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Morphology and Phylogeny of the Cypraeoidea

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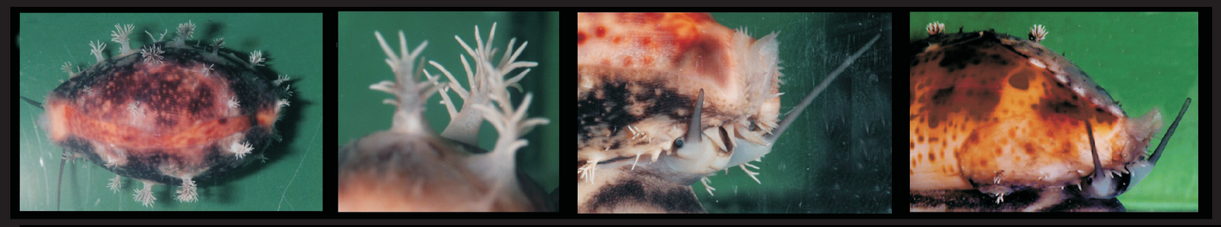

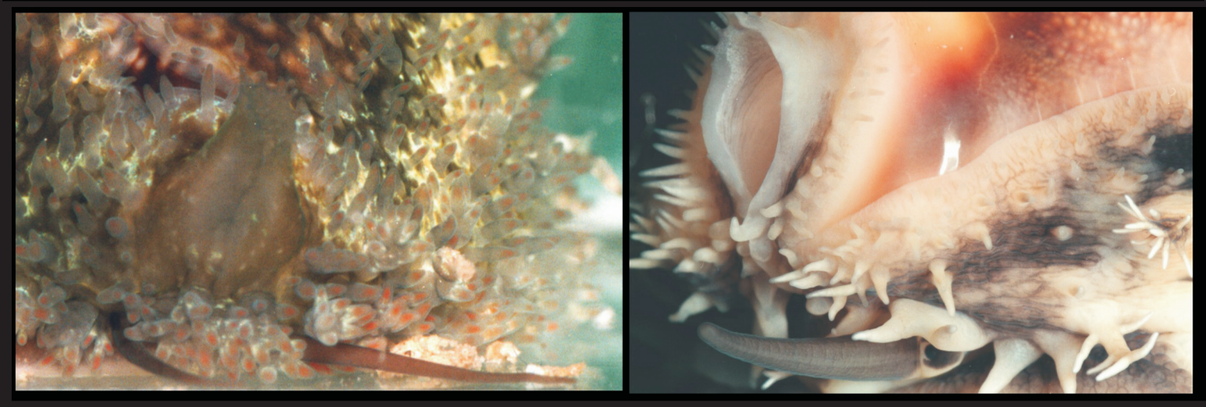

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FAPESP

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Morphology and phylogeny of the Cypraeoidea (Mollusca, Caenogastropoda).

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SUMMARY

ABSTRACT

With the intention of searching the monophyly and the ground plan of the Cypraeoidea, including Lamellarioidea, a sample of 28 species of the former and 5 of the latter were studied in detailed comparative morphology. The species are the following: 1) Cypraeidae: *Macrocypraea zebra* (Linné) (from Brazil); *M. cervinetta* (Kiener) (from Panama, Pacific); *Erosaria acicularis* (Gmelin) (W. Atlantic); *E. spurca* (Linné) (N. Atlantic and Mediterranean); *Luria cinerea* (Gmelin) (NE Brazil); *Cypraea tigris* Linné (SW Pacific) (type species); *Lyncina lynx* (Linné) (SW Pacific); *Monetaria moneta* (Linné) (W. Pacific); *M. annulus* (Linné) (W. Pacific); *Ravitrona caputserpentis* (Linné) (Hawaii); *Muracypraea mus* (Linné) (Venezuela); *Pseudozonaria arabicula* (Linné) (Ecuador); *P. robertsi* (Hidalgo) (Ecuador); 2) Ovulidae: *Cyphoma signatum* Pilsbry & McGinty (W. Atlantic); *C. gibbosum* (Linné) (Caribbean); *Pseudocyphoma intermedium* (Sowerby) (Brazil); *Ovula ovum* (Linné) (W. Pacific); *Calpurnus verrucosus* (Linné) (Philippines); *Simnialena uniplicata* (Sowerby) (SE Brazil); *Cymbula acicularis* (Lamarck) (Caribbean); *Jenneria pustulata* (Lightfoot) (Panama, Pacific); 3) Triviidae: *Niveria pediculus* (Linné) (Brazil); *Trivirostra oryza* (Lamarck) (Australia); 4) Eratoidae: *Hespererato maugeriae* (Gray) (E. USA); 5) Pediculariidae: *Pedicularia* sp1 (Tonga); *P. californica* Newcomb (California, USA); *P. decussata* (Gould) (Bahamas); *P.* sp2 (Australia); 6) Lamelariidae: *Lamellaria branca* n. sp. (SE Brazil); *L. mopsicolor* Marcus (SE Brazil); *L. patagonica* E.A. Smith (S. Argentina); *Velutina velutina* Müller (W. USA); *Velutina* sp (Massachusetts, USA). Each species is described with a formal taxonomical treatment. A total of 132 characters were searched in 322 states. They were analyzed under formal cladistic methodology, resulting in a single most parsimonious tree, with the following indices: length: 281, CI: 68, RI: 89. The tree is the following: ((*Velutina velutina* (*Lamellaria patagonica* (*L. mopsicolor – L. branca*))) ((*Pedicularia* sp1 (*P*. sp2 (*P. decussata – P. californica*))) (*Hespererato maugeriae* ((*Niveria pediculus – Trivirostra oryza*) ((*Jenneria pustulata* ((*Simnialena uniplicata – Cymbula acicularis*) (*Ovula ovum* (*Calpurnus verrucosus* (*Pseudocyphoma intermedium* (*Cyphoma signatum – C. gibbosum*))))))) (*Ravitrona caputserpentis* ((*Pseudozonaria robertsi – M. arabicula*) ((*Luria cinerea – Lyncina lynx*) ((*Cypraea tigris* (*Macrocypraea zebra – M. cervinetta*)) ((*Erosaria acicularis – E. spurca*) (*Monetaria moneta – M. annulus*)))))))))). The monophyly of the superfamily Cypraeoidea is confirmed, supported by 34 morphological synapomorphies; the lamellarioideans can be regarded as part of the taxon. The species presently considered Eratoidae resulted as 2 successive branches, then paraphyletic; the separation into 2 families is necessary (Eratoidae and Triviidae). The Cypraeoidea groups the following monophyletic families, respectively distributed along the cladogram: Lamellariidae, Pediculariidae, Eratoidae, Triviidae, Ovulidae and Cypraeidae, being the 2 last ones sister taxa. As secondary results are: 1) the confirmation of the specific separation between *Erosaria spurca* and *E acicularis*; 2) the description of a new species of *Lamellaria* (*L. branca*); 3) the base for specific and supra-specific future revision of the taxa such as families and genera 4) some new synonyms (*Luria cinerea brasiliensis* Lorenz & Hubert, 1993 = *L. cinerea*; *Pseudocyphoma christahemmenae* Fehse, 1997, *Cyphoma guerrinii* and *Pseudocyphoma rosembergi* both Fehse, 2001, = *P. intermedium*; *Simnialena ilhabelaensis* Fehse, 2001 = *S. uniplicata*).

INTRODUCTION

The superfamily Cypraeoidea encompasses some of the most beautiful shelled gastropods – the cowries – and usually groups the following 7 families (Vaught, 1989): Cypraeidae, Ovulidae, Triviidae, Pediculariidae, Velutinidae, Lamellariidae and Pseudosacculidae. Some authors, on the other hand, consider the Lamellariidae in a superfamily proper – Lamellarioidea (e.g., Schilder, 1936), and Velutinidae as subfamily of Lamellariidae (Velutininae) (e.g., Schilder, 1936). However, some other different systematic arrangements are found in the contemporary literature.

The Cypraeidae have some conchological compendia dedicated to list all world species (e.g., Schilder & Schilder, 1971; Burgess, 1970, 1985; Taylor & Walls, 1975; Lorenz & Hubert, 1993, 2000), which facilitate the identification and bring useful comments and history. This does not occur with the other, less spectacularly shelled families; some of which have been revised by Cate (1973, ovulids; 1977, eratoids; 1979, triviids).

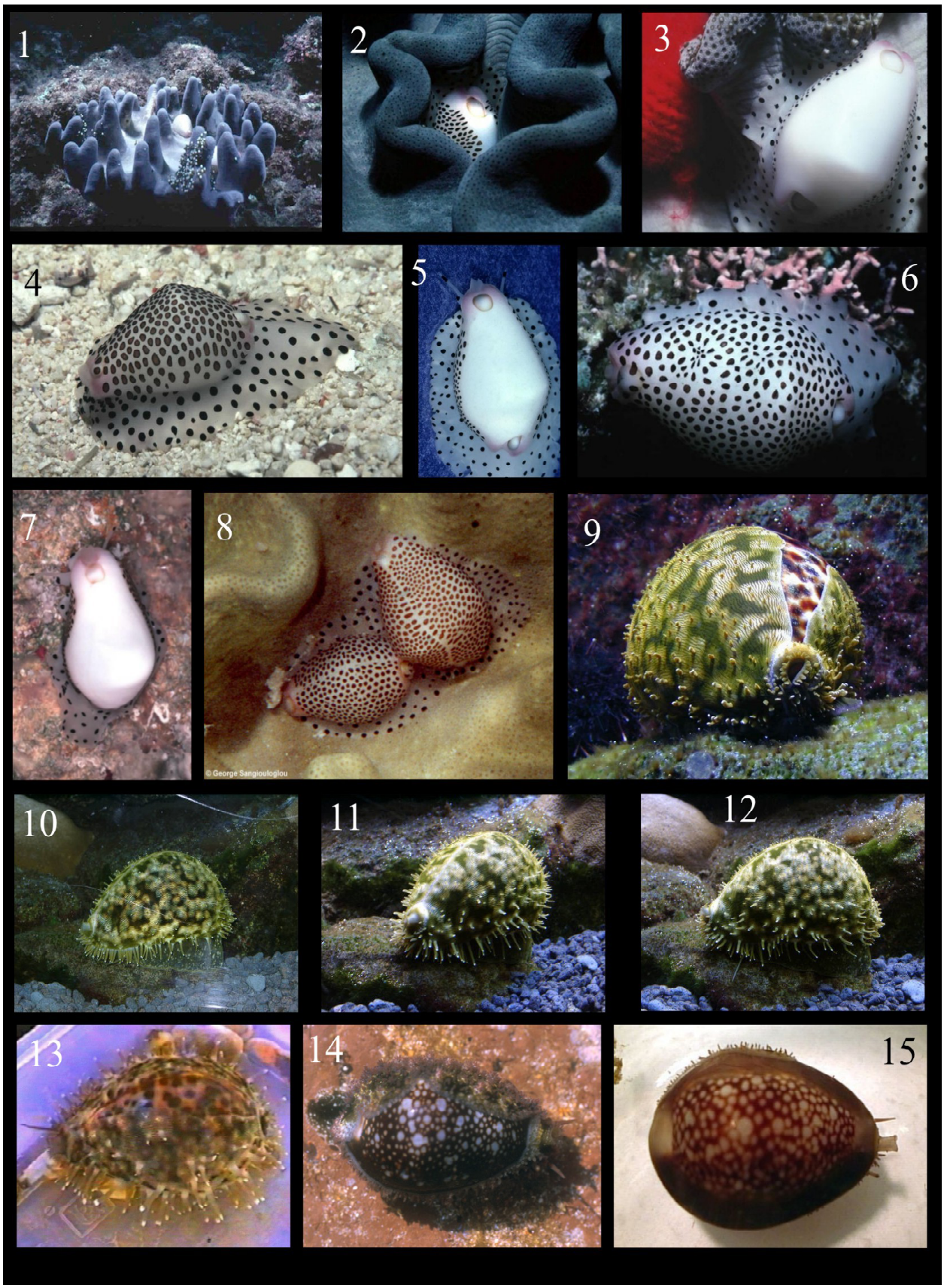
The systematics of the Cypraeoidea is mostly (if not only) based on the shell characters, and relatively few papers have been published on the characters of the inner morphology. Except for the shell, the scant knowledge of other characters precludes, the interpretation of some cypraeoidean shell variation as belonging to single or distinct species, mainly in widespread species of cypraeids (e.g., Kay, 1957, 1981), as well as in the groups with simplified shell, such as ovulids and lamellariids. Similarly, poor is the knowledge about the supra-specific taxa interrelationships, e.g., the genus *Cypraea* Linné, 1758 (according to some authors), encompassing a couple hundred species. No firm synapomorphy has been pointed out for defining the taxon Cypraeoidea, except maybe the involute shell. The lack of an involute shell is perhaps the doubtful aspect for the inclusion of the lamellariids and velutinids within the taxon. On the other hand, when considered, anatomical attributes have helped in the resolution of cowry taxonomic troubles (e.g., Schilder, 1936; Kay, 1960b, 1961, 1964; Gosliner & Liltved, 1987).

The Lamellariidae family comprises species with reduced shell, and sometimes with the shell permanently surrounded by the mantle. This slug-like fashion is an unusual feature for a caenogastropod species. A comprehensive history on the lamellariids is provided by Behrens (1980).

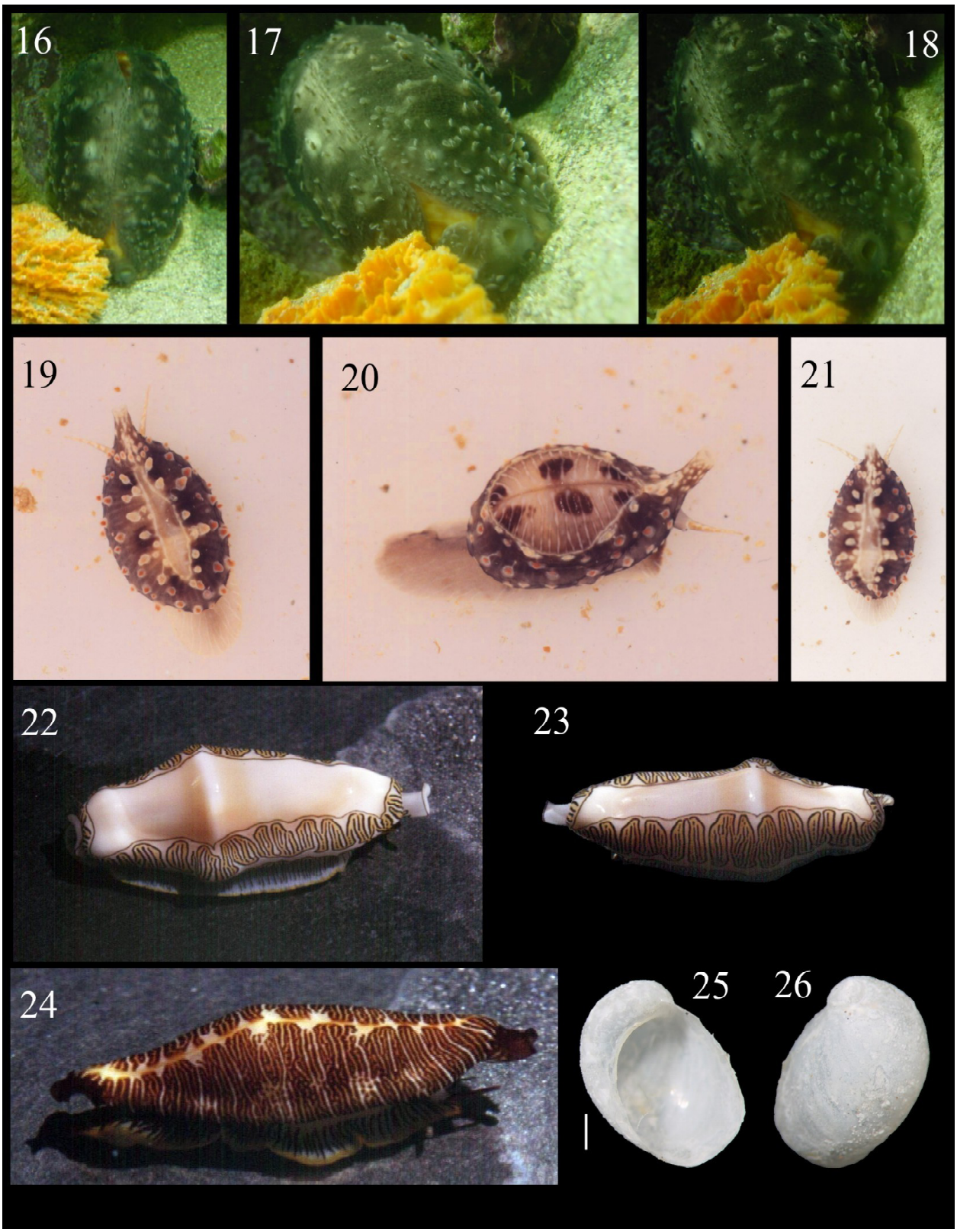
Studies on the cypraeoideans, with the phylogenetic approach, have been produced, such as Schilder (1936, pls. 11-12), Gosliner & Liltved (1985, fig. 35), as well as a more recent one, including molecular aspects (Meyer, 1998). Those studies have brought new additional insights to the cowry taxonomy and, therefore, are important for the current study.

Kay (1996), referring to the Cypraea as the oldest ascribable fossil of the Upper Jurassic, explored the early geological and taxonomical history of the cypraeoideans, particularly of the Cypraeidae. Groves (1994) was more direct and elected *Zittelia* Gemmellaro, 1869, a fossil genus from the Late Jurassic (Kimmeridgian), as the probable cypraeoidean ancestor.

As part of a larger project on phylogeny of the Caenogastropoda, representatives of each family of all superfamilies have been studied under a detailed morphological and comparative scenario. For each caenogastropod superfamily the following attributes have been searched: 1) monophyly of the group; 2) validity of the taxon, really separated from the other superfamilies; and 3) it has the ground plan of the superfamily, i.e., the hypothetical ancestral attributes. These 3 parameters are only searchable by means of a phylogenetic analysis. The Cypraeoidea (*sensu lato*, including Lamellariidae) is the focus of the present paper, with the main objective of searching the above mentioned information, but also providing a foundation for future revisional papers of each particular subgroup. Previously published phylogenies are part of the project (Simone, 1999, in press a, on Terebridae; Simone in press b, on Cerithioidea and Simone in press c, on Stromboidea), as well as taxa treated in other smaller papers serving as outgroups.



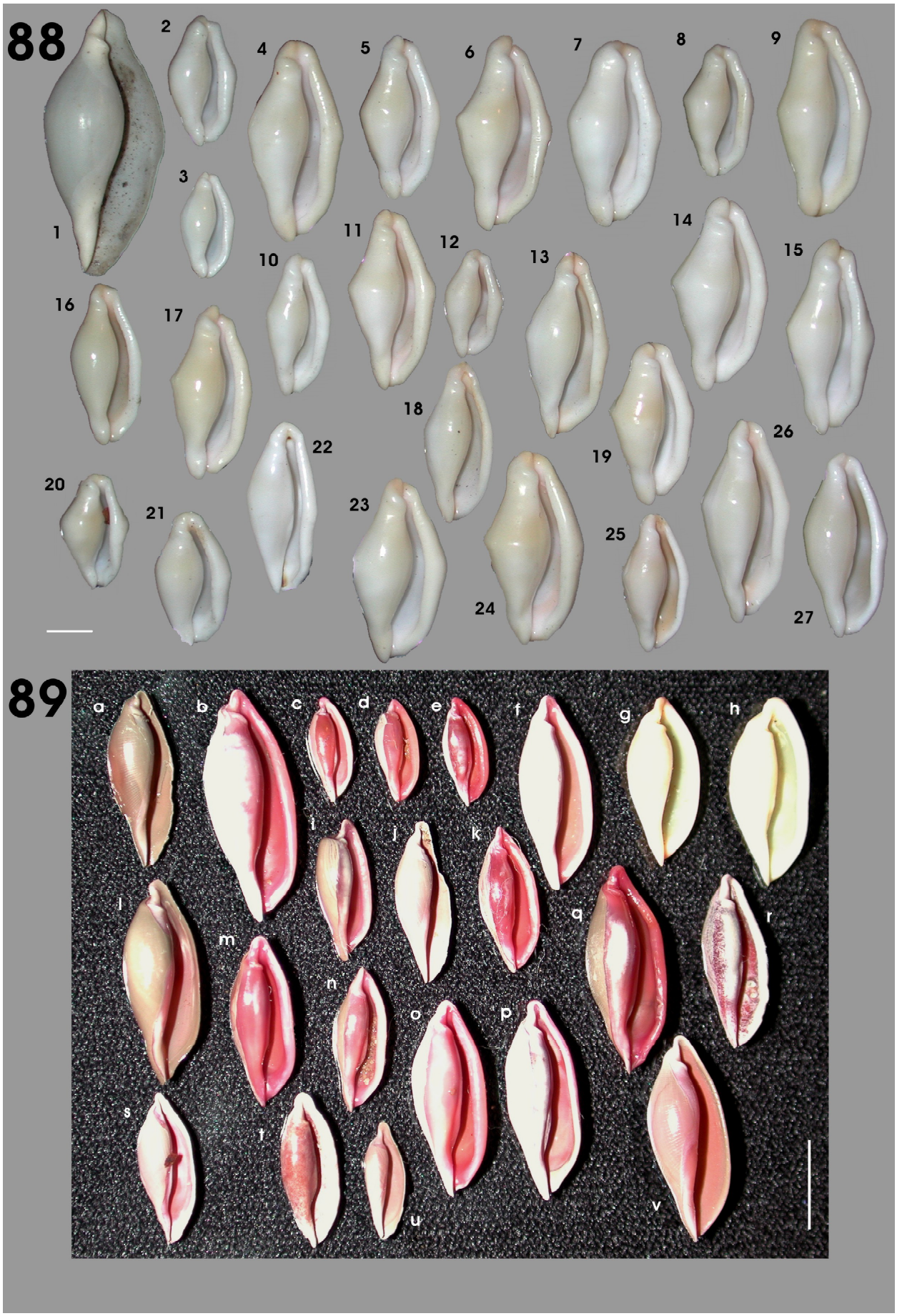
Figs. 1-15, alive crawling specimens: **1-8**, *Calpurnus verrucosus*, 1-7, from Okinawa, Japan, courtesy of Robert F. Bolland, 8, courtesy of George Sangioulouglou; **9-13**, *Cypraea tigris*, 9-12, courtesy of Fabio Moretzsohn, 13, courtesy of George Sangioulouglou; **14-15**, *Ravitrona caputserpentis*, 14, courtesy of Patty Jansen, 15, courtesy of Fabio Moretzsohn.



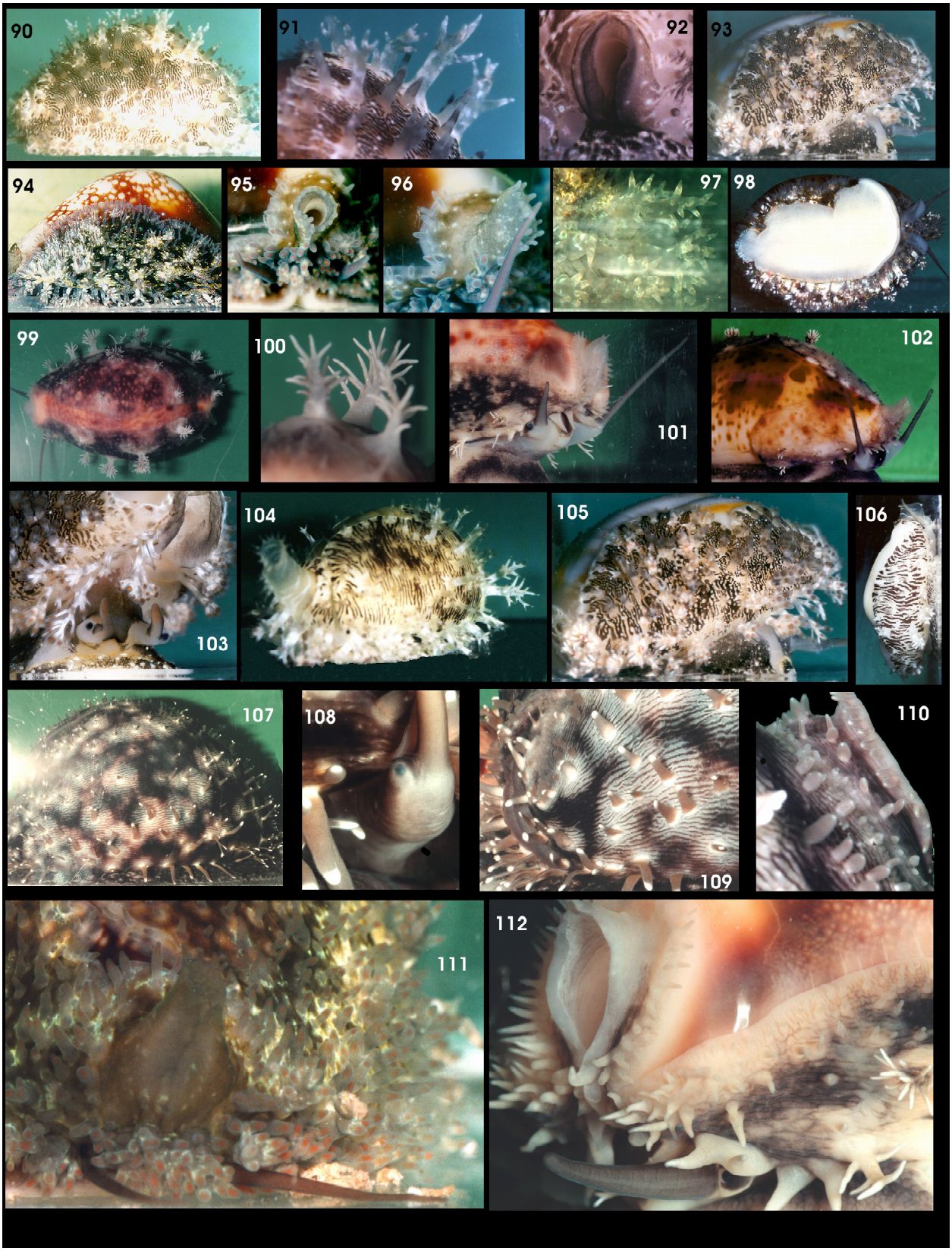
Color plate. Figs. 16-26, alive crawling specimens and shells: **16-18**, *Macrocypraea zebra* living in Poços de Caldas Aquarium, specimen of about 80 mm; **19-21**, *Niveria pediculus* from Salvador, Bahia, courtesy of Carlo Magenta; **22-23**, *Cyphoma signatum*, courtesy of Paulo M. Costa; **24**, *Pseudocyphoma intermedium*, courtesy of Paulo M. Costa; **25-26**, *Lamellaria mopsicolor*, shell found in Marcus' collection (type?), apertural and dorsal views, MZSP 35008, scale = 1 mm.

Color plate. Figs. 27-56, shells: **27**, *Lamellaria mopsicolor*, shell found in Marcus' collection, MZSP 35008, lateral view; **28**, label of shell of Figs 25-27 with Dr. Eveline Marcus' calligraphy; **29-30**, *Lamellaria patagonica*, dorsal and ventral views, courtesy of Guido Pastorino, scale = 10 mm; **31-32**, *Jenneria pustulata*; **33**, *Velutina velutina*; **34**, *Niveria pediculus*; **35**, *Cyphoma signatum*; **36-37**; *Cyphoma gibbosum*; **38**, *Erosaria spurca*; **39**; *Ovula ovum*; **40**, *Macrocypraea zebra*; **41**, *Cypraea tigris*; **42**, *Pseudozonaria robertsi*; **43**, *Ravitrona caputserpentis*; **44**, *Muracypraea mus*; **45**, *Monetaria moneta*; **46**, *Luria cinerea*; **47-48**, *Lyncina lynx*; **49**, *Calpurnus verrucosus*; **50**, *Monetaria annulus*; **51**, *Macrocypraea cervinetta*; **52**, *Erosaria acicularis*; **53**, *Pseudocyphoma intermedium*; **54**, *Niveria pediculus*; **55**, *Pseudocyphoma intermedium*; **56**, *Calpurnus verrucosus*. (All same specimens of grayscale plates.)

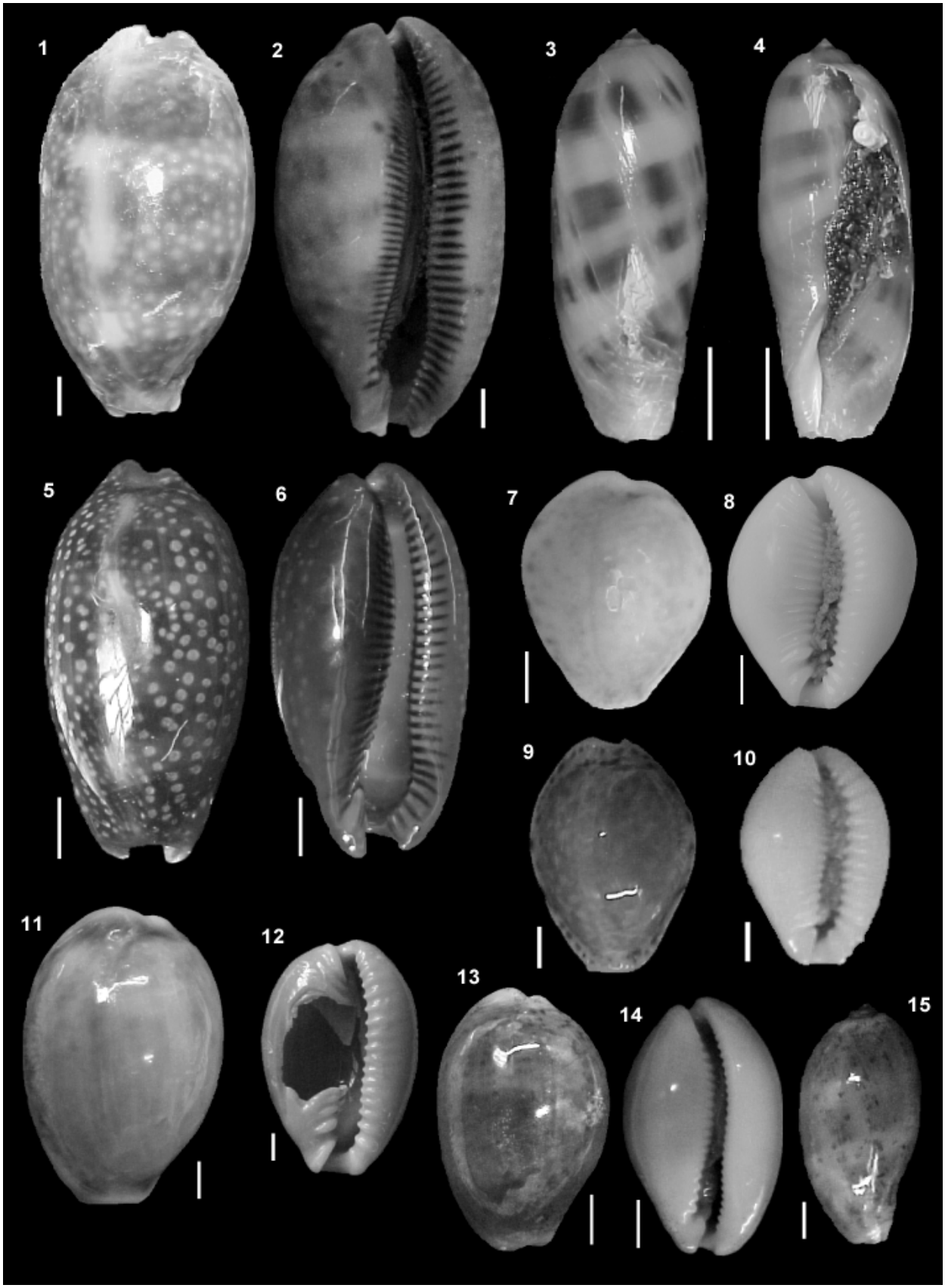
Color plate. Figs. 57-87, shell of specimens from other localities rather than those studies herein. All courtesy of Femorale Ltda. Marcus & José Coltro. **57-58**, *Erosaria acicularis*, from Salvador, Bahia, Brazil; **59-60**, *Monetaria annulus*, from Tutula Is., Samoa; **61-62**, *Pseudozonaria arabicula*, from Manabi, Ecuador; **63-64**, *Ravitrona caputserpentis*, from Mozambique; **65-66**, *Macrocypraea cervinetta*, from Veraguas Province, Panama; **67-69**, *Luria cinerea*, 67, from Salvador, Bahia, Brazil, 68-69, from Alcobaça, Bahia; **70-72**, *Monetaria moneta*, 70, from Taiwan, 71-72, from Fakarawa Atoll, French Polynesia; **73-74**, *Pseudozonaria robertsi*, from La Perla Is., Panama; **75-76**, *Erosaria spurca* from Murcia, Spain; **77**, *Cypraea tigris*, from Thailand; **78-80**, *Macrocypraea zebra*, from Alcobaça, Bahia; **81-82**, *Cyphoma gibbosum*, from Puerto Francos, Venezuela; **83**, *Calpurnus verrucosus*, from Nacala, Mozambique; **84-85**, *Jenneria pustulata*, from Sonora, Mexico; **86-87**, *Pseudocyphoma intermedium*, from Ilha Bela, São Paulo, Brazil (as *P. gerrini*).



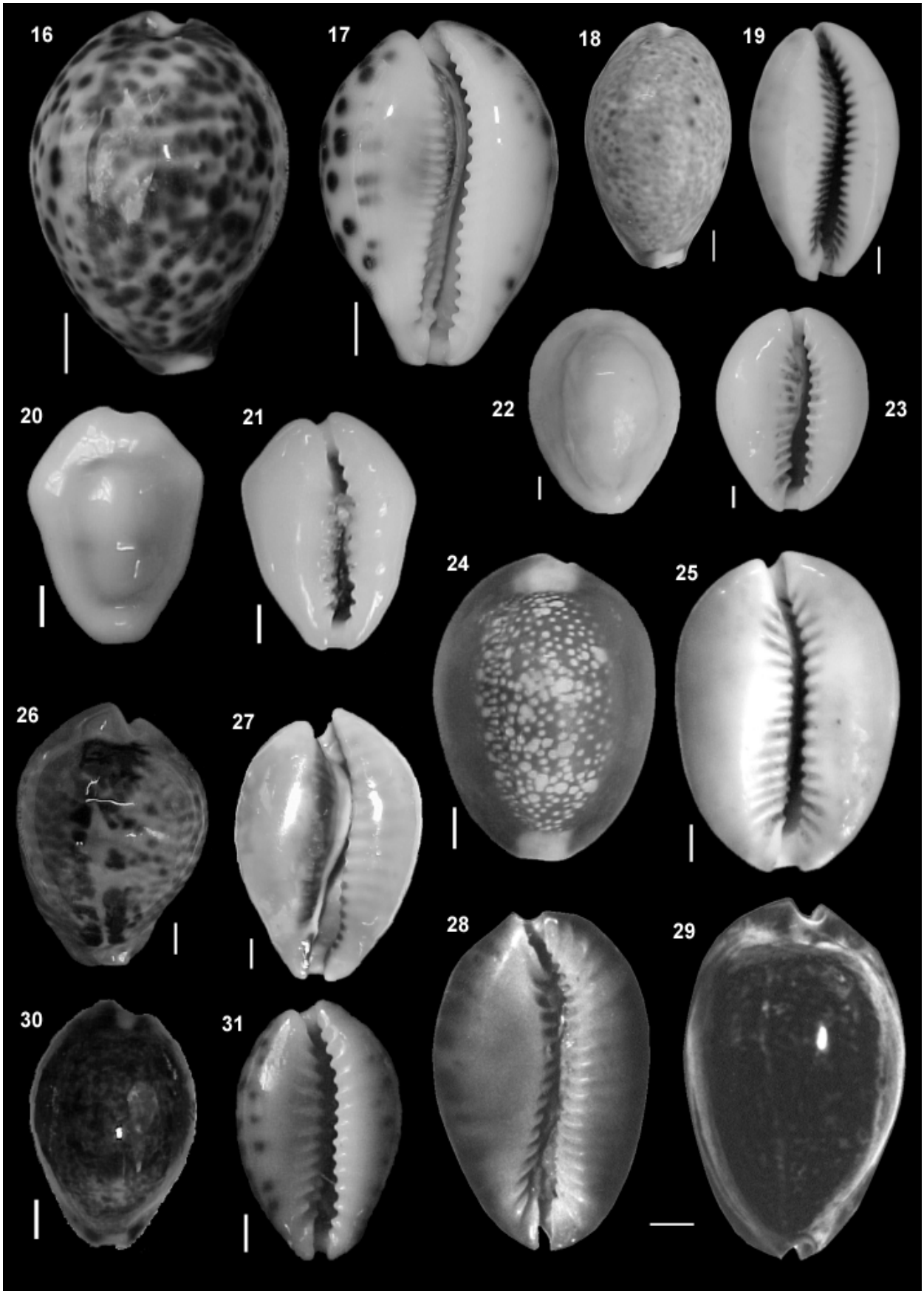
Color plate. Examples of shell variation in two ovulid species. **88**, *Pseudocyphoma intermedium*, specimens collected from Angra dos Reis (south Rio de Janeiro) to Ilha Bela (north São Paulo), specimens of Coltro collection; **89**, *Simnialena uniplicata*, from Angra dos Reis (south Rio de Janeiro) to Ilha Bela, (north São Paulo), most MZSP 34832. Scales = 5 mm.



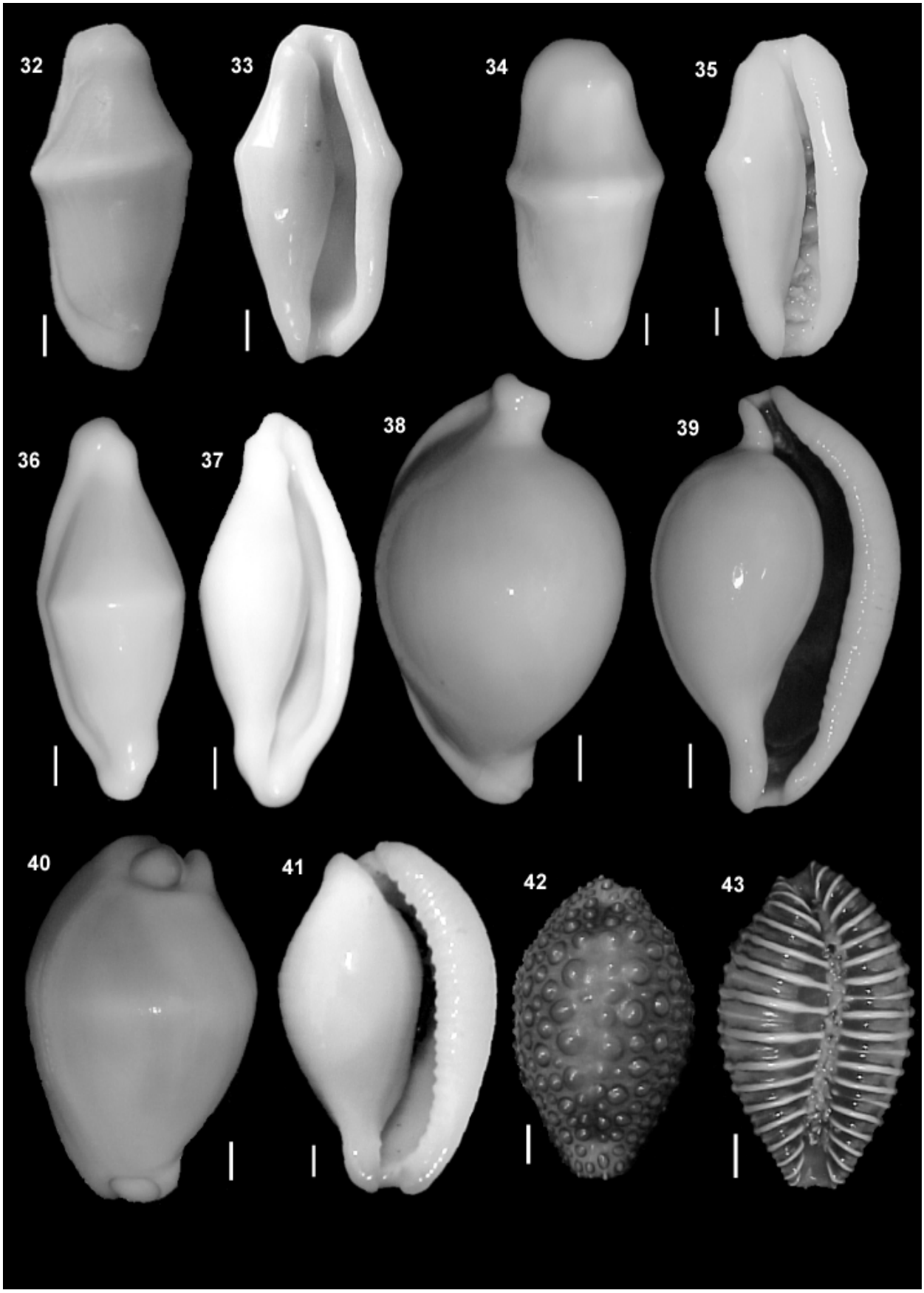
Color plate. Cypraeidae living specimens, courtesy of Wesley M. Thorsson's *Cypraea* graphic files (an internet Hawaiian shell news project). **90-93**, *Monetaria annulus*, 90, lateral view; 91, detail of papillae; 92, detail of siphon; 93, lateral view of another specimen; **94-98**, *Ravitrona caputserpentis*, 94, lateral view; 95-96, details of siphon; 97, detail of papillae; 98, crawling sole in a glass, ventral view; **99-102**, *Lyncina lynx*, 99, dorsal view; 100, detail of papillae; 101-102, cephalic region; **103-106**, *Monetaria moneta*, 103, cephalic region; 104-106, lateral views of different specimens; **107-110**, *Cypraea tigris*, 107, lateral view; 108, detail of right cephalic tentacle; 109, posterior region of mantle surface; 110, detail of siphon, lateral-right view; **111**, *Ravitrona caputserpentis*, cephalic region, frontal view; **112**, *Lyncina lynx*, cephalic region, lateral-left view.



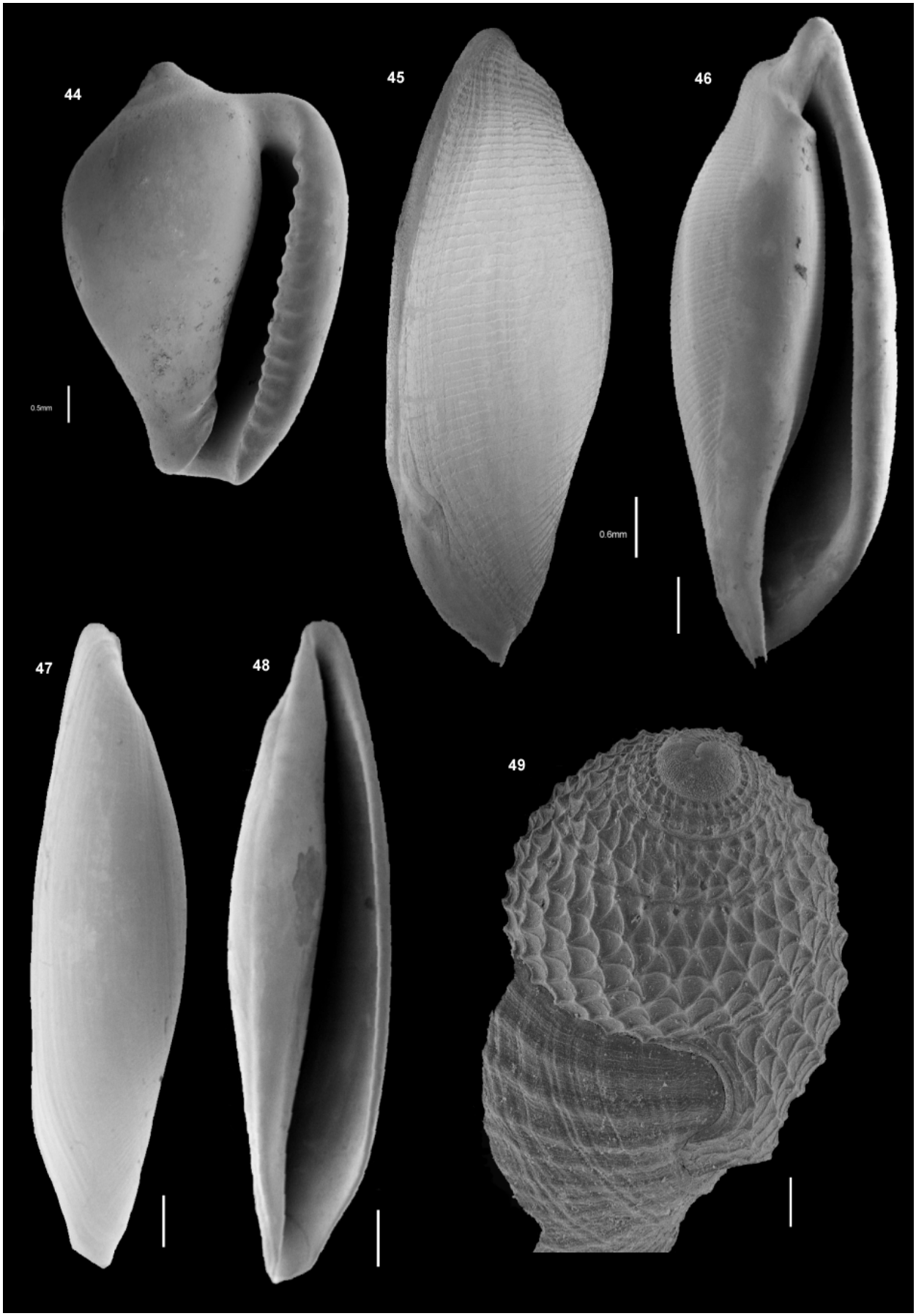
Figs. 1-15, cypraeid shells. **1**-**4**, *Macrocypraea zebra*, 1-2, dorsal and apertural views of adult specimen MZSP 32841, 3-4, same for young specimen MZSP 28311, scales = 10 mm; **5**, **6**, *M. cervinetta*, dorsal and apertural views, AMNH 276910, scales = 10 mm; **7**-**10**, *Erosaria acicularis*, 7-8 dorsal and apertural views, DMNH 202013 (from Florida), scales = 5 mm, 9-10, same, MZSP 28570 (Brazil), scales = 3 mm; **11**, **12**, *E. spurca*, dorsal and apertural (partially broken) views, BMNH, scales = 10 mm; **13**, **15**, *Luria cinerea*, 13-14, dorsal and apertural views of adult specimen MZSP 28569, scales = 5 mm; 15, young specimen MZSP 30942, scale = 3 mm.



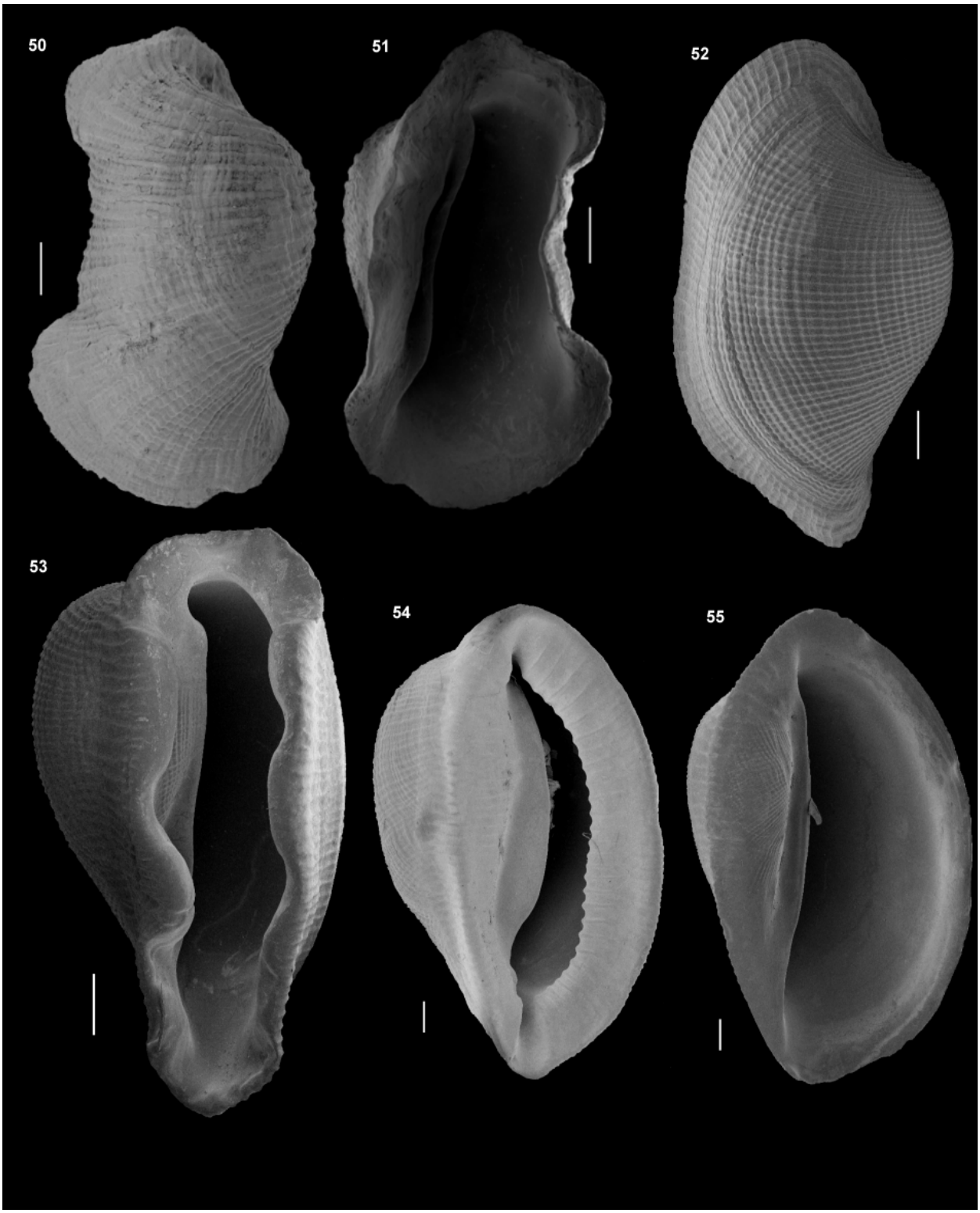
Figs. 16-31, cypraeid shells. **16**, **17**, *Cypraea tigris*, dorsal and apertural views, ANSP 200894, scales = 10 mm; **18**, **19**, *Lyncina lynx*, dorsal and apertural views, MZSP 2044, scales = 5 mm; **20**, **21**, *Monetaria moneta*, dorsal and apertural views, MZSP 30764, scales = 3 mm; **22**, **23**, *M. annulus*, dorsal and apertural views, MZSP 8154, scales = 3 mm; **24**, **25**, *Ravitrona caputserpentis*, dorsal and apertural views, MZSP 8220, scales = 5 mm; **26**, **27**, *Muracypraea mus*, dorsal and apertural views, AMNH 181455, scales = 5 mm; **28**, **29**, *Pseudozonaria arabicula*, apertural and dorsal views, MZSP 32147, scales = 3 mm; **30**, **31**, *Pseudozonaria robertsi*, dorsal and apertural views, MZSP 32148, scales = 3 mm.



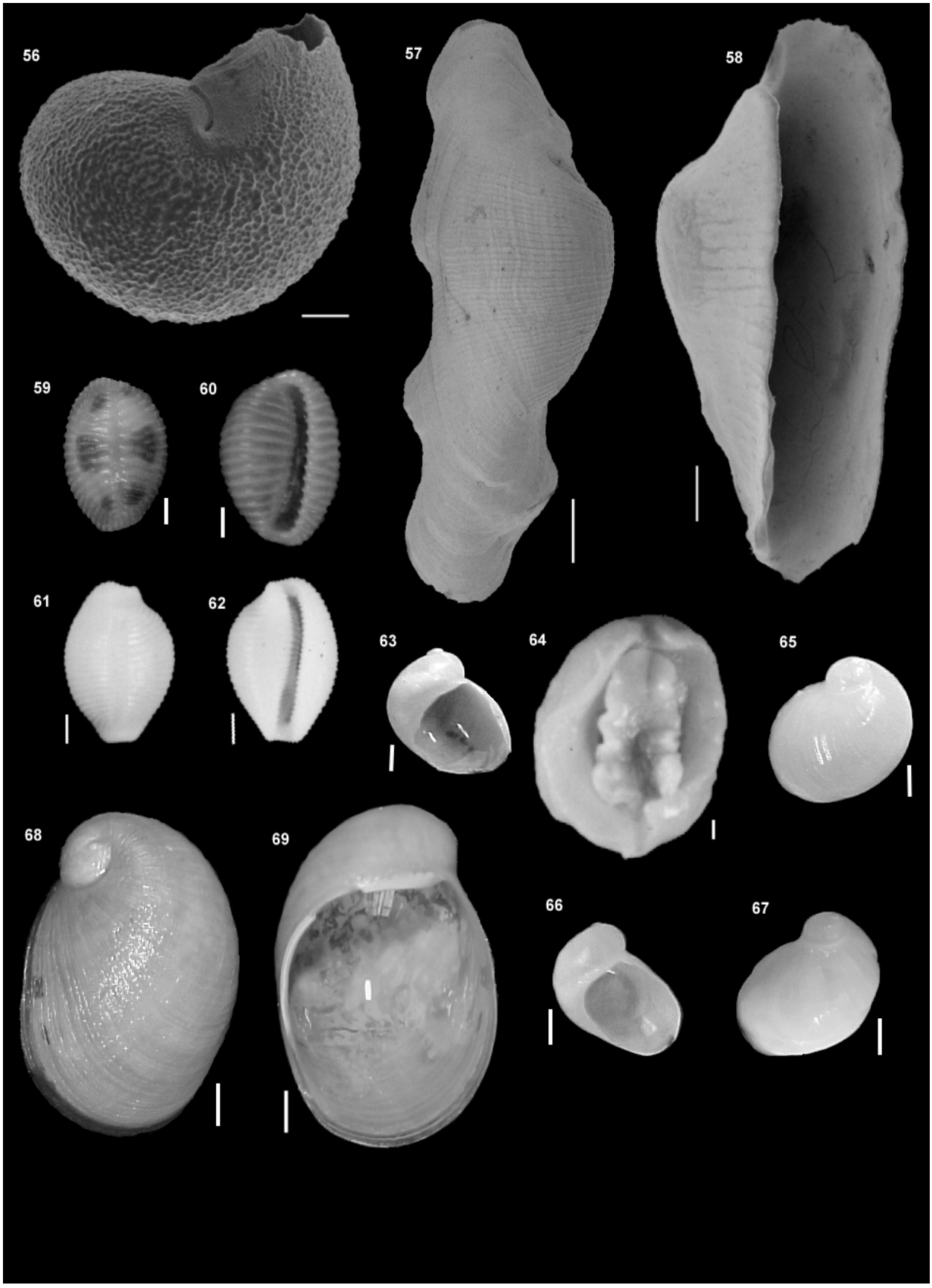
Figs. 32-43, ovulid shells. **32**, **33**, *Cyphoma signatum*, dorsal and apertural views, MZSP 29248; **34**, **35**, *C. gibbosum*, dorsal and apertural views, ANSP A5540; **36**, **37**, *Pseudocyphoma intermedium*, dorsal and apertural views, MZSP 19198; **38**, **39**, *Ovula ovum*, dorsal and apertural views, USNM 836355; **40**, **41**, *Calpurnus verrucosus*, dorsal and apertural views, ANSP Z30676; **42**, **43**, *Jenneria pustulata*, dorsal and apertural views, ANSP 276915. Scales = 3 mm, except 38-39= 10 mm.



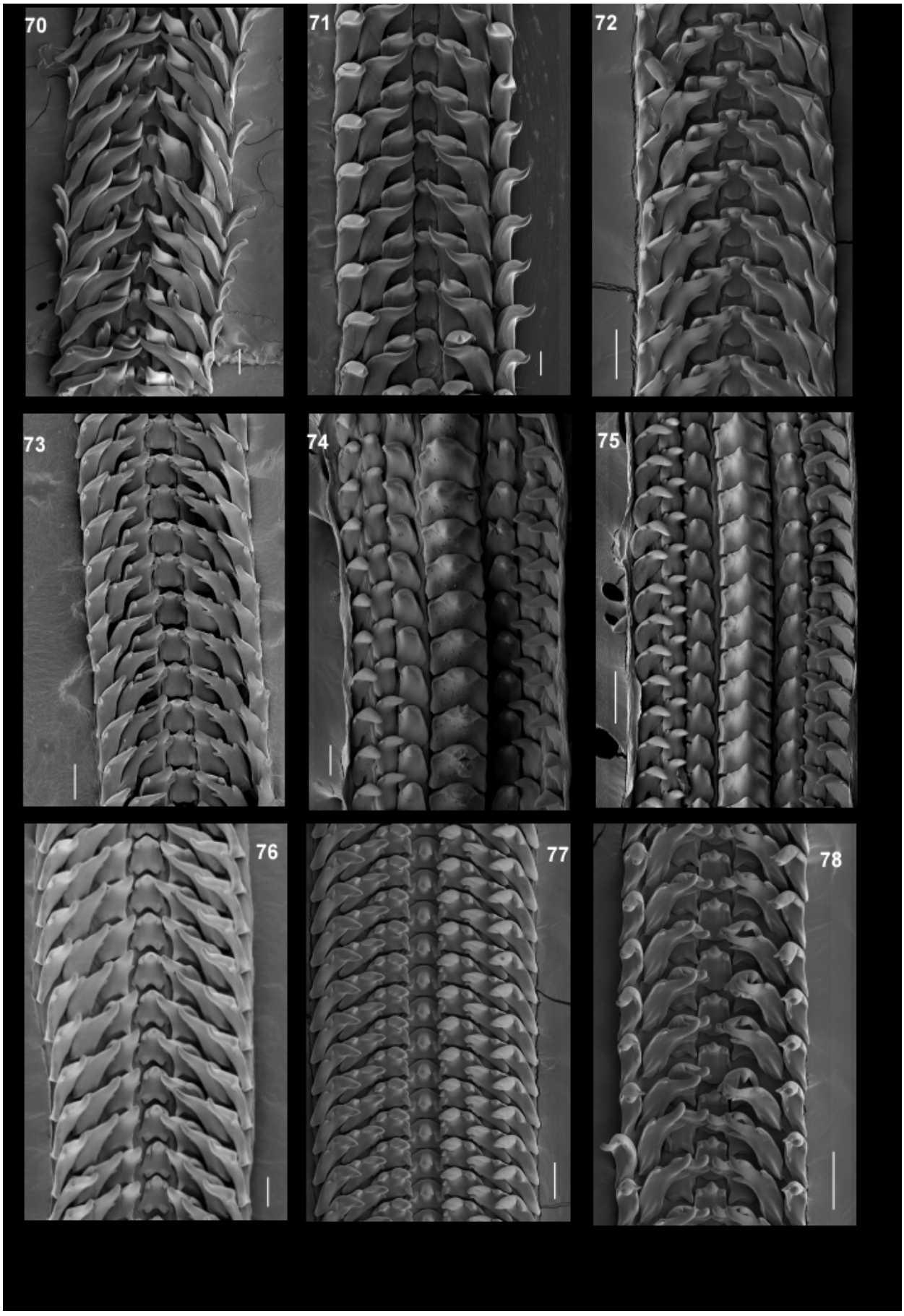
Figs 44-49, eratoid and pediculariid shells in SEM. **44**, *Hespererato maugeriae*, apertural view, USNM 850684, scale = 500 µm; **45**, **46**, *Simnialena uniplicata*, dorsal and apertural views, MZSP 29233, scales = 600 µm; **47**, **48**, *Cymbula acicularis*, dorsal and apertural views, AMNH 163747, scales = 600 µm; **49**, *Pedicularia decussata*, detail of very young specimen, DMNH 201879, scales = 60 µm.



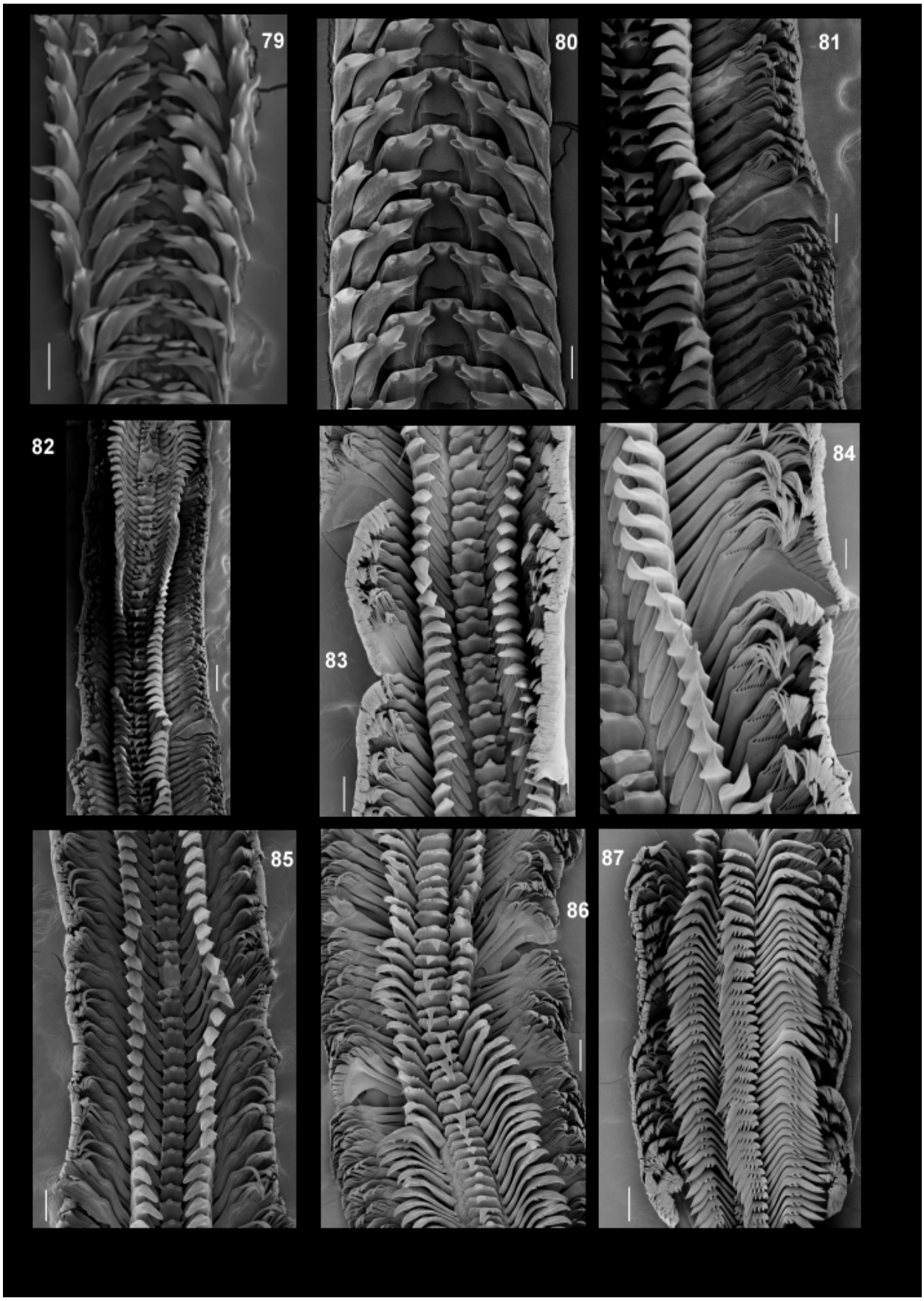
Figs. 50-55, pediculariid shells in SEM. **50**, **51**, *Pedicularia* sp1, dorsal and apertural views, USNM 857666; **52**, **53**, *P. decussata*, dorsal and apertural views, DMNH 201879; **54**, **55**, *P. californica*, apertural views, FMNH 24040. Scales = 500 µm.



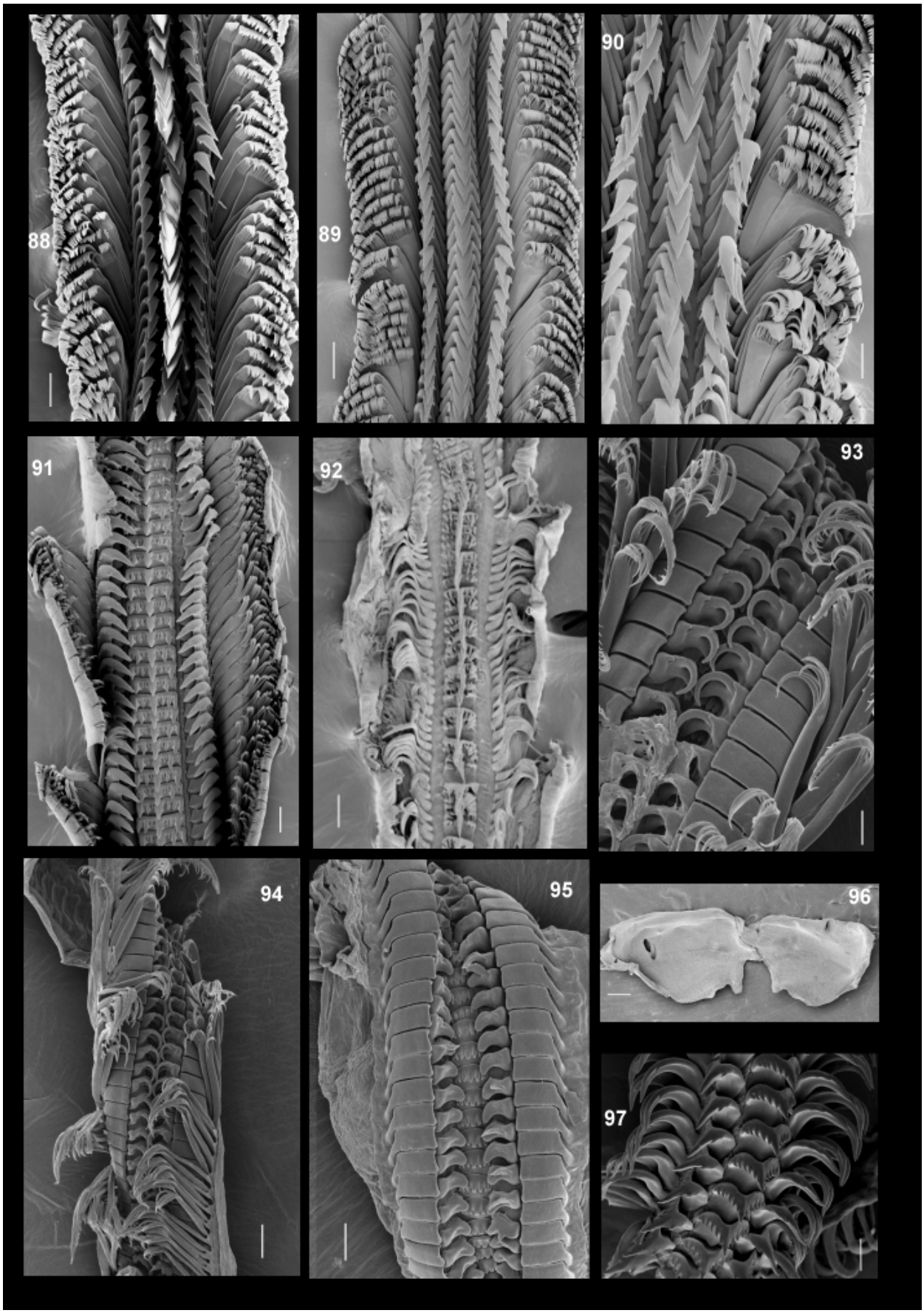
Figs. 56-69, pediculariid, triviid and lamellariid shells. **56**, *Pedicularia californica*, protoconch, SEM, scale = 20 µm; **57**, **58**, *Pedicularia* sp2, dorsal and apertural views, MAS 353021, scales = 0.5 mm; **59**, **60**, *Niveria pediculus*, dorsal and apertural views, MZSP 28520, scales = 2 mm; **61**, **62**, *Trivirostra oryza*, dorsal and apertural views, AMS 160778, scales = 2 mm; **63**- **65**, *Lamellaria branca*, 63, 65, apertural and dorsal views of MZSP 19498, 64, whole specimen MZSP 30679, ventral view, scales = 2 mm; **66**, **67**, *L. mopsicolor*, apertural and dorsal views, MZSP 30684, scales = 2 mm; **68**, **69**, *Velutina velutina*, dorsal and apertural views, LACM 68-74, scales = 3 mm.



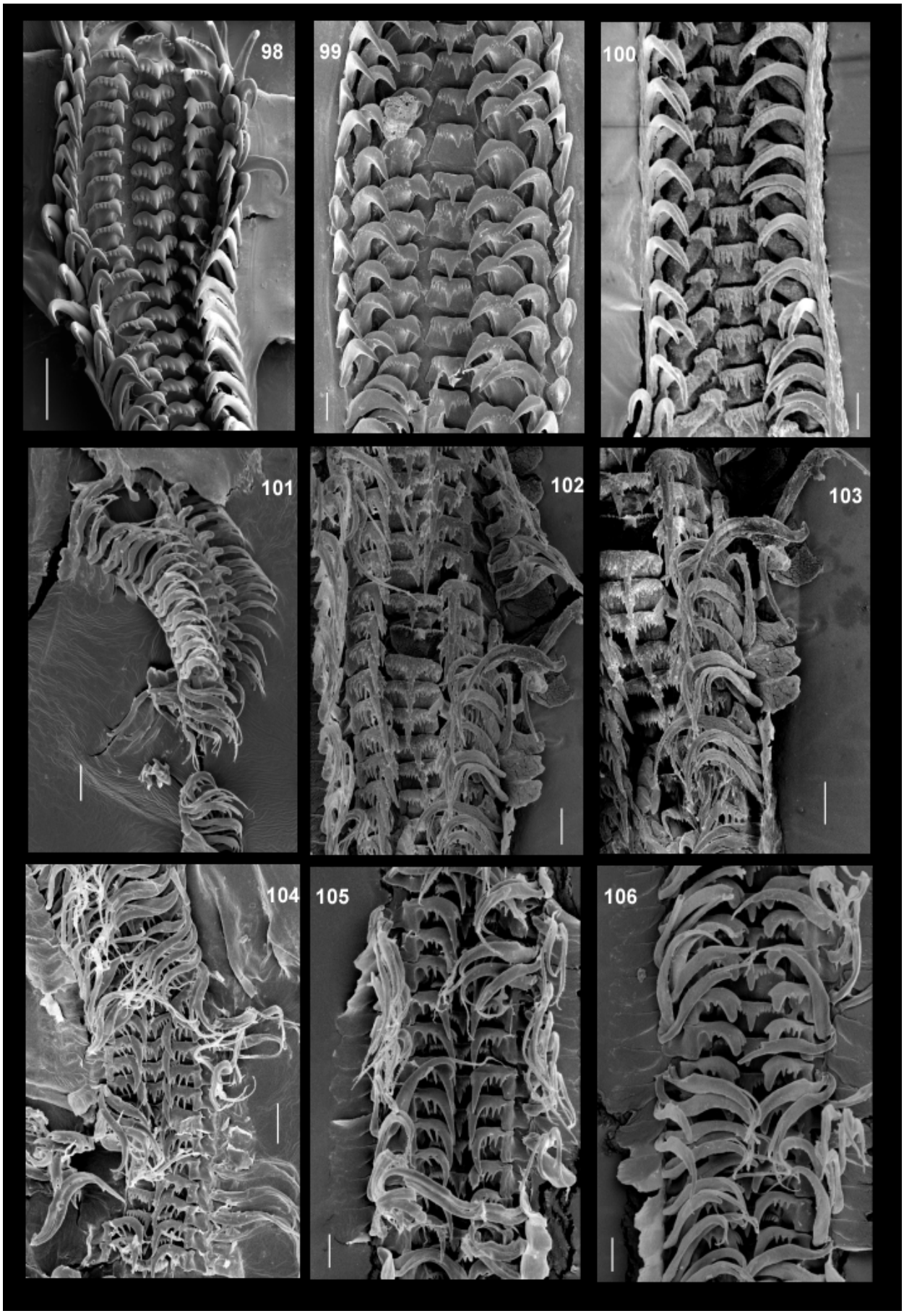
Figs. 70-78, radulae in SEM: **70**, *Macrocypraea zebra*, scale = 200 µm; **71**, *M. cervinetta*, scale = 200 µm; **72**, *Erosaria acicularis*, scale = 100 µm; **73**, *E. spurca*, scale = 100 µm; **74-75**, *Luria cinerea*, scales = 100 µm; **76**, *Cypraea tigris*, scale = 200 µm; **77**, *Lyncina lynx*, scale = 100 µm; **78**, *Monetaria moneta*, scale = 100 µm.



