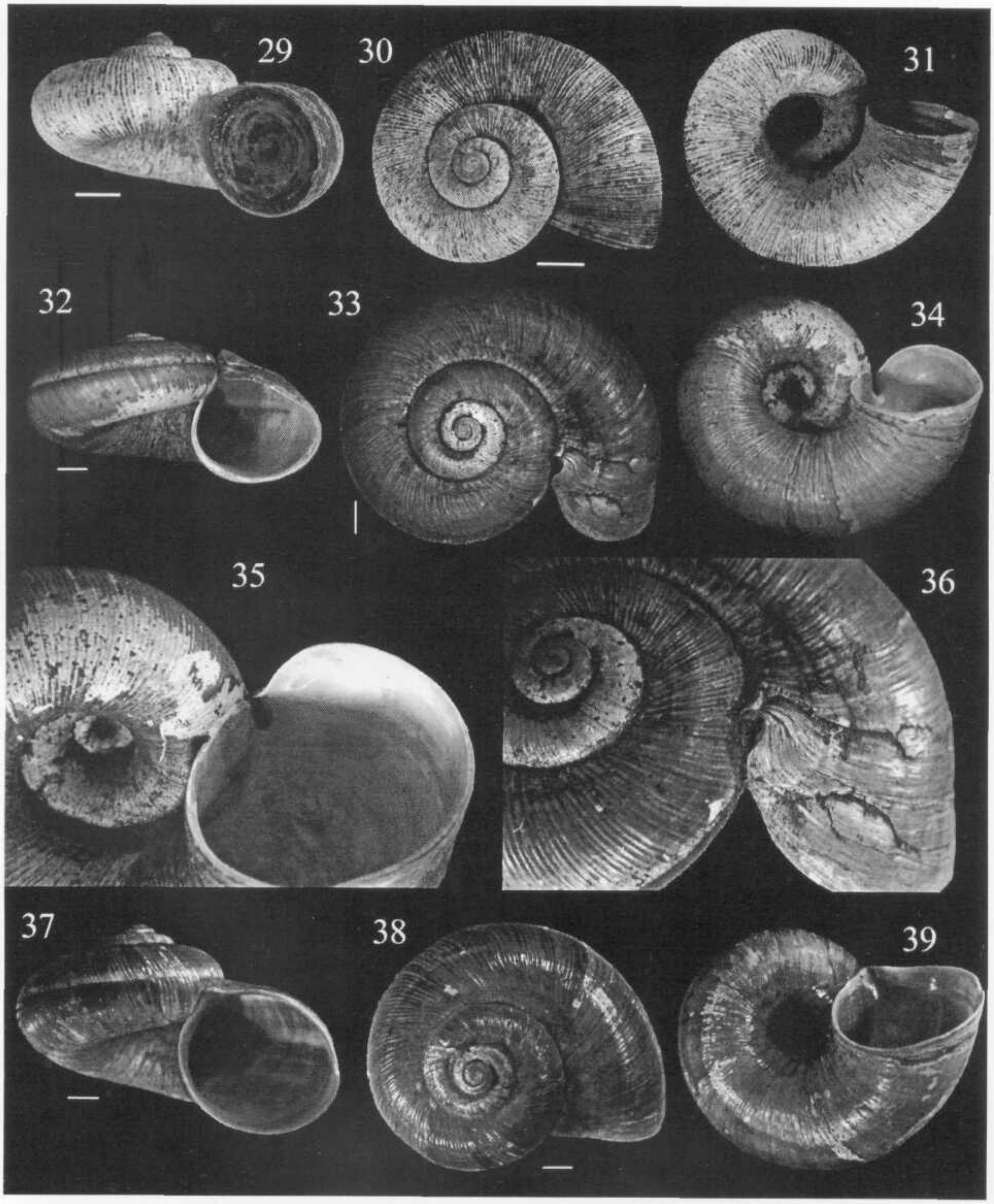
Ampullariid shells: fig. 1-2- *Pomacea crosseana*, frontal and dorsal views, MZSP 20158 (9 4); fig.3-4- *Pomacea carumim* frontal and dorsal views, holotype MZSP 30760. Pomacea *scalaris* MZSP 29590, fig.5-6- *d* , frontal and dorsal views, fig.7-9- 9 2, frontal, dorsal and apical views; fig. 10- *Viviparuscontectus*, MZSP 29402. Scale bars: (1-2 5-9) = 5mm (3-4) = 2mm, (10) = 3mm



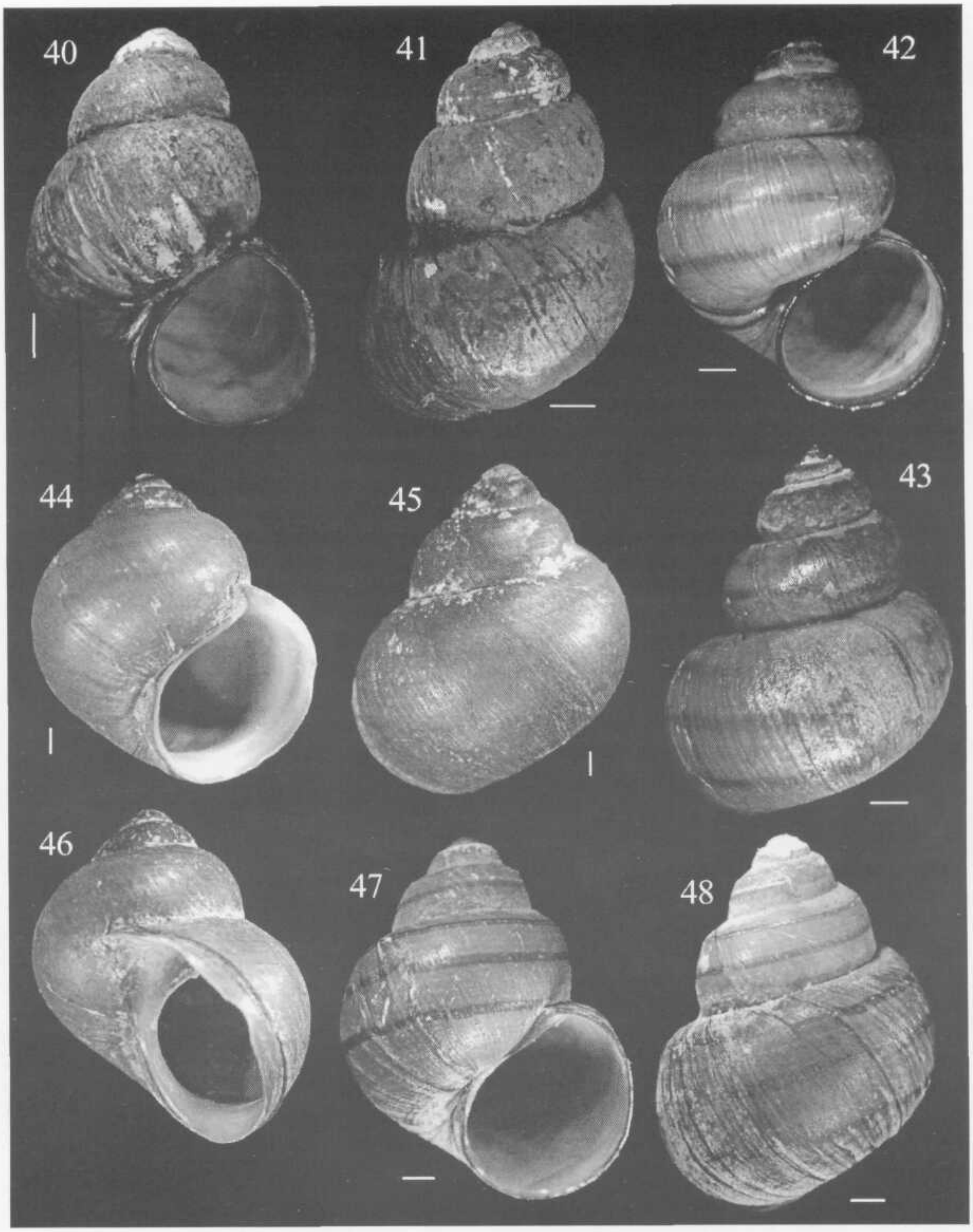
Ampullariid shells: fig.11-12- *Pomacea canaliculata*, MZSP 29633, frontal and dorsal views; fig.13-15- *Pomacea lineata*, fig. 13-14- MZSP 26684, frontal and dorsal views, fig. 15- MZSP 31147 (from Fernando de Noronha Archipelago), frontal view; fig.16-17- *Pomacea sordida*, MZSP 32195, frontal and dorsal views; fig.18-19- *Pomacea bridgesi*, MZSP 27880, dorsal and frontal views. Scale bars = 5mm.



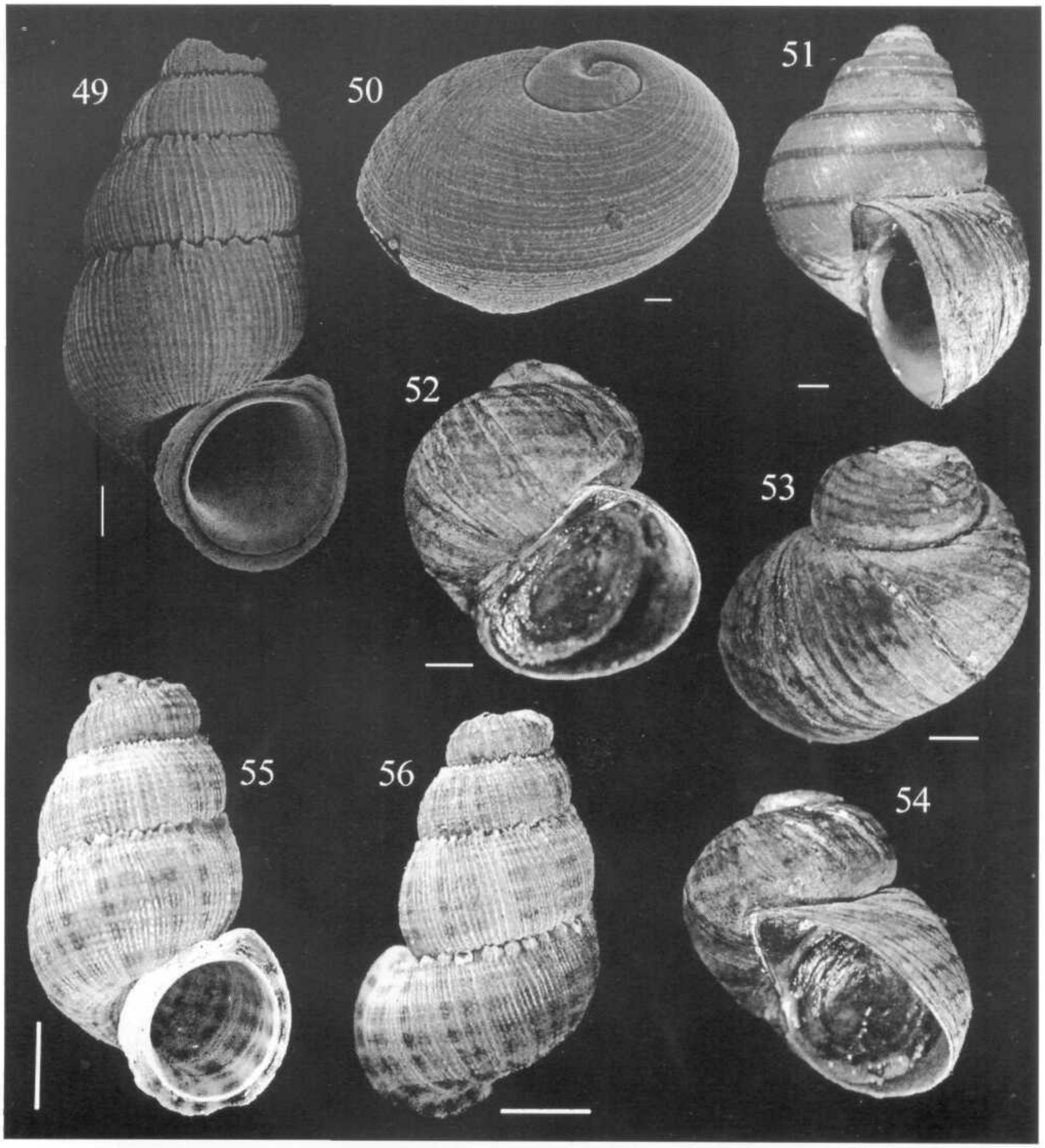
Ampullariid shells: fig.20-21- Pomacea *bridgesi*, MZSP 32196, frontal and dorsal views; fig.22- Marisa planogyra, MZSP 29674, specimens with uniform color, right view; fig.23-24- *Asolene megastoma*, MZSP 250, frontal and dorsal views; fig.25-28- Marisa *planogyra*, MZSP 29674. fig.25-27- specimen with uniform color (same than figure 22), left, frontal and oblique views; fig.28- specimen with bands in color, dorsal view. Scale bars = 5mm.



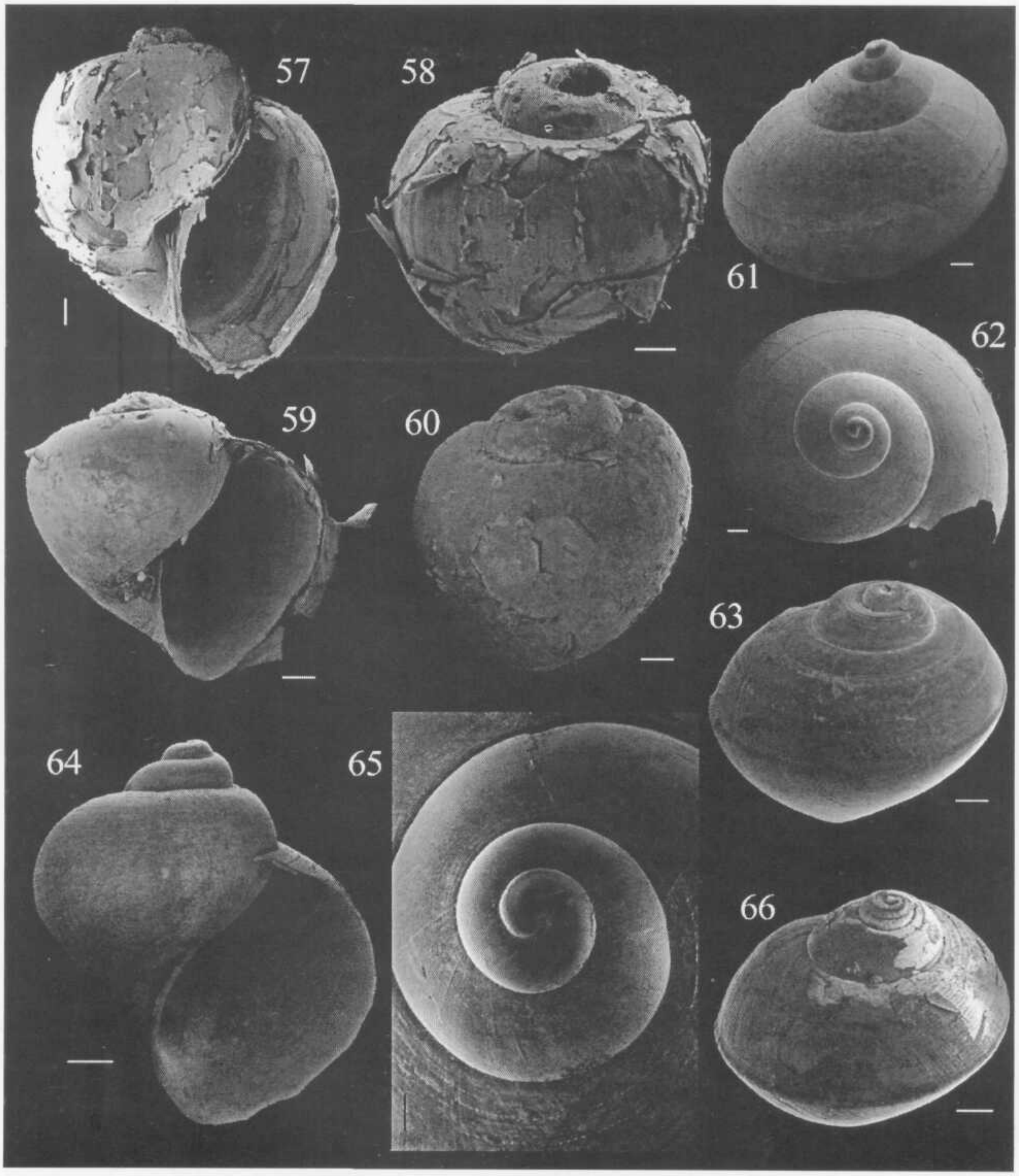
Cyclophorid shells: figs.29-31- *Neocyclotus prominulus*, MZSP 24546, frontal, apical and umbilical views. *Incidostoma tupy*, holotype, MZSP 29560, fig.32-34- frontal, apical and umbilical views, fig.35- detail of aperture, inner view, fig.36- same, dorsal view; fig.37-39- Aperostoma *blanchetiana* frontal, apical and umbilical views. Scale bars: (29-31, 37-39) = 2mm, (32-36) = 3mm.



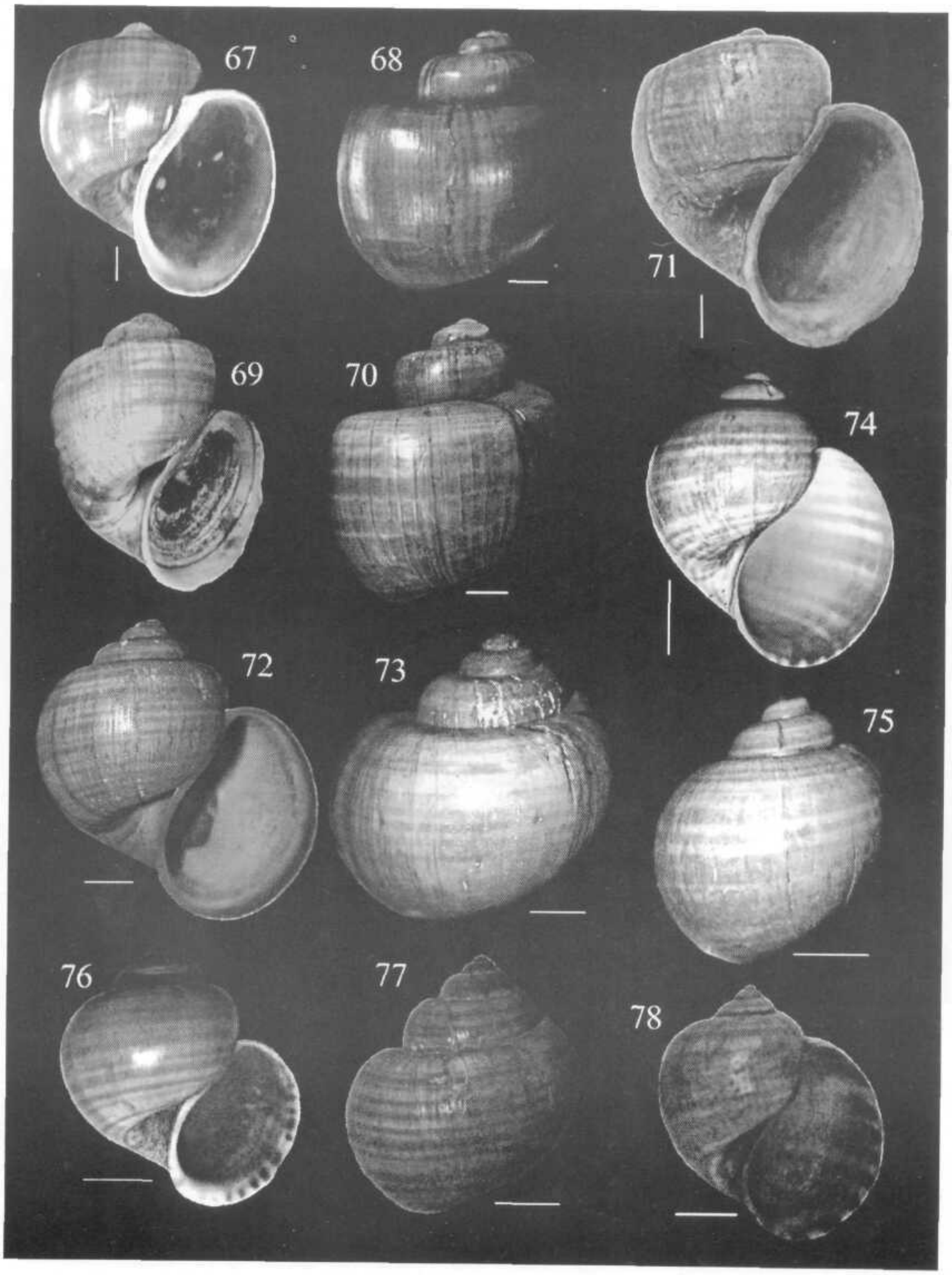
Viviparid shells: fig.40-41- *Viviparus acerosus*, MZSP 29403, frontal and dorsal views; fig.42-43- *Viviparus contectus*, MZSP 29402, frontal and dorsal views; fig.44-46- *Notopala ampullaroides*, AMS 202766 (9 1), frontal, dorsal and lateral-left views; fig.47-48- *Notopalaessintonensis*, AMS 153577 (9 1), frontal and dorsal views. Scale bars: (40-41) = 5mm, (42-43) = 3mm, (44-48) = 2mm.



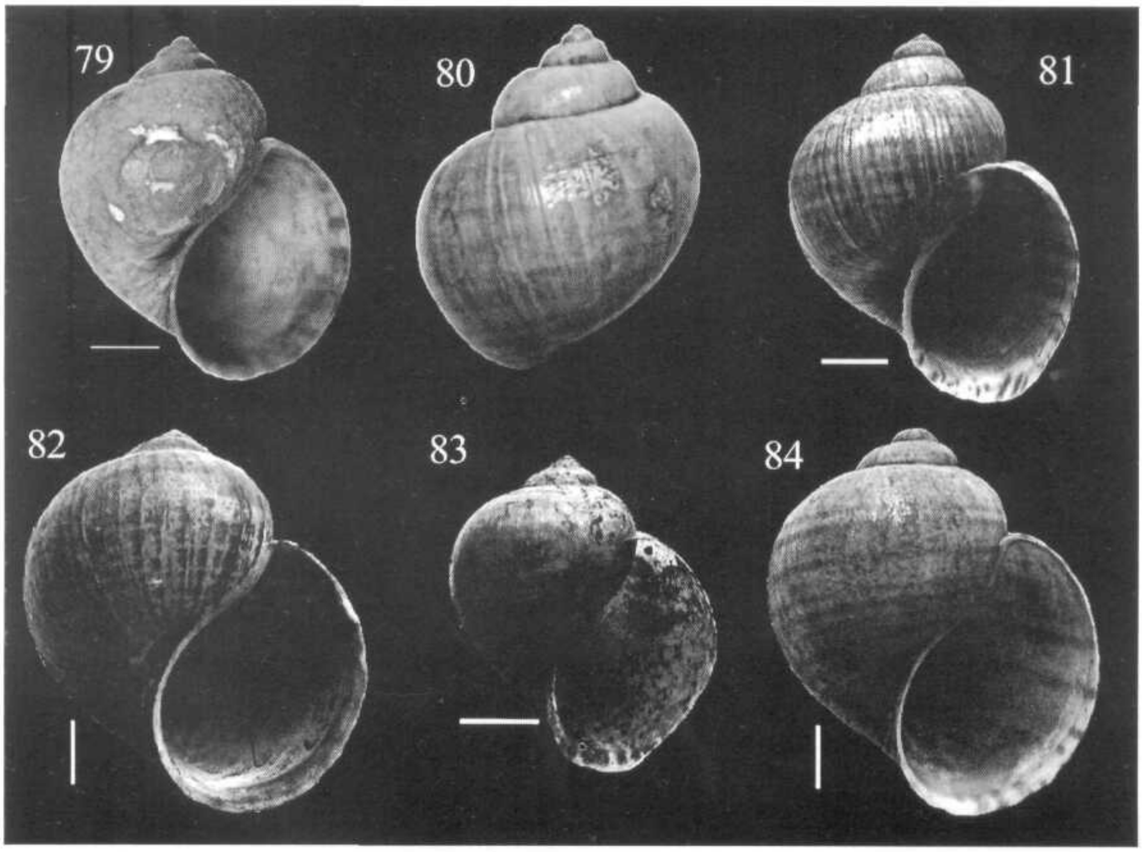
Shells: fig.49- *Annularia sp,* MZSP 28266, SEM, frontal view; fig.50- *Larina* cf *strangei,* AMS 338590, SEM, young specimen extracted from brood pouch, dorsal view; fig.51- *Notopala essingtonensis,* AMS 153577, lateral-left view; fig.52-54- *Larina* cf *strangei,* AMS 338590, frontal, dorsal and lateral-left views; fig.55-56- *Annularia sp.,* MZSP 28266, frontal and dorsal views. Scale bars: (49) = 1mm, (50-56) = 2mm.



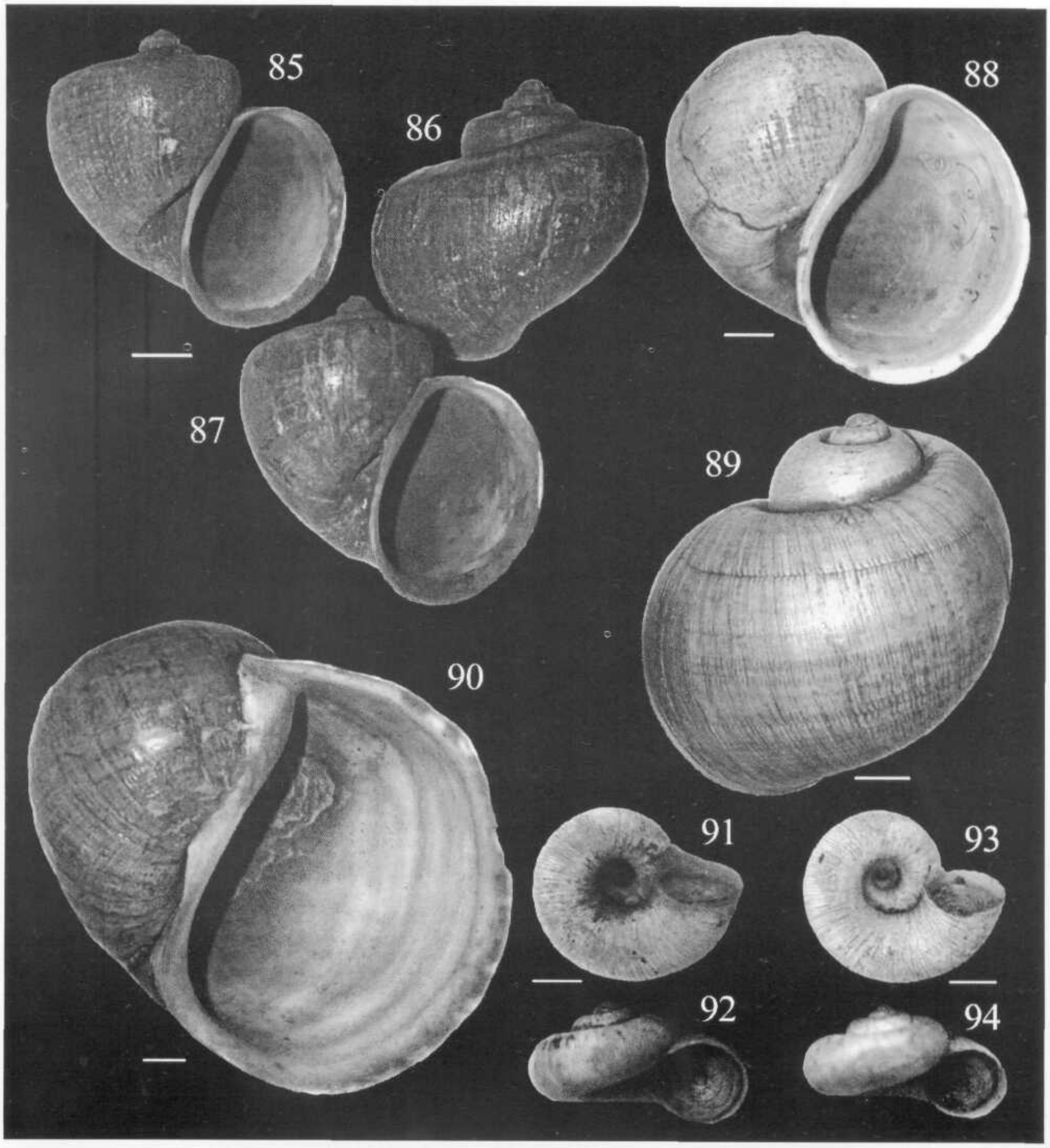
Shells in SEM: *Pomacea curumim*, paratypes, fig.57-58- specimens with intact periostracum, frontal and dorsal views; fig.59-60- specimen with most periostracum removed, frontal and dorsal views; fig.61-62- *Viviparus contectus*, young specimen removed from brood pouch, dorsal and apical views; fig.63- *Notopala ampullaroides*, young specimen removed from brood pouch, dorsal view; fig.64-65-. *Pomacea lineata*, MZSP 31147 (from Fernando de Noronha Archipelago); fig.64- young specimen, frontal view; fig.65- same, detail of apex, apical view; fig.66- *Notopala essingtonensis*, young specimen removed from brood pouch, dorsal view. Scale bars: (57-60) = 0.6mm, (61-62) = 0.5mm, (63, 65-66) = 0.4mm, (64) = 1mm.