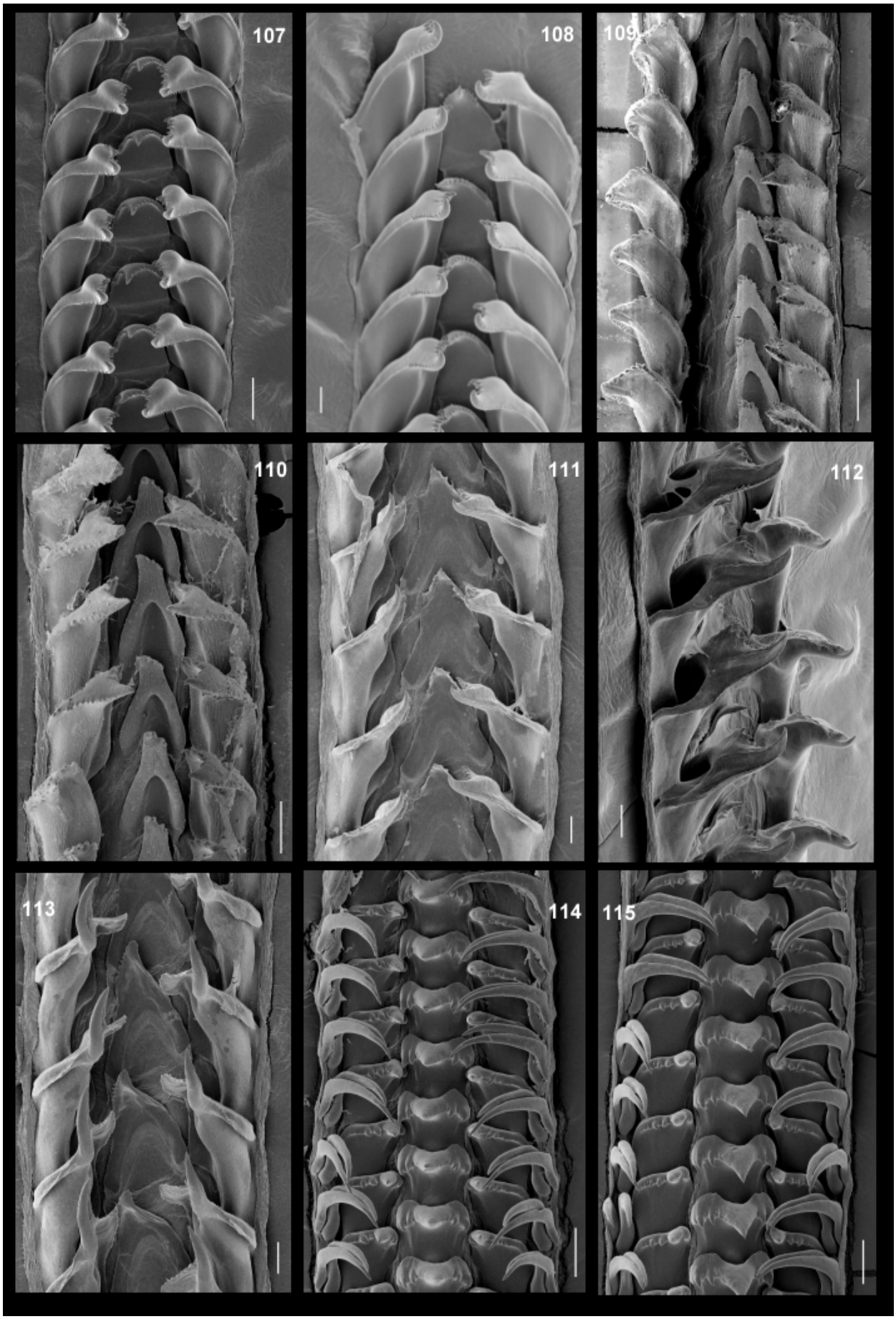
Figs. 79-87, radulae in SEM: **79**, *Monetaria annulus*, scale = 100 µm; **80**, *Ravitrona caputserpentis*, scale = 60 µm; **81**, *Cyphoma signatum*, scale = 100 µm; **82**, same, scale = 200 µm; **83**, *C. gibbosum*, scale = 100 µm; **84**, same, scale = 60 µm; **85**, *Pseudocyphoma intermedium*, scale = 100 µm; **86**-**87**, *Ovula ovum*, scales = 200 µm.



Figs 88-97, hard structures in SEM (radulae, except if indicated): **88-90**, *Calpurnus verrucosus*, scales: 88, 90 = 60 µm, 89 = 100 µm; **91**, *Simnialena uniplicata*, scale = 30 µm; **92**, *Cymbula acicularis*, scale = 60 µm; **93-95**, *Jenneria pustulata*, 93, middle portion of the ribbon, scale = 20 µm; 94, same, scale = 40 µm; 95, distal portion, after in use area, scale = 30 µm; **96**, *Lamellaria branca*, jaws, ventral view, anterior region down, scale = 200 µm; **97**, *Niveria pediculus*, scale = 50 µm.



Figs. 98-106, radulae in SEM: **98**, *Niveria pediculus*, scale = 100 µm; **99**, *Trivirostra oryza*, scale = 40 µm; **100**, *Hespererato maugeriae*, scale = 10 µm; **101**, *Pedicularia* sp1, scale = 20 µm; **102-103**, *P. californica*, scales = 20 µm; **104**, *P. decussata*, scale = 20 µm; **105-106**, *P.* sp2, scales = 10 µm.



Figs. 107-115, radulae in SEM: **107**, *Lamellaria branca*, scale = 100 µm; **108**, same, scale = 50 µm; **109-110**, *L. mopsicolor*, scales = 50 µm; **111-113**, *L. patagonica*, 112 slightly lateral view, scales = 50 µm; **114-115**, *Velutina velutina*, scales = 50 µm.

MATERIAL AND METHODS

Although some living specimens of *Macrocypraea zebra* were examined at the laboratories of the Centro de Biologia Marinha (CEBIMar- USP), most of the specimens studied were fixed in 70% ethanol. The shells were broken (except those of the lamellariids) for extraction of the specimens. The dissections were performed under a stereomicroscope following traditional techniques, with the specimens immerse in fixative (70% ETOH). All drawings were made with aid of a camera lucida. For comparative drawings of the outer surface of the mantle lobes, the middle portion of the left lobe of all specimens was arbitrarily chosen to be pictured. The hard parts, such as shells (of small specimens), jaws and radulae, were also examined in SEM, at the Laboratório de Microscopia Eletrônica, MZSP.

A more detailed description is supplied for the first species, *M. zebra*, which represents the most common and largest cypraeoidean species in southeastern Brazil. In the remainder species, and when possible, the description is basically comparative to *M. zebra*, without the description of the similar characters. This measure decreases considerably the length of this volume. A similar approach is used in the figures.

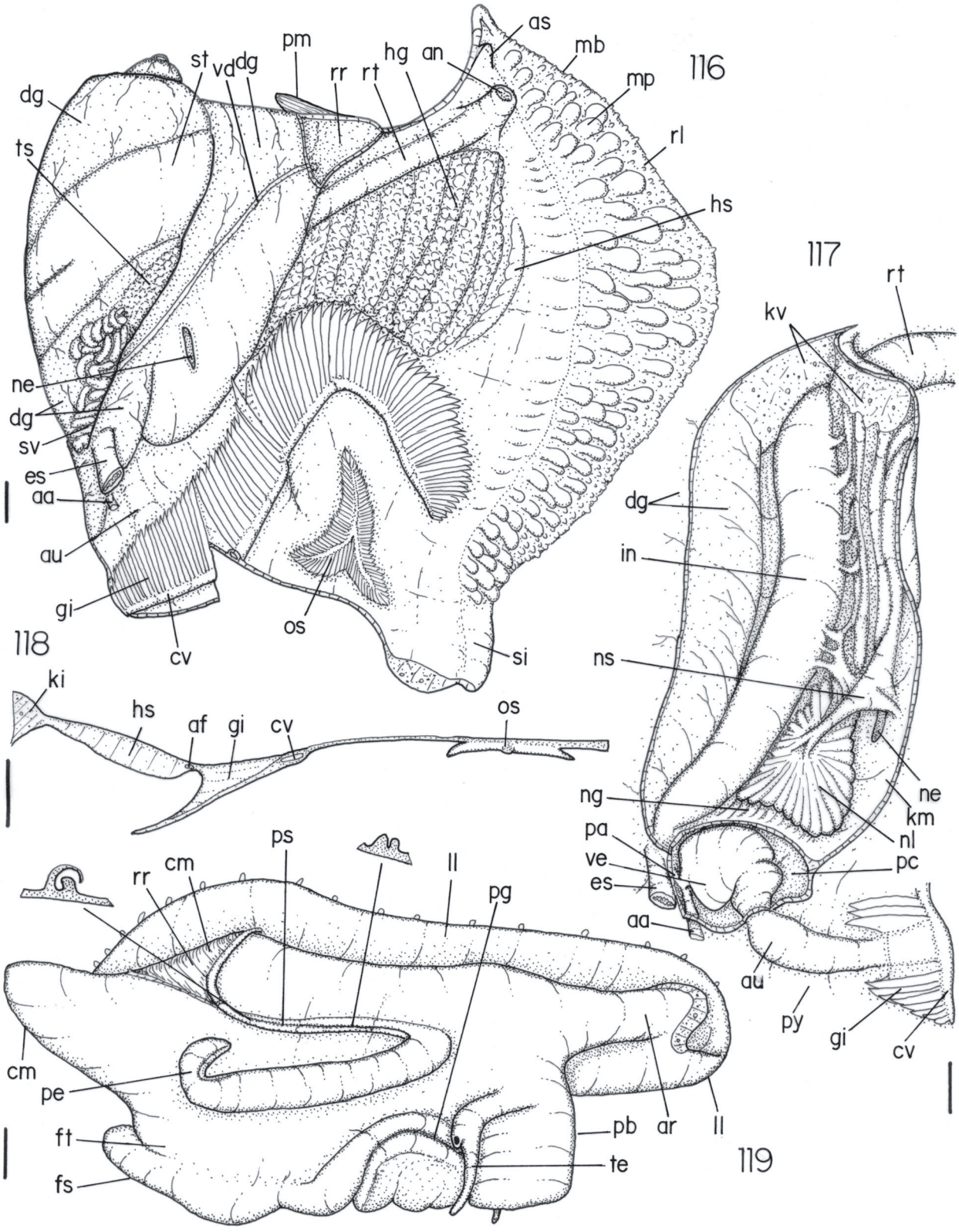
In the final stage of the cladistic analysis the computer program "Tree Gardner 2.2" (Ramos, 1997) was used, which basically works as an interface of the program "Hennig86" (Farris, 1988), the algorithm used was mh*, bb* and ie. For the polarization of the character states the outgroup method was used. The outgroup choice is explained in section of discussion of the characters.

Abbreviations in the figures are: **aa**, anterior aorta; **ac**; anterior extremity of ctenidial vein; **af**, afferent gill vessel; **ag**, albumen gland; **an**, anus; **ap**, aperture of pallial gonoducts; **ar**, anterior projection of head-foot; **as**, anal siphon; **au**, auricle; **ba**, brood pouch aperture; **bb**, bulged region of br; **bc**, bursa copulatrix; **bg**, buccal ganglion; **bm**, buccal mass; **bp,** brood pouch; **br**, subradular membrane; **bt**, buccal (oral) tube; **bv**, blood vessel; **ce**, cerebral ganglion; **cg**, capsule gland; **ci**, circular muscle fibers; **cm**, columellar muscle; **co**, connection haemocoel-visceral mass; **cv**, ctenidial vein; **da**, duct to digestive gland close to esophageal insertion; **dc**, dorsal chamber of buccal mass; **dd**, duct to digestive gland; **df**, dorsal fold of buccal mass; **dg**, digestive gland; **dw**, dorsal wall of buccal mass; **ec**, esophageal gland; **ed**, ejaculatory duct free in haemocoel; **ef**, esophageal folds; **ep**, esophageal pouch; **es**, esophagus; **et**, esophageal typhlosole; **ey**, eye; **ff**, furrowed part of dorsal folds of buccal mass; **fo**, female papilla or atrium; **fp**, female pore; **fs**, foot sole; **ft**, foot; **gc**, cerebral ganglion; **gd**, pallial gonoduct; **gi** gill; **go**, gonad; **gp**, parietal ganglion; **gr**, gonopericardial duct; **hg**, hypobranchial gland; **hs**, mantle septum trough hypobranchial gland; **in**, intestine; **ir**, insertion of m4 in tissue on radula (to); **is**, insertion of m5 in radular sac; **jw**, jaw; **kc**, kidney chamber; **ki**, kidney; **km**, membrane between kidney and pallial cavity; **kv**, ventral lobe of kidney generally attached to intestine; **ll**, left mantle lobe; **ls**, left shell muscle; **m1** to **m14**, extrinsic and intrinsic odontophore muscles; **ma**, mouth abductor muscle; **mb**, mantle border; **mc**, buccal sphincter and circular muscles of oral tube; **mf**, middle fold of pallial oviduct; **mj**, jaws, buccal, and oral tube muscles; **mo**, mouth; **mp**, mantle papilla; **mr**, mantle posterior concavity; **mt**, mantle portion covering shell; **nc**, nephridial gland central vessel; **ne**, nephrostome; **ng**, nephridial gland; **nl**, lobe of nephridial gland; **nr**, nerve ring; **ns**, nephridial gland vessel inserted at right from nephrostome; **nv**, nerve; **oc**, odontophore cartilage; **od**, odontophore; **os**, osphradium; **ot**, oral tube; **ov**, pallial oviduct; **oy**, ovary; **pa**, posterior aorta; **pb**, proboscis; **pc**, pericardium; **pd**, penis groove or duct; **pe**, penis; **pg**, pedal glands anterior furrow; **pl**, penis basal muscles; **pm**, pallial muscle (derived from columellar muscle) **pn**, pedal ganglion; **pp**, penis papilla; **ps**, pallial spermgroove or duct; **pt**, prostate; **pu**, pedal ganglion; **py**, pallial cavity; **ra**, radula; **rh**, rhynchostome; **rm**, retractor muscle of proboscis; **rn**, radular nucleus; **rp**, radular distal sac; **rr**, anterior triangular sinus of visceral mass connected to pallial floor; **rs**,

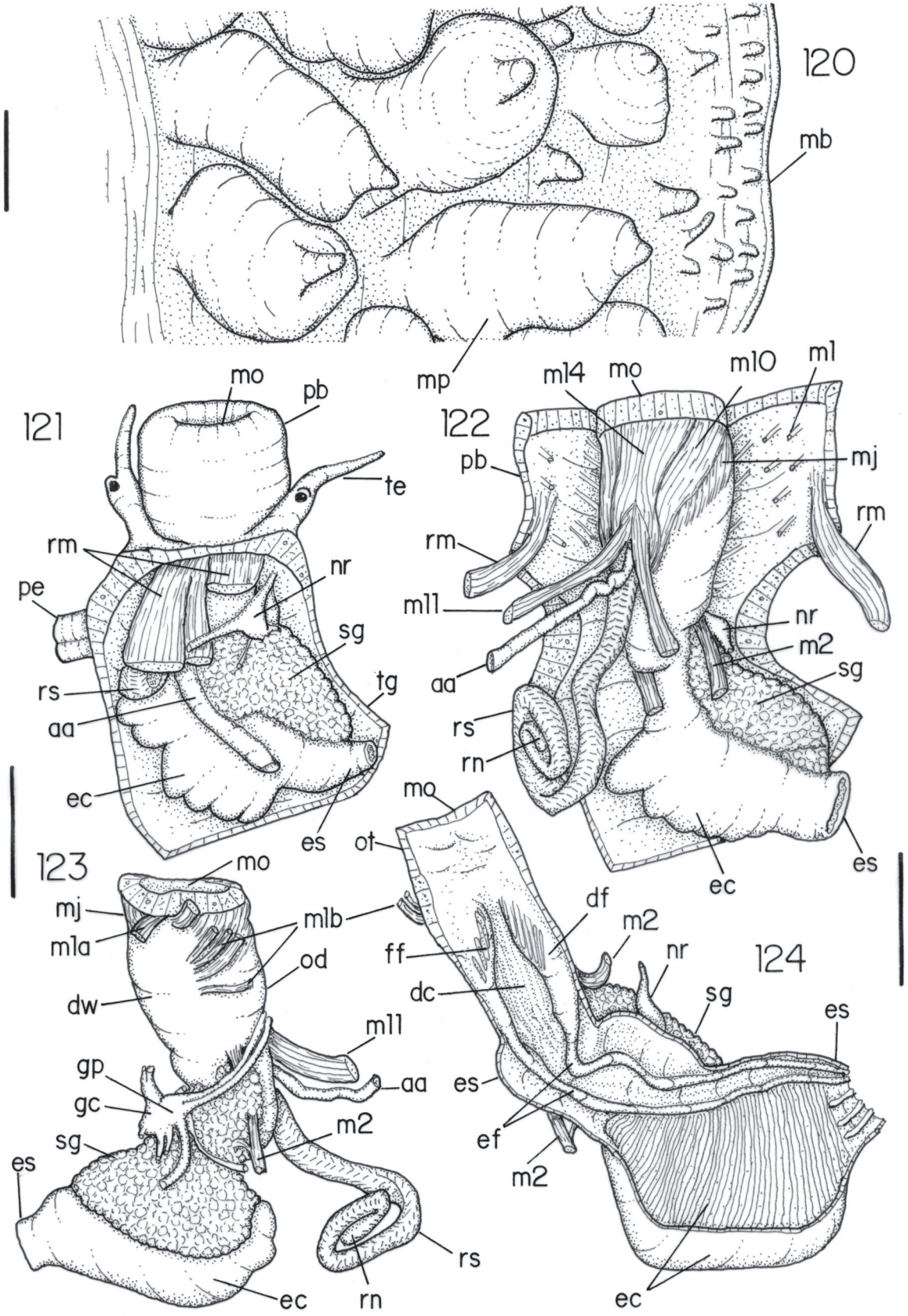
radular sac; **rt**, rectum; **sc**, subradular cartilage; **sd**, salivary duct; **se**, septum between esophagus and odontophore in buccal mass; **sg**, salivary gland; **sh**, shell; **si**, siphon; **sl**, snout (or oral tube) gland(s); **sm**, right shell muscle; **so**, salivary orifice; **sr**, seminal receptacle; **st**, stomach; **su**, subesophageal ganglion; **sv**, seminal vesicle; **sy** statocyst; **te** cephalic tentacle; **tg**, integument; **to**, tissue on middle region of radula preceding its exposure; **ts**, testis; **vd**, visceral vas deferens; **ve**, ventricle; **vg**, vaginal groove/duct; **vi**, visceral ganglion; **vo**, visceral oviduct; **vp**, vestigial penis of female; **vs**, seminal vesicles of pallial oviduct.

Abbreviations of institutions are: **AMNH**, American Museum of Natural History, New York; **AMS**, Australian Museum, Sydney; **ANSP**, Academy of Natural Sciences of Philadelphia; **BMNH**, The Natural History Museum, London; **BMSM**, The Bayley-Mattews Shell Museum, Sanibel Island, Florida; **DMNH**, Delaware Museum of Natural History, Delaware; **FMNH**, Field Museum of Natural History, Chicago, IL; **LACM**, Natural History Museum of Los Angeles County, California, USA; **MACN**, Museo Argentino de Ciencias Naturales, Argentina; **MNHN**, Muséum National d'Histoire Narurelle, Paris; **MZSP**, Museu de Zoologia da Universidade de São Paulo; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

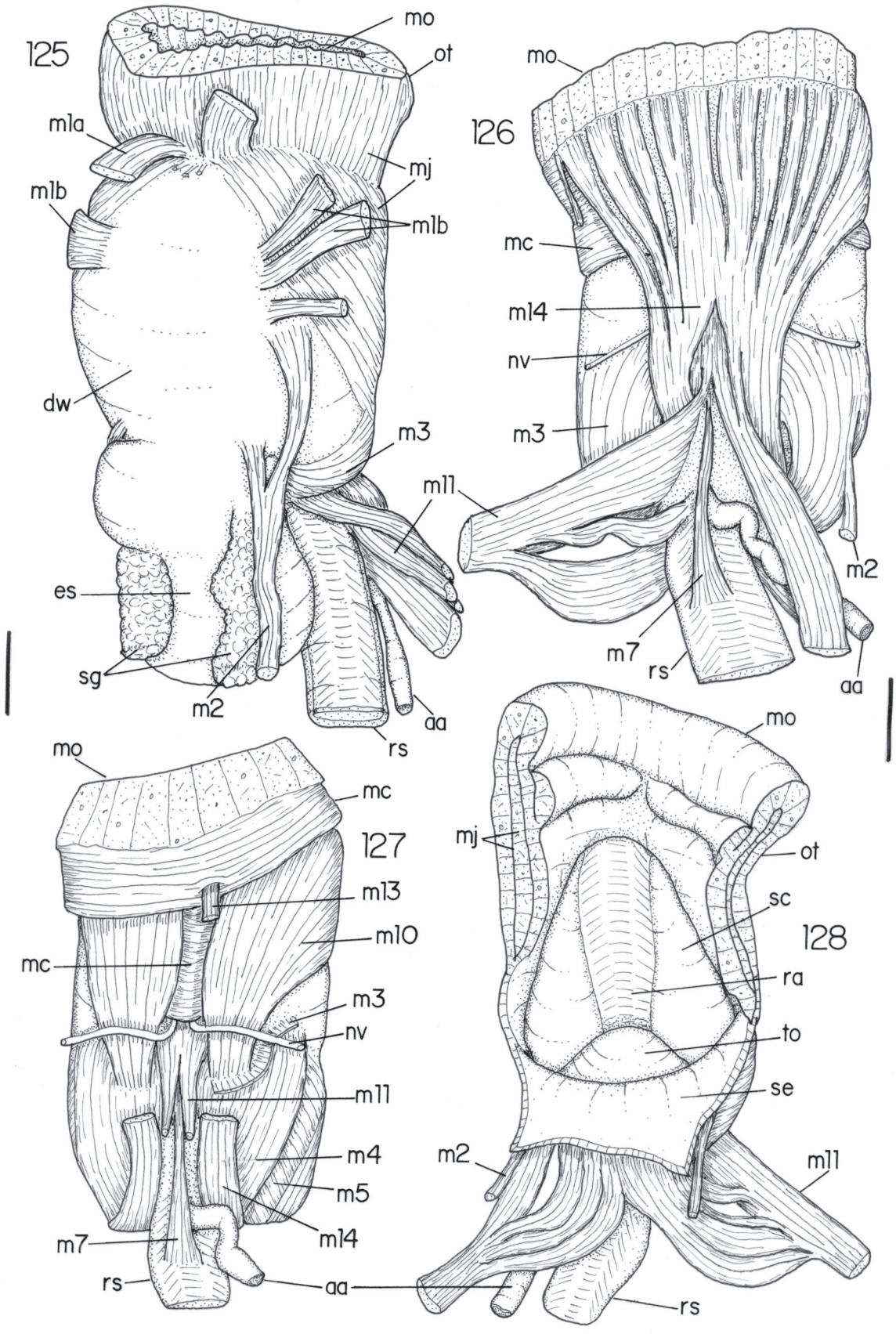
Some data extracted from Malacolog website were also used (Rosenberg, 1996), mainly depth and distribution of the Western Atlantic species.



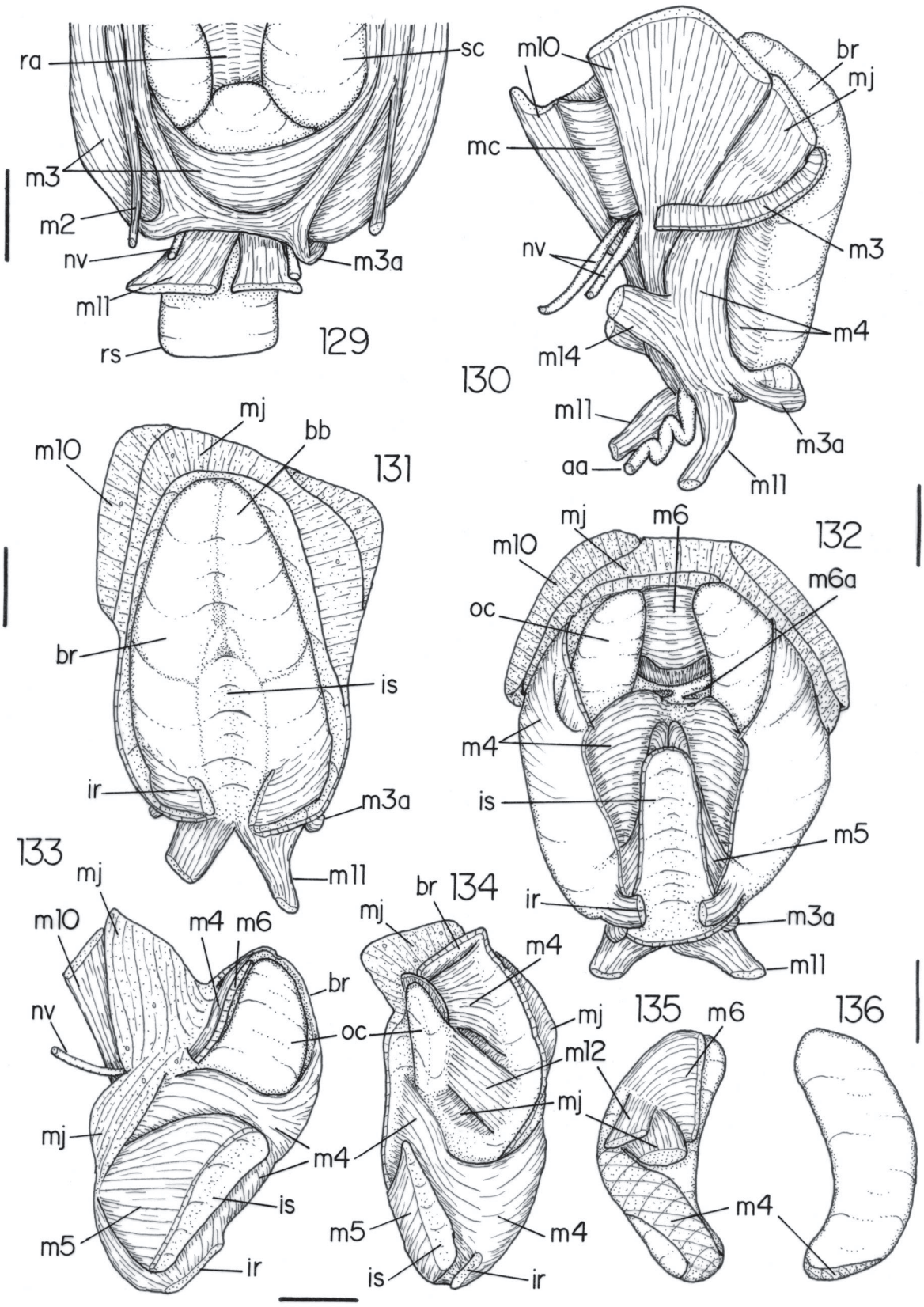
Figs. 116-119, *Macrocypraea zebra* anatomy: **116,** pallial cavity and visceral mass, male, inner-ventral view; **117,** kidney and pericardium, ventral view, both opened along ventral wall, a portion of adjacent region of pallial cavity also shown, with some gill filaments on auricle removed; **118,** pallial cavity, transversal section in middle level of posterior osphradium branch; **119**, head-foot, male, lateral-right view, specimens with proboscis extended, transversal sections of sperm groove in 2 indicated levels also shown. Scales = 5 mm.



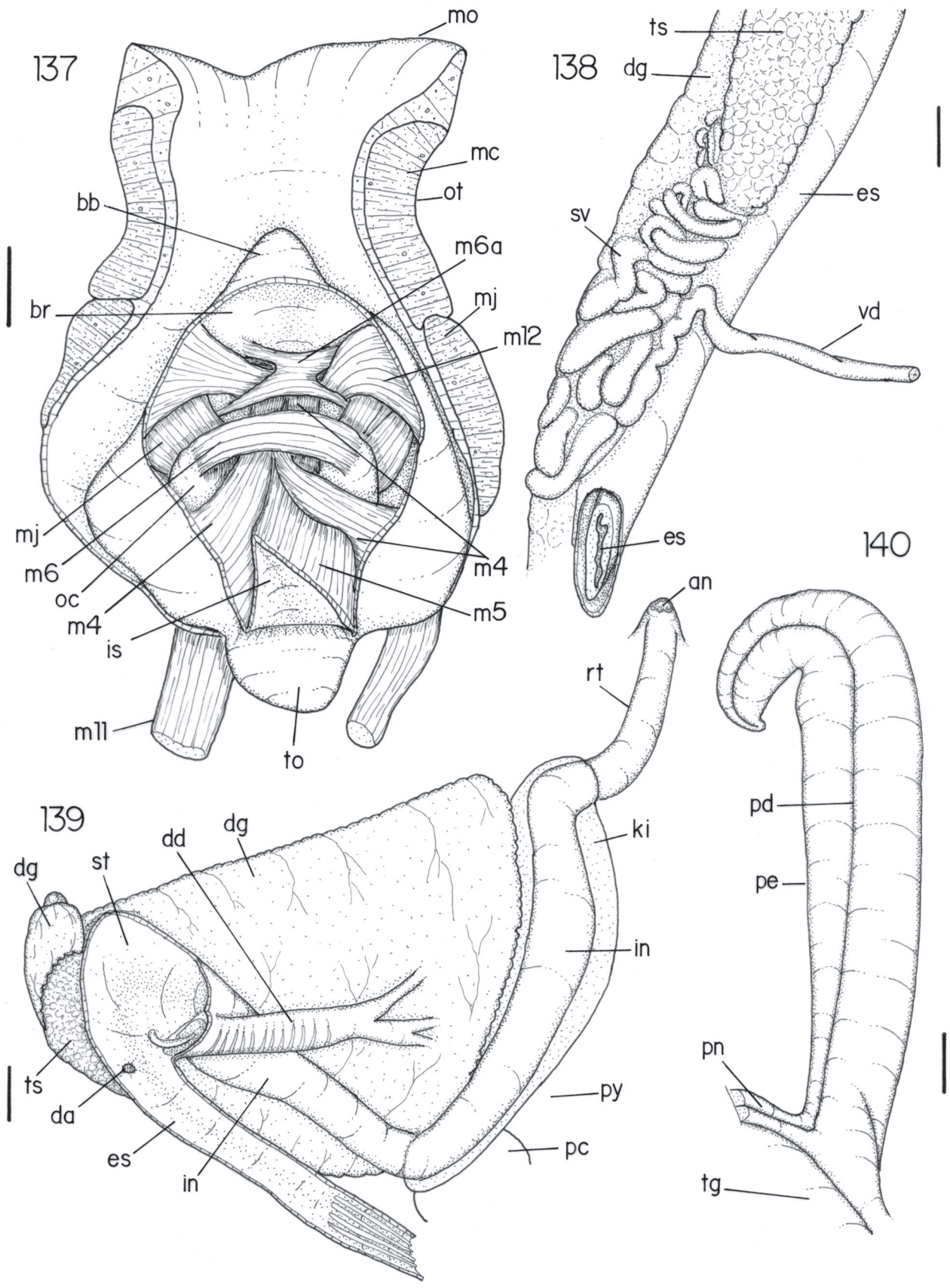
Figs. 120-124, *Macrocypraea zebra* anatomy: **120,** right mantle lobe, outer surface, detail of its middle portion; **121,** head and haemocoel, ventral view, foot removed, proboscis extended, nerve ring and penis only partially shown; **122,** same, head and proboscis opened longitudinally along median line; **123**, foregut, dorsal-slightly right view; **124**, same, odontophore removed remaining dorsal wall of buccal mass, esophagus opened longitudinally with inner surface exposed. Scales: 120= 2 mm, remainder = 10 mm.



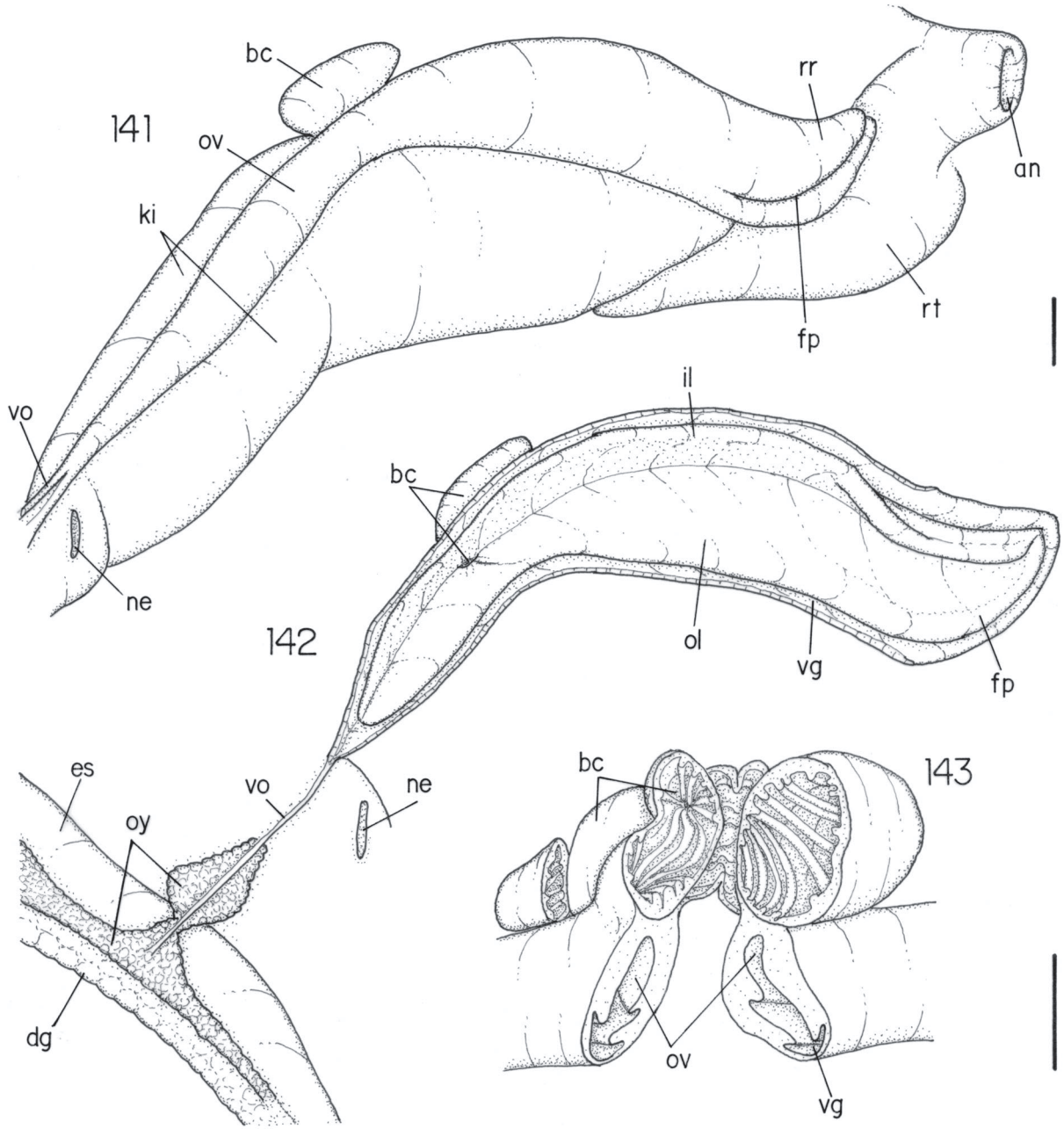
Figs. 125-128, *Macrocypraea zebra* buccal mass: **125,** dorsal, slightly lateral-right view, radular sac only partially shown; **126,** same, ventral view; **127**, same, ventral layer of muscle partially removed; **128,** odontophore and ventral part of buccal mass removed from buccal mass, dorsal view. Scales = 2 mm.



Figs. 129-136, *Macrocypraea zebra* odontophore: **129,** posterior half, dorsal view, superficial layer of tissue removed; **130,** lateral-left view, some muscles cut close to insertions; **131,** dorsal view, radula and subradular cartilage removed; **132,** same, subradular membrane (br) partially removed to show inner musculature; **133,** right half sectioned sagitally, lateral-left view; **134,** same, slightly anterior view, cartilage (oc) deflected to show muscles inserted in its outer surface; **135,** right cartilage, outer view, most adjacent muscles removed; **136,** same, inner view. Scales = 2 mm.



Figs. 137-140, *Macrocypraea zebra* anatomy: **137,** odontophore and ventral portion of oral tube, dorsal view, subradular membrane partially removed, cartilages deflected outside; **138,** anterior-left extremity of visceral mass, male, ventral view; **139,** visceral mass, male, ventral-inner view, esophagus opened longitudinally, ventral wall of stomach removed, kidney and pericardium only indicated, pallial portion of digestive tubes also shown; **140,** penis, lateral-right view. Scales = 2 mm, except 139 = 5 mm.



Figs. 141-143, *Macrocypraea zebra* female gonoducts: **141,** pallial oviduct and adjacent structures, ventral view; **142,** broad look, ventral view in situ, ovary partially shown, pallial oviduct opened longitudinally along vaginal groove (vg), localization of nephrostome shown; **143**, detail of bursa copulatrix, sectioned transversally in some regions, inner surface exposed, adjacent region of pallial oviduct also sectioned transversally. Scales = 2 mm.

DESCRIPTIONS

Family Cypraeidae
Genus *Macrocypraea* Schilder, 1930
(Type species: *Cypraea exantema* Linné, 1767=*C. zebra* Linné, 1758)

Macrocypraea zebra Linné, 1758

(Figs. 1-4, 70, 116-143)
(Color plate Figs. 16-18, 40, 78-80)

Synonymy see Burgess (1985: 100). Complement:

Cypraea zebra Linné, 1758: 719 [no locality]; Matthews & Rios, 1967: 96; Burgess, 1970: 229 (pl. 21, figs. B, C); Crovo, 1971: 292-295 (figs. 2, 3, 5); Taylor & Walls, 1975: 189 (figs.); Donohue, 1977: 160; Domaneschi, 1983: 12 (fig. 1); Abbott & Dance, 1983: 96 (fig.); Bandel, 1984: 82-84 (fig. 135; pl. 7, fig. 3); Burgess, 1985: 100 (fig.); Calvo, 1987: 109 (fig. 68); Trew, 1987b: 22; Jong & Coomans, 1988: 65; Azevedo, 1989: 33; Merlano & Hegedus, 1994: 166-167 (pl. 52, fig. 615); Abbott & Morris, 1995: 194 (pls. 10, 51).

Cypraea (Trona) zebra: Abbott, 1954: 180 (pl. 6, fig. d); Warmke & Abbott, 1962: 91-92 (fig. 17; pl.2, fig. e; pl. 16, fig. n); Rios, 1970: 61 (pl. 11); Humfrey, 1975: 105-106 (pl. 9, figs. 1-1c).

Cypraea (Macrocypraea) zebra: Matthews, 1967: 17 (fig. 1); Abbott, 1974: (pl. 5, fig. 1638); Rios, 1975: 72 (pl. 20, fig. 294); Oliveira *et al*., 1981: 147; Rios, 1985: 65 (pl. 23, fig. 286); Leal, 1991: 99; Rios, 1994: 74 (pl. 25, fig. 284).

Macrocypraea zebra: Schilder & Schilder, 1971: 33; Lorenz Jr. & Hubert, 1993: 53 (pl. 10, figs. 12-14, 17-20); Bradner & Kay, 1996: 78 (fig. 117).

Description

Shell. Medium to large sized; elliptical, slightly long antero-posteriorly. Color brown with beige circular spots throughout outer surface (Figs. 1, 2; color plate Figs. 40, 78-80), not uniform in size. Young and immature specimens with successive dark and pale purple-brown transversal bands (Figs. 3, 4). Other details in Abbott (1974:149) and Rios (1994: 74).

Head-foot (Figs. 119, 121). Color of exposed areas dark brown with irregular, sometimes coalescent paler sports. Form compressed laterally. Head outstanding. Snout/proboscis cylindrical, large, with almost total capacity of retraction (Fig. 119). Cephalic tentacles long, origin slight ventral of lateral surface of snout base; basal half clearly broader than distal half. Ommatophore small, in ventral-middle region of tentacles. Eyes dark, slightly small. Foot large, somewhat plane and broad. Anterior furrow of pedal glands well developed. Columellar muscle short (about half whorl) and distally thin. Anterior projection of head solid-muscular, originating in nuchal region turned forward; located protected at left of shell siphon canal. An accessory muscle of columellar muscle running in its right edge attached to pallial cavity right margin, where it gradually faints (Fig. 116: pm). Haemocoel relatively broad, elliptical. Haemocoel connection with visceral mass (where esophagus and aorta runs) in middle level of haemocoel left margin. Pair of large and powerful retractor muscles of proboscis (Figs. 121, 122: **rm**), originating in ventral-posterior region of haemocoel, running edging ventral haemocoel inner surface in median line towards anterior, inserting along ventral and lateral wall of snout/proboscis. [See discussion on denomination between snout and proboscis in discussion section, the structure will be named only as proboscis below.]

Mantle organs (Figs. 116-118, 120). Mantle border very ample and broad, presents two lobes (left and right) exceeding shell aperture, which cover shell completely when animal is active. Outer surface of exposed part of mantle dark brown in color, covered by many papillae; inner and medium regions of each lobe possessing large and broad papillae (Figs. 116, 120; Color plate Figs. 16-18); their base narrow, suddenly becoming broad and circular in section, distally narrowing again, presenting a pointed, central apex; papillae of outer region (close to border) gradually become smaller and of uniform width. Siphon separated from mantle border, shallow, with several small

papillae in its margin. Anal siphon present, separated from mantle border, slightly shallower and in opposite side of incurrent siphon. Osphradium slightly large, located at some distance from siphon; presents 3 somewhat isometric and equidistant branches; anterior branch turned forwards, towards siphon; other two branches turned laterally, to left and to right. Each osphradium branch bipectinate, each filament low and thin, its base almost entire connected to mantle, except for pointed, turned externally tip. Osphradium ganglion thick, running in central region of each branch. Osphradium nerve running from intersection of 3 osphradium ganglion branches directly to left, between anterior and left branches. Between osphradium and gill a considerable distance. Gill large, long and curved (concavity left), with about same length of cavity. Ctenidial vein slightly broad, of uniform width along its length; connection with auricle sub-terminal (Fig. 117) (described below). Each gill filament tall, triangular, tip long, slender and sharp (Fig. 118). Distance between gill and visceral mass narrow in posterior half, successively far from visceral mass and rectum in anterior half. Hypobranchial gland very developed, thick, white; occupies area between gill and rectum in anterior half of pallial roof. Several transversal, thin septa from adjacent mantle running through hypobranchial gland. Rectum slightly broad, running in right margin. Anus siphoned, close to anal siphon. Genital gonoducts running ventral and at right from rectum, most in floor of pallial cavity.

Visceral mass (Figs. 116, 139). Slightly small. Of about 3 whorls posterior to pallial cavity, first whorl visible (not covered by next whorls). Right anterior region more anterior than left one, encroaching pallial cavity. Gonad occupies first whorl and opens in a V-shape in second whorl, surrounding digestive gland; left branch of gonad running towards left up to anterior region of animal, close to esophagus, anterior and at left to pericardium; right branch running edging upper surface of visceral mass up to middle region of its last whorl. Stomach and adjacent esophagus and intestine occupy obliquely central region of first visceral whorl. Digestive gland dark brown, almost black, fills space between stomach (and adjacent digestive tubes) and gonad, being more massive anterior to stomach in last visceral whorl. Kidney and pericardium as anterior border of digestive gland.

Circulatory and excretory systems (Fig. 117). Heart relatively large, located in anterior-left region of visceral mass. Auricle long and narrow, connects with ctenidial vein before its posterior end, running immersed in mantle, crosses transversal and dorsal to gill, after runs an approximately equal distance towards posterior up to pericardial cavity (a pericardium membrane is present in this pallial region). Auricle, in pericardial cavity, slightly broader. Ventricle large, walls thick muscular. Aortas running attached to left pericardial wall, anterior aorta about 3 times broader than posterior aorta, running parallel to esophagus. Anterior aorta within haemocoel easily visible up to buccal mass, where possesses a main branch penetrating in ventral region of radular sac (Fig. 126), just in region where it connects with odontophore (between m11 connection to radular sac, see below). Kidney narrow and long, located in central and right regions of posterior limit of pallial cavity (Figs. 116, 139). Kidney chamber mostly hollow, intestine running in its dorsal inner surface, digestive gland as its posterior limit. Kidney lobe single, a solid glandular mass in right-anterior region of kidney, attached to adjacent intestine; gradually becomes a flattened mass attached to membrane between kidney and pallial chambers, with a longitudinal folded inner surface; this flattened region gradually detaches from intestine, except for some sparse projection of its folds. Nephridial gland with two regions: 1) smaller and thin, triangular in section, located in dorsal region of membrane between kidney and pericardium, presents several transversal folds (Fig. 117: **ng**); 2) large, massive, slightly triangular, possesses a longitudinal vessel from which its folds converge, this vessel becomes outstandingly large and inserts at right and ventral to nephrostome (Fig. 117: **nl**). Nephrostome a broad transversal slit in left region of membrane between kidney and pallial cavity, near pericardium (Fig. 116).

Digestive system (Figs. 121-137, 139). Buccal mass massive, occupies about half of haemocoel volume. Localization within haemocoel varies according to retraction of proboscis. Oral tube relatively long, broad, thick muscular (**mj**), presenting several muscular layers of different fiber dispositions, most of them disposed longitudinally (Figs. 122, 123, 125). Mouth circular, broad,

inner surface irregular, covered by yellowish-transparent chitinous layer, maybe homologue to jaws (Figs. 124, 128). Differentiable jaws absent. Dorsal wall of buccal mass (which continues to esophagus) covered externally by small muscular fibers uniting it with adjacent inner surface of haemocoel (**m1**). Some of these muscles more developed – jugal muscles – forming differentiated pairs (Figs. 123, 125): **m1a**) pair of broad muscles, relatively flattened, originating in anterior-dorsal surface of haemocoel, close to median line, running towards ventral, inserting in short distance just between oral tube and buccal mass limit, close to median line; **m1b**) vary from 2 to 3 pairs, flattened, originating in lateral region of haemocoel inner surface, running towards medial, inserting in lateral-dorsal region of buccal mass dorsal wall more or less aligned. Inner surface of dorsal wall with a pair of broad folds that gradually narrow towards posterior. Anterior ventral surface of these dorsal folds with a series of oblique furrows – called "furrowed part of dorsal folds" (Fig. 124). One pair of these furrows bears aperture of salivary glands. Between dorsal folds a relatively deep dorsal chamber with inner surface covered by narrow longitudinal folds. Odontophore relatively large (about ¾ of buccal mass volume), protruded within buccal cavity. Odontophore muscles as following (Figs. 122-137): **mc**) buccal sphincter and circular muscles of oral tube; **mj**) jaws, oral tube and peri-buccal muscles (part described above), presenting a portion connected to odontophore, working as odontophore protractors, inserting in posterior-ventral region of odontophore cartilages, mj forms a muscular platform-like structure that some odontophore muscles inset in region preceding their insertion; **m2**) pair of narrow dorsal retractor muscles of buccal mass (retractor of pharynx), originating in ventral-posterior region of haemocoel inner surface, in same localization of pair retractor muscle of proboscis origin (rm), runing towards dorsal and after towards anterior edging attached to esophagus lateral surface, inserting part in lateral-dorsal-posterior surface of buccal mass, and part running more anterior and inserting close to m1b (Fig. 125); **m3**) broad and very thin pair of muscles, originating in lateral-ventral region of odontophore surface, covering almost completely lateral and ventral regions of odontophore posterior surface, connecting with each other in region dorsal to radular sac; **m3a**) small muscle accessory of m3 in "H"-fashion, originating and inserting similarly, running in m3 surface (Fig. 129); **m4**) large pair of dorsal tensor muscle of radula, originating broad in mj muscular platform close to median line, running towards dorsal edging medial surface of posterior half of odontophore cartilages, surrounding radular sac just anterior to its region within odontophore, inserting in a tissue which covers radula in region just posterior to its exposure (**to**); part of m4 also running from its origin in outer surface of odontophore cartilages, with fibers towards dorsal, covering ¾ of outer surface of cartilages, inserting with its medial branch in "to"; another small part of m4 pair (**m4a**) running from their origin towards anterior, close to median line, surrounding mj insertion on cartilages, inserting in subradular membrane anterior-lateral region; m4 also working as tensor of subradular membrane (**br**), covering dorsal and lateral regions of odontophore, connecting with (and probably secretes) subradular cartilage, m4 present ample connection with br (Figs. 131-134); **m5**) large pair of ventral tensor muscle of radula, originating in mj muscular platform just by side and medial to m4 origin, very close to medial line, running towards ventral a relatively short distance, inserting in a long area of radular sac ventral surface just ventral to m4 insertion and extending anteriorly; **m6**) horizontal muscle, relatively thin, connecting anterior-ventral margin of both odontophore cartilages at about 1/3 of their length; **m6a**) accessory horizontal muscle, same function than m6 but located posterior to it, presenting a connection with mj muscular platform in ventral surface, along median line (Figs. 132, 135, 137); **m7**) very narrow, non-paired muscle, originating in posterior region of m4 origin, running towards posterior within radular sac, inserting like a fan in radular sac region just before its connection in odontophore (Fig. 126); **m10**) pair of ventral protractor muscle of buccal mass, originating very broad and thick in ventral, lateral and part of dorsal regions around mouth (except close to median line) running towards posterior attached to mc, inserting somewhat narrow and thin in middle level of odontophore ventral surface (Figs. 127, 130); **m11**) a broad and powerful pair of ventral retractor muscles of buccal mass, originating in ventral-posterior region of haemocoel inner surface in same localization of retractor

muscle of proboscis origin (rm), running towards anterior, dorsally to rm, inserting multiple, surrounding completely radular sac in its region connected to odontophore, both more ventral branches thicker, inserting part in platform region of mj and part in m14 (Fig. 126); **m13**) non-paired small muscle (Fig. 127), originating in ventral surface of proboscis close to mouth, running towards dorsal through mc fibers, inserting along ventral peribuccal muscle; **m12**) small pair of muscles, originating in lateral-anterior surface of cartilages, running towards posterior covering mj, inserting in subradular membrane inner-lateral surface (Fig. 134); **m14**) pair of accessory ventral protractor muscle of buccal mass, slightly thin, same origin of m10 but ventral, running towards posterior covering m10, gradually becoming narrower, inserting in posterior limit of odontophore on m4 (Fig. 126). Some branches of rm, pairs m2 and m11 pass through nerve ring. Pair of odontophore cartilages long, flattened, slightly elliptical, most of muscles inserted in their outer surface (Figs. 135, 136). Radula long, about 4 times odontophore length, coiled distally (Figs. 122, 123). A branch of anterior aorta inserts in radular nucleus. Radular teeth (Fig. 70): rachidian tooth narrow, central cusp broad and low, slightly spherical, pair of secondary cusps smaller; lateral tooth broad, tall, flattened, curved inwards, tip pointed, pair of small secondary cusps in each side at some distance from tip; inner and outer marginal teeth similar with each other, long, tall, tip pointed, very small cusp in outer margin at some distance from tip, outer marginal tooth slightly narrower than inner marginal tooth (in Fig. 70, some teeth artificially divided, but this is an artifact). Salivary glands cluster around anterior and middle esophagus, posterior to nerve ring (Figs. 121-123); salivary ducts pass through nerve ring jointed with a small and narrow part of glandular tissue; in level just posterior to buccal mass penetrate in its dorsal wall and runs immerse in dorsal folds base; open in anterior-median limit of these folds. Anterior esophagus slightly narrow, inner surface with a pair of tall longitudinal folds (continuation from dorsal folds of buccal mass) (Fig. 124), remainder smooth. Middle esophagus broad; esophageal gland massive and broad, well delimited, located in posterior-right region of haemocoel (Fig. 124); inner surface of esophageal gland entirely filled by many thin septa, which evolve friable glandular tissue; pair of longitudinal folds (continuation from those of anterior esophagus) in opposite side of esophageal gland. Posterior esophagus narrow (Fig. 139), long (about half of total esophagus length), inner surface with about 8 longitudinal, narrow folds (2 of them continuation from those of middle esophagus); running towards left, somewhat perpendicular to frontal plane of head. Posterior esophagus, in visceral mass, gradually become slightly broader, with inner surface smooth (Fig. 139). Stomach large (Fig. 139), "U"-shaped, located about in penultimate whorl of visceral mass (Fig. 116); esophagus inserts in its left side. Duct to posterior lobe of digestive gland in transition between esophagus and stomach, narrow, turned towards posterior. Duct to anterior lobe of digestive gland very broad, originating between esophageal insertion and intestinal origin, in its ventral region; a small, longitudinal, short fold in dorsal surface of this duct; inner surface of this duct with several, transversal, successive, thin septa along its left surface (Fig. 139); these septa series end in a duct bifurcation, at considerable distance from its origin. Intestine originating broad, as right branch of stomach. Intestine running towards anterior and left, parallel to posterior esophagus (Fig. 139); inner surface smooth. Digestive gland described above. Intestine, in left extremity of kidney, suddenly towards right, running attached to posterior surface of kidney all along its length, crossing from left to right side of visceral mass anterior limit. Rectum short, running along right margin of pallial cavity. Anus broad, siphoned, located close to anal siphon of mantle border (Fig. 116).

Genital system. **Male**. Testis running in columellar surface of visceral mass up to level of pallial cavity posterior limit. Seminal vesicle intensely coiled, occupies anterior projection of visceral mass parallel and at left from esophagus, as continuation from testis (Fig. 116). Posterior region of seminal vesicle narrow, gradually becoming broader. In median region of right surface of seminal vesicle mass, vas deferens suddenly runs perpendicular towards right by a distance approximately half of visceral mass width (Fig. 138), opens in a triangular sinus located posterior to anus and in ¾ posterior level of columellar muscle (Fig. 119: **rr**). This sinus possesses a small aperture to pallial cavity in its anterior extremity. From this aperture a sigmoid sperm groove begins, running initially towards ventral and after anterior up to penis base (Fig. 119). Penis long, massive, with about ¾ of head-foot length, almost cylindrical, curved distally (Figs. 119, 140). Penis groove running along its ventral surface up to penis tip. Penis tip with a small, broad papilla.

Female (Figs. 141-143). Ovary occupies approximately same regions than testis of males, but broader posteriorly and very narrow anteriorly. Visceral oviduct running in a perpendicular and sub-terminal fashion from anterior projection of visceral mass at left from esophagus. Visceral oviduct very slender and still possessing glandular ovarian tissue along its length (Fig. 142). At level of nephrostome, oviduct suddenly expands and becomes thick glandular. Pallial oviduct with a pair of glandular laminas, similarly sized, gradually increasing along its length. Both laminas united with each other in right margin and folded in left margin, this left margin connected by a thin walled vaginal duct. Bursa copulatrix U-shaped, thick walled, located between posterior and middle third parts of pallial oviduct; dorsal branch a conic blind-sac with some longitudinal inner folds, connects with ventral branch by a narrow orifice; ventral branch almost spherical, with some transversal, slightly tall inner folds, connects with pallial oviduct by a narrow orifice of its posterior region (Fig. 143). Bursa orifice located just between both laminas of pallial oviduct posterior third part. Female genital aperture a simple slit close to floor of pallial cavity posterior to anus.

Central nervous system. Nerve ring typical caenogastropod, epiathroid, located just posterior to buccal mass. Pedal ganglia far removed from cerebral-pleural complex, deeply introduced in pedal muscles. Statocyst with single and large statolith.

Measurements of shells (in mm). MZSP 29698: 88.3 by 44.6; MZSP 28311: 84.0 by 43.6; MZSP 28589: 106.4 by 57.2.

Distribution. North Carolina, USA to Santa Catarina, Brazil

Habitat. Rocks and corals, subtidal, up to 10 m depth.

Material examined. BRAZIL. **Bahia**; Salvador; Farol da Barra, MZSP 28504, 11 specimens (Simone col. 22-24/ii/1997), MZSP 28589, 1 specimen (B.L. Albuquerque col., 1997); Alcobaça, MZSP 34884, 1♂ (Coltro leg. 2001). **Rio de Janeiro**; Arraial do Cabo, Enseada do Forno, 1-4 m depth, MZSP 32444, 1 specimen (P.J.S.Souza Jr. col., 7/v/2000). **São Paulo** (Simone col.); Ilha Bela; Siriúba Beach, 6 m depth, MZSP 29698, 1♀ observed alive (27/ix/1998); in front of Cabras Island, 3 m depth, MZSP 32868, 12 specimens (12/v/1990), MZSP 32869, 6 specimens (19/ii/1987), Parcel da Praia Grande, 1 m depth, MZSP 32841, 1 specimen (11/x/1996); Alcatrazes Island, Faloreiros harbor, MZSP 28311, 2 specimens (01/xii/1996).

Macrocypraea cervinetta (Kiener, 1843)

(Fig. 5, 6, 71, 144-153)

(Color plate Figs. 51, 65, 66)

Synonymy see Burgess (1985: 99). Complement:

Cypraea cervinetta Kiener, 1843 (pl. 6, figs. 1-2); Phillips, 1967: 12; Burgess, 1970: 228 (pl. 21, fig. A); Keen, 1971: 493 (pl. 4); Abbott, 1974: 149; Taylor & Walls, 1975: 168 (figs.); Donohue, 1977: 160; Oliveira *et al*., 1981: 147; Abbott & Dance, 1983: 96 (fig.); Burgess, 1985: 99 (figs.).

Macrocypraea cervus cervinetta: Cate, 1969: 110 (pl. 11, fig. 1).

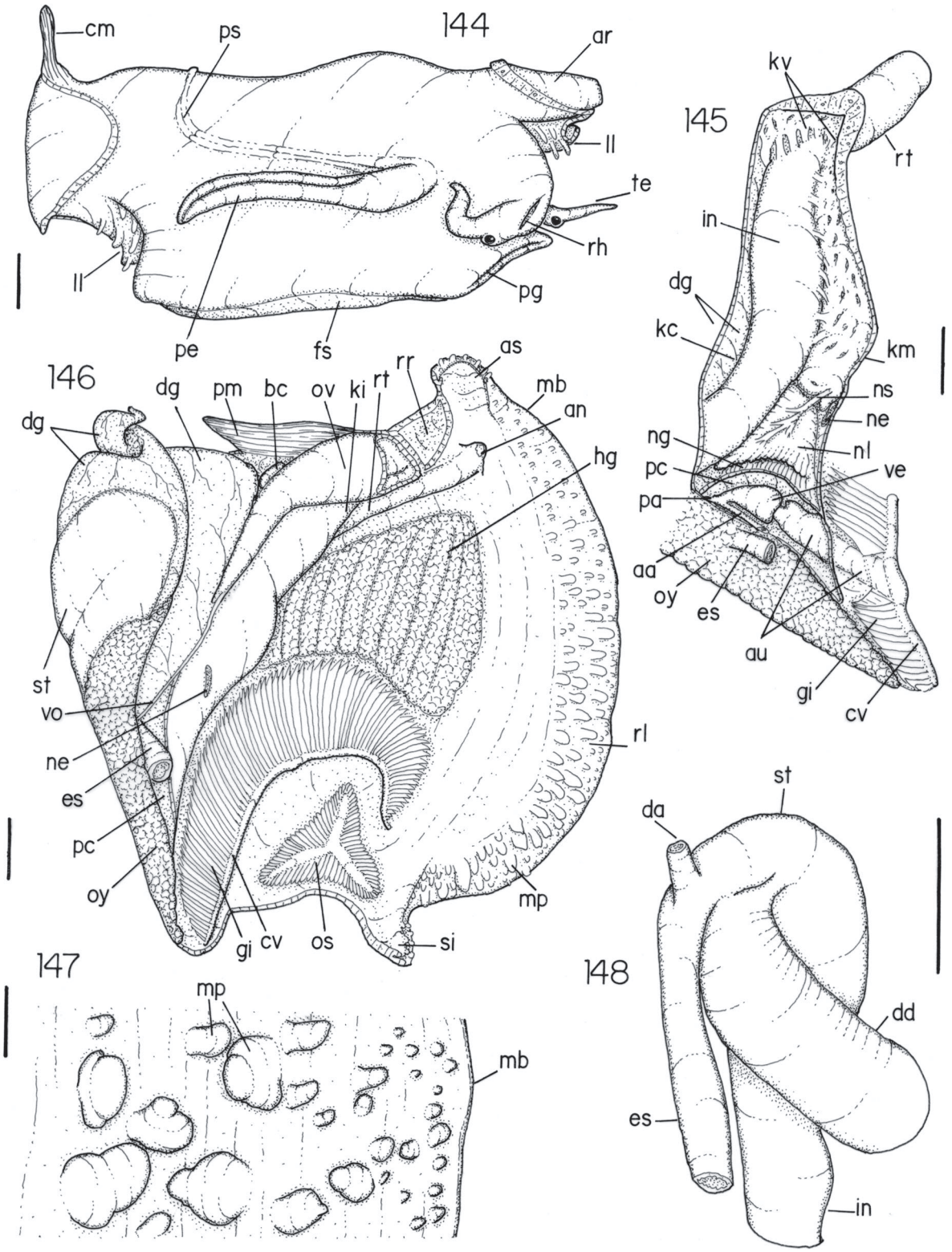
Macrocypraea cervinetta: Schilder & Schilder, 1971: 33; Lorenz & Hubert, 1993: 54 (pl. 10, figs. 8-11, 15, 16); Bradner & Kay, 1996: 77 (fig. 115).

Description

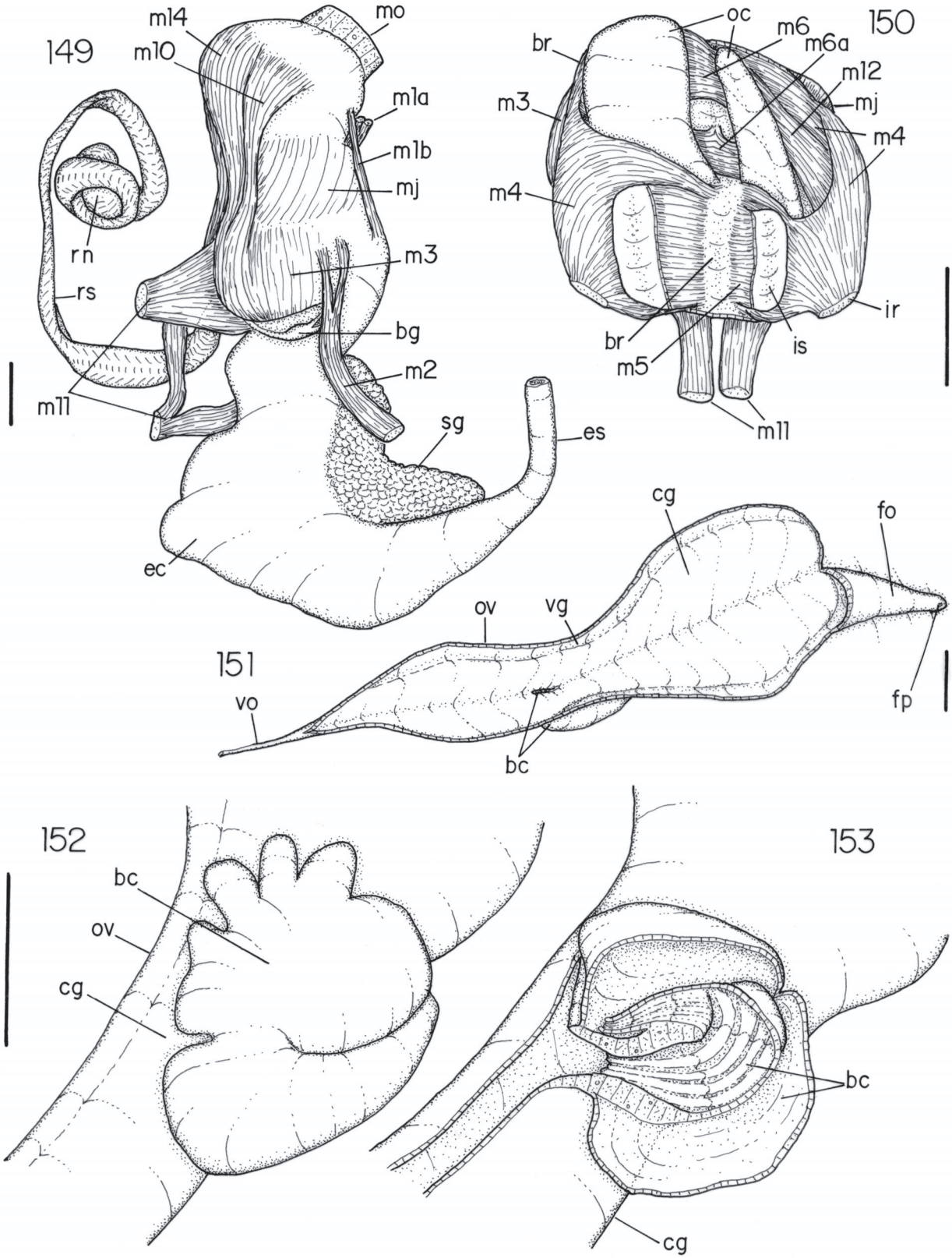
Shell (Figs. 5, 6; Color plate Fig. 51). Characters very similar to those of *M. zebra*. Differs mainly by generally smaller size and by ampler anterior region of aperture. Other details in Keen (1971: 493).

Head-foot (Fig. 144). Similar to that of *M. zebra*, except for a broader anterior projection. Inside haemocoel, a powerful muscle accessory of retractor muscle of proboscis, originating in anterior projection, running towards posterior, inserts in ventral-right region of haemocoel, by side of buccal mass.

Mantle organs (Figs. 145-147). Mantle lobe papillae similar to those of *M. zebra*, but proportionally fewer in total, and more numerous in anterior region, some scanty broadly papillae bifurcated.



Figs. 144-148, *Macrocypraea cervinetta* anatomy: **144,** head-foot, male, lateral-right view; **145**, kidney, pericardium and adjacent structures, ventral view, kidney opened longitudinally, pericardium ventral wall removed, some gill filaments on auricle also extracted; **146,** pallial cavity and visceral mass, female, inner-ventral view; **147,** right lobe of mantle, detail of its middle region; **148,** stomach and adjacent digestive tubes, ventral view as in situ. Scaled = 5 mm, except 147= 1 mm.



Figs. 149-153, *Macrocypraea cervinetta* anatomy: **149,** foregut, lateral-right view, radular sac partially uncoiled; **150,** odontophore, ventral view, superficial tissues removed, both cartilages deflected externally, left cartilage (right in fig.) still deflected posteriorly; **151,** pallial oviduct, whole ventral view, most opened longitudinally along vaginal groove; **152,** same, dorsal view, detail of bursa region; **153,** same, bursa opened along outer edge and along its inner duct, cut still continues along vaginal groove of adjacent posterior region of capsule gland. Scales = 2 mm.

Incurrent siphon with border presenting several small papillae. Mantle organs features as those described for *M. zebra* (Fig. 146).

Circulatory and excretory systems (Fig. 145). Heart characters similar to those described for preceding species, except for more anterior origin of auricle and consequent longer portion of ctenidial vein posterior to it with contrary circulation. Kidney features also similar to those of *M. zebra*, but ventral lobe presents a mosaic of pores (and not longitudinal folds).

Digestive system. Buccal mass characters very similar to those of *M. zebra*, including very long radular ribbon (about 3 times buccal mass length) (Figs. 149, 150), **m11** with muscular tissue surrounding entirely radular sac in its region penetrating in odontophore, and presence of **m6a** and **m12**. Radular tooth (Fig. 71) features closely similar to those of *M. zebra*, differing in narrow fashion of rachidian tooth. Esophagus, esophageal gland, salivary glands and stomach features similar to those described for preceding species. Middle esophagus with a tall fold that covers aperture of esophageal gland. Duct to anterior lobe to digestive gland also broad, with several, thin, transversal septa along its dorsal inner surface (Fig. 148). Intestine, rectum and anus as those of *M. zebra*.

Genital system. **Male**. Visceral and pallial organs very similar to those of *M. zebra*, including lack of prostate gland. Seminal vesicle relatively narrower. Penis also similar, but generally straight and with a rounded tip (Fig. 144).

Female (Figs. 151-153). Visceral and pallial organs with same features as those of *M. zebra*, including localization of bursa copulatrix. Bursa also U-shaped (Fig. 152). Distal, blind-sac portion of bursa with walls thin, inner surface smooth and some broad and short projections along its right margin. Proximal portion of bursa smaller, curved, muscular walls thick and some inner longitudinal folds; connection with distal portion by means of a long, narrow papilla projected inside right region of distal portion; connection with pallial oviduct a small pore localized between posterior and middle thirds of oviduct between both laminas (Fig. 153). Anterior region of pallial oviduct without glandular walls, conic, ends in a small, papilla-like genital pore.

Measurements of shells. 1) 59.1 by 29.6; 2) 57.0 by 28.0; 3) 55.5 by 28.0 (Figs. 5, 6).

Distribution. Sonora, Mexico to Peru.

Material examined. PANAMA; Pacific Ocean; Gobernadora Island, North Shore, AMNH 276910, 23 specimens (Walter Sage col., 30/i/1991).

Genus *Erosaria* Troschel, 1863

(Type species: *C. erosa* Linné, 1758)

Erosaria acicularis (Gmelin, 1791)

(Figs. 7-10, 72, 154-173)

(Color plate Figs. 52, 57, 58)

Synonymy see Burgess (1985: 219) and Leal (1991: 98). Complement:

Cypraea acicularis Gmelin in Linné, 1791: 3421 (no locality).

Cypraea spurca acicularis: Abbott, 1954: 180 (pl. 6, fig. a); Warmke & Abbott, 1962: 92 (pl. 16, fig. i); Matthews & Rios, 1967: 96; Kempf & Matthews, 1969: 92; Rios, 1970: 61 (pl. 11); Abbott, 1974: 150 (pl. 5, fig. 1643); Rios, 1975: 72 (pl. 20, fig. 293); Domaneschi, 1983: 12 (fig. 4); Abbott & Dance, 1983: 85 (fig.); Bandel, 1984: 84 (fig. 139; pl. 7, fig. 5); Rios, 1985: 64 (pl. 23, fig. 285); Calvo, 1987: 107 (fig. 67); Jong & Coomans, 1988: 65; Azevedo, 1989: 33; Merlano & Hegedus, 1994: 166 (pl. 52, fig. 614).

Cypraea (Ravitona) spurca acicularis: Matthews, 1967: 17 (figs. 5-6).

Cypraea acicularis: Burgess, 1970: 156 (in synonymy) (pl. 10, fig. L); 1985: 219 (fig.).

Erosaria spurca acicularis: Schilder & Schilder, 1971: 62; Talavera et al, 1986: 107-114 (fig. 2); Bradner & Kay, 1996: 28, 170.

Cypraea (Erosaria) spurca acicularis: Humfrey, 1975: 106 (pl. 9, figs. 7, 7a).

Erosaria (Erosaria) acicularis: Massilia, 1982a: 11-14 (figs.).

Cypraea (Erosaria) acicularis: Leal, 1991: 98 (pl. 15, fig. f-h).