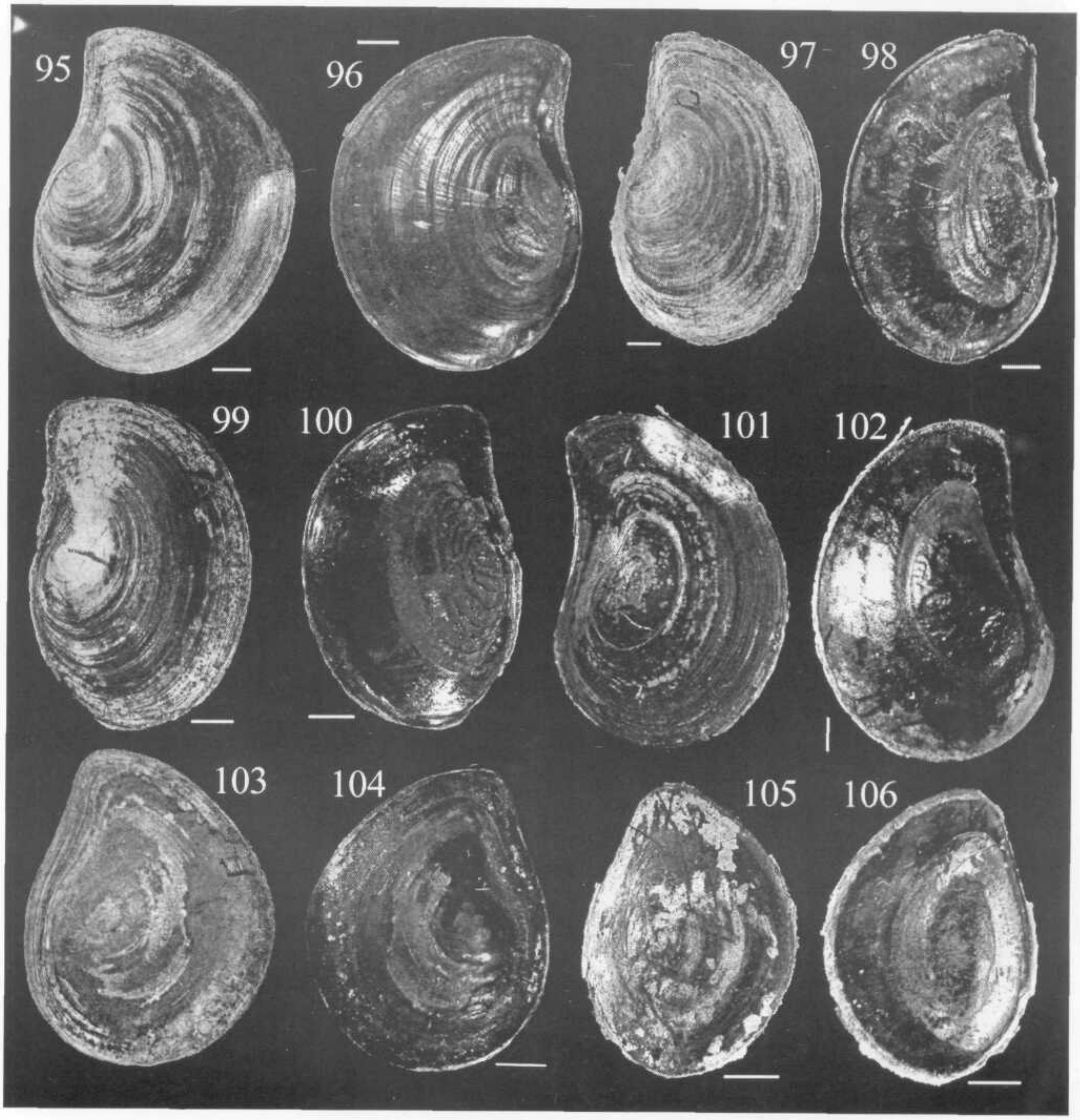
Some shell TYPES: *Pomacea bridgesi* syntypes, BMNH, flg.67-68- specimen 1, frontal and dorsal views fig 69-70- same for specimen 2; fig.71- P. *bridgesi*, MNHN, labeled as "*Ampullaria scalaris* var B *major viridescens*" Orbigny 1835 frontal view, Bolivie; fig.72-73- P. sordida, BMNH, holotype of *Ampullaria melanocheila* Reeve, frontal and dorsal views; fig 74-75- P. *lineata*, BMNH, holotype of *Ampullaria testudinea* Reeve, frontal and dorsal views; fig.76-77- P *lineata*, MNHN syntype 1 (of 2), Brazil, frontal and dorsal views; fig. 78- *P. lineata*, MNHN, syntype 1 (of 2) of *Ampullatia physis* Hupé 1857 frontal view. Scale bar = 10mm.



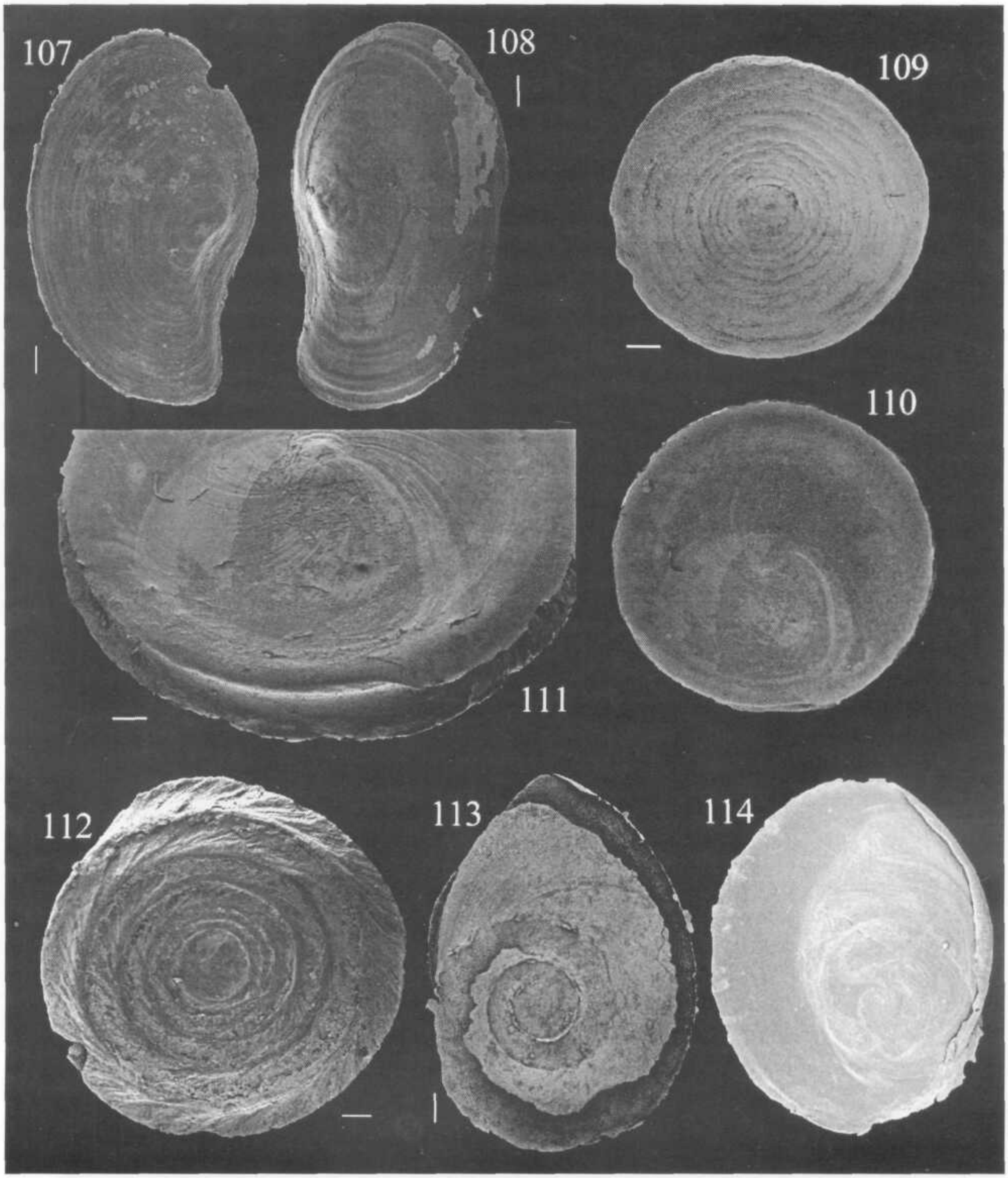
Pomacea lineata TYPES: fig.79-80- MNHN, syntype 2 (of 2, see figs.76-77), Brazil, frontal and dorsal views; fig.81-82- ZSM, Spix's types of Pomus *lineatus fasciatus*, Bahia; fig.83-84- ZSM, Spix's types *of Pomus fingulinus*, Bahia. Figs.81-84 courtesy of Silvana Thiengo (Fundação Oswaldo Cruz, Rio de Janeiro). Scale bars = 10mm.



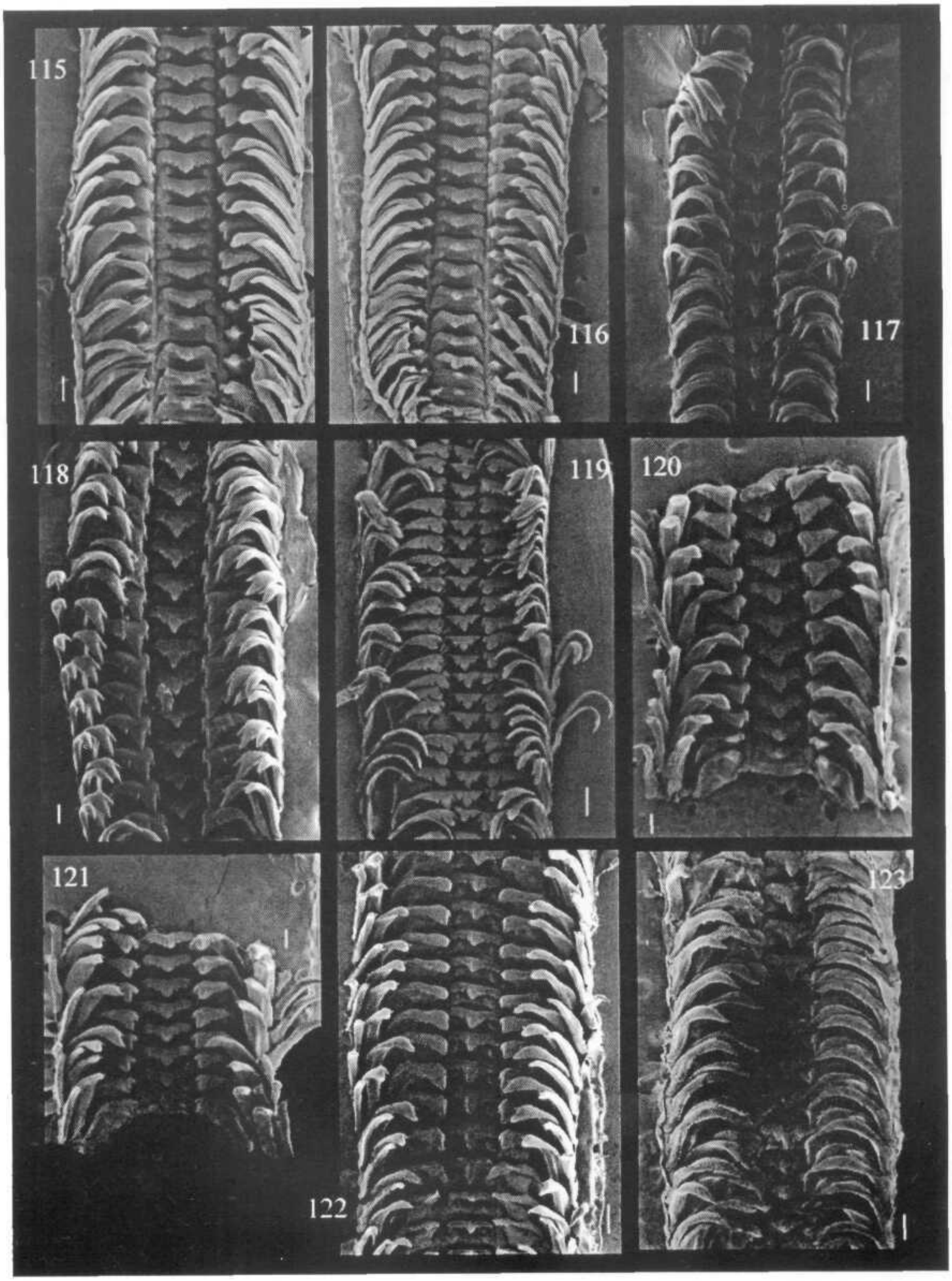
Some shell TYPES: fig.85-87- *Pomacea scalaris*, 3 syntypes, MNHN, Bolivia; fig.88-89- P. *canaliculata*, MNHN, Rio de la Plata, syntypes of Pita *insularum* Orbigny, fig.88- frontal view of syntype 1, fig.89- dorsal view of syntype 2; fig.90- *Asolene megastoma*, MNHN, probable type of *Ampullaria neritoides* Orbigny, Rio Uruguay, frontal view. *Neocyclotas prominulus*, MNHN, 2 probable syntypes of *Cyclostoma prominula* Fer. in Orbigny, Brazil, coll. Deshayes, fig.91-92- specimen 1, umbilical and frontal views, fig.93-94- same for specimen 2. Scale bars: (85-90) = 10mm, (91-94) = 3mm.



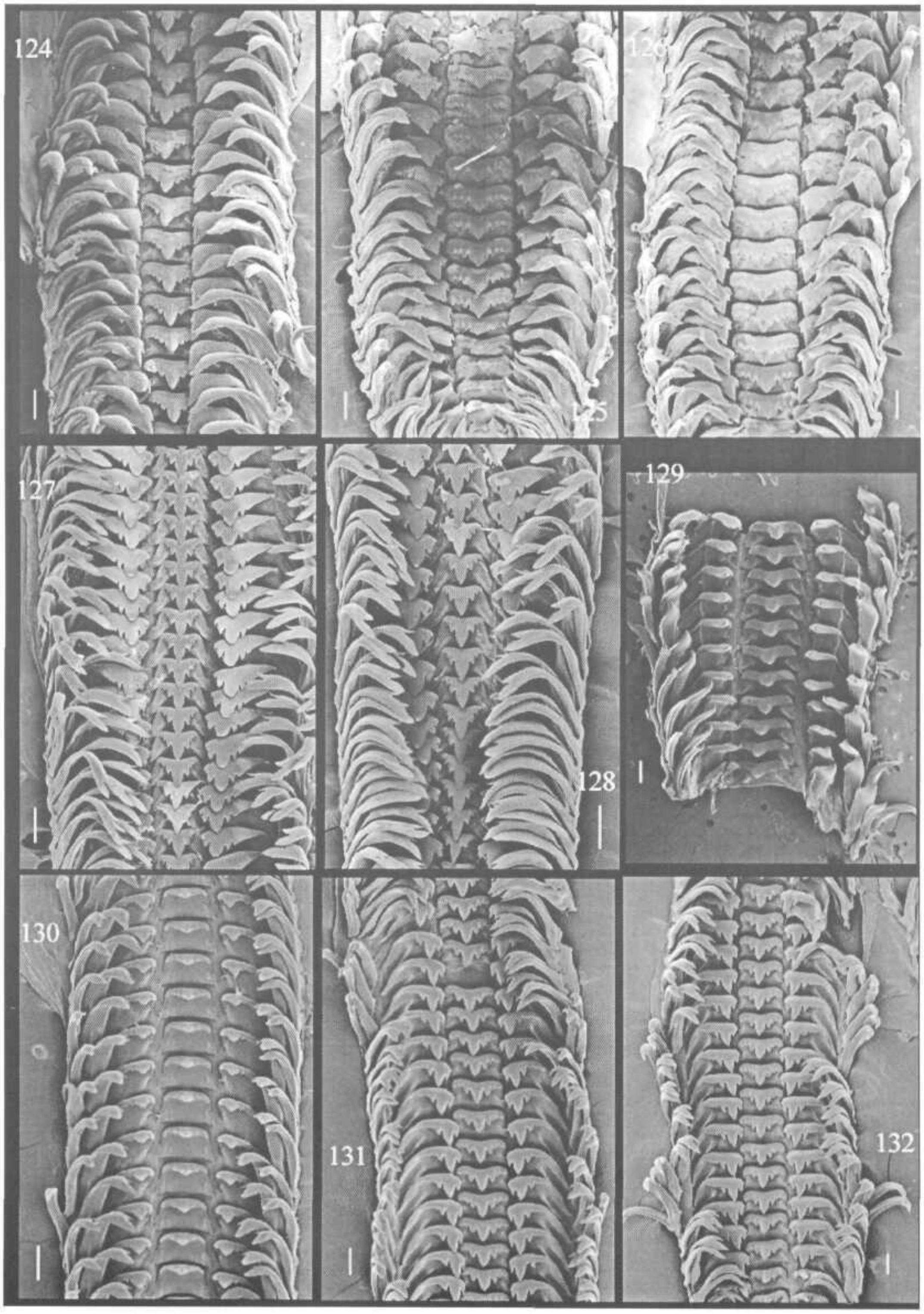
Opercula: fig.95-96- *Pomacea lineata*, outer and inner views; fig.97-98- *Pomacea crosseana*, outer and inner views; fig.99-100- *Pomacea sordida*, outer and inner views; fig. 101-102- *Marisaplanogyra*, outer and inner views; fig. 103-104- *Viviparus acerosus*, outer and inner views; fig. 105-106- *Notopala ampullaroides*, outer and inner views. Scale bars: (95-100 103-104) = 3mm, (101-102, 105-106) = 2mm.



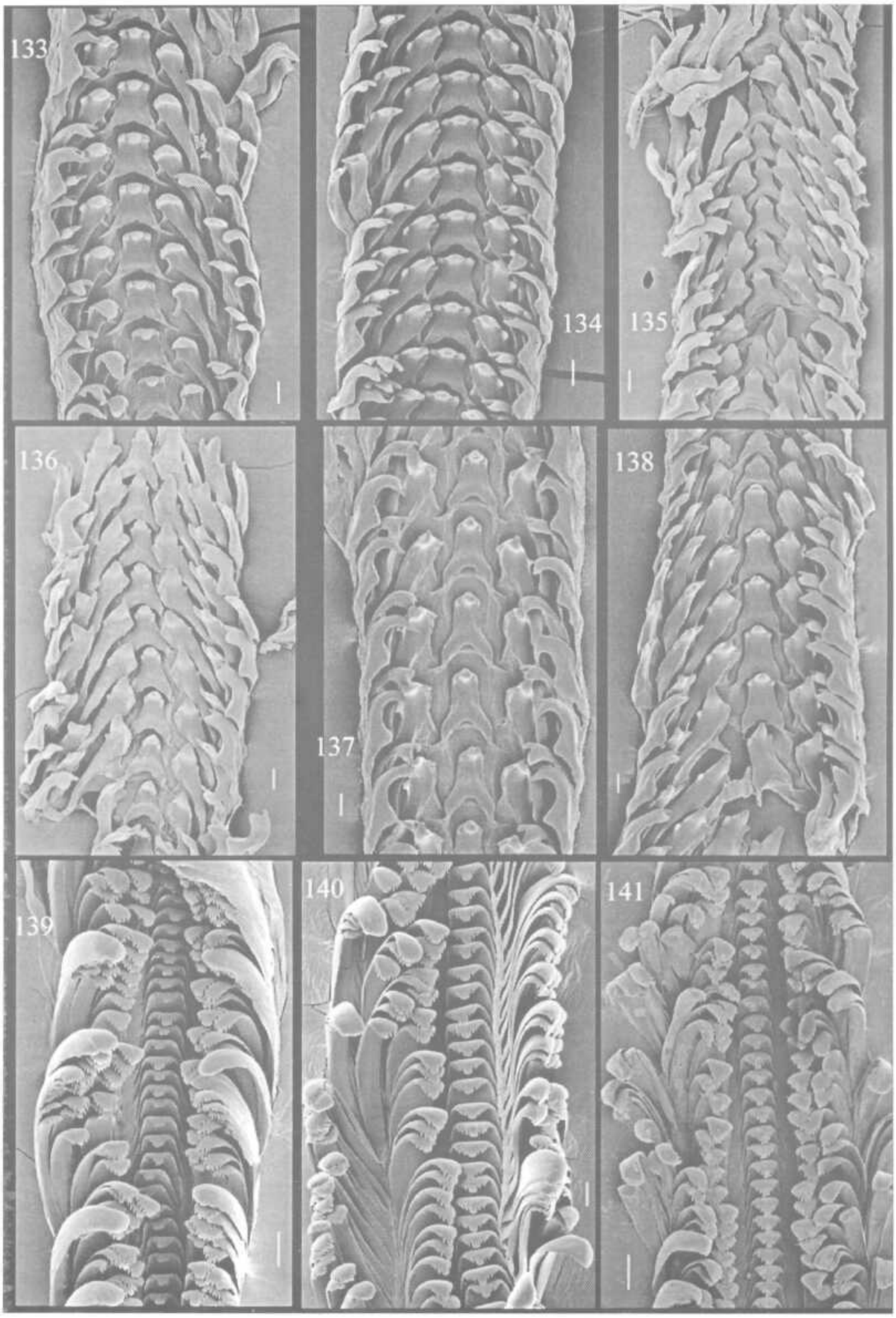
Opercula in SEM: fig. 107-108- *Pomacea curumim*, outer and inner views; 109-111, *Neocyclotus prominulus*; fig. 109-110- outer and inner views; fig. 111- detail of border, inner-shghtly oblique view; fig. 112- *Aperostoma blanchetiana*, outer view; fig. 113-114- *Annularia sp*, outer and inner views. Scale bars: (107-108, 111, 113-114) = 0.3mm, (109-110, 112) = 0.5mm.



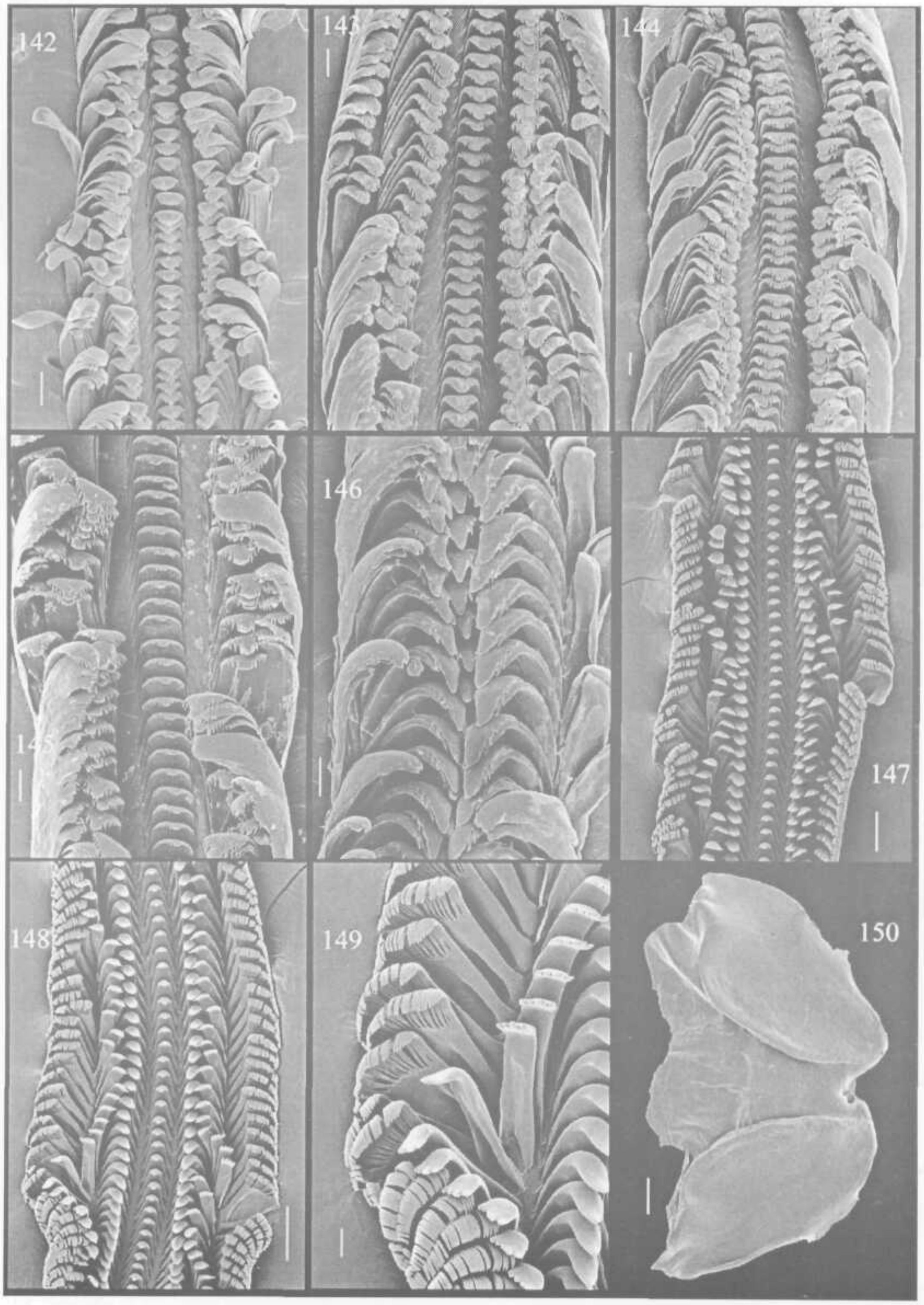
Pomacea radulae in SEM: fig.115-116- *Pomacea crosseana*; fig.117-118- P. curumim; fig.119- P. scalaris; fig.120-121- P. *canaliculata*; fig.122- P. *lineata*; fig.123- P. sordida Scale bars: (115-116, 119-123) = 200μm, (117-118) = 60μm.



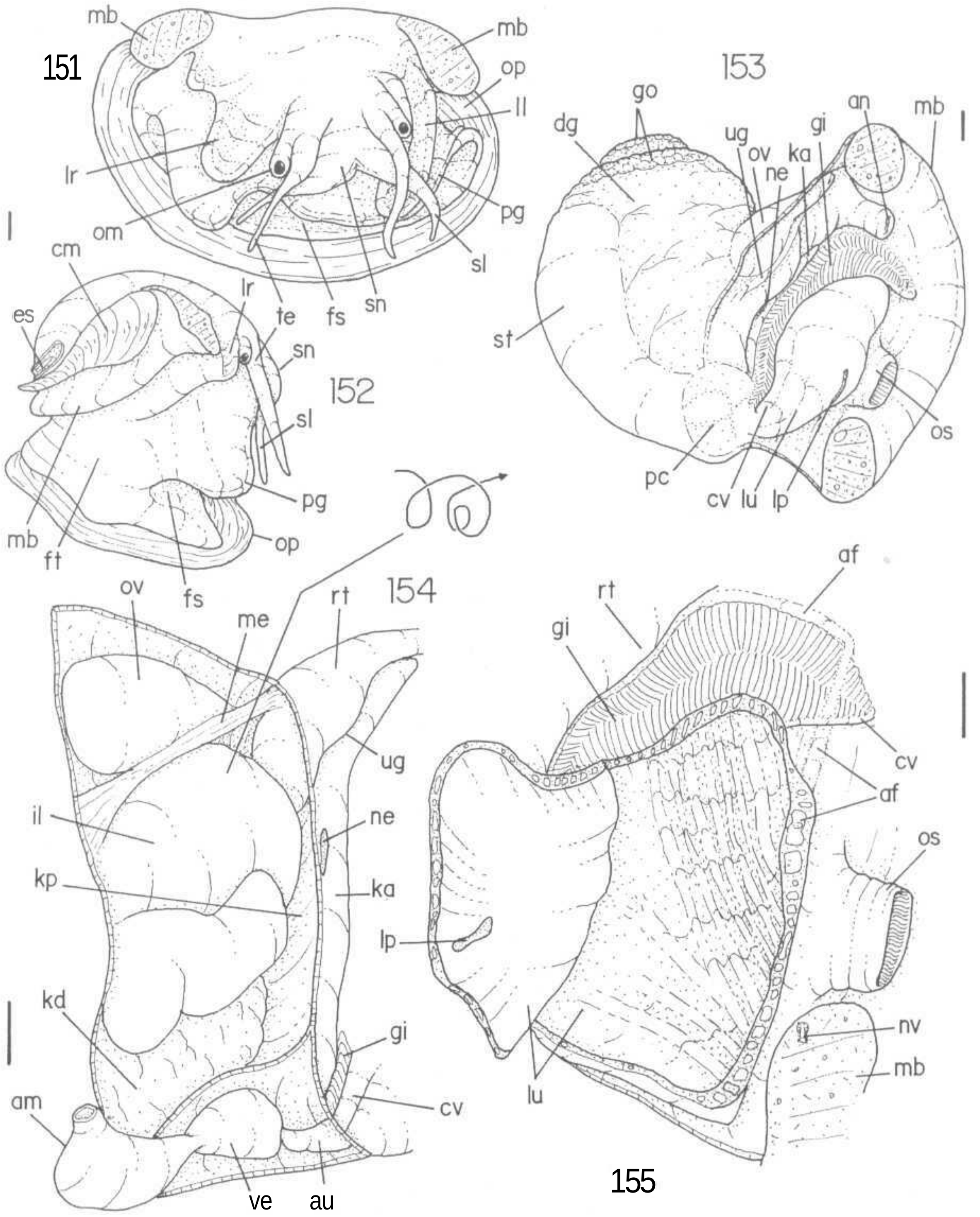
Ampullariid radulae in SEM: fig.124- *Pomacea sordida*; fig.125-126- P. *lineata* (from Fernando de Noronha Archipelago); fig.127-128- P. *bridgesi;* fig.129- *Asolene megastoma*; fig.130- *Felipponea neritiniformis;* fig.131-132- Marisa *planogyra*. Scale bars: (124-128, 130) = 200μm, (129) = 400μm, (131-132) = 100μm.



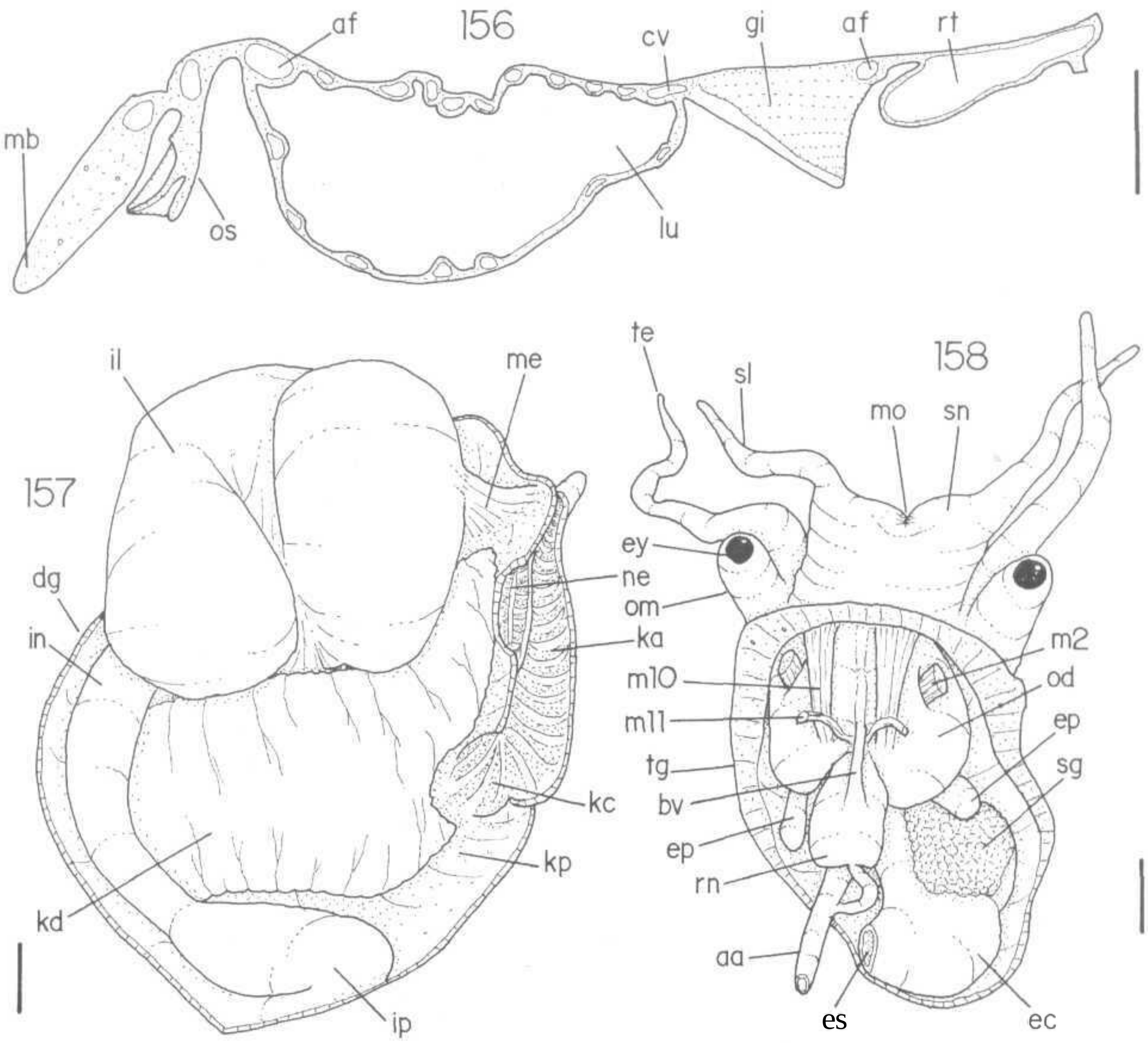
Radulae in SEM: fig. 133-134- *Neocyclotus prominulus*; fig. 135-136- *Incidostoma typy;* fig. 137-138- *Aperostoma blanchetiana*; fig.139-140- *Viviparus acerosus;* fig.141- *Viviparus contectus.* Scale bars: (133-134, 137-138) = 30μm, (135-136, 140) = 60μm, (139, 141) = 100μm



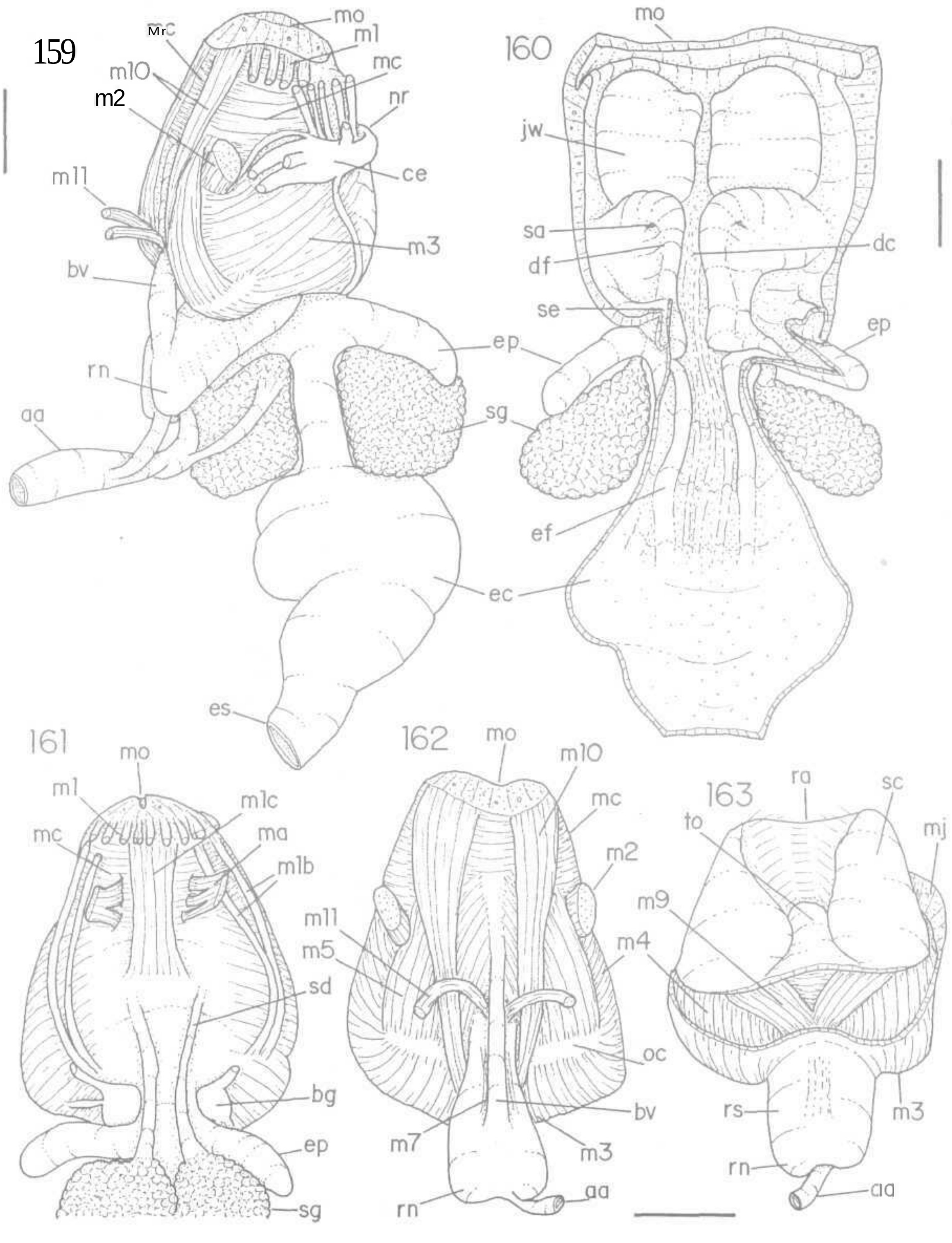
Hard structures (radula, except if indicated) in SEM: fig.142- *Viviparus contectus;* fig.143-144- *Notopala ampullaroides;* fig.145- *Notopala essingtonensis;* fig.146- *Larina* cf *strangei;* fig.147-148- *Annularia* sp.; fig.149- same, detail; fig.150- *Pomacea crosseana,* jaws. Scale bars: (142, 147-148) = 100μm, (143-146) = 40μm, (149) = 20μm, (150) = 200μm.



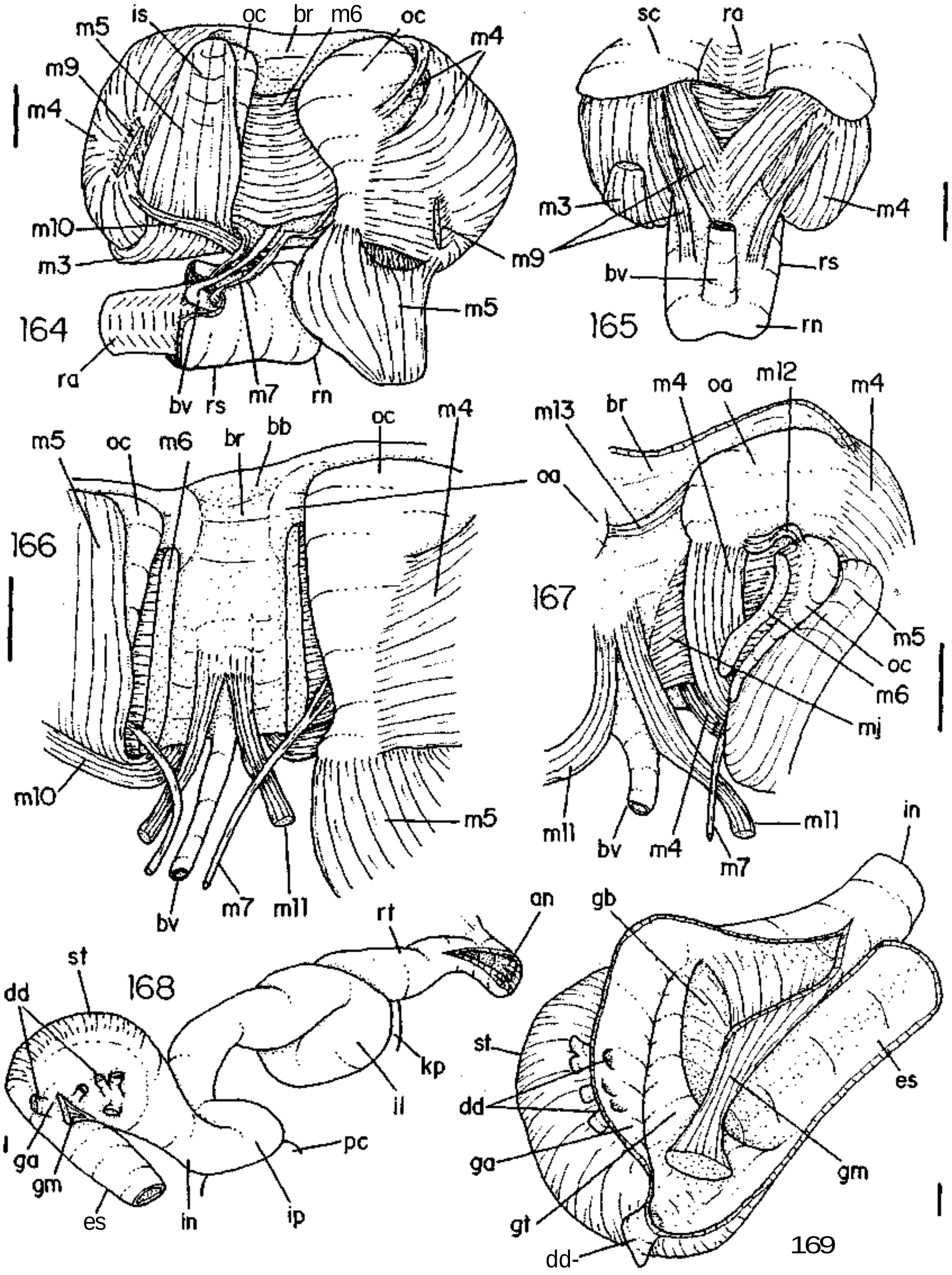
Pomacea crosseana anatomy: fig. 151- head-foot, 9 , frontal view; fig. 152- same, lateral-right view; fig. 153- pallial cavity roof in inner-ventral view, and visceral mass; fig. 154- anterior region of visceral mass and adjacent portion of pallial cavity, ventral view, ventral walls of pericardium and kidney removed, an schematic representation of in situ intestinal loops inside kidney shown in a separated detail; fig. 155- detail of pallial cavity in region of lung, ventral wall of lung most removed and deflected posteriorly (to left in fig.). Scale bars = 2mm.



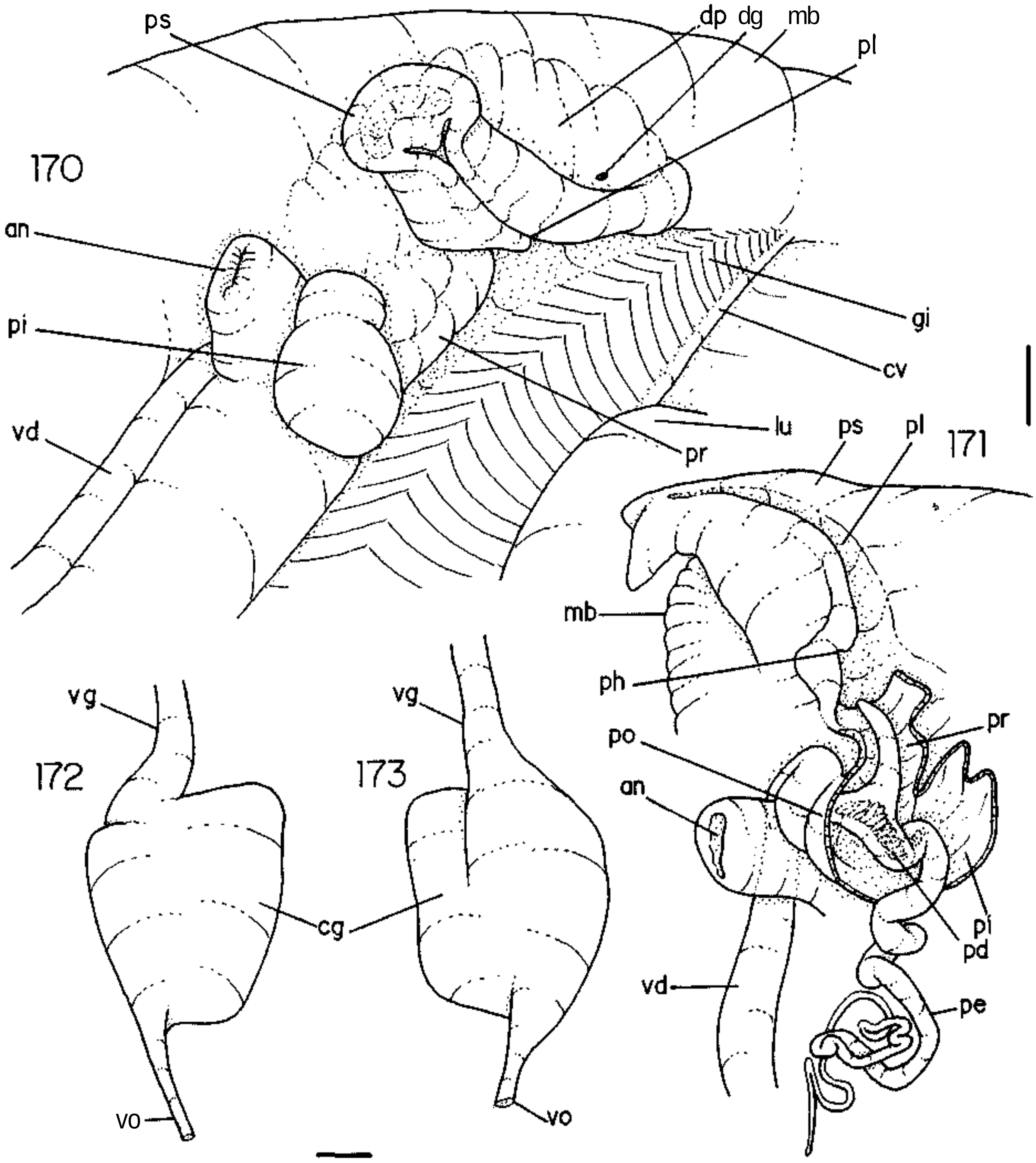
Pomacea crosseana anatomy: fig. 156- pallial cavity roof, transversal section in middle region of osphradium; fig. 157- kidney, ventral view, ventral wall removed, intestinal loops deflected, anterior lobe (ka) opened longitudinally; fig. 158- head and haemocoel, ventral view, foot removed. Scale bars = 2mm.



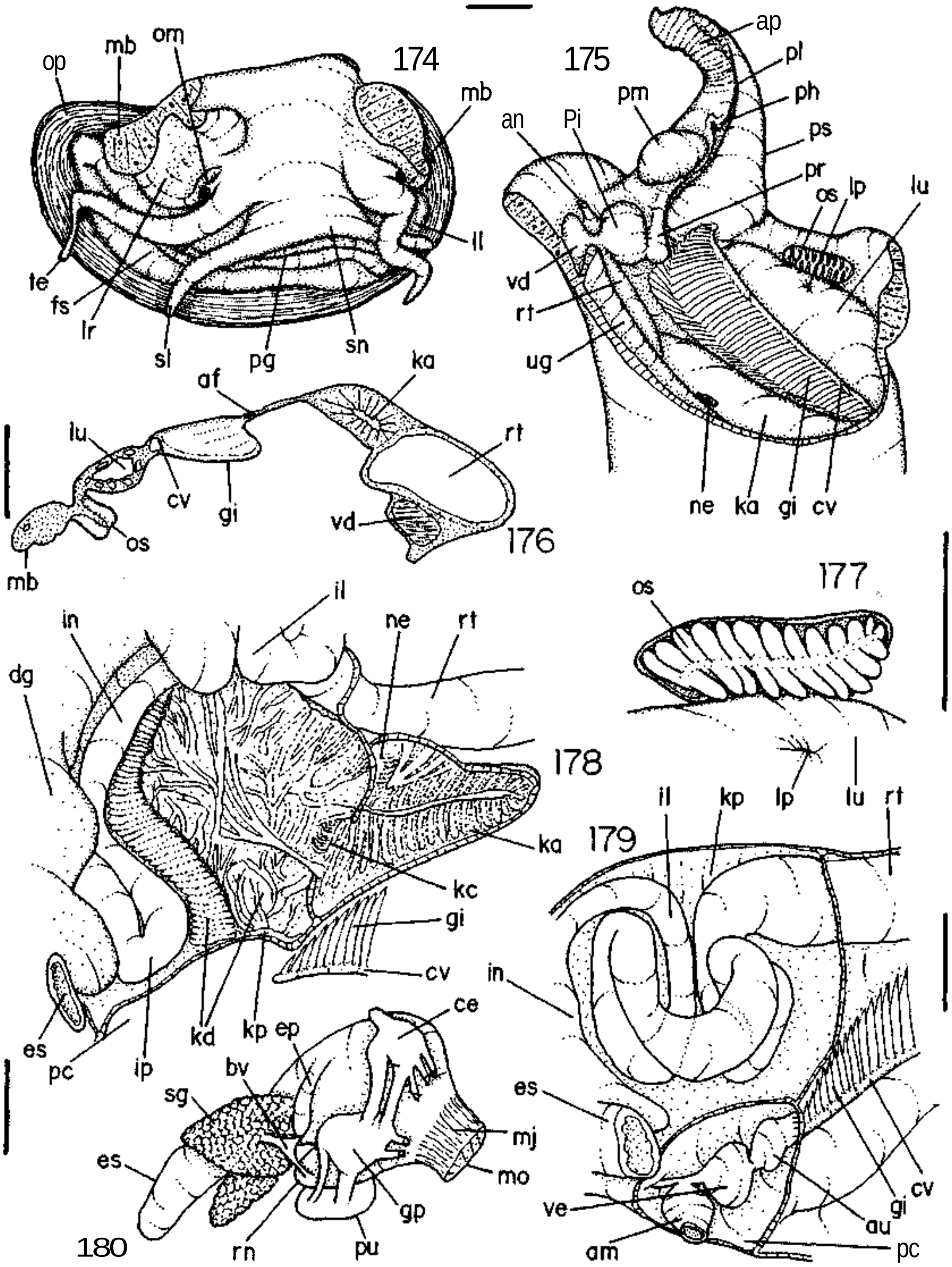
Pomacea crosseana anatomy: fig. 159- foregut, buccal mass in lateral-left view, remainder structures in ventral view; fig. 160- same, ventral view, odontophore removed, esophagus and left esophageal pouch (right in fig.) opened longitudinally; fig. 161- buccal mass, dorsal view; fig. 162- same, ventral view; fig. 163- same, dorsal view, dorsal wall and esophagus removed. Scale bars = 2mm.



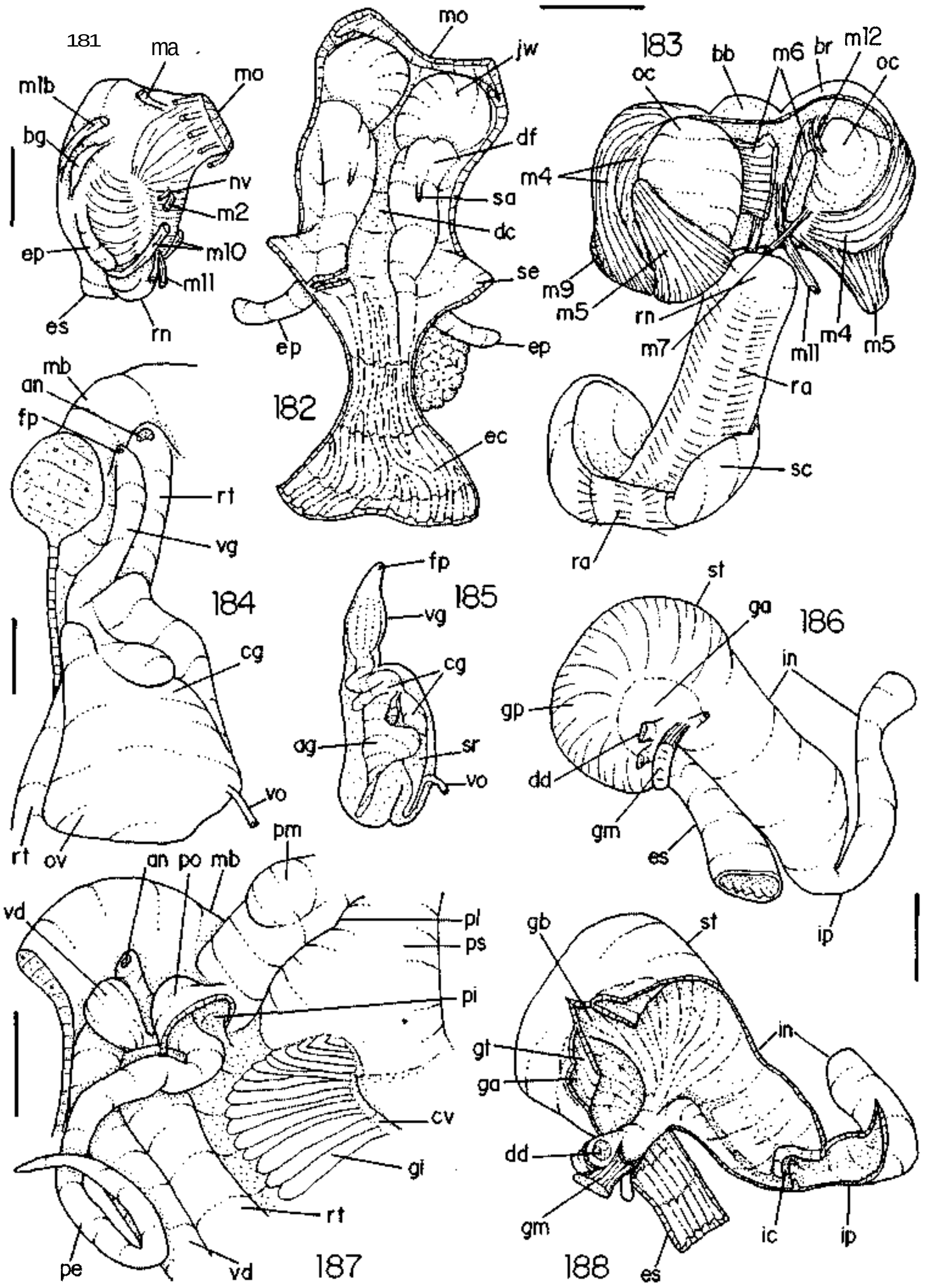
Pomacea crosseana anatomy: fig. 164- odontophore, dorsal **view**, radular ribbon deflected and only partially shown, both cartilages and **right** m5 deflected; fig. 165- **same**, dorsal view, detail of **its** posterior region with radular ribbon and subradular cartilage in situ; fig. 166- detail of fig. 164, with horizontal muscle (m6) sectioned longitudinally and deflected; fig. 167- **same**, only right **hemi-odontophore** shown, odontophore cartilage (oc) deflected to show its opposed side; fig. 168- middle and hindgut seen as in situ, ventral view; **fig.** 169- stomach, ventral view, esophageal portion opened longitudinally, ventral gastric wall sectioned and deflected. Scale bars = 1mm.



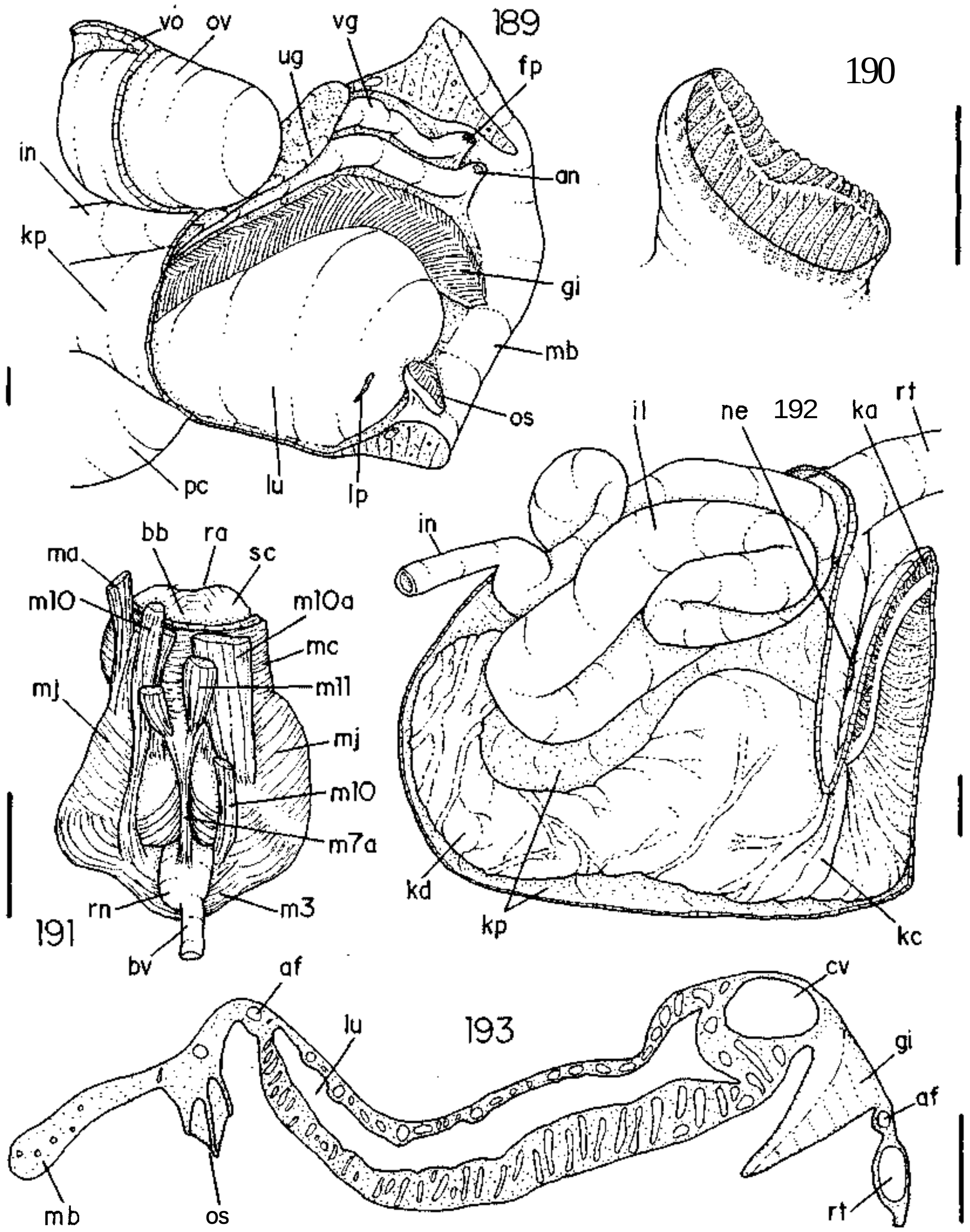
Pomacea crosseana anatomy: fig. 170-detail of pallial cavity in region of penis shield; fig. 171- same, with penis shield deflected externally, penis sac opened, penis stretched; fig. 172-173- pallial oviduct, ventral and dorsal views. Scale bars = 1mm.