Erosaria acicularis acicularis: Lorenz Jr. & Hubert, 1993: 197 (pl. 85, figs 17-27).
Cypraea spurca acicularis: Abbott & Morris, 1995: 194 (pls. 10, 51)

Description

Shell (Figs. 7-10; Color plate Figs. 52, 57, 58). Adequate description in Abbott (1974: 150). Most of Brazilian examined specimens with an almost cylindrical shell (Figs. 9, 10), however some lots from Florida (e.g., DMNH 202013) possess thickness (callus) along peripheral surface (Figs. 7, 8). Protoconch see Leal (1991, pl. 15, fig. f-h).

Head-foot (Figs. 156, 159). Very similar characters to those of preceding species, including anterior projection. Basic color pale beige, covered by dark brown small spots sometimes coalescent.

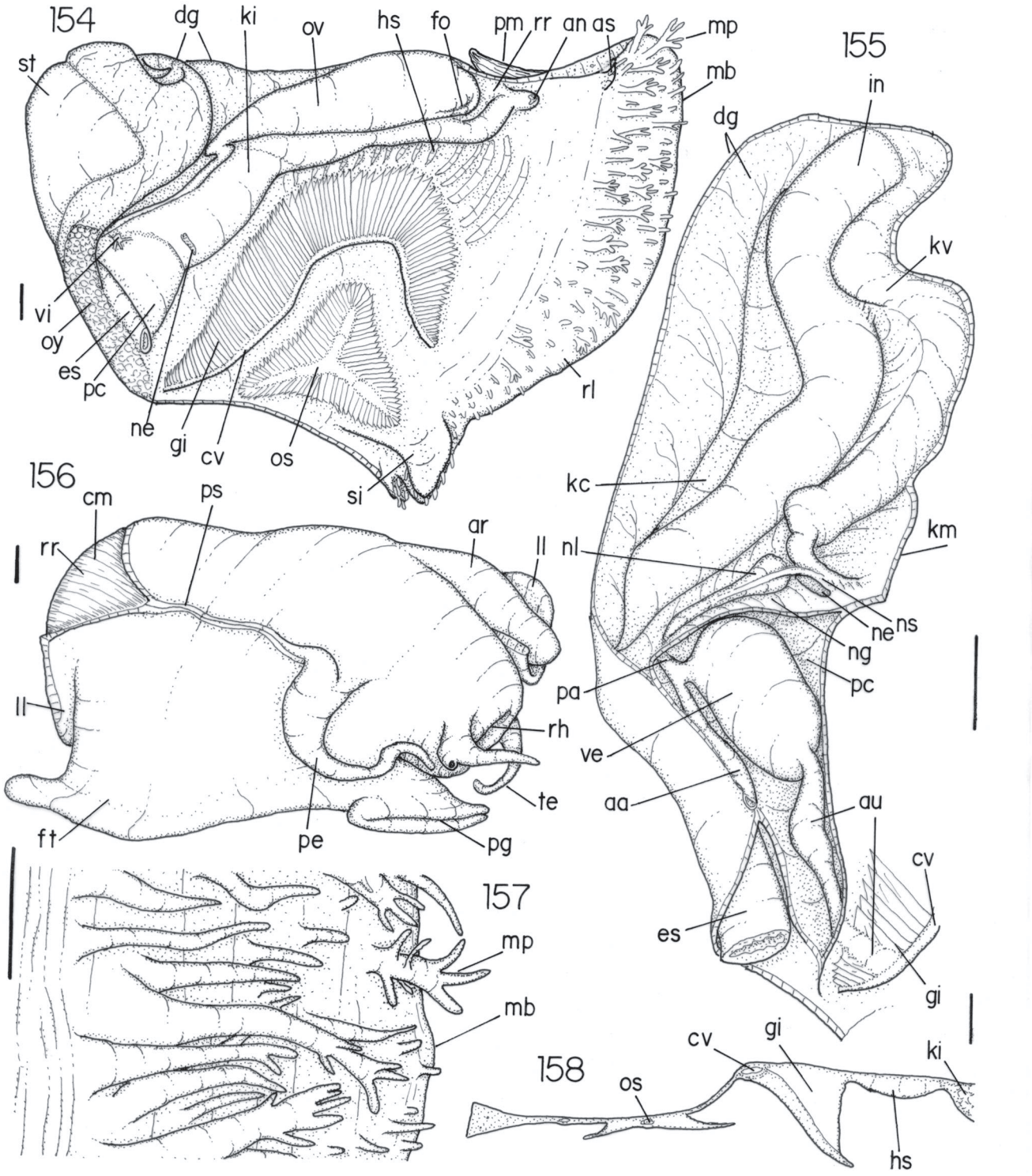
Mantle organs (Figs. 154, 157, 158). Mantle lobes characters similar to those of *M. zebra*, included incurrent and anal siphons, differing in papillae constitution. Mantle papillae with 4 basic types (Fig. 157): 1) simple and short, 2) simple and long; 3) bifurcated in tip and long; 4) long, with several (generally 4) pairs of lateral projections along its length, each pair situated orthogonal to neighbors, and 3 terminal projections. Distribution of papillae types slightly random, but in general longer papillae located far from mantle edge and more concentrated in middle and posterior regions; and more concentrated also close to siphon. Siphon with small papillae in border. Anal siphon low, generally with dark brown edges. Mantle organs characters similar to those of preceding species, including osphradium form and transversal septa of mantle in hypobranchial gland (Fig. 154). Osphradium proportionally larger and located at some distance from gill. Osphradium filaments with a long distal projection. Gill filaments with a broader base (Fig. 158).

Visceral mass (Figs. 167, 171). Similar characters than *M. zebra*.

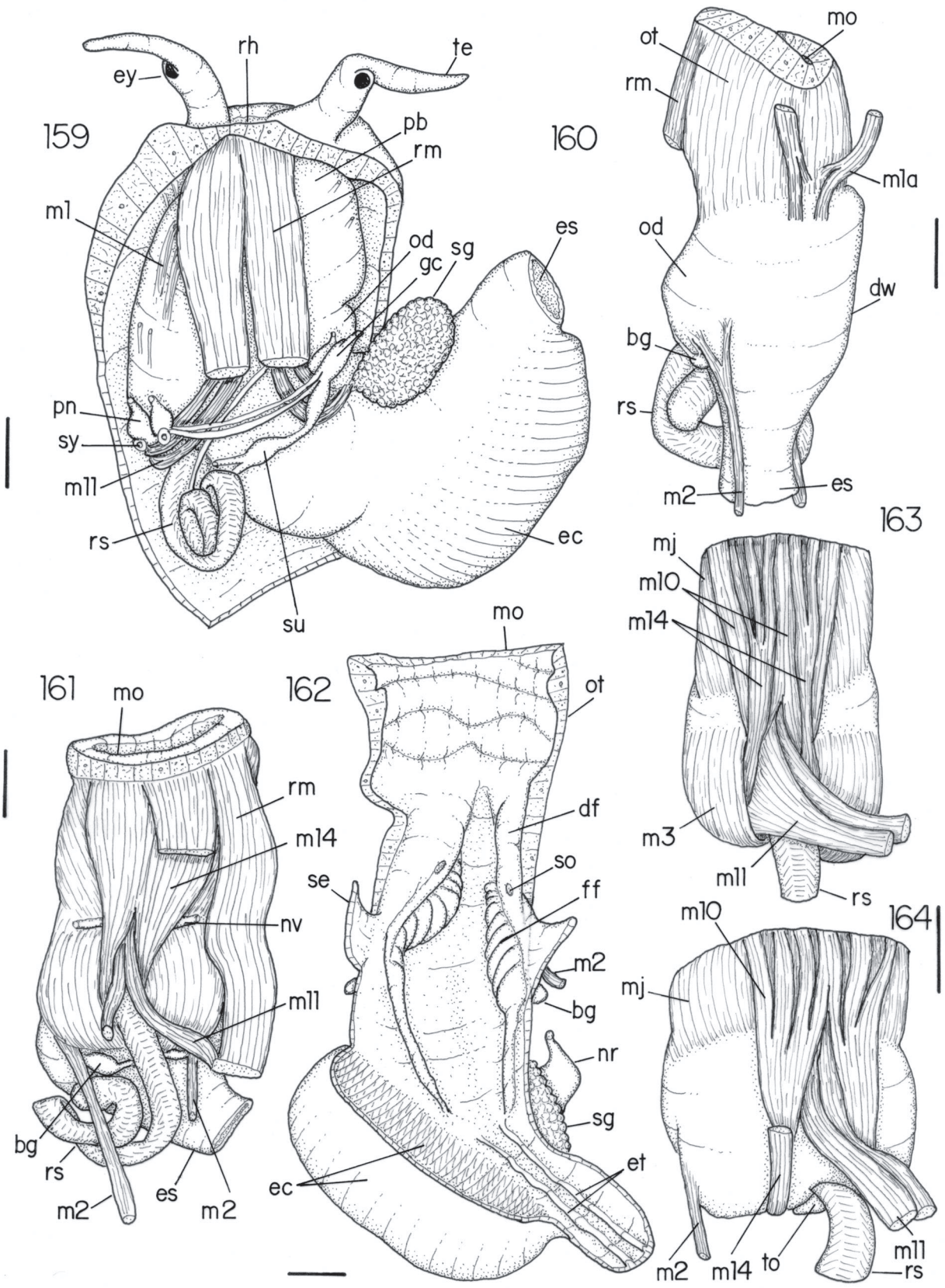
Circulatory and excretory systems (Fig. 155). Heart very similar to that of *M. zebra*, including narrow region of auricle running dorsal to gill posterior region and a short portion of ctenidial vein as a bind-sac. Kidney characters and situation similar to those of preceding species (Figs. 170, 171). Nephridial gland accessory lobe narrower and simpler, but also with longitudinal vessel inserted at right from nephrostome. Kidney ventral lobe with uniform surface, without detectable folds.

Digestive system (Figs. 159-169). Buccal mass features and odontophore muscles very similar to those of *M. zebra*, distinctive or notable features following. Proboscis short, pair of retractors thick and broad. Jaws also missing. Furrowed part of dorsal folds well developed. Aperture of salivary glands ampler, located just anterior to furrowed part, on ventral region of dorsal folds (Fig. 162). Odontophore muscles (Figs. 160-166, 168, 169): **m11** pair with muscular tissue only in their lateral and ventral regions; a thin, transparent membrane connected in their lateral regions surrounding radular sac (in its region where penetrates in odontophore) dorsal surface (this membrane presents muscular tissue in *M. zebra*); **m3a** and **m7** absent; **m1a**, **m4a**, **m6a** and **m12** present; **m14** pair narrower and inserted closer to median line, part covered by m3. Radular ribbon long, about twice buccal mass length (Fig. 161). Radular teeth (Fig. 72): rachidian tooth small, short, with 3 broad terminal cusps, central cusp with about double secondary cusps size; lateral and both marginal tooth similar with each other, differing only in width (lateral tooth broad – slightly broader than rachidian, outer marginal slender, inner marginal intermediary in width), curved inwards, with 3 broad cusps, central cusp slightly pointed, terminal, secondary cusps small, inner cusp closer to tooth apex than outer cusp. Esophagus and salivary glands characters similar to those of anterior species, including esophageal gland filled by thin, transversal septa (Fig. 162). Stomach and intestine features also as those described for *M. zebra*, except for absence of transversal septa in duct to anterior lobe of digestive gland and lack of inner gastric folds (Fig. 167). Digestive gland (pale beige in color), rectum and anus similar to those of *M. zebra* (Fig. 167).

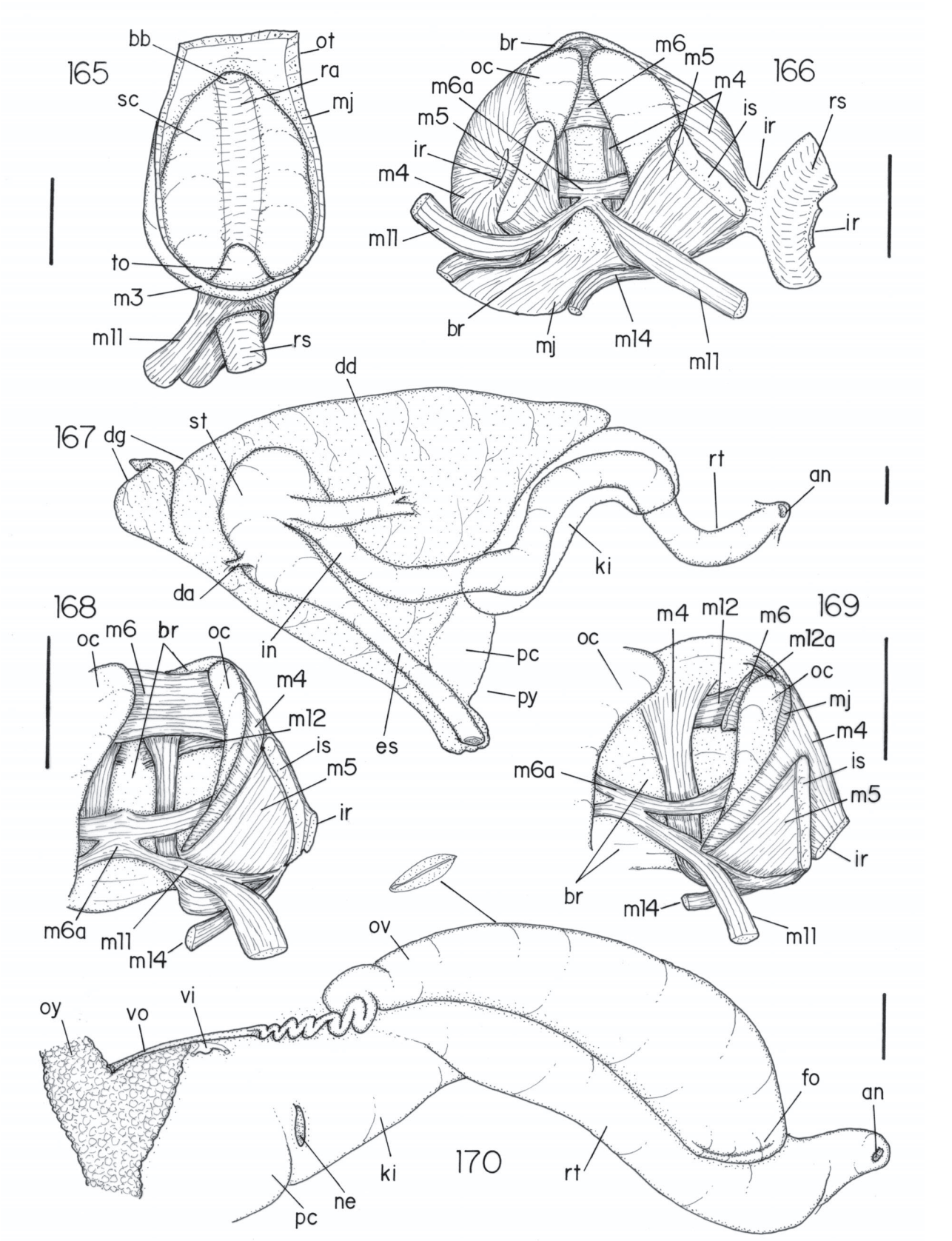
Genital system. **Male**. Visceral and pallial organs similar in characters and location to those of *M. zebra*, distinctive and notable features following. Seminal vesicle coiled in a longer and narrower fashion (Fig. 171). Vas deferens, after seminal vesicle and running along ventral renal surface, very



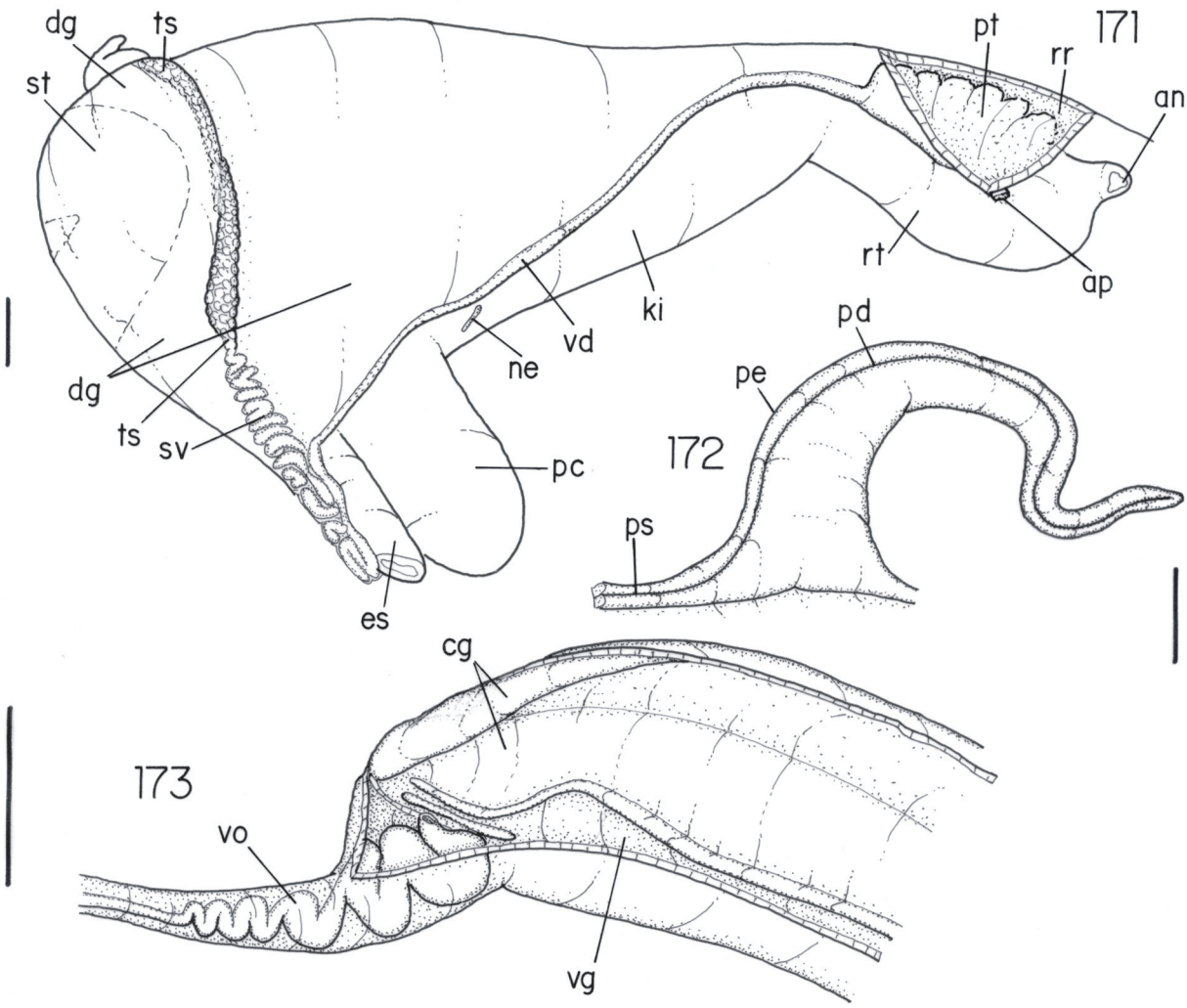
Figs. 154-158, *Erosaria acicularis* anatomy: **154,** pallial roof and visceral mass, female, ventral-inner view; **155,** kidney and pericardium region, both opened longitudinally, some gill filaments on auricle removed; **156,** head-foot, male, right view; **157,** right mantle lobe, outer surface, detail of its middle region; **158,** pallial cavity roof, transversal section in middle region of osphradium posterior branch. Scales = 1 mm.



Figs. 159-164, *Erosaria acicularis* anatomy: **159,** head and haemocoel, ventral view, foot and columellar muscle removed, proboscis wholly retracted; **160,** buccal mass and short portion of esophagus, dorsal-slightly lateral-left view; **161,** same, ventral view; **162,** dorsal wall of buccal mass and esophagus, ventral view, odontophore removed, esophagus opened longitudinally; **163,** odontophore, ventral view, radular sac only partially shown; **164,** same, ventral-slightly lateral-right view, some superficial muscles sectioned. Scales = 1 mm.



Figs. 165-170, *Erosaria acicularis* anatomy: **165,** odontophore, dorsal view; **166,** same, ventral view, both cartilages deflected, radular sac deflected to right and only partially shown; **167,** visceral mass, middle and distal portions of digestive tubes, ventral view, kidney and pericardium only indicated; **168,** odontophore, ventral view mainly of right side, right cartilage greatly deflected; **169,** same, m6 sectioned; **170,** visceral and pallial oviducts and adjacent structures, ventral view, ovary only partially shown, female terminal papilla extracted. Scales = 1 mm.



Figs. 171-173, *Erosaria acicularis* anatomy: **171,** visceral mass and posterior part of pallial roof schematically drown, ventral view, with main concern to male genital structures; **172,** penis, lateral view; **173,** region between visceral and pallial oviducts, ventral view, anterior 2/3 opened longitudinally. Scales = 1 mm.

narrow; inserts in prostate gland in short distance from triangular sinus (Fig. 171). Prostate gland as a sudden expansion of vas deferens, most located inside triangular sinus, dorso-ventrally flattened, with about 5-6 lobes at right from its duct. Prostate aperture to pallial cavity in anterior-left end of triangular sinus. Penis conical, long, base broad, gradually narrows up to a slender distal region (Figs. 156, 172). Distal region of penis very long and coiled in some specimens (e.g., DMNH 40547).

Female (Figs. 170, 173). Characters of visceral organs similar to those of *M. zebra*. Visceral oviduct, before its insertion on pallial oviduct, possesses a gradually large zigzag fashion, covered by a thin, transparent membrane. After this zigzag oviduct opens as a small papilla somewhat subterminally in ventral region of pallial oviduct. Pallial oviduct gradually increasing along its length, with thick glandular walls. Both glandular laminas similar to those of *M. zebra*, except for a pair of posterior, narrow folds in margin of outer lamina, ventral fold short, dorsal folds longer, running almost entire lamina length. Vaginal tube present, thin walled. Female genital aperture simple, slit-

like.

Central nervous system. Similar in attributes to that of *M. zebra* (Fig. 159).

Measurements of shells (in mm). MZSP 28510, 1) 18.5 by 12.2; 2) 16.3 by 10.7. DMNH 202013, ♂ 1) 23.8 by 17.4; ♀ 20 24.2 by 18.5.

Distribution. From North Carolina, USA, to Rio de Janeiro, Brazil.

Habitat. Under rocks and corals, subtidal up to 81 m depth.

Material examined. UNITED STATES OF AMERICA. **Florida**; off West Florida, Gulf of Mexico, 26º44'N 83º25'W, off shore, 56 m depth, DMNH 202013, 1♂, 1♀ (Mikkelsen col., 17/iii/1980); Key West, Sand Key, Monroe Co., 1 m depth, DMNH 40547, 2♂ (Beers & Abbott col., 18/vii/1970). BONAIRE; DMNH 82975, 1♂ (Abbott col., ii/1983). BRAZIL. **Pernambuco**; Fernando de Noronha Archipelago, Conceição Beach, MZSP 31410, 2 shells (Simone & Souza Jr. col., vii/1999). **Bahia**; Baia de Todos os Santos, MZSP 28570, 5 specimens (B.L. Albuquerque col. 1998), MZSP 32858, 1♂, 1♀ (L. Trinchão col.); Salvador, Farol da Barra, MZSP 28510, 3 specimens (Simone col., 22-28/ii/1997); off Alcobaça, MZSP 31566, 1♀ (Coltro col., viii/1999). **Espírito Santo**; off Guarapari, MZSP 32857, 2 specimens, 2 shells (Coltro col., 1999).

Erosaria spurca (Linné, 1758)

(Figs. 11, 12, 73, 174-186)

(Color plate Figs. 38, 75, 76)

Synonymy see Burgess (1985: 218). Complement:

Cypraea spurca: Burgess, 1970: 156 (pl. 10, figs J, K); Taylor & Walls, 1975: 182 (figs.); Geisel, 1976: 24-26; Donohue, 1977: 160; Lavenir, 1984: 614; Burgess, 1985: 218 (fig.); Trew, 1987b: 18 (part).

Erosaria spurca spurca: Schilder & Schilder, 1971: 63; Talavera et al., 1986: 107-114 (fig.).

Erosaria spurca: Massilia, 1982b: 11-14 (figs.); Nicolay, 1986: 29 (figs.); Poppe & Goto, 1991: 123 (pl. 19, fig. 1-5); Lorenz Jr. & Hubert, 1993: 197 (pl. 86, figs 1-16, 19, 20, 22); Bradner & Kay, 1996: 38 (fig. 48).

Description

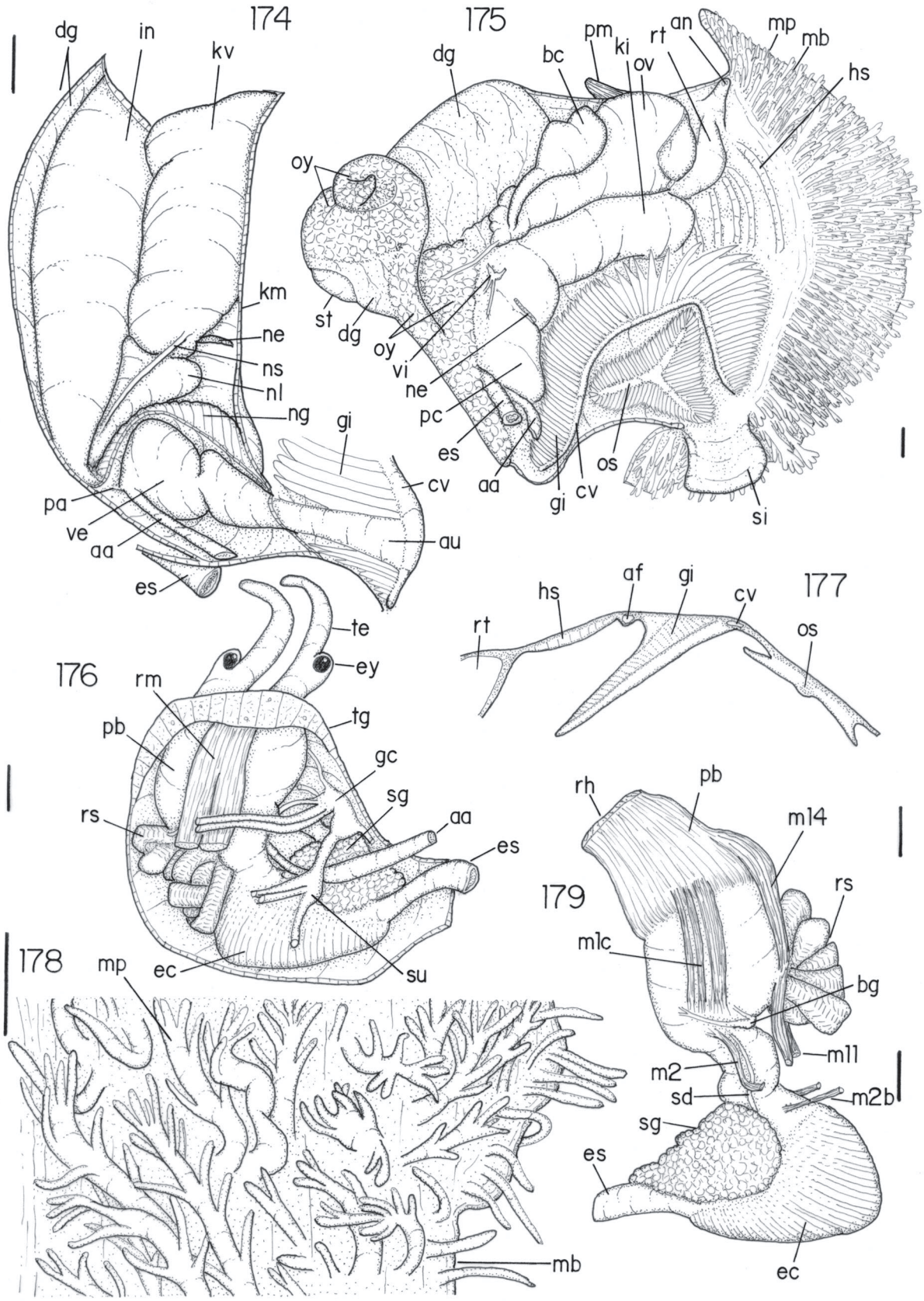
Shell (Figs. 11, 12; Color plate Figs. 38, 75, 76). Similar to that of *E. acicularis*, but in general more rounded and darker. Color pale brown. Other details in Lorenz & Hubert (1993).

Head-foot (Figs. 176, 186). Very similar characters to *M. zebra*.

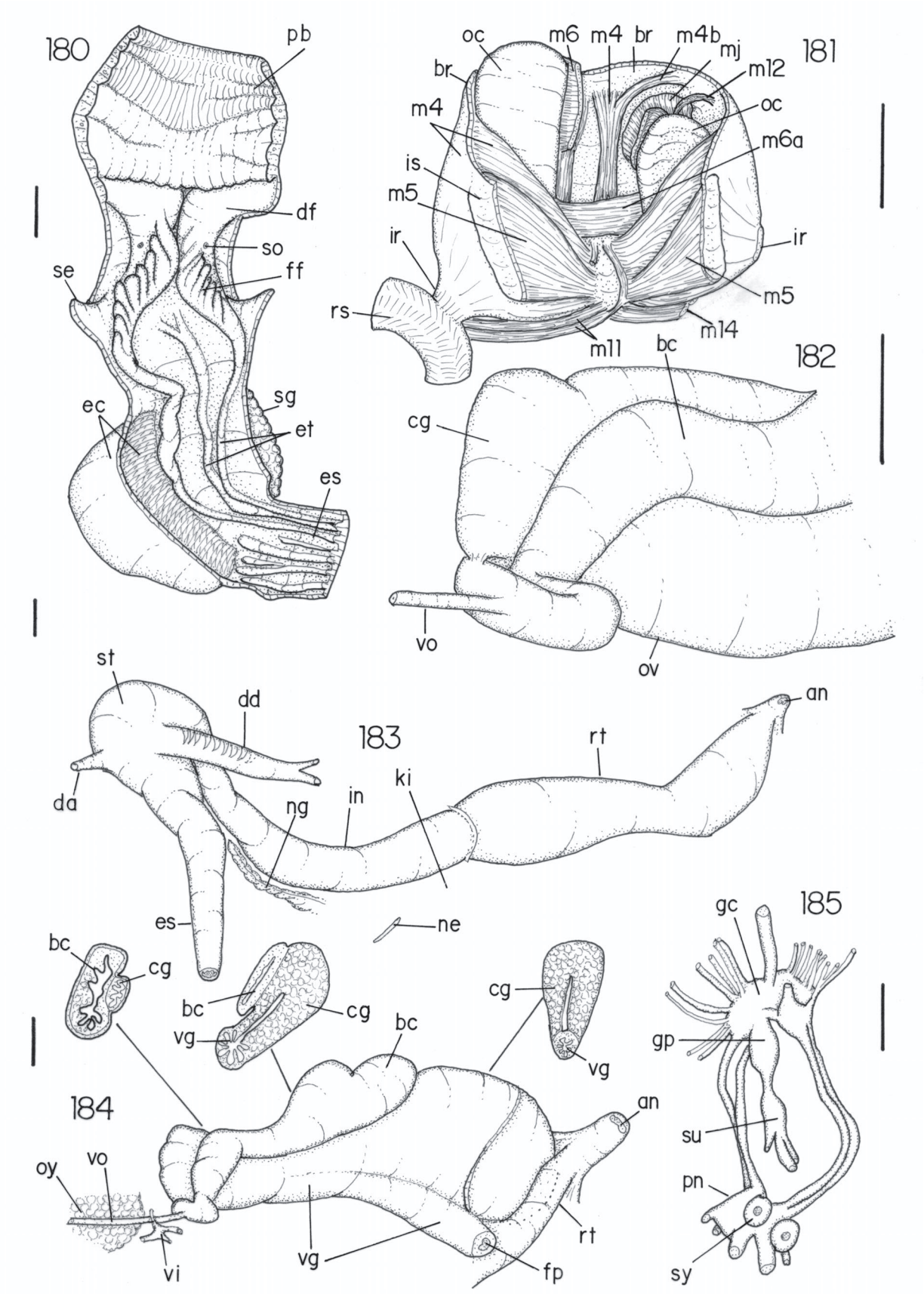
Mantle organs (Figs. 175, 177, 178). Mantle lobe papillae similar to those types of *E. acicularis*, but more numerous and concentrated, mainly complex papillae (type 4 of anterior species), with 5-6 alternate pairs of projections (Fig. 178). Incurrent and anal siphons present; incurrent siphon with small papillae in border. Pallial organs very similar to those of *E. acicularis*, except for taller and slender gill filaments (Fig. 177).

Circulatory and excretory systems (Fig. 174). Heart and kidney characters very similar to those of *E. acicularis*, included portion of auricle located dorsal to gill, accessory lobe of nephridial gland (but slightly broader) and uniform, almost smooth surface of ventral renal lobe. Kidney slightly longer, with a narrow portion of lobe of nephridial gland running towards posterior, between esophagus and adjacent intestine, by about half whorl (Fig. 183).

Digestive system (Figs. 176, 179-181, 183). Most features similar to those described for *E. acicularis*, distinctive characters following. Odontophore muscles (Figs. 179-181): **m1c**, a broad, thin, differentiated pair of jugal muscles, originating in lateral-posterior region of proboscis, running towards posterior, inserting on m3 in posterior region of odontophore; **m4b**, a pair of small projection of m4 ventral and anterior region, surrounding median and anterior surface of mj attached to subradular membrane (br); **m11** narrower; **m12** narrow. Radula very long (about 3 times buccal mass length) and intensely coiled. Radular teeth characters essentially same as in *E. acicularis*, but with a slightly



Figs. 174-179, *Erosaria spurca* anatomy: **174,** kidney and pericardium regions, ventral view, both opened longitudinally, some gill filaments on auricle removed; **175,** pallial roof and visceral mass, female, ventral view; **176,** head and haemocoel, ventral view, foot and columellar muscle removed; **177,** pallial cavity roof, transversal section in middle level of osphradium posterior branch; **178,** right mantle lobe, outer view, detail of its middle region; **179,** foregut, lateral-right view. Scales = 1 mm.



Figs. 180-185, *Erosaria spurca* anatomy: **180,** dorsal wall of buccal mass and esophagus, ventral view, odontophore removed, esophagus opened longitudinally; **181,** odontophore, ventral view, both cartilages deflected, m6 sectioned, right cartilage still deflected posteriorly, radular sac only partially shown; **182,** pallial oviduct, ventral view, detail of posterior region; **183,** middle and distal digestive tubes, ventral view, shown as in situ, some renal structures also shown; **184,** part of visceral, whole pallial oviducts and some adjacent structures, ventral view, female papilla only partially shown, 3 transversal sections in indicated regions also shown; **185,** central nervous system, ventral view. Scales = 1 mm.

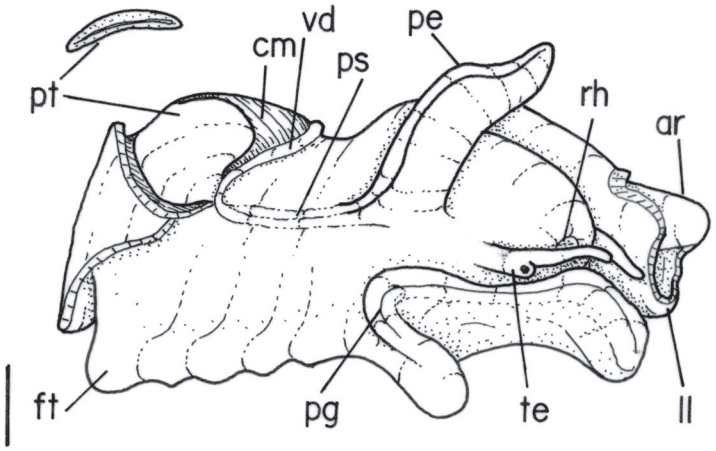


Fig. **186**, *Erosaria spurca*, head-foot, male, lateral-right view, a transversal section of prostate also shown. Scale = 2 mm.

broader rachidian tooth (Fig. 73). Middle and posterior esophagus with more longitudinal folds (Figs. 179, 180). Duct to anterior lobe of digestive gland with several transversal septa in its ventral-right surface (Fig. 183). Both ducts to digestive gland and intestine proportionally broader.

Genital system. **Male** (Fig. 186). Pallial and visceral structures with characters similar to those of *M. zebra*. Distinctive or notable features following. Coiled seminal vesicle extending up to anterior projection of visceral mass, close to esophagus; narrow in posterior and broader in anterior region. Prostate gland flat and broad, located inside triangular sinus on posterior-dorsal surface of columellar muscle. Connected with pallial vas deferens by a small region preceding its aperture. Vas deferens aperture just anterior to triangular sinus, between this aperture and penis base a thick walled sperm furrow. Penis short and stubby, tip weakly pointed. Penis furrow running all along its posterior edge.

Female (Figs. 175, 182, 184). Visceral structures with similar characters to those of *E. acicularis*, but pallial oviduct differs. Slender visceral oviduct inserts in posterior 1/3 of a thick posterior tube (Fig. 182). This tube curves towards posterior and in short distance towards right, gradually increases up to a broad, somewhat bilobed tip located in middle level of pallial oviduct; this blind-sac chamber, regarded as bursa copulatrix, possesses muscular walls and some longitudinal, narrow inner folds. From posterior end of posterior tube a narrow connection to remainder pallial oviduct, which suddenly increases and becomes thick glandular. Capsule gland most of this part of oviduct, connected to vaginal tube only in its posterior half, anterior half a blind-sac. Vaginal tube with muscular walls and some slightly tall inner longitudinal folds; its posterior half opened to capsule gland, gradually becoming an independent, somewhat long tube, opens as a papilla (female genital pore) in left side of pallial oviduct, close to floor of pallial cavity.

Central nervous system (Figs. 176, 185). Similar to that described for *M. zebra*.

Measurements of shells (in mm). MZSP 30681, ♀ 25.0 by 15.4; ♂ 22.1 by 13.6. BMNH: 25.0 by 16.1.

Distribution. NE Atlantic and Mediterranean Sea.

Habitat. Under rocks, subtidal.

Material examined. CANARY ISLANDS; **Lanzarote**, Arrecife, BMNH, 1♀ (Capt A.K. Lotton col iii-v/1955). MALTA (C. Mifsud col.); Blaka, MZSP 30680, 1♀ (xii/1991); Qalev Marku, 3 m depth, MZSP 30681, 1♂, 1♀ (viii/1997).

Discussion. Although there are long known conchological differences, several authors consider *E. acicularis* an Atlantic subspecies of European *E. spurca* (e.g., Talavera et al., 1986). Other authors, however, consider them as separated species (e.g., Rios, 1994). Based on the above explored morphological differences, mainly those of pallial oviduct, is it possible to establish that both are close, but undoubtedly separated species.

Genus *Luria* Jousseaume, 1884

(Type species *C. lurida* Linné, 1758)

Luria cinerea (Gmelin, 1791)

(Figs. 13-15, 74, 75, 187-204)

(Color plate Figs. 46, 67-69)

Synonymy see Burgess (1985: 182). Complement:

Cypraea cinerea Gmelin in Linné, 1791: 3402 (no locality); Abbott, 1954: 180 (pl. 6, fig. c); Warmke & Abbott, 1962: 92 (pl. 16, fig. h); Matthews & Rios, 1967: 96; Kempf & Matthews, 1969: 92; Burgess, 1970: 51 (pl. 2, fig. A); Bandel, 1973: 335 (fig. 1); Taylor & Walls, 1975: 101 (figs.); Burgess, 1975: 1, 9; Donohue, 1977: 160; Domaneschi, 1983: 12 (fig. 3); Abbott & Dance, 1983: 95 (fig.); Bandel, 1984: 83 (fig. 137; pl. 7, fig. 4); Burgess, 1985: 182 (fig.); Sutty, 1986: 45 (fig.); Calvo, 1987: 105, 107 (fig. 66); Trew, 1987b: 5; Jong & Coomans, 1988: 64; Azevedo, 1989: 33; Merlano & Hegedus, 1994: 166 (pl. 52, fig. 613); Abbott & Morris, 1995: 194 (pl. 51).

Cypraea (Luria) cinerea: Matthews, 1967: 16-17 (figs. 2-4); Rios, 1970: 60 (pl. 11); Abbott, 1974: 149-150 (pl. 5, fig. 1641); Humfrey, 1975: 106 (pl. 9, fig. 3); Rios, 1975: 71 (pl. 20, fig. 292); Oliveira *et al*., 1981: 145-146; Rios, 1985: 65 (pl. 23, fig. 287); Leal, 1991: 97 (pl. 15, fig. d, e); Rios, 1994: 75 (pl. 25, fig.285).

Luria cinerea cinerea: Schilder & Schilder, 1971: 40.

Luria cinerea: Lorenz Jr. & Hubert, 1993: 79 (pl. 30, figs 1-3, 7-14); Bradner & Kay, 1996: 97 (fig. 149).

Luria cinerea brasiliensis Lorenz & Hubert, 1993: 79 (pl. 30, figs. 8-11).

Talparia cinerea: Kay, 1996: 212 (figs. 18.1A, G).

Description

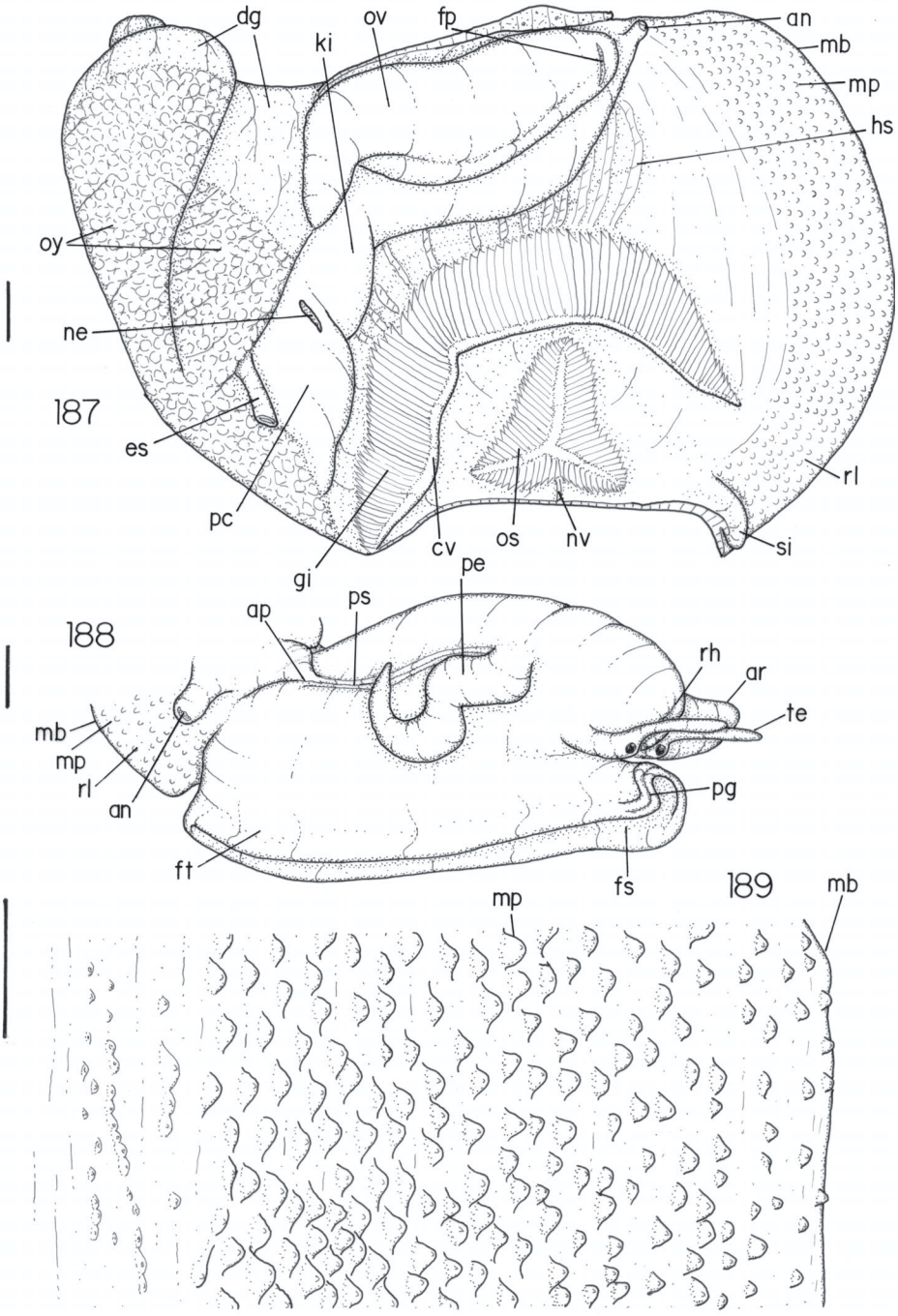
Shell (Figs. 13-15; color plate Figs. 46, 67-69). Adequate shell description in Abbott (1974: 149-150). Young specimens possessing shell color patterns similar to mature ones (Fig. 15). Larval shell in Leal (1991, pl. 15, figs d, e) and Kay (1996, fig. 18.1G).

Head-foot (Figs. 188, 192). Characters similar to those described for *M. zebra*. Anterior projection well-developed. Color uniform brownish purple, inclusive in sole, darker in tentacles. Some females presented small penis jointed with mature female organs.

Mantle organs (Figs. 187, 189-191). Mantle lobes entirely covered by small, rounded papillae, somewhat uniformly distributed, close with each other (Fig. 189). Each papilla mammillate, with a small projection in its central tip. Papillae of small size in inner and outer limits of each mantle lobe. Color uniform brownish purple. Incurrent siphon with smooth borders (without papillae). Anal siphon low. Both siphons white, with edges of same color of mantle lobes. Pallial organs very similar to those of *M. zebra* (Figs. 187, 190). Osphradium at some distance from gill left margin. A small projection of ctenidial vein as anterior end of gill, without gill filaments.

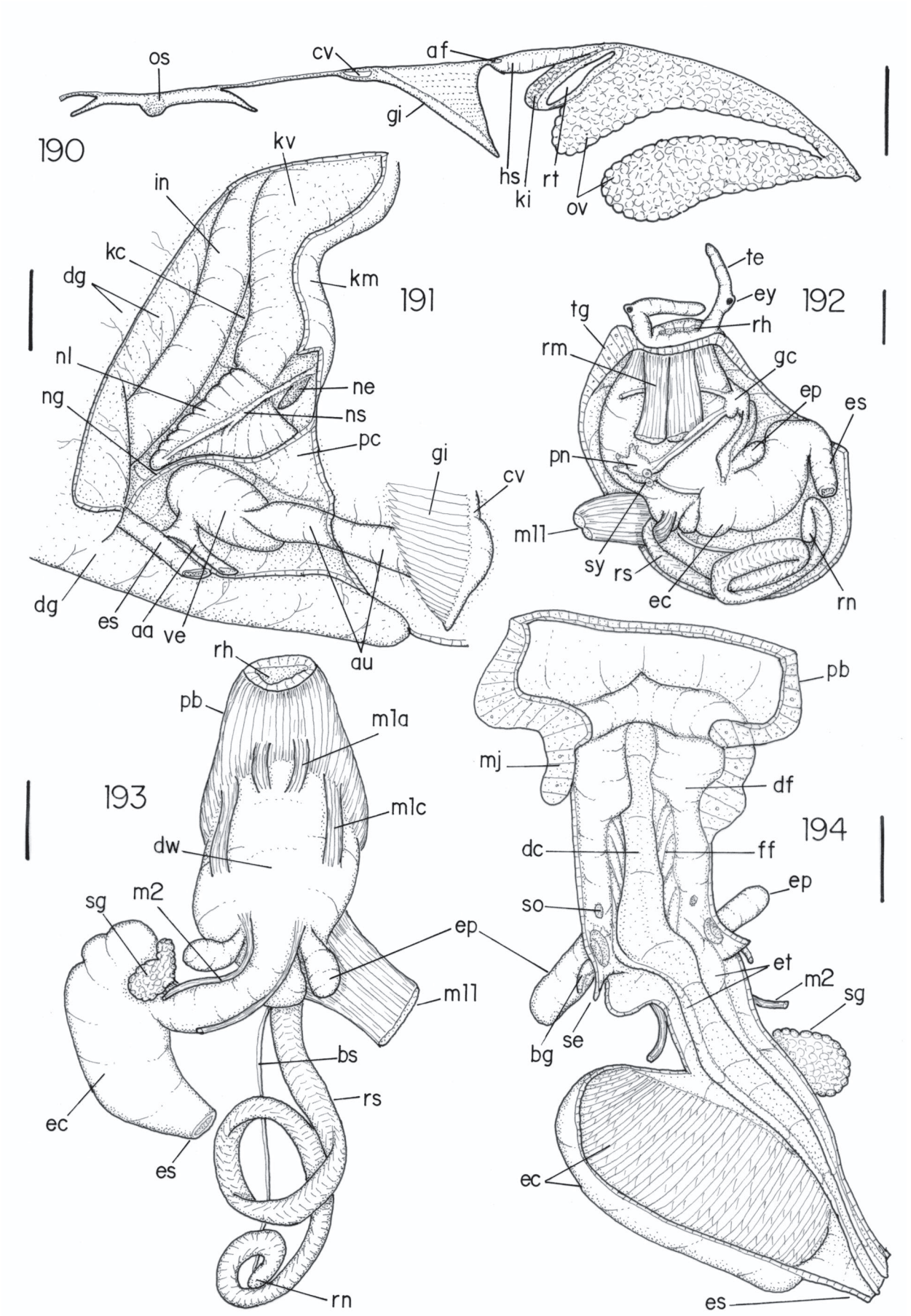
Circulatory and excretory systems (Figs. 191, 203). Heart characters similar to those of *M. zebra*, including dorsal narrow portion of auricle dorsal to posterior region of gill. Kidney also similar to that of *M. zebra*, lobe of nephridial gland also large, with several furrows converging to central, longitudinal vessel; this vessel also inserts at right and ventral to nephrostome. Ventral lobe of kidney solid, massive, without any detectable special arrangement of folds in its surface.

Digestive system (Figs. 192-198). Buccal mass characters similar to those of *M. zebra*, distinctive or notable features following. Odontophore muscles (Figs. 193-197): **m1a** and **m1c** pairs present; **m6a** present, with its median-dorsal surface connected to adjacent subradular membrane (Figs. 196, 197); **m7** absent; **m11** pair surrounding with muscle entire radular sac region penetrating in odontophore; **m12** pair present. Pair of dorsal folds also broad, furrowed part long, with very oblique furrows (Fig. 194). Aperture of salivary glands posterior (almost in posterior limit of buccal mass) and in middle-ventral surface of each fold. Radula very long (about 3 times buccal mass length) (Figs. 192, 193). Radular teeth (Figs. 74, 75): rachidian tooth broader than long, slightly large, base rectangular, cut edge

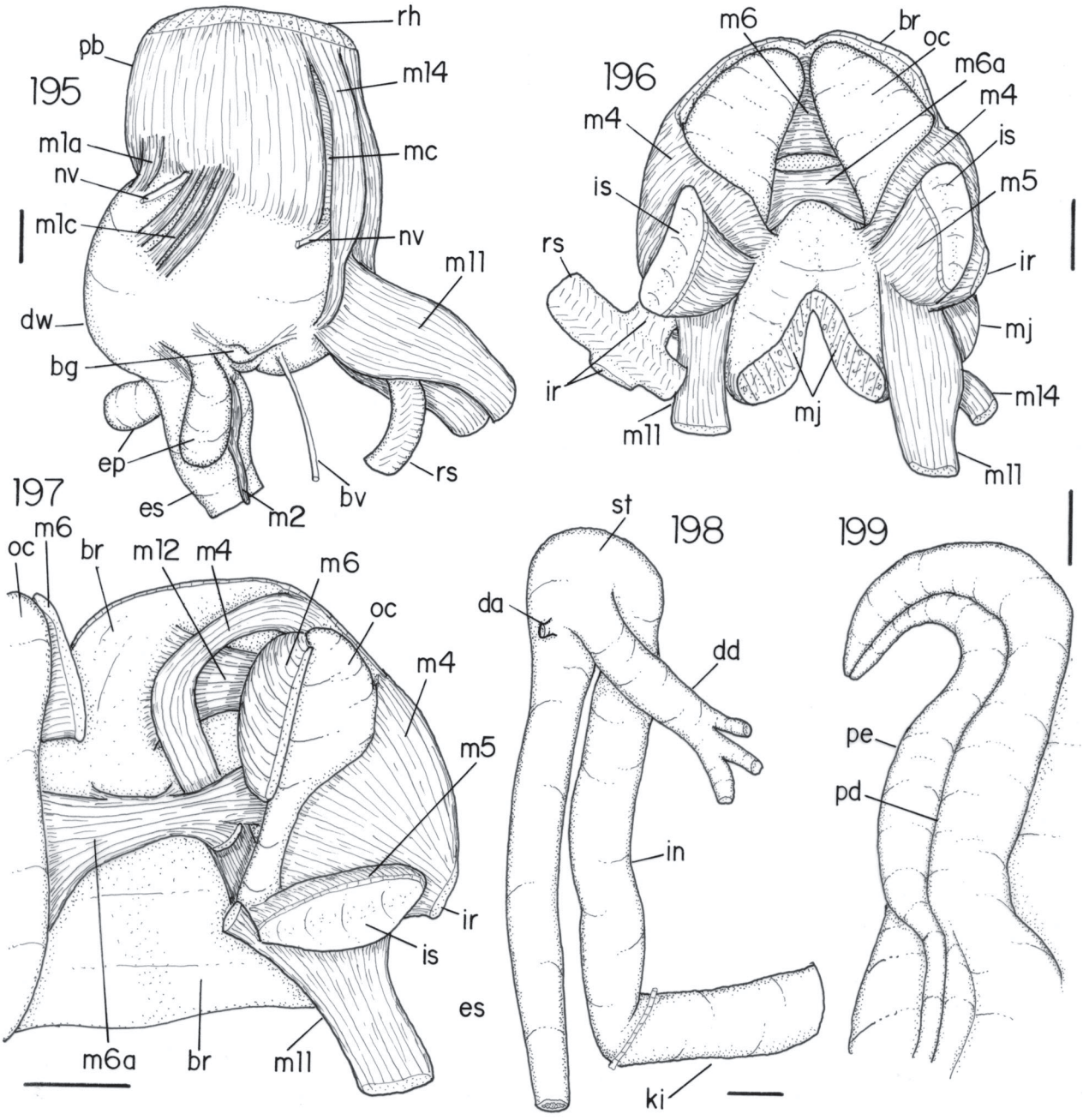


Figs. 187-189, *Luria cinerea* anatomy: **187,** pallial roof and visceral mass, female, ventral view; **188,** head-foot and small portion of adjacent posterior pallial roof, male, lateral-right view; **189,** right mantle lobe, outer view, detail of middle region. Scales: 187-188 = 2 mm; 189 = 1 mm.

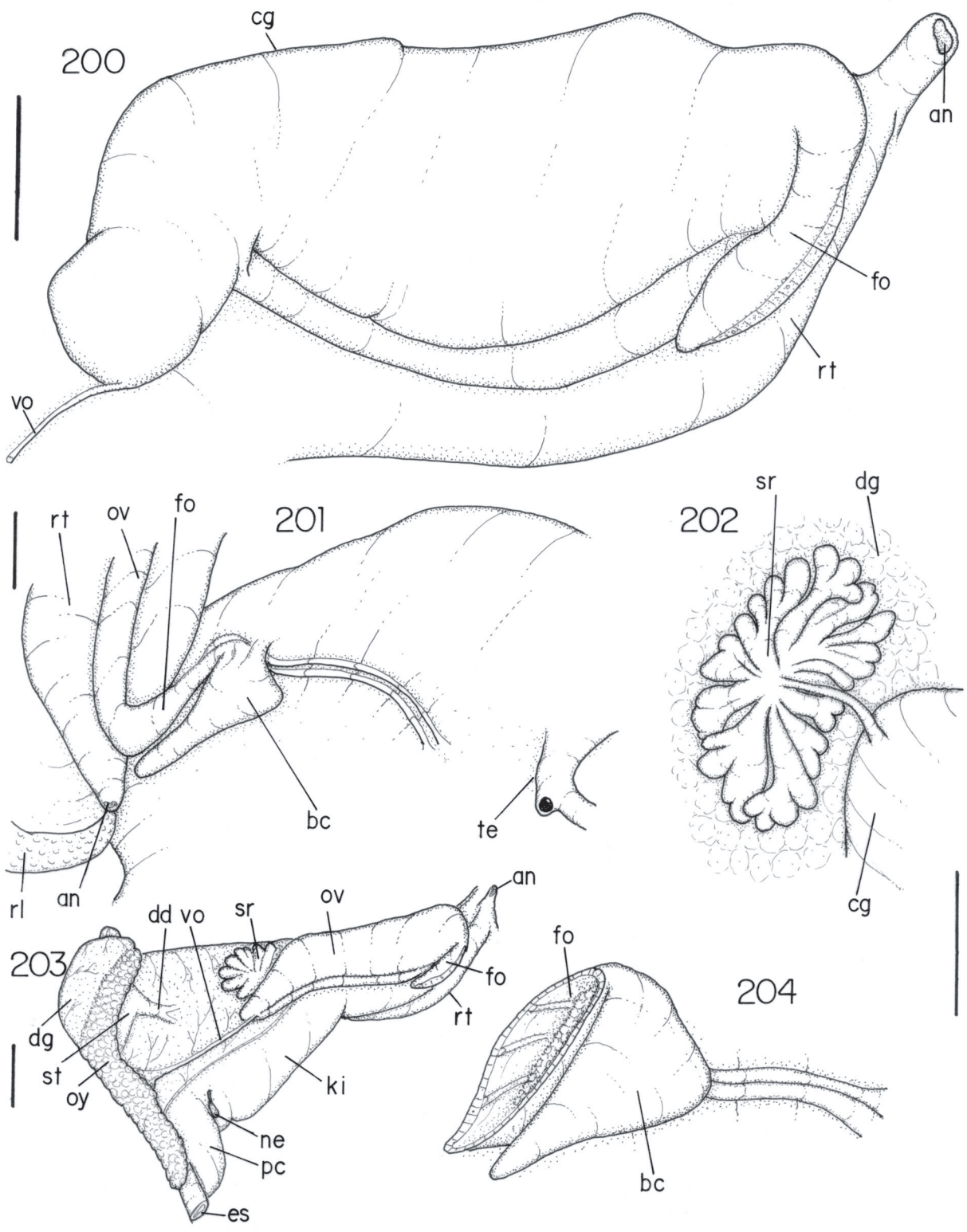
triangular and low, central cusp broad, 2 pairs of secondary cusps very smaller; lateral tooth narrow, slightly elliptical, tip with a broad and short cusp, a pair of secondary cusps small, inner cusp closer than tip the outer cusp; inner marginal tooth similar to lateral but narrower and with central cusp suddenly curved inwards; outer marginal tooth similar to inner marginal, but broader and more curved inwards, base slightly elliptical. Anterior esophagus with a pair of pouches located just posterior to buccal mass posterior limit (Figs. 193, 194), each one long, walls thin and transparent, inner surface smooth, distal end rounded, closed. Stomach and intestine features (Fig. 198) similar to those of *M. zebra*, except for location of duct to posterior lobe of digestive gland closer to duct to anterior lobe and lack of inner septa in duct to anterior lobe of same gland.



Figs. 190-194, *Luria cinerea* anatomy: **190,** pallial roof, transversal section in middle level of posterior osphradium branch; **191,** kidney and pericardium regions, ventral view, both opened longitudinally; **192,** head and haemocoel, ventral view, foot and columellar muscle removed, proboscis wholly retracted; **193,** foregut, dorsal view, radular sac partially uncoiled; **194,** dorsal wall of buccal mass and esophagus, ventral view, odontophore removed, esophagus opened longitudinally. Scales = 2 mm.



Figs. 195-199, *Luria cinerea* anatomy: **195,** buccal mass, lateral-left view; **196,** odontophore, ventral view, both cartilages deflected, radular sac removed, deflected and only partially shown; **197,** same, detail of its left side, m6 sectioned, m5 partially deflected, left cartilage (right in fig.) deflected laterally; **198,** middle digestive tubes, ventral view, shown as in situ; **199,** penis, lateral-ventral view. Scales = 3 mm.



Figs. 200-204, *Luria cinerea* anatomy: **200,** pallial oviduct and some adjacent structures, ventral view; **201,** detail of female anterior-right region of pallial cavity, both roof and floor (roof deflected), part of head also shown; **202,** pallial oviduct, dorsal view, detail of seminal receptacle (sr) region; **203,** visceral mass and posterior part of pallial roof, female, ventral view; **204,** anterior portion of pallial oviduct and short region of adjacent pallial floor, dorsal view, capsule gland removed. Scales = 2 mm.

Genital system. **Male** (Figs. 188, 199). Visceral and pallial structures similar to those described for *M. zebra*. Penis long, almost cylindrical (slightly flattened), tip slightly pointed, penis groove running up to penis tip extremity.

Female (Figs. 200-204). Visceral structures with similar characters to those of *M. zebra*. Pallial oviduct more complex. Narrow visceral oviduct inserts sub-terminally in very broad pallial thin walled in its left margin. Seminal receptacle located dorsal, between posterior and middle thirds of capsule gland; possesses several hollow branches in a same plane (Figs. 202, 203), all converging to a same central small chamber; from this chamber a slender and slightly long duct originating, runs a distance and inserts in capsule gland right surface (between inner and outer laminas). Anterior end of pallial oviduct with a sudden zigzag (Figs. 201, 203, 204); in anterior end of capsule gland, glandular tissue finishes, walls become thin, narrower and suddenly curving towards posterior end; runs a short distance narrowing gradually; after inserts in posterior end of a tall, triangular bursa copulatrix with walls thin, semi-transparent, internally hollow. Ventral surface of these structures amply connected to pallial cavity floor. Female genital pore small, in anterior-right end of bursa. A shallow furrow starts from genital pore, running towards anterior, faint after a distance relative to 1/3 of foot length.

Measurements of shells (in mm). MZSP 28568: ♀ 1: 24.8 by 15.0; ♂ 3: 24.7 by 15.7; ♀ 5: 19.3 by 12.8; MZSP 31039: 38.0 by 23.0.

Distribution. North Carolina, USA, to Rio de Janeiro, Brazil.

Habitat. Under rocks and corals, subtidal up to 97 m depth.

Material examined. BRAZIL; **Pernambuco**; Fernando de Noronha Arquipelago (Simone & Souza Jr. col.); Porcos Bay, MZSP 30914, 1 specimen (21/vii/1999); Praia do Meio, 4-6 m depth, MZSP 31039, 1 specimen (22/vii/1999); Rata Island, Cagaras, MZSP 30942, 2 specimens (21/vii/1999), Buraco do Inferno, 10 m depth, 3 specimens (19/vii/1999). **Bahia**; Salvador, MZSP 28569, 8 specimens (B.L. Albuquerque col., 1997); Itapuã Beach, MZSP 28408, 1 specimen (Simone col., 23-27/ii/1997); Alcobaça, 10 m depth, MZSP 31567, 1 specimen (Coltro col., viii/1999), Recife da Escalada, 5-10 m depth, MZSP 34058, 2 specimens (A. Bodart col., vii/2001, Coltro leg.).

Genus *Cypraea* Linné, 1758

(Type species: *C. tigris* Linné, 1758)

Cypraea tigris Linné, 1758

(Figs. 16, 17, 76, 205-516)

(Color plate Figs. 9-13, 41, 77, 107-110)

Synonymy see Burgess (1985: 76). Complement:

Cypraea tigris: Shaw, 1909: 291 (fig. 1); Vayssière, 1927: 136; Schilder, 1962: 43; Burgess, 1970: 229 (pl. 22, figs. A-D); Wilson & Gillett, 1972: 43-44 (figs. 14, pl. 20); Foin, 1972: 211-218 (figs. 1, 2); Leehman, 1972: 6; 1973: 5; Old, 1974: 4 (figs. 1-9); Taylor & Walls, 1975: 17, 20, 21, 53, 176 (figs.); Donohue, 1977: 160; Brock, 1979: 166-170 (figs. 1, 2); Abbott & Dance, 1983: 97 (fig.); Bandel, 1984: 89 (fig. 138); Burgess, 1985: 76 (fig.); Fainzilber, 1985: 19-21 (figs. 1-21B); Trew, 1987b: 20; Haywood & Wells, 1989: 34-35 (fig.), 154-155 (fig.); Kay & Schoenberg-Dole, 1991: 37 (fig. 45); Lorenz Jr. & Hubert, 1993: 65 (pls. 18, 19, 105, 107); Bradner & Kay, 1996: 5, 87 (figs. 5, 132).

Cypraea tigris tigris: Schilder & Schilder, 1971: 36.

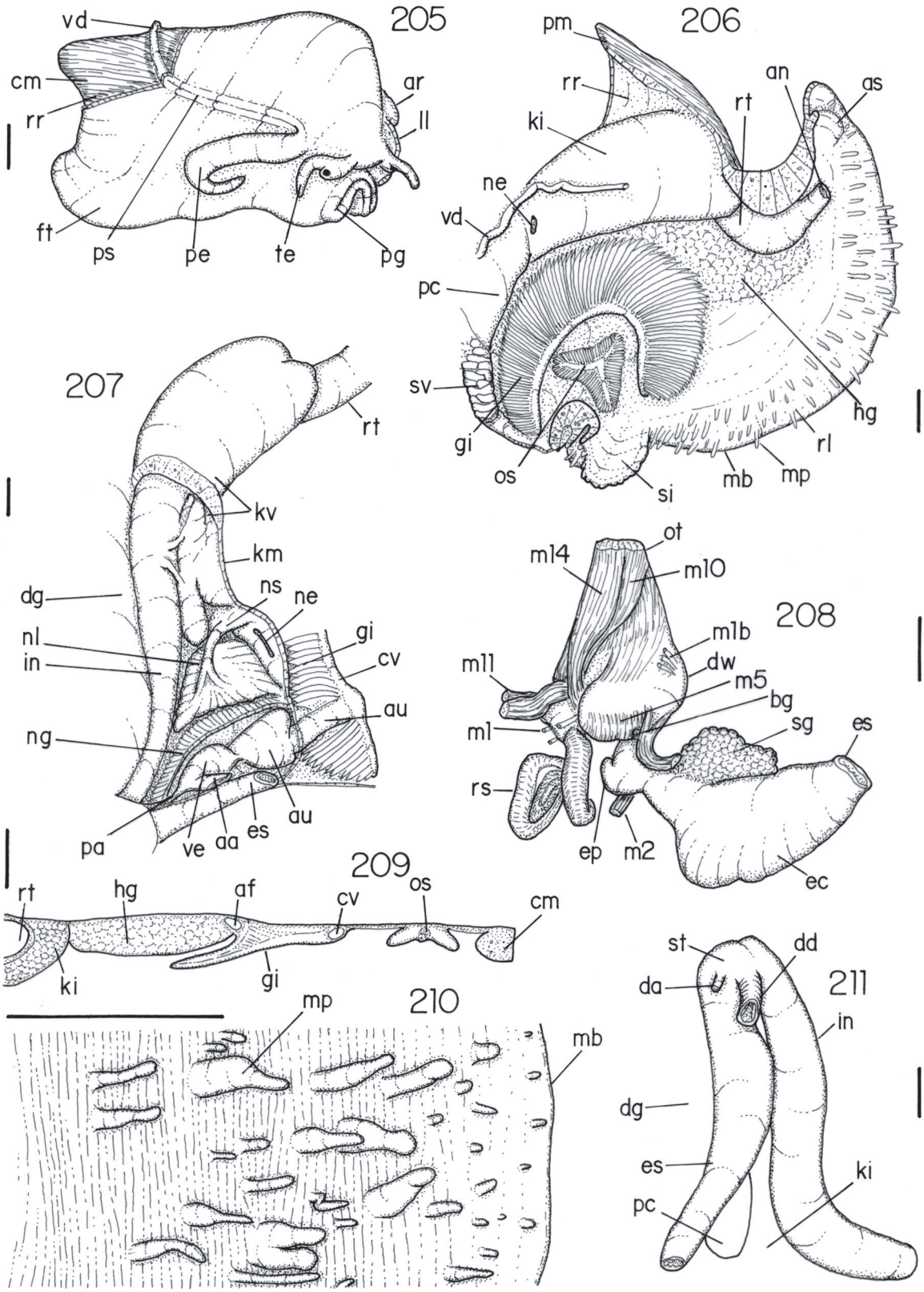
Cypraea (Vulgusela) tigris: Oliveira *et al*., 1981: 157.

Description

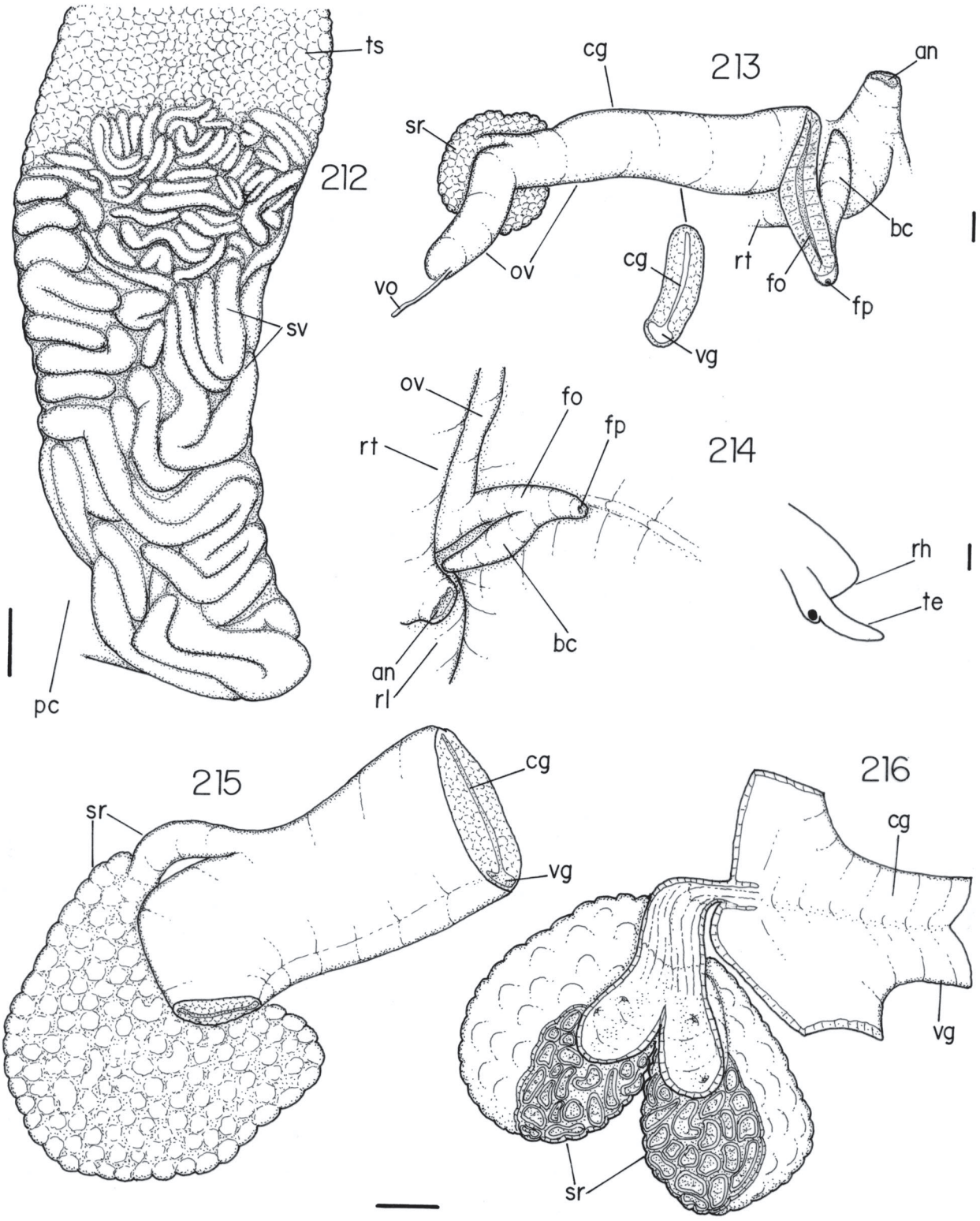
Shell (Figs. 16, 17; color plate Figs. 41, 77). Generally large, rounded, white, with circular dark spots in dorsal surface. Other details in Burgess (1970: 229).