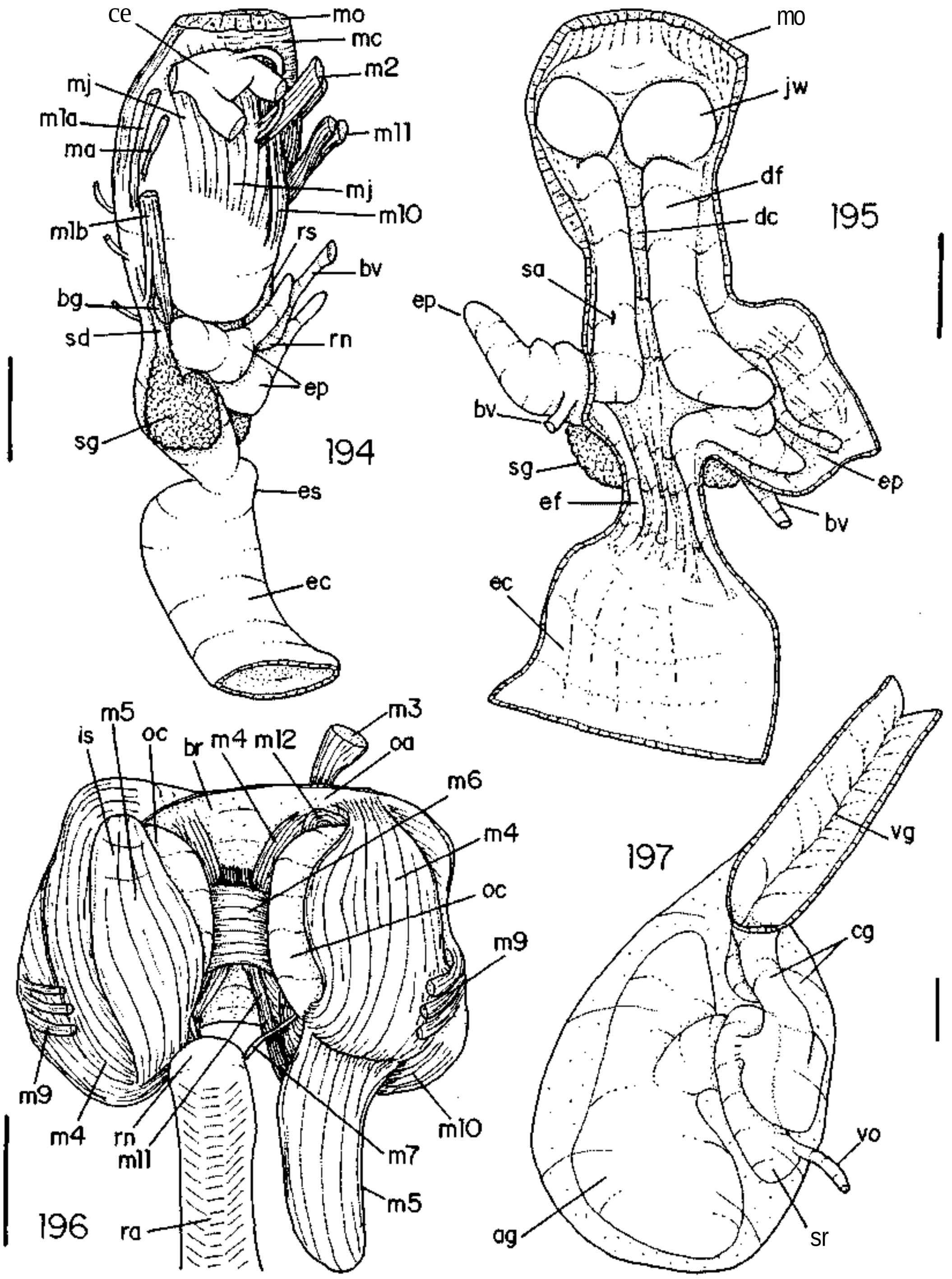
Pomacea curumim anatomy: fig. 174- head-foot, 9 , frontal view; fig. 175- pallial cavity roof, ♂, inner-ventral view, penis shield deflected outside; fig. 176- pallial cavity roof, transversal section in middle region of osphradium; fig. 177- detail of osphradium and adjacent region, ventral view; fig. 178- kidney, ventral view, ventral wall removed, Intestinal loops deflected, anterior lobe (ka) opened longitudinally; fig. 179- anterior region of visceral mass and adjacent region of pallial cavity, ventral view, ventral walls of kidney and pericardium removed, special attention to fashion of renal Intestinal loops; fig. 180- foregut, lateral-right view. Scale bars = 1mm.



Pomacea curumim anatomy: fig. 181- buccal mass, lateral-right view; fig. 182- foregut, ventral view, odontophore removed, esophagus opened longitudinally right dorsal fold (left in fig.) sectioned in the level of esophageal pouch; fig. 183- odontophore, dorsal view, radular ribbon extracted and deflected, both cartilages deflected, left cartilage in slightly apical view, horizontal muscle (m6) sectioned longitudinally and part deflected, left m5 also deflected; fig. 184- pallial oviduct and adjacent structures of pallial roof, ventral view; fig. 185- same, seen as a transparent structure; fig. 186- midgut, ventral view as in situ; fig. 187- right-anterior region of pallial cavity roof, male, penis shield deflected, penis sac opened and penis stretched; fig. 188- midgut most opened longitudinally, ventral view, ventral gastric wall deflected, its transversal septum (gt) partially sectioned. Scale bars = 1mm.



Pomacea scalaris anatomy: fig. 189- pallial cavity roof and anterior region of visceral mass, female, ventral view, oviduct deflected; fig. 190- detail of osphradium, ventral view; fig. 191- buccal mass, ventral view; fig. 192- kidney, ventral view, ventral wall removed, intestinal loops deflected, anterior lobe (ka) opened longitudinally; fig. 193- pallial cavity roof, transversal section in middle region of osphradium. Scale bars = 2mm.



Pomacea scalaris anatomy: fig. 194- foregut, lateral-right view; fig. 195- same, ventral view, odontophore removed, esophagus and left esophageal pouch (right in fig.) opened longitudinally; fig. 196- odontophore, dorsal view, radular ribbon removed, deflected and only partially shown, both cartilages and right m5 deflected; fig. 197- pallial oviduct, ventral view, seen as a transparent structure. Scale bars = 2mm.

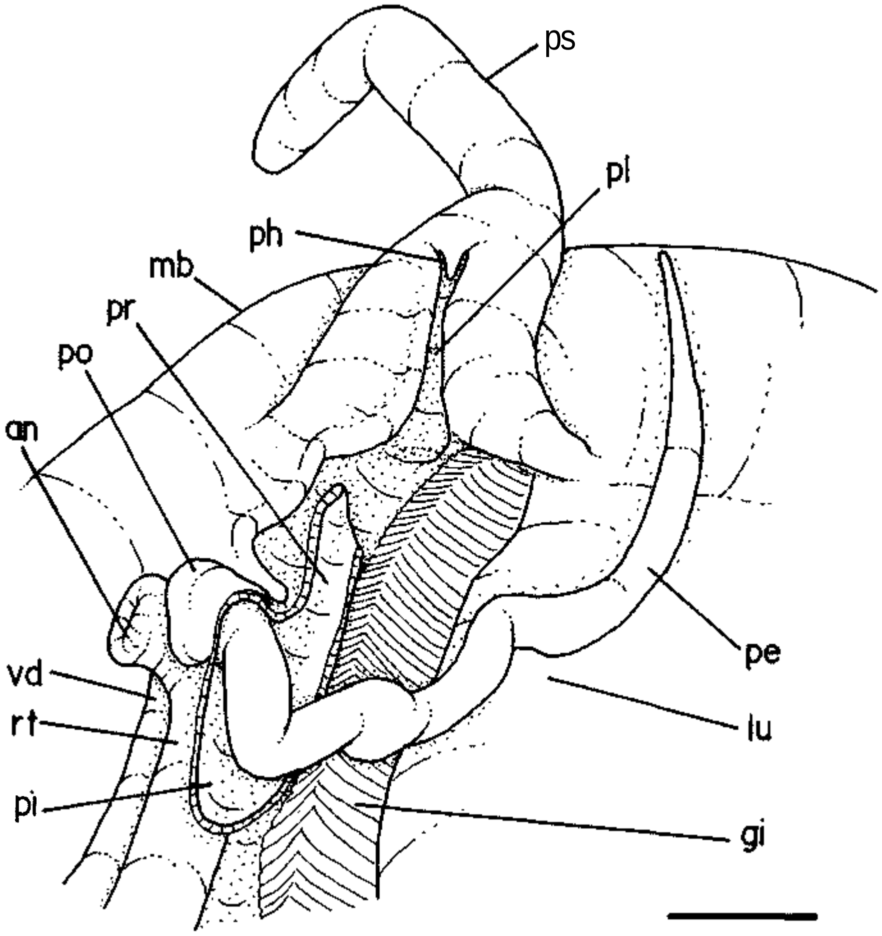
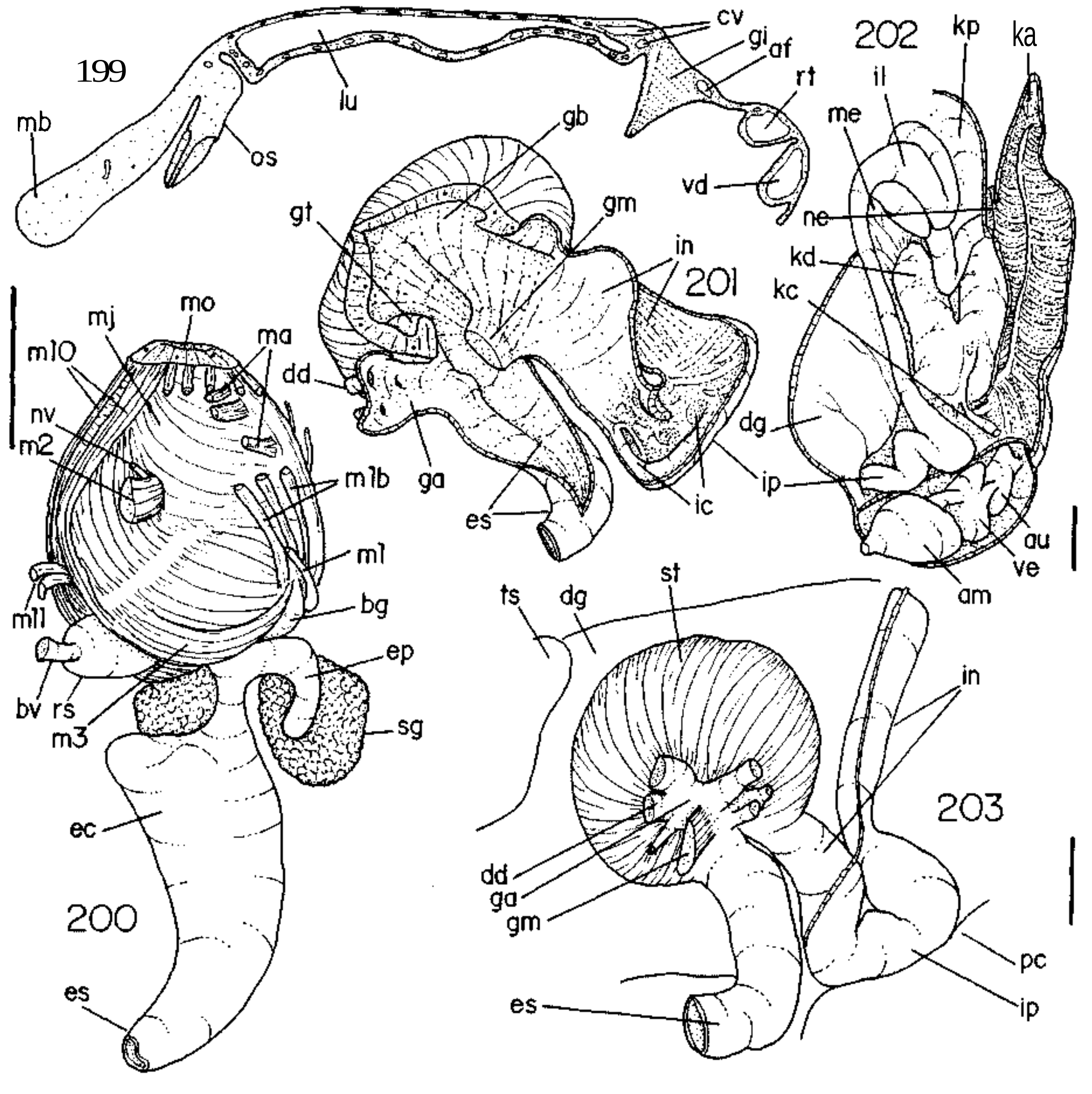
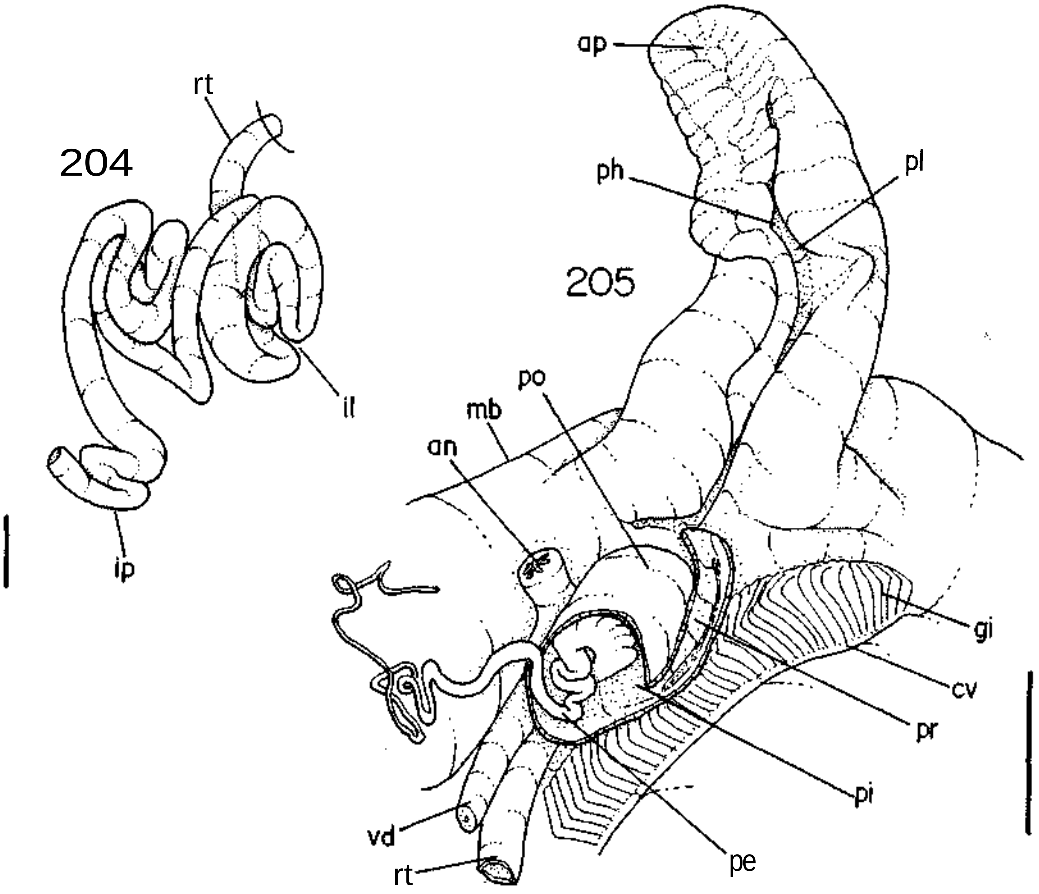


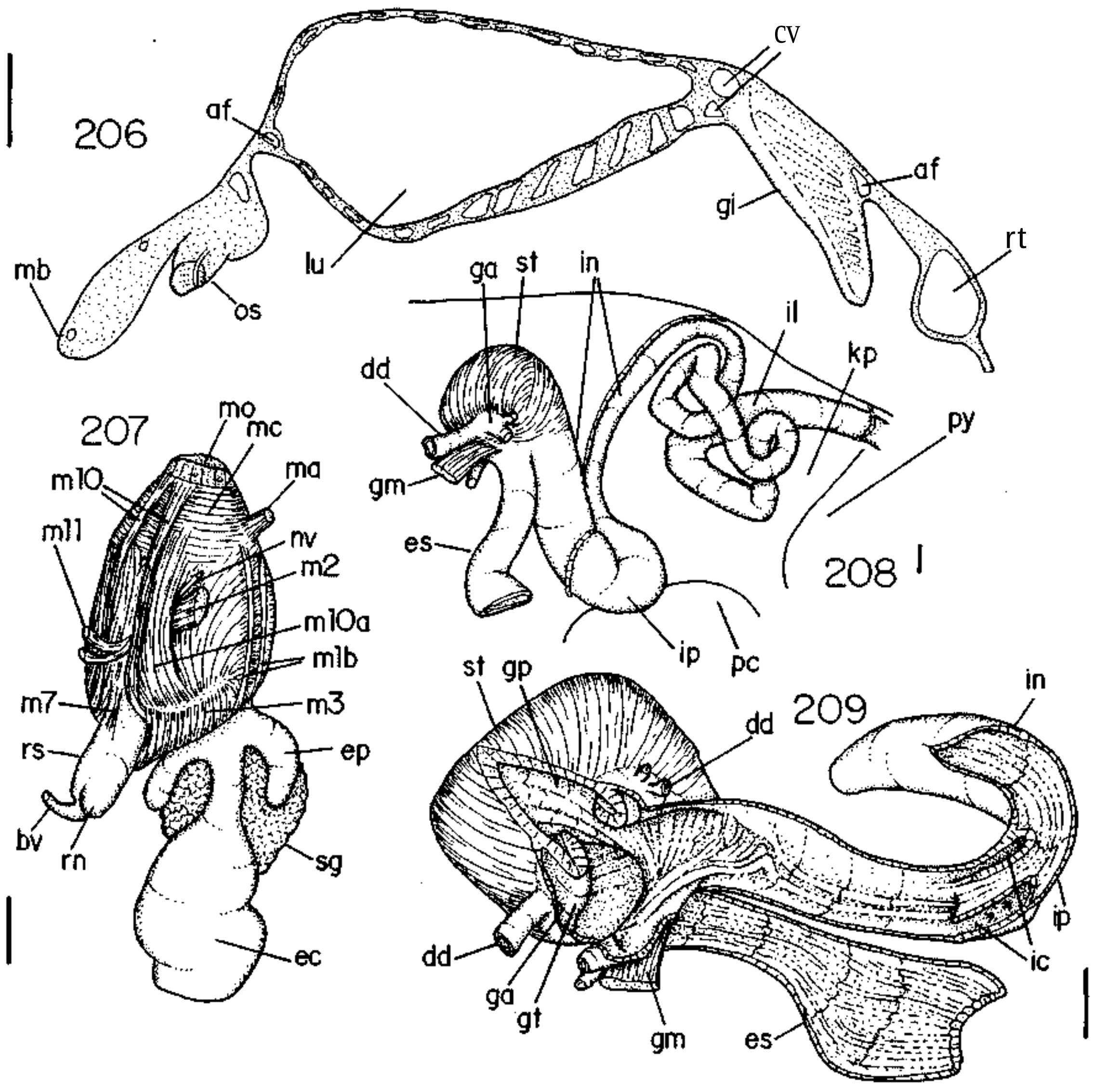
Fig. 198- *Pomacea* scalaris anterior region of male reproductive system, penis shield deflected outside, penis sac opened, penis stretched. Scale bar = 2mm.



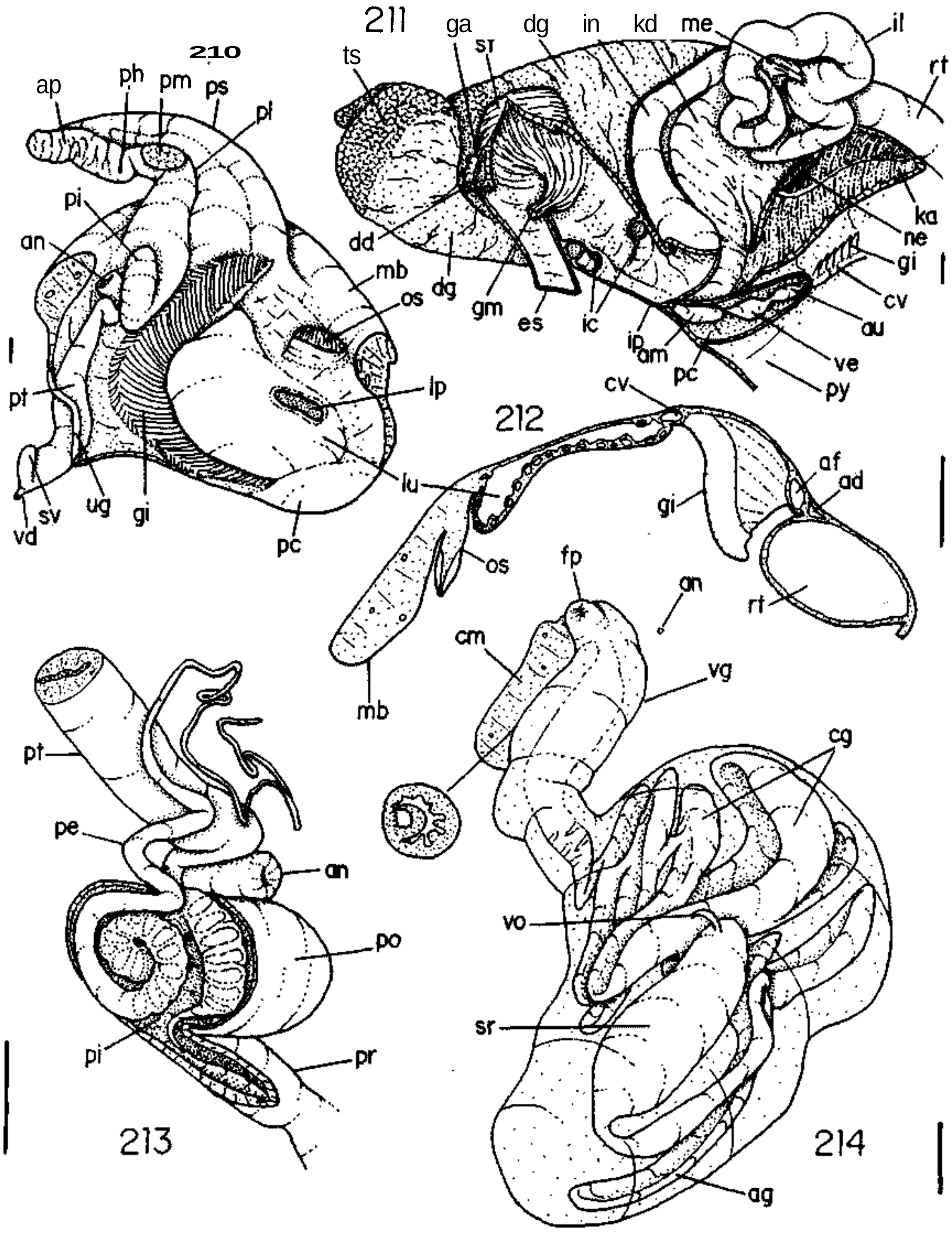
Pomacea canaliculata anatomy: fig. 199- pallial cavity roof, transversal section in middle region of osphradium; fig.200- foregut, buccal mass in lateral-left view, remainder structures in ventral view; fig.201-midgut, ventral view, most opened longitudinally, ventral gastric wall greatly deflected; fig.202- kidney and pericardium, ventral view, ventral walls removed, intestinal loops deflected, anterior lobe (ka) opened longitudinally; fig.203- midgut, ventral view as in situ. Scale bars = 5mm.



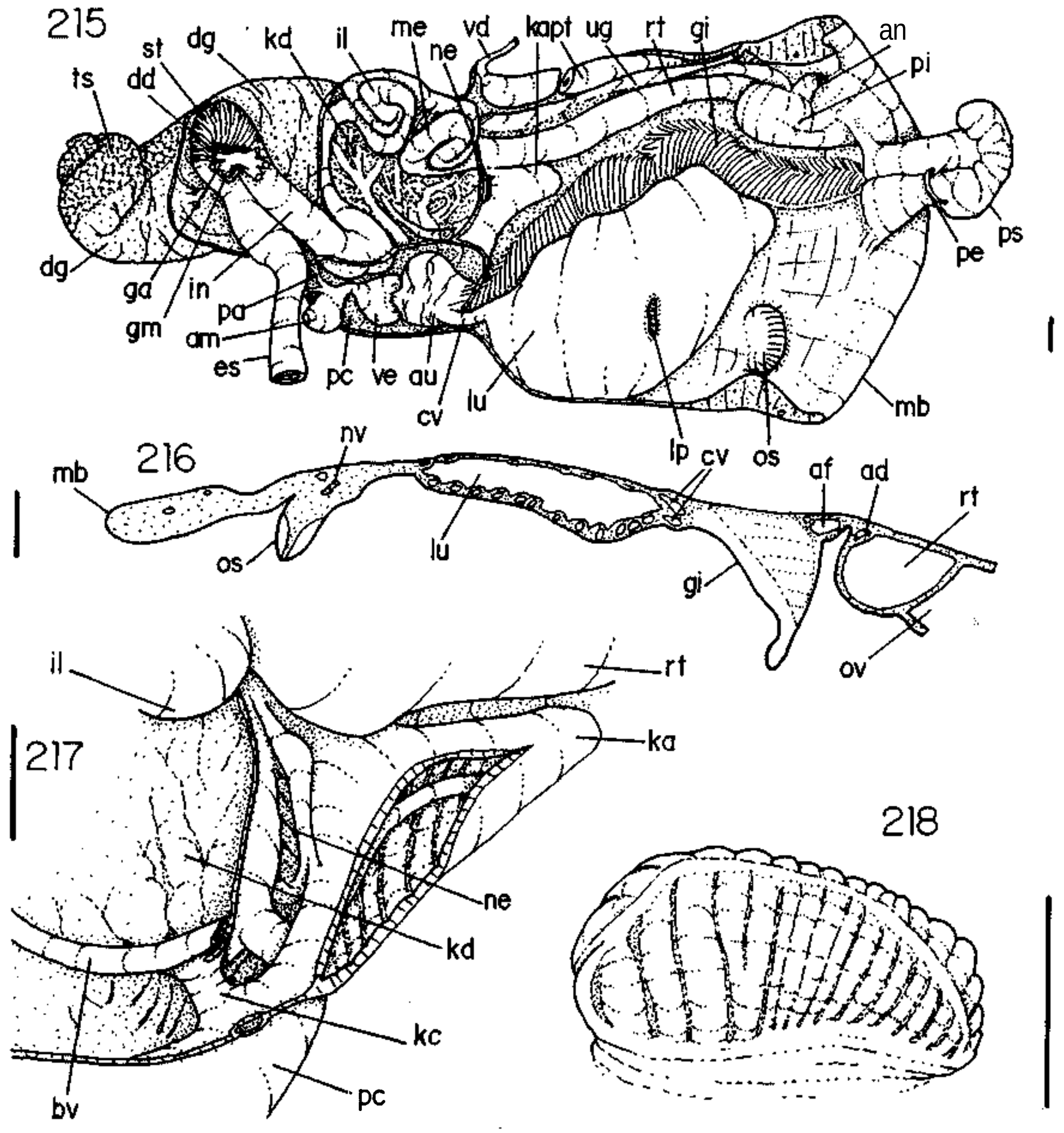
Pomacea canaliculata anatomy: fig.204- renal intestinal loops seen as in situ, ventral view; fig.205- anterior region of male reproductive system and adjacent pallial structures, penis shield deflected outside, penis sac opened, penis almost stretched. Scale bars = 5mm.



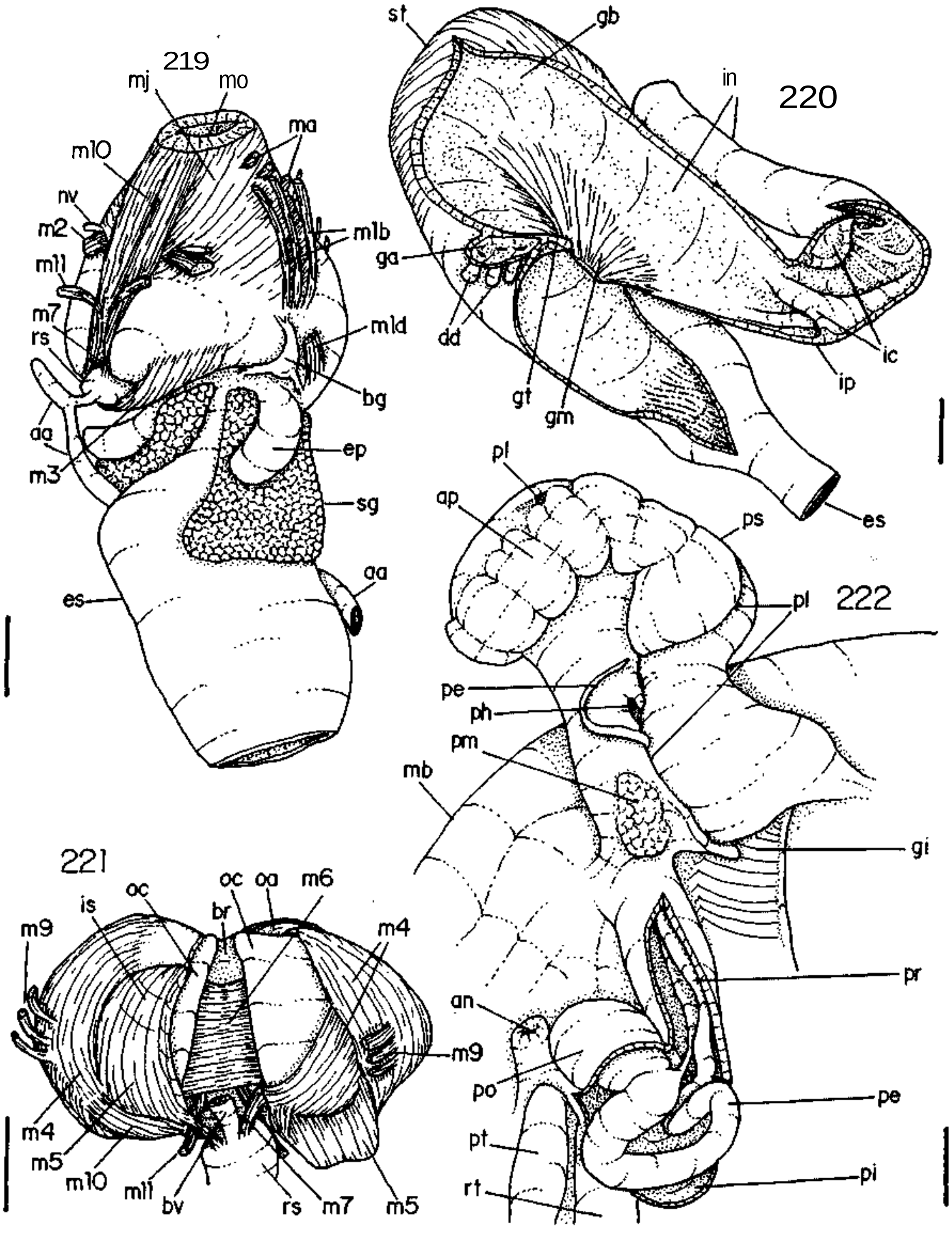
Pomacea lineata anatomy, mainland samples: fig.206- pallial cavity roof, transversal section in middle region of osphradium; fig.207- foregut, ventral-slightly left view; fig.208- middle and hindgut, ventral view as in situ; fig.209- midgut most opened longitudinally, ventral view. Scale bars = 2mm.