Head-foot (Fig. 205, color plate Fig. 108). Characters very similar to those of *M. zebra*, but broader, anterior projection short.

Mantle organs (Figs. 206, 207, 209, 210). Mantle lobes color cream, with irregular large



Figs. 205-211, *Cypraea tigris* anatomy: **205,** head-foot, male, lateral-right view; **206,** pallial cavity roof and anterior portion of visceral mass, ventral view; **207,** kidney and pericardium region, ventral view, both opened longitudinally (kidney only partially opened); **208,** foregut, lateral-left view; **209,** pallial roof, transversal section in middle level of posterior osphradium branch; **210,** right mantle lobe, outer view, detail of its middle region; **211,** middle portion of digestive tubes, ventral view, seen as in situ, some adjacent structures also indicated. Scales = 5 mm.



Figs. 212-216, *Cypraea tigris* anatomy: **212,** anterior-left end of visceral mass, male, outer (dorsal) view; **213,** pallial oviduct and some adjacent structures, ventral view, female papilla (fo) extracted from pallial floor, a transversal section in indicated level also shown; **214,** anterior end of pallial oviduct and some adjacent structures, dorsal view, head also shown; **215,** pallial oviduct posterior half, ventral view; **216,** same, receptacle duct and capsule gland opened longitudinally to show their connection. Scales = 2 mm.

dark brown spots. Papillae somewhat sparse throughout outer surface, more concentrated close incurrent siphon. Papillae generally simple, tall, rounded tip, most small, some bigger (Fig. 210) (see figs. of live specimens in Wilson & Gillett, 1972; Haywood & Wells, 1989; Kay & Schoenberg-Dole, 1991; and discussion on camouflage in Smith, 1962) (color plate Figs. 9-13, 107-110). Incurrent and anal siphons present, some small papillae in margin of incurrent siphon (color plate Fig. 110). Pallial organs characters (Figs. 206, 209) similar to those of *M. zebra*. Osphradium proportionally small, at some distance from gill. Osphradium filaments with detached distal region, tip rounded. Gill greatly curved, running almost in a half circle. Gill filaments tall and sharp, curved to right (Fig. 209).

Circulatory and excretory systems (Fig. 207). Heart characters similar to those of *M. zebra*. Narrow portion of auricle, running dorsal to gill posterior region, connected to ctenidial vein at considerable distance from its posterior extremity. Kidney features similar to those of *M. zebra*. Accessory lobe of nephridial gland large and broad. Ventral lobe of kidney about half connected to intestine, surface irregular, with some longitudinal furrows.

Digestive system (Figs. 208, 211). Buccal mass very similar in characters to that of *M. zebra*. Distinctive or notable features following. Pair of dorsal folds broader, their furrowed portion with almost longitudinal furrows. Odontophore muscles: **m1** with some of them aligned transversally in middle portion of dorsal surface; **m1a**, **m1c** not developed; **m5** pair short and thick; **m6** very thin and ateriorized; **m6a** thick, located about in middle region of cartilages inner margin, with dorsal median region connected to subradular membrane; **m7** absent; **m11** without muscular fibers in dorsal region around radular sac, only a membrane; **m12** pair thin, broad, covering mj insertion. Esophagus characters close to those of *M. zebra*, but pair of folds of anterior and middle esophagus taller, especially one of then in region of esophageal gland, covering its aperture. Stomach (Fig. 211) also of similar characters to that of *M. zebra*, except for: 1) closer located ducts to digestive gland; 2) duct to anterior lobe of digestive gland running towards left (and not anterior) and 3) presence of 2 series of septa in this duct, a series in each side, each septa thin and low. Intestine, rectum and anus similar to those of preceding species, except by intestine running in a V-shape.

Genital system. **Male**. Visceral and pallial organs characters similar to those of *M. zebra*. Seminal vesicle, however, very much coiled in several series, occupying a broad space in anterior-left region of visceral mass (Fig. 212). Posterior whorls of seminal vesicle narrower than anterior whorls. Pallial sperm groove with tall margins, left margin slightly taller, covering sperm furrow. Penis slightly short (about half of foot length), somewhat cylindrical (Fig. 205), tip curved. Penis groove ends in penis tip.

Female (Figs. 213-216). Visceral structures similar in characters to those of *M. zebra*. Pallial oviduct slightly narrow. Capsule gland most of pallial oviduct, with a pair of glandular laminas connected with each other in right side. Vaginal tube thin walled, uniting left margin of laminas. Narrow visceral oviduct inserted in capsule gland sub-terminally. Seminal receptacle located dorsally, between posterior and middle third parts of pallial oviduct. Seminal receptacle with several hollow, thin walled, coiled, narrow tubes; each one with rounded, closed tip; all tubes converge to a central, slightly large chamber with walls thin and inner surface smooth (Figs. 215, 216). This seminal receptacle central chamber becoming a tube with slightly thick walls and inner surface with several longitudinal folds. Receptacle aperture narrow, papilla-like, between both laminas of capsule gland (Fig. 216). Anterior region of pallial oviduct with sudden zigzag (Figs. 213, 214). After anterior end of capsule gland laminas, vaginal tube becoming an isolated tube suddenly running towards perpendicular, attached to pallial floor by a distance relative to ¼ of capsule gland length; inner surface with slightly tall longitudinal folds. Bursa copulatrix long, elliptical, walls thick, inner surface with tall longitudinal folds; inserting close (slightly posterior) to genital pore, in short distance detaches from vaginal tube and runs projected backwards. Genital pore small, papilla alike (Fig. 214).

Measurements of shells. ANSP 200894: 1) 59.9 by 44.0.

Distribution. Central and West Pacific, Indian Oceans.

Habitat. Rocky, 5 to 20 m depth.

Material examined. CAROLINE ISLANDS; Palau Islands; Babelthuap Island, 2.7 km of

West Passage, 07º31'30"N 134º25'30"E, ANSP 200894, 3♂, 2♀ (15/vii/1955); Peleliu Island, MZSP 29222, 1♂ (Fabio Moretzsohn col. i/1996).

Genus *Lyncina* Troschel, 1863

(Type species: *C. lynx* Linné)

Lyncina lynx (Linné, 1758)

(Figs. 18, 19, 77, 217-228)

(Color plate Figs. 47, 48, 99-102, 112)

Synonymy see Burgess (1985: 87). Complement:

Cypraea lynx: Kay, 1964: 52-53 (figs. 6e, 8-2); Burgess, 1970: 241 (pl. 24, figs. C-F); Donohue, 1977: 160; Abbott & Dance, 1983: 97 (fig.); Burgess, 1985: 87 (fig.); Trew, 1987b: 12; Krommenhoek, 1997: 86.

Lyncina lynx: Schilder & Schilder, 1971: 37; Taylor & Walls, 1975: 15 (fig. radula), 111 (figs.); Lorenz Jr. & Hubert, 1993: 67 (pls. 20, 107); Bradner & Kay, 1996: 5, 17 (figs 7, 11); Kay, 1996: 212 (fig. 18.1C).

Cypraea (Lyncina) lynx: Oliveira *et al*., 1981: 158;

Description

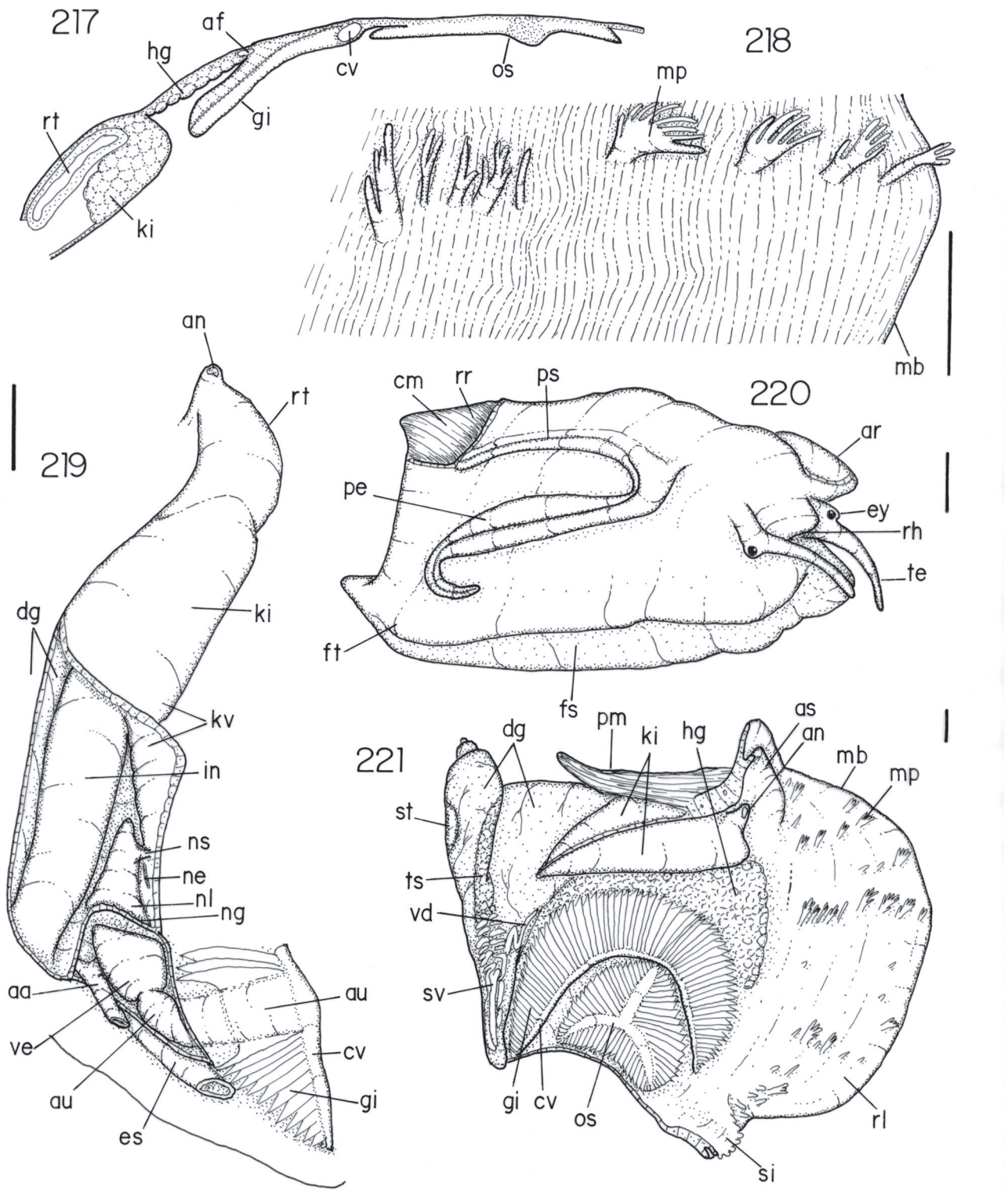
Shell (Figs. 18, 19; color plate Figs. 47-48). Adequate description in references listed in synonymy. Remarkable purple color separating aperture teeth.

Head-foot (Fig. 220; color plate Figs. 101, 102, 112). Characters very similar to those of *M. zebra*.

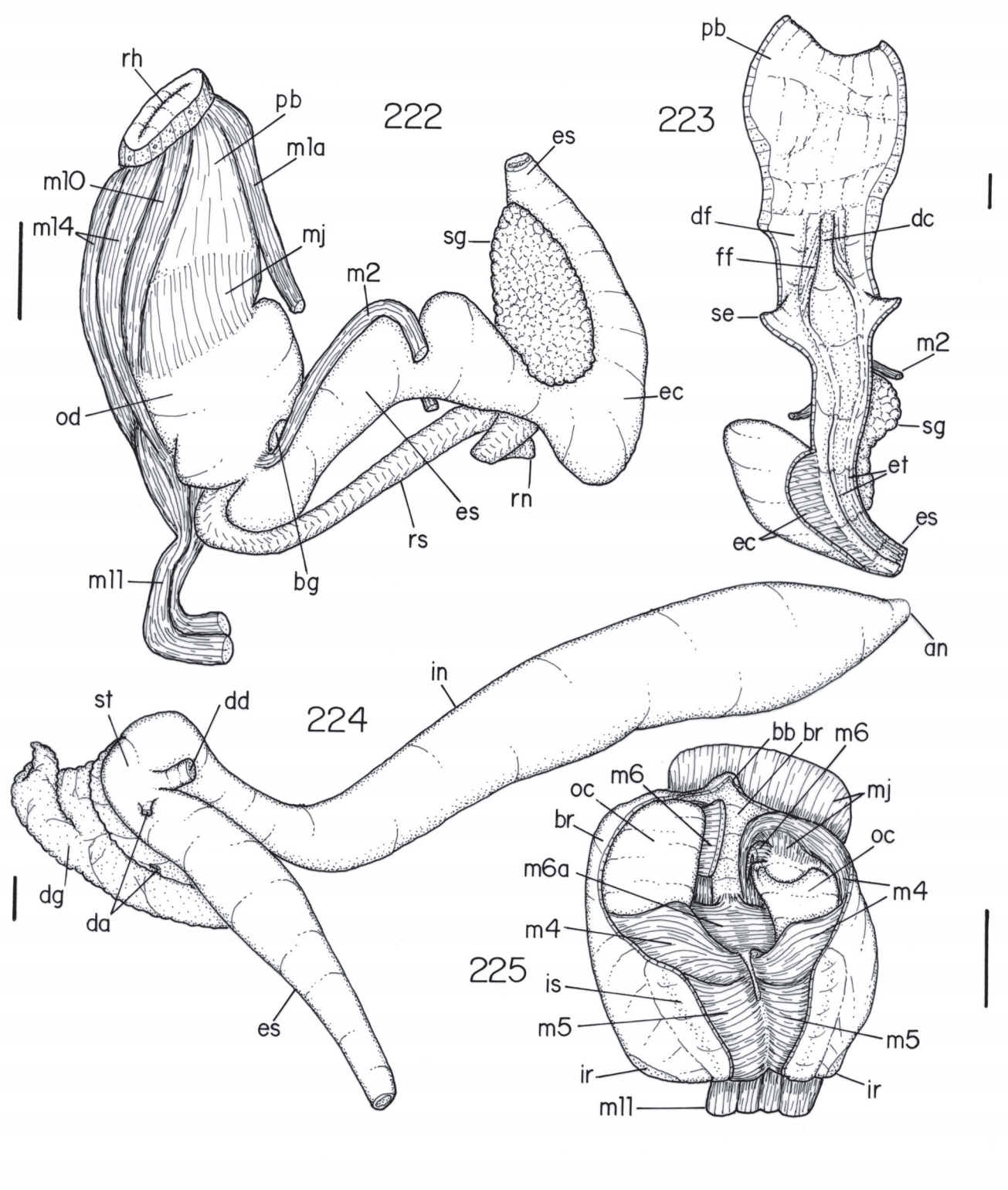
Mantle organs (Figs. 217, 218, 221; color plate Figs. 99-102, 112). Mantle lobes color cream, with dark brown spots in transversal irregular bands; outer surface covered by narrow, low folds, close with each other, parallel to mantle edge. Papillae in general aligned in series, perpendicular to mantle edge, 5-6 series along each lobe (Figs. 218, 221). Papillae varies from simple, slender and tall ones to some with a narrow base and 8-10 terminal, long, slender projections (brush like), most of them intermediary between both extreme forms; in general all papillae present same height (dendritic papillae, sic Kay, 1964) (color plate Fig. 100). Incurrent and anal siphons present, incurrent siphon with a series of small papillae in its free border (color plate Fig. 101). Pallial organs (Figs. 217, 221) with similar characters to those of *M. zebra*. Osphradium also with 3 branches, but with outline almost rounded, its right and posterior margins close to gill. Gill large, curved as a semi-circle. Gill filaments long, with broad base, suddenly narrow, tip rounded and slightly broad (Fig. 217). Other details in Kay (1964: 52).

Circulatory and excretory systems (Fig. 219). Heart characters similar to those of *M. zebra*, included slender region of auricle dorsal to gill posterior region. Kidney features also similar to those of *M. zebra*, distinguishing by: 1) accessory lobe of nephridial gland smaller, with smooth outer surface; its central vessel shorter, also inserted at right to nephrostome; 2) Ventral renal lobe mostly solid and ampler connected to intestine (about ½ to 2/3 of its length); 3) smooth surface of renal lobe.

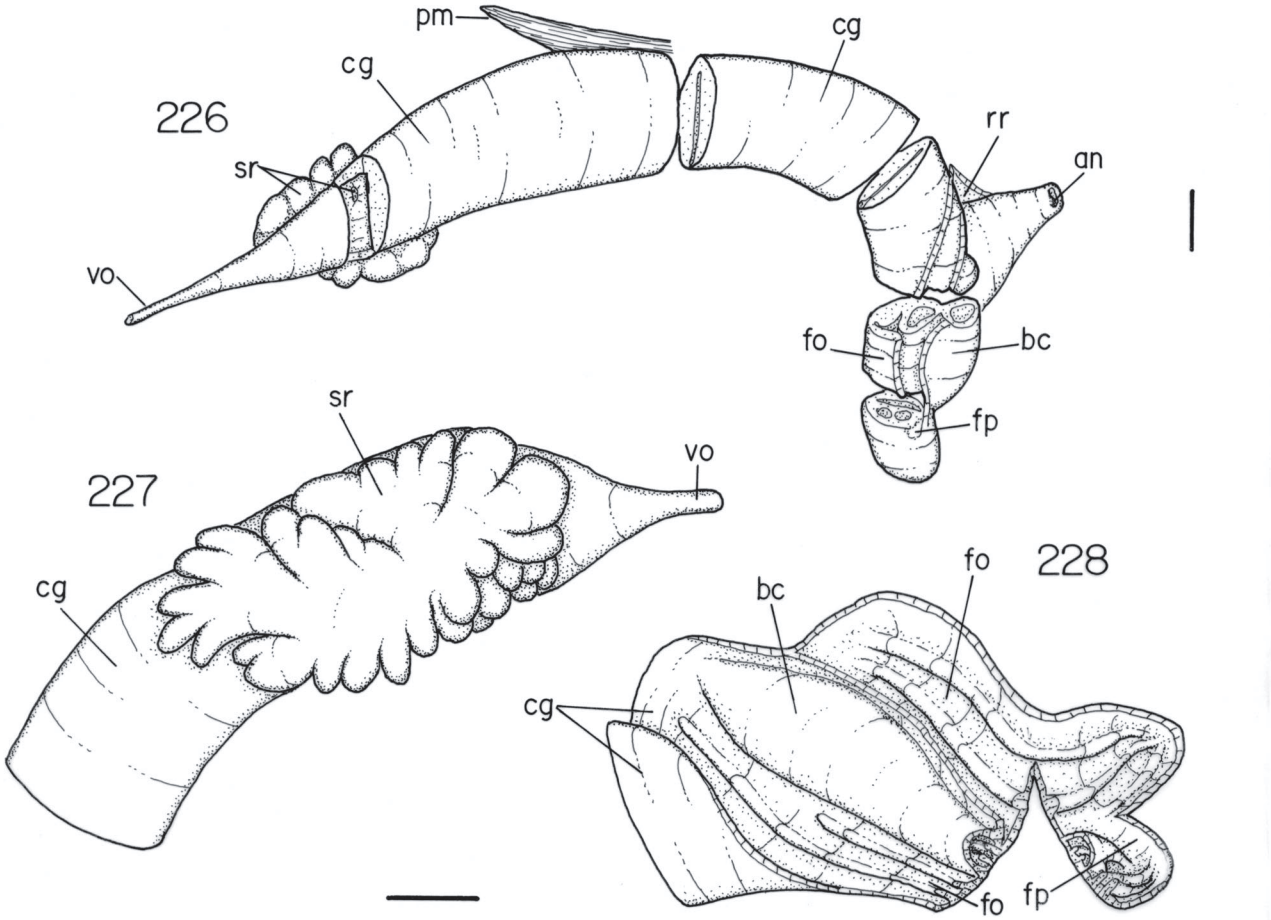
Digestive system (Figs. 222-225). Buccal mass characters similar to those of *M. zebra*, distinctive or notable features following. Dorsal folds narrow, its furrowed part also narrower, with almost longitudinal furrows (Fig. 223). Odontophore muscles (Figs. 222, 225): **m1a** pair present; **m1c**, **m7** and **m12** absent; **m11** pair without muscular fibers in dorsal region surrounding radular sac, only a membrane. Radular sac shorter than twice buccal mass length. Radular teeth (Fig. 77): rachidian tooth slightly narrow and triangular, 3 sub-terminal cusps, central cusp larger (about double than neighbor cusps); lateral tooth broad (about double than rachidian width), cusp terminal large, slightly amorphous, projected inwards, 2 additional small cusps in inner edge and another in outer edge; inner marginal tooth similar to marginal tooth but more straight, 3 cusps, middle cusp terminal and preceded by a thick, long reinforcement; outer marginal tooth narrow, curved inwards, very large terminal pointed cusp and a pair of small secondary cusps (other detail in Kay, 1964: 53). Salivary glands, esophagus and esophageal gland characters (Fig. 222) similar to those of *M. zebra*, except for proportionally longer anterior esophagus. Stomach (Fig.



Figs. 217-221, *Lyncina lynx* anatomy: **217,** pallial roof, transversal section in middle level of posterior osphradium branch; **218,** right mantle lobe, outer view, detail of its middle region; **219,** kidney and pericardium region, ventral view, both opened longitudinally (kidney only partially opened); **220,** head-foot, male, lateral-right view; **221,** pallial cavity roof and anterior portion of visceral mass, ventral view. Scales = 2 mm.



Figs. 222-225, *Lyncina lynx* anatomy: **222,** foregut, lateral-right view; **223**, dorsal wall of buccal mass and esophagus, ventral view, odontophore extracted, esophagus opened longitudinally; **224,** middle and distal digestive tubes and posterior lobe of digestive gland, ventral view, seen as in situ; **225,** odontophore, ventral view, both cartilages deflected and left cartilage (right in fig.) also deflected posteriorly, m6 sectioned. Scales = 1 mm.



Figs. 226-228, *Lyncina lynx* pallial oviduct: **226,** ventral view, some transversal sections artificially made in 5 regions, some adjacent structures also shown; **227,** dorsal view, detail of receptacle region; **228,** detail of anterior region opened longitudinally, dorsal view, a transversal sub terminal section also done. Scales = 1 mm.

224) also similar to that of *M. zebra*, except for closer located ducts to digestive gland and for duct to anterior lobe lacking inner septa. Posterior lobe of digestive gland very small, about 1 whorl posterior to stomach, connected to anterior lobe by a thin portion dorsal to stomach (Fig. 224). Intestine very broad, almost straight. Rectum and anus as in *M. zebra*.

Genital system. **Male** (Fig. 220). Visceral and pallial structures similar in characters to those of *M. zebra*. Seminal vesicle of proportional smaller size (Fig. 221). Pallial sperm groove with thick, tall borders. Penis long, clearly narrow, apical region curved. Penis groove running up to apex (Fig. 220).

Female (Figs. 226-228). Visceral structures characters similar to those of *M. zebra*. Pallial oviduct with several distinctive features as following. Visceral oviduct insertion in posterior end of pallial oviduct as a gradual increase. Seminal receptacle located dorsal to posterior region of pallial oviduct; possesses several broad, thin walled, irregular branches (Fig. 227), all them converging to a central region. This central region shortly connected to outer lamina of pallial oviduct orifice, located nearer to right side (Fig. 226). Pallial oviduct long and slightly narrow, mostly composed by a capsule gland. Both capsule gland laminas connected with each other in right side. Vaginal tube thin walled connects left side of these laminas. Anterior end of capsule gland very complex (Figs. 226, 228): at anterior to capsule gland laminas end, oviduct walls become thin, with inner longitudinal folds by a considerable distance. Bursa copulatrix as an elliptical chamber attached to dorsal (outer) wall and bulged inwards; bursa aperture small, turned to left, close to genital aperture. Female genital aperture small, located in anterior end of oviduct, in floor of

pallial cavity. Another accessory chamber present, walls thin, inner folds longitudinal, starting close to genital pore and running towards posterior attached to mantle and to right surface of anterior region of pallial oviduct; posterior end closed as blind-sac; anterior end opened by a small, sub-terminal orifice, turned to left, just posterior to genital pore. Other details in Kay (1964: 53)

Measurements of shells. MZSP 2044: 1) 40.6 by 25.0; 2) 37.5 by 21.2.

Distribution. Central and West Pacific, Indian Oceans.

Habitat. Under corals slabs, intertidal.

Material examined. CAROLINE ISLANDS; **Palau**; Koror, MZSP 30763, 1♂, 1♀ (sta. FM41, Fabio Moretzsohn col., i/1996). SOUTH AFRICA; Natal, MZSP 2044, 3 shells (1901).

Genus *Monetaria* Troschel, 1863

(Type species: *C. moneta* Linné)

Monetaria moneta (Linné, 1758)

(Figs 20, 21, 78, 229-244)

(Color plate Figs. 45, 70-72, 103-106)

Synonymy see Burgess (1985: 228). Complement:

Cypraea moneta: Shaw, 1909: 312; Vayssière, 1927: 138 (pl. 24, fig. 13) Morris, 1952: 181 (pl. 172); Kay, 1960b: 279; Burgess, 1970: 343 (pl. 41, figs. B-I); Keen, 1971: 493; Wilson & Gillett, 1972: 56 (pl. 35, fig. 2); Taylor & Walls, 1975: 149 (figs.); Renaud, 1976: 147-158 (figs. 1-8); Donohue, 1977: 160; Abbott & Dance, 1983: 87 (fig.); Burgess, 1985: 228-229 (fig.); Finet, 1987: 22-24 (figs. 1-14); Trew, 1987b: 13; Kay & Schoenberg-Dole, 1991: 37 (fig. 44-2).

Monetaria moneta: Schilder & Schilder, 1971: 59; Lorenz Jr. & Hubert, 1993: 205 (pls. 96, 106, 108); Bradner & Kay, 1996: 42 (fig. 56).

Pustularia (Monetaria) moneta: Llabador, 1971: 5-14.

Cypraea (Monetaria) moneta: Oliveira *et al*., 1981: 154-155.

Erosaria moneta: Kay, 1996: 216.

Description

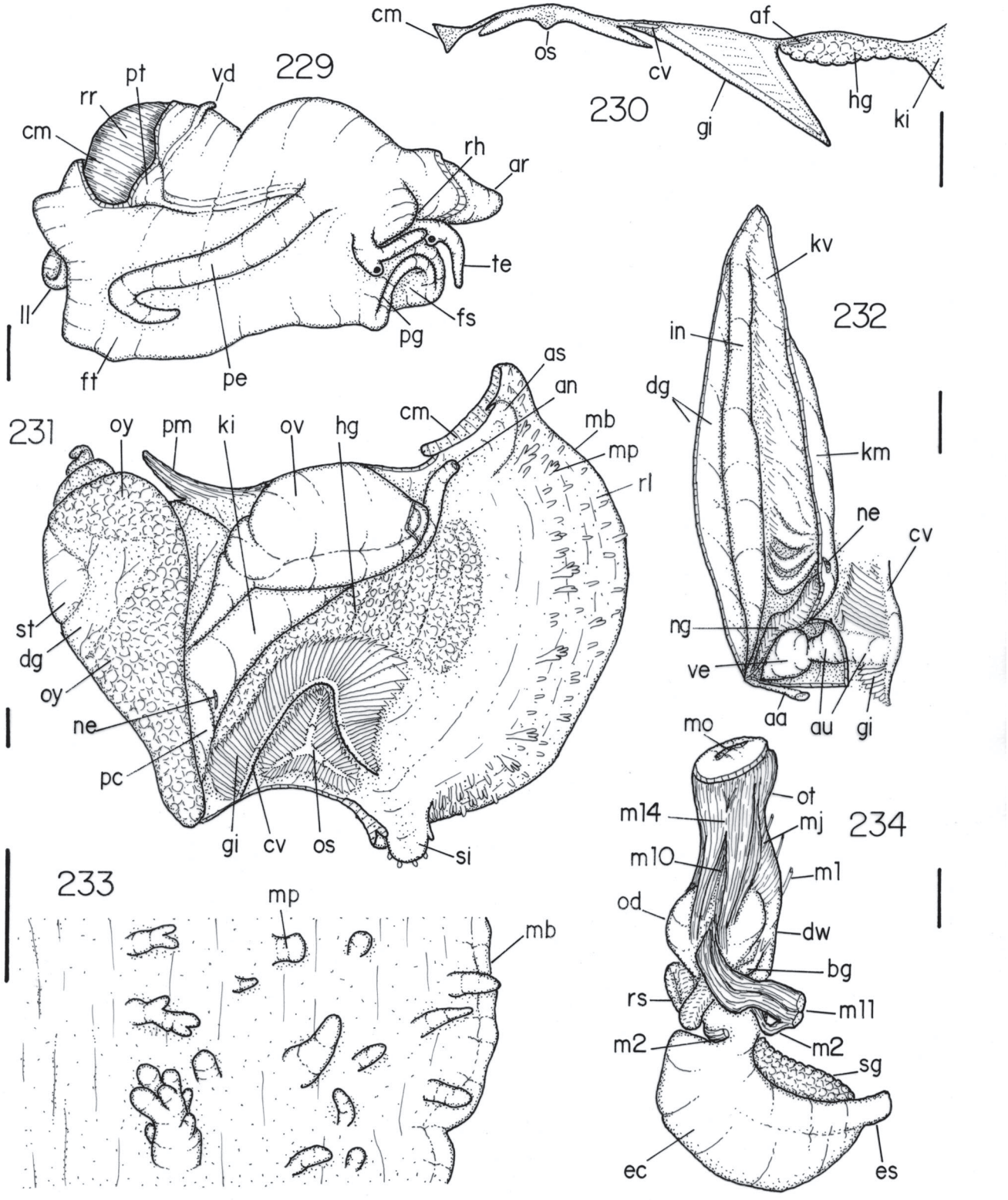
Shell (Figs. 21, 21; color plate Fig. 45, 70-72). For description see Burgess (1985).

Head-foot (Figs. 229, 239; color plate Fig. 103). Very similar characters to those of *M. zebra*, but with proportionally shorter and broader anterior projection.

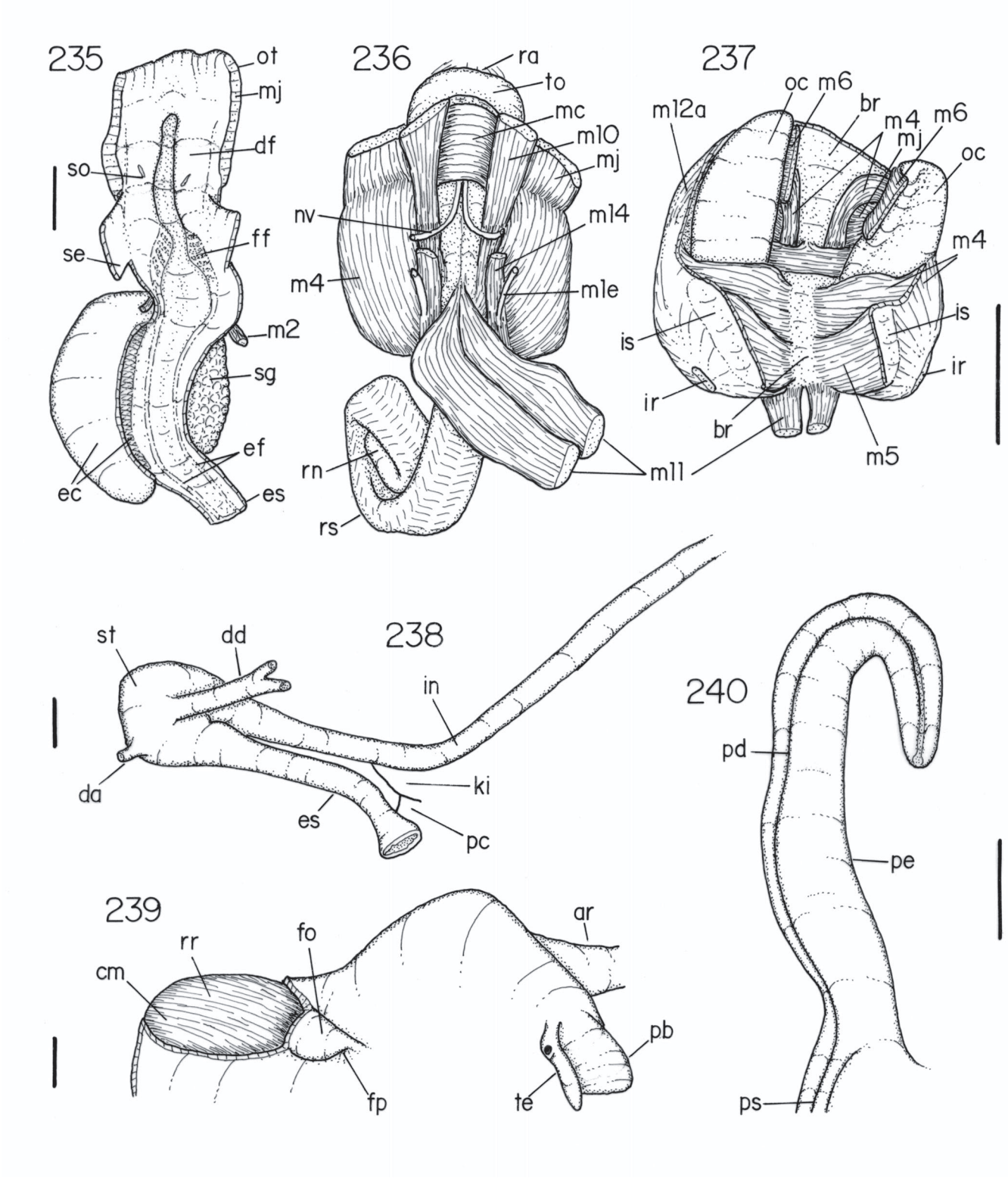
Mantle organs (Figs. 230-233; color plate Figs. 103-106). Mantle lobes pigmented with several, narrow, transversal bands alternate pale cream and dark brown. Mantle papillae mostly short and sparse, of 4 main types (Fig. 233): 1) most simple; 2) bifid tip; 3) bifid tip and also another pair of projection in middle level; 4) 4 tip projections and 1 or 2 pairs of projections along its length, in alternate positions. These more complex papillae in general located far from mantle edge. Siphon with small papillae in its edge. Pallial organs characters (Figs. 230, 231) similar to those of *M. zebra*, distinctive characters following. Osphradium proportionally larger, its posterior and right margin close to gill. Gill filaments tall, with almost straight margins (Fig. 230).

Circulatory and excretory systems (Fig. 232). Heart characters similar to those of *M. zebra* but proportionally smaller. Kidney also similar in characters to those of *M. zebra*, except for: 1) narrower lobe of nephridial gland, with almost smooth surface; 2) ventral lobe of kidney longer, narrower, surface with several successive oblique furrows, most not attached to intestine (only a small portion in its right extremity), color cream.

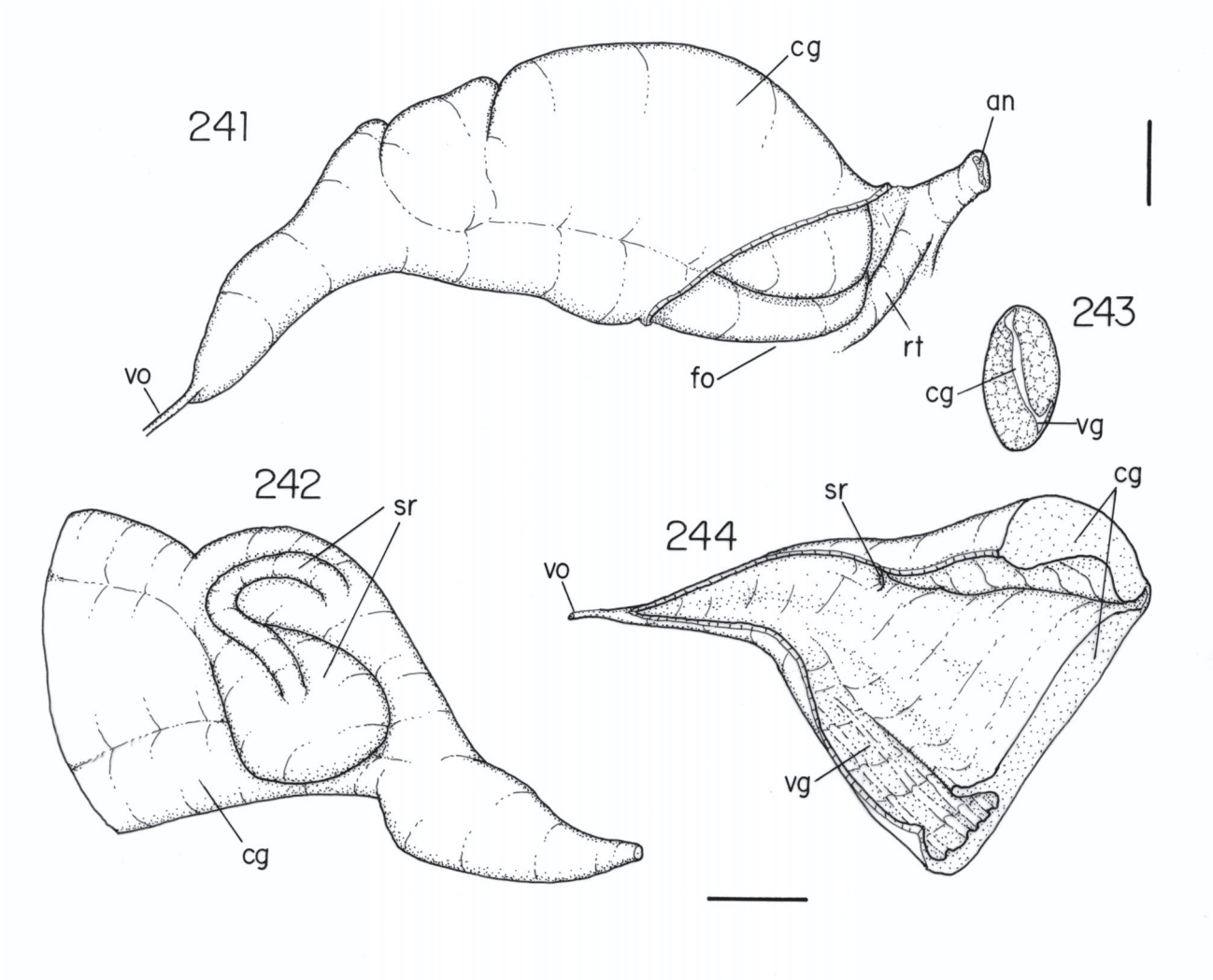
Digestive system (Figs. 234-238). Buccal mass characters similar to those of *M. zebra*, distinctive or notable features following. Dorsal folds also broad; its furrowed part short, posteriorly located (Fig. 235). Aperture of salivary glands a slit located in middle region of folds ventral surface. Odontophore muscles (Figs. 234, 236, 237): **m1e**, a differentiable pair of jugal muscle inserted



Figs. 229-234, *Monetaria moneta* anatomy: **229,** head-foot, male, lateral-right view; **230,** pallial roof, transversal section in middle level of posterior osphradium branch; **231,** pallial cavity roof and visceral mass, ventral view; **232,** kidney and pericardium region, ventral view, both opened longitudinally, some gill filaments on auricle extracted; **233,** right mantle lobe, outer view, detail of its middle region; **234,** foregut, ventral-slightly lateral-left view. Scales = 1 mm.



Figs. 235-240, *Monetaria moneta* anatomy: **235,** dorsal wall of buccal mass and esophagus, ventral view, odontophore extracted, esophagus opened longitudinally; **236,** odontophore, ventral view; **237,** same, both cartilages deflected and left cartilage (right in fig.) also deflected posteriorly, m6 sectioned; **238,** middle and distal digestive tubes, ventral view, seen as in situ; **239,** head-foot, female, lateral-right view, detail of its dorsal surface with pallial oviduct partially extracted; **240,** penis, lateral view. Scales = 1 mm.



Figs. 241-244, *Monetaria moneta* pallial oviduct: **241,** whole ventral view, some adjacent structures also shown, female papilla extracted; **242,** detail of its posterior region, dorsal view; **243,** transversal section in middle level of capsule gland; **244,** posterior end opened longitudinally, ventral view. Scales = 1 mm.

dorsal to m14 insertion; **m6a** narrow, connected dorsally in median line to subradular membrane; **m11** pair without muscular tissue in dorsal region of radular sac, only a transparent membrane; **m12a** pair of thin and narrow muscles, originating in anterior-outer surface of odontophore cartilages, running towards posterior covering mj, inserting in subradular membrane lateral region, close to m4; **m14** pair narrow. Radula slightly short, with about same length than that of buccal mass. Radular teeth (Fig. 78): rachidian long and narrow, 3 cusps, central cusp about double of secondary cusp; lateral and both marginal teeth similar with each other, curved inwards, with 3 terminal cusps, apical cusp very larger, curved forwards, tip rounded, a secondary, small cusp in each side, inner cusp closer to tip than outer cusp; marginal tooth with about same width as rachidian, outer marginal tooth with about half of rachidian width, inner marginal tooth of intermediary width. Salivary glands, esophagus and esophageal gland characters (Figs. 234, 235) similar to those of *M. zebra*, but with esophageal gland proportionally longer. Stomach characters (Fig. 238) also similar to those of *M. zebra*, except for lack of inner septa in duct to anterior lobe of digestive gland. A distinct typhlosole running from dorsal region by side of duct to anterior lobe of digestive gland, running along intestine dorsal surface for a short distance and faints. Intestine narrow and proportionally long, with a pair of small, inner, longitudinal folds in its ventral surface only in its renal portion, remainder inner surface smooth.

Genital system. **Male** (Figs. 229, 239). Visceral and pallial structures with features similar to those of *M. zebra*. Seminal vesicle proportionally shorter, but with thicker walls; its perpendicular portion

(in direction of pallial cavity) possessing thick walls and even some coils. Prostate gland small, just posterior to triangular sinus where vas deferens opens. Penis long, cylindrical, tip curved. Penis groove running up to tip.

Female (Figs. 231, 239, 241-244). Visceral structures characters similar to those of *M. zebra*. Visceral oviduct gradually increases in posterior extremity of pallial oviduct, originating as a thin walled, triangular chamber; after a short distance walls become thick glandular (capsule gland). Both laminas of capsule gland narrowly united with each other in right margin. Vaginal tube broad, walls somewhat thick, inner surface covered by narrow longitudinal folds; a tall fold of outer capsule gland lamina protects vaginal tube; vaginal tube unites left margin of capsule gland laminas. Seminal receptacle almost spherical, located attached to dorsal surface of posterior region of capsule gland. A narrow and curved tube connects middle dorsal surface of receptacle with capsule gland posterior region (Fig. 242), opening just between both laminas (Fig. 244). Capsule gland laminas finish at short distance from genital aperture suddenly narrow, walls become thin. Genital pore papilla-like (Fig. 239).

Measurements of shells (in mm). MZSP 30764: 1) 17.8 by 14.3; 2) 17.7 by 13.5.

Distribution. Indo-Pacific.

Habitat. Lagoon reefs, intertidal.

Material examined. JAPAN; **Okinawa**, Sesoko Island, MZSP 29253, 2♂, 3♀ (M. Tsuchiya col., ix/1998). FANNING ATOLL, MZSP 30764, 9 specimens (sta. FM70, E.A. Kay col., viii/1972). MICRONESIA; **Kosrae**, Lelu, MZSP 30762, 5♂, 5♀ (F. Moretzsohn col., sta. FM54-1/2, xii/1995).

Monetaria annulus (Linné, 1758)

(Figs. 22, 23, 79, 245-262)

(Color plate Figs. 50, 59, 60, 90-93)

Synonymy see Burgess (1985: 227). Complement:

Cypraea annulus: Vayssière, 1927: 138 (pl. 26, figs 44, 45); Kay, 1960b: 279; Burgess, 1970: 341: (pl. 41, fig. A); Wilson & Gillett, 1972: 56 (pl. 35, fig. 5); Taylor & Walls, 1975: 36, 136 (figs.); Donohue, 1977: 160; Pelletier, 1982: 24; Abbott & Dance, 1983: 87 (fig.); Bandel, 1984: 89 (fig. 133); Burgess, 1985: 227 (fig.); Trew, 1987b: 1-2.

Cypraea annulata: Morris, 1952: 181 (pl. 172).

Monetaria (Ornamentaria) annulus annulus: Schilder & Schilder, 1971: 60.

Cypraea (Ornamentaria) annulus: Oliveira *et al*., 1981: 155.

Monetaria annulus: Lorenz Jr. & Hubert, 1993: 204 (pls. 97, 106, 108); Bradner & Kay, 1996: 42 (fig. 57).

Erosaria annulus: Lorenz, 1997: 13.

Description

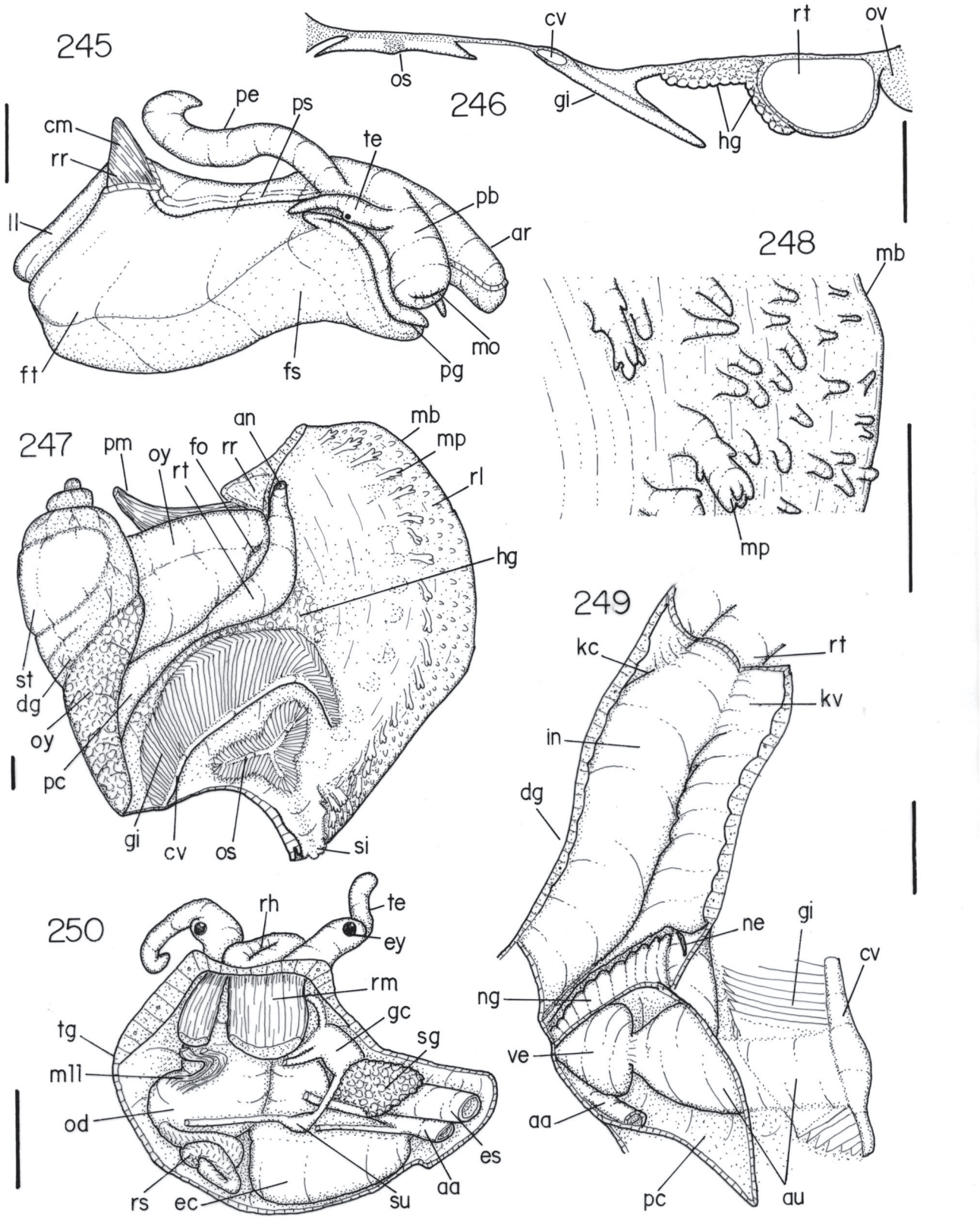
Shell (Figs. 22, 23; color plate Figs. 50, 59, 60). Description in Burgess (1985) and others above listed.

Head-foot (Figs. 245, 250). Characters similar to those of *M. moneta*.

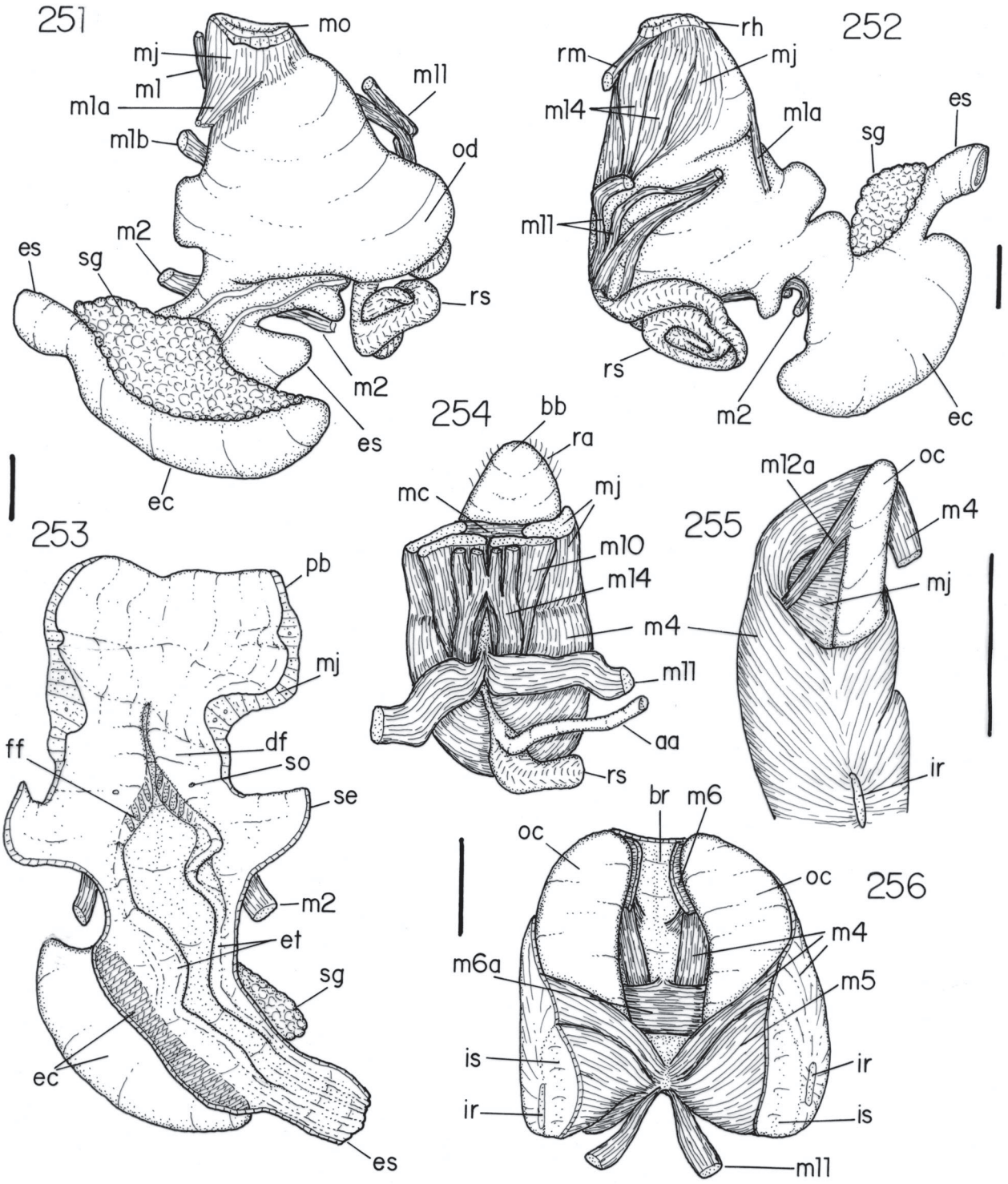
Mantle organs (Figs. 246-248; color plate Figs. 90-93). Mantle lobes characters very similar to those of *M. moneta*, including papillae types and color, however presents more quantity of complex papillae (Fig. 248, color plate Fig. 91), in general located far from mantle edge. Pallial organs features (Fig. 247) also similar to those of *M. moneta*, including osphradium size, close to gill, and anal siphon (color plate Fig. 92). Gill filaments with narrower distal region, concave in right margin (Fig. 246).

Circulatory and excretory systems (Fig. 249). Heart and kidney characters similar to those of *M. moneta*.

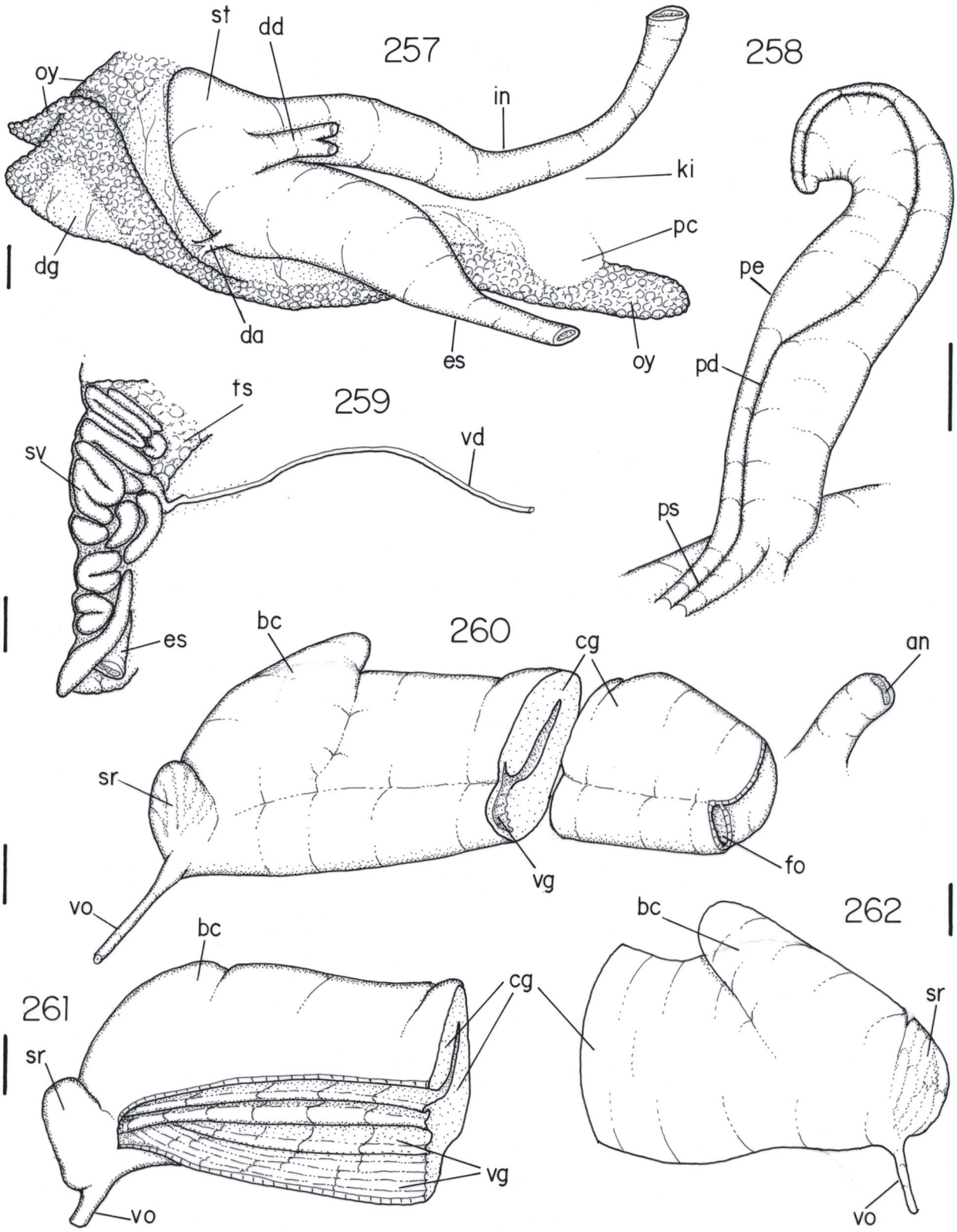
Digestive system (Figs. 251-257). Buccal mass characters similar to those described for *M. moneta*, including dorsal folds and odontophore muscles. Aperture of salivary gland differs in being smaller, as a single pore (Fig. 253). Radular attributes very similar to those of *M. moneta* (Fig. 79). Esophagus and



Figs. 245-250, *Monetaria annulus* anatomy: **245,** head-foot, male, lateral-right, slightly ventral view; **246,** pallial roof, transversal section in middle level of posterior osphradium branch; **247,** pallial cavity roof and visceral mass, ventral view; **248,** right mantle lobe, outer view, detail of its middle region; **249,** kidney and pericardium region, ventral view, both opened longitudinally, some gill filaments on auricle extracted; **250,** head and haemocoel, ventral view, foot and columellar muscle extracted. Scales = 2 mm.



Figs. 251-256, *Monetaria annulus* anatomy: **251,** foregut, dorsal-slightly lateral-right view; **252,** same, lateral-left view; **253,** dorsal wall of buccal mass and esophagus, ventral view, odontophore extracted, esophagus opened longitudinally; **254,** odontophore, ventral view; **255,** same, dorsal view, left half only, subradular membrane extracted; **256,** same, ventral view, both cartilages deflected m6 sectioned. Scales = 1 mm.



Figs. 257-262, *Monetaria annulus* anatomy: **257,** part of visceral mass and middle digestive tubes seen as in situ, female, ventral view; **258,** penis, lateral view; **259,** visceral mass, male, dorsal view, detail of its left-anterior end, vas deferens shown as in situ; **260,** pallial oviduct, ventral view, a transversal section artificially made, female papilla extracted, anus also shown; **261,** same, posterior half with vaginal groove opened longitudinally; **262,** same, dorsal view. Scales = 1 mm.

stomach features (Figs. 251-253, 257) similar to those of *M. moneta*, except for in general broader esophagus insertion and intestine origin.

Genital system. **Male**. Visceral and pallial structures similar in characters to those of *M. moneta*, except for vas deferens region narrower, running perpendicularly from seminal vesicle mass lacking coils (Fig. 259). Penis long, cylindrical, broad, tip curved (Figs. 245, 258).

Female (Figs. 247, 260-262). Visceral structures with similar features as those of *M. zebra*. Pallial oviduct attributes similar to those of *M. moneta*, including slightly complex vaginal tube (with inner longitudinal folds, especially those of outer lamina of capsule gland) and papilla-like female pore. Posterior region of pallial oviduct presents, however, some differences. Seminal receptacle located just after visceral oviduct inserting in pallial oviduct, almost spherical with some long, irregular acina, confined in a transparent, thin membrane; connects with pallial oviduct by a narrow aperture in its posterior-right margin. Bursa copulatrix slightly long, located just anterior to receptacle and posteriorly in capsule gland, diverticulum-like, walls thin. Vaginal groove with several longitudinal folds (Fig. 261)

Measurements of shells (in mm). MZSP 8154: 1) 27.0 by 20.7; 2) 27.4 by 20.2.

Distribution. Central and West Pacific, Indian Oceans.

Habitat. Intertidal reef.

Material examined. MICRONESIA; Kosrae; Lelu, MZSP 30762, 1♂, 1♀ (sta. FM54-1/2, Fabio Moretzsohn col., xii/1995). JAPAN; MZSP 8154, 3 shells (Stearns col., 1896); Okinawa; Sesoko Island, MZSP 29254, 2♂, 3♀ (M. Tsuchiya col., ix/1998).

Discussion. *M annulus* and *M. moneta* are very close to each other morphologically, the main differences are explored above. However, the main difference is in the pallial oviduct features. The similarity is the reason for considering *M. annulus* in the genus *Monetaria* and not in *Ornamentaria* M. & F. Schilder, 1936, which it is the type species. Some authors consider *Ornamentaria* a subgenus of *Monetaria* (e.g., Wenz, 1938).

Genus *Ravitrona* Iredale, 1930

(Type species: *C. caputserpentis* L.)

Ravitrona caputserpentis (Linné, 1758)

(Figs. 24, 25, 80, 263-271)

(Color plate Figs. 14, 15, 43, 63, 64, 94-98, 111)

Cypraea caput-serpentis: Vayssière, 1927: 139 (pl. 24, fig. 14); Morris, 1952: 179 (pl. 172).

Erosaria caputserpentis: Rau, 1934: 102 (fig. 15); Kay, 1996: 216.

Cypraea caputserpentis: Kay, 1960a: 175-195 (figs. 1-8); 1960b: 278, 282, 285 (figs. 1-1, 7); Griffiths, 1960: 13; Keen, 1971: 492; Wilson & Gillett, 1972: 54 (pl. 34, fig. 5); Taylor & Walls, 1975: 243 (figs.); Donohue, 1977: 160; Oliveira *et al*., 1981: 153-154; Abbott & Dance, 1983: 86 (fig.); Tissot, 1984: 106-119 (figs. 1-5); Trew, 1987b: 3; Foin, 1989: 506-517 (fig. 1); Cantera, 1991: 85-97 (fig. 1); Krommenhoek, 1997: 86.

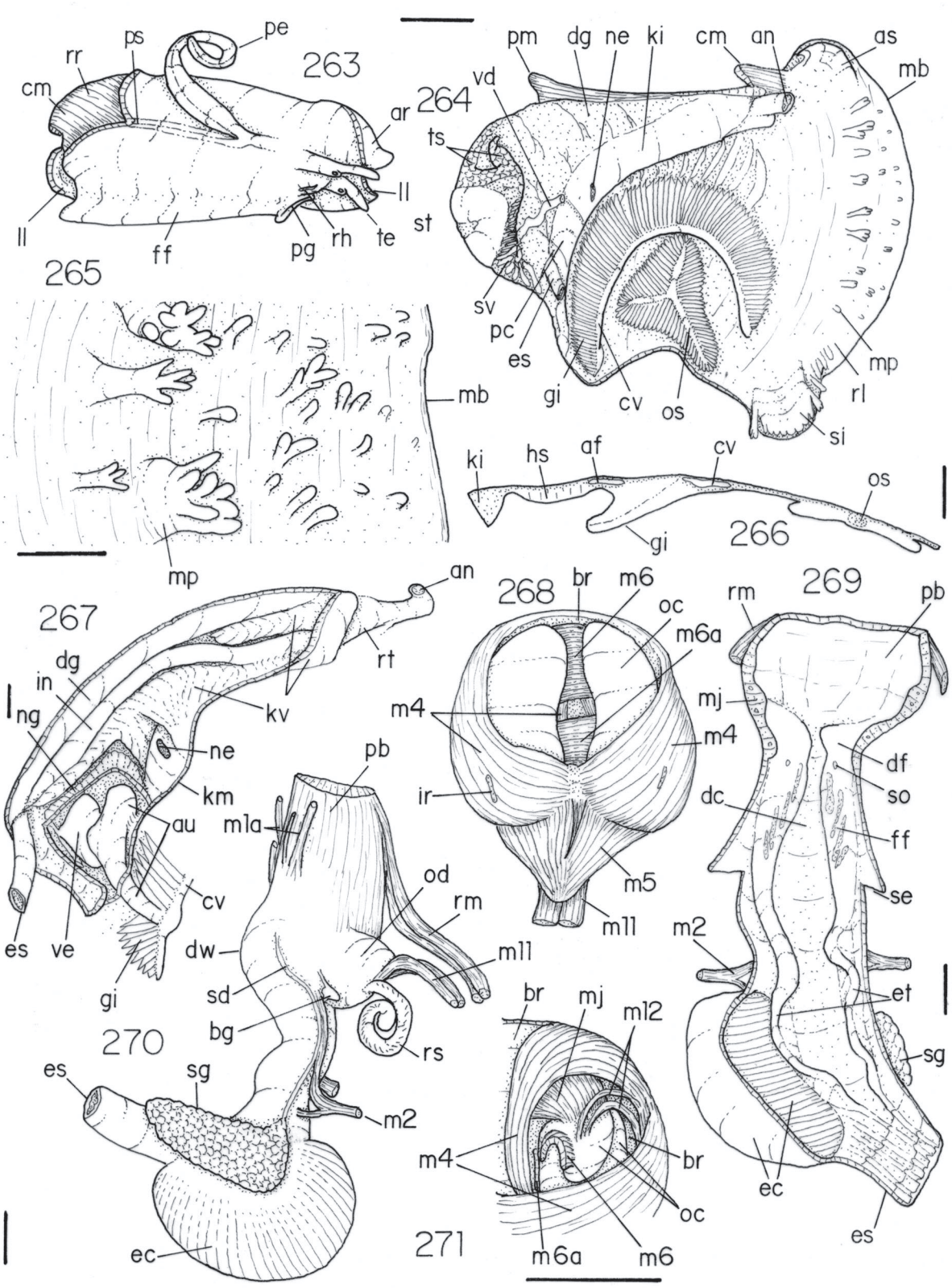
Erosaria (Ravitrona) caputserpentis: Schilder & Schilder, 1971: 65.

Description

Shell (Figs. 24, 25; color plate Figs. 43, 63, 64). Characterized by a strong peripheral keel, producing an almost semispherical form. More details in Wilson & Gillett (1972: 54).

Head-foot (Fig. 263). Characters somewhat similar to those of *M. zebra*, except for anterior projection of head amply connected to columellar muscle.

Mantle organs (Figs. 264-266). Similar features to those of *M. zebra*. Distinctive or notable attributes following. Mantle lobes covered by sparse, randomly located papillae (Color plate Figs. 14, 15, 94-98); papillae simple and small in region close to border, tip rounded, gradually more complex papillae appear towards internal, some simpler and smaller, with apex bifid or with 3 or 4 branches; others (close to inner region) tall and broad, with several (5-10) apical and sub-apical narrow branches, each branch short, with tip rounded (Fig. 265; color plate Fig. 97). Siphon tall, with papillate edge (color plate Figs. 95, 96); central (anterior) papillae small, posterior papillae gradually taller and sometimes bifid. Anal siphon



Figs. 263-271, *Ravitrona caputserpentis* anatomy: **263,** head-foot, male, lateral-right view; **264,** pallial cavity roof and visceral mass, ventral view; **265,** right mantle lobe, outer view, detail of its middle region; **266,** pallial roof, transversal section in middle level of posterior osphradium branch; **267,** kidney and pericardium region, ventral view, both opened longitudinally, some gill filaments on auricle extracted; **268,** odontophore, ventral view, radular ribbon and subradular cartilage extracted, m5 deflected; **269,** dorsal wall of buccal mass and esophagus, ventral view, odontophore extracted, esophagus opened longitudinally; **270,** foregut, lateral-right view; **271,** odontophore, left half, ventral view, detail of its anterior region with cartilage deflected posteriorly. Scales = 1 mm, except 263-264 = 5 mm.

low. Osphradium at some distance from gill. Osphradium filaments low, with rounded tip. Gill strongly arched, its filaments low, curved towards right, tip rounded. Afferent gill vessel broad. Hypobranchial gland cut by transversal septa from mantle. More details in Kay (1960a, fig. 6A).

Circulatory and excretory systems (Fig. 267). Both with similar attributes as those of *M.*

zebra, remarkable features following. Auricle connection with ctenidial vein at some distance from gill posterior end, running narrowly dorsal to gill. Anterior surface of auricle attached to adjacent region of pericardium. Nephridial gland narrow, section triangular, edges entire wall between kidney and pericardium, without apparent connection with any lobe. Renal lobe single, its posterior region narrow, section triangular, compressed by intestine and nephridial gland (not attached to them); suddenly becoming broad close to nephrostome, surrounding pericardium; a pair of folds appear at right from nephrostome protecting it; towards right of renal lobe surrounding intestine, becoming attached to it initially in its anterior surface and, after, its anterior, ventral and posterior surfaces in a short distance before anterior kidney extremity. Nephrostome a broad slit close to pericardium (Figs. 264, 267).

Digestive system (Figs. 268-271). Foregut organization somewhat similar to that of *M. zebra*, distinctive characters following. Buccal mass dorsal folds with shorter furrowed portion, having 3-5 oblique furrows. Aperture of salivary glands anterior to furrowed portion. Odontophore muscles: **m2** pair narrow and thin, inserted close to buccal ganglion and also in middle esophagus; **m3** and **m7** absent; **m5** thinner, originated in m4; **m6** broad (about half of cartilages length); **m6a** not connected to adjacent dorsal platform; **m12** as 2-3 narrow pairs, originating in odontophore cartilages close to and by side of m6, running towards dorsal and external, inserting in m4 inner surface. Radular teeth (Fig. 80): with similar features of preceding cypraeids, rachidian slightly narrow; rachidian, lateral and marginal teeth tricuspid and similar with each other, all teeth differing in being less curved and broader towards median. Anterior and middle esophagus with tall pair of folds, covering esophageal gland aperture (Fig. 269). Posterior esophagus with 5-7 narrow and low longitudinal folds, being 2 of them continuation from those pair of middle esophagus. Stomach as described by Kay (1960a, fig. 4), anterior duct to digestive gland with bilateral pairs of small and thin septa. More details in Kay (1960a, figs. 2-5).

Genital system. **Male**. Organization of visceral and pallial structures similar to that of *M. zebra*, with following distinctive or notable characters (Fig. 264). Testis small, color pale-beige, fills first visceral whorls. Seminal vesicle very narrow (slightly broader anteriorly) located far from anterior-left end of visceral mass; its perpendicular portion (running in columellar surface) presenting some coils in posterior region. Pallial vas deferens opens in anterior extremity of triangular sinus, without prostate gland. Penis somewhat narrow, tip almost pointed (Fig. 263). Other details in Kay (1960a, fig. 6).

Female. No female examined, but a good female description is found in Kay (1960a: 187-189, fig 7), showing a large seminal receptacle located posterior, bearing 3 distal branches.

Measurements of shells (in mm). 1: 27.8 by 21.5; 2: 24.0 by 18.2.

Distribution. Central and West Pacific, Indian Oceans.

Habitat. Intertidal reef.

Material Examined. UNITED STATES OF AMERICA; **Hawaii**; Oahu, Diamond Head, MZSP 30678, 2♂ (F. Moretzsohn col. viii/1996, sta.66). JAPAN; MZSP 8220, 3 shells (Stearns col., 1896).

Genus *Muracypraea* Woodring, 1957

(type species: *C. mus* Linné)

Muracypraea mus (Linné, 1758)

(Figs 26-27)

(Color plate Fig. 44)

Synonymy see Burgess (1985: 168). Complement:

Cypraea mus: Abbott, 1954: 181 (pl. 6, fig. e); Taylor & Walls, 1975: 116 (figs.); Abbott & Dance, 1983: 94 (fig.); Burgess, 1985: 168 (fig.); Sutty, 1986: 44 (fig.).

Siphocypraea mus mus: Lorenz Jr. & Hubert, 1993: 39 (pl. 1, figs 5-8, 12, 17).

Muracypraea mus: Bradner & Kay, 1996: 90 (fig. 137).

N.B.: a single female of this species was studies, but, because of fixation problem, it was not good enough for anatomical study. Remarkably, it was possible to note the mantle lobes uniformly covered by low, broad, simple papillae.

Material examined. VENEZUELA; **Falcon**; Judibana, AMNH 181455, 1♀ .

Genus *Pseudozonaria* Schilder, 1927

(Type species: *C. arabicula* Linné)

Pseudozonaria arabicula (Linné, 1758)

(Figs 28, 29, 272-277)

(Color plate Figs. 61, 62)

Zonaria (Zonaria) arabicula: Cate, 1969: 115 (pl. 13, fig. 15).

Cypraea (Pseudozonaria) arabicula: Abbott, 1974: 150 (pl. 5, fig. 1649); Oliveira *et al*., 1981: 154.

Cypraea arabicula: Taylor & Walls, 1975: 166 (figs.); Donohue, 1977: 160; Abbott & Dance, 1983: 88 (fig.); Trew, 1987b: 2.

Mauritia arabicula: Bradner & Kay, 1996: 72 (fig. 108a-d).

Description

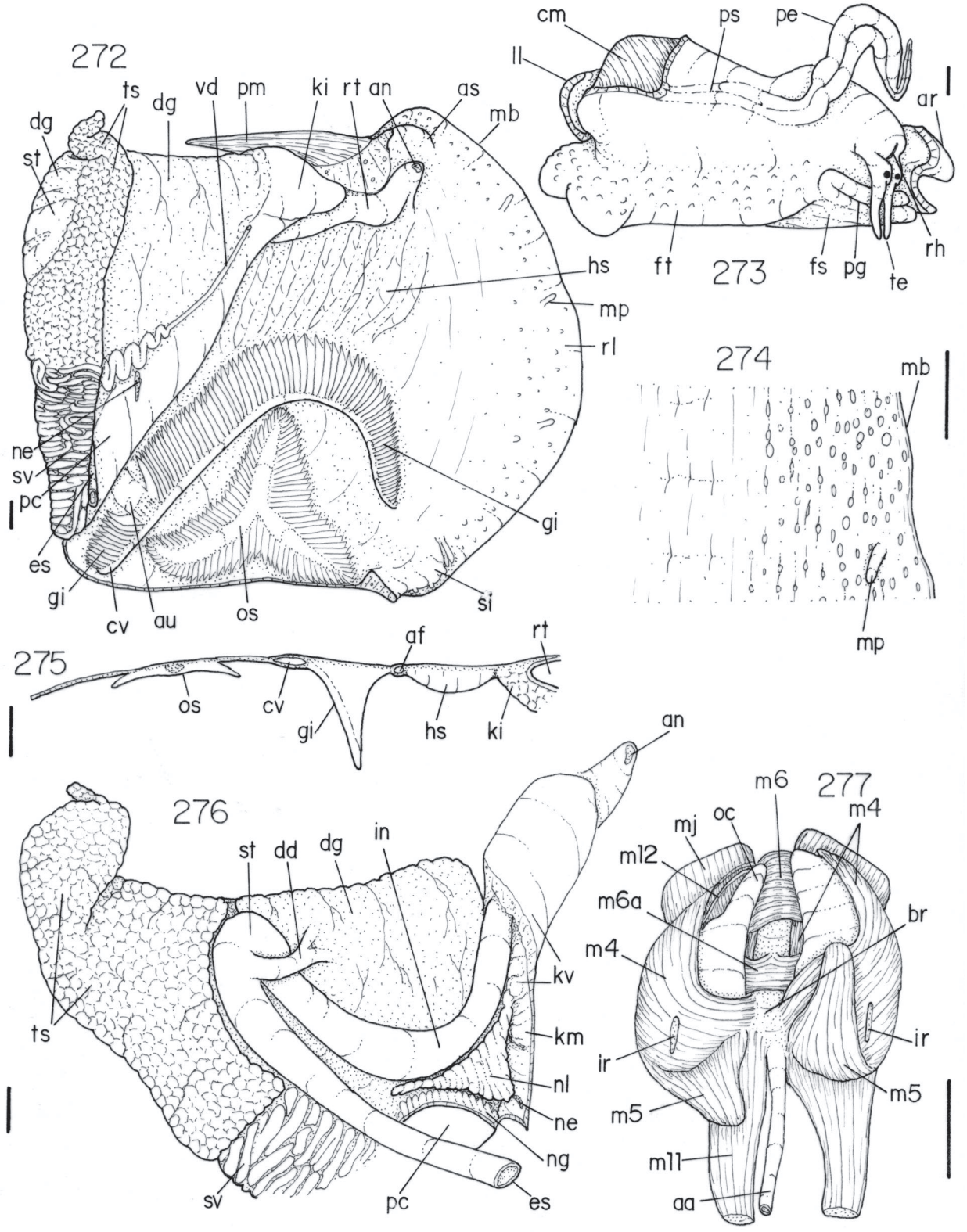
Shell (Figs. 28, 29, color plate Figs. 61, 62). Of small size, with a weal keel in periphery, aperture surrounded by narrow and many tooth. Other details in Cate (1969: 115).

Head-foot (Fig. 273). Characters similar to those of *M zebra*, except for shorter outline and by dorsal surface of foot covered by several papillae, in an arrangement somewhat similar to that of mantle lobes.

Mantle organs (Figs. 272, 274, 275). Organization somewhat similar to that of *M. zebra*, remarkable features following. Mantle lobes uniformly covered by small, low and slightly spherical papillae; about 4-5 larger papilla in each lobe present, very spaced from each other, generally located in middle position between border and inner edges. Siphon low, edge papillate, outer papillae taller and simple. Anal siphon also low. Osphradium with slightly narrow branches, at some distance from gill. Osphradium filaments low, tip pointed, turned externally. Gill arched; filaments tall, triangular, pointed, both edges concave. Hypobranchial gland with transversal pallial septa.

Circulatory and excretory systems (Fig. 276). Both with similar characters to those of *M. zebra*. Distinctive or notable features following. Auricle connection with ctenidial vein relatively far from its posterior end. Auricle portion running dorsal to gill narrow. Kidney long, its chamber edged entire intestine loop in visceral mass, posterior end close to stomach. Nephridial gland narrow, section triangular, edging entire wall between kidney and pericardium, no apparent connection with any renal lobes. Renal lobe posterior end very narrow, located dorsal, by side of nephridial gland, compressed by it and adjacent intestine. Renal lobe gradually increases up to nephrostome level, covered by a mosaic of irregular, transversal folds. Renal lobe narrowing gradually anterior to nephrostome, after crossing towards ventral, running up to anterior renal end with long portion attached to intestine (about 1/3 of its length).

Digestive system (Figs. 276, 277). Foregut characters similar to those of *M. zebra*, with following remarkable features. Dorsal folds wit about 8 oblique, deep furrows. Aperture of salivary glands in second or third furrow. Odontophore muscles (Fig. 277): **m2** pair thick, running attached to anterior esophagus; **m5** relatively thin and short; **m6a** connected to adjacent dorsal platform; **m7** absent; **m11** pair with muscular fibers surrounding dorsal to radular sac; **m12** pair present, originating close to m6, running towards external and posterior, inserting in inner surface of m4 close to mj. Radular sac about 3 times longer than odontophore. Radular teeth as in Bradner & Kay (1996: 74, fig. 108). Stomach (Fig. 276) with single duct to digestive gland just between esophageal insertion and intestinal origin. This duct broad, without inner septa. Stomach a simple, broad curve. Posterior lobe of digestive gland absent. Intestine



Figs. 272-277, *Pseudozonaria arabicula* anatomy: **272,** pallial cavity roof and visceral mass, male, ventral view; **273,** head-foot, male, lateral-right view; **274,** right mantle lobe, outer view, detail of its middle region; **275,** pallial roof, transversal section in middle level of posterior osphradium branch; **276,** visceral mass, male, ventral view, digestive tubes shown as in situ, kidney in part opened longitudinally, heart extracted, anterior-left region not shown; **277,** odontophore, ventral view, radula extracted, both cartilages deflected, right cartilage (left in fig.) still deflected posteriorly, right m5 also deflected. Scales = 1 mm.

broad, with a single, U-shaped loop.

Genital system. **Male** (Figs. 272, 273). Organization of visceral and pallial male structures somewhat similar to those of *M. zebra*, with following remarks (Fig. 272). Testis greenish beige and very large, occupies most of visceral mass first whorls up to esophagus and stomach (no digestive gland posterior to stomach). Testis acina convolute. Seminal vesicle also very voluminous, occupies a broad and long area of anterior-left side of visceral mass up to connection to head-foot. Perpendicular portion of vas deferens, running between digestive gland and kidney, possessing coiled seminal vesicle up to its middle level. Prostate absent. Aperture of vas deferens just after triangular sinus. Pallial sperm furrow edged by thick and broad folds (Fig. 273). Penis broad in basal and middle thirds, distal third slender as a papilla. Penis furrow running entire penis length, including apical papilla.

Female. All examined females are not well preserved and with most of genital structures destroyed, only massive ovary (of similar size than testis of males) and vaginal tube running in pallial cavity floor observed.

Measurements of shells (in mm). MZSP 32147 ♂ 1: 23.0 by 15.0; ♂ 3: 20.1 by 12.7; ♀ 5: 21.8 by 14.0.

Distribution. From Mexico to North Peru.

Habitat. Under rocks, intertidal to 10 m depth.

Material examined. ECUADOR; Isla de La Plata, MZSP 32147, 3♂ , 4♀ (Coltro col. ix/1999).

Pseudozonaria robertsi (Hidalgo, 1906)

(Figs. 30, 31, 278-287)

(Color plate Figs. 42, 73, 74)

Zonaria robertsi: Cate, 1969: 114 (pl. 13, fig. 13); Bradner & Kay, 1996: 72 (fig. 125a-d).
Cypraea (Pseudozonaria) robertsi: Abbott, 1974: 150; Oliveira *et al*., 1981: 154.
Cypraea robertsi: Taylor & Walls, 1975: 154 (figs.); Donohue, 1977: 160; Abbott & Dance, 1983: 91 (fig.); Trew, 1987b: 17.

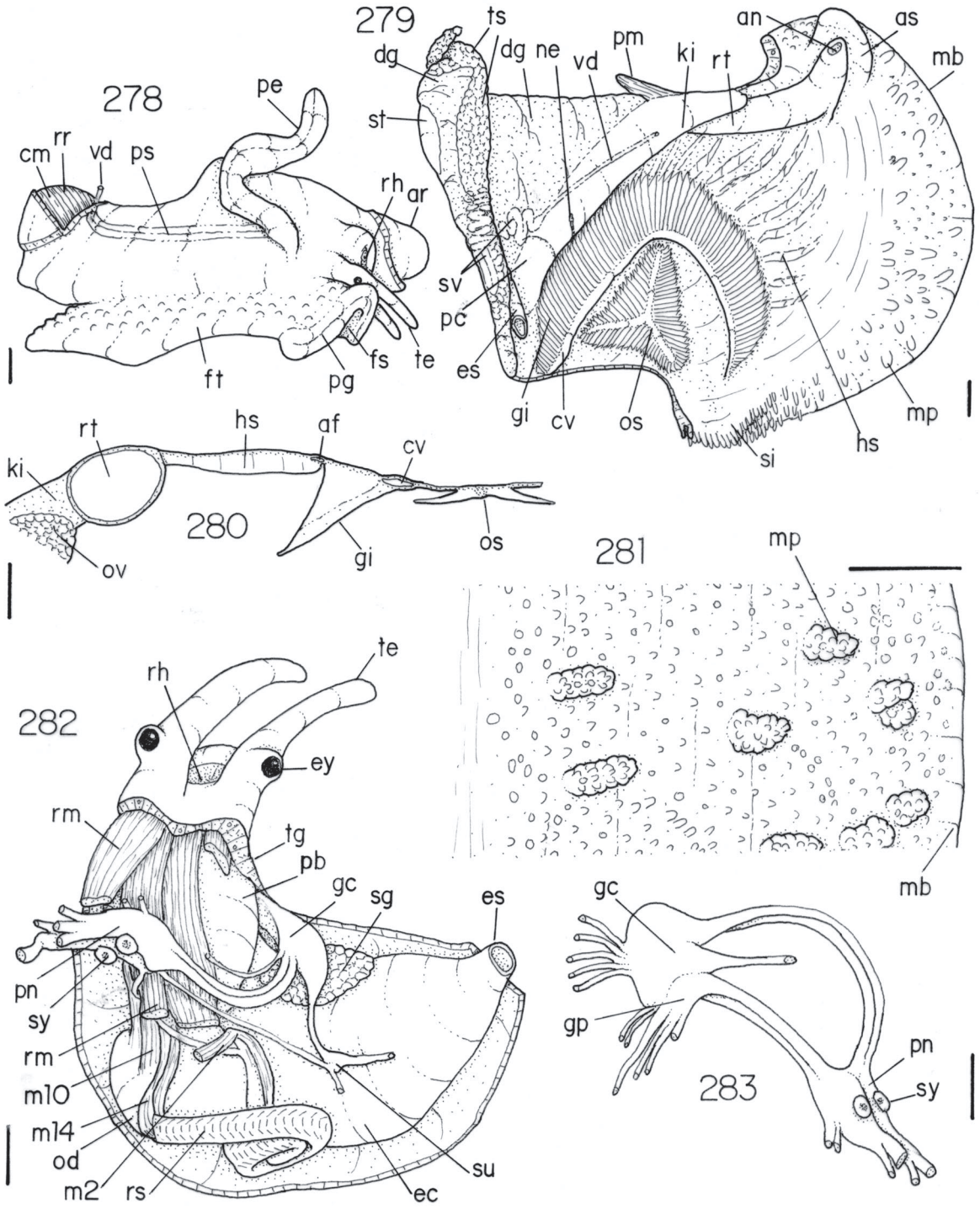
Description

Shell (Figs. 30, 31; color plate Figs. 42, 73, 74). Characters similar to those of *P. arabicula*, differs mainly in having fewer teeth in aperture and in lacking a developed furrow by side of siphon. Other details in Cate (1969: 114).

Head-foot (Figs. 278, 282)**.** Similar features as those of *P. arabicula*, including dorsal surface of foot covered uniformly by low papillae. Differs mainly in being longer antero-posteriorly.

Mantle organs (Figs. 279-281). Close morphological attributes to those of *P. arabicula*, distinctive or notable features following. Mantle lobes also possessing small, simple, and low papillae uniformly distributed; differs by presence of several tall papillae, each one composed by several others sub-papillae of similar size as those of remainder lobe surface; these composed papillae somewhat randomly distributed (Fig. 281). Siphon low, edges papillate. Lateral regions of siphon marked by a high concentration of tall papillae, most of them simple (not-composed). Anal siphon also low. Osphradium somewhat triangular, its posterior border close to gill. Osphradium filaments with a very long, pointed tip turned externally. Gill strongly arched. Gill filaments slightly broad, slightly turned towards right, edges almost straight, tip pointed, rod broad (Fig. 280). Hypobranchial gland with transversal pallial septa; these septa edges up to anterior gill region.

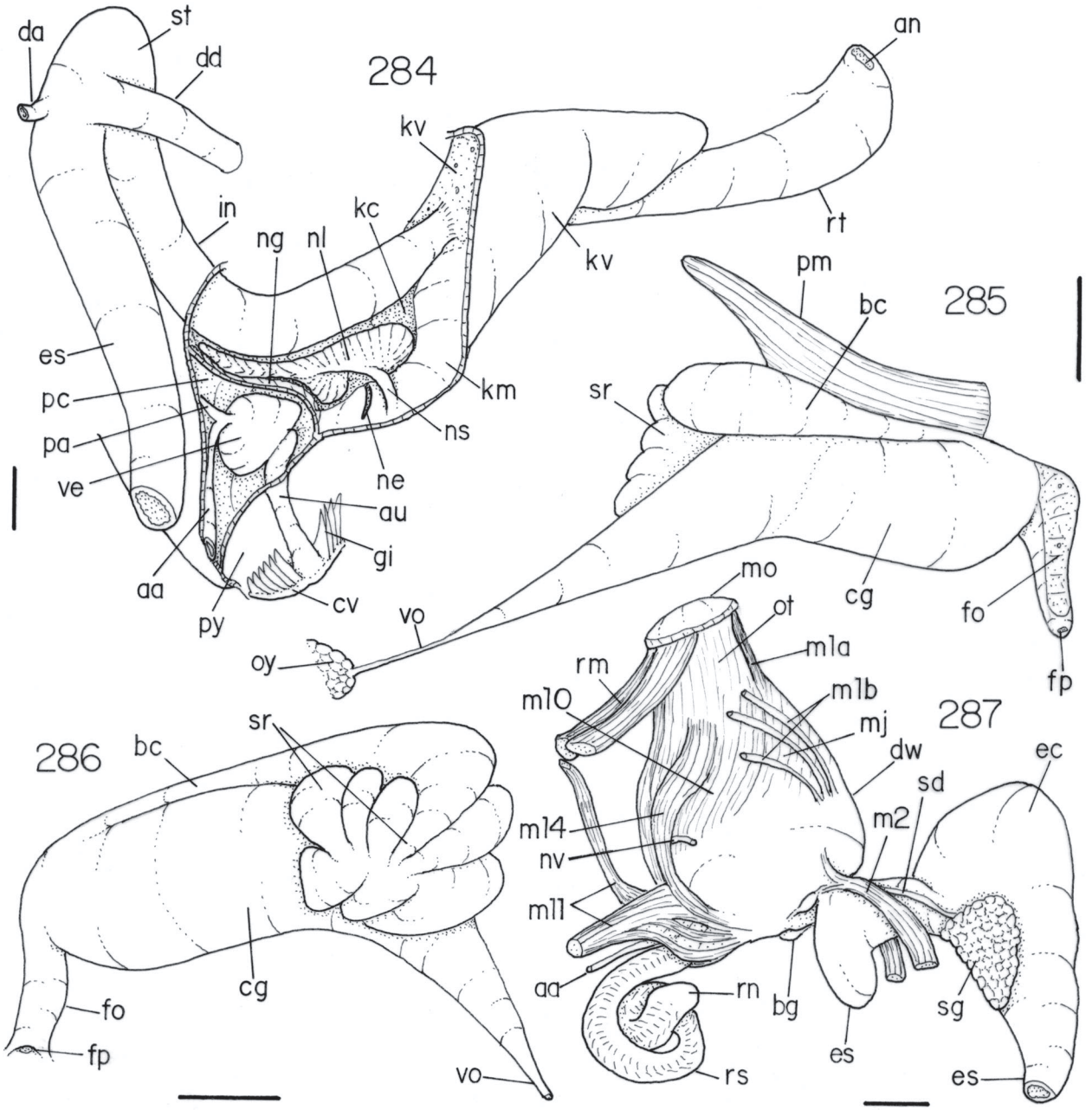
Circulatory and excretory systems (Fig. 284). Both presenting features similar to those of preceding cypraeids, with following remarkable characters. Auricle portion dorsal to gill long and narrow, connected to ctenidial vein at some distance from its posterior end. Auricle portion inside main pericardium chamber not attached to anterior surface of this chamber. Kidney somewhat short, its posterior end stays in posterior third level of visceral loop of intestine; its anterior end at some



Figs. 278-283, *Pseudozonaria robertsi* anatomy: **278,** head-foot, male, lateral-right view; **279,** pallial cavity roof and visceral mass, male, ventral view; **280,** pallial roof, transversal section in middle level of posterior osphradium branch; **281,** right mantle lobe, outer view, detail of its middle region; **282,** head and haemocoel, ventral view, foot and columellar muscle removed; **283,** central nervous system, lateral-left view. Scales = 1 mm.

distance from anus. Nephridial gland narrow and thin, section triangular, restricted to wall between kidney and pericardium, without connections to renal lobes. Posterior renal lobe compressed between nephridial gland and adjacent intestine portion; posterior half narrow, gradually increases towards anterior; a central longitudinal vessel present, inserted at right from nephrostome. Left side of posterior lobe shorter than its right side. Ventral-anterior lobe solid, of uniform surface; its posterior half flat, attached only to membrane between kidney and pallial cavities; its anterior half also attached to dorsal renal wall, surrounding and attached to local intestine. Nephrostome close to pericardium (Fig. 279).

Digestive system (Figs. 282, 284, 287). Characters similar to those of *M. zebra*, with following



Figs. 284-287, *Pseudozonaria robertsi* anatomy: **284,** middle and distal digestive tubes seen as in situ, and kidney-pericardium region, both opened longitudinally (kidney only partially opened), ventral view, some gill filaments on auricle removed; **285,** pallial oviduct and some adjacent structures, ventral view; **286,** same, dorsal view; **287,** foregut, lateral-left view. Scales = 1 mm.

distinctive or notable features. Dorsal folds of buccal mass with portion of oblique furrows similar to preceding species. Aperture of salivary glands anterior to furrowed portion of dorsal folds, located in their central region. Odontophore muscles (Fig. 287): **m1b**, in several, thin, narrow pairs, **m11** pair with portion surrounding dorsally radular sac with muscular tissue; their origin jointed with **mr** origin, passing through nerve ring. Remainder of odontophore features closely similar to those described for *P. arabicula*. Radula with about double of odontophore length if straightened. Radular teeth as in Bradner & Kay (1996: 72, fig. 125). Anterior esophagus with a low diverticle just posterior to buccal mass. Salivary gland small, cluster

around middle esophagus; their ducts very narrow, running attached to anterior esophagus lateral surface, penetrate in dorsal wall of buccal mass, open as described above. Inner surface of anterior and middle esophagus similar to those of *M arabicula*. Posterior esophagus with low, longitudinal, narrow folds. Between esophagus and stomach a narrow duct to posterior lobe of digestive gland. Duct to anterior lobe of digestive gland broad, its inner surface smooth, without septa. Digestive gland lobes as those of *M. zebra*, color greenish beige. Intestine broad, weakly sigmoid. Anus siphoned, located in base of anal siphon.

Genital system. **Male**. Organization somewhat similar to those of *M. zebra*, with following remarks (Fig. 279). Testis narrow, occupying first whorls, color strong orange, iridescent. Seminal vesicle as continuation of testis, intensely coiled, posteriorly narrow and anteriorly broader, its coils finish at some distance of anterior-left extremity of visceral mass. Seminal vesicle still present, coiled, along about 1/3 of perpendicular portion of vas deferens running ventral to anterior lobe of digestive gland; after seminal vesicle becomes a very narrow duct, opens in anterior-left region of triangular sinus without prostate. From this aperture to penis base a long, thick edged, narrow furrow. Penis (Fig. 278) slightly small, width somewhat uniform along its length (except for a broader sub-terminal region). Penis tip rounded. Penis sperm groove running along central region of its ventral surface.

Female (Figs. 285, 286). Visceral and pallial structures attributes similar to those of preceding cypraeids, distinctive or notable features following. Ovary similar located, but larger than testis of males, pale orange in color. Ovary present in region running ventral to anterior lobe of digestive gland, after short distance only a very narrow visceral oviduct present. Visceral oviduct running narrow for a distance, gradually becoming broad. Albumen gland inside this broader region of oviduct, with thin, whitish walls. Capsule gland with very thick, beige walls, appearing suddenly anterior to albumen gland, amply connected to it. Bursa copulatrix inserted in anterior-right region of capsule gland, running towards posterior edging remainder pallial oviduct, its anterior portion very narrow, gradually increases becoming an elliptical chamber with thick-muscular walls up to middle level of albumen gland. In this region, bursa suddenly curved, becoming gradually narrow and with thin walls. Another ample, multi-lobed chamber inserted in final portion of bursa, walls thin and transparent, located on dorsal-posterior region of pallial oviduct. Vaginal tube just anterior to capsule gland, running obliquely attached to pallial floor a considerable distance. Genital pore a small aperture in vaginal tube end.

Central nervous system (Figs. 282, 283). Similar to those of preceding cypraeids, cerebral and pleural pairs of ganglia forming a single mass. Pedal ganglia large, long towards anterior, somewhat far from remainder ganglia, united with them by long pairs of connectives being dorsal-right pair shorter. Statocysts with single, large statolith. Pair of pedal ganglia running through pedal musculature towards anterior by a considerable distance, after bifurcates.

Measurements of shells (in mm). MZSP 32148 ♂ , 20.1 by 12.7; ♀ , 20.0 by 13.0

Distribution. From Panama to Ecuador.

Habitat. Subtidal rocks.

Material examined. ECUADOR; Isla de La Plata, MZSP 32148, 1♂ , 2♀ (Coltro col., ix/1999).

Family Ovulidae

Genus *Cyphoma* Röding, 1798

(Type species *Bulla gibbosa* Linné, 1758)

Cyphoma signatum Pilsbry & McGinty, 1939

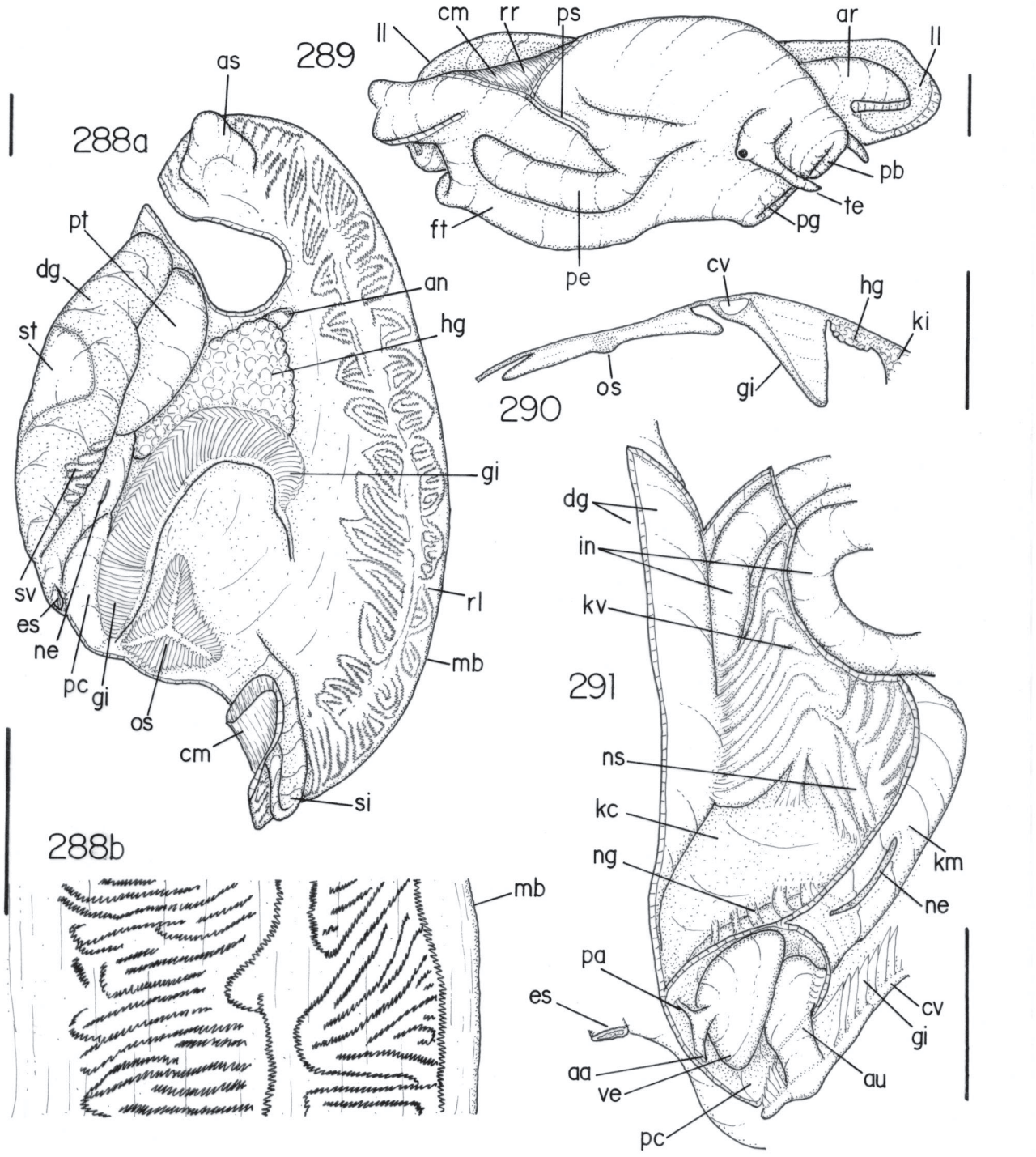
(Figs. 32, 33, 81, 82, 288-306)

(Color plate Figs. 22, 23, 35)

Cyphoma signatum Pilsbry & McGinty, 1939: 3 (pl. 1, figs. 1, 1a, 2, 2a, 9, 10) (loc: South of Key Vaca); Abbott, 1954: 184 (pl. 4); Warmke & Abbott, 1962: 93 (pl. 16, fig. g); Ghiselin & Wilson, 1966: 133-

138; Matthews & Rios, 1967: 96; Kempf & Matthews, 1969: 92; Rios, 1970: 62; Cate, 1973: 68 (fig. 152); Abbott, 1974: 153 (fig. 1666); Humfrey, 1975: 108 (pl. 9, figs. 6, 6a); Rios, 1975: 73 (pl. 20, fig. 298); Oliveira *et al*., 1981: 139; Abbott & Dance, 1983: 100 (fig.); Domaneschi & Penna-Neme, 1984: 10 (figs 2, 6); Rios, 1985: 66 (pl. 23, fig. 291); Trew, 1987b: 26; Jong & Coomans, 1988: 65; Leal, 1991: 97; Rios, 1994: 75 (pl.25, fig. 287); Merlano & Hegedus, 1994:167-168 (pl. 52, fig. 620).

Cyphoma signata: Schilder & Schilder, 1971: 76.



Figs. 288-292, *Cyphoma signatum* anatomy: **288a,** pallial cavity roof and visceral mass, male, ventral view; **288b,** right mantle lobe, outer view, detail of its middle region; **289,** head-foot, male, lateral-right view; **290,** pallial roof, transversal section in middle level of posterior osphradium branch; **291,** kidney and pericardium region, both opened longitudinally, ventral view, some gill filaments on auricle removed. Scales = 2 mm.

Cyphoma macumba: Hetzel, 1994: 124 (fig.); Rocha *et al*., 1994:149-160 (figs. 2, 4, 7, 8) [non Petuch, 1979(?)] (see following discussion).

Description

Shell (Figs. 32, 33; color plate Fig. 35). Highly involute (no trace of apex), long, slightly elliptical. Outer and inner lip tick, without teeth. Color white, yellowish of pale brown. Other details in Cate (1973: 68).

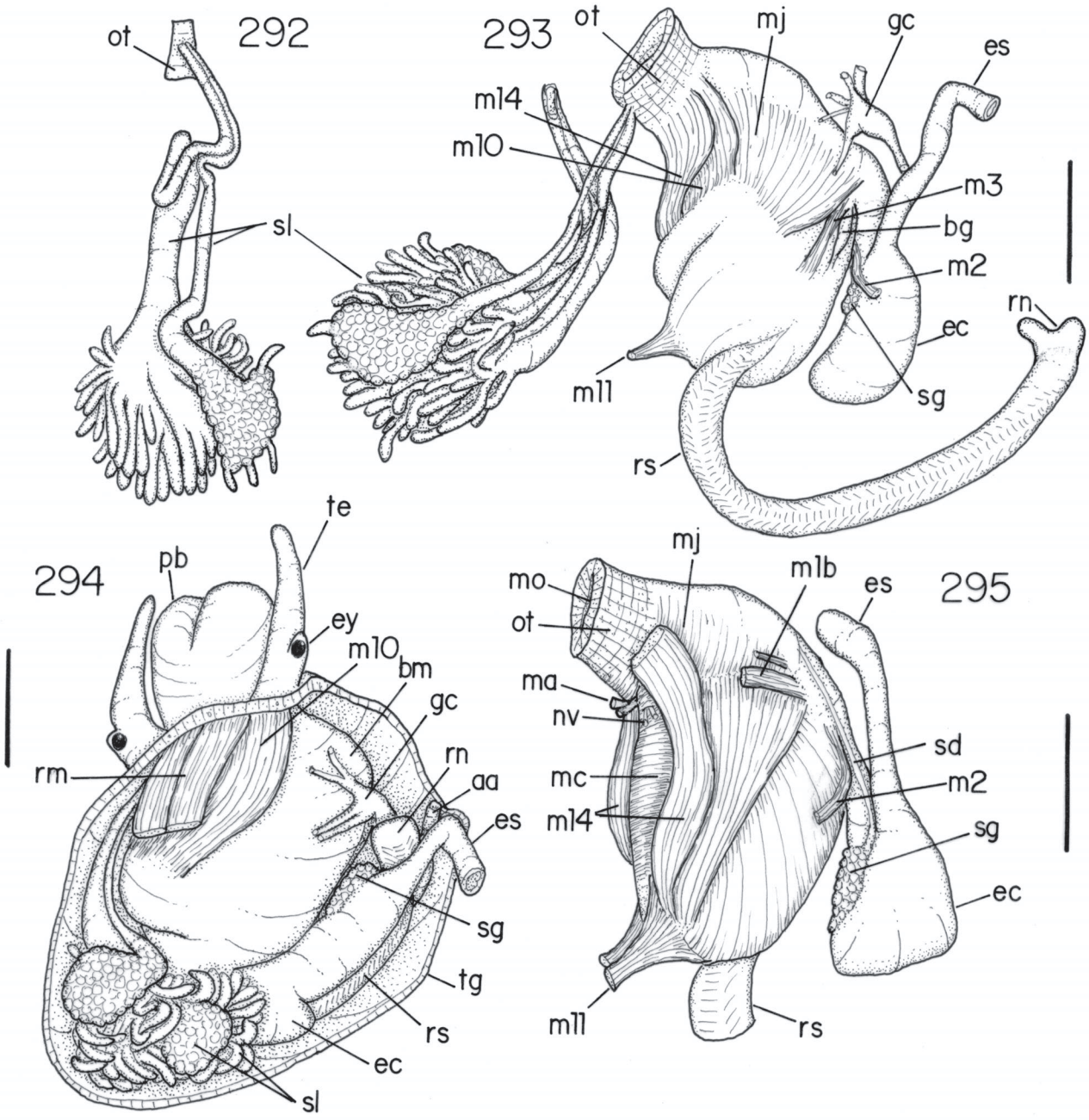
Head-foot (Figs. 289, 294). Characters somewhat similar to those described for *M. zebra*, distinctive or notable features following. Color pale cream, with dark brown, transversal bands in exposed areas, particularly on dorsal foot surface; some isolated bands present surrounding snout anterior margin and longitudinal in tentacles. Snout-proboscis broad and short. Tentacles stubby, laterally located, basal half clearly broader than distal half. Eyes dark, located on small ommatophores on middle-outer side of tentacles. Foot long antero-posteriorly and narrow laterally. Anterior furrow of pedal glands with thick margins, restricted to anterior edge. Dorsal surface of pedal gland furrow (propodium) with well-developed folds perpendicular to anterior edge; each fold slightly tall, separated from each other, with a dark brown, longitudinal band on its distal surface. Anterior muscular projection long. A similar projection, but narrower, present in opposite side, towards posterior. Columellar muscle of about ½ whorl, involute (almost symmetrical). Triangular sinus, from which in general gonoducts open, more anteriorized, located just posterior to middle level of head-foot longitudinal axis.

Mantle organs (Figs. 288, 291). Left and right mantle lobes as large as those of cypraeids, covering most of shell when extended. Color cream, with a mosaic of dark brown transversal bands, especially organized as shown in Fig. 288b and color plate Figs. 22, 23. Papillae absent. Siphon large, separated from mantle edge, connected to left head surface, smooth borders (without papillae). Anal siphon slightly smaller than incurrent siphon and in opposite side. Pallial organs (Fig. 288a) also similarly organized as those of *M. zebra*. Pallial cavity slightly shallow (about 1 whorl) and triangular. Osphradium proportionally small, located far from siphon and from gill. Osphradium form similar to that of cypraeids, with 3 bipectinate branches. Osphradium filaments with detached, rounded tip. Gill long and curved. Ctenidial vein of uniform width along its length, with anterior portion projected beyond gill filaments. Gill filaments slightly short, apex rounded, in general central or slightly turned to right (Fig. 290). Hypobranchial gland white, thick, transversal folded, more developed in median level of gill right side. Intestine possesses some coils in right-posterior region of pallial cavity described below.

Visceral mass (Figs. 288a, 303). Similar organization to that of cypraeids, except for being highly involute, i.e., each whorl covers entirely precedent whorl. Precedent whorls slightly dislocated to right.

Circulatory and excretory systems (Fig. 291). Heart and pericardium characters similar to those described for *M. zebra*, inclusive narrow part of auricle running dorsal to posterior gill region. Auricle inserting sub-terminally in ctenidial vein. Auricle presents its anterior surface (at right from its long portion) connected to anterior inner surface of pericardium. Kidney also slightly similar in characters to those of cypraeids. Nephridial gland very smaller, with some transversal glandular folds in wall between kidney and pericardium. Nephridial annex lobe absent. Ventral lobe of kidney large, section somewhat triangular, color pale cream, almost entirely detached from intestine (only a narrow connection in middle-posterior region of this lobe) thicker in its middle and anterior region, where attaches to membrane between kidney and pallial cavity. A special vessel of anterior region of ventral renal lobe inserts at right and ventral to nephrostome (probably homologue to that vessel of accessory lobe of nephridial gland).

Digestive system (Figs. 292-303). Proboscis and its ventral pair of retractor muscles with similar fashion to those of cypraeids (Figs. 289, 294). Two pairs of glands of oral tube (snout gland), forming a large mass of several long acina, located in posterior-left region of haemocoel (Fig. 294); all acina of each gland irregularly converge to a slender chamber which gradually narrow towards anterior as a duct; running slightly sinuously contouring at left of buccal mass (Figs. 292, 293); insertion of all 4 ducts side-by-side in ventral region of oral tube, close to median line and close to mouth. A pair of oral tube gland of larger size and with acina hollow, transparent; other pair smaller and with acina solid-glandular,



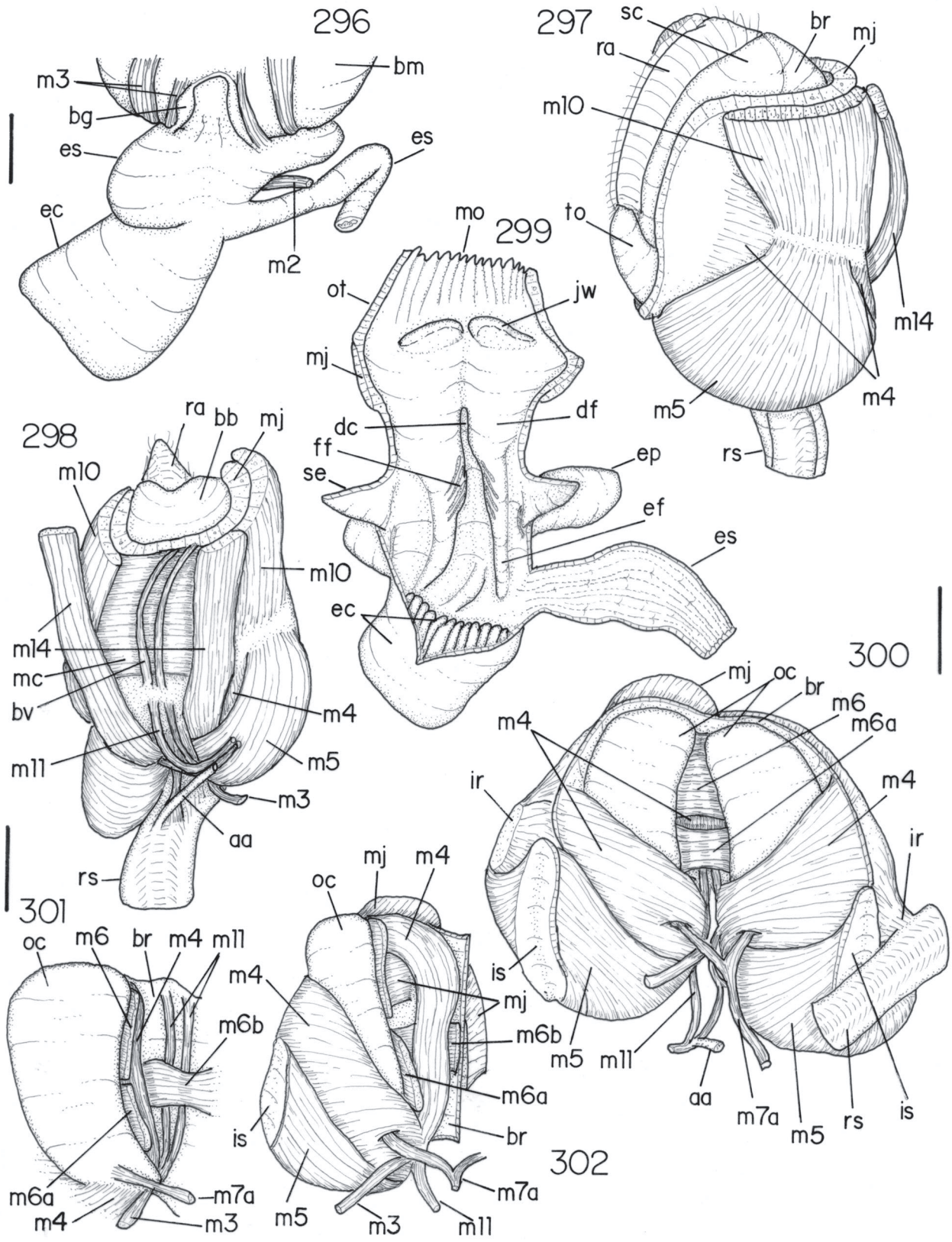
Figs. 292-295, *Cyphoma signatum* anatomy: **292,** left snout (or oral tube) glands isolated; **293,** foregut, lateral-left view; **294,** head and haemocoel, ventral view, foot and columellar muscle removed, proboscis extended; **295,** odontophore and anterior esophagus, lateral-left view. Scales = 2 mm.

whitish. Buccal mass characters similar to those of *M. zebra*, distinctive or notable features following. Pair of jaw plates present (Fig. 299), each one slightly elliptical, thin, close to median line. Pair of dorsal folds broad, clearer at some distance posterior to jaws. Dorsal chamber between both dorsal folds shallow. Furrowed part of dorsal folds short, with oblique, deep furrows (Fig. 299). Aperture of salivary glands inside of anterior furrows of this furrowed part. Pair of nerves posterior to oral tube close to median line (Fig. 295: nv). Odontophore muscles (Figs. 293-302): **m1a** absent; **m1b** pair present; **ma**, pair of short and broad muscles, originating in ventral surface of haemocoel, running towards dorsal a short distance, penetrating just posterior to mc, inserting in mj ventral region; **m2** pair also narrow, running attached to esophagus, inserting jointed with that of proboscis retractor muscles (Fig. 293); **m3** pair very narrow, close to median line; **m6**, slightly thin and long; **m6a** just posterior to m6, not attached to subradular

membrane (Figs. 300-302); **m7** absent; **m7a,** pair of slender and long muscles, originating in posterior-median region of odontophore cartilages, running towards ventral through m4 fibers, in short distance unite with each other and penetrate within radular sac ventral surface, after another short distance inserts in radular sac like a fan (Figs. 300-302); **m10** pair slightly lateral located; **m11**, a small pair of narrow retractor muscles of odontophore, originating in ventral surface of haemocoel just posterior to odontophore, running towards dorsal and anterior, penetrating in odontophore by side of m7, inserting in posterior-median extremity of odontophore cartilages (no muscular branches surrounding radular sac, only a transparent membrane) (Fig. 295); **m12** absent; **m14** pair narrow. Radular sac about 1.5 times buccal mass length (Fig. 293). Radular nucleus broad, somewhat bifid (Fig. 293). Radular teeth (Figs. 81-82): rachidian narrow, short, central cusp very large, pointed, base broad, 2 pairs of secondary, small cusps slightly far from central cusp; lateral tooth curved, tip sharp pointed, flattened, without secondary cusps; inner and outer marginal teeth similar with each other, inner marginal narrower, outer marginal broader, with a lateral projection, marginal teeth base flattened, long and 20-30 terminal, very long, curved cusps (brush-like). Anterior esophagus with a pair of esophageal pouches as broad diverticles (Figs. 296, 299), walls thin, inner surface smooth; inner surface of anterior esophagus only with a pair of folds continuating from those of buccal mass. Middle esophagus with esophageal gland similar to those of cypraeids (Fig. 299); anterior esophagus folds finish in middle esophagus. Posterior esophagus narrow, long, inner surface with several narrow longitudinal folds. Stomach (Fig. 303) similar in characters to those of *M. zebra*, except for narrow ducts to digestive gland and by lack of inner septa in duct to anterior lobe of this gland. Intestine originating broad, running parallel to esophagus, in left renal region suddenly towards right and becomes narrow, running all along renal length up to right-posterior limit of pallial cavity. In pallial cavity (Fig. 303) intestine presents a loop towards anterior returning close to its preceding region; suddenly turns 180º running edging externally its preceding loop, becoming slightly broader. Close to anterior-right extremity of visceral mass (also close to mantle border), intestine once again turns 180º, presenting a sigmoid loop. Anus siphoned, narrow. Digestive gland of cream color, surrounding visceral digestive tubes, larger anteriorly, encroaches in pallial cavity jointed and at right of intestinal loops up to close mantle border. Distal loops of intestine full of elliptical fecal pellets compacted without any apparent especial organization.

Genital system. **Male**. Testis cream in color, lying right surface of visceral mass by about 1 whorl, finishes about 1 whorl posterior to digestive gland anterior end (Fig. 303). Vas deferens with a coiled seminal vesicle running along columella towards left (Figs. 288, 303). At some distance from anterior-left extremity of digestive gland, seminal vesicle suddenly runs perpendicular towards anterior, and as happens in most cypraeids, runs as a broad tube up to triangular sinus, forming a prostate gland (Fig. 288a). From this sinus, vas deferens still runs as a closed tube attached in floor of pallial cavity by about half of distance between this sinus and penis base, after which becomes a thick edged sperm groove (Fig. 289). Penis presenting clearly 2 regions (Figs. 289, 304): 1) basal region flattened, broad, triangular, amply connected to integument by a side like a fold; 2) distal region long, cylindrical, separated by basal region by a shallow constriction. Penis groove running in ventral surface of outer edge of basal region and in middle of distal region of penis. Penis tip with a small pointed papilla; penis groove finishes sub-terminally.

Female (Figs. 305, 306). Visceral structures characters similar to those of *M. zebra*. Very narrow visceral oviduct inserts in pallial oviduct sub-terminally, in ventral-middle side of albumen gland. Albumen gland spherical, relatively small. From albumen gland 2 anterior branches gradually begin, bursa copulatrix as right branch and capsule gland as left branch. Bursa copulatrix long and broad (about as large as capsule gland), thick glandular walled, dorso-ventrally flattened. Seminal receptacle small, straight, cylindrical and long, located along posterior surface of bursa; left extremity closed as a blind-sac; right extremity suddenly narrows and curves towards anterior, connecting with middle level of bursa posterior wall. Capsule gland broad, walls thick glandular, dorso-ventrally flattened, part connected to bursa in its posterior half. Vaginal tube running along left margin of capsule gland, thin walled; after anterior end of capsule gland laminas, vaginal tube running perpendicularly towards left by a short distance, attached to pallial floor. Genital pore small, papilla-like.



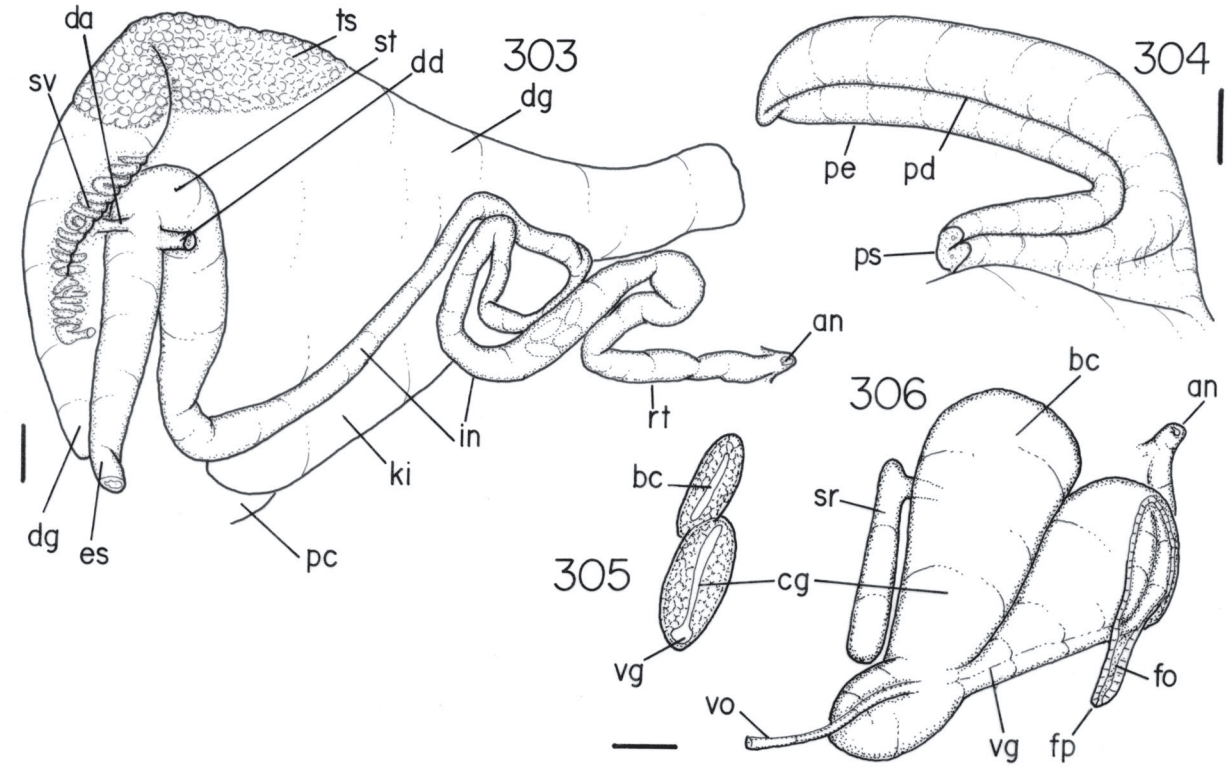
Figs. 296-302, *Cyphoma signatum* buccal mass: **296,** detail of posterior region still connected to anterior and middle esophagus, ventral view; **297,** odontophore, lateral-right view, radular sac only partially shown; **298,** same, ventral view; **299,** dorsal wall and esophagus, ventral view, odontophore removed, esophagus opened longitudinally; **300,** odontophore, ventral view, radula removed and deflected to right (partially shown), both cartilages deflected; **301,** same, right half, most muscle deflected, m6 and m6a sectioned, most m4 extracted; **302,** same with muscles still in situ. Scales = 1mm.

Measurements of shells (in mm). MZSP 19364 ♀ : 32.3 by 15.2; MZSP 29248 ♀ : 25.2 by 12.9; AMNH 177648 ♂ 38.2 by 16.6, ♀ 38.3 by 18.4.

Distribution. From Florida, USA, to São Paulo, Brazil.

Habitat. On gorgonians, from intertidal to 20 m depth.

Material examined. HAITI; **Port au Prince**, SW side of Grand Banc, 2-5 m depth, AMNH 177648, 2♂ , 2♀ (G. Goodfriend leg., 20/vi/1972). BRAZIL; **Bahia**; Salvador; MZSP 29248, 1♂ , 2♀ (L. Trinchão col.); Barra, MZSP 26964, 1♂ , 3 shells; Alcobaça, MZSP 28724, 1♂ (L.M.L. Couto col., 1977). **Espirito Santo**; Santa Cruz, MZSP 29252, 1♀ (sta. 5306, vii/1976). **Rio de Janeiro**; off Cabo Frio, 23º20'S 42º54'W, 105 m depth, MZSP 19364, 1♀ (R. V. "W. Besnard" sta. 1477, 09/iii/1971); MZSP 29249, 1 ♂ (Coltro leg., 1997); Búzios, Praia de João Fernandes, 3-4 m depth, MZSP 35051, 2♀ (of color plate Figs. 22, 23) (P.M. Costa col., ii/2002).



Figs. 303-306, *Cyphoma signatum* anatomy: **303,** visceral mass (uncoiled), middle and distal digestive tubes shown as in situ, ventral view; **304,** penis and its base, lateral view; **305,** pallial oviduct, transversal section in its middle region; **306,** same, whole ventral view, some adjacent structures also shown. Scales = 1 mm.

Cyphoma gibbosum (Linné, 1758)

(Figs. 34, 35, 83, 84, 307-319)

(Color plate Figs. 36, 37, 81, 82)

Synonymy see Cate (1973: 66). Complement:

Bulla gibbosa Linné, 1758: 726 (loc: Brasilia).

Cyphoma gibbosum: Abbott, 1954: 183 (pl. 8); Warmke & Abbott, 1962: 93 (pl. 16, fig. k); Ghiselin & Wilson, 1966: 133-138 (figs. 1-3); Rios, 1970: 62; Cather & Crovo, 1972: 111-114 (fig. 1); Cate, 1973: 66-67 (fig. 146); Bandel, 1973: 336 (fig. 2); Abbott, 1974: 152-153 (pl. 3, fig. 1664); Graaf, 1974: 312-315 (figs.); Crovo, 1974: 53-55 (figs 1-3); Humfrey, 1975: 108 (pl. 9, figs. 4, 4a); Taylor & Walls, 1975: 12, 13 (figs.); Rios, 1975: 72-73 (pl. 20, fig. 296); Birkeland & Gregory, 1975: 57-67 (figs. 38-39); Berman, 1979: 45-47 (figs.); Behety, 1980: 76-84 (figs. 1-4); Hazlett & Bach,

1982: 305-309 (fig.1); Main, 1982: 257; Abbott & Dance, 1983: 100 (figs.); Domaneschi & Penna-Neme, 1984: 10 (figs 1, 5); Bertsch, 1984a: 100-101 (fig.); 1984b: 119-122 (figs 1-6); Bandel, 1984: 84-85 (fig. 148; pl. 7, fig. 6; pl. 8, fig. 1); Gerhart, 1986: 255-263 (figs 1-4); Harvell & Suchanek, 1987: 37-44 (figs. 1-4); Trew, 1987b: 26; Jong & Coomans, 1988: 65; Lasker & Coffroth, 1988: 285-295 (figs 1-4); Lasker *et al*., 1988: 254-266 (fis 14); Haywood & Wells, 1989: 156 (fig.); Rios, 1994: 75 (pl. 25, fig. 289); Merlano & Hegedus, 1994: 167 (pl. 52, fig. 619); Abbott & Morris, 1995: 187 (pls. 9, 49).

Cyphoma gibbosa gibbosa: Schilder & Schilder, 1971: 76.

Cyphoma alleneae Cate, 1973: 67-68 (figs. 151, 151c).

Cyphoma gibbosa: Oliveira *et al*., 1981: 139.

Description

Shell (Figs. 34, 35; color plate Figs. 36, 37, 81, 82). Virtually similar to that of *C. signatum*. Other details in Cate (1973: 66-67).

Head-foot (Fig. 307). Same characters of those of preceding *C. signatum*, including transversal folds of propodium and posterior projection.

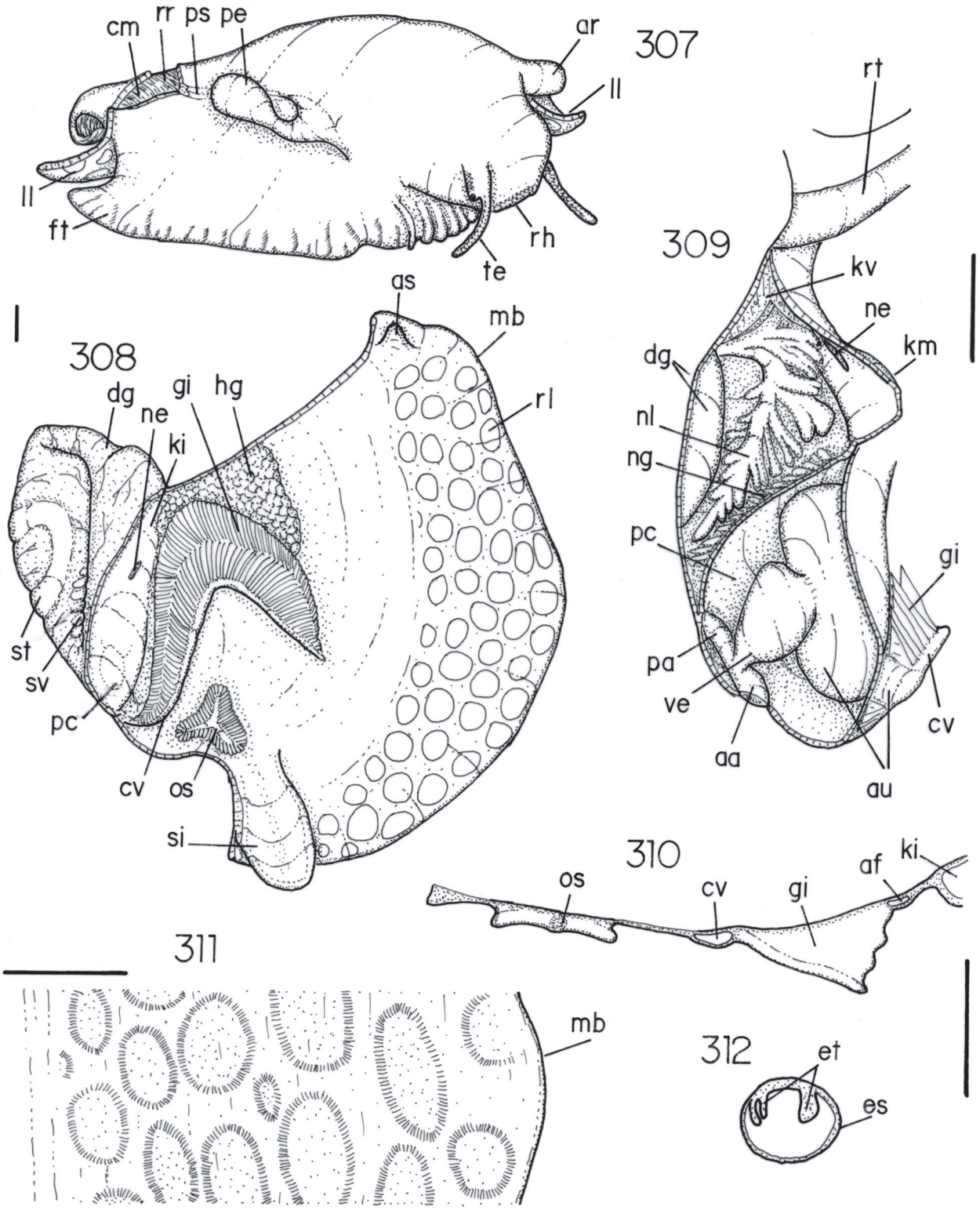
Mantle organs (Figs. 308-311). Mantle lobes characters similar to those of *C. signatum*, differing only in spots. Color clear beige with several dark-brown rings, most of uniform size (some rings smaller) (Figs. 308, 311) and close with each other. In some specimens a pale brown pigment present inside of each ring (see figures of living specimens in Haywood & Wells, 1989; Abbott & Morris, 1995: pl. 9). A dark band in margin of incurrent and anal siphons. Incurrent siphon very larger than anal siphon. Pallial organs (Figs. 308, 310) similar to those of anterior species, distinctive features following. Osphradium of smaller size, far from gill and siphon margins. Gill filaments with almost central tip (Fig. 310). Other details in Ghiselin & Wilson (1966: 133-134, fig. 1).

Circulatory and excretory systems (Fig. 309). Heart of similar attributes to those of *C. signatum*. Kidney characters also similar to those of anterior species, except for presence of a ramified accessory lobe of nephridial gland entirely separated from nephridial gland, and part connected to ventral lobe of kidney (this homology is possible due to vessel inserting at right and ventral to nephrostome).

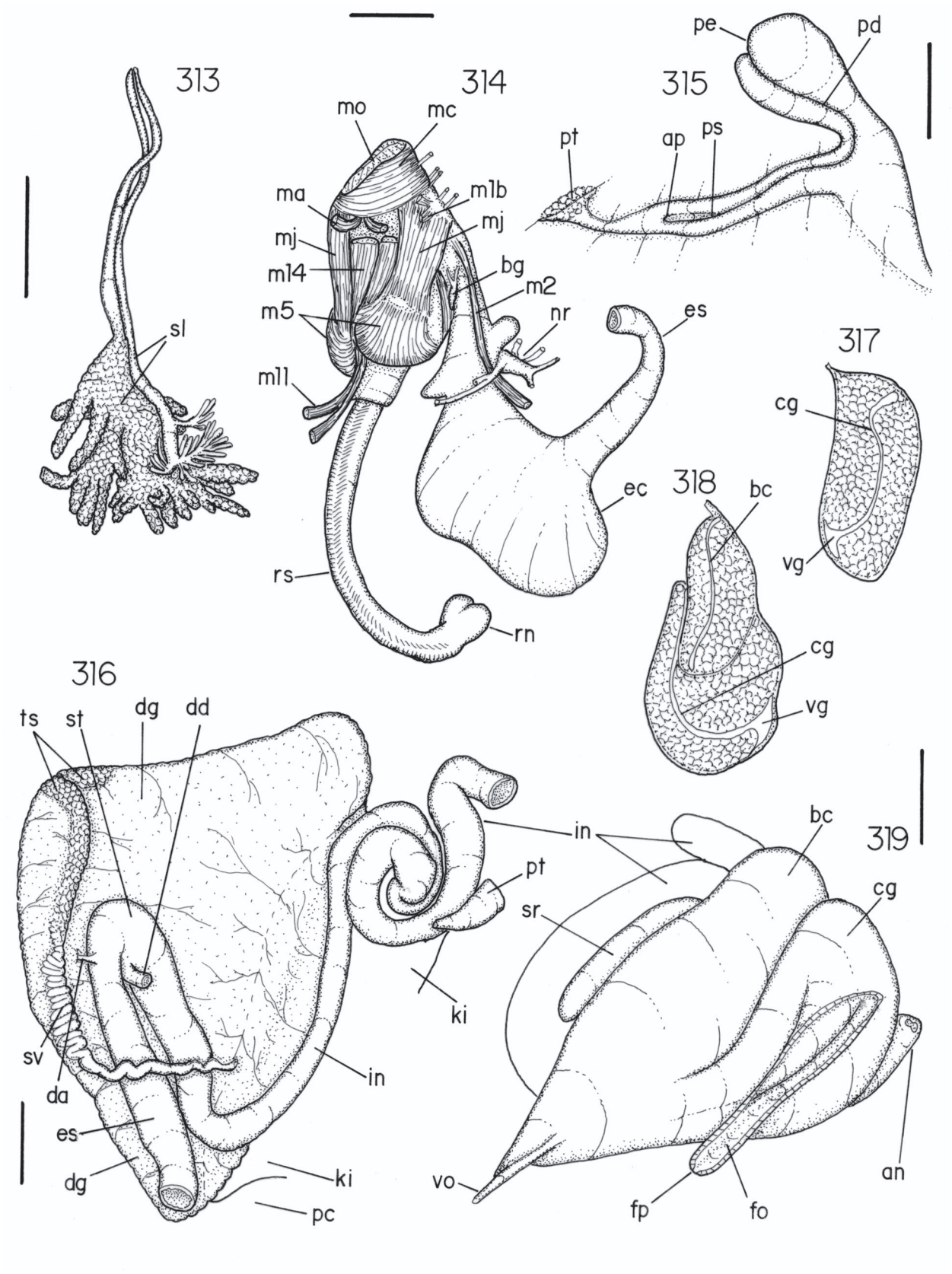
Digestive system (Figs. 312-314, 316). Glands of oral tube very similar to those of *C. signatum*, except for smaller pair of hollow gland and larger pair of solid glandular gland (Fig. 313). Buccal mass characters similar to those described for *C. signatum*, including odontophore muscles (Fig. 314). Radular sac almost twice longer than buccal mass, radular nucleus also broad and somewhat bifid (Fig. 314). Radular teeth features (Figs. 83, 84) similar to those of *C. signatum*, remarkable attributes following: rachidian and lateral slightly less curved; inner marginal tooth narrow, with about 20 long, curved cusps; outer marginal tooth very broader (about double), with about 70 cusps successively shorter towards external. Salivary glands almost reduced. Esophagus, esophageal pouches pair and esophageal gland characters similar to those of anterior species; except for anterior esophagus with left inner fold double (Fig. 312). Stomach, ducts to digestive gland and intestine also similar to those of *C. signatum*, except for broader fashion of intestinal loops after kidney, with penultimate loop running ventral to preceding loop (Fig. 316).

Genital system. **Male**. Visceral structures with similar features as those of *C. signatum*, except for coiled seminal vesicle longer (Fig. 308), present also in perpendicular portion of vas deferens towards triangular sinus. Sperm duct in pallial floor also half-closed (tubular). Penis also similar to that of *C. signatum*, except for larger basal portion and smaller distal portion (Figs. 307, 315). Penis tip broad, penis groove separates a pair of broad, rounded tips. More details in Ghiselin & Wilson (1966, fig. 3).

Female. Visceral and pallial organ characters similar to those of *C. signatum*, distinctive or notable features following (Figs. 317-319). Albumen gland not so clear. Seminal receptacle narrow and long. Bursa copulatrix and capsule gland also thick glandular. Vaginal tube part anterior to capsule gland located ventrally to it, also running in floor of pallial cavity. Genital pore small, papilla-like. More details in Ghiselin & Wilson (1966, fig. 2).



Figs. 307-312, *Cyphoma gibbosum* anatomy: **307,** head-foot, male, lateral-right view; **308,** pallial cavity roof and visceral mass, male, ventral view; **309,** kidney and pericardium region, both opened longitudinally, ventral view, some gill filaments on auricle removed; **310,** pallial roof, transversal section in middle level of posterior osphradium branch; **311,** right mantle lobe, outer view, detail of its middle region; **312,** anterior esophagus, transversal section in its middle region. Scales = 2 mm.



Figs. 313-319, *Cyphoma gibbosum* anatomy: **313,** left snout (or oral tube) glands isolated; **314,** foregut, lateral-left view; **315,** pallial vas deferens and penis, dorsal-slightly lateral view; **316,** visceral mass (uncoiled), middle and distal digestive tubes shown as in situ, ventral view; **317,** pallial oviduct, transversal section in its posterior region; **318,** same for its anterior region; **319,** same, whole ventral view, some adjacent structures also shown. Scales = 2 mm.

Measurements of shells (in mm). AMNH 177644: 1) 31.2 by 16.6; 2) 32.4 by 16.2; 3) 29.6 by 15.1.

Distribution. From Georgia, USA, to Espirito Santo, Brazil.

Habitat. On gorgonians, intertidal to 29 m depth.

Material examined. UNITED STATES OF AMERICA; Georgia, 31º41'24"N 80º21'00"W, 27 m depth, USNM 848730, 1♂ (31/i/1980). HAITI; off Port-au-Prince, SW side of Grand Banc, 8 m depth, AMNH 177644, 19 specimens (Glenn Goodfriend leg. 20/vi/1972). TOBAGO; North End, Reef off N end Anse, Bateau, ANSP A-5540, 24 specimens (sta. 13, G. M. Davis col., 24/xii/1973).

Discussion. In the tropical western Atlantic, assisted by Cate (1973), who described and figured the types, practically only 3 species of flamingo-tongue snails were considered: *C. signatum, C. gibbosum* and *P. intermedium*. The 2 former species are practically indistinguishable in shell attributes (Cate, 1973, figs. 152 and 146 respectively). It is possible to point out morphological "tendencies" of each species, but there is always overlapping of anyone. The key for easy specific separation between both is in the mantle color patterns, as *C. gibbosum* has rings or circles, and *C. signatum* a mosaic of oblique spots forming successive bands (color plate Figs. 22-23). *P. intermedium*, on the other hand, has shell characters easily differentiable from the other 2 species, mainly in the more pointed form of shell anterior and posterior ends (Cate, 1973, figs. 155, 156). However, the mantle color pattern resembles that of *C. signatum*, distinguishing in being simpler fashioned, darker and denser.

When Petuch (1979) described his *C. macumba*, the problem in identifying those taxa started. According to the Petuch's photos and drawings, *C. macumba* apparently has a shell with *C. gibbosum-C. signatum* fashion, with mantle color looking like *P. intermedium*. Those facts apparently have raised insecurity in the identification of these animals, as talks with several malacologist, and even in some publications, the problematic appears. Hetzel (1994: 124), for example, figured a *"C. macumba"* specimen certainly collected close to (or possibly in) the type locality (Abrolhos Archipelago, South Bahia). However, analyzing the mantle color pattern and the shell of the figured specimen, certainly it is *C. signatum*. Rocha *et al*. (1994), on the other hand, performed a comparative morphological study of samples of *C. macumba* and *C. signatum*. They reported additional differences between both species, mainly in the penis form, and the size of the osphradium branches. Unfortunately, nothing is reported by the authors about the geographic distribution of the both species, and a personal search for the studied specimens in the University of Ceará and Labomar (where that study was developed), for including them in present study, was fruitless. Analyzing the figures and descriptions given by Rocha *et al*. (1994), it is clear that what they called "*C. signatum*" is actually *P. intermedium*, and what they called "*C. macumba*" is *C. signatum*.

Although the resolution of this kind of systematics problem is beyond of the scope of this study, I tried to resolve it. The type of *C. macumba* at USNM was examined, but helped little, because it is only a shell. Specimens from neighborhood places of *C. macumba* type locality were examined, but all they were *C. signatum*.

Because of no surely identified *C. macumba* was available for examination, the differences in the mantle color pattern explored by Petuch (1979) remain the main (or unique) difference between this species and *C. signatum*. Some specimens of *C. signatum* with darker-colored mantle, such as MZSP 29252, present some similarity with mantle color pattern figured by Petuch for *C. macumba*. This maybe can indicate that *C. macumba* can be only a form of *C. signatum*. Moreover, Rosenberg (1996) considered *C. macumba* synonym of *C. signatum*.

Due to the fact that no specimen with the same morphological attributes of Petuch's description of *C. macumba* was examined, the synonymy of this species with *C. signatum*, although mostly probable, is not confirmed. Then, both species are provisionally considered as valid herein until more material become available.

If *C. macumba* is a valid species, it is highly endemic of Abrolhos archipelago, and does not occur in the remainder Central and South America Atlantic coasts, as have been observed in examined material.

Genus *Pseudocyphoma* Cate, 1973

(Type species: *Ovulum intermedium* Sowerby)

Pseudocyphoma intermedium (Sowerby, 1828)

(Figs. 36, 37, 85, 320-330)

(Color plate Figs. 24, 53, 55, 86, 87, 88)

Synonymy see Cate (1973: 69). Complement:

Cyphoma intermedium: Warmke & Abbott, 1962: 93 (pl. 16, fig. j); Kempf & Matthews, 1969: 92; Rios, 1970: 62; Matthews & Rios, 1974: 49; Rios, 1975: 73 (pl. 20, fig. 297); Oliveira *et al*., 1981: 139; Domaneschi & Penna-Neme, 1984: 12 (fig. 3); Calvo, 1987: 109 (fig. 69).

Cyphoma intermedia intermedia: Schilder & Schilder, 1971: 76.

Pseudocyphoma intermedium: Cate, 1973: 69-70 (fig. 156); Abbott & Dance, 1983: 99 (fig.); Trew, 1987b: 26; Merlano & Hegedus, 1994: 168 (pl. 52. fig. 621); Fehse, 1997: 36.

Cyphoma (Pseudocyphoma) intermedium: Abbott, 1974: 153; Rios, 1985: 66 (pl. 23, fig. 293); 1994: 76 (pl. 25, fig. 290).

Cyphoma signatum: Rocha et al., 1994: 149-159 (figs. 1, 3, 5, 6) (not Pilsbry & McGinty, 1939).

Pseudocyphoma christahemmenae Fehse, 1997: 35-37 [Guarapari, Espirito Santo].

Cyphoma guerrinii Fehse, 2001: 37-39 (fig. 1) [Jiboia Is., São Paulo].

Pseudocyphoma rosenbergi Fehse, 2001: 39-40 (fig. 3) [Guarapari, Espírito Santo].

Description

Shell (Figs. 36, 37; color plate Figs. 53, 55, 86, 87, 88). Considerably different from preceding *Cyphoma* species, with bi-conic fashion, thinner outer lip. Other details in Cate (1973: 69-70). Some mature specimens present outer lip not thickened. Other comments see following discussion.