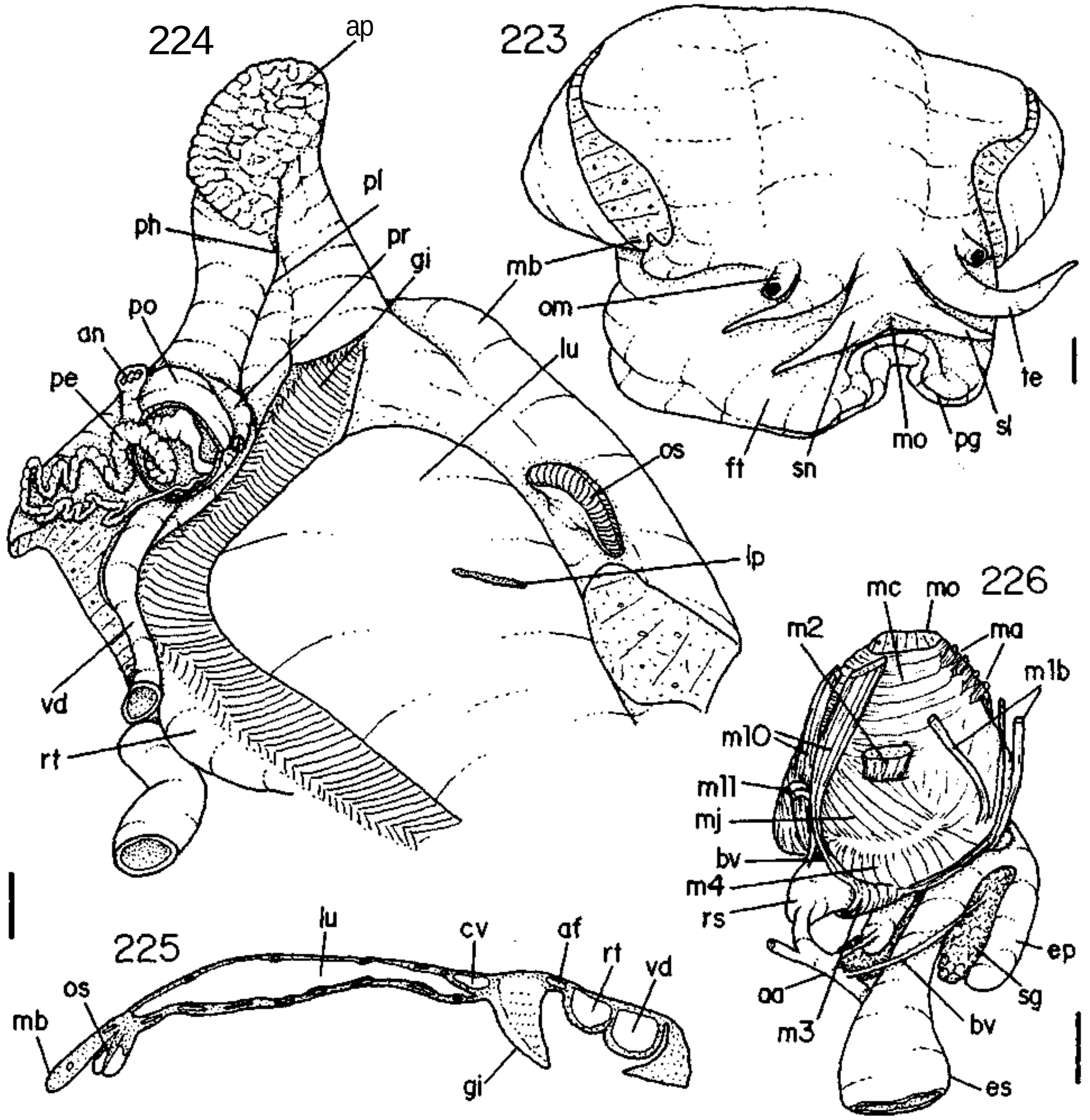
Pomacea lineata anatomy, Fernando de Noronha sample: **fig.210- pallial roof, ♂**, ventral-inner view, penis shield deflected outside, rectum extracted; **fig.211-** visceral mass partially uncoiled and posterior region of pallial cavity, ventral view, midgut opened longitudinally, ventral walls of kidney and pericardium removed, renal intestinal loops deflected, anterior lobe (ka) opened longitudinally; **fig.212- pallial** cavity roof, transversal section in middle region of osphradium; **fig.213- penis** sac and adjacent structures, ventral view, penis sac opened, penis partially stretched; fig.214- **pallial** oviduct, ventral view, seen as a transparent structure, a transversal section of indicated level of vaginal tube also shown. Scale bars = 2mm.



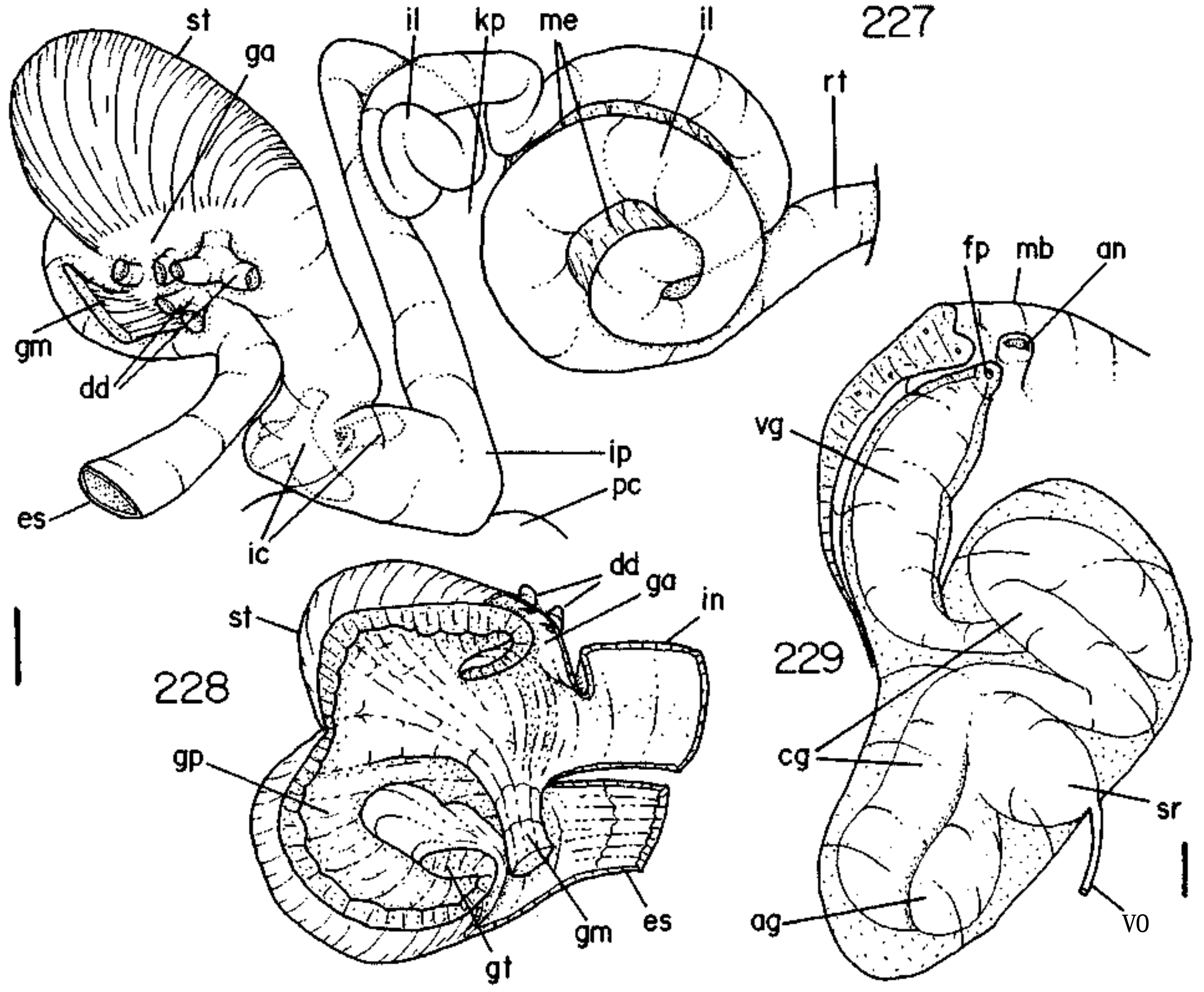
Pomacea sordida anatomy: **fig.215-** pallial cavity and visceral mass partially uncoiled, ♂, ventral view, penis shield deflected outside, prostate artificially sectioned transversally, ventral walls of kidney and pericardium removed, renal intestinal loops slightly deflected outside, portion of digestive gland ventral to midgut removed; **fig.216-** pallial cavity roof, transversal section in middle region of osphradium; **fig.217-** detail of anterior region of kidney, ventral view, ventral renal wall removed, nephrostome opened, anterior renal chamber (ka) partially opened longitudinally; **fig.218-** osphradium, ventral-slightly posterior view. Scale bars = 2mm.



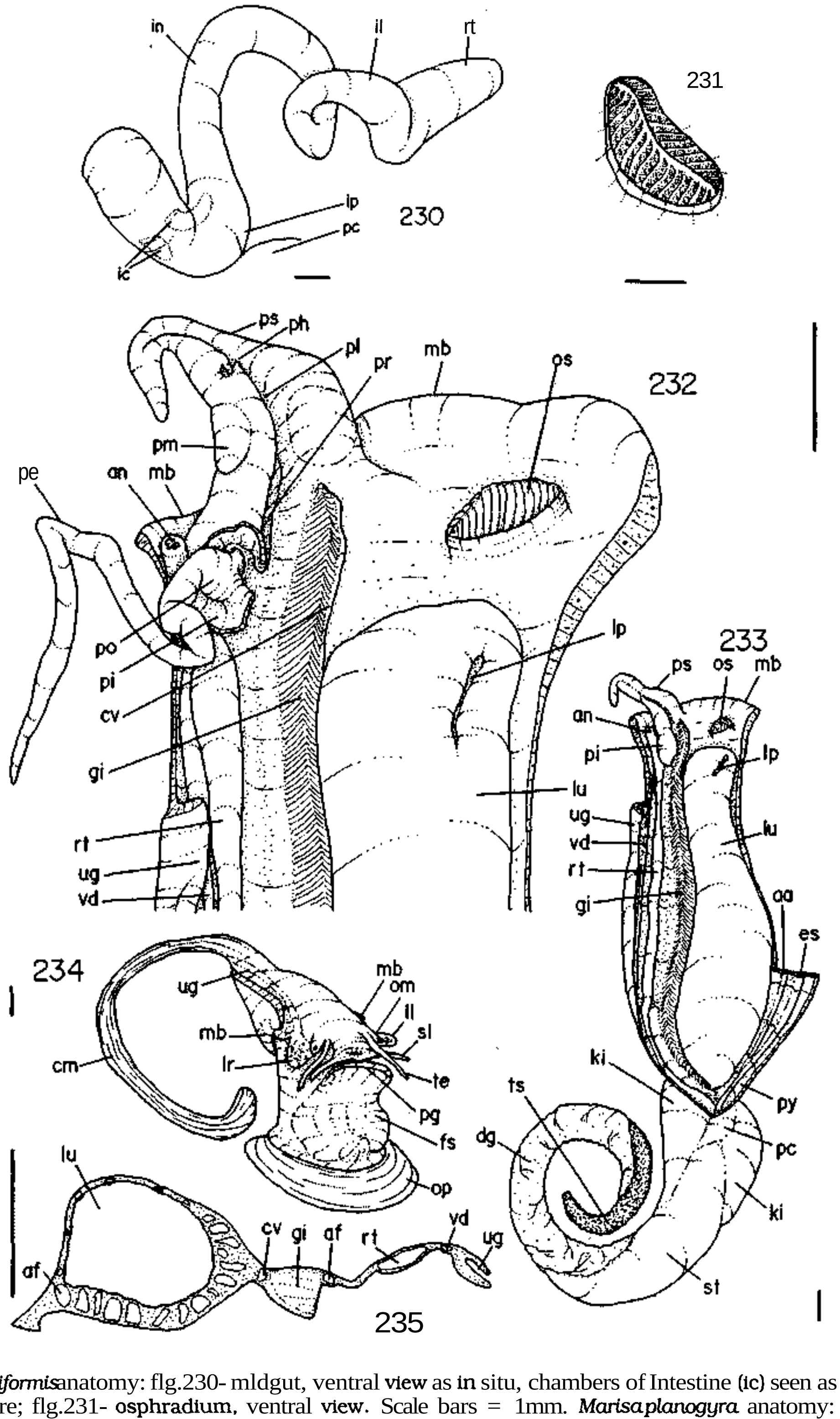
Pomacea sordida anatomy: **fig.219-** foregut, lateral-right view; **fig.220- midgut**, ventral **view**, most opened longitudinally; **fig.221-** odontophore, dorsal **view**, radula removed, deflected (only **radular** nucleus shown), both cartilages and left m5 deflected; fig.222- anterior region of male genital system and adjacent **pallial** structures, ventral view, penis shield deflected outside, penis sac opened, penis partially uncoiled, but **with** its apical portion still passing through its groove **in** penis shield. Scale bars = 2mm.



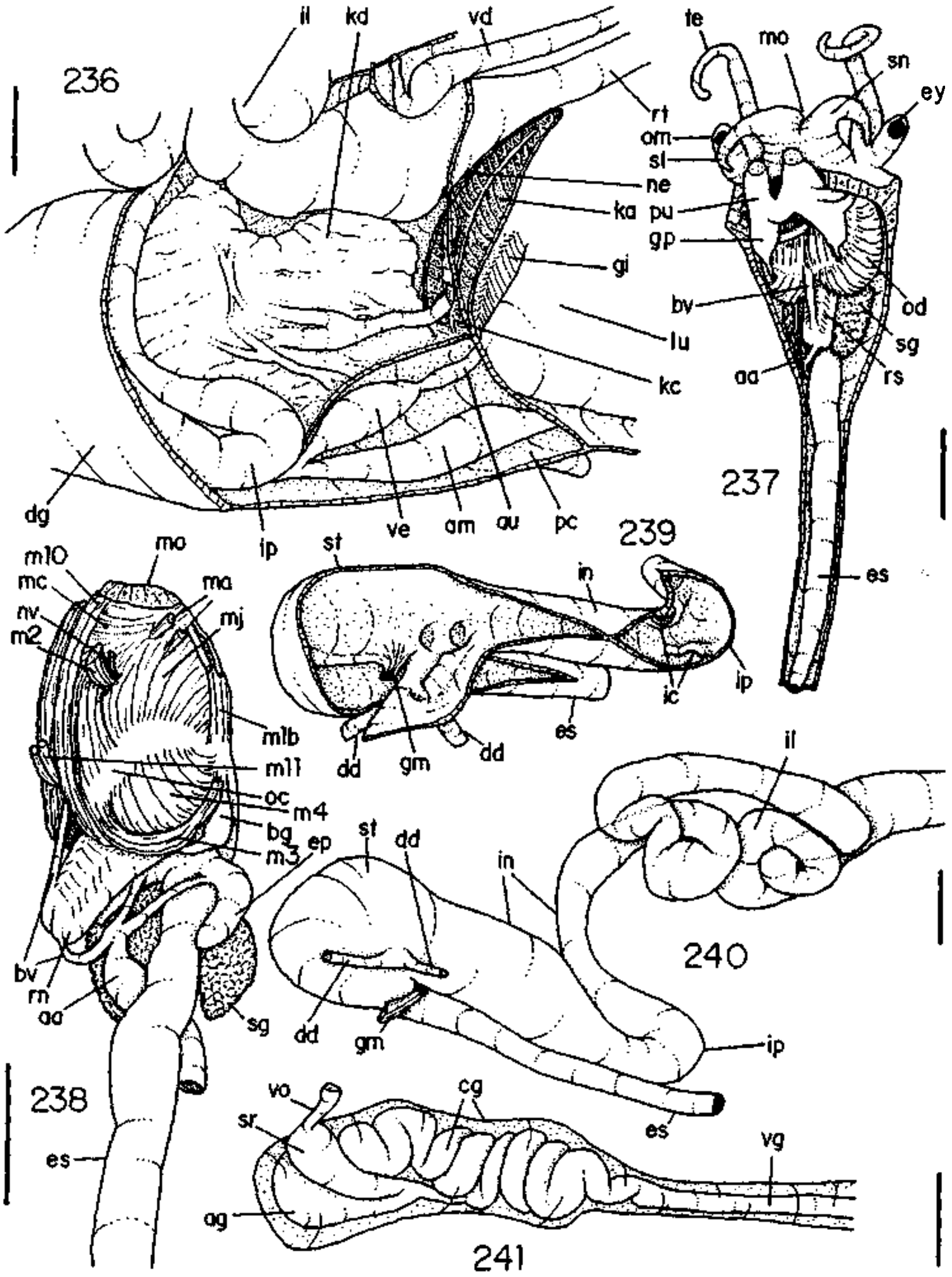
Asolene megastoma anatomy: fig.223- head-foot, ♂, frontal view; fig.224- pallial cavity, ♂, ventral-inner view, penis shield deflected outside, penis sac opened, penis partially stretched, prostate posterior region sectioned; fig.225- pallial cavity roof, transversal section in middle region of osphradium; fig.226- foregut, lateral-left view. Scale bars = 5mm.



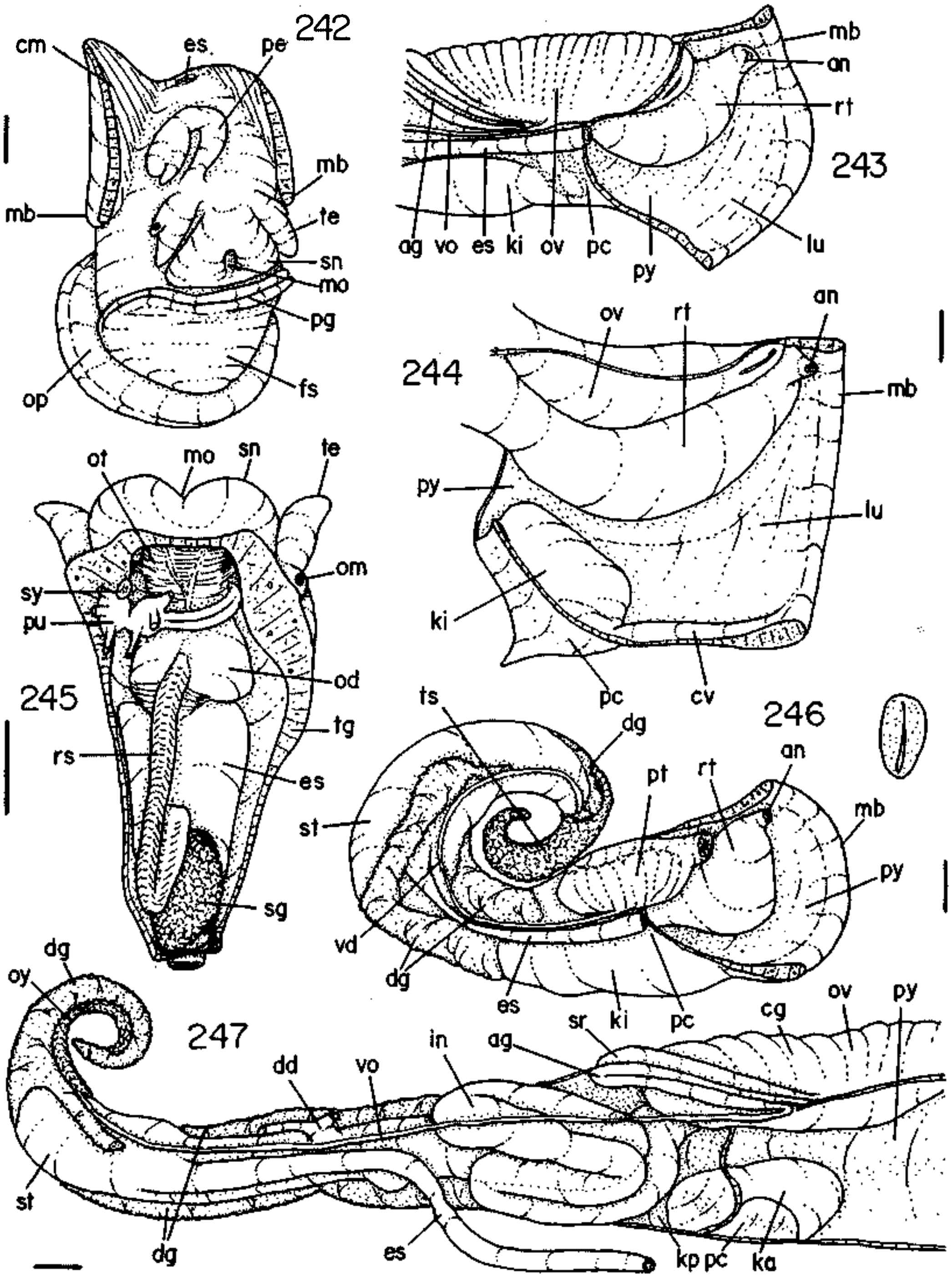
Asotene megastoma anatomy: *fig.227-* midgut, ventral view as in situ, chambers of Intestine (ic) seen as if Intestine was a transparent structure; fig.228- stomach and adjacent portions of stomach and Intestine, ventral view, entirely opened longitudinally; fig.229- pallial oviduct and adjacent region of pallial cavity, ventral view, oviduct seen as a transparent structure. Scale bars = 5mm.



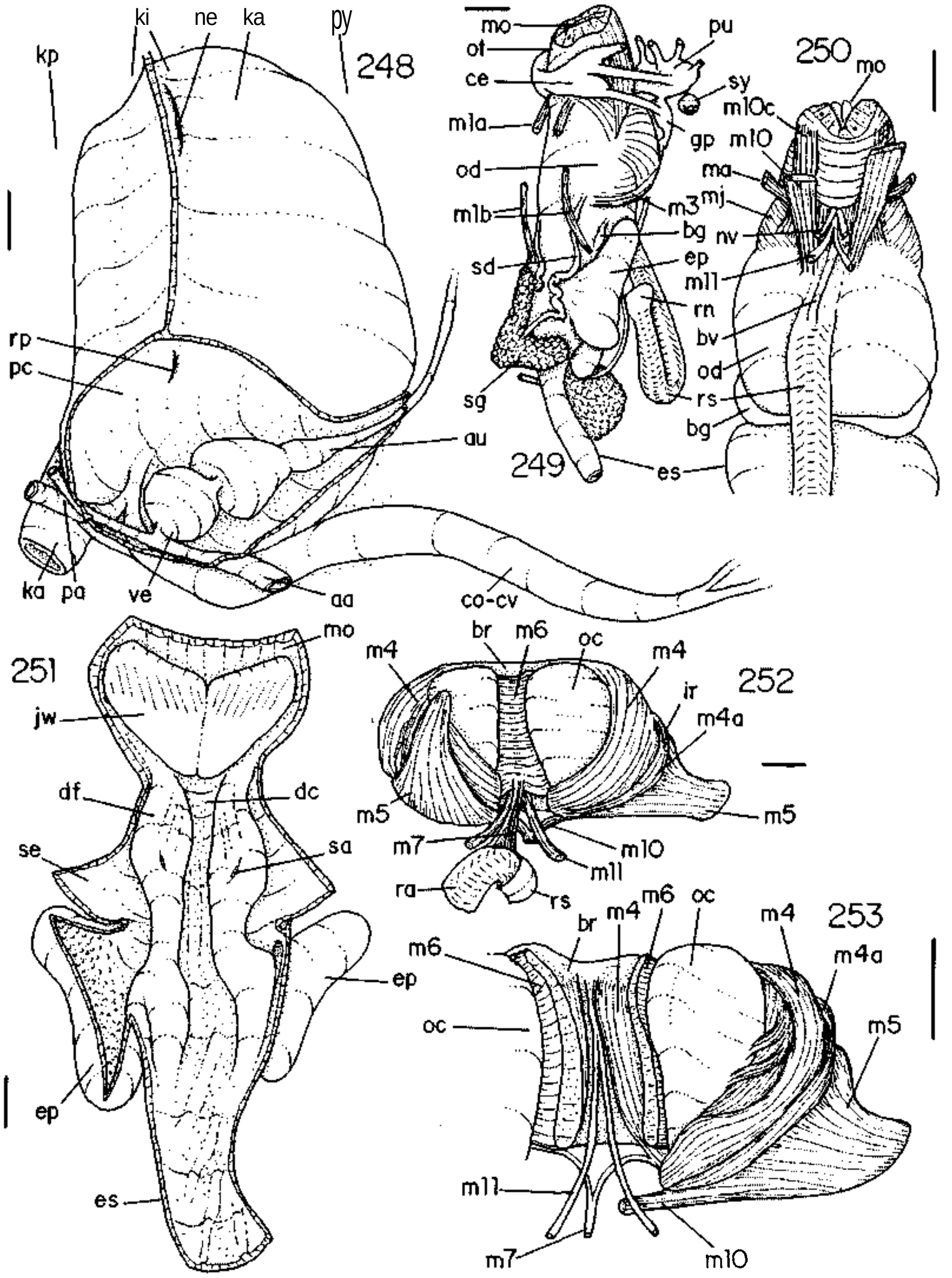
Felipponea neritiniformis anatomy: fig.230- midgut, ventral view as in situ, chambers of intestine (ic) seen as if intestine was a transparent structure; fig.231- osphradium, ventral view. Scale bars = 1mm. *Marisa planogyra* anatomy: fig.232- anterior portion of pallial cavity, ♂, ventral-inner view, penis shield deflected outside, penis sac opened, penis partially stretched; fig.233- pallial cavity and visceral mass partially uncoiled, male, ventral view, penis shield deflected outside; fig.234- head-foot, ♂, frontal view; fig.235- pallial cavity roof, transversal section in middle region of lung. Scale bars = 2mm.



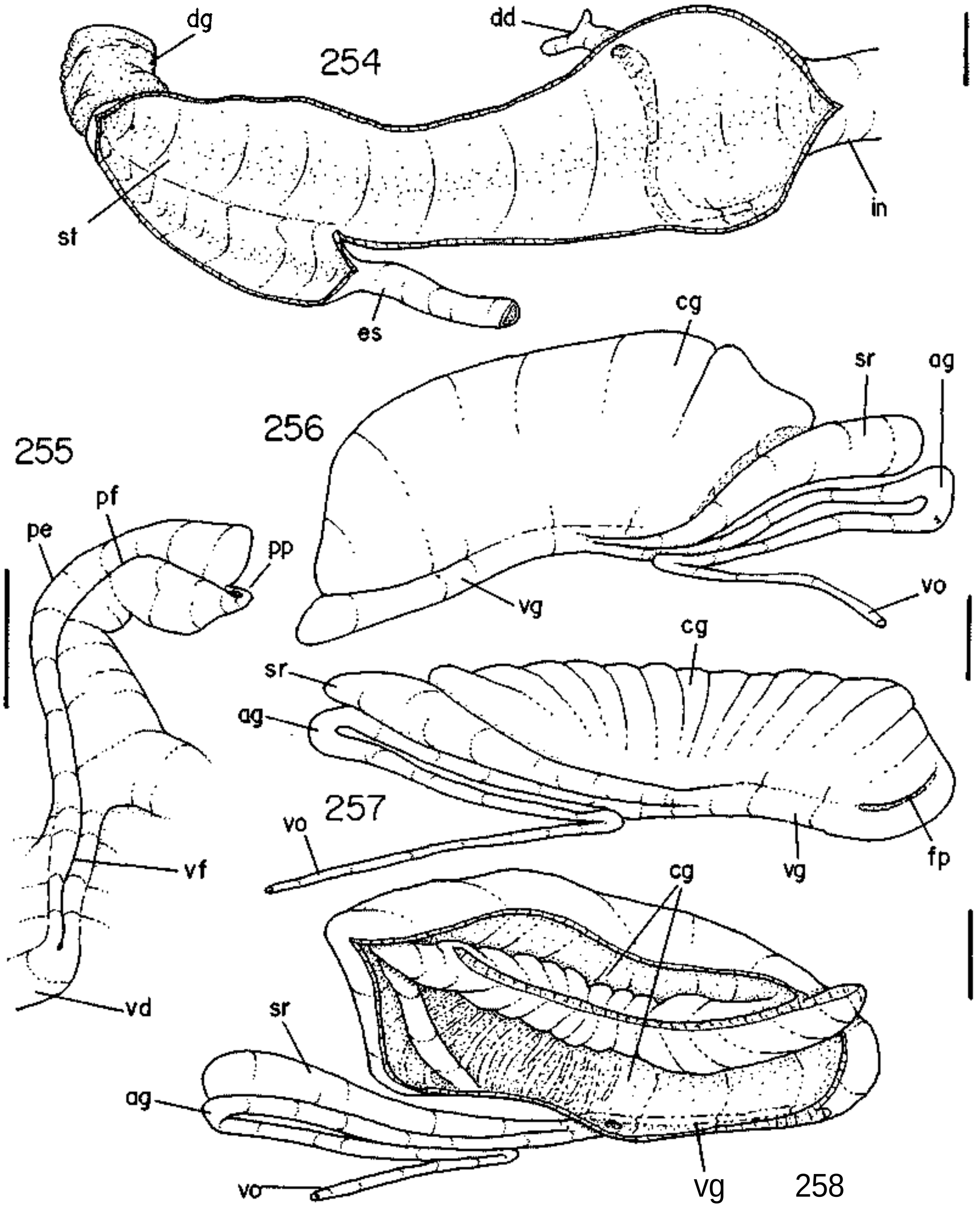
***Marisa planogyra* anatomy:** fig.236- kidney and adjacent structures, ventral view, ventral walls of kidney and pericardium removed, renal intestinal loops deflected outside and only partially shown, anterior renal chamber opened longitudinally; fig.237- head and haemocoel, ventral view, foot removed; fig.238- foregut, lateral-left view; fig.239- midgut, ventral view, most opened longitudinally, ventral gastric wall deflected; fig.240- midgut, ventral view as in situ; fig.241- pallial oviduct posterior region, not fully mature, ventral view, seen as a transparent structure. Scale bars = 2mm.