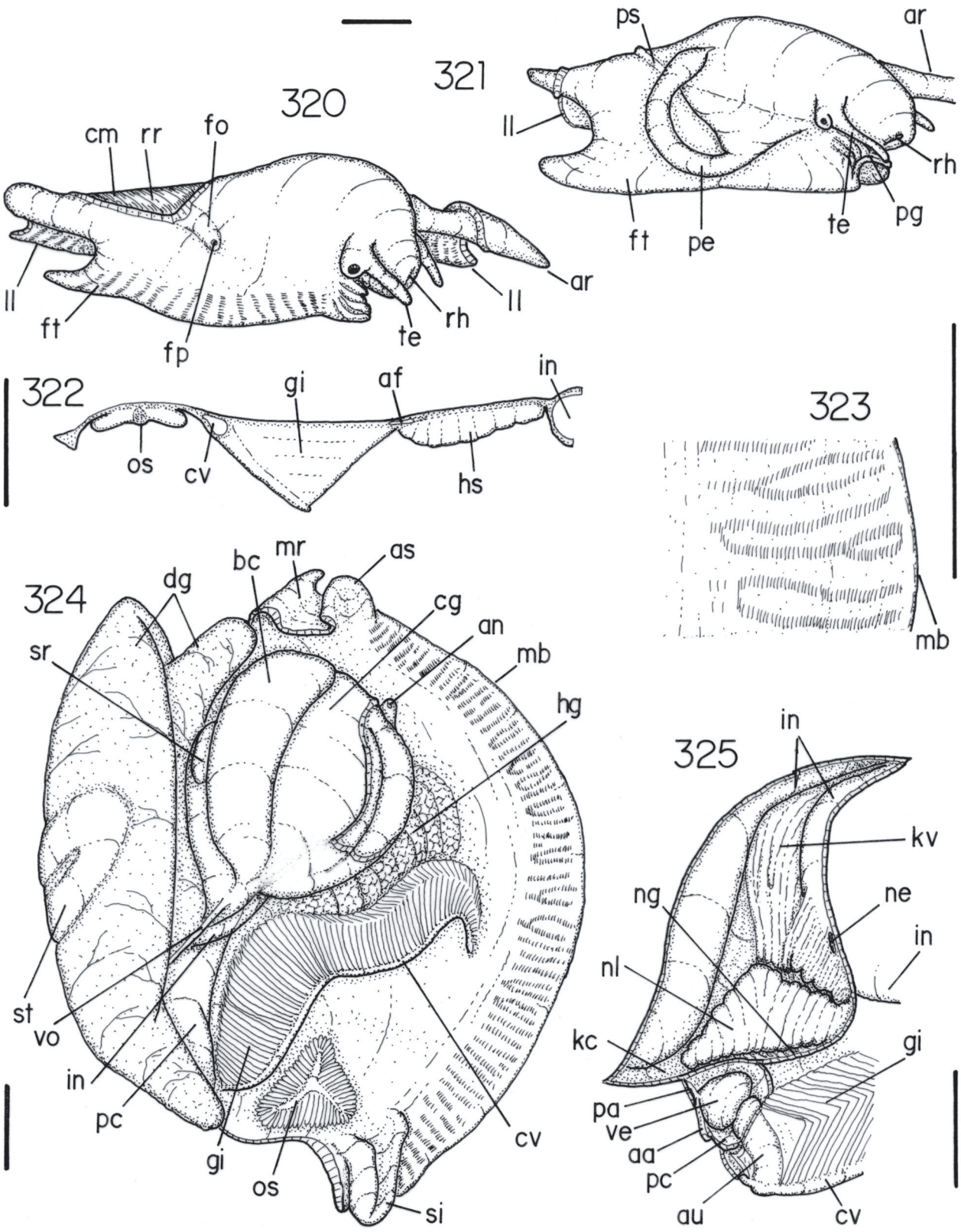
Head-foot (Figs. 320, 321, 326). Characters similar to those of *C. signatum*, including color, posterior projection and transversal folds of propodium. Anterior muscular projection slender and longer.

Mantle organs (Figs. 322-324). Mantle lobes not so broad as those of preceding species, but also well developed. No papillae. Color pale cream with a series of transversal bands (Figs. 323, 324), presenting irregular fashion of dichotomy or fusion somewhat similar to those of *C. signatum*, but usually more crowded and dense (color plate Fig. 24). Incurrent siphon slightly larger than anal siphon. Pallial organs similar in features to those of *C. signatum*, but dislocated to left by visceral mass. Gill slightly sigmoid. Gill filaments apex almost central (Fig. 322). Hypobranchial gland thick, with mantle septa crossing transversally through it. Anus small, far removed at left from anal siphon.

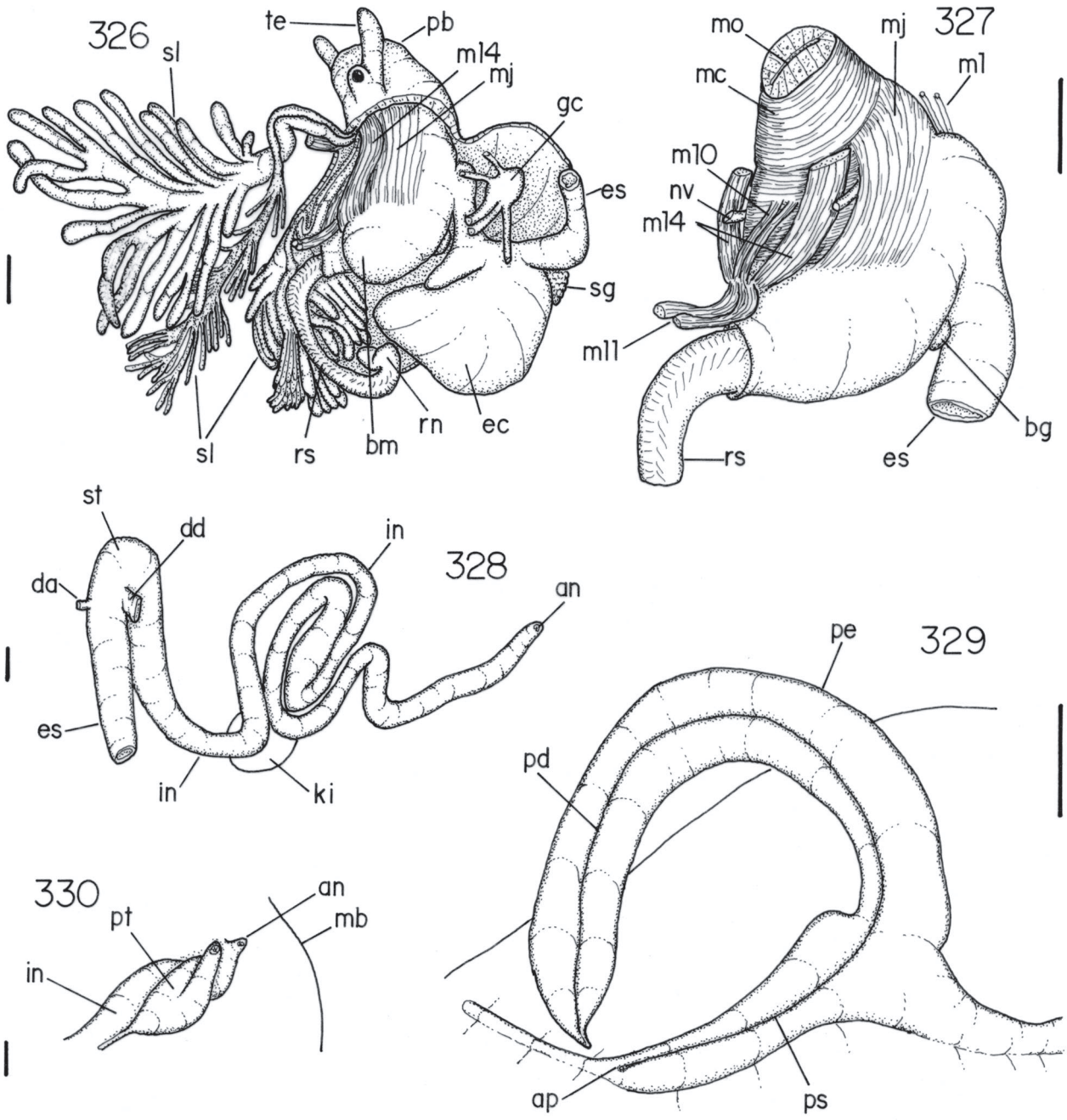
Visceral mass (Fig. 324). Very similar characters to those of *C. signatum*, except in being more encroached in posterior-right region of pallial cavity and by anterior-right projection of digestive gland located protected in a transparent sac of mantle, just posterior to anal siphon.

Circulatory and excretory systems (Fig. 325). Heart characters similar to those of *C. signatum*, but proportionally smaller, auricle narrow portion dorsal to gill inserting almost terminal in ctenidial vein. Kidney slightly narrow, compressed by intestine loops. Accessory lobe of nephridial gland broad, large, with some irregular transversal furrows in its surface. Renal lobe fills inner space among 2 intestinal loops and nephridial lobe, most constituted by longitudinal, tall, whitish folds, some of them weakly attached to intestine and amply connected to dorsal renal wall. Nephrostome a broad slit just at right from nephridial lobe level.

Digestive system (Figs. 326-328). As in preceding *Cyphoma* species, 2 pairs of oral tube glands present (Fig. 326). Larger pair with several long acina, most solid-glandular, acina inserted along a longitudinal tubular axis. Smaller pair slender, with very narrow and long acina, mostly hollow, also inserted in a narrow longitudinal tube. Both gland pairs possess a long and narrow, slightly convolute tube inserted, as in preceding *Cyphoma* species, in ventral-anterior side of oral tube close to median line. Buccal mass features also similar to those described for *C. signatum*, distinctive features following (Fig.



Figs. 320-325, *Pseudocyphoma intermedium* anatomy: **320,** head-foot, female, lateral-right view; **321,** same, male; **322,** pallial roof, transversal section in middle level of posterior osphradium branch; **323,** right mantle lobe, outer view, detail of its middle region; **324,** pallial cavity roof and visceral mass, female, ventral view; **325,** kidney and pericardium region, both opened longitudinally, ventral view, some gill filaments on auricle removed. Scales = 2 mm.



Figs. 326-330, *Pseudocyphoma intermedium* anatomy: **326,** head and haemocoel, ventral-slightly lateral-left view, two of snout gland deflected and uncoiled, proboscis extended; **327,** buccal mass, lateral-left view, radular sac only partially shown; **328,** middle and distal digestive tubes shown as in situ, ventral view, some adjacent structures also indicated; **329,** pallial vas deferens and penis, dorsal-slightly lateral view; **330,** prostate and adjacent structures, ventral view. Scales = 1 mm.

327). Dorsal folds broad, with aperture of salivary gland located in anterior 1/3 of their length. Furrowed part of these folds with some longitudinal furrows. Odontophore muscles: **m1a**, **m1b**, **m2** and **m3** absent; **m11** and **m10** pairs narrow; **m14** pair inserted just anterior to radular sac. Pair of nerves laterally located. Radular sac with about same length than buccal mass. Radular nucleus broad and bifid. Radular teeth characters (Fig. 85) similar to those of preceding *Cyphoma* species, with following remarks: rachidian tooth little curved; lateral tooth well curved; marginal teeth narrower, with about 30 long cusps along their tip. Esophagus, esophageal gland and salivary glands similar in characters to those of *C. signatum* except for longer and taller fold of middle esophagus, covering esophageal gland aperture. Stomach (Fig. 328) also similar to that of *C. signatum*. Intestine longer and more coiled than those of preceding *Cyphoma* species; loops fashion shown in Fig. 238; most of them compress kidney and encroach in pallial cavity. Rectum narrow, running slightly far from right pallial cavity edge, compressed by dorsal surface of pallial oviduct of females. Anus above described.

Genital system. **Male**. Visceral organs with similar characters as those of *C. signatum*. Prostate gland elliptical, located just posterior to anus, walls thick glandular (Fig. 330), inner duct narrow. Vas deferens, after prostate, suddenly narrows and runs attached to floor of pallial cavity, in half way between prostate and penis base suddenly expands and becomes a furrow (Fig. 329). Penis similar in fashion to that of *C. signatum*; basal portion low and long; distal portion long, cylindrical, curved; penis tip with a small papilla in which penis groove finishes (Figs. 321, 329).

Female (Fig. 324). Visceral and pallial structures features very similar to those of *C. signatum*. Albumen gland not so clear. Bursa copulatrix slightly narrow and more ventral located. Seminal receptacle shorter, of similar location. Female genital pore a small papilla (Fig. 320).

Measurements of shells (in mm). MZSP 24887♀ : 26.1 by 11.5; MZSP 29240♂ : 23.6 by 11.8.

Distribution. From Texas, USA, to Rio Grande do Sul, Brazil.

Habitat. On octocorallia. From intertidal to 300 m depth.

Material examined. BRAZIL; **Rio de Janeiro**; off Cabo Frio, MZSP 29250, 1♀ (P.M. Costa col.); Búzios, Praia de João Fernandes, 3-4 m depth, MZSP 35052, 2♀ (of color plate Fig. 24) (P.M. Costa col., ii/2002); off Niterói, MZSP 34772, 7 specimens (otter trawl, xi-xii/2001, Coltro leg.); Angra dos Reis, MZP 29240, 1♂ (sta. 282, 14/vii/1966), MZSP 34833, 1♂ (Coltro leg, 2001). **São Paulo**; Bertioga, Guaratuba Beach, MZSP 24887, 1♀ (Antonio C. Prado col., 19/v/1984); off Santos, 50-60 m depth, MZSP 34946, 1♀ (otter trawl, Carlo Magenta leg., iv/2000); Praia Grande, off Boqueirão, MZSP 29251, 1♂ (otter trawl). **Rio Grande do Sul**; off Mostardas, 31º31'S 49º47'W, 294 m depth, MZSP 19198, 2♀ (R. V. "W. Besnard" sta. 444, 6/xii/1968).

Discussion. This species has a highly variable shell [color plate (c. p.) Fig. 88]. Some specimens are thinner walled (c. p. Fig. 88-1), while others are thicker (c. p. Fig. 88-20), with thick outer lips. Some adult specimens are larger than 30 mm (c. p. Fig. 88-1), while others have little more than 10 mm (c. p. Fig. 88-3). The transversal callus is weak in some slender specimens (c. p. Fig. 88-9) and well marked in shorter specimens (c. p. Fig. 88-23). Specimens of all kind of variations were examined, showing uniform characters of the soft parts. Besides, in the shell characters, all degree of variation is observable between 2 extremes. This is the reason for considering the recently described species of Fehse as forms of *P. intermedium*. For example, the c. p. Fig. 88-9 and 27 have the shell attributable to *P. kathiewayae* (sensu Fehse, 2000, figs. 2-5, not Cate, 1973); the shell of c. p. Fig. 88-7 looks closely to *C. guerrini* Fehse (2001, fig. 1); the shell of c. p. Fig. 88-14 is similar to *C. macumba* sensu Fehse (2001, fig. 2, not Petuch); while the c. p. Fig. 88-26 shows a specimen with shell of *P. rosembergi* Fehse (2001, fig. 3). The c. p. Fig. 88-10 is closely similar to the *P. intermedium* type specimen (Cate, 1973, fig. 155-156). As well as several other forms.

Genus *Ovula* Bruguière, 1789

(Type species: Ovula oviformis Lamarck, 1801 = Bulla ovum Linné, 1758)

Ovula ovum (Linné, 1758)

(Figs. 38, 39, 86, 87, 331-344)

(Color plate Fig. 39)

Synonymy see Cate (1973: 64). Complement:

Ovula ovum: Schilder & Schilder, 1971: 74; Wilson & Gillett, 1972: 61-62 (pl. 42; pl. 44, fig. 6); Taylor & Walls, 1975: 4, 8, 9 (figs.); Webb & Coll, 1983: 61 (figs.); Abbott & Dance, 1983: 99 (fig.); Trew, 1987b: 26; Webb, 1988: 155-160 (figs. 1-3); Haywood & Wells, 1989: 102-103 (fig.), 155 (fig.).

Description

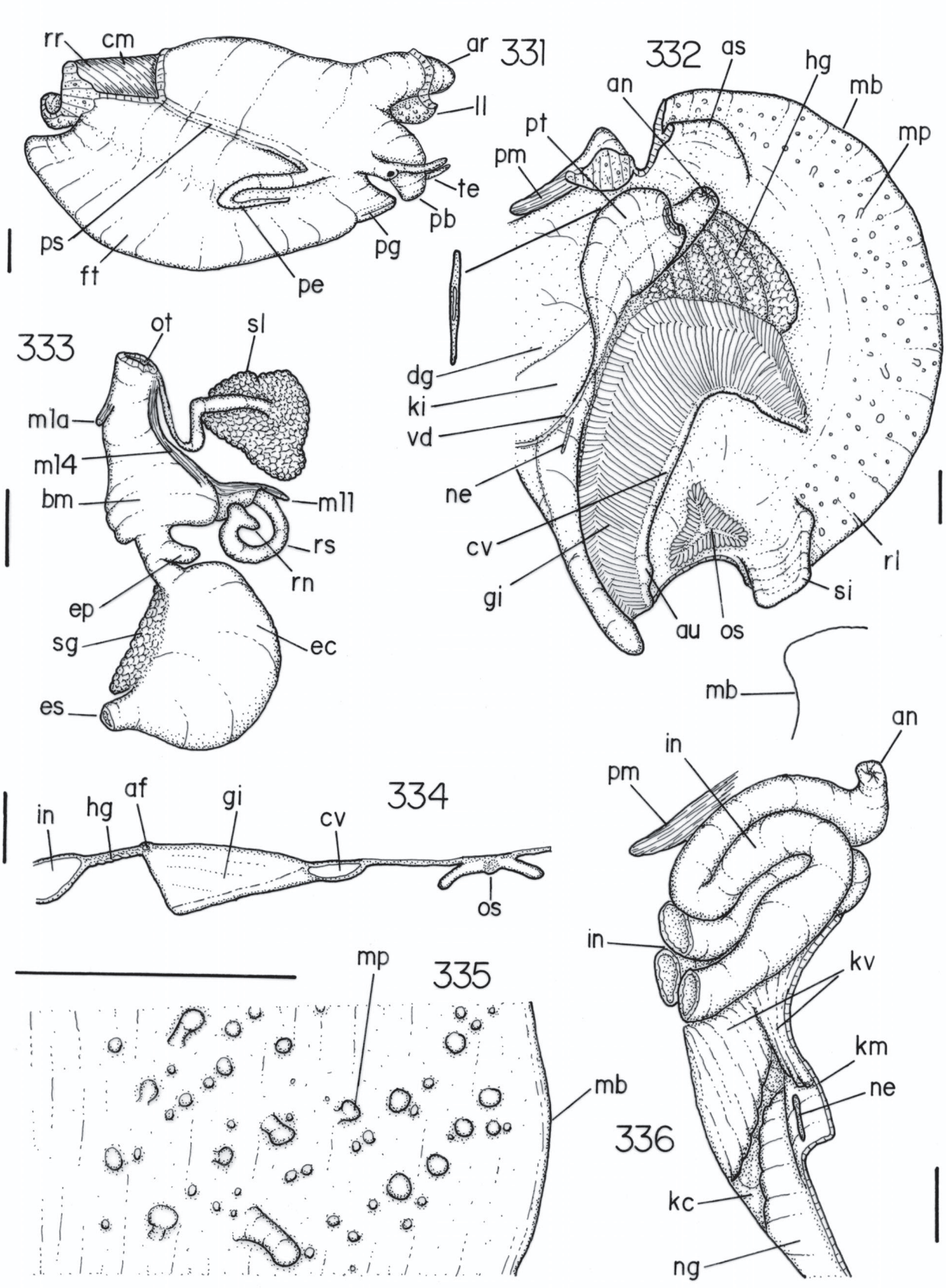
Shell (Figs. 38, 39; color plate Fig. 39). Of large size, homogeneous white in outer surface, dark brown in inner surface. Other details in Cate (1973: 64-65).

Head-foot (Fig. 331). Color dark brown, almost black, in exposed areas, remainder (e.g., pallial cavity roof) pale beige. General fashion similar to those described for *M zebra*, but slightly broader. Anterior projection long and robust. Posterior projection lacking. Penis proportionally small (described below).

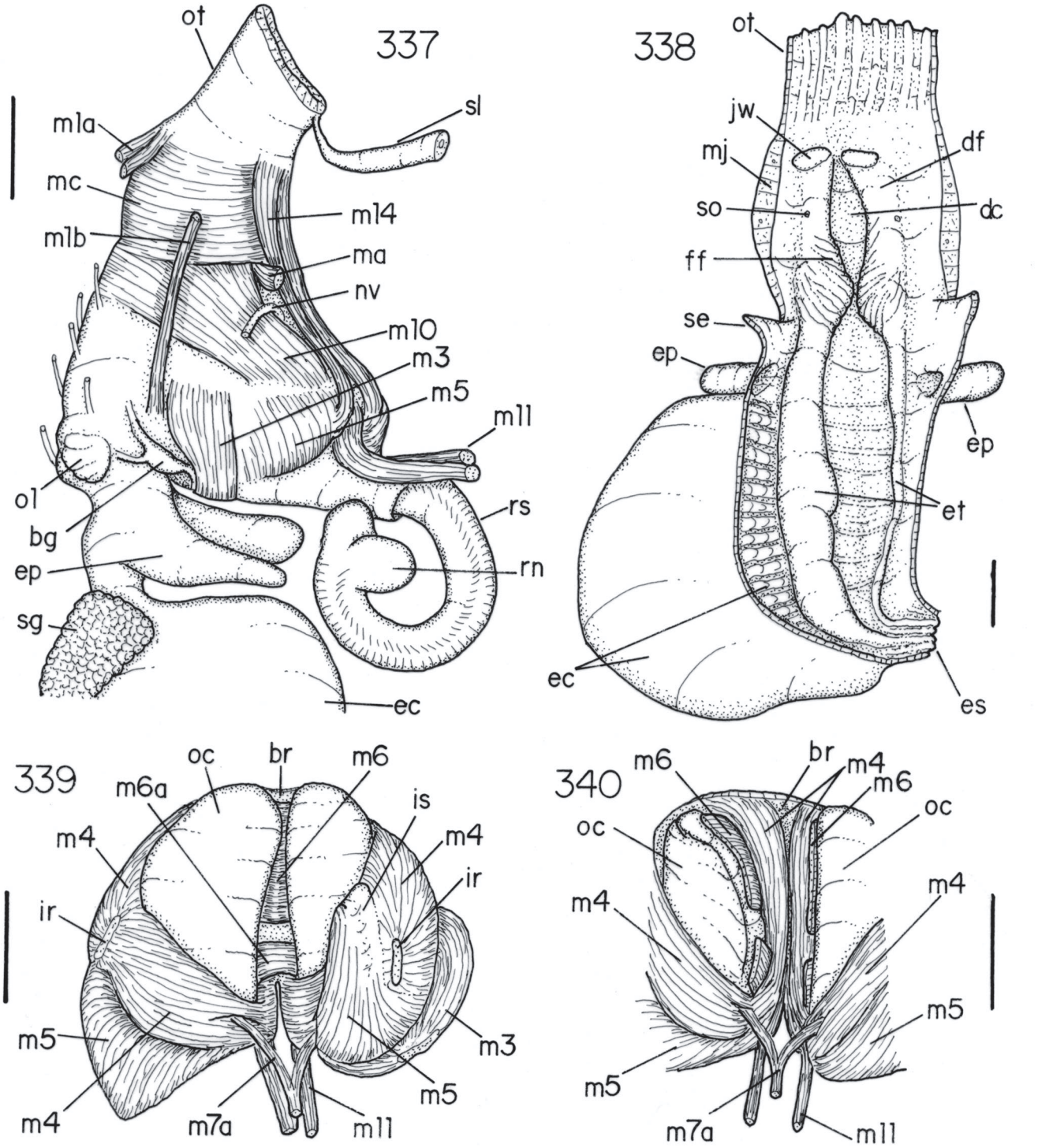
Mantle organs (Figs. 332, 334, 335). Mantle lobe color homogeneously dark brown, almost black, with pale cream papillae (see figs. of living specimens in Wilson & Gillett, 1972; Haywood & Wells, 1989). Papillae of several sizes, but small if compared to most cypraeids (Fig. 335); papillae simple, absent close to mantle edge, most sessile, some larger peduncled, tip broad. Incurrent and anal siphons well developed and slightly same sized; both of smooth margins. Pallial organs characters (Fig. 332) similar to those of *M. zebra*, distinctive or notable features following. Osphradium also with 3 branches, but narrower and smaller, somewhat far removed from siphon and gill. Osphradium filaments with a slightly long detached distal region, tip rounded. Gill large, broad, curved. Gill filaments broad, slightly low, apex almost central (Fig. 334). Hypobranchial gland large, thick, transversal folded, color cream.

Circulatory and excretory systems (Figs. 332, 336). Heart characters similar to those of *M. zebra*. Narrow region of auricle, running dorsal to gill, inserted in ctenidial vein at short distance from its posterior end. Kidney compressed by intestine loops. Nephridial gland slightly large, triangular in section, located in dorsal region of membrane between kidney and pericardium, without accessory lobe. Kidney lobe massive, with longitudinal, tall folds, connected to dorsal and ventral renal walls and also to adjacent intestinal loops. Nephrostome free of any inner vessels.

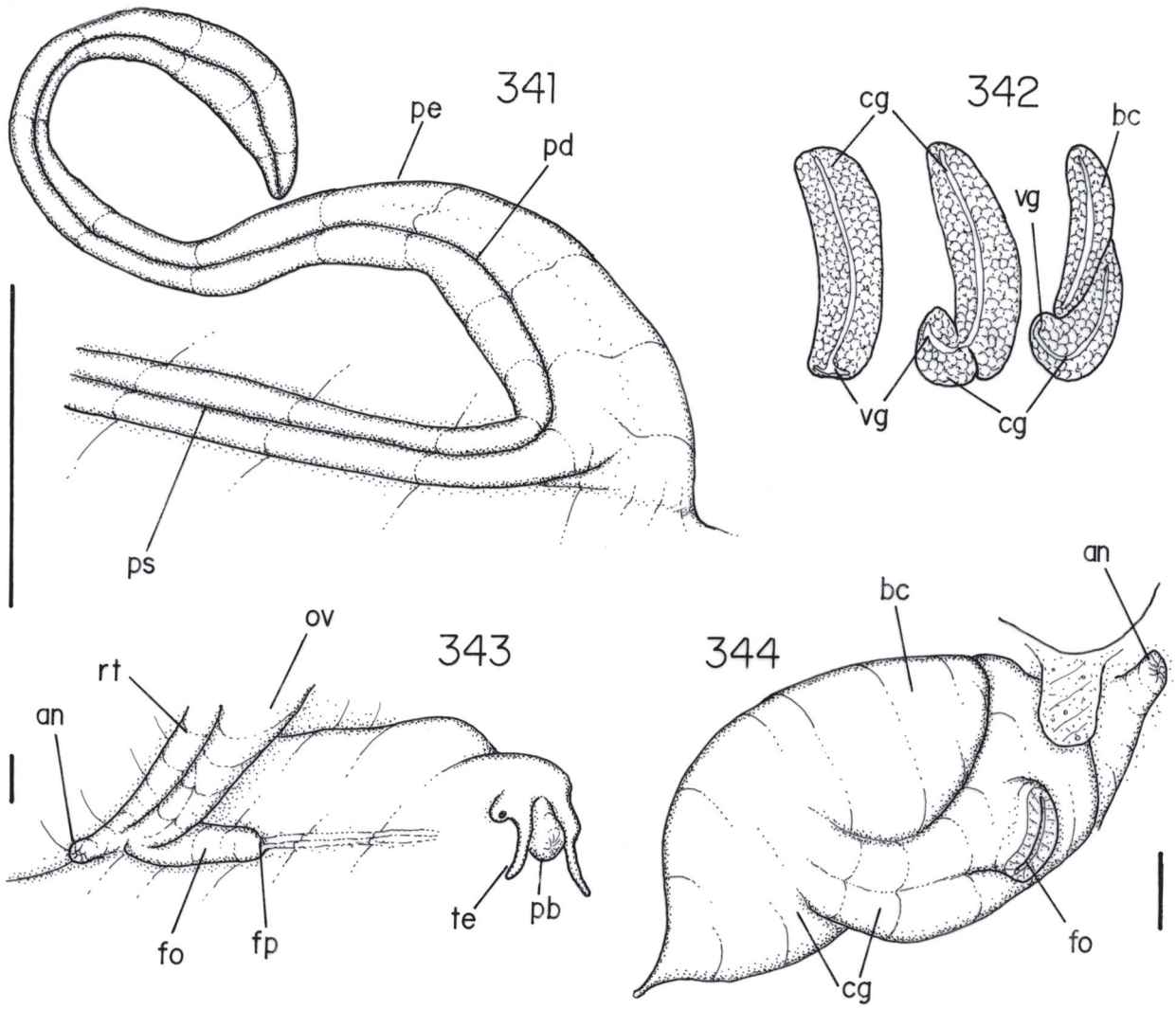
Digestive system (Figs. 333, 336-340). Oral tube gland single (Fig. 333), located in right-posterior region of haemocoel, amorphous, soft, color cream, surface slightly smooth; duct long, stubby, hollow; inserts in ventral surface of oral tube close to mouth and to median line. Proboscis and retractor muscles similar to those of *M. zebra*. Buccal mass characters also similar to those of *M. zebra*, distinctive or notable features following (Figs. 337-340). Pair of jaw plates present, small, thin, elliptical (Fig. 338). Dorsal folds broad and tall; their furrowed part large (almost half of their length), with several oblique furrows (Fig. 338). Aperture of salivary gland a small pore just anterior to furrowed part, located laterally. Odontophore muscles (Figs. 337, 339, 340): **m1a** pair present; **m1b** pair long and narrow; **m2** absent; **m3** pair narrow, transversal, close to esophageal origin; **m6** long; **m6a** narrow, detached from subradular membrane; **m7** absent; **m7a** (see *Cyphoma signatum*) present; **m10** pair broad, lateral located, some fibers running in dorsal-anterior surface; **m11** pair narrow and long, without muscular tissue surrounding radular sac, only a thin membrane; **m14** narrow, close to median line, inserting just anterior and medial to those of m10. Radular sac of about same length of that of buccal mass. Radular nucleus broad, bifid (Fig. 337). Radular teeth (Figs. 86, 87) somewhat similar in features to those of *Cyphoma* species, with following remarks: rachidian tooth tall and broad, with about 7 pointed cusps, central cusp several times larger than neighbor cusps; lateral tooth tall and narrow; tip pointed, a pair of small cusps in



Figs. 331-336, *Ovula ovum* anatomy: **331,** head-foot, male, lateral-right view; **332,** pallial cavity roof and anterior part of visceral mass, male, ventral view, a transversal section of indicated region of prostate also shown; **333,** foregut, lateral-right view, single snout (or oral tube) gland partially deflected; **334,** pallial roof, transversal section in middle level of posterior osphradium branch; **335,** right mantle lobe, outer view, detail of its middle region; **336,** kidney and visceral-pallial region at right from it, ventral view, ventral kidney membrane part removed and part deflected anteriorly, intestinal loops exposed, mantle border location also shown. Scales = 5 mm.



Figs. 337-340, *Ovula ovum* buccal mass: **337,** buccal mass and anterior region of esophagus, lateral-right view; **338,** dorsal wall and esophagus, ventral view, odontophore removed, esophagus opened longitudinally; **339,** odontophore, ventral view, radula removed, both cartilages deflected, right m5 (left in fig.) deflected posteriorly; **340,** same, detail of its central region, m6 and m6a sectioned. Lettering: **o1**, secondary glandular esophageal pouch. Scales = 2 mm.



Figs. 341-344, *Ovula ovum* anatomy: **341,** pallial vas deferens and penis, dorsal-slightly lateral view; **342,** pallial oviduct, transversal sections respectively in its posterior, middle and anterior regions; **343,** pallial roof and floor, female, dorsal view, mantle partially deflected to show anterior end of oviduct; **344,** pallial oviduct and some adjacent structures, ventral view. Scales = 5 mm.

each side located about in middle region of each tooth, outer pair slightly closer to tip than inner pair; marginal teeth also brooch-like, inner marginal tooth narrower, with about 18 long cusps; outer marginal tooth broader, mainly at tip, with about 35 long cusps gradually decreasing towards external. Two pairs of esophageal pouches; a pair small, located anterior and dorsal, to buccal ganglia, transversal folded; other pair diverticle-like, long, thin walled, inner surface smooth. Middle and posterior esophagus (Figs. 333, 338) characters similar to those of *M. zebra*, with esophageal gland very large. Esophageal right fold broad and irregular, partially covering esophageal gland aperture. Stomach constitution also similar to that of *M. zebra*, but duct to anterior lobe of digestive gland lacks inner septa. Intestine narrow and long, in pallial region possesses 2 loops (Fig. 336), a dorsal and other ventral to this; this last loop sigmoid, in short distance ends in anus. Anus broad, siphoned, close to anal siphon.

Genital system. **Male**. Visceral structures not examined. Prostate just posterior to triangular sinus, broad, elliptical, greatly flattened. Prostate inner duct slightly narrow. From triangular sinus, pallial sperm groove running towards anterior region in pallial floor, entirely open (a furrow) and with thick

margins. Penis somewhat small, long, base flattened and broader, gradually narrows and becomes slender (Figs. 331, 341). Penis sub-apical region slightly broader. Penis apex rounded, with penis groove ending terminally.

Female. Visceral structures characters similar to those of *M. zebra*. Features of pallial oviduct similar to those of *Cyphoma signatum*, except for (Figs. 342, 344): 1) insertion of visceral oviduct in pallial oviduct posterior extremity; 2) albumen gland not so clear; 3) vaginal tube presenting a portion beyond capsule gland running perpendicular to pallial oviduct longitudinal axis. Genital pore small, from this a shallow furrow starts, running towards anterior, fainting posterior to head (Fig. 343).

Measurements of shells (in mm). USNM 836355: 91.7 by 55.6; USNM 802036: 79.2 by 49.0.

Distribution. Tropical and sub-tropical Indo-Pacific.

Material examined. PHILIPPINES; 09º04'00"N 123º08'48"E, USNM 802036, 1♂ (Siphil Exp. 78, sta. SP78-44, 16/vi/1978); Negros Oriental, near Giligaon, N. of Maloh, 09º06'30"N 122º55'24"E, 0-2m depth, USNM 828725, 1♂ (Knapp et al. col. 26/iv/1979). PAPUA NEW GUINEA, Bootless Inlet, SE of PNG University Marine Laboratory, USNM 836355, 2♀ (Pettit col., 26/v/1981).

Genus *Calpurnus* Montfort, 1810

(Type species *Bulla verrucosa* Linné)

Calpurnus verrucosus (Linné, 1758)

(Figs. 40, 41, 88-90, 345-356)

(Color plate Figs. 1-8; 49, 56, 83)

Synonymy see Cate (1973: 63). Complement:

Calpurnus verrucosus: Schilder & Schilder, 1971: 74; Wilson & Gillett, 1972: 18-19 (pl. 6), 62 (pl. 44, fig. 5); Cate, 1973: 63 (figs. 135, 136); Abbott & Dance, 1983: 99 (fig.); Trew, 1987b: 26.

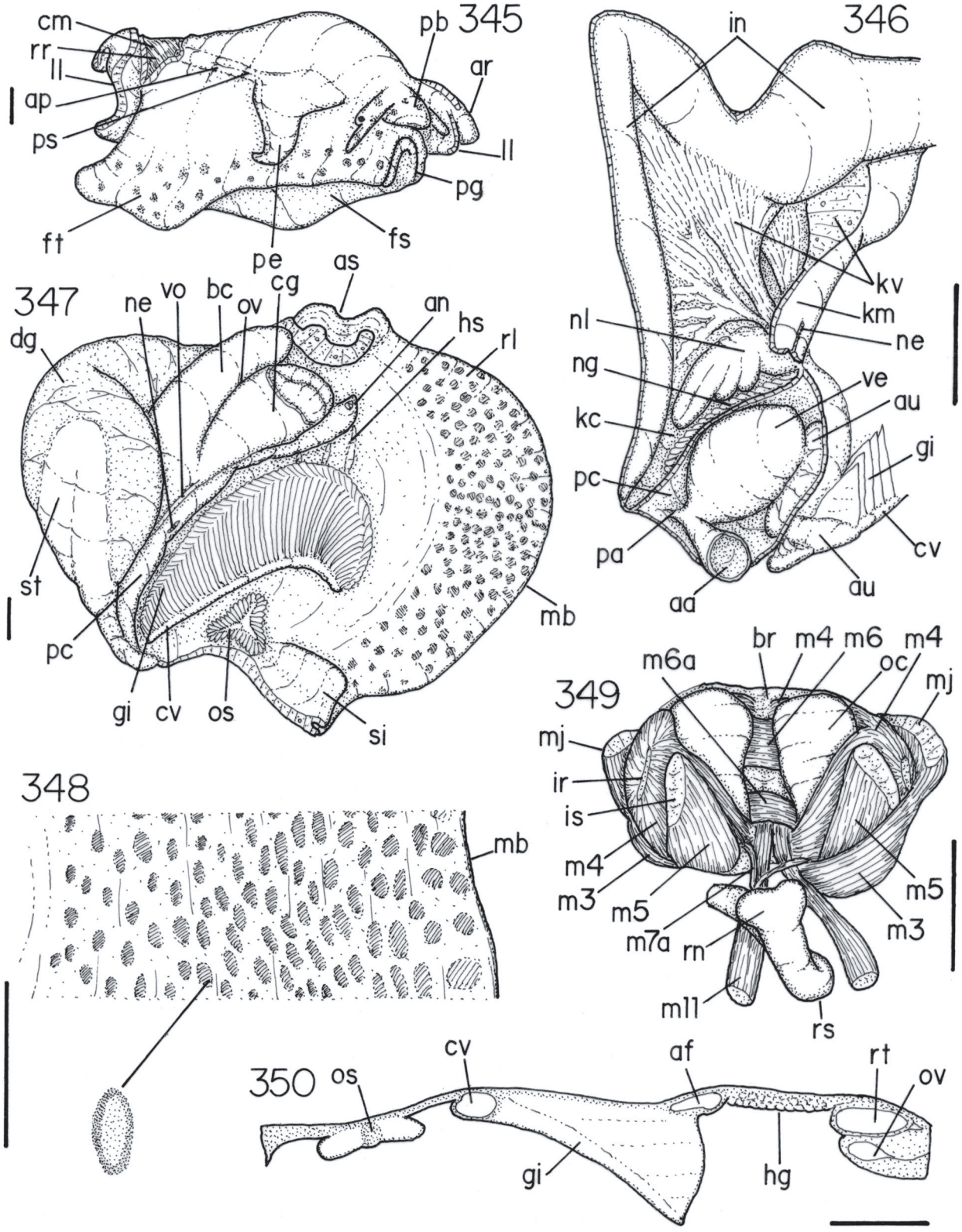
Description

Shell (Figs. 40, 41; color plate Figs. 49, 56, 83). Color white. Protuberances rounded and small, just dorsal to incurrent and anal siphons. Outer lip with inner teeth. Other details in Cate (1973: 63).

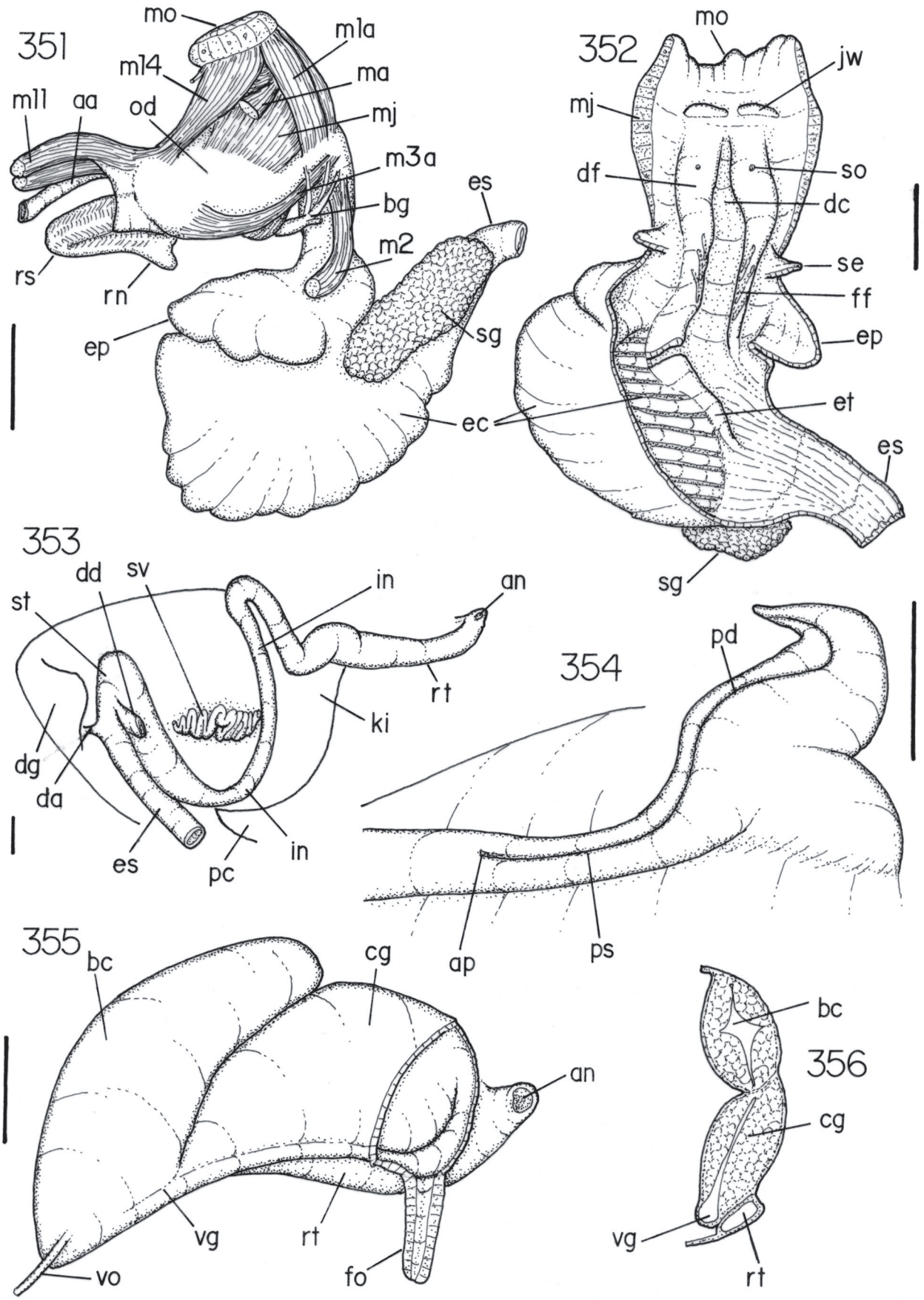
Head-foot (Fig. 345). Color pale beige with rounded brown spots uniformly distributed in exposed areas (except foot sole) (Color plate Figs. 5-8). Characters in general similar to those of *M. zebra*, including proboscis and anterior projection. Posterior projection lacking.

Mantle organs (Figs. 347, 348, 350). Mantle lobes smooth, without papillae. Color pale beige to white with brown spots uniformly distributed and sized (Figs. 347, 348; color plate Figs. 1-8), each spot with a darker marginal region and a paler central region (see other colors in Wilson & Gillett, 1972, pl. 42). Spots organized in about 20 alternate successive rows. Siphon large, with smooth margins, base thick muscular. Anal siphon thick muscular, partly connected to columellar muscle. Pallial organ characters (Fig. 347) similar to those of *M. zebra*. Osphradium small, also with 3 branches, slightly far from gill. Osphradium filaments slightly tall, with rounded extremities. Gill broad, curved. Gill filaments with apex located at right; right margin straight (Fig. 350). Hypobranchial gland thick, with some transversal thin septa of mantle crossing through it.

Circulatory and excretory systems (Fig. 346). Heart features similar to those of *M. zebra*, narrow region of auricle, running dorsal to gill, inserted at short distance from its posterior end. Kidney characters also similar to those of *M. zebra*. Accessory lobe of nephridial gland large, slightly irregular. Renal lobe fills most of remainder inner space, part attached to dorsal and ventral renal walls, and also to adjacent intestine loops. Renal lobe with several folds and vessels, most converging to a same insertion at right and ventral to nephrostome (jointed with vessel of nephridial gland accessory lobe). Anterior-right



Figs. 345-350, *Calpurnus verrucosus* anatomy: **345,** head-foot, male, lateral-right view; **346,** kidney and pericardium region, both opened longitudinally, ventral view, some gill filaments on auricle removed; **347,** pallial cavity roof and visceral mass, female, ventral view; **348,** right mantle lobe, outer view, detail of its middle region, one of spots seen in larger magnification; **349,** odontophore, ventral view, radula removed and partially shown down, both cartilages deflected, right m3 (left in fig.) partially removed; **350,** pallial roof, transversal section in middle level of posterior osphradium branch. Scales = 2 mm.



Figs. 351-356, *Calpurnus verrucosus* anatomy: **351,** foregut, lateral-left view; **352,** dorsal wall and esophagus, ventral view, odontophore removed, esophagus opened longitudinally; **353,** visceral mass seen as a transparent structure, male, with special concern to middle and distal digestive tubes (shown as in situ) and seminal vesicle; **354,** pallial vas deferens and penis, lateral view; **355,** pallial oviduct and some adjacent structures, ventral view; **356,** same, transversal section in its middle region. Scales = 2 mm.

region of kidney lobe solid.

Digestive system (Figs. 349, 351-353). No oral tube gland. Buccal mass characters similar to those of *Ovula ovum*, except for (Figs. 351, 352): a) dorsal folds: a1) furrowed part shorter, with few oblique furrows; a2) aperture of salivary glands in middle level of their anterior region; b) odontophore muscles (Fig. 349): b1) **m1a** pair broader; b2) **m2** pair present, broad and thick; b3) **m3** pair located towards dorso-ventral b4) **ma** pair also present but more lateral. Radular sac and nucleus also similar to those of *O. ovum*. Radular teeth features (Figs. 88-90) somewhat similar to those of *Cyphoma* species, with following remarkable characters: rachidian narrow and tall, strongly curved and close to similar of neighbor rows, tip broadly pointed, a pair of very small cusps in middle region of outer edges; lateral tooth narrow and tall, tip broadly pointed and curved, a pair of small, sub terminal cusps at some distance from tip; marginal teeth also brooch-like as those of remainder ovulids; inner marginal tooth with about 25 long cusps; outer marginal tooth broader, with about 50 long cusps. Salivary glands, esophagus and esophageal gland features similar to those of *M. zebra* with following distinctive features. A single and broad pouch, diverticle-like, lies ventral just anterior to esophageal gland. Right fold longer and taller, running in middle esophagus, covering part of esophageal gland aperture (Fig. 352). Stomach attributes (Fig. 353) similar to those of *M. zebra*, except for absence of inner septa in duct to anterior lobe of digestive gland. Intestine in visceral region U-shaped (right concavity). In right extremity of kidney, intestine suddenly towards left, running a short distance and after towards anterior (Fig. 353). Rectum slightly short and broad. Anus siphoned, small, located posteriorly from anal siphon (Fig. 347).

Genital system. **Male**. Testis characters similar to those of *M. zebra*. Seminal vesicle, different from preceding species, running in middle of ventral surface of visceral mass (but not along its left margin), Connects directly in triangular sinus. Prostate not differentiated. From triangular sinus, vas deferens runs towards anterior, approximately in its middle level opens and becomes a thick edged furrow (Figs. 345, 354). Penis short, stubby, base broad and flattened, distal half curved, tapering gradually (Fig. 354). Penis groove running in ventral surface, close to posterior penis edge. Penis tip pointed, with penis groove finishing in its end.

Female. Visceral and pallial structures with characters similar to those of *Cyphoma signatum*, distinctive or notable features following (Figs. 347, 355, 356). Seminal receptacle lacking. Vaginal tube, after capsule gland anterior end, runs perpendicularly towards anterior-left for a short distance. Genital pore small, papilla-like, on pallial floor.

Measurements of shells (in mm): ANSP 230676 ♀ : 25.6 by 15.8; ♂ : 26.0 by 17.4.

Distribution. Tropical Indo-Pacific.

Material examined. PHILIPPINES; Sulu Archipelago, SW end of Sanga Sanga Island, Bongao Channel, ANSP 230676, 18 specimens (duPont-Academy Expedition, John Root col., vii/1958).

Genus *Simnialena* Cate, 1973

(Type species: *S. marferula* Cate, 1973)

Simnialena uniplicata (Sowerby, 1848)

(Figs. 45, 46, 91, 357-367)

(Color plate Fig. 89)

Synonymy see Cate (1973: 76). Complement:

Neosimnia uniplicata: Abbott, 1954: 182 (pl. 7, fig. e); Warmke & Abbott, 1962: 92 (pl. 16, fig. m); Rios, 1970: 62; Humfrey, 1975: 107 (pl. 9, figs. 5, 5a); Neck, 1977: 367; Main, 1982: 257.

Simnia inflexa uniplicata: Schilder & Schilder, 1971: 76.

Simnialena uniplicata: Cate, 1973: 76-77 (fig. 168); Trew, 1987b: 27.

Simnia uniplicata: Abbott, 1974: 152 (fig. 1657); Rios, 1975: 73 (pl. 20, fig. 300); Domaneschi & Penna-Neme, 1984: 12 (fig. 4); Leal, 1991: 100; Merlano & Hegedus, 1994: 168 (pl. 52, fig. 624); Abbott & Morris, 1995: 197 (pl. 53).

Simnia (Simnialena) uniplicata: Rios, 1985: 66 (pl. 23, fig. 289); 1994: 76 (pl. 25, fig. 292).
Simnialena ilhabelaensis Fehse, 2001: 40-42 (fig.4).
Simnialena antillarum: Fehse, 2001: 41-42 (fig. 5).

Description

Shell (Figs. 45, 46; color plate Fig. 89). Slender, small and thin, characteristic sigmoid fold in inner lip close to anal siphon. Other details see Cate (1973: 76-77) and discussion following.

Head-foot (Fig. 357). Characters similar to those described for *Cyphoma signatum*, including anterior and posterior projections, transversal folds in propodium and color. Differs in being slender and long antero-posteriorly. Head outstandingly large.

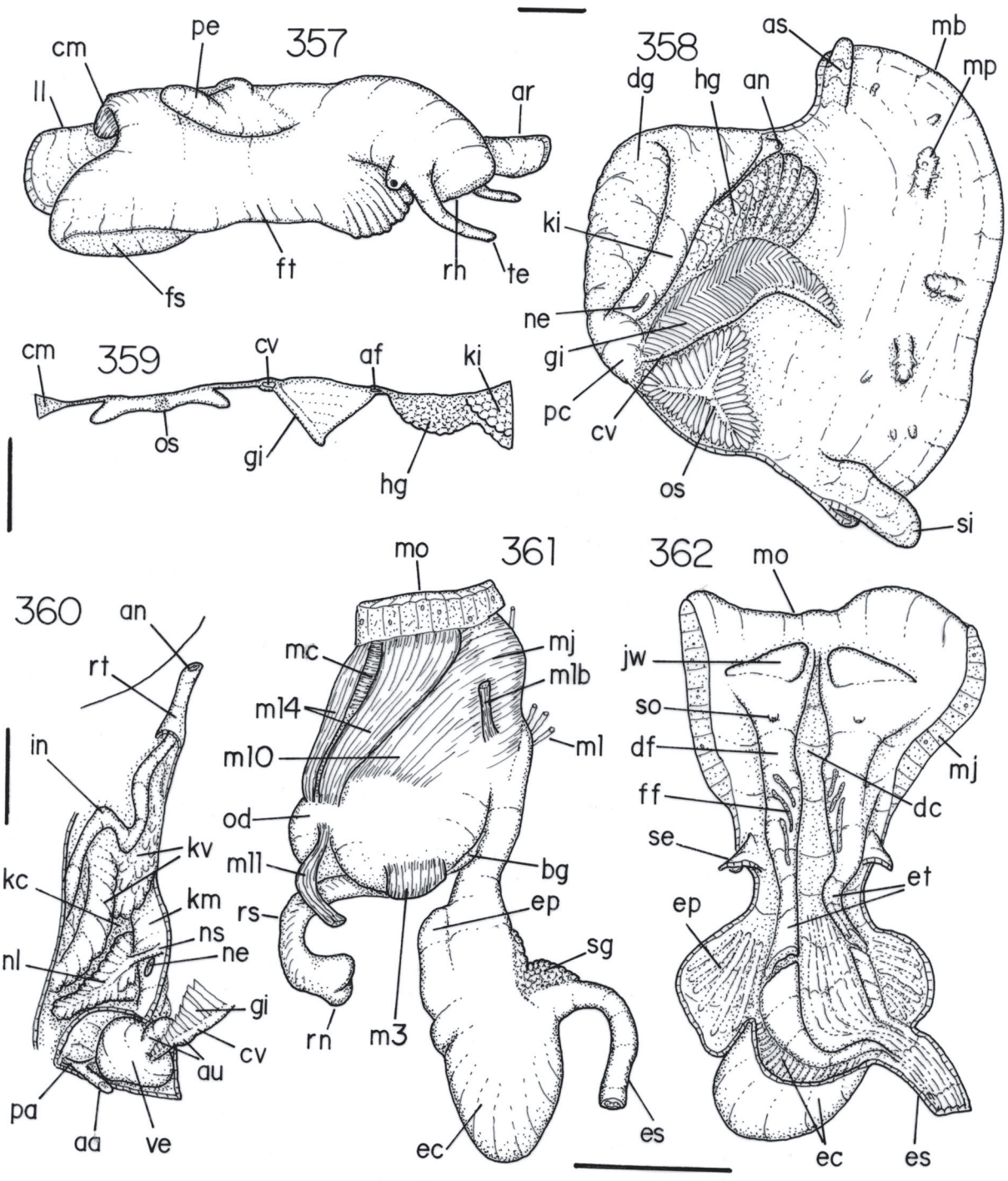
Mantle organs (Figs. 358, 359). Mantle lobes color pale cream with a mosaic of brown narrow bands. About 3 large and 5 small papillae irregularly distributed in each lobe. Papillae simple, cylindrical, tip rounded; larger papillae with narrow projections and cilia. Incurrent and anal siphon narrow and long, incurrent about double size of anal siphon, edges smooth. Pallial organs characters somewhat similar to those of *M. zebra*, distinctive or notable features following. Osphradium proportionally large, slightly triangular, close to gill and somewhat far from siphon. Osphradium filaments with rounded ends. Gill slightly elliptical and short, tapered anterior region. Hypobranchial gland thick, broad, with tall transversal folds.

Circulatory and excretory systems (Fig. 360). Heart characters similar to those of *M. zebra*, except in being smaller and dislocated forwards, about half of auricle and adjacent part of pericardium located dorsally to posterior end of gill. Auricle originating in ctenidial vein sub-terminal. Kidney features similar to those of *M. zebra*, but shorter. Accessory lobe of nephridial gland also broad, with similar folds and vessel. Ventral renal lobe small, part attached to intestine, surface irregular, wrinkled. Dorsal lobe broader, low, attached to dorsal wall of renal chamber, without intestinal connections; surface with several transversal folds.

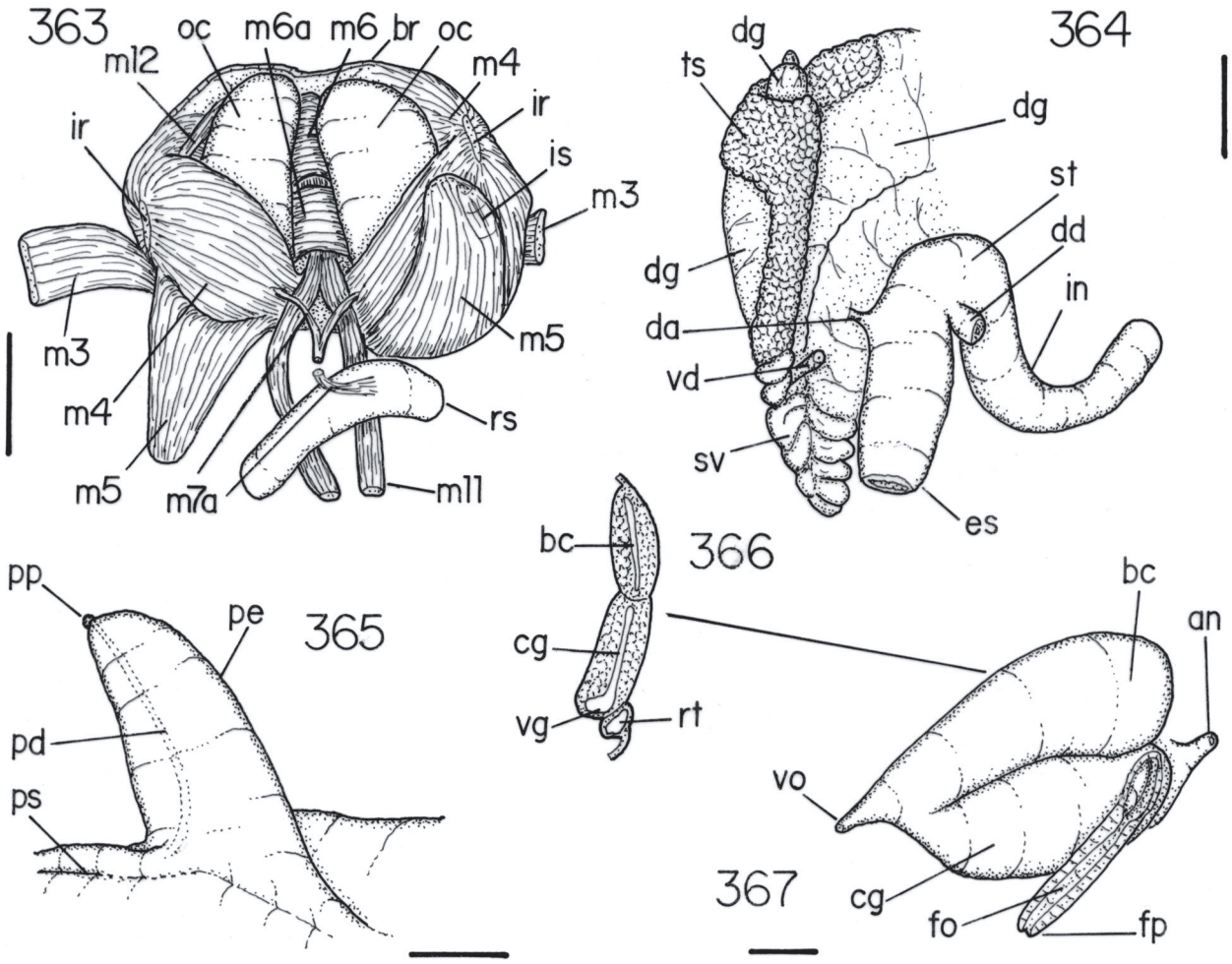
Visceral mass (Fig. 358). Organization similar to that of *C. signatum*, but proportionally smaller. Small chamber protecting right extremity of digestive gland (similar to that of *Pseudocyphoma intermedium*) present.

Digestive system (Figs. 360-364). No oral tube gland. Buccal mass characters similar to those of *C. signatum*, following distinctive or notable attributes. Jaw plates thin, slightly large, triangular (Fig. 362). Dorsal folds somewhat narrow; their furrowed part with 3 or 4 oblique furrows. Aperture of salivary glands in middle level of anterior dorsal folds region. Odontophore muscles (Figs. 361, 363): **m1a**, **ma** and **m2** absent; **m6a** broad; **m11** pair narrow; **m12** pair similar to those of *M. moneta*. Radular sac shorter than buccal mass length. Radular nucleus also broad and bifid (Fig. 361). Radular teeth with some similar attributes as those of preceding ovulids (Fig. 91), with following remarks: rachidian tooth broad and short, with 11 irregularly sized cusps, central cusp larger, remainder alternate between larger (about half of central cusp size) and small cusps, outer cusp pair larger (great variation along same ribbon present); lateral tooth narrow and tall, curved inwards, tip sharp pointed, about 4 small cusps along middle region of outer edge; marginal teeth also brooch-like as in preceding ovulids; inner marginal with about 6 long and slightly broad cusps; outer marginal broader, with about 40 tall cusps, lateral cusps becoming gradually very slender. Esophagus with similar characters to those of *M. zebra*, but shorter, other notable features following (Figs. 361, 362). Pair of pouches broad, diverticle-like, inner surface covered by transversal, narrow, low folds. Esophageal gland short. Right esophageal fold tall, covering esophageal gland aperture. Stomach organization (Fig. 364) similar to that of *C. signatum*. Intestine narrow, running sinuously edging at left of anterior digestive gland region and at right kidney (Fig. 360). Anus at short distance from kidney, siphoned, small, posterior removed from anal siphon.

Genital system. **Male**. Visceral structures (Fig. 364) similar in features to those of *M. zebra*, except for fewer and broader loops of seminal vesicle. Vas deferens running from seminal vesicle to penis base (passing through triangular sinus) altogether closed (tubular), protruded on mantle floor. Penis (Figs.



Figs. 357-362, *Simnialena uniplicata* anatomy: **357,** head-foot, male, lateral-right view; **358,** pallial cavity roof and visceral mass, male, ventral view; **359,** pallial roof, transversal section in middle level of posterior osphradium branch; **360,** kidney and pericardium region, both opened longitudinally, ventral view, gill shown as in situ; **361,** foregut, lateral-left view; **362,** dorsal wall of buccal mass and esophagus, ventral view, odontophore removed, esophagus opened longitudinally. Scales = 1 mm.



Figs. 363-367, *Simnialena uniplicata* anatomy: **363,** odontophore, ventral view, radula removed and partially shown down, both cartilages deflected, right m5 (left in fig.) deflected posteriorly; **364,** visceral mass and middle digestive tubes, ventral view, stomach slightly deflected; **365,** penis and its basal region, lateral view; **366,** pallial oviduct, transversal section of its middle region; **367,** same, ventral view, some adjacent structures also shown. Scales = 0.5 mm.

357, 365) short, flattened, base broad, gradually narrows, tip rounded with a small terminal papilla. Penis duct entirely closed (tubular), running close to posterior penis margin, opens on papilla tip.

Female. Visceral structures similar to those described for *M. zebra*. Pallial oviduct organization (Figs. 366, 367) close to that of *C. signatum*, except for terminal insertion of visceral oviduct, albumen gland not so clear and by seminal receptacle missing. Vaginal tube running beyond anterior end of capsule gland perpendicularly, towards left, as a tube. Genital pore small, papilla-like, close to mantle floor.

Measurements of shells (in mm). MZSP 29233: 10.4 by 4.0; 7.5 by 3.0.

Distribution. From Florida, USA to São Paulo, Brazil.

Habitat. On gorgonians up to 37 m depth.

Material examined. BRAZIL; **Rio de Janeiro**; Angra dos Reis, MZSP 34832, 20 shells (Coltro leg. 2001). **São Paulo**; São Sebastião and Ilha Bela, MZSP 29233, 8 specimens (A. Barreto col., 1979); Araçá Beach, MZSP 29228, 1♂ (Montouchet col.). Between Itajai, SC, and Santos, MZSP 30847, 17 specimens (Fishermen col., o. t., C. Magenta leg. 1999).

Discussion. The recently species *S. ilhabelaensis* Fehse, fits among the shell variation found in examined specimens of *S. uniplicata* (color plate Fig. 89), being considered only a form of the species. Besides, specimens with typical shell fashion of *S. ilhabelensis, S. antillarum* (sensu Fehse, 2001), and many others, were examined and revealed a uniformity of soft parts characters. An example of shell variation of *S. uniplicata* is shown in the color plate (c.p.) Fig. 89, in specimens collected in less than 100

km of geographic range. The color varies from brown (c.p. Figs. 89a, l), to yellow (c.p. Figs. 89g, h), and the more common purple (c.p. Fig. 89, remainder specimens). The size varies from more than 10 mm (c.p. Fig. 89b) to half of this length (c.p. Figs. 89c, d). The shell figured in c.p Fig. 89f is virtually identical to the representation of *S. antillarum* of Fehse (2001, fig. 5), as well as the c.p. Fig, 89m to *S. ilhabelensis* of same paper (fig. 4).

Genus *Cymbula* Cate, 1973

(Type species *Ovula acicularis* Lamarck)

N.B.: David Reid, from BMNH, has indicated that the name *Cymbula* is pre-occupied by *Cymbula* H. & A. Adams, 1854, a Patellidae. As *C. acicularis* is the type species of the Cate's genus, it is maintained herein until the resolution of this nomenclatural problem.

Cymbula acicularis (Lamarck, 1810)

(Figs. 47, 48, 92, 368-372)

Synonymy see Cate (1973: 81). Complement:

Neosimnia acicularis: Abbott, 1954: 182 (pl. 7, fig. a); Warmke & Abbott, 1962: 92 (pl. 16, fig. l); Rios, 1970: 61; Humfrey, 1975: 107; Main, 1982: 257.

Simnia acicularis acicularis: Schilder & Schilder, 1971: 76.

Cymbula acicularis: Cate, 1973: 81 (fig. 181); Trew, 1987b: 27.

Cymbula bahamaensis Cate, 1973: 80-81 (fig, 178) (Bahamas).

Simnia acicularis: Abbott, 1974: 151-152 (fig. 1656); Rios, 1975: 73 (pl. 20, fig. 29); Oliveira *et al*., 1981: 139; Bandel, 1984: 85-86 (fig. 144; pl. 7, fig. 7; pl. 8, fig. 2); Jong & Coomans, 1988: 65; Merlano & Hegedus, 1994: 168 (pl. 52, fig. 623); Abbott & Morris, 1995: 197 (pls. 9, 53).

Simnia acicularia: Abbott & Dance, 1983: 100 (fig.);

Simnia (Cymbula) acicularis: Rios, 1985: 66 (pl. 23, fig. 290); 1994: 76 (pl. 25, fig. 293).

Description

Shell (Figs. 47, 48). Long and slender. Other details in Cate (1973: 81).

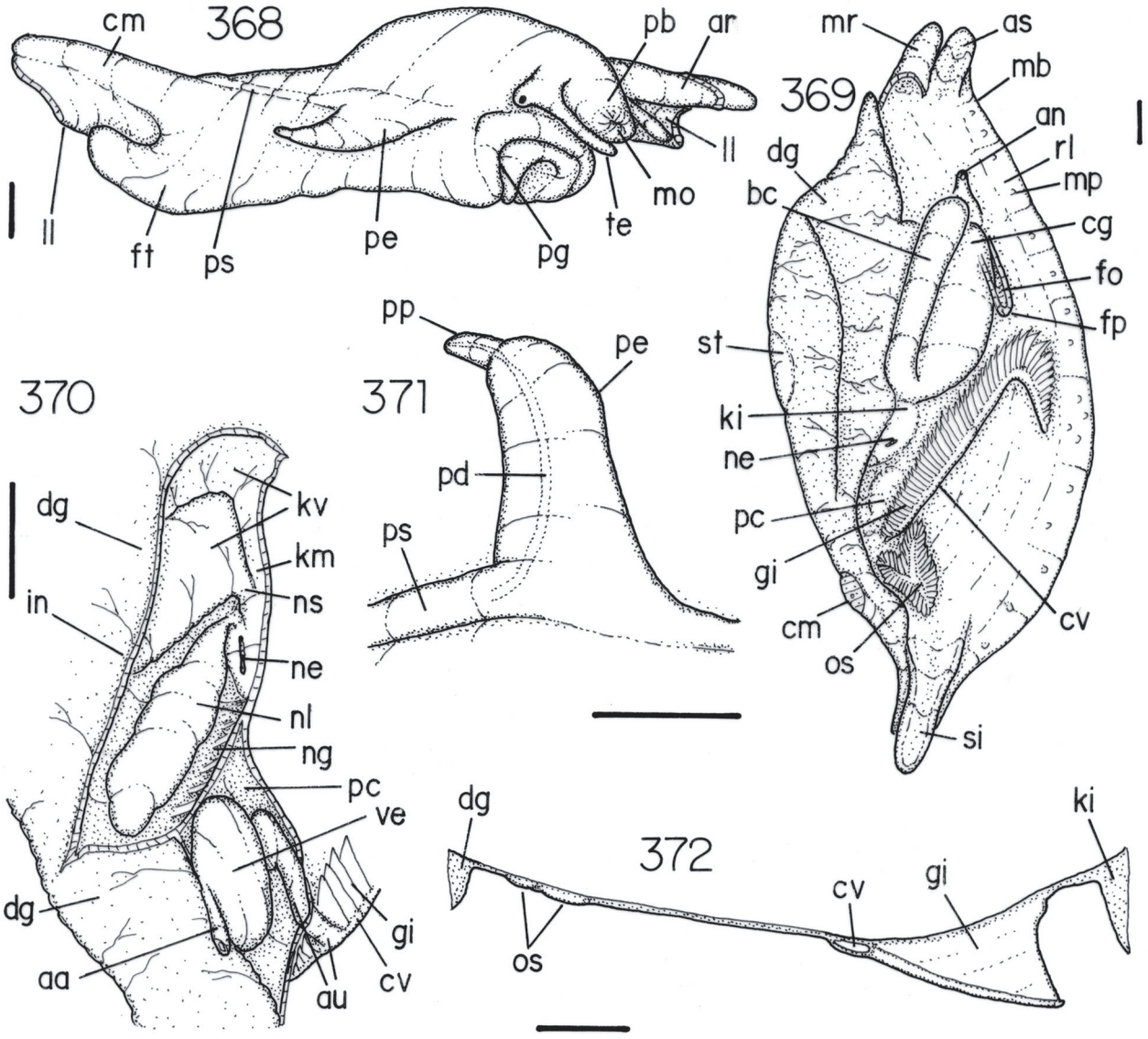
Head-foot (Fig. 368). Very similar characters to those of *S. uniplicata*, including outstanding head. Differs in lacking transversal folds in propodium and by longer posterior projection.

Mantle organs (Figs. 369, 372). Mantle lobes narrow. Papillae very small, simple, of uniform size, sparse distributed along lobes. Incurrent and anal siphons long, of almost same size (anal siphon slightly smaller), edges smooth. Pallial organs features very similar to those of *S. uniplicata*, distinctive or notable attributes following. Pallial cavity dislocated to left. Osphradium small, low, asymmetric, close to gill posterior end. Gill long, narrow, mostly straight, curved only in its anterior region. Gill filaments tall, apex almost central, slightly dislocated to right. Hypobranchial gland thinner, white, with immersed transversal septa of mantle.

Circulatory and excretory systems (Fig. 370). Heart characters similar to those of *S. uniplicata*. Kidney characters also similar to those of anterior species, except for smoother, most solid renal lobe (without divisions into 2 lobes).

Digestive system. Buccal mass characters similar to those described for *S. uniplicata*, except for narrower **m3** and **m12**. Radular teeth characters similar to those of *S. uniplicata*, differing in very longer rachidian tooth central cusps. Esophagus features also similar to those of anterior species, differing only in longer pair of pouches, with localization posterior to nerve ring. Stomach and intestine attributes also close to those of *S. uniplicata*, but intestine less sinuous, broader after kidney. Anus small, far from anal siphon.

Genital system. **Male** (Figs. 368, 371). Visceral and pallial organs characters similar to those of *S. uniplicata*, including form of seminal vesicle and closure of pallial and penis sperm ducts. Penis differs by larger apical papilla.



Figs. 368-372, *Cymbula acicularis* anatomy: **368,** head-foot, male, lateral-right view; **369,** pallial cavity roof and visceral mass, female, ventral view; **370,** kidney and pericardium region, both opened longitudinally, ventral view, some gill filaments on auricle removed; **371,** penis and its basal region, lateral view; **372,** pallial roof, transversal section in middle level of posterior osphradium branch. Scales = 0.5 mm.

Female (Fig. 369). Visceral and pallial structures also similar in characters to those of *S. uniplicata*, including details of pallial oviduct and vaginal tube.

Measurements of shells (in mm). AMNH 163747 ♀ : 12.0 by 3.5.

Distribution. Florida, USA, to Rio de Janeiro, Brazil.

Habitat. On gorgonians, from 2 to 100 m depth.

Material examined. CUBA; 24º25'N 82º43'W, 27 m depth, UMML 3010898, 1♂ , 1♀ (otter trawl, 27/iv/1969). BAHAMAS; New Providence Island, S side of Pirate's Nest, 1 m depth, AMNH 163747, 1♂ , 5♀ (R.W. Miner leg., 10/iii/1930).

Genus *Jenneria* Josseaume, 1884

(Type species: *Cypraea pustulata* Lightfoot)

Jenneria pustulata (Lightfoot, 1786)

(Figs. 42, 43, 93-95, 373-389)

(Color plate Figs. 31, 32, 84, 85)

Synonymy see Cate (1973: 5). Complement.

Jenneria pustulata: Burch, 1964: 88; Asaro, 1969: 182-184 (figs. 1-3); Keen, 1971: 799 (fig. 940; pl. 18); Abbott, 1974: 151 (pl. 3, fig. 1652); Oliveira *et al*., 1981: 138; Trew, 1987b: 23.

Jenneria pustulata pustulata: Schilder & Schilder, 1971: 71.

Cryptopterina (Jenneria) pustulata: Biraghi, 1988: 17 (figs.).

Description

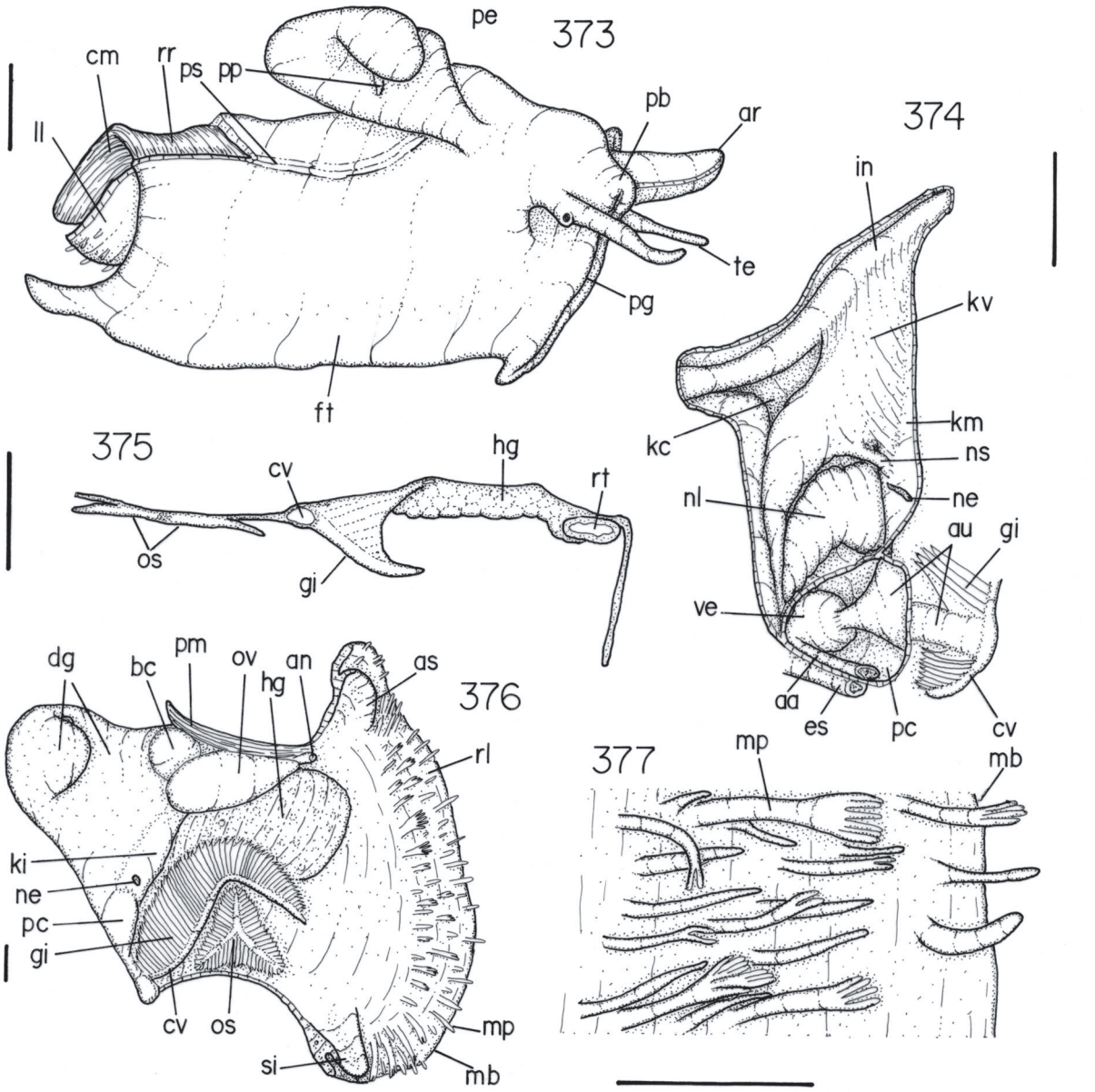
Shell (Figs. 42, 43; color plate Figs. 31, 32, 84, 85). Dorsal surface covered by nodes, ventral surface covered by transversal folds originated from aperture teeth. Other details in Cate (1973: 5, fig. 2).

Head-foot (Fig. 373). Characters similar to those of *M. zebra*. Anterior projection long. Anterior edge of foot, with pedal gland furrow, broader, with small lateral projections.

Mantle organs (Figs. 375-377). Mantle lobes color pale beige with large, dark brown, irregular, coalescent spots. Several papillae randomly distributed, but more concentrated near to siphons. Papillae in general slender and long, with 3 main types (Figs. 376, 377): 1) simple; 2) with tip bifid; 3) with multi-papillate tip (brush-like). Incurrent and anal siphons of almost same size and large. Pallial organs (Fig. 376) constituted similarly to those of *M. zebra*, distinctive or notable features following. Osphradium slightly far from siphon and close to gill. Osphradium filaments with pointed lateral tip. Gill curved, broader posteriorly. Anterior end of ctenidial vein with short portion without filaments. Gill filaments arched, base broad, tip narrow, curved to right (Fig. 375). Hypobranchial gland thick, color cream, surface transversal folded, pallial transversal septa through this gland present.

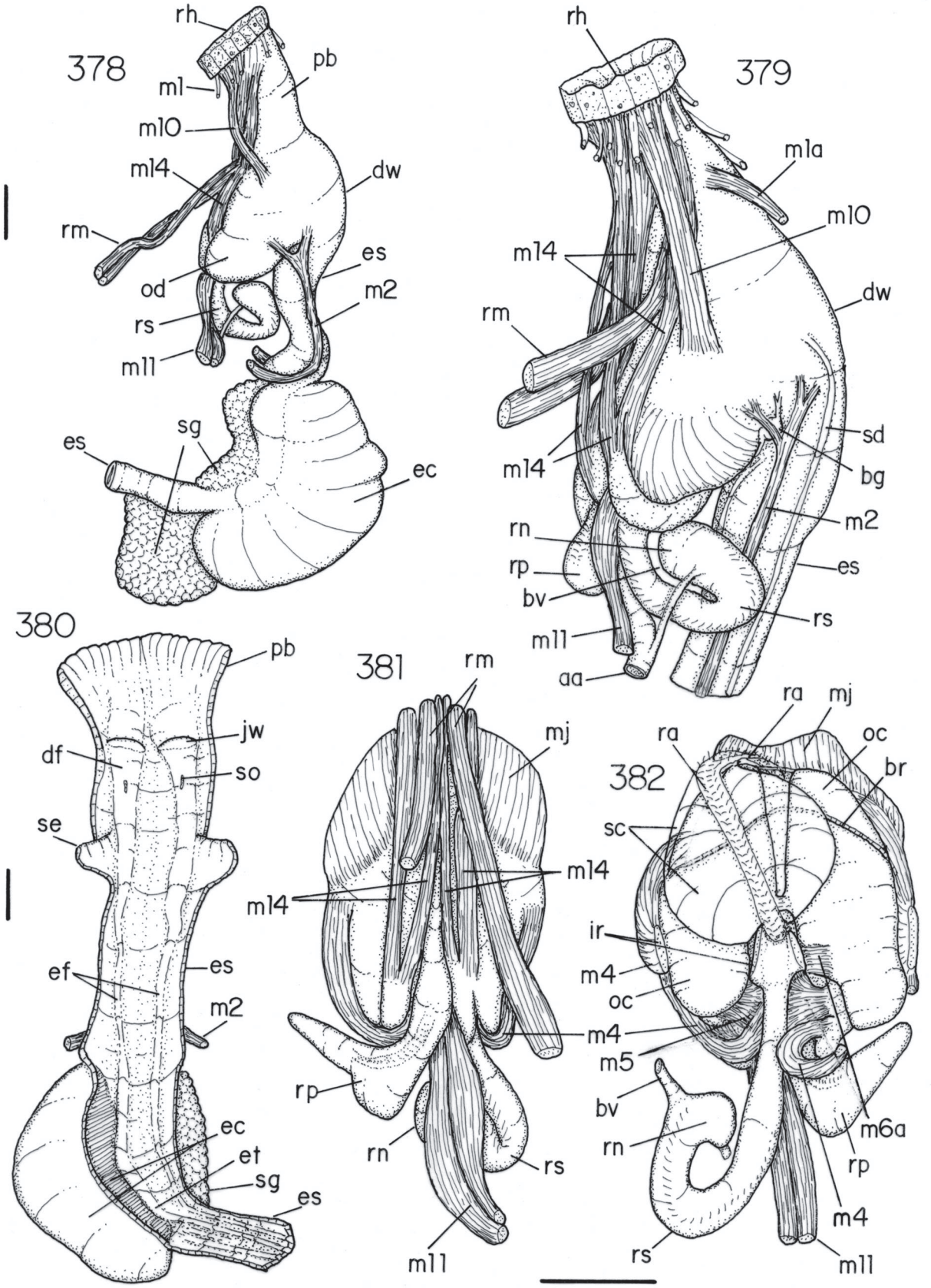
Circulatory and excretory systems (Fig. 374). Heart attributes similar to those of *M. zebra*, except for connection of auricle in anterior wall of pericardium (just posterior to its pallial, narrow portion running dorsal to gill). Kidney features also similar to those of *M. zebra*, differing by following characters. Accessory lobe of nephridial gland with smooth surface, no clear vessel inserting close to nephrostome. Renal lobe flattened and triangular, color cream; a short anterior portion connected to intestine. Renal lobe attached to dorsal and ventral kidney chamber walls in anterior half, and as a tall fold in posterior half, which left margin possesses a vessel inserted at right and ventral to nephrostome.

Digestive system (Figs. 378-384, 388). Proboscis and retractor muscles with same characters as those of *M. zebra*. Buccal mass somewhat different from those of all preceding species, as follows. Pair of jaw plates very narrow and thin. Pair of dorsal folds narrow, furrowed part missing. Aperture of salivary glands as a small slit located in middle region of each fold (Fig. 380). Odontophore muscles (Figs. 378, 379, 381-384): **m1a** pair present; **m1b**, **m1c**, **ma**, **m3**, not developed; **m2** pair as those of *M. zebra*; **m4** and **m5** pairs similar to those of *M. zebra*, but with ventral portion of m4 thick; **m6** very small, thin and narrow; **m6a** similar to m6; **m7** absent; **m10** pair narrow, located laterally; **m11** pair broad, inserted very anterior, without muscular part surrounding radular sac (only a short membrane); **m14** pair narrow, originating double (part close to median line, and part lateral to retractor muscles of proboscis) (Figs. 379, 381), running towards posterior, both branches of each m14 unite close to insertion, insertion in ventral-posterior region of m4 close to median line. Odontophore cartilages flattened, with a pair of median projections just where m6 and m6a insert (Fig. 383). Radula with about double length than that of buccal mass. Radular nucleus simple. Radula, up to in-use area (Figs. 93, 94) (along connection of subradular cartilage) running in usual way. A long portion of radula beyond this part present. In this portion (Fig. 95), subradular cartilage

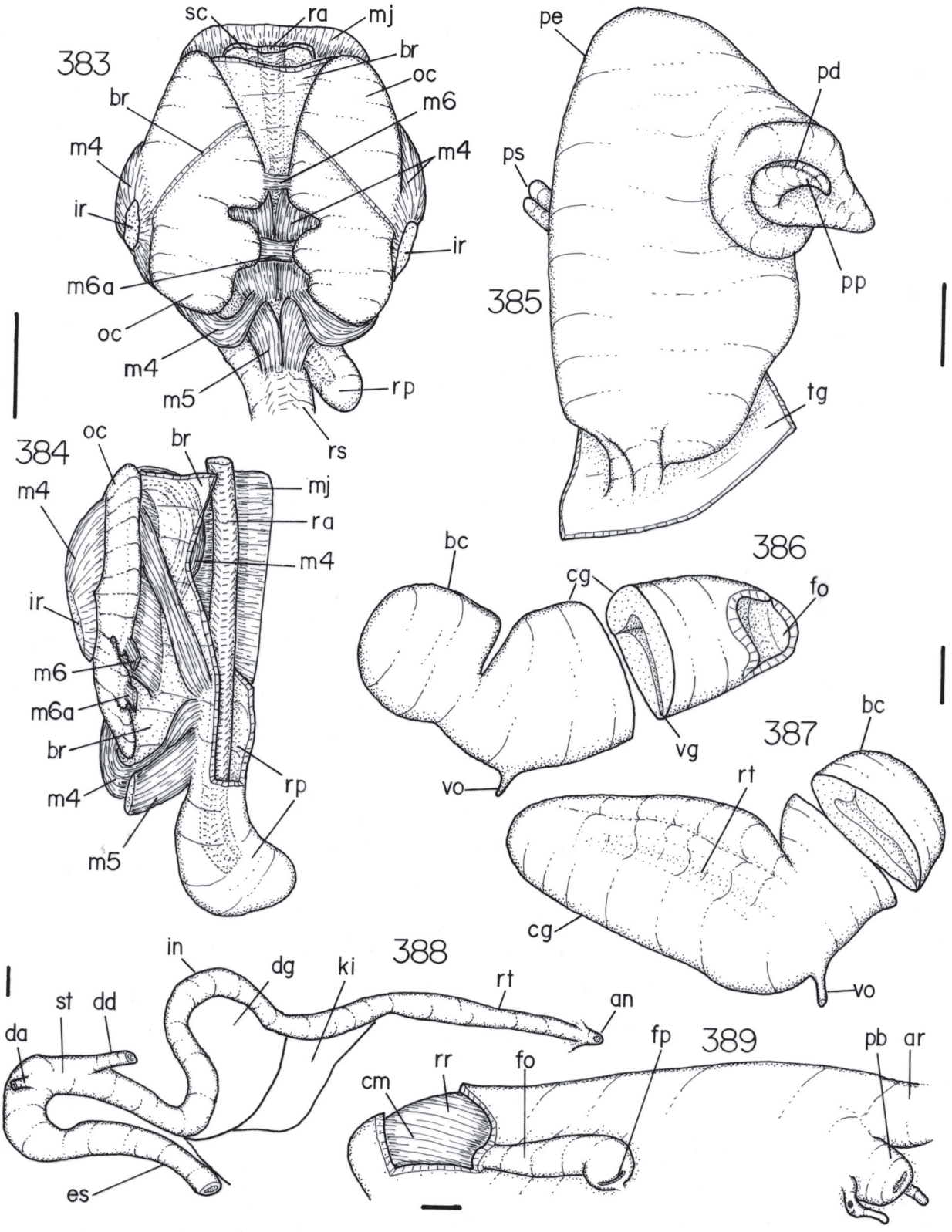


Figs. 373-377, *Jenneria pustulata* anatomy: **373,** head-foot, male, lateral-right view; **374,** kidney and pericardium region, both opened longitudinally, ventral view, some gill filaments on auricle removed; **375,** pallial roof, transversal section in middle level of posterior osphradium branch; **376,** pallial cavity roof and visceral mass, female, ventral view; **377,** right mantle lobe, outer view, detail of its middle region. Scales = 2 mm.

narrows and, jointed with radula, running through odontophore in a special space between subradular membrane (with reinforcement of m4 ventral part) and oral-jaw muscles (mj) platform (Figs. 382, 384). Radula still running by an accessory sac with walls transparent and thin, located ventral to m1 connection to radular sac, towards posterior (Figs. 379, 381, 384: **rp**). Radula also very different from preceding species, as follows (Figs. 93-94): rachidian tooth broad, short, with 5 broad cusps in central level of its length, central cusp slightly larger than neighbors; two pairs of lateral teeth; inner lateral tooth with base slightly rectangular, two projections turned internally, inferior projection flattened with margin rounded, superior projection as a strong hook; outer lateral tooth almost a simple rectangular platform; inner and outer marginal teeth similar with each other, long, slender, flattened, with about 6 cusps long, pointed, curved and distal. Radular part after in-use area with marginal teeth missing and with superior, hook-like projection of inner lateral tooth lost (Fig. 95). Esophagus, esophageal and salivary glands characters (Figs. 378, 380) similar to those of *M. zebra*, but with right inner fold tall, covering part of esophageal gland aperture. Stomach narrow and U-shaped (Fig. 388), inner surface



Figs. 378-382, *Jenneria pustulata* foregut: **378,** whole left view; **379,** same, detail of buccal mass; **380,** dorsal wall of buccal mass and esophagus, ventral view, odontophore removed, esophagus opened longitudinally; **381,** odontophore, ventral view, note distal radular sac (rp); **382,** same, both cartilages deflected, radular ribbon and subradular cartilage partially removed, with structures covered by them seen by transparency. Scales = 1 mm.



Figs. 383-389, *Jenneria pustulata* anatomy: **383,** odontophore, ventral view, both cartilages deflected, middle region of radula removed, remaining radular sac and its distal region enclosed within distal radular sac; **384,** same, right half, left view; **385,** penis and its basal region, dorsal view; **386,** pallial oviduct, ventral view, with a transversal section artificially done in capsule gland; **387,** same, dorsal view, transversal section in bursa; **388,** middle and distal digestive tubes, ventral view, seen as in situ, some adjacent structures also shown; **389,** pallial floor, female, dorsal-slightly right view, mantle and oviduct extracted. Scales = 1 mm.

smooth, without folds. Ducts to digestive gland located at some distance from each other and turned to opposite side. No inner septa in duct to posterior lobe of digestive gland. Intestine narrow, sigmoid in visceral mass portion crossing anterior region of digestive gland (Fig. 388); after runs almost straight forwards, passing in right margin of kidney and of pallial cavity (Fig. 374); in females rectum running dorsal to pallial oviduct. Anus small, siphoned, posterior removed from anal siphon.

Genital system. **Male**. Visceral and pallial structures similar in characters as those of *M. zebra*. Penis large (Figs. 373, 385), base flattened and thick; after base, penis twist about 90º still broad and flattened. Penis tip a projected spiral, located in middle level of dorsal margin. Penis groove running in dorsal margin of basal and middle penis regions and in inner margin of spiral tip. A portion of penis tip projected beyond penis groove end as a flattened, triangular papilla.

Female. Visceral structures of similar characters as those of *M. zebra*. Pallial oviduct (Figs. 376, 386, 387) V-shaped, large, located also attached to pallial floor. Narrow visceral oviduct inserts almost in middle level of pallial oviduct left margin. Bursa copulatrix projected obliquely towards posterior and right, circular, flattened, walls thick glandular; connection with capsule gland as an anterior constriction. Capsule gland long (about twice bursa length), elliptical, flattened, walls thick glandular. Vaginal tube in left junction of capsule gland laminas, very narrow, becoming broader after capsule gland end, in this region running slightly perpendicular in floor of pallial cavity, up to half distance between capsule gland and head (Fig. 389). Genital pore a slit close to pallial floor (Fig. 389).

Measurements of shells (in mm). AMNH 276915: Fig 42: 22.0 by 13.7; 1) 20.3 by 12.5; 2) 20.1 by 11.8.

Distribution. Gulf of California to Ecuador.

Material examined. PANAMA; Cebaco Island (Pacific), AMNH 276915, 13 specimens (Walter Sage col., 28/i/1991).

Family Triviidae

Genus *Niveria* Jousseaume, 1884

(Types species *Cypraea nivea* Gray = *Trivia nix* Schilder)

Niveria pediculus (Linné, 1758)

(Figs. 59, 60, 97, 98, 390-409)

(Color plate Figs. 19-21; 34, 54)

Synonymy see Cate (1979: 48) and Leal (1991: 103)

Cypraea pediculus Linné, 1758: 724 (Loc: Jamaica).

Trivia (Trivia) pediculus: Olsson & Harbison, 1953: 265 (pl. 60, figs. 1-1a).

Trivia pediculus: Abbott, 1954: 177 (pl. 21, fig. bb); Warmke & Abbott, 1962: 90 (pl. 16, fig. f); Matthews & Rios, 1967: 96; Kempf & Matthews, 1969: 91; Rios, 1970: 60; Humfrey, 1975: 103 (pl. 22, fig. 1); Matthews & Matthews, 1976: 74 (fig. 1); Oliveira *et al*., 1981: 138; Jong & Coomans, 1988: 64; Leal, 1991: 103; Calvo, 1987: 105 (fig. 65); Abbott & Morris, 1995: 195-196 (pls. 11, 53).

Niveria (Niveria) pediculus pediculus: Schilder & Schilder, 1971: 20; Rios, 1985: 63 (pl. 23, fig. 281).

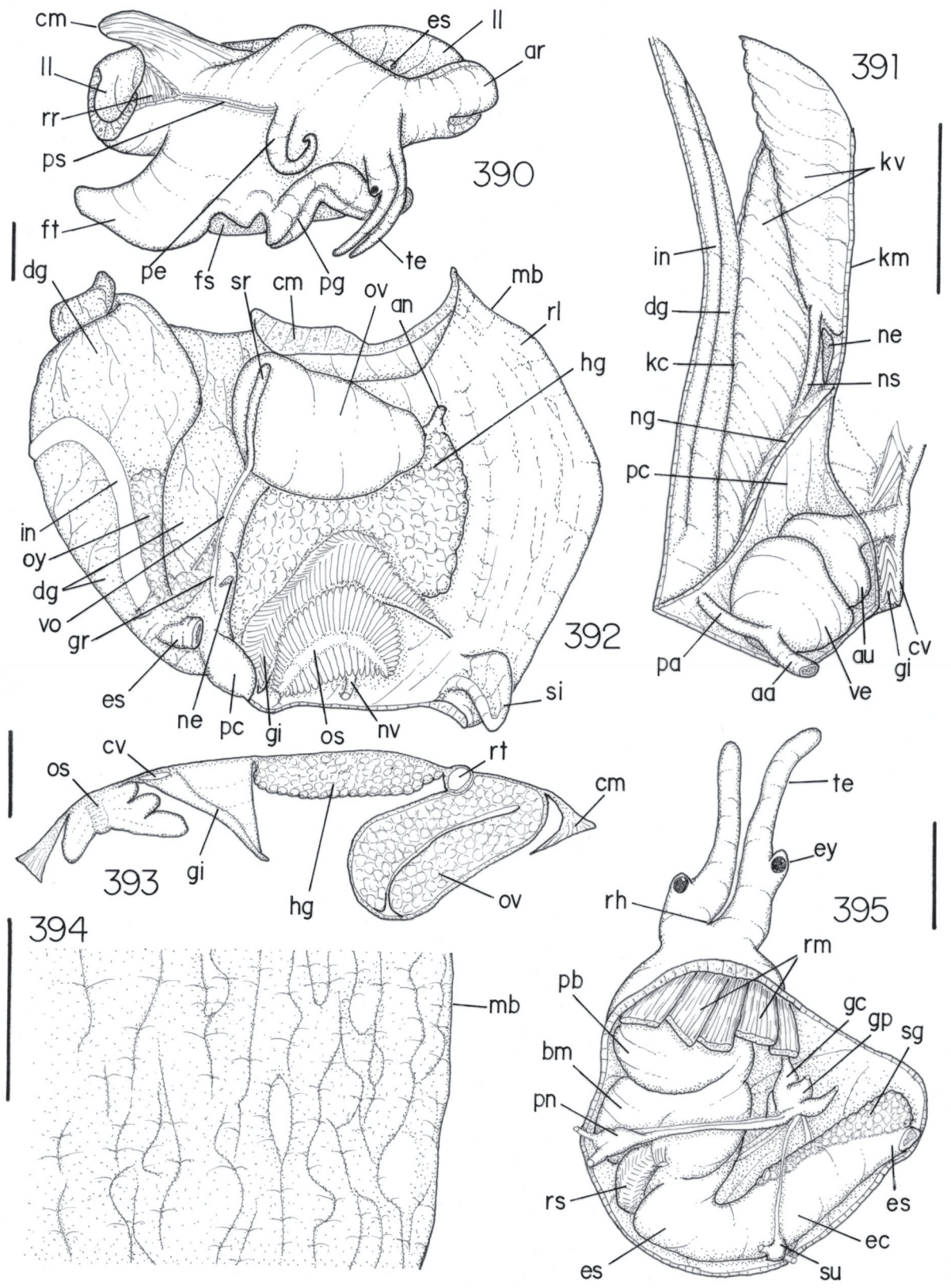
Trivia (Pustula) pediculus: Abbott, 1974: 147 (pl. 3, fig. 1623); Rios, 1975: 71 (pl. 20, fig. 289).

Niveria (Ellatrivia) pediculus pediculus: Cate, 1979: 48-49 (figs. 55, 55a).

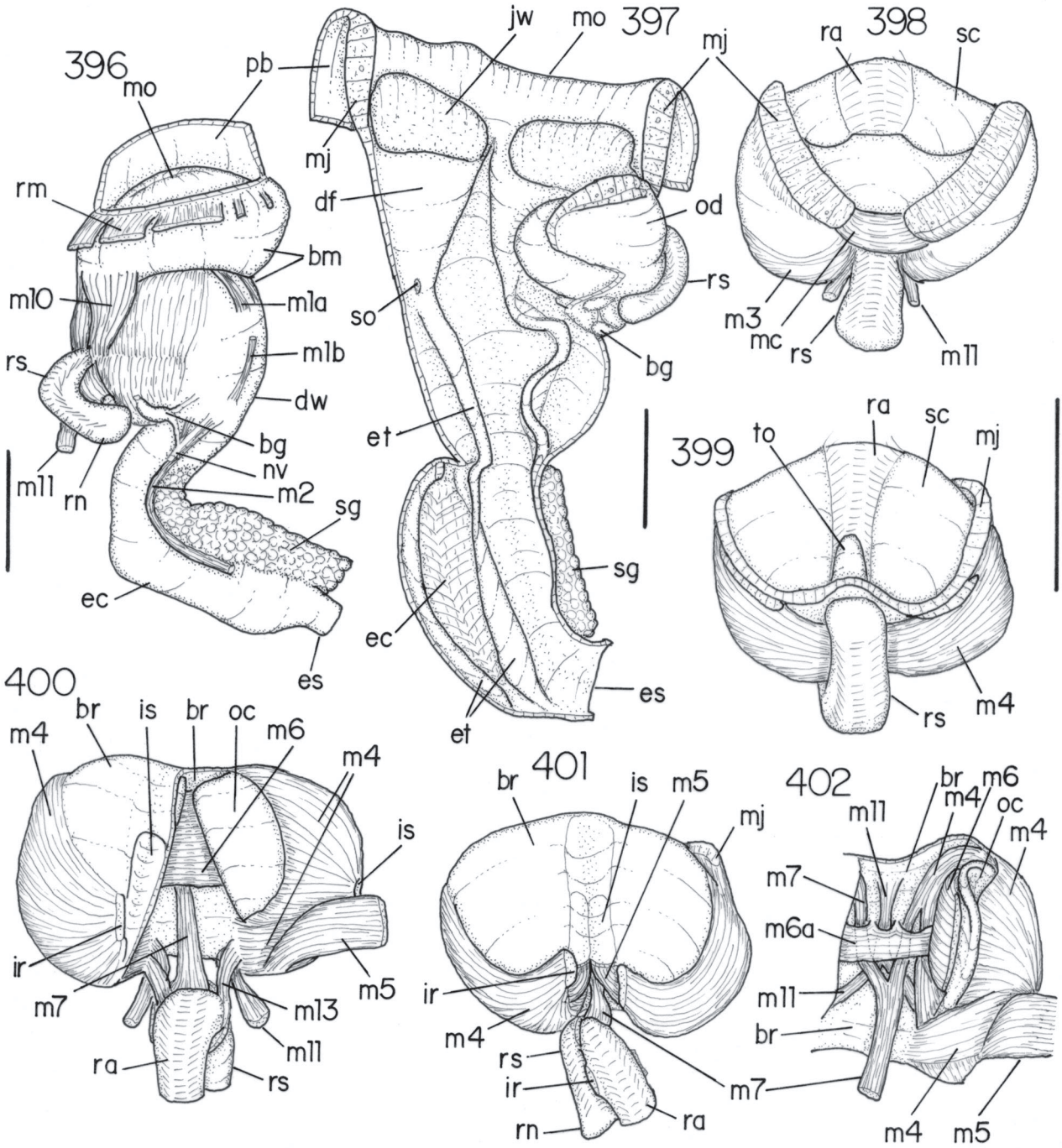
Trivia pedicula: Abbott & Dance, 1983: 83 (fig.);

Niveria pediculus: Trew, 1987a: 6.

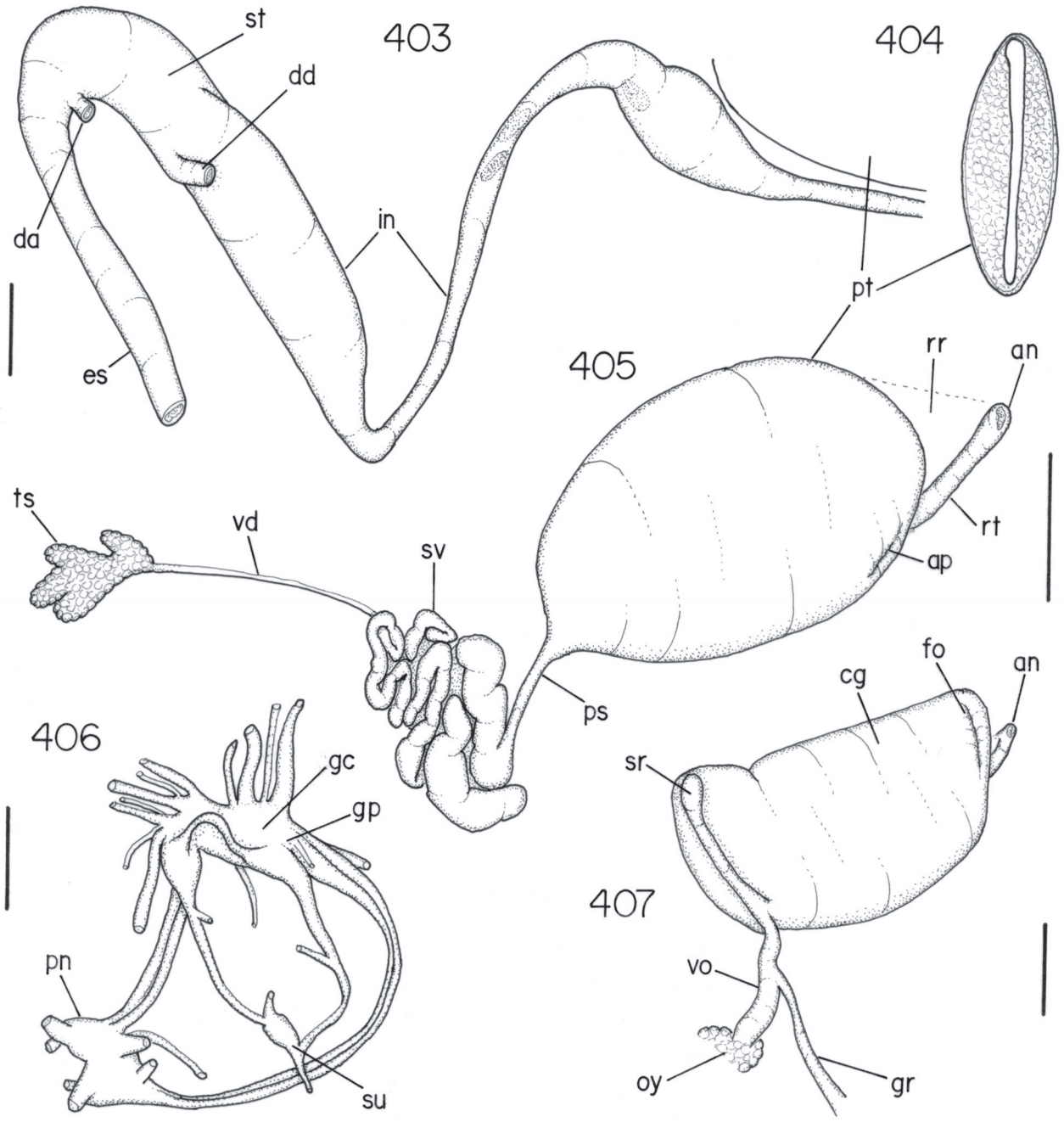
Trivia (Niveria) pediculus: Rios, 1994: 77 (pl. 26, fig. 296); Merlano & Hegedus, 1994: 165-166 (pl. 51, fig. 610).



Figs. 390-395, *Niveria pediculus* anatomy: **390,** head-foot, male, lateral-right view; **391,** kidney and pericardium region, both opened longitudinally, ventral view, some gill filaments on auricle removed; **392,** pallial cavity roof and visceral mass, female, ventral view; **393,** pallial roof, transversal section in middle level osphradium; **394,** right mantle lobe, outer view, detail of its middle region; **395,** head and haemocoel, ventral view, foot and columellar muscle removed. Scales = 1 mm.



Figs. 396-402, *Niveria pediculus* foregut: **396,** right view; **397,** dorsal wall of buccal mass and esophagus, ventral view, odontophore removed, esophagus opened longitudinally; **398,** odontophore, ventral view; **399,** same, dorsal view; **400,** same, ventral view, both cartilages deflected, right muscles (left in fig.) most deflected, radula deflected down and only part shown; **401,** same, with simple extraction of radular structures; **402,** same, right half, cartilage deflected, m6 sectioned. Scales = 1 mm.

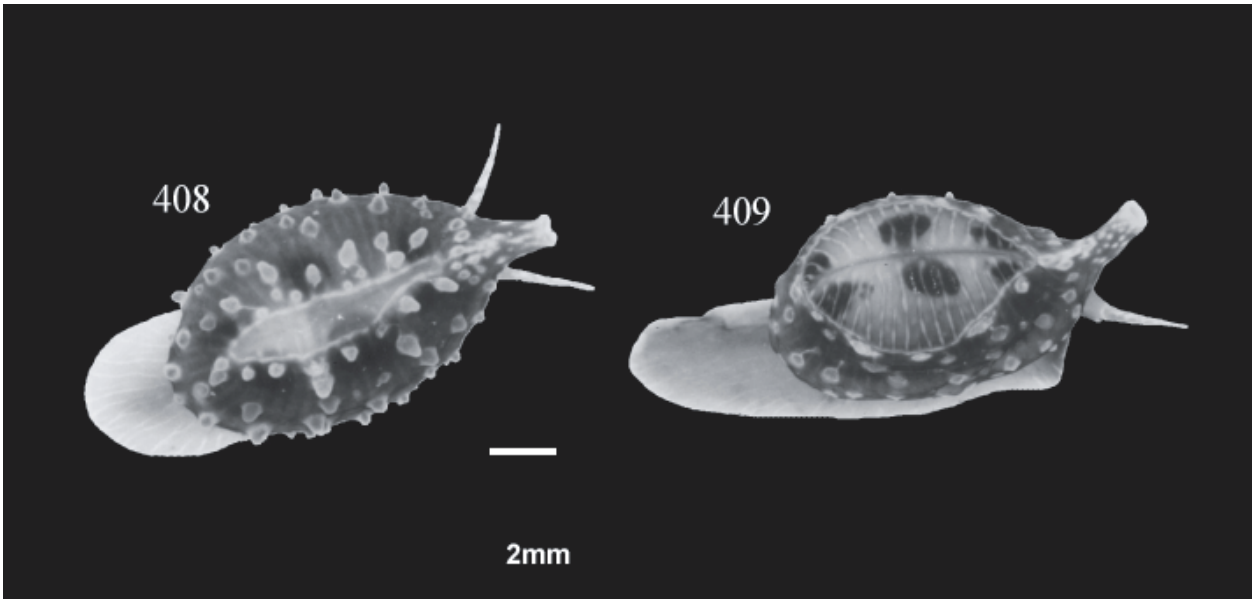


Figs. 403-407, *Niveria pediculus* anatomy: **403,** middle and distal digestive tubes (except anal region), ventral view, seen as in situ, some adjacent structures also shown; **404,** prostate, transversal section in its middle region; **405,** male genital structures, ventral view, seen as in situ, some adjacent structures also shown; **406,** central nervous system, dorsal view; **407,** female genital structures, ventral view, seen as in situ, some adjacent structures also shown. Scales = 1 mm.

Description

Shell (Figs. 59-60; color plate Figs. 34, 54). Os small size, involute. Dorsal transverse folds interrupted in middle level. Ventral transverse folds as continuation from aperture teeth. Immature specimens with white, smooth surfaced, thin shell. More details in Abbott (1974: 147), Cate (1979: 48-49).

Head-foot (Figs. 390, 395, 409). General characters similar to those of *M. zebra*, but shorter outline. Color beige with very small dark brown spots in head and dorsal foot surface. Anterior projection also present. Columellar muscle with a projection posterior (certainly homologous to pallial muscle of cypraeids. Anterior foot edge broad, with lateral projections. Pedal gland furrow in entire anterior edge.



Figs. 408-409, *Niveria pediculus* live specimen in activity showing mantle functional papillae: **408,** dorsal view, mantle covering most of shell; **409**, dorsal- slightly lateral-right view, with small portion of the shell shown. Scale = 2 mm.

Mantle organs (Figs. 392-394, 408, 409). Mantle lobes broad, outer surface almost smooth, presenting only irregular undulations (Fig. 394). Mantle lobes color pale brown, with sparse circular pale cream spots; some specimens with sparse small reddish spots. Mantle lobes possess some functional papillae, appearing during activity (Figs. 408, 409, color plate Figs. 19-21), which disappear during contraction. Siphon narrow and long, with smooth margins. Anal siphon absent. Pallial organs organization and localization (Fig. 392) somewhat similar to those of *M. zebra*, distinctive or notable features following. Osphradium bipectinate of normal fashion, with a single axis, elliptical, large, curved. Osphradium filaments asymmetrical, left filaments smaller, fewer, simple, slightly projected to left and ventral; right filaments larger, scalloped, with 3 successive larger projections, distal projection towards right and ventral, covering left part of gill. Gill narrow, curved, edging right osphradium margin and shortly longer than it. Gill anterior edge sharp, with a small portion of ctenidial vein beyond filaments anterior end. Gill filaments tall, apex projected to right, both margins almost straight (Fig. 393). Hypobranchial gland very thick, white, occupies most of broad surface between gill and rectum. Pallial gonoducts occupy considerable space of mantle cavity right region. Rectum very narrow, edge left margin of pallial gonoducts and short distance beyond them. Anus small, slightly siphoned, far from mantle edge.

Circulatory and excretory systems (Fig. 391). Heart characters and localization somewhat similar to those of *M. zebra*, except in being more anterior, with auricle connected directly to ctenidial vein sub-terminal region (i.e., auricle does not runs narrowly dorsal to gill, but so entire pericardium does). Kidney characters and localization also slightly similar to those described for *M. zebra*, with notable or distinguish features following. Nephridial gland white, massive and tall, occupying most of membrane between kidney and pericardium. Two yellowish lobes of kidney. Dorsal lobe thin, surface uniform with discrete oblique furrows, located in dorsal wall of kidney chamber. Ventral lobe somewhat thicker, connected to intestine in anterior-right region, attached to membrane between kidney and pallial cavity in middle and right regions, right end close to nephrostome; a conspicuous vessel running dorsal to nephrostome.

Visceral mass (Fig. 392). Organization somewhat similar to that of *M. zebra*, slightly less involute (apex not covered by next whorls).

Digestive system (Figs. 395-403). Proboscis short, slightly similar characters to those of *M.*

zebra, but with closer similarity to a pleurembolic proboscis (a buccal mass protruded inside in retracted condition) (Fig. 396). Proboscis retractor muscle (**rm**) multiple, in general 2 pairs broad inserted along ventral and lateral proboscis surface (Fig. 395), some extra muscles common. Pair of jaw plates very large (Fig. 397), each one slightly rectangular, thick, iridescent, yellow, tall anterior cut-edge, separated with each other. Dorsal folds broad anteriorly, gradually narrow, no furrowed part (Fig. 397). Aperture of salivary gland small, posterior. Dorsal chamber shallow, smooth. Odontophore muscles (in comparison with those of *M. zebra*) (Figs. 396, 398-402): **m1a** pair present; **m1b** pair narrow; **mj** platform no so clear; **mc** similar; **m2** pair similar; **m3** pair similar localized, but thin and divided into 2 lateral branches except in region just dorsal to radular sac; **m4** pair more similar to those of other basal caenogastropod than those of cypraeids, surrounding most of odontophore cartilages (except their median surface), with ventral and dorsal branches amply connected with each other; **m5** pair thinner, not connected with its pair; **m6** longer and slightly thicker; **m6a** narrow, thin, located just dorsal to m6 posterior region, connected to dorsal subradular membrane (**br**) in 2 points, just between m7 and m11 (Fig. 402); **m7** pair similar to those of basal caenogastropods, originating in median margin of m4 dorsal branch, running attached to br towards posterior, after m6a unite with each other and penetrate in radular sac, inserting like a fan within radular sac ventral inner surface; **m10** pair similar; **m11** pair broad, separated from each other, originating also with rm, connection one in each side with radular sac just where it entrances in odontophore, within odontophore portion narrow and thin, crossing by each side of odontophore cartilages median-posterior region jointed with m4, running attached to br in direction posterior, inserting on br anterior surface; **m13**, pair of m4 accessory muscles narrow and short, originating in m4 median-posterior-dorsal region, running within radular sac, inserting in its lateral inner surface; **m14** absent. Odontophore cartilage similar to those of *M. zebra*. Radular sac short, little longer than odontophore (Fig. 396). Radular teeth (Figs. 97, 98): rachidian tooth broad and short, strongly curved, distal edge concave, 7 to 11 pointed cusps, being central cusp about double of neighbor cusps size; lateral tooth broad, tall, curved inwards, tip sharp pointed, a single cusp in inner edge and 5-7 small cusps in outer edge, both cusp assemblages far from tooth tip; inner and outer marginal teeth tall, slender, curved, similar with each other, tip sharp pointed, a single small cusp located between middle and distal thirds of inner edge. Anterior esophagus with a pair of tall and thin folds (continuation from those of buccal mass), remainder inner surface smooth (Fig. 397). Middle esophagus also with a pair of tall folds (continuation from those of anterior esophagus), both projected inwards, covering aperture of esophageal gland (Fig. 397). Esophageal gland slightly narrow, inner surface filled by 2 series of oblique septa; each septum united with its opposite pair in middle region of gland in a V-shape. Posterior esophagus long (about half of total esophageal length) narrow, inner surface smooth. Stomach U-shaped and narrow (Fig. 403). Pair of ducts to digestive gland slender, located in inner gastric curve, at some distance from each other. Digestive gland color pale yellow, occupies apical region of visceral mass and region around stomach and adjacent digestive tubes. Intestine initially broad (Fig. 403), an inner longitudinal typhlosole running in dorsal surface since duct to posterior lobe of digestive gland (inclusive through stomach), remainder intestinal inner surface smooth. Intestine running towards left and anterior though digestive gland, close to pericardium narrows and curves slightly perpendicular towards anterior and right; elliptical fecal pellets present since this region. Intestine, close to right posterior end of pallial cavity running in direction anterior, dorsal to pallial gonoducts, initially broad (about 1/3 of pallial portion) and after very narrow. Anus above described.

Genital system. **Male** (Figs. 390, 405). Testis very small, color pale cream, located close to visceral mass apex in columellar surface. Visceral vas deferens very slender, running in middle region of visceral mass ventral surface. Seminal vesicle just posterior to pericardium and kidney, successively broader and coiled, forming a slightly circular mass in ventral surface of visceral mass anterior region. Vesicle suddenly narrows and runs forward a short distance in floor of pallial cavity. Prostate gland very large, broad, somewhat flattened dorso-ventrally, walls thick glandular, inner lumen broad and flattened; insertion of vas deferens in its posterior extremity; aperture a slit in left region of triangular sinus. From prostate aperture a shallow furrow begins and runs in pallial cavity floor up to penis base. Penis slightly small, conical, curved, tapers gradually, tip slender. Penis groove in middle of ventral surface up to

penis tip.

Female (Figs. 392, 404, 407). Ovary small, color orange, located in anterior-left region of visceral mass close to columella; some sparse small portions throughout ventral surface of digestive gland. Visceral oviduct very narrow, running perpendicularly to ovary towards right and anterior, accompanied by some ovary tissue. Gonopericardial duct very narrow, inserts in visceral oviduct at short distance from its insertion in pallial oviduct. Visceral oviduct inserts in left-posterior region of pallial oviduct. Bursa copulatrix originated directly from visceral oviduct, running towards right, slender, long, tip slightly broader and rounded. A small conjunctive tissue ligament connects bursa tip with adjacent region of visceral mass. Capsule gland very large, broad, elliptical, walls thick glandular. Capsule gland connection with visceral oviduct via bursa base, this connection located in ventral surface of capsule gland posterior-left region. Capsule gland inner lumen broad and flattened. Genital aperture a slit close to pallial floor. Some females present vestigial penis in equivalent localization of males.

Central nervous system (Fig. 406). Features similar to those of *M. zebra*.

Measurements of shells (in mm). MZSP 28520: ♀ 1, 9.8 by 7.0 by 5.8; ♀ 2, 12.4 by 9.0 by 7.3; ♂ 3, 9.8 by 6.4 by 5.2.

Distribution. North Carolina, USA, to São Paulo, Brazil.

Habitat. Under rocks and corals, subtidal up to 23 m depth.

Material examined. BRAZIL; **Pernambuco**; Fernando de Noronha Archipelago (Simone & Souza Jr. col.); Porto Beach, MZSP 31186, 1 specimen (17/vii/1999); Porcos Beach, MZSP 30934, 1 specimen (21/vii/1999); Meio Beach, MZSP 31056, 1 specimen (22/vii/1999); Rata Island, Buraco do Inferno, 10 m depth, MZSP 31094, 5 specimens (19/vii/1999), Cagaras, MZSP 30948, 2 specimens (21/vii/1999), canal with Meio Island, 10 m depth, MZSP 30983, 3 specimens (21/vii/1999); **Bahia**; Salvador; Farol da Barra, 2-5 m depth, MZSP 28520, 15 specimens (Simone col., 22-28/ii/1997), MZSP 31374, 10 specimens (C. Magenta col., vii/1999); Alcobaça, MZSP 34909, 2 specimens (Coltro leg. 2001), Parcel de Paredes, Pedra da Lixa, 1-5 m deep, MZSP 32316, 2 specimens, MZSP 32461, 1 young specimen (P.J. Souza Jr. & E.P. Gonçalves col., i/2000).

N.B.: Specimens of ***Niveria nix*** (Schilder, 1922) (type species of the genus) were also studied, but they are not well preserved enough for anatomical studies. It was possible to observe a developed siphon, no anal siphon, some transversal folds (parallel to edge) in mantle lobes without papillae and a very large penis in male. The females are immature, without visible pallial oviduct.

Material examined: BRAZIL; Espirito Santo, off Guarapari, MZSP 30682, 1♂, 2♀

Genus *Trivirostra* Jousseaume, 1884

(Type species: *Cypraea oryza* Lamarck)

Trivirostra oryza (Lamarck, 1810)

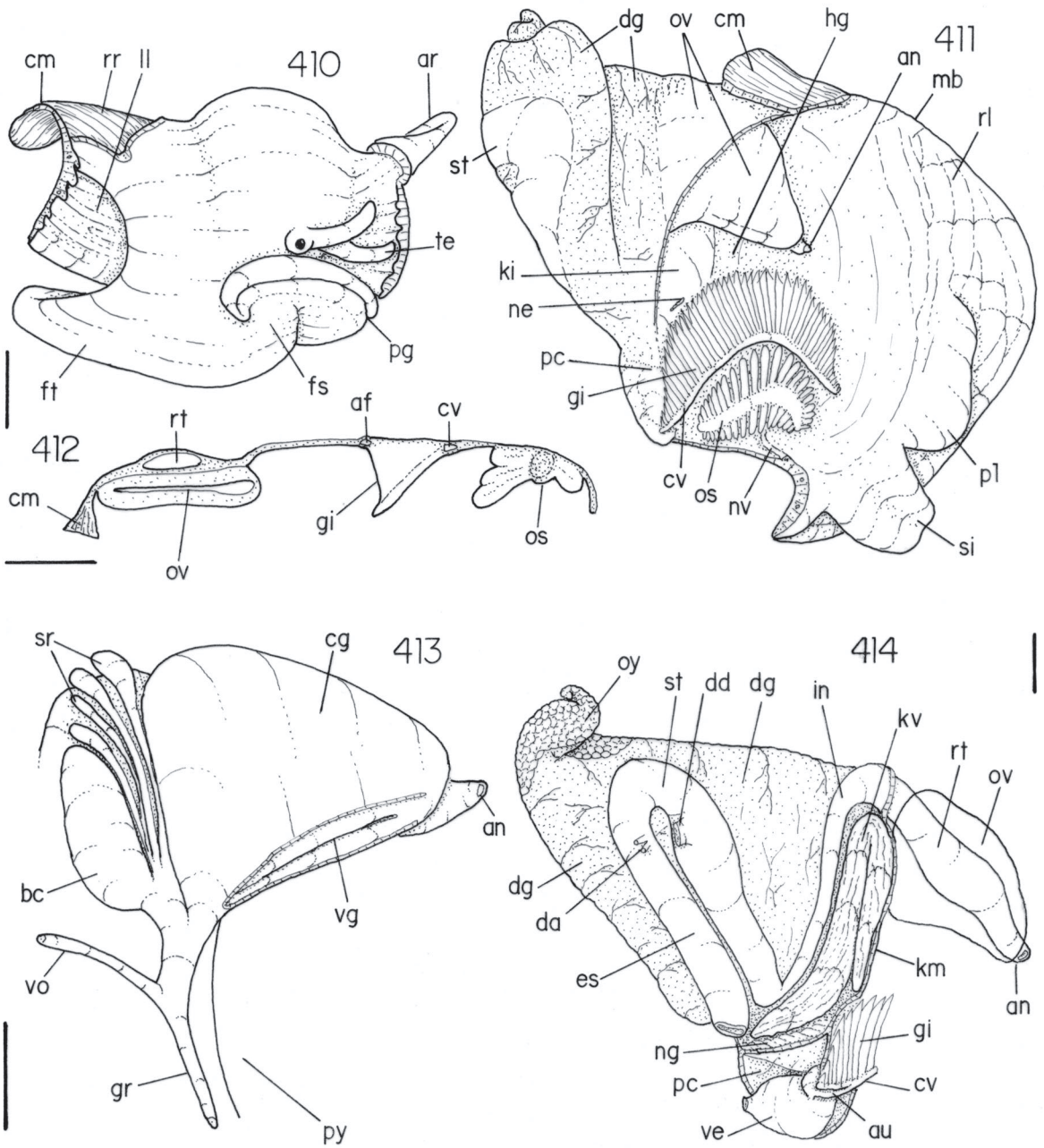
(Figs. 61, 62, 99, 410-414)

Trivia oryza: Shaw, 1909: 308; Gosliner & Liltved, 1987: 248.
(?) Trivia boswellae Cate, 1979 (sic Gosliner & Liltved, 1987).
Trivirostra oryza: Trew, 1987a: 8.

Description

Shell (Figs. 61, 62). Involute, color white, sculptured by about 24 transversal threads without interruption in dorsal middle line and secondary intercalated threads in periphery. Other details in Shaw (1909).

Head-foot (Fig. 410). Characters similar to those of preceding triviid, differences or notable features following. Color uniform pale beige. Anterior projection long and narrower. Anterior edge of foot with a small projection in each side extending little beyond remainder sole. Edged of pedal gland furrow very thick. Columellar muscle flat and short. Right pallial muscle as part of columellar muscle.



Figs. 410-414, *Trivirostra oryza* anatomy: **410,** head-foot, male, lateral-right view; **411,** pallial cavity roof and visceral mass, female, ventral view; **412,** pallial roof, transversal section in middle level osphradium; **413,** pallial oviduct, ventral view, seen as in situ, some adjacent structures also shown; **414,** Visceral mass uncoiled and posterior and right pallial structures, ventral view, kidney and pericardium opened longitudinally, posterior gill region shown as in situ. Lettering: **p1**, accessory mantle fold of siphon. Scales = 1 mm.

Mantle organs (Figs. 411, 412). Very similar features as those described for *N. pediculus*, remarkable attributes following. Mantle lobes without papillae, possessing transversal, irregular, tall folds, pigments lacking. Siphon large and ample, edges smooth; a tall satellite fold located at right from siphon, running parallel to mantle border at about half of right lobe length. Osphradium large, with proportionally fewer filaments. Left osphradium filaments smaller and simple; right filaments larger and with outer edge trilobed. Between osphradium and gill a narrow space. Gill curved, relatively small (equivalent to osphradium area and little longer than it). Gill filaments low, with edges somewhat straight and with same length; filament rod extending little beyond membranous part in a small pointed tip. Hypobranchial gland tick, white, lacking mantle septa. Anal siphon absent.

Circulatory and excretory systems (Fig. 414). Also with features similar to those of *N. pediculus*, remarkable characters following. Pericardium located part dorsal to posterior gill end and part (about

2/3) in visceral mass anterior-left extremity. Auricle connected to ctenidial vein sub-terminally, but close to its posterior end. Kidney narrow, located edging anterior end of visceral mass exposed in pallial cavity. Kidney chamber located along middle third of intestine. Nephridial gland thin, triangular in section, limited to membrane between kidney and pericardium. Renal lobe white, large, single, filling most of inner renal space, attached only to dorsal surface of renal chamber and not to intestine. Renal lobe ventral surface covered by irregular, narrow, longitudinal folds, extend from posterior region of nephridial gland to renal anterior-right end, where curves abruptly and runs parallel and close at about 2/3 of its preceding region, ending close to nephrostome. Nephrostome a transversal slit close to pericardium.

Digestive system (Fig. 414). Characters of foregut similar to those described for *N. pediculus*, including those of proboscis, jaws and buccal mass. Remarkable features following. Jaw plates also very large. Odontophore muscles: **m1a** pair similar, **mj** thick, occupying almost half of buccal mass size; **m2** pair narrower and inserted far from buccal ganglia; **m6** longer, almost entire length of cartilages; **m6a** broad, also located dorsal to m6; **m11** pair narrower. Buccal ganglia located close to median line, just between esophagus and buccal mass. Radular teeth characters (Fig. 99) similar to those of *N. pediculus*, with following remarks: rachidian and lateral teeth cups more pointed, in same number; outer marginal tooth lacking sub terminal cusp. Esophageal gland with a central, longitudinal fold and 2 series of oblique, tall folds edging it. Stomach (Fig. 414) a simple curve, ducts to posterior lobe of digestive gland double, narrow, located close from each other in limit between esophagus and stomach. Duct to anterior lobe of digestive gland broad, located in limit between stomach and intestine. Digestive glands lobes narrowly connected with each other at right from stomach (Fig. 414), color pale beige. Intestine running as a "Z", with central portion edging renal chamber and distal portion running in pallial cavity, part covered by pallial oviduct. Anus shortly siphoned, located far from mantle edge.

Genital system. **Female** (Fig. 413). (No male available). Visceral and pallial characters similar to those of *N. pediculus*, differentiable or notable features following. Ovary pale beige in color, filling first whorls covering posterior lobe of digestive gland. Visceral oviduct very narrow, running in ventral surface of anterior lobe of digestive gland. Gonopericardial duct present, narrow, inserts in visceral oviduct close to its insertion in pallial oviduct. Pallial oviduct large and flat, occupies about ¼ of pallial cavity area, running attached to pallial floor covered dorsally by rectum. Visceral oviduct anterior end, after connection with gonopericardial duct, suddenly curved almost perpendicularly and becomes thicker. Bursa copulatrix large (about ¼ of oviduct volume), located as posterior structure. Bursa internally hollow, walls thick-muscular, inner surface with irregular, longitudinal folds. Bursa duct narrow and very short, inserted just posterior to insertion of main part of pallial oviduct. Seminal receptacles as 4 vesicular, tall, long projections, located compressed between bursa and remainder pallial oviduct. Each seminal receptacle with broader tip and very long and narrow duct, all inserted side by side just anterior to bursa duct, forming a broader common duct. Just anterior from this duct, remainder pallial oviduct begins in a similar sized duct that shortly expands. Albumen and capsule glands united with each other, albumen gland as posterior 1/5, whitish portion, capsule gland as remainder, cream in color, portion. Albumen and capsule glands walls thick, as 2 flat laminas. Vaginal tube amply connected to capsule gland, edging its left border, attached to pallial floor. Female aperture a simple slit covered by anterior end of capsule gland.

Central nervous system. Similar in features to those of preceding triviid, differing in lacking additional connective between both cerebral ganglia.

Measurements of shells (in mm). AMS 160778 1: 16.0 by 7.5; 2: 9.2 by 6.6.

Habitat. Under rocks and chorally reef.

Material examined. AUSTRALIA; **Darwin**, Waigait, 11º28'S 130º50'E, AMS 160778, 3♀ (sta. 38614 NT, P.H. Colman col. 25/x/1969).

Family Eratoidae

Genus *Hespererato* Schilder, 1832

(Type species: *Erato vitellina* Hinds)

Hespererato maugeriae (Gray, 1832)

(Figs. 44, 100, 415-427)

Erato maugeriae Gray in Sowerby, 1832: 14 (fig. 47); Olsson & Harbison, 1953: 266 (pl. 60, fig. 7); Abbott, 1954: 176 (pl. 22, fig. w); Rios, 1970: 59; Abbott, 1974: 147 (fig, 1618); Matthews & Matthews, 1976: 76-77 (fig. 6); Oliveira *et al*., 1981: 137; Rios, 1985: 63 (pl. 23, fig. 279); Jong & Coomans, 1988: 63; Rios, 1994: 78 (pl. 26, fig. 300); Merlano & Hegedus, 1994: 165 (pl. 51, fig. 607); Abbott & Morris, 1995: 194 (pl. 53).

Persicula dalli Morretes, 1940: 252-253 (pl. 1, fig. 4-7) (loc: Bertioga, SP).

Erato (Hespererato) maugeriae: Warmke & Abbott, 1962: 90 (pl. 23, fig. c); Rios, 1975: 71 (pl. 20, fig. 291).

Hespererato maugeriae: Schilder & Schilder, 1971: 14; Cate, 1977: 361 (fig. 42, 42a); Trew, 1987a: 4.

Description

Shell (Fig. 44). Spire low; surface glossy; aperture narrow; outer lip thick, without teeth. Other details in Cate (1977: 361).

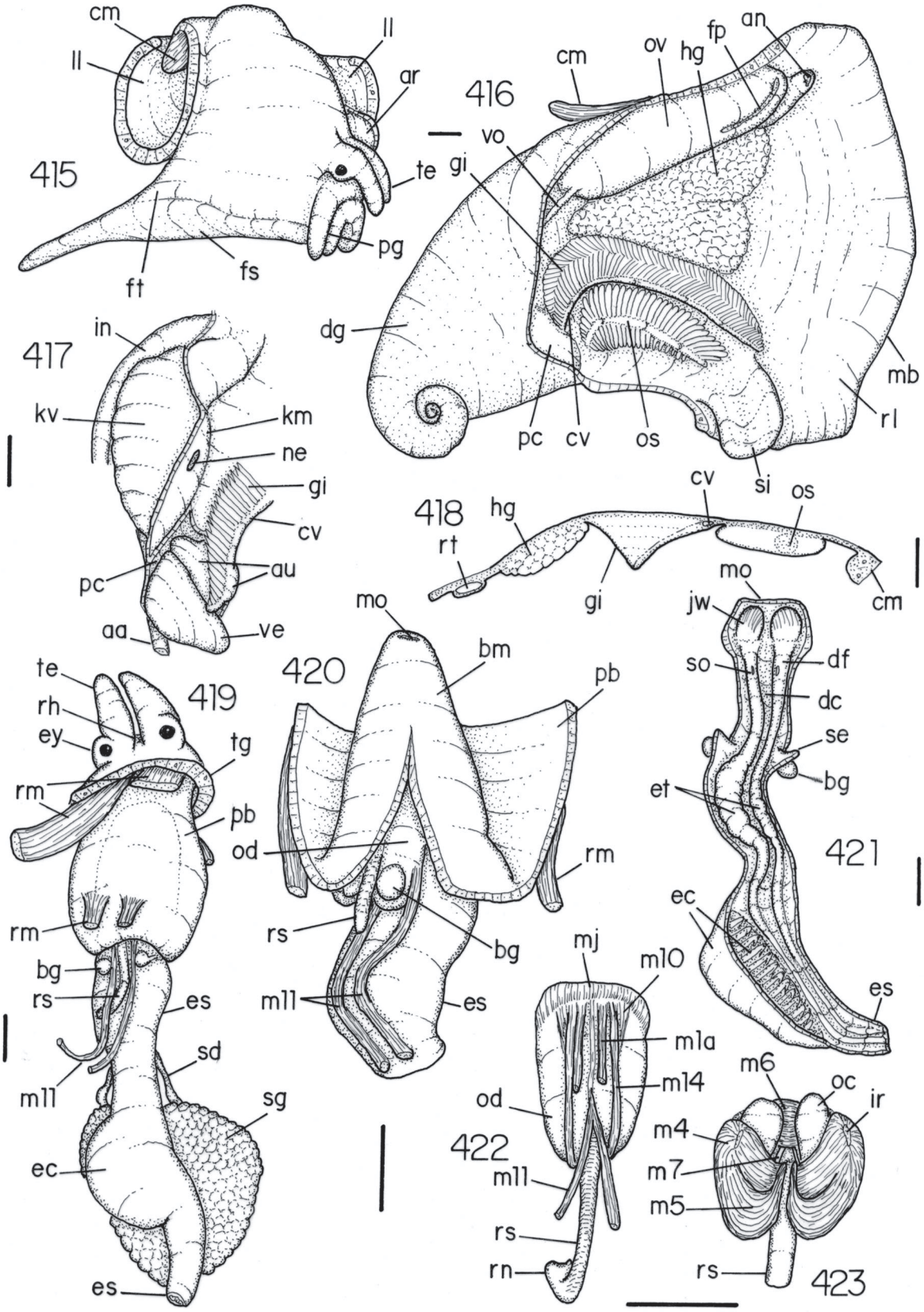
Head-foot (Figs. 415, 419, 426). Color uniform pale cream. Head somewhat inlaid. Tentacles stubby, close with each other. Ommatophore small, slightly over tentacles base. Eyes dark. Rhynchostome a small pore between and ventral to tentacles. Foot long, slightly narrow, posterior projections long. Anterior furrow of pedal glands with thick borders. Columellar muscle flat, of half whorl. Pleurembolic proboscis and its retractor muscles well developed (more details below). Haemocoel narrow, connection with visceral mass posterior (not lateral like preceding species). No triangular sinus.

Mantle organs (Figs. 416-418). Mantle lobes broad, exceeding beyond shell aperture. Lobes surface almost smooth, only with undulations (no papillae). Siphon separated from mantle border, margins smooth. No anal siphon. Pallial cavity of about 1 whorl. Osphradium large, long, bipectinate, with single antero-posterior axis. Osphradium filaments with rounded distal end; left filament smaller and fewer than right filaments; left filaments missing in anterior region. Gill long, narrow, curved, edging right margin of osphradium and extending little beyond its limits. Gill filaments low, apex almost central, edges straight. Between gill and rectum a broad area, mainly in anterior portion. Hypobranchial gland thick, white, without mantle septa. Rectum narrow, runs at short distance from left margin of pallial cavity (but not on this margin), generally dorsal to gonoducts. Anus siphoned, small, close to mantle border.

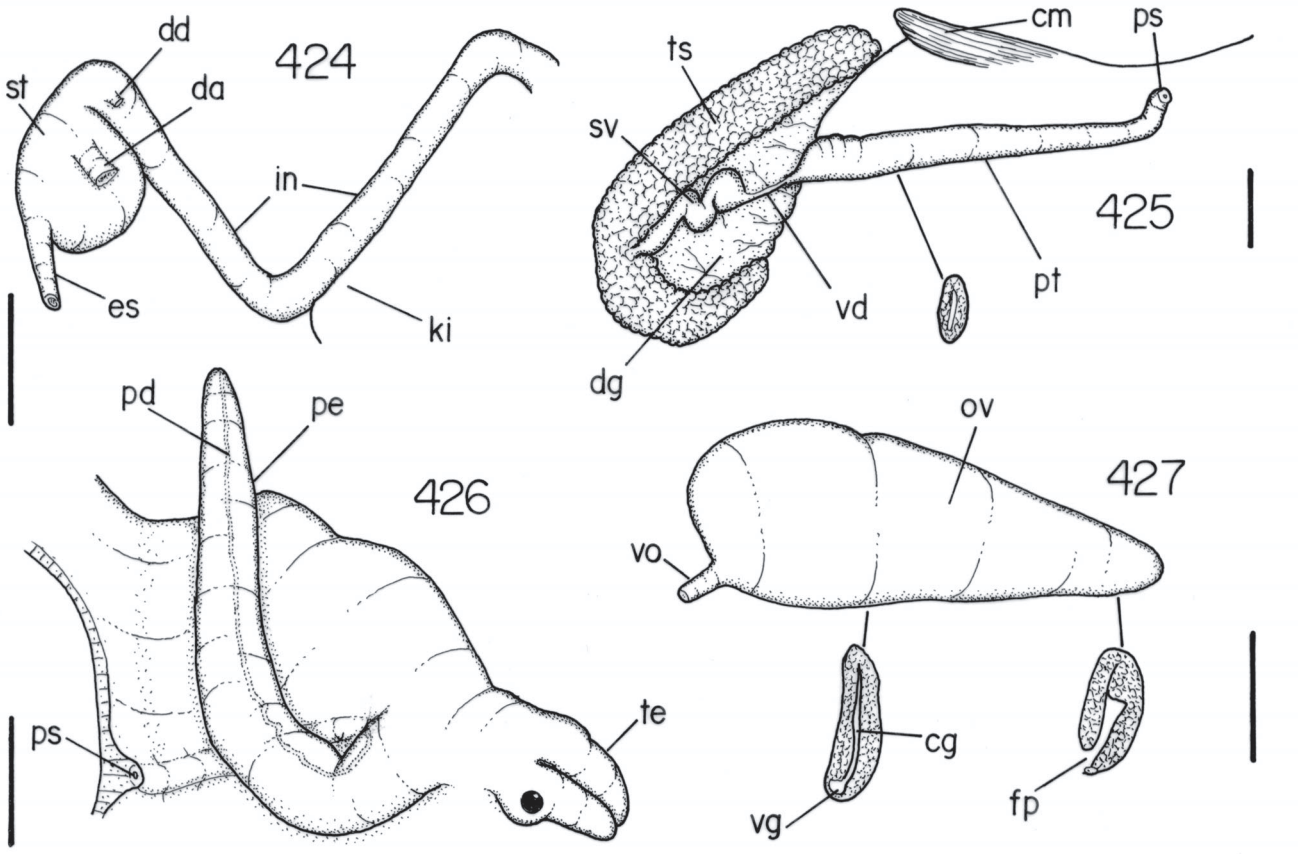
Circulatory and excretory systems (Fig. 417). Heart characters similar to those of *N. pediculus*, including position of auricle dorsal to posterior gill region and its sub-terminal connection with ctenidial vein (no narrow area of auricle dorsal to gill). Kidney massive, almost entirely filled by glandular tissue connected to ventral and dorsal renal walls. Intestine running along posterior renal wall; attachment with intestinal lobe only in anterior-right extremity. Nephrostome a small slit in middle region of membrane between kidney and pallial cavity. Hollow region just posterior and left from nephrostome. Accessory muscle of columellar muscle present.

Visceral mass (Figs. 416, 425). Organization similar to most caenogastropod, spiral, not-involute fashion. Except this, remainder characters somewhat similar to those of *M. zebra*.

Digestive system (Figs. 419-424). Proboscis of normal pleurembolic type, slightly short (Figs. 419, 420). Rhynchodeal wall thin, semi-transparent. Buccal mass part of proboscis conic, almost of same length than rhynchodeal part, thick muscular. Pair of proboscis retractor muscles narrow, originating in middle level of haemocoel ventral inner surface, inserting in posterior-ventral region of rhynchodeal wall (Fig. 419). Mouth small, slit-like. Oral tube broad and long (about half of buccal mass length). Odontophore with about half of buccal mass volume. Pair of jaw plates large, thick, each plate almost circular, cut-edge elevated (Fig. 421). Pair of dorsal folds broad, just posterior to jaws. Aperture of salivary gland in middle region of each dorsal fold. No furrowed part of dorsal folds developed. Odontophore muscles (in relation to characters of *M. zebra*) (Figs. 422, 423): **m1a** pair narrow; **m1b**, **m1c**, **m2**, **m3**, **m11**, **m12**, not developed; **mc**, **mj**, **m10**, similar; **m4** pair more similar to those of *N. pediculus*; **m5** pair broad, posterior located, inserted in radular sac in long and lateral region of its portion preceding exposition; **m6**, thin, with



Figs. 415-423, *Hespererato maugeriae* anatomy: **415,** head-foot, female, lateral-right view; **416,** pallial cavity roof and visceral mass, female, ventral view; **417,** kidney and pericardium region, ventral view, both opened longitudinally, posterior gill region shown as in situ; **418,** pallial roof, transversal section in middle level osphradium; **419,** head and foregut, ventral view, proboscis retracted; **420,** proboscis, buccal mass and anterior esophagus, ventral view, proboscis partially opened longitudinally; **421,** dorsal wall of buccal mass and esophagus, ventral view, odontophore removed, esophagus opened longitudinally; **422,** odontophore, ventral view; **423,** same, radula partially removed, both cartilages deflected, both m5 still connected to radular sac. Scales = 0.25 mm.



Figs. 424-427, *Hespererato maugeriae* anatomy: **424,** middle digestive tubes, ventral view, shown as in situ, some adjacent structures also indicated, **425,** middle and posterior male genital structures, ventral view, some adjacent structures and a transversal section in indicated region of prostate also shown; **426,** head and pallial floor of male, dorsal-slightly lateral-right view; **427,** pallial oviduct, ventral view, two transversal sections in indicated regions also shown. Scales = 0.5 mm.

about half of odontophore cartilages length; **m6a** absent; **m7** pair similar to those of *N. pediculus*; **m11** pair very slender; **m14** pair narrow and thin, similar origin and insertion. Radular sac narrow and long, with about twice buccal mass length. Radular nucleus broad and slightly bifid. Radular teeth (Fig. 100): rachidian tooth broad, 7 to 11 cusps, central cusp about 3 times larger than neighbors, secondary cusps of almost uniform size; lateral tooth long, flat, curved, about 6 cusps, second cusp several times larger than neighbors and terminal; inner and outer marginal teeth similar with each other, slender, long, curved, hook-like, tip pointed, a small cusp in inner margin far from tip. Esophagus narrow and long, anterior esophagus with a single pair of longitudinal folds (continuation from those of buccal mass) thick and glandular (Fig. 421). Middle esophagus with esophageal gland similar to that of *M. zebra* but with fewer and thicker septa; in opposite side of gland a pair of narrow longitudinal folds (continuation from those of anterior esophagus) (Fig. 421). Posterior esophagus characters as those of *M. zebra*. Stomach marked by a sudden increase after esophagus (Fig. 424), almost spherical, walls thin, inner surface smooth. A pair of ducts to digestive gland in ventral surface. Intestine narrow, running similarly to that of *M. zebra*. Rectum and anus above described.