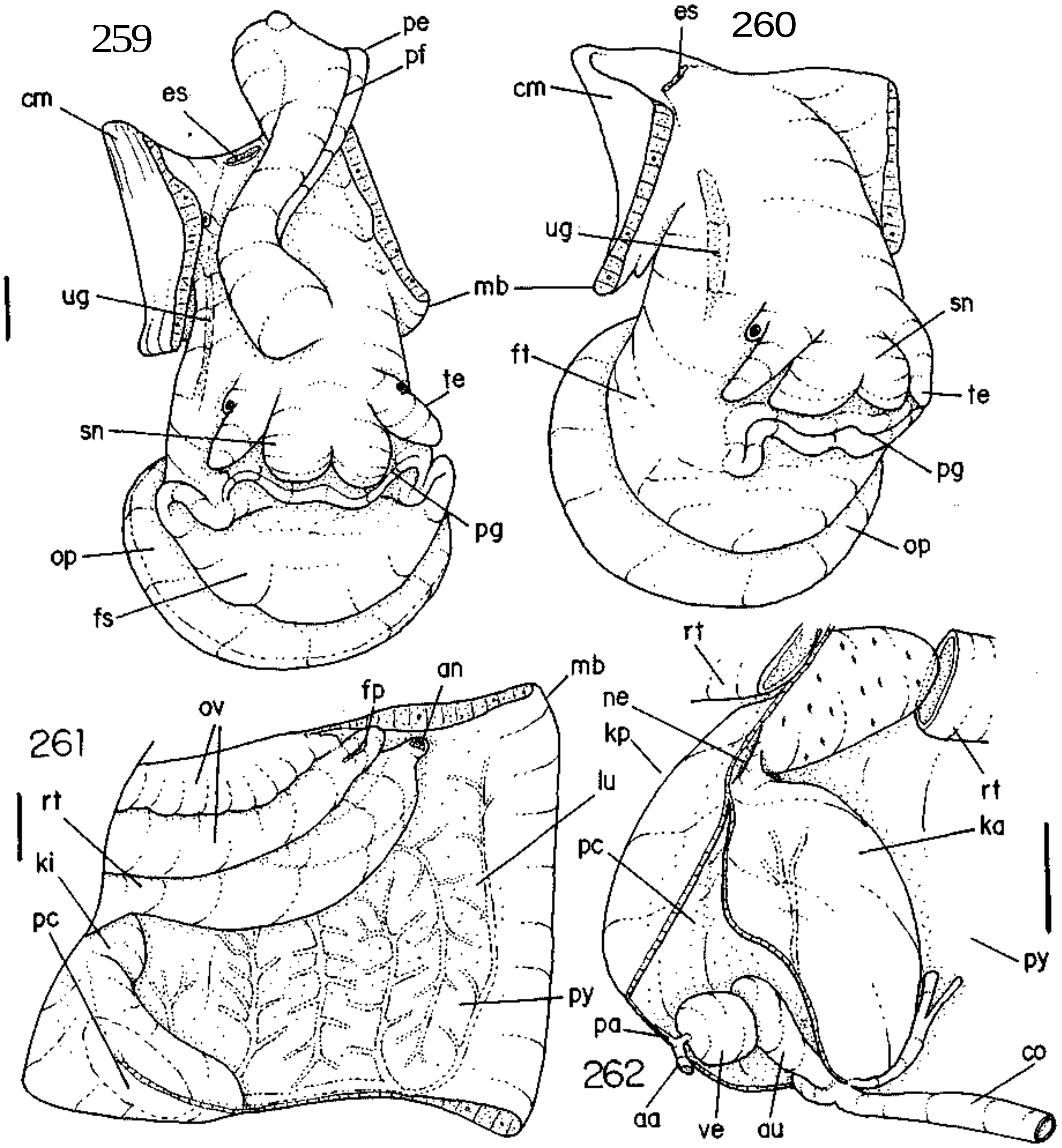
Neocyclotus prominulus anatomy: fig.242- head-foot, ♂, frontal view; fig.243- pallial cavity and anterior region of visceral mass, 5 . ventral view; fig.244- same, mantle posterior region deflected; fig.245- head and haemocoel, ventral view, foot removed; fig.246- pallial cavity and visceral mass partially uncoiled, ♂, ventral view, a detail of a transversal section of prostate shown at right; fig.247- partially uncoiled visceral mass and posterior region of pallial cavity, ventral view, esophagus deflected, digestive gland portion ventral to stomach partially removed. Scale bars = 1mm.



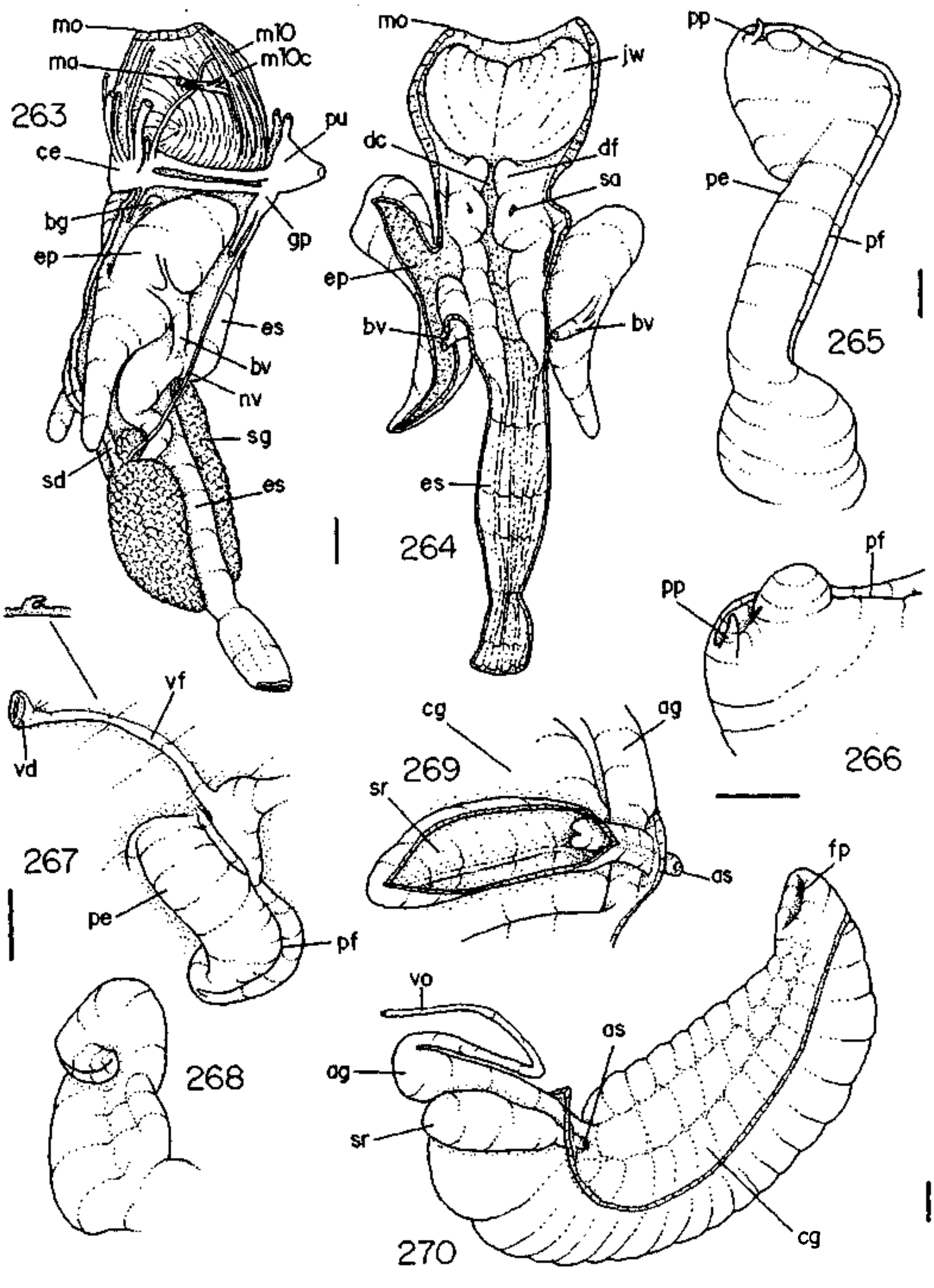
Neocyclotus prominulus anatomy: fig.248- kidney and adjacent structures, ventral view, ventral wall of pericardium removed; fig.249- foregut, lateral-right view; fig.250- buccal mass and anterior region of esophagus, ventral view; fig.251- foregut, ventral view, odontophore removed, esophagus and right esophageal pouch (left in fig.) opened longitudinally; fig.252- odontophore, dorsal view, radula removed, deflected and only partially shown, both cartilages and left m5 deflected; fig.253- same, m6 sectioned longitudinally, only middle and right structures shown, m4 partially separated from cartilage. Scale bars = 0.5mm.



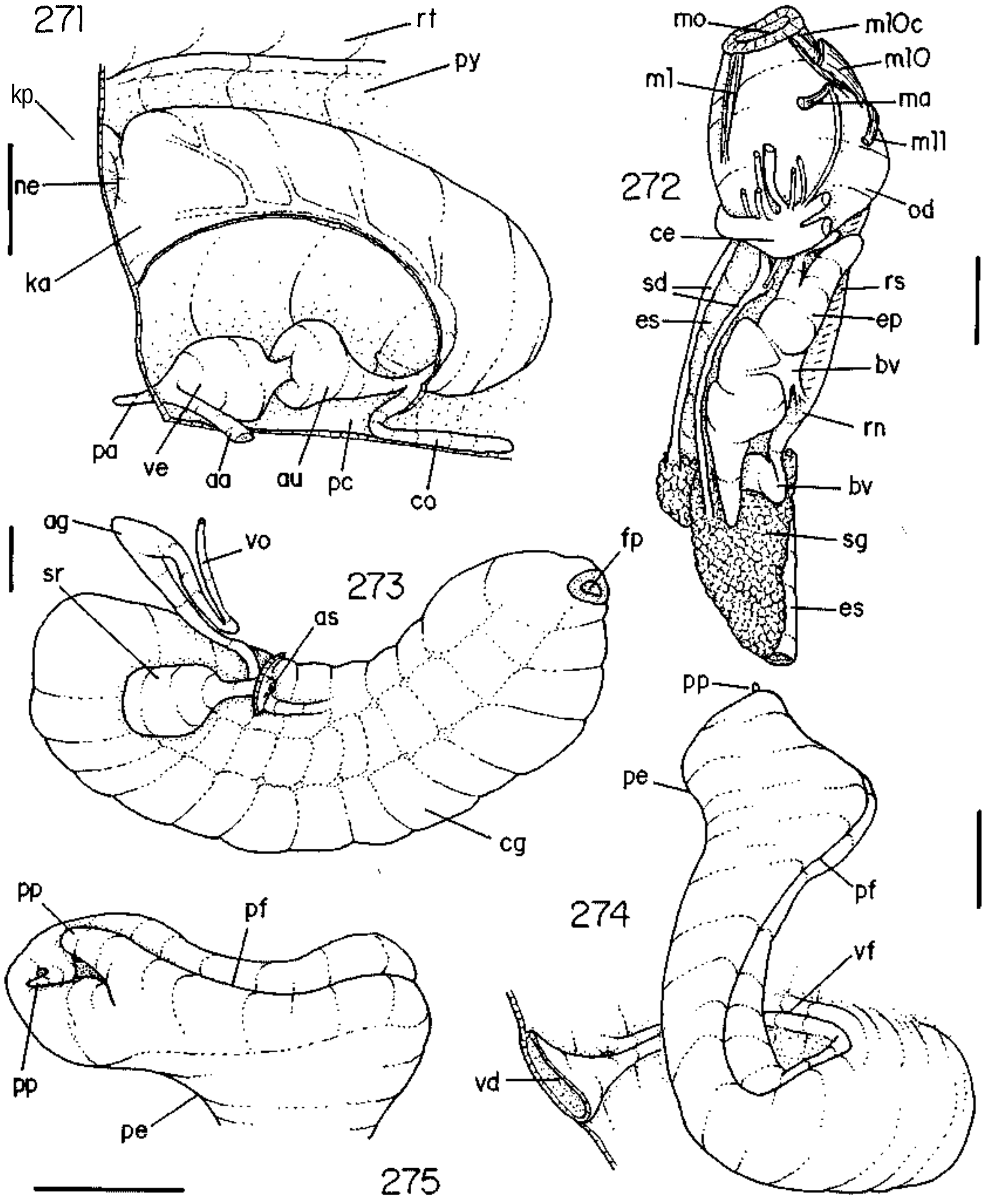
Neocyclotus prominulus anatomy: fig.254- stomach and adjacent portions of esophagus and intestine, ventral view, most opened longitudinally; fig.255- penis and adjacent region of pallial floor, dorsal view; fig.256- pallial oviduct, dorsal view as in situ; fig.257- same, ventral view; fig.258- same, capsule gland (cg) opened longitudinally. Scale bars = 1mm.



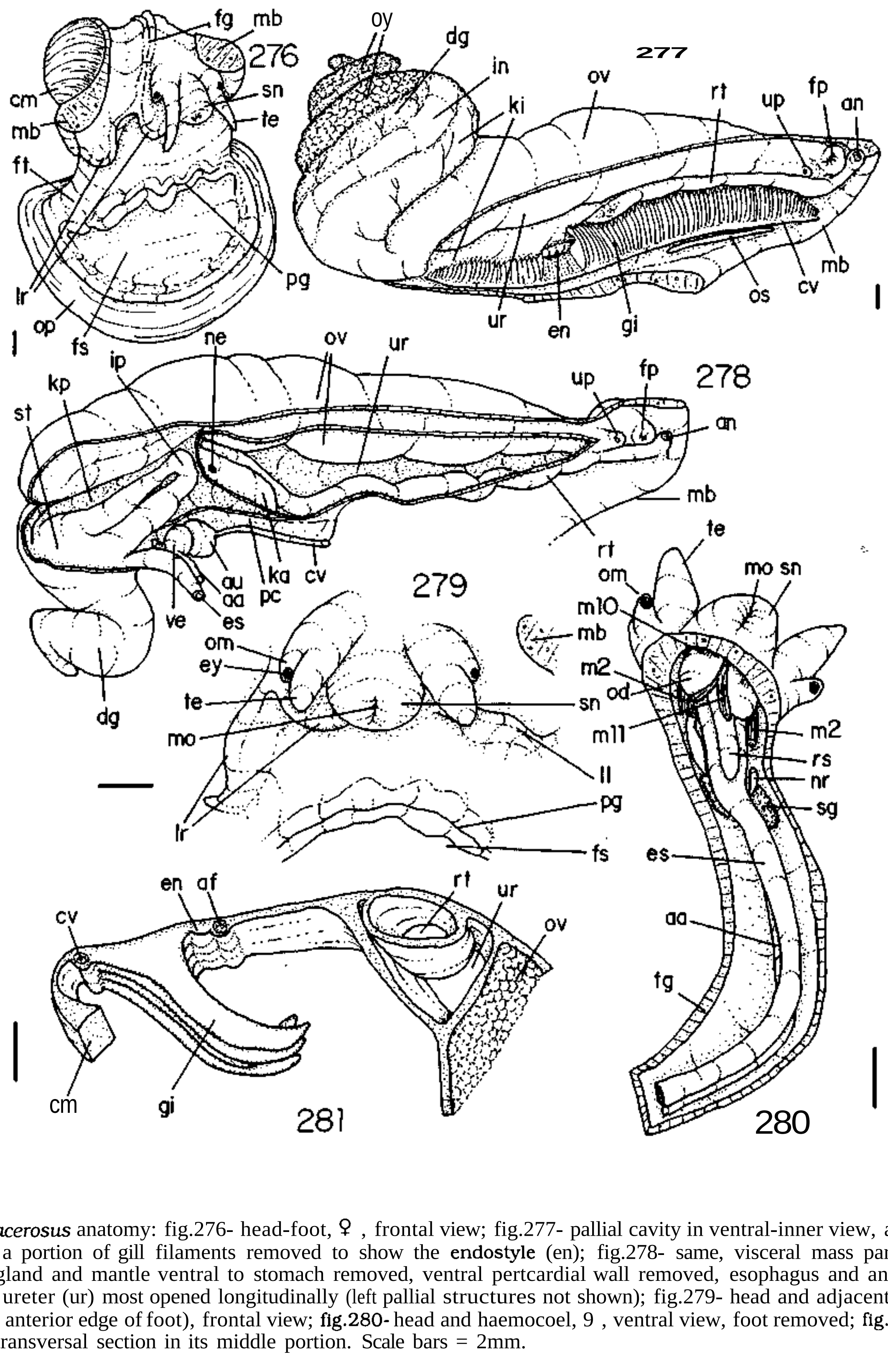
Incidostoma tupy anatomy: fig.259- head-foot, ♂, frontal view; fig.260- head-foot, 9 , frontal-slightly left view; fig.261- pallial cavity (lung), 9 , ventral-inner view; fig.262- region between visceral mass and pallial cavity, ventral view, ventral wall of pericardium and portion of rectum ventral to kidney removed. Scale bars = 2mm.



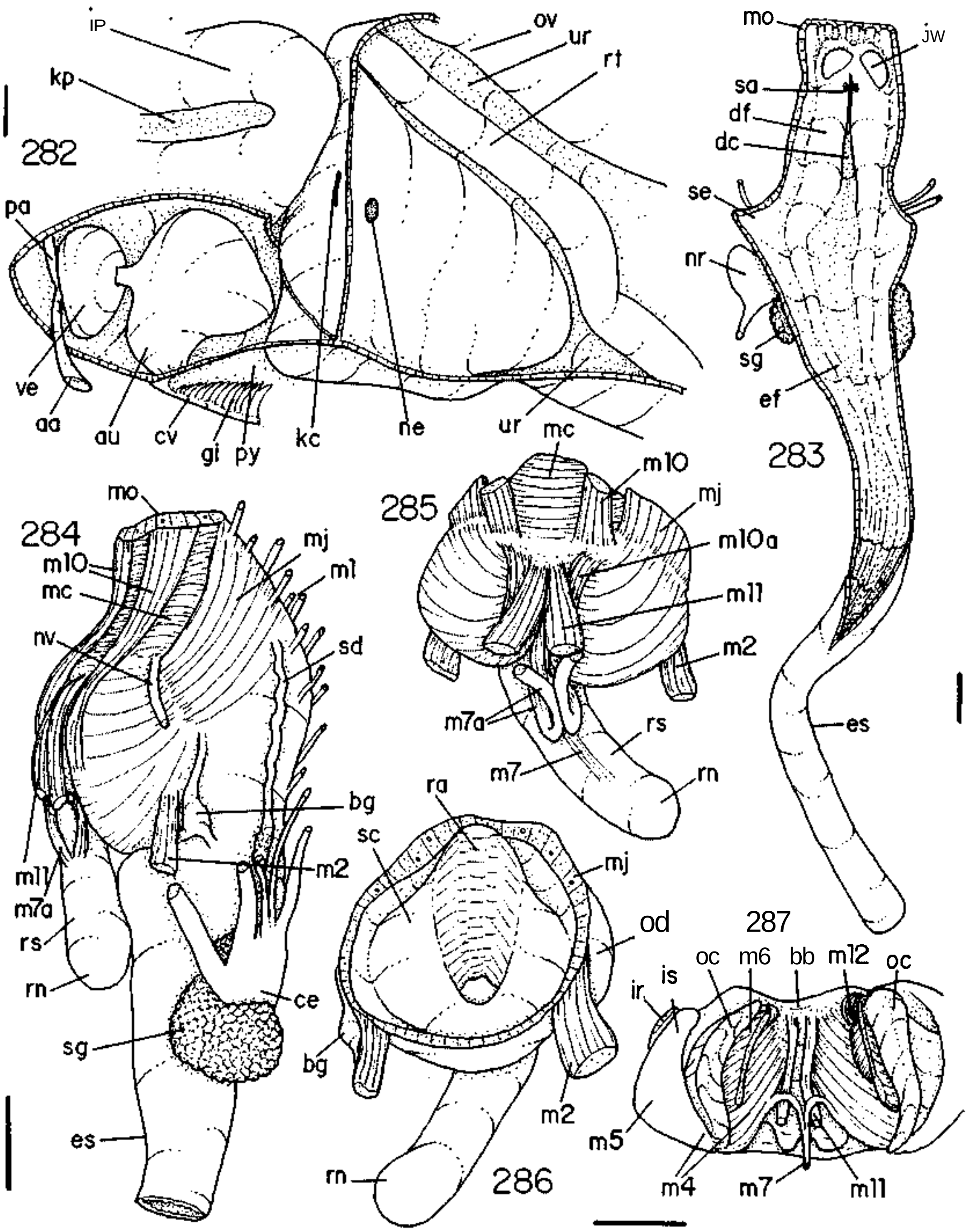
Incidostoma tupy anatomy: fig.263- foregut, lateral-left view; fig.264- same, ventral view, odontophore removed, esophagus and right esophageal pouch (left in fig.) opened longitudinally; fig.265- penis, dorsal view; fig.266- same, detail of its apical region; fig.267- penis and adjacent region of pallial cavity floor of Immature male, dorsal view, detail of a transversal section in indicated region of sperm groove also shown; fig.268- same, ventral view; fig.269- detail of posterior region of pallial oviduct, ventral view, seminal receptacle (sr) opened longitudinally; fig.270- pallial oviduct, ventral view as in situ. Scale bars = 1mm.



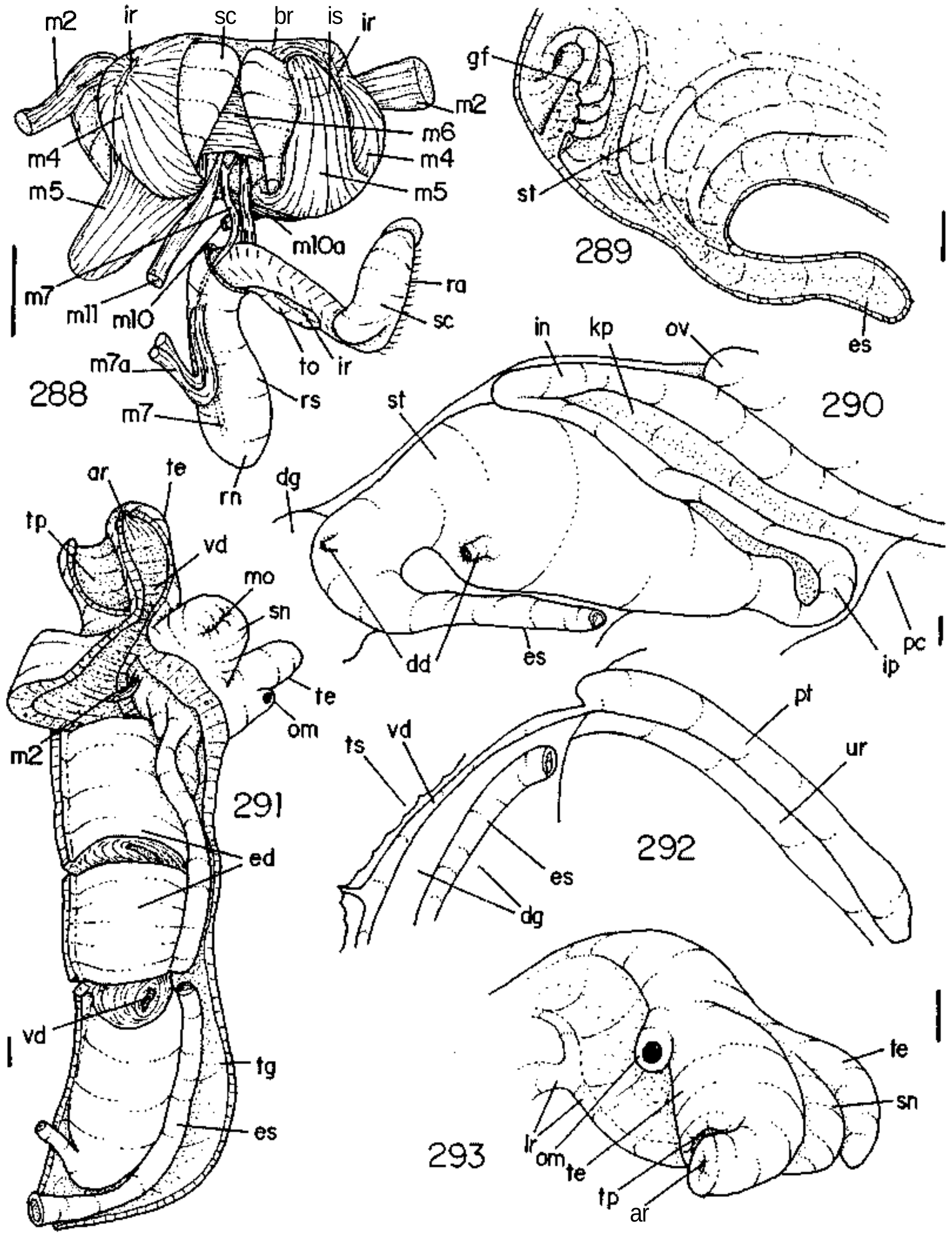
Aperostoma blanchetiana anatomy: fig.271- kidney and adjacent structures, ventral view, ventral wall of pericardium removed; fig.272- foregut, lateral-left view; fig.273- pallial oviduct, ventral view, posterior structures shown as in situ; fig.274- penis and adjacent region of pallial floor, dorsal view; fig.275- same, detail of its apical region. Scale bars = 1mm.



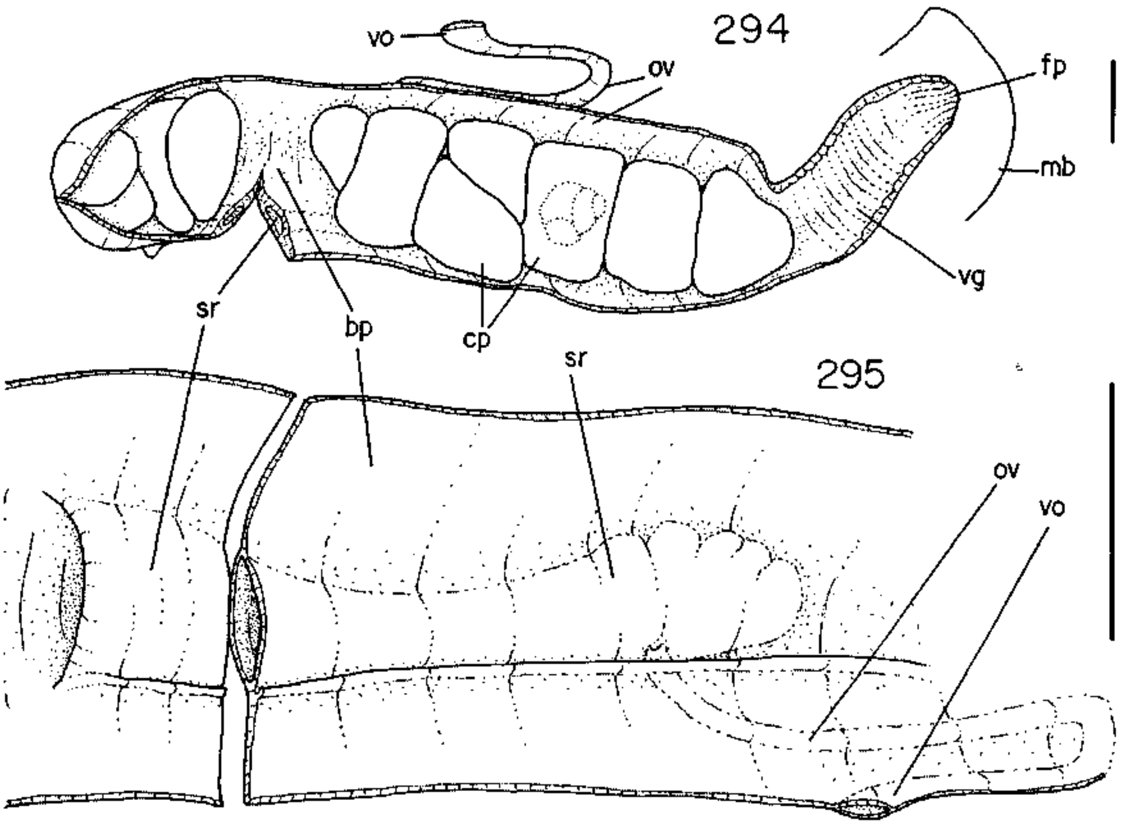
Viviparus acerosus anatomy: fig.276- head-foot, ♀ , frontal view; fig.277- pallial cavity in ventral-inner view, and visceral mass, 9 , a portion of gill filaments removed to show the endostyle (en); fig.278- same, visceral mass part uncoiled, digestive gland and mantle ventral to stomach removed, ventral pertcardial wall removed, esophagus and anterior aorta deflected, ureter (ur) most opened longitudinally (left pallial structures not shown); fig.279- head and adjacent structures (including anterior edge of foot), frontal view; fig.280- head and haemocoel, 9 , ventral view, foot removed; fig.281- pallial roof, 9 , transversal section in its middle portion. Scale bars = 2mm.



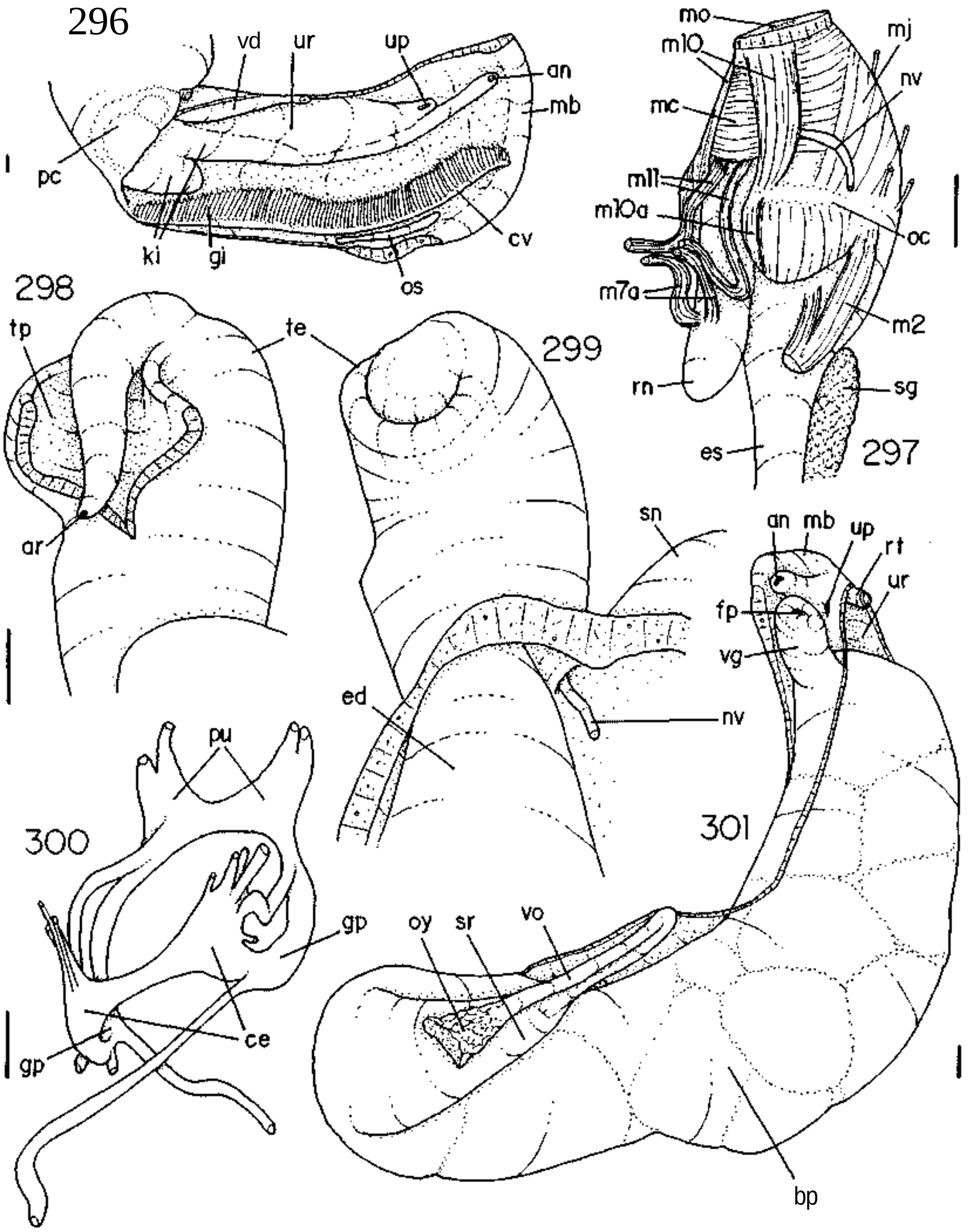
Viviparus acerosus anatomy: fig.282- kidney and adjacent structures, ventral view, ventral wall of pericardium removed, ureter opened longitudinally; fig.283- foregut, ventral view, odontophore removed, esophagus partially opened longitudinally; fig.284- foregut, lateral-left view; fig.285- odontophore, ventral view; fig.286- same, dorsal view; fig.287- same, dorsal view, radular ribbon extracted, both cartilages deflected, m6 sectioned longitudinally, lateral structures weakly shown. Scale bars = 1mm.



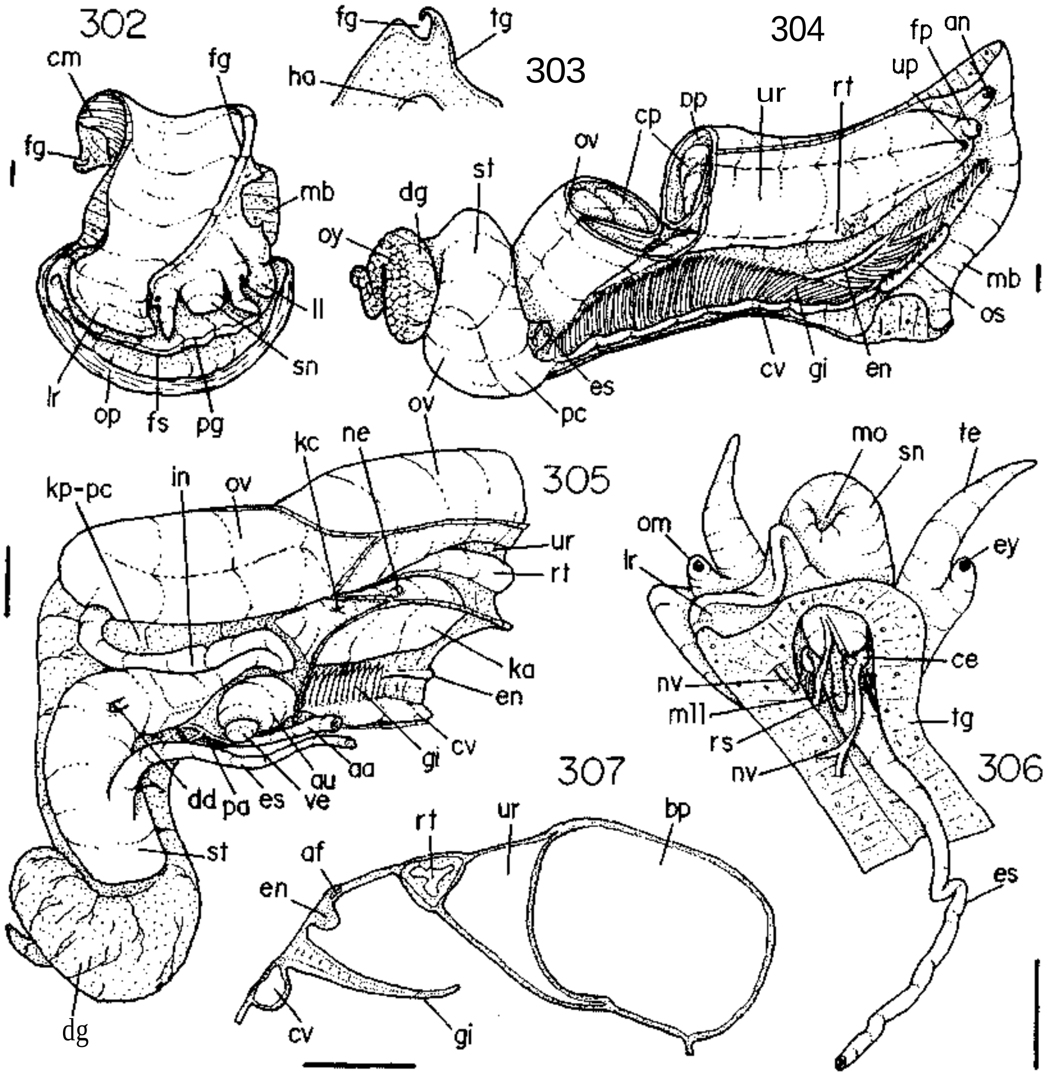
Viviparus acerosus anatomy: fig.288- odontophore, dorsal view, radular ribbon removed and deflected downwards, both cartilages and left m5 deflected; fig.289- stomach opened longitudinally, ventral view, distal region not shown; fig.290- midgut, ventral view, seen as in situ; fig.291- head and haemocoel, ♂, ventral view, foot removed, some transversal sections along vas deferens artificially done, right tentacle (left in fig.) opened longitudinally; fig.292- middle region of male genital system, dorsal view, seen as in situ; fig.293- head, ♂, lateral-right view. Scale bars = 1mm.



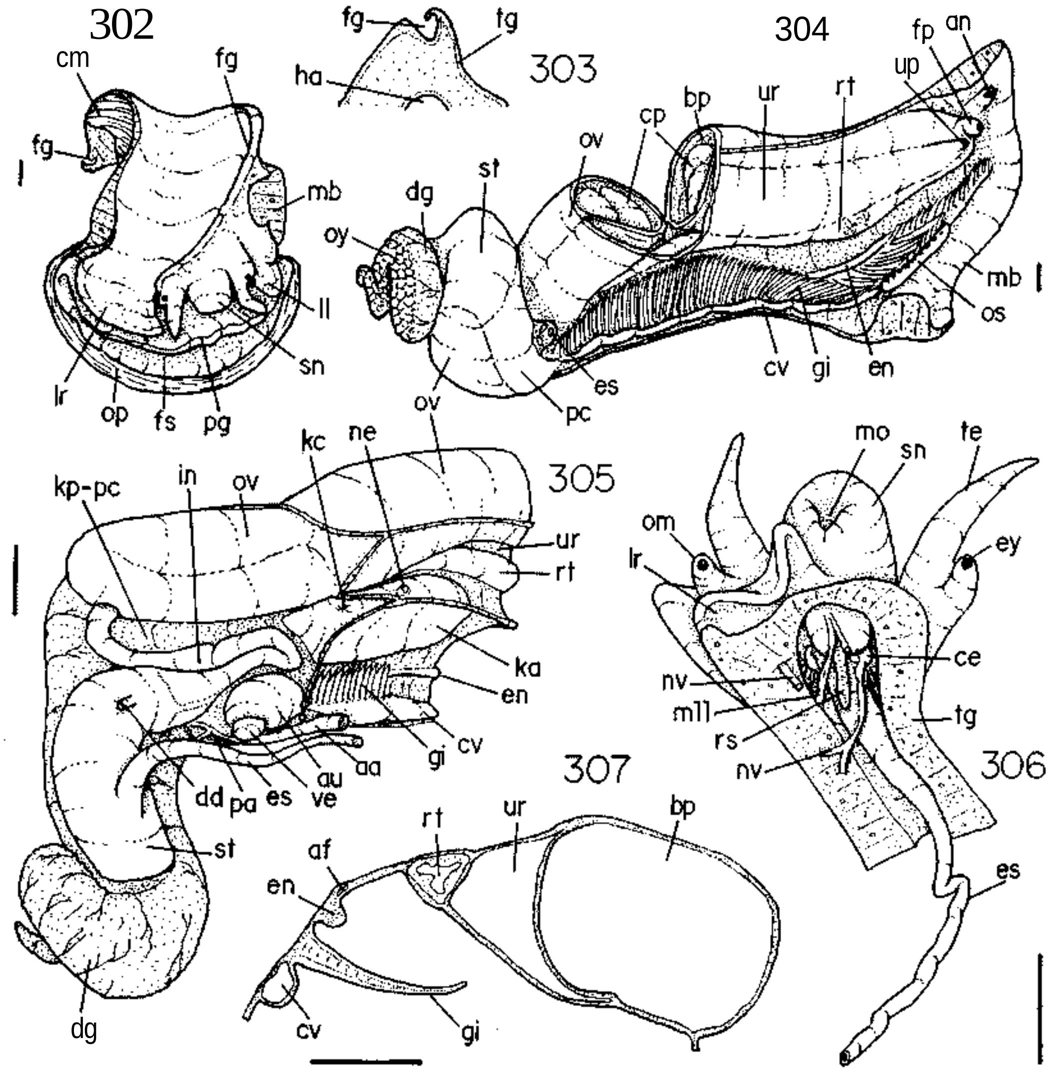
Viviparus acerosus pallial oviduct, ventral view: fig.294- whole view, uterus most opened longitudinally, some capsules still inside, an incomplete transversal section in its posterior region artificially done; fig.295- detail of uterus posterior region, showing middle portion of oviduct by transparency. Scale bars = 5mm.



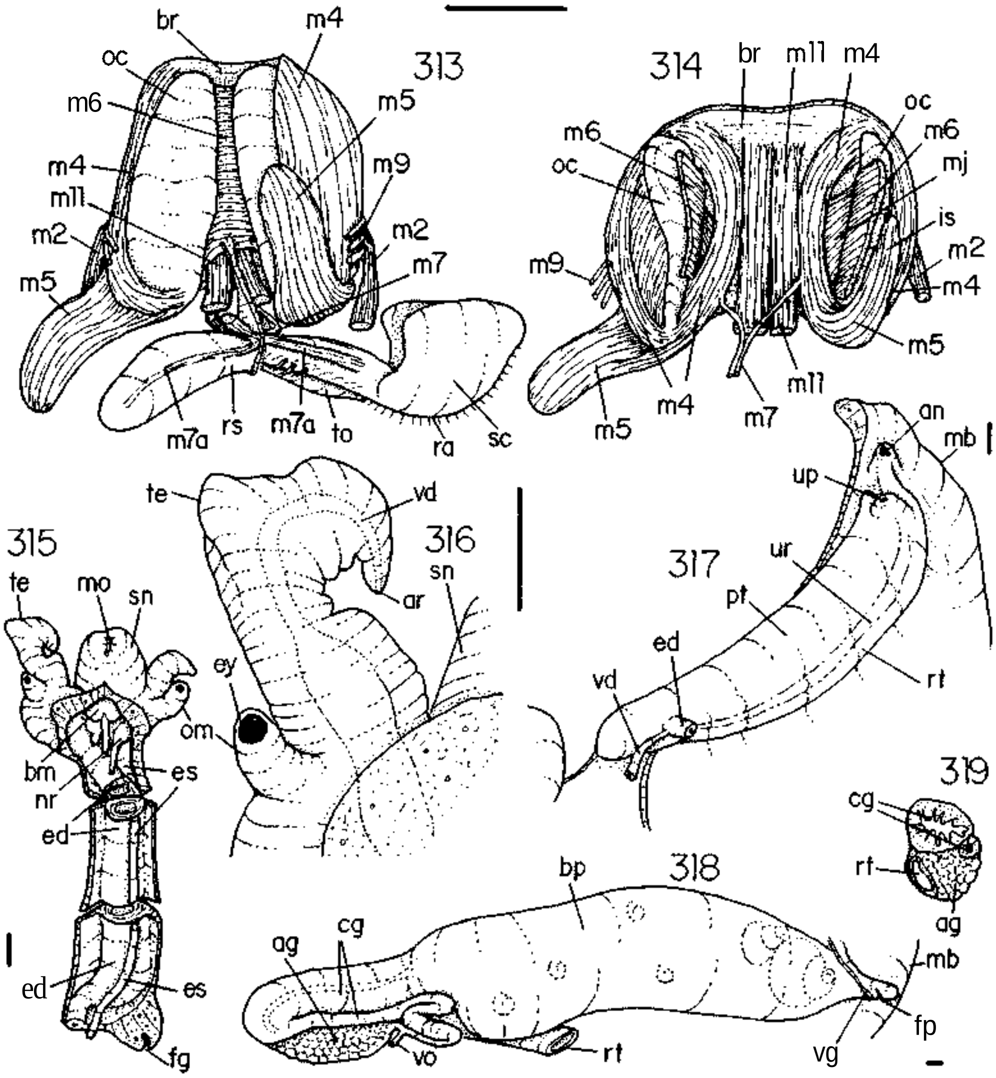
Viviparus contectus anatomy: fig.296- pallial cavity, ♂, ventral-inner view, a portion of visceral mass also shown; fig.297- buccal mass, lateral-left view; fig.298- right copulatory cephalic tentacle, ♂, ventral view, its distal chamber opened longitudinally; fig.299- same, intact, a portion of adjacent region of haemocoel also shown; fig.300- central nervous system, posterior view; fig.301- pallial oviduct and part of adjacent region of pallial cavity. Scale bars = 1mm.



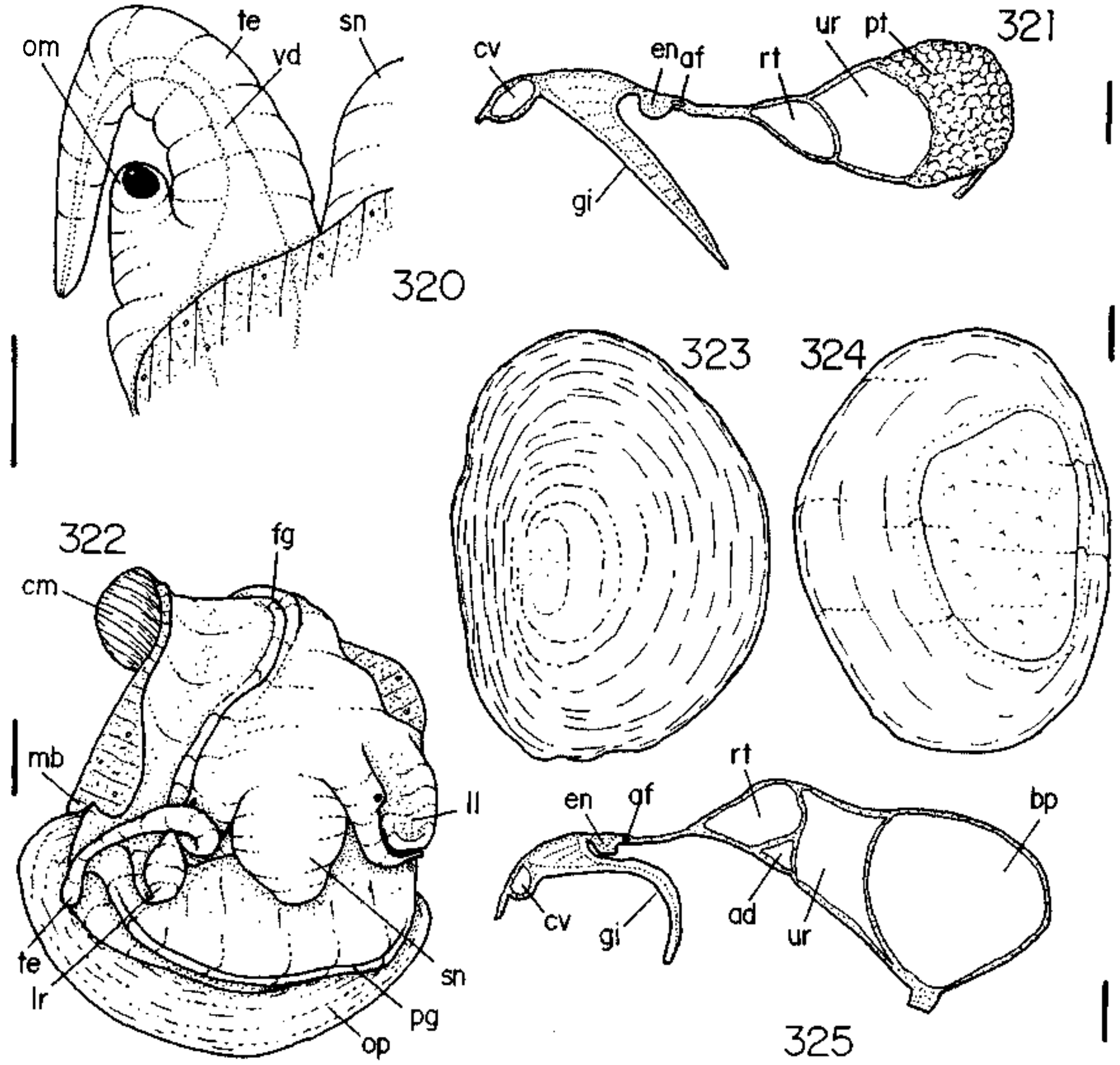
Notopala ampullaroides anatomy: fig.302- head-foot, 2 , frontal view; fig.303- transversal section on the middle region of pallial floor; fig.304- pallial cavity, ventral-inner view, and visceral mass, female, a transversal section in uterus artificially done; fig.305- visceral mass partially uncoiled, and posterior region of pallial cavity, ventral view, digestive gland and mantle potions ventral to stomach removed, ureter opened longitudinally; fig.306- head and part of haemocoel, 2 , ventral view, foot removed; fig.307- pallial cavity roof, transversal section in its middle region. Scale bars = 2mm.



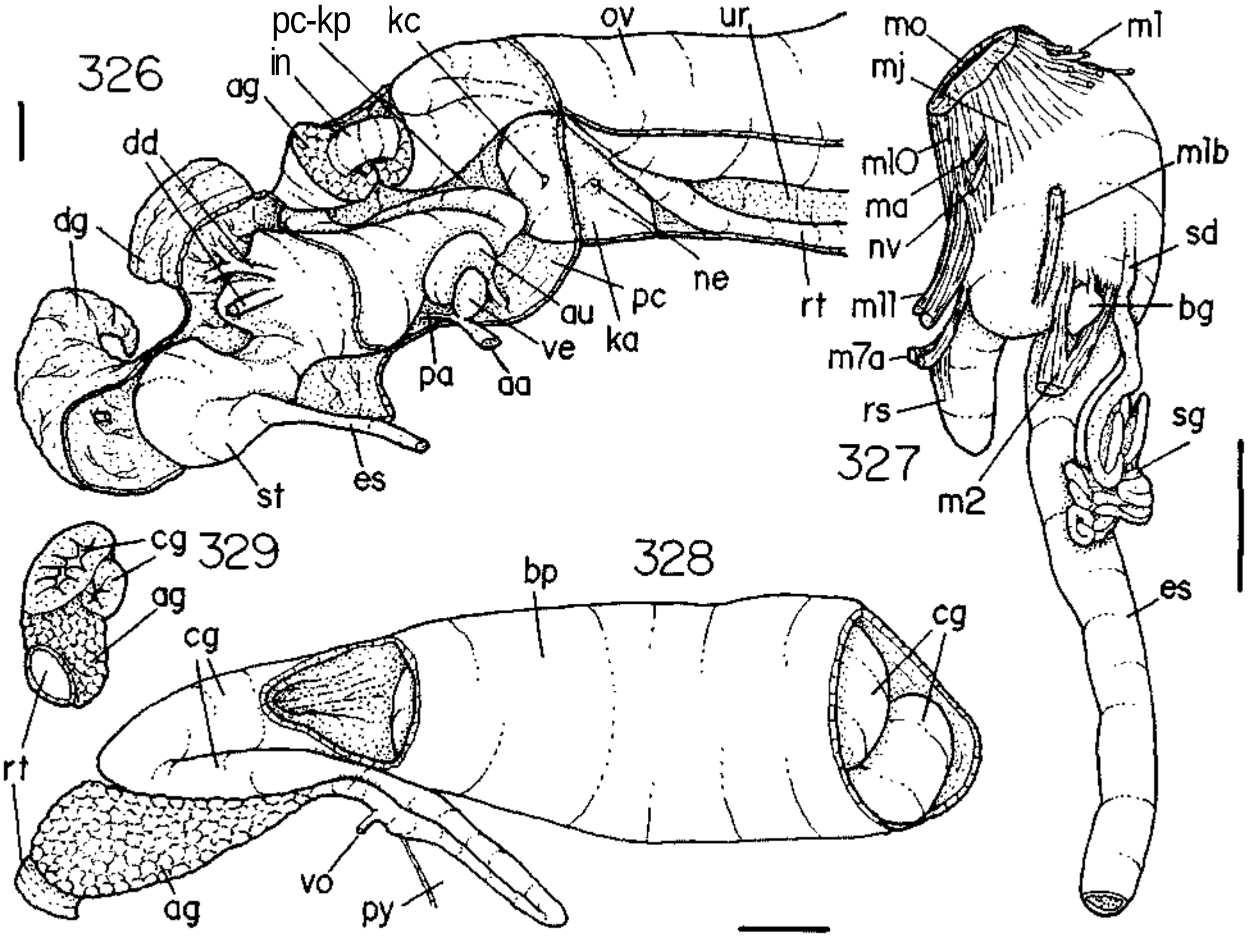
Notopala ampullaroides anatomy: flg.308- foregut, dorsal view; flg.309- same, ventral view; flg.310- same, odontophore removed, esophagus opened longitudinally; fig.311- odontophore, ventral view; fig.312- same, dorsal view. Scale bars = 1mm.



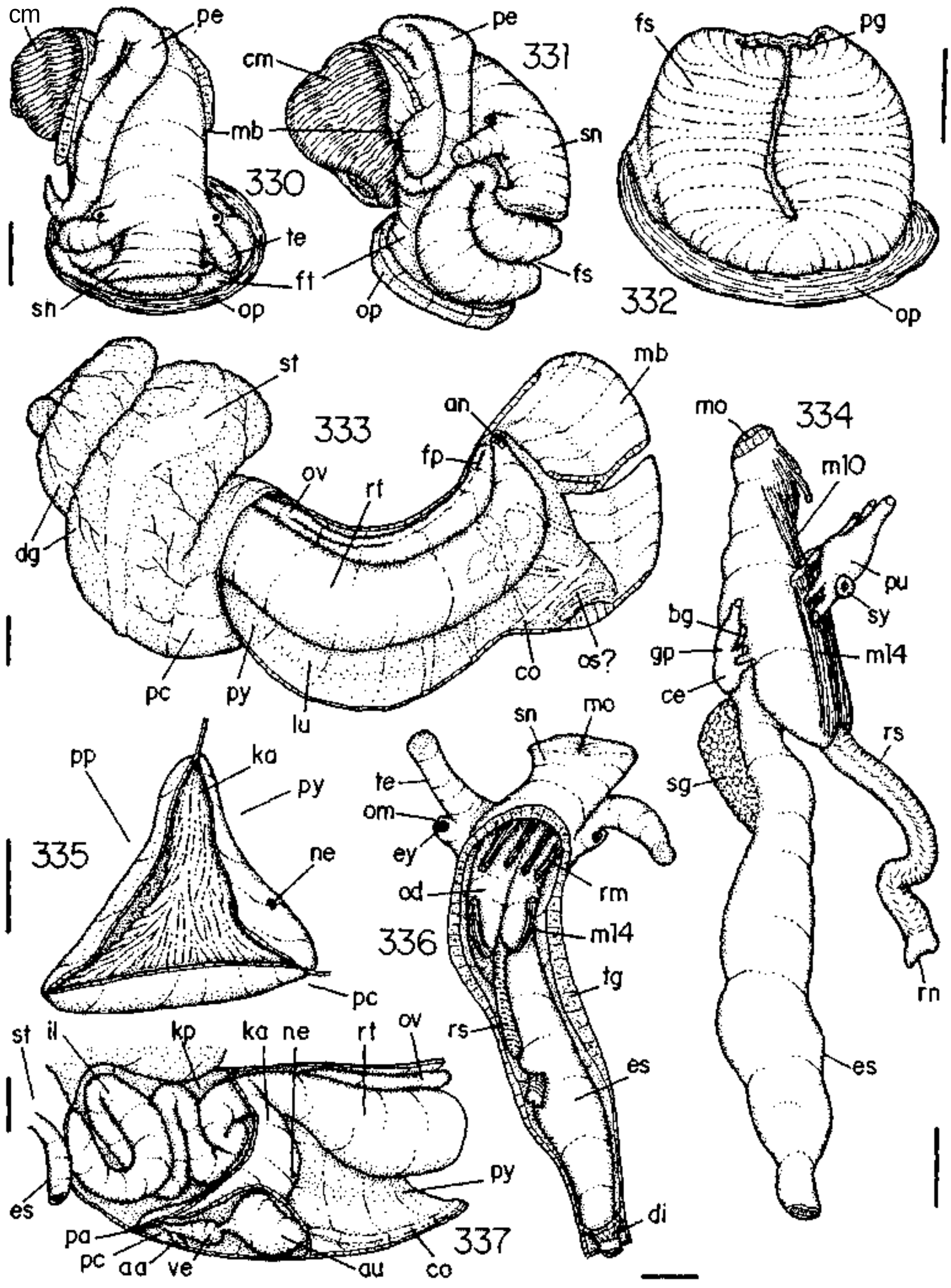
Notopala ampullaroides anatomy: fig.313- odontophore, dorsal view, radular ribbon removed and deflected, both cartilages and left m5 deflected; fig.314- same, m6 sectioned longitudinally and both cartilages still more deflected; fig.315- head and part of haemocoel, ♂, ventral view, foot removed, some transversal sections along vas deferens done; fig.316- right copulatory cephalic tentacle, ♂, ventral view, some adjacent head structures also shown; fig.317- pallial portion of male genital system, and some adjacent structures, ventral view; fig.318- pallial oviduct, ventral view as in situ; fig.319- same, transversal section in its posterior region. Scale bars = 1mm.



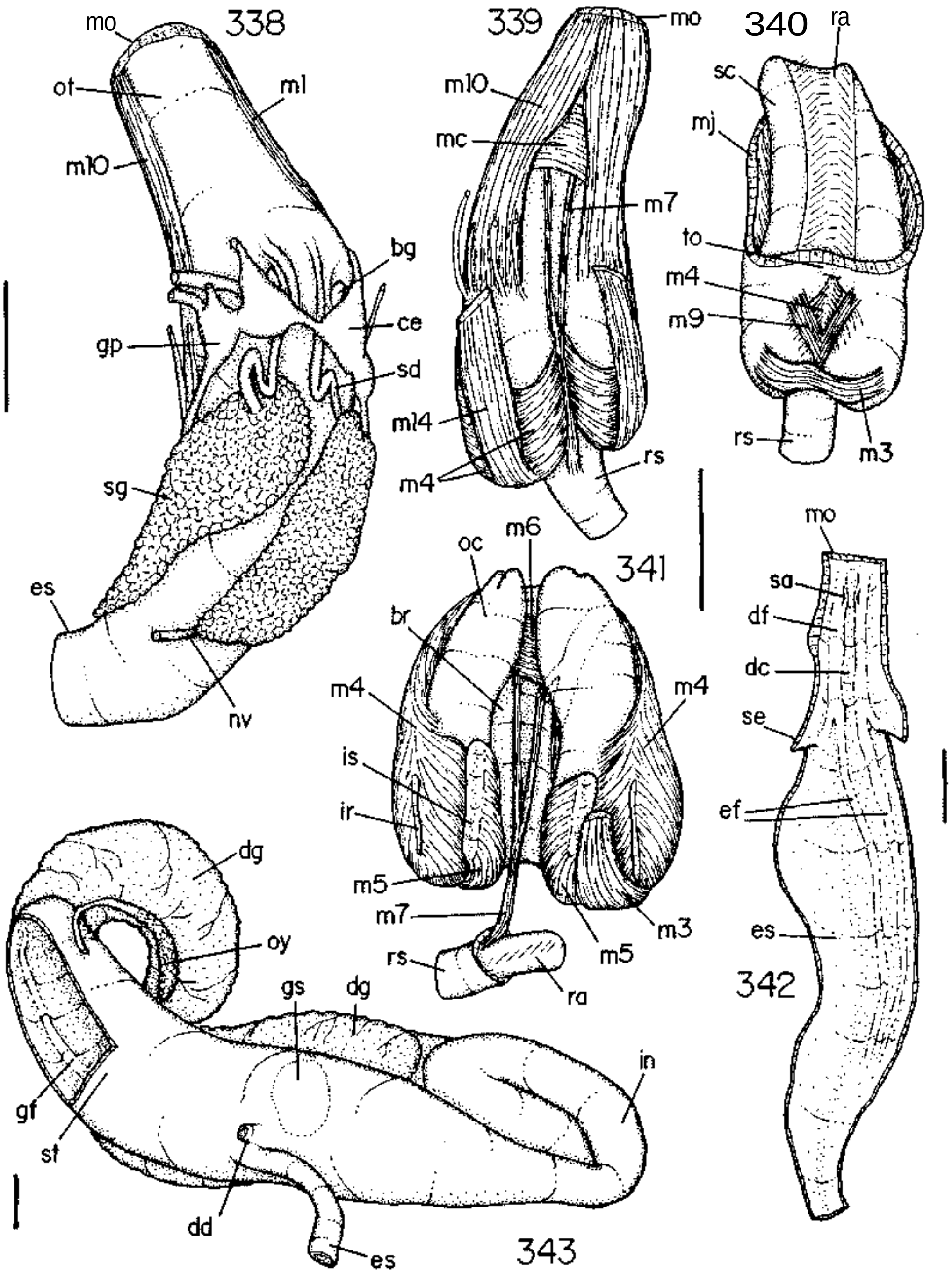
Anatomy of some Australian viviparids - *Notopala essingtonensis*: fig.320- right copulatory cephalic tentacle, ♂, ventral view, some adjacent head structures also shown; fig.321- pallial cavity roof, ♂, transversal section in its middle region; *Larina* cf *strangei*: fig.322- head-foot, ♂, frontal view; fig.323- operculum, outer view; fig.324- same, inner view; fig.325- pallial cavity roof, ♀, transversal section in its middle region. Scale bars = 1mm.



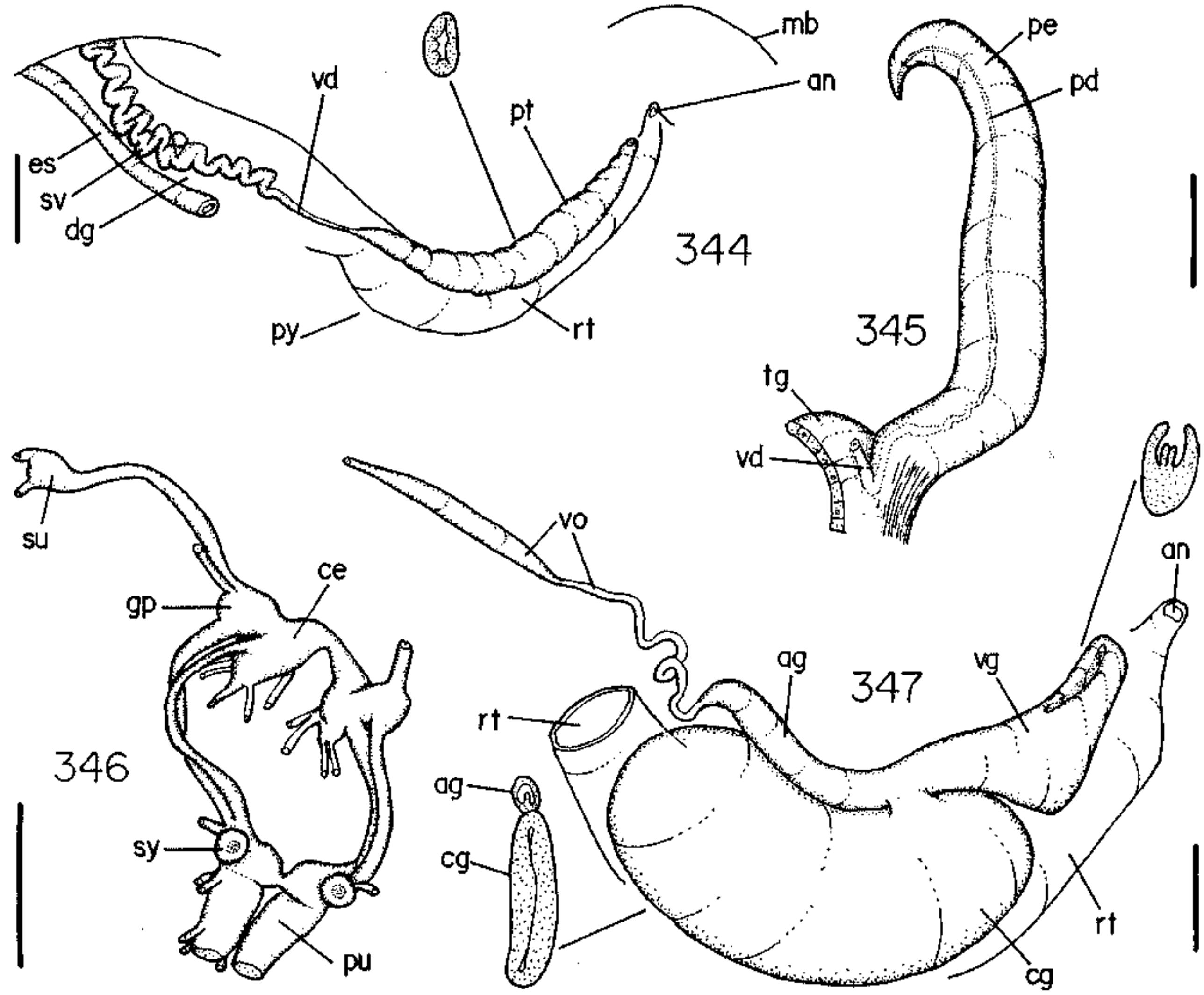
Larina cf *strangei* anatomy: fig.326- visceral mass partially uncoiled and posterior region of pallial cavity, ventral view, structures ventral to stomach removed or deflected, albumen gland transversal sectioned, ureter opened longitudinally; fig.327- foregut, lateral-left view; fig.328- posterior 2/3 portion of pallial oviduct, ventral view as in situ; fig.329- same, transversal section in its posterior region. Scale bars = 1mm.



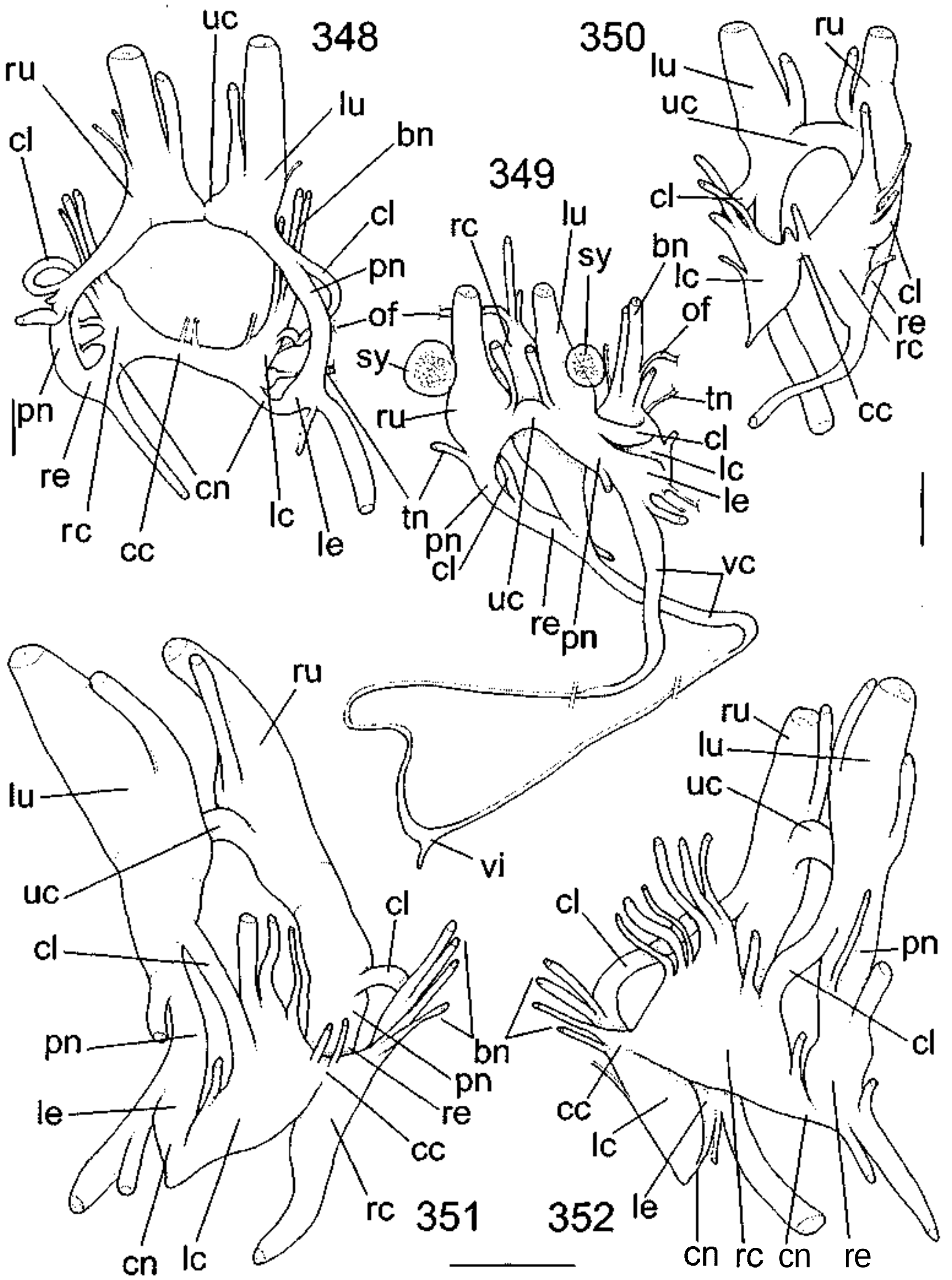
Annularia sp. anatomy: fig.330- head-foot, ♂, frontal view; fig.331- same, lateral-right view; fig.332- foot sole, ventral view; fig.333- pallial cavity, ventral-Inner view, and visceral mass, *9* ; fig.334- foregut, lateral-right view; fig.335- kidney anterior chamber, ventral view, its ventral wall opened and deflected; fig.336- head and haemocoel, ventral view, foot removed; fig.337- kidney and adjacent structures, ventral view, ventral walls of kidney posterior chamber and pericardium removed. Scale bars = 1mm.



Annularia sp. anatomy: fig.338- foregut, dorsal view; fig.339- buccal mass, ventral view; fig.340- same, dorsal view; fig.341- odontophore, dorsal view, radular ribbon removed, deflected and only partially shown, both cartilages deflected (right more than left one), insertion of m7 shown as if cartilage was transparent, left m3 removed; fig.342- foregut, ventral view, odontophore removed, esophagus opened longitudinally; fig.343- stomach and adjacent visceral structures, ventral view, digestive gland portion ventral to stomach removed, a region of posterior gastric wall extracted, gastric shield (gs) seen by transparency. Scale bars = 1mm.



Annularia sp. anatomy: fig.344- middle region of male genital system and adjacent structures, ventral view as in situ, a transversal section in indicated portion of prostate also shown; fig.345- penis and a small portion of adjacent pallial floor, dorsal view; fig.346- central nervous system, ventral view; fig.347- anterior portion of visceral and whole pallial oviduct, ventral view as in situ, transversal sections of 2 indicated portions also shown. Scale bars = 1mm.



Central nervous system of viviparids: fig.348- *Viviparuscontectus*, ventral view; *Notopala ampullaroides*;fig.349- ventral view as in situ, including visceral ganglion, its connectives not shown in total length; fig.350- dorsal view; fig.351- lateral-left view; fig.352- lateral-right view. (bn) nerves to buccal mass; (cc) cerebral commissure; (cl) cerebro-pedal connective; (cn) rebebro-pleural connective; (lc) left cerebral ganglion; (le) left pleural ganglion; (lu) left pedal ganglion; (of) ophthalmic nerve; (pn) pleuro-pedal connective; (rc) right cerebral ganglion; (re) right pleural ganglion; (ru) right pedal ganglion; (sy) statocyst; (tn) tentacular nerve; (uc) pedal commissure; (vc) visceral connectives; (vi) visceral ganglion. Scale bars = 0.5mm.

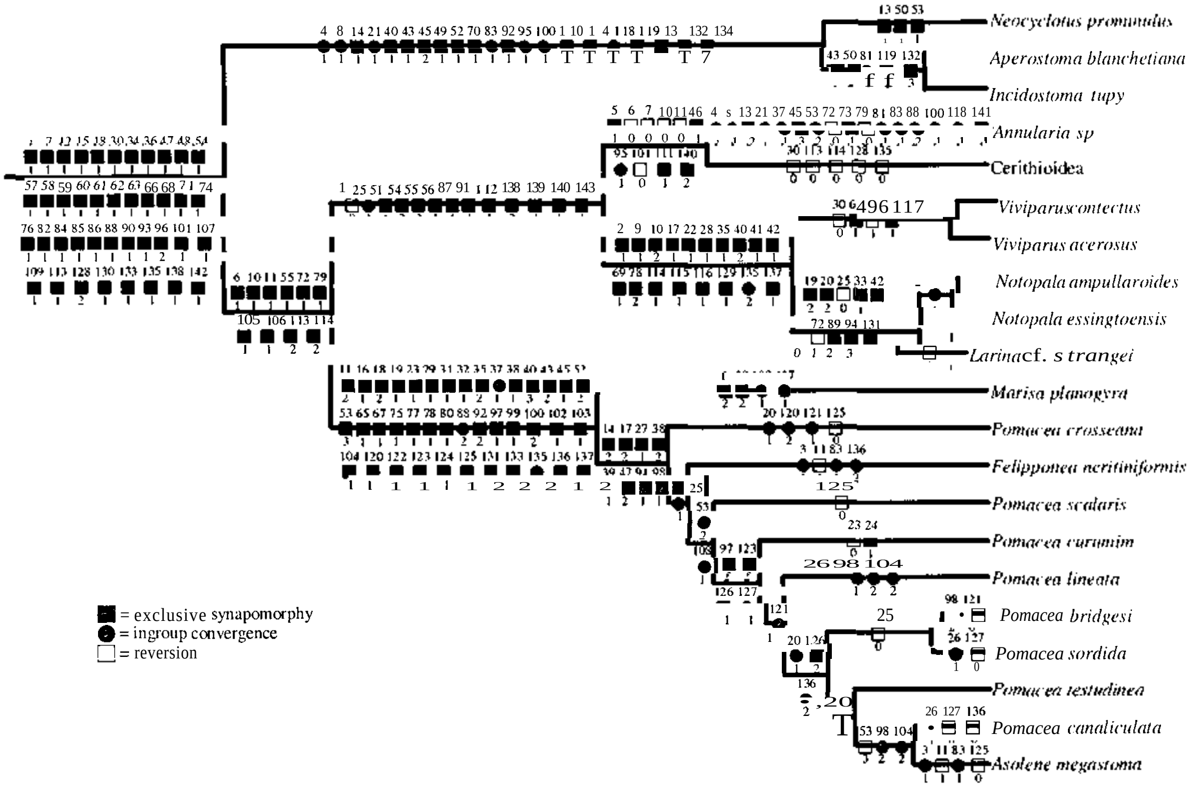


Fig.353- cladogram with synapomorphies of each node shown. Uppermost number indicates the character, the lower the state. Note that two outgroups (*Annularia* sp and Cerithioidea ground plan) resulted inside the ingroup. Length: 252; CI= 76; RI= 91.

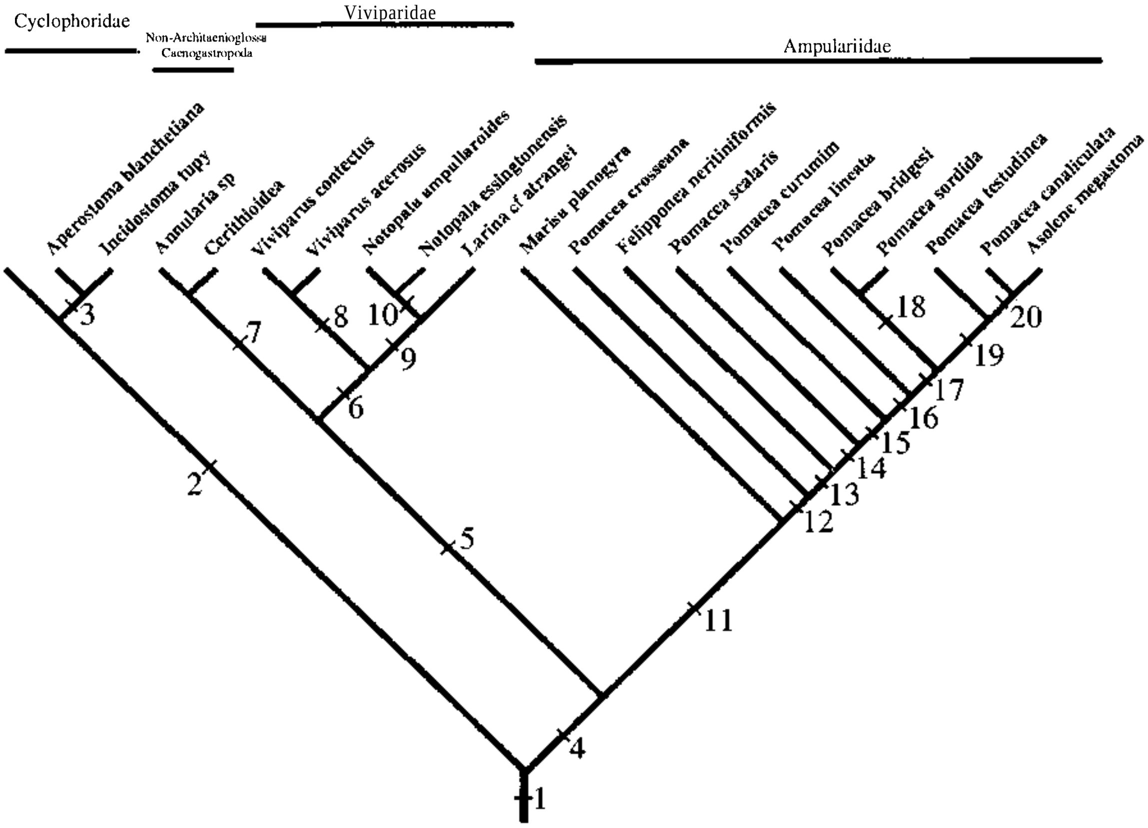


Fig.354- the single cladogram obtained cladogram; each node is numbered and the family of the ingroup taxa also indicated in the superior region, the line corresponds to the terminal branch of the cladogram.

DISCUSSION OF THE CLADOGRAM

As referred in the Material and Methods section, each character was polarized one by one, analyzing each case separately, and deciding which outgroups are selected for separating its states, for polarization, and, in the cases of multistate characters, for deciding the optimization is additive or not. Those parameters can be easily changed in the computer programs, and where changes were made, any modification in the results or indices was reported. Taking into consideration that whether all outgroups are analyzed effectively as outgroups, the monophyly of the ingroup is not tested, since it will absolutely result reunited in a branch. For testing the monophyly of any taxon, it is important to insert in the analysis some outgroups belonging to close taxa, which will be analyzed operationally as part of the ingroup. A more distant taxon (in present study a set of archaeogastropod taxa) was used as the effective outgroup. If the Architaenioglossa is actually monophyletic, the caenogastropod taxa should appear outside of the architaenioglossans clade.

This procedure was applied in the present study. The *Annularia* sp., as well as the Cerithioidea ground plan, appeared inside the architaenioglossans taxa. Both these taxa are undoubtedly considered caenogastropods. The present result suggests that the taxon "Architaenioglossa" is non-monophyletic. The two non-architaenioglossans taxa formed a single terminal branch, and the architaenioglossans formed three successive branches, indicating its paraphyly.

Most nodes and branches (Figs.353-354) are analyzed in the following text. The more important synapomorphies that support them are also reported, but are discussed in the previous section.

The node number 1 (Fig.354) is supported by 41 synapomorphies (Fig.353). From those, the outstanding are: ommatophore located on tentacles (character 12); osphradium elongated and more complex (18); decrease of the hypobranchial gland (30); duplication of the lobe of the single kidney (34, 36); appearance of a pair of inner dorsal folds in buccal mass (47); jaw muscles separated in a pair of bundles (48); formation of the m4 pair of odontophore muscles from several pairs (54); reduction of ventral tensor muscle of the radula (57); enlargement of dorsal tensor muscle of the radula (58); m5 pair of odontophore muscles becoming longer and inserted on m4 (instead of on the cartilage) (59, 60); horizontal muscle becoming shorter and broader (61, 62); arising the pair m7 (63); loss of approximator muscles of cartilages (or incorporation to m4) (66); loss of the posterior pair of odontophore cartilages (74); enlargement of subradular cartilage (76); reduction of the radular teeth to 7 per row (82, 85); esophagus origin in posterior region of buccal mass (90); loss of gastric caecum (96); absence of visceral structures in haemocoel (107); fecal pellets (109); pallial vas deferens at least partially closed (113); large and complex pallial oviduct located at right from rectum (128, 130); capsule gland (133); developed female pore (135); nerve ring positioned more posterior from mouth (138); and buccal ganglia positioned far removed from the nerve ring (142). Being the node 1 followed by the 3 architaenioglossan branches plus the remainder caenogastropods (represented by *Annularia* and Cerithioidea ground plan), it is a quite possible that it represents the order Caenogastropoda as a whole. This affirmation is considered still premature, since another study concerned to the phylogeny of the entire order is in progress. The present study is part of it. For a secure affirmation on the caenogastropod synapomorphies and monophyly depends on a deeper analysis of remainder superfamilies of the group and of the sister-group taxon, the Heterobranchia. Those studies are still being performed.

HASZPRUNAR (1988) regarded Architaenioglossa as non-caenogastropod prosobranchs (archaeogastropods). He considered it as the sister taxon of the Caenogastropoda plus Heterobranchia branch. PONDER & LINDBERG (1996, 1997), on the other hand, considered the architaenioglossans as basal caenogastropods. However, as also pointed out by HASZPRUNAR (1988), those authors suggested that there is a possibility that the architaenioglossans are paraphyletic (1997:225) as corroborated with the present result. Harasewych *et al.* (1997) performed a molecular analysis (18S rDNA and cytochrome c oxidase I), included the viviparid *Cipangopaludina japonica* (von Martens, 1860), with this architaenioglossan in the first branch of the Caenogastropoda.

The node 2, supported by 21 synapomorphies, represents the family Cyclophoridae, the single one reunited in the superfamily Cyclophoroidea. From the synapomorphies, those more remarkable are: calcareous operculum (character 8); loss of pallial structures for becoming a lung (21); posterior located nephrostome (40); urinary gutter (43); fusion of jaw plates (45); odontophore muscle pair m1a and m10c (49, 70); esophageal pouches covered internally by papillae (92); the exophalic penis (114, 118, 119); albumen gland as a loop

(131); and special conformation of pallial oviduct (132, 134). Despite the very well supported node, the cyclophorids are a very diverse and widespread group. They have some endemic supra-specific taxa that were not analyzed in present study. It is possible that the family synapomorphies would be diluted when a larger number of representatives will be analyzed. However, a set of synapomorphies of the taxon is here presented by the first time, and is considered important for defining the taxon and for analyzing its relationship with the remainder gastropods.

The node 3 separates *Aperostoma* and *Incidostoma* from *Neocyclotus*. It is supported by 5 synapomorphies, being the more important the different organization of the lung vessels (44), the modification of the odontophore pair of muscles m1a (50); the duplication of the penis papilla (119); and the bursa copulatrix opening directly to the pallial cavity instead of opening to the pallial oviduct (132).

The node 4 encompasses the remainder ingroup except the cyclophoroideans. It is supported by 10 synapomorphies, being the more remarkable the following: the head-foot siphons (10, 11, which reverted in the node 7); the connection of the m4 with tissue on the radula (55); the odontophore muscle pair m12 (72); the closure of the pallial vas deferens (113, 114). The arrangement of the taxa on the cladogram shows that the cyclophorids are the more basal taxon of the caenogastropods, and that the remainder taxa represent another branch, uniting the ampullariids and remainder caenogastropods.

For operational reasons, we will analyze the node 11 to 18, and after them we return to numerical order.

The node 11 represents the Ampullariidae, the single family of the superfamily Ampullarioidea. The node is supported by 40 synapomorphies, being the more remarkable: snout tentacles (character 16); osphradium with bipectinated and pedunculated fashion (18, 19); lung sac (29); ampulla in anterior aorta (32); intestinal loops inside kidney (37); anterior septate renal chamber (38); multiple jaw ditator muscles (ma) (52); odontophore muscle pairs m7b and m9 (65, 67); pair of accessory odontophore cartilages (75); muscular stomach walls (97); gastric muscle (99); multiplication of ducts to digestive gland (100); special arrangement of intestinal chambers in its portion close to pericardium (103, 104); penis and penis shield structures (120-127); enormous capsule gland surrounding most of remainder pallial oviduct structures (131, 133); special brooding strategy (137). The ampullariids have been the goal of some important papers on their anatomy (*e.g.*, Scott, 1957), and even including phylogenetic approach (BERTHOLD, 1989, 1991; BIELER, 1993). However, several of here presented synapomorphies are apparently introduced by the fist time. They are the cases, for example, of the gastric muscle (that connect the stomach with shell columella), the intestinal chambers close to pericardium, and the renal intestinal loops. BIELER (1993), based on the data searched by BERTHOLD (1991), selected 70 ampullariid characters, and obtained 3 equally parsimonious trees. The author showed 3 cladograms (that paper figs. 1-3), the first based on the BERTHOLD's preferences, and the other 2 based on the data matrix. All cladograms are so different from each other and from that obtained herein that it is impracticable to compare. Bieler searched 23 synapomorphies for the family, most of them taken into consideration in the present study and presented in preceding discussion.

The remaining nodes, 12-20, refer to the internal organization of the family Ampullariidae. The first branch is *Marisa*, separated from the remaining branches by 8 synapomorphies. The lasting taxa are, in a broad sense, representatives of the genus *Pomacea*. However, species belonging to the genera *Asolene and Felipponea,* considered by some authors as subgenera of *Pomacea,* where mixed. The scattered organization of the ampullariids in the cladogram is considered provisional, since some organs and structures have been under-analyzed *(e.g.,* the kidney, pallial oviduct). This happened because of the insufficient or poorly-preserved material available. For this reason no taxonomical change is proposed. However, on the basis of this result, it appears that a reanalysis of ampullariid taxonomy may necessary.

The node 5 is supported by 13 synapomorphies, including: the appearance of the pair of retractor muscle of buccal mass (m2) (character 51); the simplification and enlargement of the odontophore muscle pair m4 (54-56); the loss of the esophageal pouches (91); the prostate gland located in pallial cavity (112); the nerve ring positioned posterior to buccal mass (138); the approach of the pleural ganglia to the cerebral ganglia (epiathroid organization) (139, 140); and the lateral position of buccal ganglia in buccal mass (143). This branch represents the caenogastropods except the Cyclophoroidea and the Ampullarioidea, encompassing the Viviparioidea and the Sorbeoconcha. PONDER & LINDBERG (1997:225) introduced this taxon, comprising the Cerithioidea and the rest of the caenogastropods. The current literature usually considers the Viviparidae as Ampullarioidea *(e.g.,* BOSS, 1982; VAUGHT, 1989). The viviparids actually share some characters with the ampullariids, such as the head-foot left and right siphons, the type of operculum, and the freshwater environment. Those characters were here considered homologous between the representatives of both groups. However, despite this, the two groups are paraphyletic. This resultindicates that the viviparids should be included in a monotypic superfamilyVivipariolidea.

The node 6 is supported by 18 synapomorphies, and represents the viviparids. The more important synapomorphies are: adaptations to filter feeding (characters 9, 10, 17, 22, 28); ureter (40, 41); male pallial ducts running by integument and opening in the right cephalic tentacle (114-117); brood pouch in pallial oviduct (129, 137). An internal organization of the viviparids was obtained, represented by the nodes 8 and 9, separating respectively the *Viviparus* sample from the Australian sample. As this organization is considered provisional, then no deeper analysis or taxonomic implications is here proposed. The Australian viviparids studied here belong to the subfamily Bellamyinae (ANNANDALE & SEWELL, 1921; ROHRBACH, 1937; VAIL, 1977; SMITH, 2000), characterized mainly by the testis positioned in the pallial cavity, by side of the rectum (Fig.317:pt); this character is not explored here because the studied material is not well-preserved enough for observing this character in all samples. The Australian sample of *Notopala* and *Larina* are separated from each other (node 10) by a single synapomorphy (single gastric duct to digestive gland, character 100, state 1, convergent with other branches).

The node 7 encompasses supposedly outgroups, representing the "true" caenogastropods, or the Sorbeoconcha, in this study. The node is supported by 10 synapomorphies, being half of them reversions. The more remarkable are: the determinate shell growth (character 5); the reversion of the left and right head-foot siphons (10-11); the reduction of the dorsal chamber of buccal mass (46); the gastric style sac (101); the male seminal vesicle (111); and the approach of the pairs of connectives pedal-cerebral to pedal-pleural ganglia in the nerve ring (140).

As reported above, a more un-depth study on the caenogastropod phylogeny is still been performed, which this study, is part. Apparently, the architaenioglossans can be regarded as true Caenogastropoda, being its basal branches. However, further analysis on caenogastropod phylogeny is still in progress, and depends on the study of remainder superfamilies, as well as of more outgroups. On the other hand, the present studied sample is considered sufficient for analyzing the monophyly and phylogenetic relationship of the contemplated supra-generic taxa, just the main goals of this study.

CONCLUSIONS

1. The taxon Architaenioglossa is not monophyletic, but so paraphyletic, then it should not be used as a formal taxon.

2. The architaenioglossans can be regarded as the 3 first branches of the order Caenogastropoda, respectively: Cyclophoroidea (Cyclophoridae); Ampullarioidea (Ampullariidae) and Viviparioidea (Viviparidae).

3. The combination among the architaenioglossans and remaining caenogastropods are supported by 41 morphological synapomorphies.

4. The Cyclophoroidea, Ampullarioidea and Viviparioidea are supported respectively by 21, 40 and 18 synapomorphies.

5. The Viviparioidea are a separated taxon from the Ampullarioidea.

6. The three architaenioglossan branches presented internal, well-resolved organizations; however, they are considered provisional and no systematic change was proposed.

7. The analysis of all organs and systems are useful for phylogenetic analysis.

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