Genital system. **Male** (Figs. 425, 426). Testis pale yellow, located in right surface of visceral mass. Seminal vesicle very broad, with few coils, running in middle region of last whorl of visceral mass ventral surface. Vas deferens narrows at short distance from pallial cavity. In pallial cavity suddenly expands. Prostate narrow and long, walls thick glandular, pale yellow, entirely closed (tubular). Prostate running edging at some distance right margin of pallial cavity by about 2/3 of its length, after suddenly towards left and run in floor of pallial cavity up to penis base, entirely closed. Penis slender, slightly flat-

-tened; base somewhat broad and curved located posterior to right tentacle; gradually narrows up to rounded tip. Penis duct closed, very slender, running close to penis posterior margin. Aperture in penis tip.

Female (Figs. 416, 427). Visceral organs similar in localization to those equivalent from males. Pallial oviduct broad, flattened, located along right margin of pallial cavity attached to pallial floor. Albumen gland in posterior region, whitish. Separation between albumen and capsule gland not clear. Capsule gland long (about twice albumen gland length) initially with same width from albumen gland, gradually narrows up to rounded anterior extremity. Genital pore a lateral slit close to floor of pallial cavity.

Measurements of shells (in mm). USNM 850684 (Fig. 44): 5.7 by 4.3.

Distribution. From North Carolina, USA, to Santa Catarina, Brazil.

Habitat. Sand and algae, 4 to 120 m depth.

Material examined. UNITED STATED OF AMERICA. **North Carolina**; 32º49'30"N 78º39'48"W, 34 m depth, USNM 850687, 1 specimen (15/iii/1981). **Georgia**; 31º41'06"N 80º20'48"W, 28 m depth, USNM 850686, 1 specimen (10/iii/1981); 31º23'42"N 80º52'54"W, 16 m depth, USNM 850683, 1♂ (28/vii/1981); 30º37'00"N 81º10'42"W, 20 m depth, USNM 848671, 1♀ (6/ii/1980); 31º23'36"N 80º53'12"W, 19 m depth, USNM 850684, 1♀ (26/ii/1981).

Family Pediculariidae

Genus *Pedicularia* Swainson, 1840

(Type species: *P. sicula* Swainson, 1840)

Pedicularia sp1.

(Figs. 50, 51, 101, 428-439)

Description

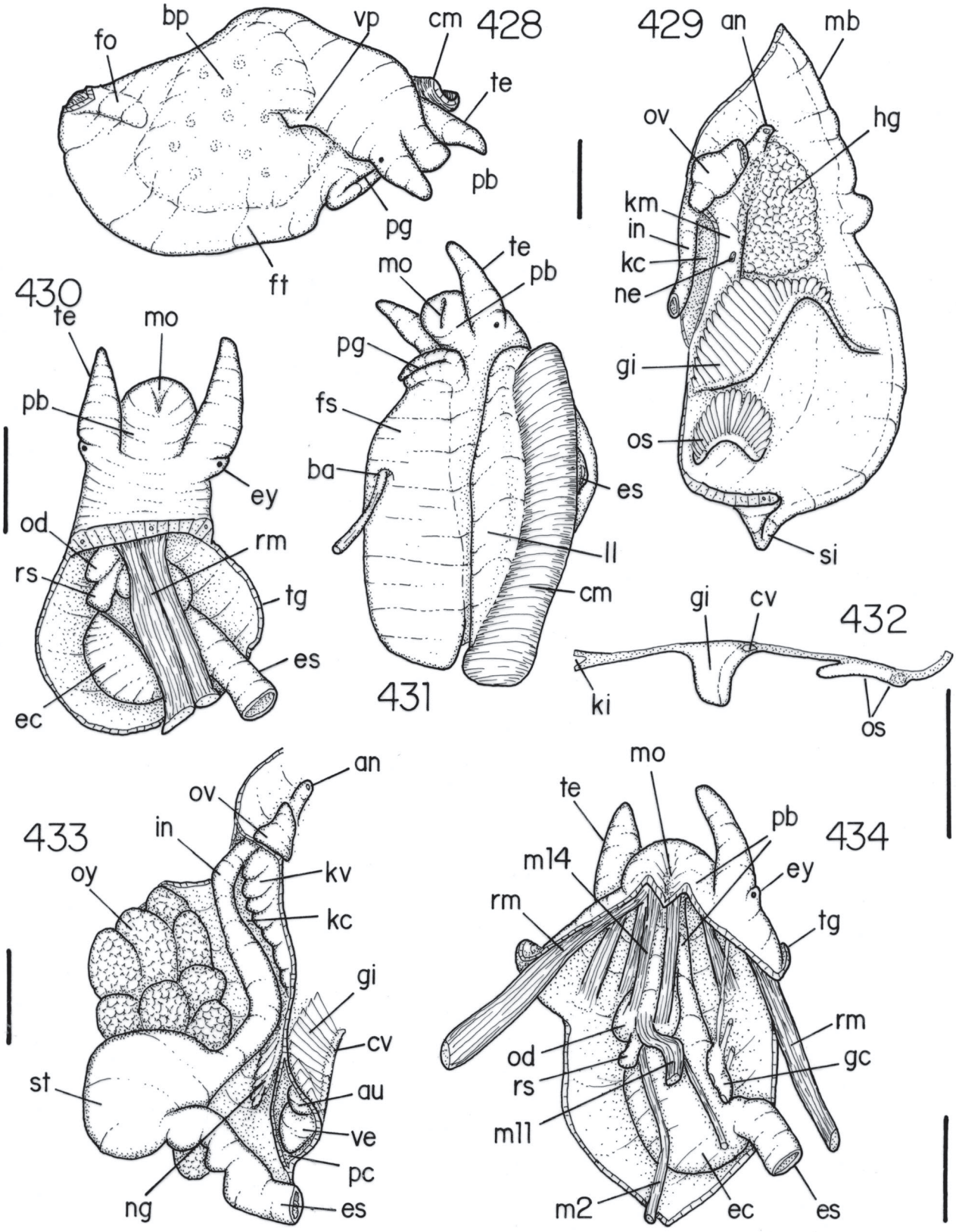
Shell (Figs. 50, 51). Outer surface opaque, pale beige. Spire involute, small, located just posterior to middle region of left size. Sculpture successive spiral and axial threads, with predominance of spiral threads. A small node in intersection of spiral and axial threads. Inner lip smooth, slightly irregular. Callus covering about half of spire. Outer lip projected, siphon and anal regions amply opened; constricted in middle. Outer lip with thin cut-edge.

Head-foot (Figs. 428, 430, 431, 434). Head outstanding, slightly peduncled. Tentacles stubby, tip rounded, no ommatophores. Eyes dark, very small, located in tentacles base. Foot large, ample. Anterior furrow of pedal glands somewhat short, edges thick. Anterior projection short. Brood pouch present, described below. Columellar muscle thick, broad and very short, about 1/5 whorl. Haemocoel slightly rounded, connection with visceral mass between posterior and left sides.

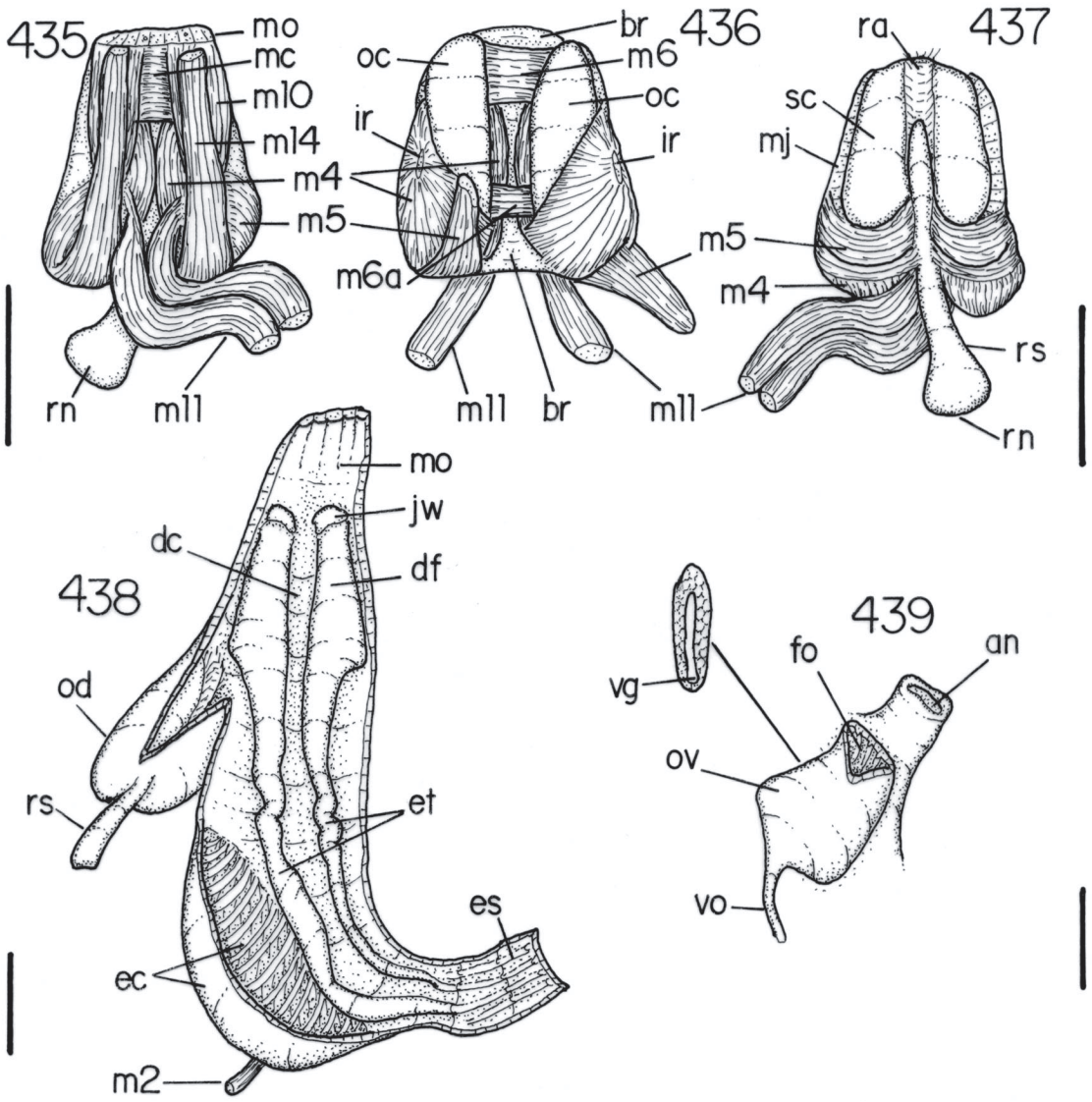
Mantle organs (Figs. 429, 432). Mantle lobes broad, limited to inner shell surface, smooth. No mantle appendices (papillae, siphons) except a weak siphonal undulation. Osphradium elliptical, curved, monopectinate, located slightly far posterior from siphon. Osphradium ganglion running in left margin. About 12 right filaments, free tip rounded. Gill broad, short, sigmoid, a short posterior portion close to osphradium. Gill filaments broader in posterior 2/3, tall, tip central, broad-rounded; gill filaments suddenly narrow in anterior 1/3. Ctenidial vein narrow all along its length, a long, curved portion beyond anterior end of gill filaments, ending close to mantle edge. Posterior gill half close to kidney, anterior gill half gradually far from kidney and rectum. Hypobranchial gland thick, white, occupying anterior region between gill and rectum. Pallial oviduct small, running shortly in right margin of pallial cavity (more details below). Rectum very short, running dorsal to oviduct. Anus siphoned, small, slightly far from mantle edge.

Circulatory and excretory systems (Fig. 433). Heart small, located along 1/3 of gill dorsal surface and shortly beyond posterior to it. Auricle connected directly to ctenidial vein before its posterior end. Kidney narrow, long. A single long, flattened, white glandular mass edging along middle region of intestine, attached to it only in right-anterior extremity. This glandular mass evolves nephridial gland and ventral renal lobe, without clear division. Nephrostome a small slit located just at right from pericardium.

Visceral mass (Fig. 433). Small, involute, with organization somewhat similar to that of *M. zebra*.



Figs. 428-434, *Pedicularia* sp1 anatomy: **428,** head-foot, female, lateral-right view, note brood pouch (bp); **429,** pallial cavity roof, female, ventral view; **430** head and haemocoel, ventral view, foot and columellar muscle removed, proboscis partially extended; **431,** head-foot, female, lateral-left view; **432,** pallial roof, transversal section in middle level osphradium; **433,** anterior region of visceral mass and adjacent region of pallial cavity roof, ventral view, ventral membranes of kidney and pericardium removed, posterior end of gill deflected; **434,** same than fig 430, proboscis partially opened longitudinally. Scales = 0.5 mm.



Figs. 435-439, *Pedicularia* sp1 anatomy: **435,** odontophore, ventral view; **436,** same, radula removed, both cartilages deflected, left m5 (right in fig.) also deflected; **437,**odontophore, dorsal view; **438,** foregut, ventral view, buccal mass and esophagus opened longitudinally; **439,** pallial oviduct and adjacent structures, ventral view, genital papilla extracted (see fig 428) a transversal section in indicated level also shown. Scales = 0.25 mm.

Digestive system (Figs. 430, 433-438). Proboscis and ventral pair of retractor muscles (Fig. 434) similar in characters to those of *M. zebra*. Buccal mass long and narrow. Oral tube long, slightly broad. Odontophore small, with posterior 2/3 of its length separated from esophagus. Pair of jaw plates very small and thin. Pair of dorsal folds broad, starting just posterior to jaws. Odontophore muscles (in comparison with those of *M. zebra*) (Figs. 434-437): **m1** no differentiated pair; **mj** and **mc** thin; **m2**, **m10** pairs similar; **m3**, **m7** not developed; **m4** pair similar, but located posterior; **m5** pair narrow and thin; **m6** very narrow and thin; **m6a** narrower than m6 and far from it, not connected to subradular membrane; **m11** pair broad and long, without muscle branched in dorsal region of radular sac, only a short membrane; **m14** pair slightly broad and long, insertion very posterior. Radular sac of almost same length than buccal mass (Fig. 435). Radular nucleus broad and simple (not bifid). Radular ribbon very small, almost reduced (width about 30 µm). Radular teeth (Fig. 101): rachidian tooth very broad (more than half of radular ribbon width), central cusp long and sharp, about 7 pairs of secondary small cusps; lateral tooth slightly short, slender, curved, with generally 3 cusps, lateral cusp larger and terminal; Inner and outer marginal teeth similar with each other (outer marginal tooth about of double width than inner marginal), 3 terminal cusps, inner cusp very long, slender, pointed, filiform, of almost same length than tooth base, outer cusp pointed, several times shorter, middle cusp of intermediary length. Anterior esophagus with a pair of inner folds as narrow continuation from those of buccal mass (Fig. 438). Middle esophagus with a pair of tall,

narrow folds (continuation from those of anterior esophagus), covering partially esophageal gland. Esophageal gland similar to that of *M. zebra*, but with few and lower septa (Fig. 438). Posterior esophagus long (about half of total esophageal length), with 4-5 narrow inner longitudinal folds. Stomach slightly spherical (Fig. 433), esophagus inserts in left surface just after narrow duct to digestive gland. Other duct broader in ventral-right region of stomach. Inner gastric surface white, iridescent, without folds. Intestine narrow, short, slightly sigmoid. Intestine originating in anterior gastric region just anterior to esophageal insertion, running towards anterior and right edging posterior renal surface. After kidney, intestine running a short distance ventral to pallial oviduct (Fig. 433). Anus above described.

Genital system. Only **female** examined. Ovary occupying right regions of visceral mass (Fig. 433), whitish, acina relatively large and spherical. Visceral oviduct short and very narrow (Figs. 429, 439). Pallial oviduct simple, small and short, form somewhat triangular. Walls somewhat thick-glandular. Vaginal tube in left margin of oviduct. After anterior end of glandular walls, vaginal tube increase as continuation of pallial oviduct and runs attached to pallial floor by a short distance. Genital pore very small, close to pallial floor (Fig. 428). Brood pouch very large, with hundreds of young specimens (of single whorl shell); occupies most of middle-right region of head-foot dislocating haemocoel to left (Fig. 428). Brood pouch aperture in foot sole between its anterior and middle thirds, slightly to right (Fig. 431). Foot musculature as brood pouch ventral surface, semi-transparent integument as its dorsal surface.

Material examined. TONGA; Kapa Island, NW tip, 18º40'48"S 174º03'W, 30 m depth, USNM 857666, 1♀ (R.H. Chesher col. 14/viii/1984).

Pedicularia californica Newcomb, 1864

(Figs. 54-56, 102, 103, 440-446)

Synonymy see Schilder, 1931. Complement:

Pedicullariella californica: Schilder, 1931: 167-168 (fig. 2).

Pedicularia (Pedicullariella) californica: Abbott, 1954: 180 (pl. 7, figs. b, c); 1974: 151; Catarius, 1991: 83.

Pedicularia californica: Schmieder, 1980: 382-384; 1982: 272 (fig. 1); Gosliner & Liltved, 1985: 105 (fig. 34); Trew, 1987a: 23; Lindahl, 1991: 79 (figs. 1-2).

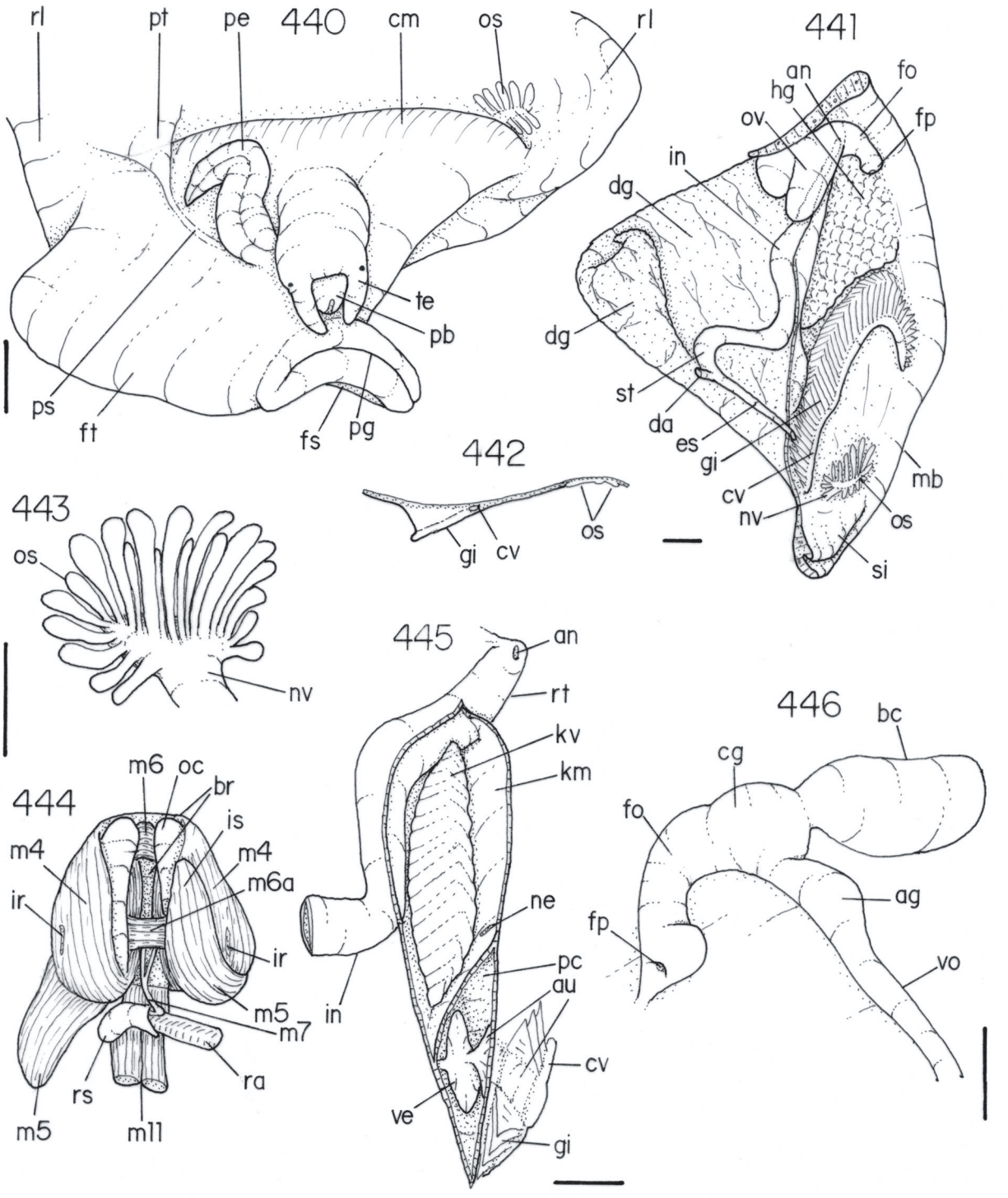
Description

Shell (Figs. 54, 55). Color pink. In young specimens a tick outer lip remembering that of *Erato* (Fig. 54). In larger forms, outer edge of outer and inner lips expands thinner and irregular (Fig. 55). Protoconch I (Fig. 56) rounded, inflate, sculptured by a mosaic of irregular undulations. Other details in Abbott (1974: 151).

Head-foot (Fig. 440). Characters similar to those of preceding pediculariid, distinctive or notable features following. Head also preceded by a very long neck, peduncled. Anterior furrow of pedal glands edged by thick borders. Eyes somewhat reduced. Anterior projection present, as part of columellar muscle.

Mantle organs (Figs. 440-443). Close similarity with characters described for preceding pediculariid, following remarkable features. Mantle lobes narrow, outer surface smooth. Siphon low, separated from mantle border. Osphradium bipectinate, except for a monopectinate central-anterior region (just in connection with osphradium nerve), with only right filaments (Figs. 441, 443). Osphradium filaments low, irregular, somewhat intercalated longer and shorter filaments. Between gill and osphradium a broad space. Gill narrow, long, anterior region curved. Gill filaments low, slightly curved to right, edges straight, tip as a short, rounded projection of rods (Fig. 442). Hypobranchial gland thick, white, solid, lacking pallial septa.

Circulatory and excretory systems (Fig. 445). Both with organization similar to that of preceding pediculariid, with following remarks. Auricle connection with ctenidial vein sub terminal; its portion dorsal to gill narrow; its portion inside main pericardium chamber partially connected to anterior pericardial wall. Ventricle large and broadly discoid. Kidney long and narrow. Nephridial gland not detectable. Renal lobe single, elliptical, connected only to renal dorsal surface (not to intestine), triangular in section,



Figs. 440-446, *Pedicularia californica* anatomy: **440,** head-foot, male, lateral-right view, mantle roof still connected, deflected and partially shown; **441,** pallial cavity roof and visceral mass, female, ventral view; **442,** pallial roof, transversal section in middle level osphradium; **443,** osphradium, ventral view; **444,** odontophore, ventral view, radula removed, deflected posteriorly and partially shown, right m5 (left in fig.) deflected; **445,** kidney and pericardium, ventral view, both opened longitudinally, some adjacent structures also shown, some gill filaments on auricle removed; **446,** pallial oviduct and adjacent visceral oviduct, dorsal view. Scales = 0.5 mm.

ventral surface with transversal furrows. Membrane between kidney and pallial cavity lacking structures attached to it.

Visceral mass (Fig. 441). Similar attributes than preceding *Pedicularia*, except for digestive tubes far removed from visceral apex, and both digestive gland lobes broadly connected.

Digestive system. Characters of foregut closely similar to those of preceding pediculariid, remarkable features following. Jaw plates thin and small. Odontophore muscles (Fig. 444): **m1b** pair, originating in dorsal inner anterior surface of proboscis, running towards posterior, inserting in posterior-dorsal surface of odontophore; **m2** pair narrow and long, running attached to anterior esophagus; **m6** narrower; **m6a** also free from adjacent dorsal surface; **m7** pair present, originating in m4 posterior-dorsal-medial edge, running towards posterior, penetrate inside radular sac becoming a single band, inserting in radular sac close to radular nucleus. Radular teeth (Figs. 102, 103): rachidian tooth broad and short, 15-17 slender cusps, central cusp several times larger than remainder cusps, with 1-2 pairs of small cusps in central cusp base; lateral tooth about as broad as rachidian, with 6 long and slender cusps, third cusp terminal, curved inwards, and several times larger than neighbor cusps; inner and outer marginal teeth tall, hook-like, inner marginal slightly broader than outer marginal and with a middle cusp in its inner margin. A series of satellite plates, somewhat rectangular, corresponding to each teeth roll, located in both sides of radular ribbon. Esophageal folds taller and broader. Esophageal gland with broader glandular transversal septa. Stomach a single, narrow curve (Fig. 441) located in middle region of visceral mass. Duct to digestive gland single (Fig. 441), located between esophagus and stomach. Intestine weakly sinuous, running obliquely most edging anterior border of visceral mass (Figs. 441, 445). Anus somewhat close to kidney anterior end.

Genital system. **Male** (Fig. 440). Visceral structures not seen in details. From triangular sinus, vas deferens opens into pallial cavity. From this aperture to penis base a very narrow furrow, edged by low borders. Penis with length equivalent to that of neck, flattened dorso-ventrally, originated by side of ventral-right region of neck base. Penis with uniform width along its length, distal 1/3 narrowing gradually. Penis tip broadly pointed. Penis groove running along middle region of penis ventral surface. Other details in Gosliner & Liltved (1985, fig. 34B).

Female (Figs. 441, 446). Visceral and pallial structures characters similar to those of preceding pediculariid, distinctive or notable features following. Pallial oviduct larger, located mostly attached to pallial floor. Albumen gland as a small expansion preceding visceral oviduct connection in capsule gland. Bursa copulatrix almost as large as remainder pallial oviduct, outline elliptical, color yellowish iridescent, dorso-ventrally flattened. Bursa connection to capsule gland by side and at some distance from albumen gland connection. Capsule gland relatively small, semispherical, color white. Vaginal tube proportionally large, running attached to pallial floor up to middle level of region between pallial oviduct and head base. Vaginal tube wall thick, anterior end slightly broader and sometimes tall. Female pore a small slit close to floor, succeeded by a low and short folds. Brood pouch in head-foot musculature similar to that of preceding species, its aperture also in anterior third level of foot sole, dislocated towards right. Most of females possess a vestigial penis.

Central nervous system. Features similar to those of cypraeids, with cerebral and plural pairs of ganglia close with each other (as a single large mass), very long connectives from these to pedal ganglia pair, and pedal ganglia close from each other, far from remainder ganglia and deeply inserted in pedal musculature.

Measurements of shells (in mm). LACM 88-356.2, ♀ 1: 12.4 by 6.6; ♀ 2: 11.7 by 7.0.

Distribution. California, USA.

Habitat. Rocky, on *Allopora californica*.

Material examined. UNITED STATES OF AMERICA; **California**; Monterey Co., 4.8 km WSW of Pt. Sur, 36º17'N 121º58'W, 37-55 m depth, LACM 88-356-2, 5♀ (sta. 88-356, RV Cordell Explorer, ix/1988-x/1989); Farnsworth Bank, 3.2 km W of Catalina Island, 50 m depth, FMNH

24044, 13 specimens (H.J. Jacobs col., 15/x/1945).

Pedicularia decussata (Gould, 1855)

(Figs. 49, 52, 53, 104, 447-452)

Synonymy see Schilder, 1931. Complement.
Pedicullariella decussata: Schilder, 1931:168.
Pedicularia (Pedicullariella) decussata: Abbott, 1954: 181 (pl. 7, fig. d); 1974: 151 (fig. 1653).
Pedicularia decussata: Rios, 1985: 66 (pl. 23, fig. 294); Trew, 1987a: 23.

Description

Shell (Figs. 52, 53). Similar to remainder pediculariids, distinct by narrow and long anterior (siphonal) region. Sculpture a slightly uniform reticulation. Aperture narrow. Protoconch I (Fig. 49) smooth, dome-shaped, 1.5 whorls. Protoconch II (Fig. 49) with 4 successively larger whorls, sculptured by a net of strong prosocline, opisthocline, and spiral cords, in such intersections form a short projection. Selenizone notch present. Other details in Abbott (1974: 151).

Head-foot (Figs. 447, 450). Very similar features as those of preceding pediculariids, including very long neck. Anterior edge of foot as a flap, in its anterior border a furrow of pedal glands edged by thin borders.

Mantle organs (Figs. 448, 449). Characters similar to those of preceding pediculariids, remarkable features following. Mantle boles relatively narrow, surface smooth. Siphon well developed. Osphradium elliptical, small, bipectinate in posterior half and monopectinate in anterior half; its anterior half only with right filaments and a relatively broad osphradium nerve at left. Osphradium filaments low, tip narrow, long, projected laterally. Between gill and osphradium a broad area, mainly anterior. Gill narrow, anterior half curved; anterior end with a broader region of ctenidial vein without filaments. Gill filaments tall, edges straight, rod extending little beyond membranous portion, tip rounded, slightly turned to right. Hypobranchial gland thin.

Circulatory and excretory systems (Fig. 448). Similar attributes as those of preceding pediculariids, with following notable features. Pericardium located also part dorsal to gill posterior region, insertion of auricle in ctenidial vein sub terminal, running free up to ventricle (not attached to pericardium wall). Kidney with a single renal lobe, color white, surface smooth, somewhat thin, connected to renal dorsal surface and anterior part of ventral surface, entirely free from intestine.

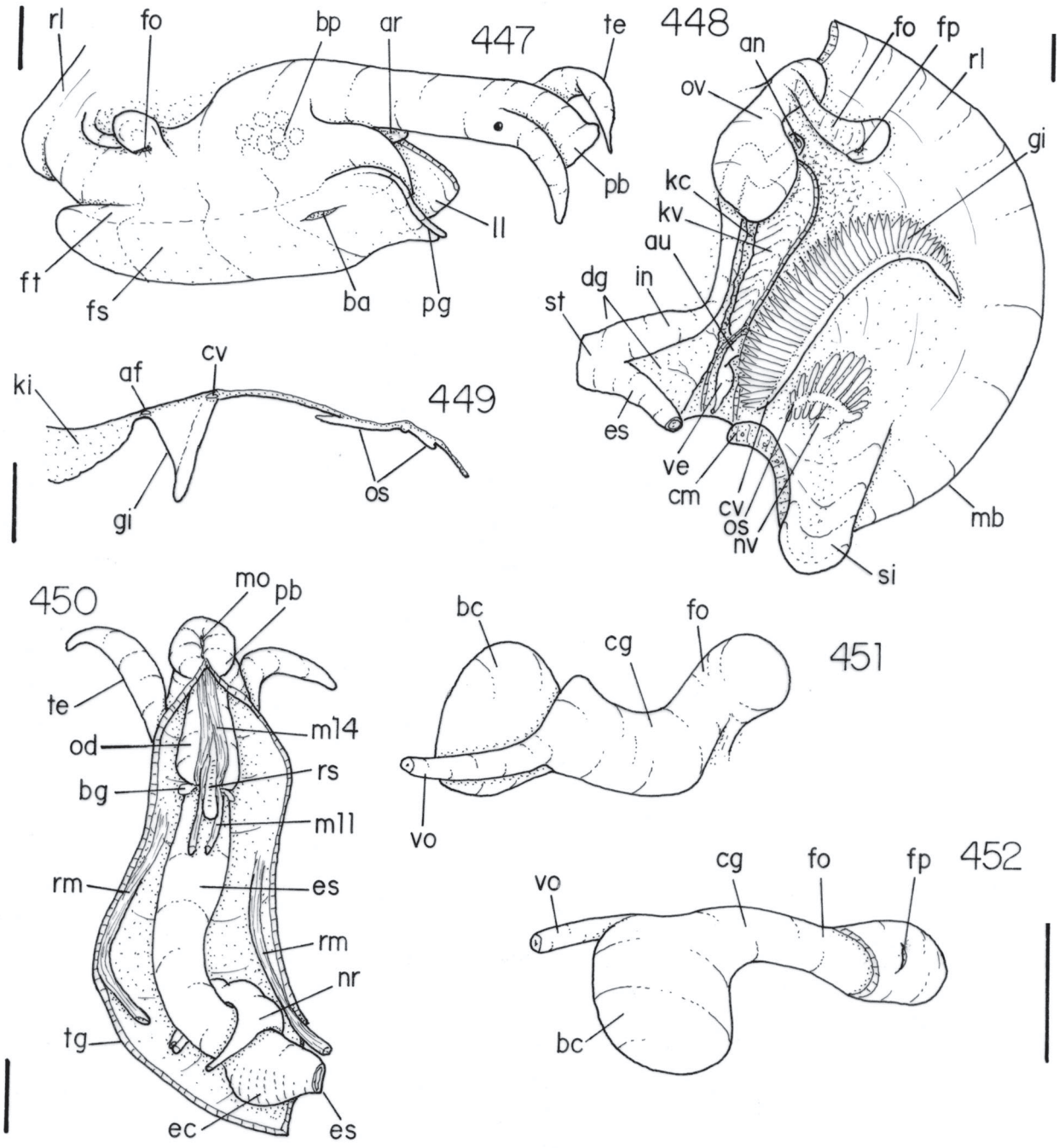
Digestive system. Foregut characters (Fig. 450) similar to those of first described *Pedicularia*, with following remarks. Odontophore muscles (Fig. 450): **m7** pair similar to those of *P. californica*, but shorter, originated in posterior edge of m4 dorsal branch. Radular teeth (Fig. 104): with similar features to those of *P. californica*, differing by curved fashion of lateral and marginal teeth. Esophageal gland proportionally small (Fig. 450), just posterior to nerve ring, inner surface covered by transversal septa. Middle and distal digestive tract as those of preceding pediculariids, except for a stronger zigzag portion preceding anus (Fig. 448). Digestive gland color pale orange.

Genital system. **Female**. (No males available.) Visceral and pallial structures similar to those of preceding pediculariids. With following remarkable attributes. Pallial oviduct (Figs. 448, 451, 452) small, albumen gland not differentiable. Capsule gland a short, thick walled tube. Bursa copulatrix present, located dorsal to visceral oviduct insertion, form somewhat rounded, dorso-ventrally flattened. Vaginal tube as continuation from capsule gland without clear separation. Female pore a small slit in base of a broad papilla (broader a taller than vaginal tube), located about in posterior 1/3 of distance between pallial oviduct and head base. Brood pouch similar to those of remainder pediculariids, its aperture differs in being located more anterior and at right (Fig. 447). A single female presents a vestigial penis.

Central nervous system. Similar to that described for preceding species.

Measurements of shells (in mm). DMNH 201879, 1: 5.8 by 3.6; 2: 5.8 by 3.8; 3: 5.6 by 3.4.

Distribution. Georgia, USA, to Caribbean Sea.



Figs. 447-452, *Pedicularia decussata* anatomy: **447,** head-foot, female, lateral-right view, mantle roof still connected posteriorly, deflected and partially shown; **448,** pallial cavity roof and anterior portion of visceral mass, female, ventral view; **449,** pallial roof, transversal section in middle level osphradium; **450,** head and haemocoel, ventral view, foot and columellar muscle removed, proboscis extended and opened longitudinally; **451,** pallial oviduct, dorsal view; **452,** same, ventral view. Scales = 0.5 mm.

Habitat. Associated with coral.

Material examined. BAHAMAS; Grand Bahama, off shore of West End, 340 m depth, DMNH 201879, 6♀ (Mikkelsen col., 19/xi/1979).

N.B.: Rosenberg (1996) consider *P. decussata* as synonym of *P. sicula* Swainson, 1840, distributed in Western and Eastern Atlantic.

Pedicularia sp2

(Figs. 57, 58, 105, 106, 453-459)

Description

Shell (Figs. 57, 58). Characters similar to preceding pediculariids. Form very narrow, antero-

posteriorly long. Sculpture almost only spiral, narrow ribs. Aperture narrow and deep.

Head-foot (Fig. 453). Characters similar to those of preceding pediculariids, notable or distinctive features following. Outline long antero-posteriorly and narrow laterally. Anterior projection present, as part of columellar muscle. Neck also very long. Eyes present, but without pigment, being invisible from an outer view. Proboscis retractor muscles running all along ventral and lateral neck length (as in preceding pediculariids), but also along dorsal surface.

Mantle organs (Figs. 454, 455). Similar features as those of preceding pediculariids, remarkable attributes following. Mantle lobes narrow and smooth, siphon low. Osphradium small, almost entirely bipectinate (a short anterior portion monopectinate). Osphradium filaments low, thin, tip rounded, turned externally. Gill proportionally small, located in middle region of pallial cavity, far from osphradium; anterior region weakly curved. Gill filaments narrow and tall, edges straight, tip pointed, slightly turned to right. Hypobranchial land thin.

Circulatory and excretory systems (Figs. 454, 456). Characters somewhat similar to those of preceding pediculariids, with following remarkable features. Auricle short and broad, inserted in ctenidial vein sub-terminally, amply attached to anterior surface of pericardium. Kidney proportionally short, with a single lobe. Kidney lobe tall, massive, solid, triangular in section, attached only to dorsal surface of renal chamber (free from intestine), covered by transversal folds. Membrane between kidney and pallial cavity thin and lacking structures attached to it.

Visceral mass (Fig. 454). First whorls narrow, increasing suddenly in penultimate whorl; anterior-left expansion weak. Digestive gland fills most of visceral mass, color pale beige. Gonad very narrow, restrict to columellar surface of each whorl, color also pale beige; its anterior-left region in a T-fashion. Visceral oviduct proportionally broad, running obliquely along visceral last whorl ventral surface.

Digestive system. Foregut characters (Fig. 457) similar to those of preceding pediculariids, notable or distinctive features following. Odontophore muscles as those described for *P. californica*, including **m7** pair and **m6a**; **m2** pair very narrow, running attached to anterior esophagus. Radular teeth (Figs. 105, 106): with similar attributes as those of preceding pediculariids, differing mainly by more cusps in rachidian (17-19), and by secondary cusp of inner marginal tooth located closer to apex. Anterior esophagus with a pair of longitudinal folds. Esophageal gland almost vestigial (Fig. 457), only some transversal folds between both longitudinal folds running along middle esophagus. Posterior esophagus, stomach and intestine short, relatively broad and weakly sinuous. Stomach broader region, with a duct to digestive gland in its anterior surface (Fig. 456).

Genital system. **Male**. Characters similar to those described for *P. californica*, except for smaller penis with tip sharper, bearing a short papilla (Fig. 458).

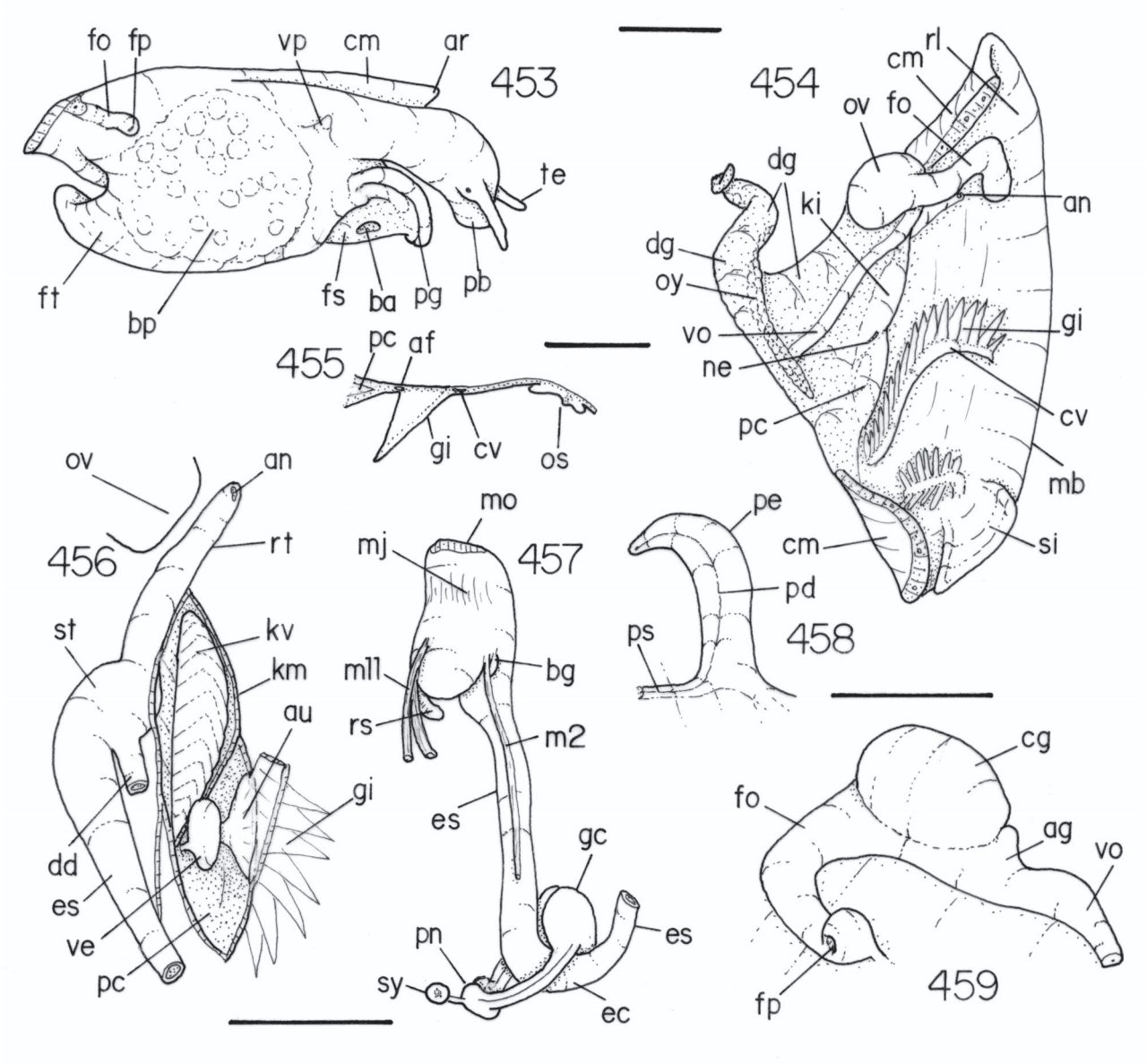
Female. Visceral and pallial attributes also similar to preceding pediculariids, with following remarks. Visceral oviduct broader and dorso-ventrally flattened (Figs. 454, 459). Albumen gland small, located in terminal region of visceral oviduct. Capsule gland spherical, following albumen gland with about double of its width. Bursa copulatrix lacking. Vaginal tube long (about 1/3 of distance between capsule gland and head base, curved, attached to pallial floor. Genital pore edged by thick borders, turned towards right. Brood pouch with similar features as those of preceding pediculariids (Fig. 453), except for more central location of its aperture, close to foot anterior edge. All females with a vestigial penis.

Measurements of shells (in mm). ♀ 1: 5.7 by 2.4; ♂ 3: 3.9 by 2.2.

Material examined. AUSTRALIA; **Queensland**; of north end of Moreton Bay, 27º01'S 153º36'E, 128 m depth, AMS 353021, 1♂, 3♀ (sta. 675C, HMAS "Kimbla", W.F. Ponder col., 29/iii/1969).

N.B.: an additional pediculariid was studied, a single immature female of another not identified species – *Pedicularia* sp3. The information obtained was very limited, then it was excluded of this study, however it is used for additional base the characters of the family.

Material examined. NEW CALEDONIE; south, 24º55'S 168º22'E, 510 m depth, MZSP 30616 (ex-MNHN), 1♀ (Sta. DW38, N.O. "Alis" Campagne SMIB4, Orston col., 07/iii.1989).



Figs. 453-459, *Pedicularia* sp2 anatomy: **453,** head-foot, female, lateral-right view; **454,** pallial cavity roof and visceral mass, female, ventral view; **455,** pallial roof, transversal section in middle level osphradium; **456,** anterior region of visceral mass and some adjacent pallial structures, ventral view, digestive tubes shown as in situ, kidney and pericardium opened longitudinally, posterior gill end deflected; **457,** foregut, lateral-left view, nerve ring also shown (as in situ); **458,** penis and its base, lateral view; **459,** pallial oviduct dorsal view. Scales = 0.5 mm.

Comments on pediculariids. Schilder (1931) produced a revision of the 11 known species of the family (considered an ovulid subfamily), and even separated them into 2 genera based mainly on characters of the columellar lip. The 11 species have their shell character distributed in a didactic table. Despite the importance of those data, the interpretation of the present material based on them was a little confused. Then, it was preferred to maintain 2 of the species still not identified and the 4 studied species in the genus *Pedicularia*.

Family Lamellariidae

Genus *Lamellaria* Montagu, 1815

(Type species: *L. tentaculata* Montagu, 1815; = *Bulla perspicua* Linné, 1758)

Lamellaria branca new species

(Figs. 63-65, 96, 107, 108, 460-481)

Types. *Holotype:* MZSP 29257, ♀ , from type locality. *Paratypes:* BRAZIL; **São Paulo**, off Ubatuba (R.V. "W. Besnard" col.), 24º08.4'S 45º01.2'W, 78 m depth, MZSP 30842, 2♂ , 1♀ (sta. 5024, 19/xii/1986), 23º57.5'S 44º52.8'W, 75 m depth, MZSP 29256, 1♀ (sta. 5021, 18/xii/1986); 24º14'S 44º32'W, 134 m depth, MZSP 30679, 3 specimens (Sta. 5148, 12/vii/1987); 24º01.5'S 44º33.5'W, 124 m depth, MZSP 32843, 3 specimens (Sta. 5019, 17/xii/1986); URUGUAY; off **Maldonado**, 35º33'S 53º48'W, 58 m depth, MZSP 19498, 1♀ (GEDIP-RS sta. 1868, RV "W. Besnard" col., 12/viii/1972).

Type locality*:* BRAZIL; São Paulo, off Ubatuba, 24º08.4'S 45º01.2'W, 78 m depth (R.V. "W. Besnard" col.).

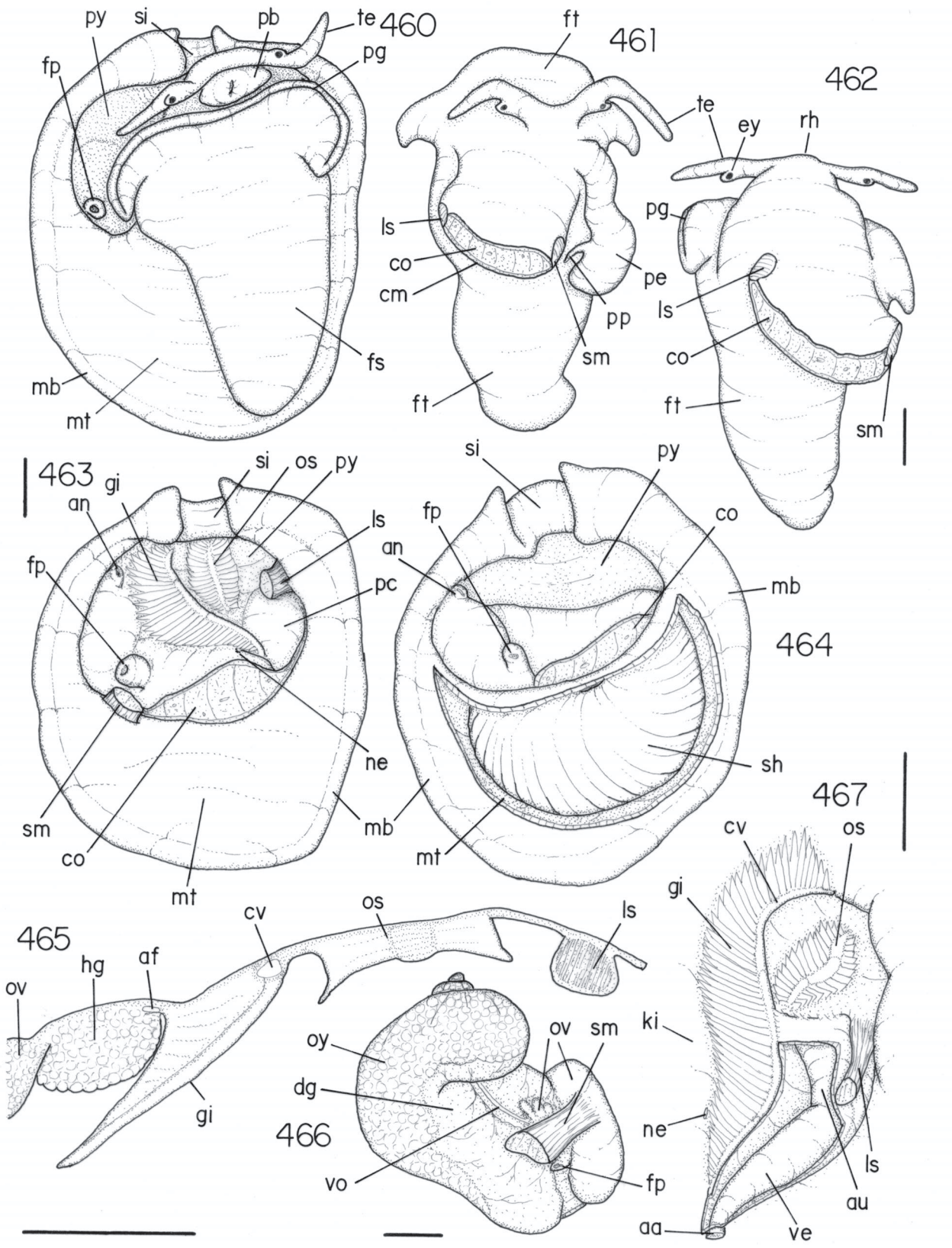
Diagnosis. Animal uniformly pale cream in color. Deepwater. Mantle smooth (lacking small papillae). Rachidian tooth with plane base (lacking concave portion). Penis with tip broad, and a lateral, small papilla in such tip penis duct opens. Pallial oviduct with a seminal receptacle with nodules, capsule gland large, as a blind-sac. Vaginal duct well marked, running on right side of capsule gland.

Description

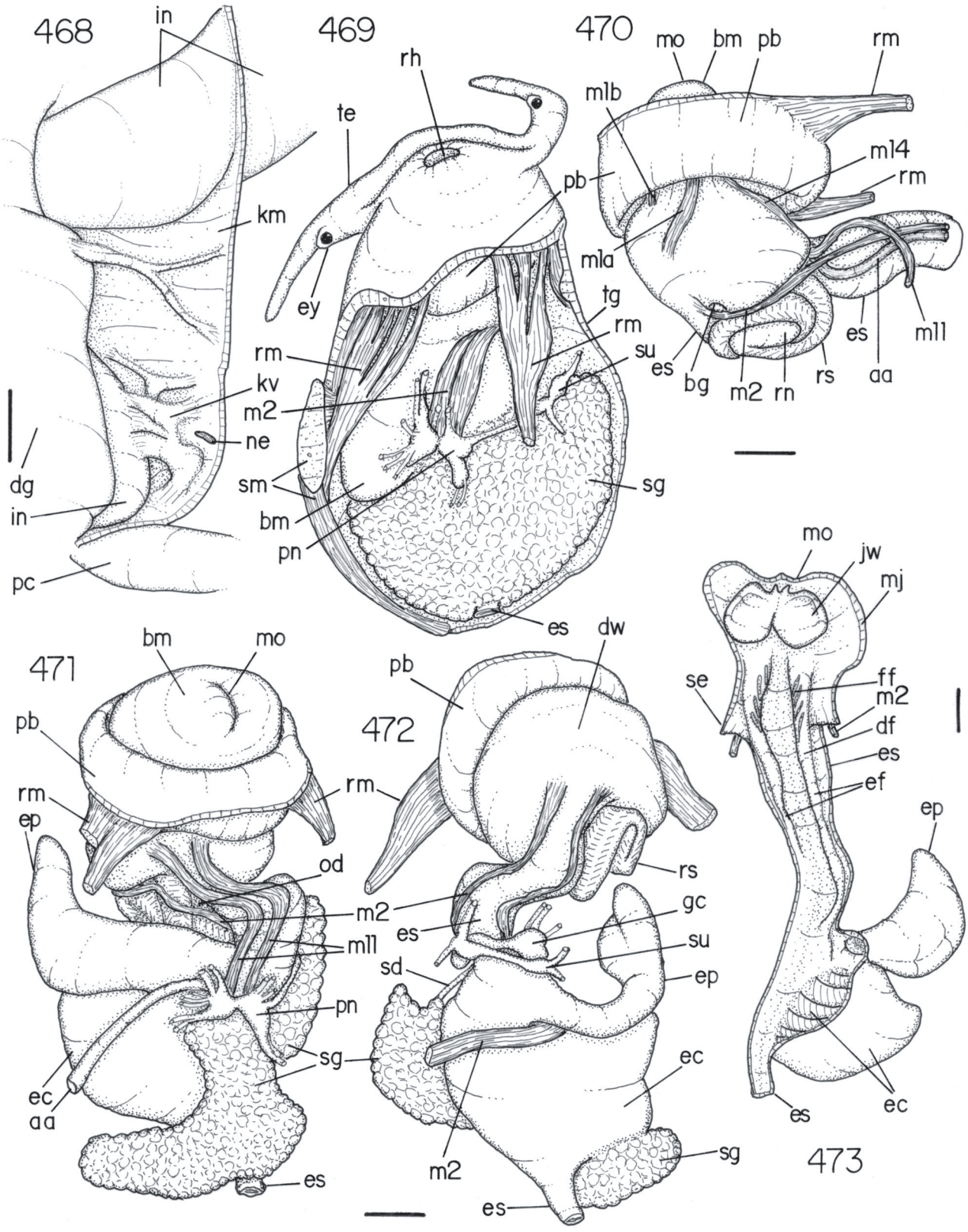
Shell (Figs. 63, 65). Entirely covered by mantle. Color whitish, semi-transparent. Periostracum opaque, transparent, very thin. Spire large, conic, of 3 whorls. Suture slightly deep. Body whorl large, inflated. Aperture ample, opisthocline. Inner lip sigmoid. Outer lip very thin.

Head-foot (Figs. 64, 460-462, 469). Color homogeneous pale cream (Fig. 64). Head outstanding, slightly peduncled (Figs. 461, 462). Tentacles lateral, a flap unites both tentacles just dorsal to rhynchostome. Ommatophore small, located about in middle region of tentacles. Eyes dark, small. Rhynchostome rounded. Foot long, flat, slightly triangular. Anterior furrow of pedal glands long, edges thick, extending beyond foot sole by lateral projections. Haemocoel broad, elliptical (Fig. 469); connection with visceral mass posterior, located about in middle region of foot. Shell muscles, homologous to columellar muscle, divided into 2, in each side of visceral connection of haemocoel (Figs. 461-463). Left shell muscle in general smaller and more anterior than right shell muscle. A thin portion of columellar muscle remains uniting both shell muscles. Each shell muscle connects with adjacent lateral and ventral muscles of head and foot. Origin of right shell muscle in superior region of inner lip and part connected to adjacent mantle and organs such as oviduct (Fig. 466). Origin of left shell muscle in inferior region of outer lip (Fig. 467), running though ventral surface of pericardium.

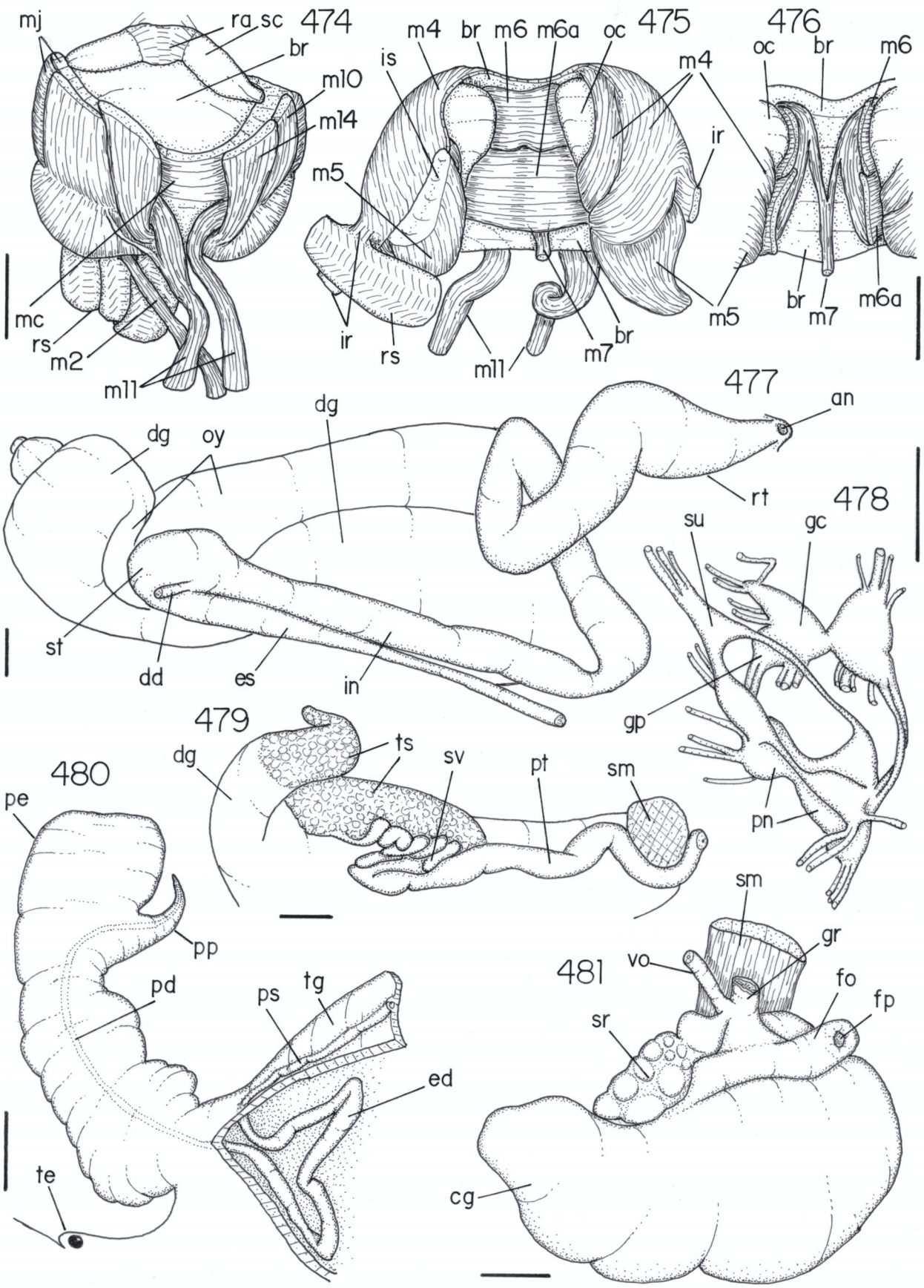
Mantle organs (Figs. 463, 465, 467). Mantle evolves completely shell, without clear dorsal division of suture. Color homogeneous pale cream. Mantle border outstandingly thick and muscular, anterior and lateral-right regions located just anterior to shell outer lip. This thick mantle region continues surrounding entire animal body as a flange (Figs. 64, 460, 463, 464). A posterior part of mantle covers ventral shell surface, localized touching dorsal surface of foot. This region bears immerse in integument a special arrangement of pallial muscles distributed asymmetrically in radial, long bands, this bands dichotomize successively through ventral surface towards periphery, where faint. These pallial muscles may be homologous to a portion of columellar muscle. Thick region of mantle forms an outstanding siphon projected anterior, just on head. Pallial cavity slightly small, occupying about anterior 1/3 of animal body. Osphradium elliptical, slightly large, bipectinate, symmetrical. Osphradium filaments tall, tip pointed (Fig. 465). Gill long, curved, with about twice osphradium length, running along middle axis of pallial cavity. Gill filaments tall, base slightly broad, narrows gradually, tip pointed. Space between gill and visceral organs slightly narrow. Hypobranchial gland relatively thick close to gill, transversal folded, color whitish or pale brown, covers thinly a part of visceral organs encroaching pallial cavity. Gonoducts running in right pallial region, described below. Rectum running dorsally to gonoducts. Anus small, low, siphoned, just anterior to gonoducts and slightly close to siphon.



Figs. 460-467, *Lamellaria branca* anatomy: **460,** whole specimen, ventral view; **461,** head-foot, male, dorsal view; **462,** same, female; **463,** pallial cavity roof and visceral mass, female, ventral view; **464,** same, mantle covering ventral shell surface removed, pallial organs not shown; **465,** pallial roof, transversal section in middle level osphradium; **466,** visceral mass just removed from shell, female, frontal view, **467,** pallial cavity roof, ventral view, detail of gill and osphradium region, pericardium (dorsal to gill) opened longitudinally. Scales = 2 mm.



Figs. 468-473, *Lamellaria branca* anatomy: **468,** kidney, ventral view, ventral wall sectioned longitudinally and deflected anteriorly; **469,** head and haemocoel, ventral view, foot and shell muscles removed, proboscis retracted; **470,** foregut, lateral-right view, only anterior esophagus shown; **471,** same, whole ventral view; **472,** same, dorsal view; **473,** dorsal wall of buccal mass and esophagus, ventral view, odontophore removed, esophagus opened longitudinally. Scales = 1 mm.



Figs. 474-481, *Lamellaria branca* anatomy: **474,** odontophore, ventral view; **475,** same, radula removed and deflected to left (partially shown), both cartilages deflected, left m5 (right in fig.) deflected; **476,** same, detail of median region with m6 and m6a sectioned; **477,** visceral mass partially uncoiled, female, ventral view, middle and distal digestive tubes seen as in situ; **478,** central nervous system, dorsal view; **479,** superior region of visceral mass partially uncoiled, male, ventral view, with special concern to genital structures; **480,** penis and its basal region, including adjacent haemocoel, ventral-slightly right view; **481,** pallial oviduct and some adjacent structures, ventral view. Scales = 1 mm.

Circulatory and excretory systems. Pericardium large, located in anterior-left extremity of visceral mass and close to mantle border. Heart running at left and part dorsal from gill, along its posterior half (Fig. 467). Auricle connected directly to middle portion of ctenidial vein. Ctenidial vein with about half of its length (posterior) with a contrary (postero-anterior) blood flow. Ventricle long, located posterior to auricle, aortas posterior to ventricle. Kidney narrow, long, compressed by intestinal loops (Fig. 468). Renal tissue white, diffuse, as several glandular, irregular folds in dorsal inner surface and also in membrane between kidney and pallial cavity plus pericardium. Renal tissue thicker at left from nephrostome, where connects with intestine and pericardium wall. Nephrostome a slit located between left and middle thirds of kidney.

Visceral mass (Figs. 464, 466). Occupies completely shell, up to fist whorl. Form spiral. Gonad in outer and digestive gland in inner sides or each whorl. Remainder characters somewhat similar to those of *M. zebra*.

Digestive system (Figs. 469-477). Proboscis pleurembolic (Figs. 470-472), short. Pair of proboscis retractor muscles in ventral-lateral region of proboscis. Mouth a longitudinal slit. Oral tube slightly long and conic. Buccal mass large (about 1/3 of haemocoel volume). Pair of jaw plates very large, thick, slightly circular, tall cut-edge, with sharp projection in median-anterior region of cut-edge (Figs. 96, 473). Dorsal folds of buccal mass slightly narrow, furrowed part somewhat long (5-6 furrows) (Fig. 473). Aperture of salivary glands in anterior furrow. Odontophore muscles (in comparison with those of *M. zebra*) (Figs. 471, 472, 474-476): **m1a**, **m1b** and **m2** pairs similar; **m3** not developed; **m4** pair similar but with ventral part divided into 2 parallel branches; **m5** pair similar but thinner; **m6** broad and slightly thick; **m6a** located just posterior, as continuation of m6 (similar fashion to m6); **m7** pair well-developed, originating in median-anterior margin of m4 dorsal branch, running towards posterior attached to subradular membrane, unite with each other in their middle level, inserting in radular sac inner surface, ventral to radula; **m11** pair broad, without muscular tissue surrounding radular sac (only a membrane), inserting sometimes with an additional branch covering m14; **m10** and **m14** similar. Radular sac with about double buccal mass length, very coiled. Radular nucleus broad and simple. Radular teeth (Figs. 107, 108): rachidian tooth tall, narrow, cut-edge curved, tip pointed, about 8 pairs of secondary, very small cusps; lateral tooth similar to rachidian, but taller and curved inwards, also with some small secondary cusps in cut-edge, about 12 in outer margin and 5-6 larger in inner margin; inner and outer marginal teeth missing. Salivary glands large (Fig. 469), clustering esophagus posterior to nerve ring. Salivary glands ducts narrow, suns similar to those of *M. zebra*. Anterior esophagus long, with a pair of low folds (continuation from those of buccal mass). Middle esophagus short, without inner folds (Fig. 473). Pouch large, long, broad, deep, as a diverticle located just anterior to esophageal gland (Fig. 473: **ep**). Esophageal gland short and deep, some inner septa thin, tall and transversal (Fig. 473). Posterior esophagus very slender and long (about 2/3 of total esophagus length), inner surface smooth. Stomach characters (Fig. 477) slightly similar to those of *M. zebra*, except for smooth inner surface and by single duct to digestive gland, originated just between esophagus and intestine. Intestine broad, inner surface smooth, running initially parallel and at right to esophagus by approximately 1 whorl, in left region of kidney suddenly towards right, running transversally up to opposite side of visceral mass, after towards posterior and left, with a loop ventral to its preceding region, after loop, newly towards anterior, crossing right end of kidney and runs in pallial cavity dorsal to gonoducts by a short distance (Fig. 477). Anus above described.

Genital system. **Male**. Testis color cream, located in right region of visceral mass up to its tip (Fig. 479). Seminal vesicle coiled, very broad in its middle region, located in middle region of visceral mass last whorl ventral surface. Prostate as a long and broad tube running after seminal vesicle towards anterior, lies close to right edge of pallial cavity and contours ventrally right shell muscle (Fig. 479). After this muscle, vas deferens narrows and runs through integument up to penis base (Fig. 480). Preceding penis base, vas deferens presents an ample free loop in haemocoel (Fig. 480). Penis long and broad (Figs. 461, 480), penis tip broad and flattened, with a lateral, sub-terminal papilla. Penis duct running along its middle region, suddenly penetrates along papilla, aperture very small in papilla tip (Fig. 480).

Female (Fig. 481). Ovary (Fig. 466) larger than testis, beige in color. Visceral oviduct narrow,

running in middle region of visceral mass ventral surface, edging ovary at right. Pallial oviduct large, bulging in right region of pallial cavity. Visceral oviduct inserts about in middle region of pallial oviduct right margin. Gonopericardial duct short, inserted close to visceral oviduct. Seminal receptacle a long and irregular sac; length about ¼ of that of capsule gland; inserting close to insertion of visceral oviduct; localization in right region of pallial oviduct turned towards posterior. Capsule gland very large, expanded to left of visceral oviduct insertion towards anterior and posterior; walls thick; inner duct brad and flattened. Vaginal tube well-developed, uniting a portion of right margin of both capsule gland laminas; becoming a separates tube at some distance from anterior end of capsule gland, running on pallial cavity floor. Genital pore small, in ventral region of vaginal tube tip.

Central nervous system (Figs. 469, 478). Features similar to those of *M. zebra*, differing in having closer ganglia and by additional connection between both pedal ganglia, probably due to proximity of subesophageal ganglion (Fig. 478).

Measurements of shells (in mm). MZSP 19498 (shell only): 9.2 by 9.7.

Distribution. Rio de Janeiro and Uruguay coast.

Habitat. Sandy, from 75 to 134 m depth.

Material examined. Types.

Discussion. *L. branca* is similar to the following described species, *L. mopsicolor*, from which differs mainly by characters listed in the Diagnosis. Further differences are reported thorough subsequent lamellariid descriptions. A complementary discussion follows the *L. mopsicolor* description. There are several species of lamellariids reported to the South Atlantic, a group with difficult identification and lacking a revisional framework. Despite this, a new species is described, mainly based on the geographic distance and by shallower depth of the remainder, mostly Patagonian and Antarctic, species (see discussion of Marcus, 1956: 10-11).

Lamellaria mopsicolor Marcus, 1956

(Figs. 66, 67, 109, 110, 482-491)

(Color plate Figs. 25-27)

Lamellaria perspicua mopsicolor Marcus, 1956: 11-14 (figs. 12-21); Rios, 1970: 59; Abbott, 1974: 145; Rios, 1975: 69-70 (pl. 19, fig. 284); 1985: 62 (pl. 23, fig. 277); 1994: 78 (pl. 26, fig. 302).

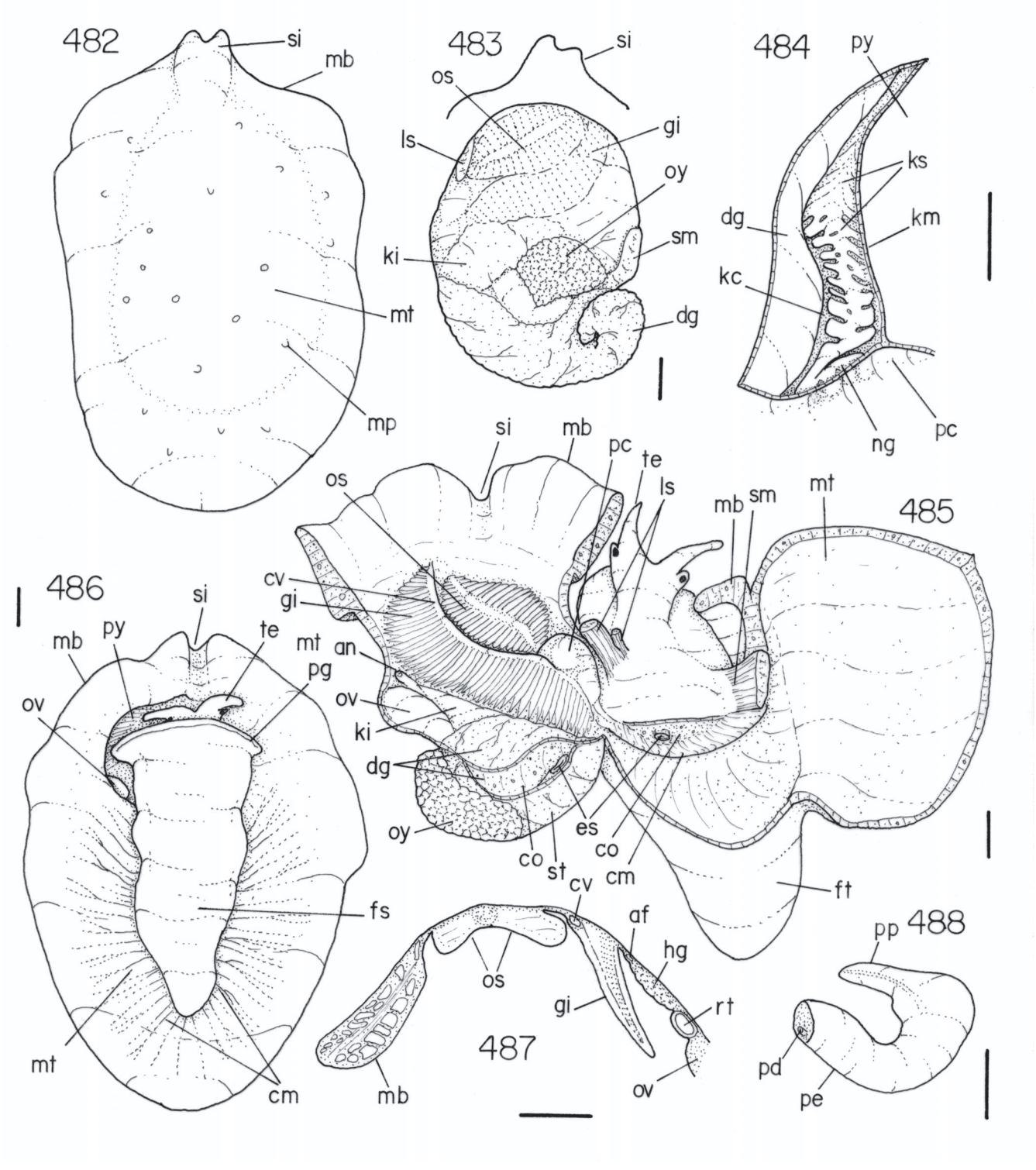
Description

(Adequate morphological description in Marcus, 1956, a complement and notable features following).

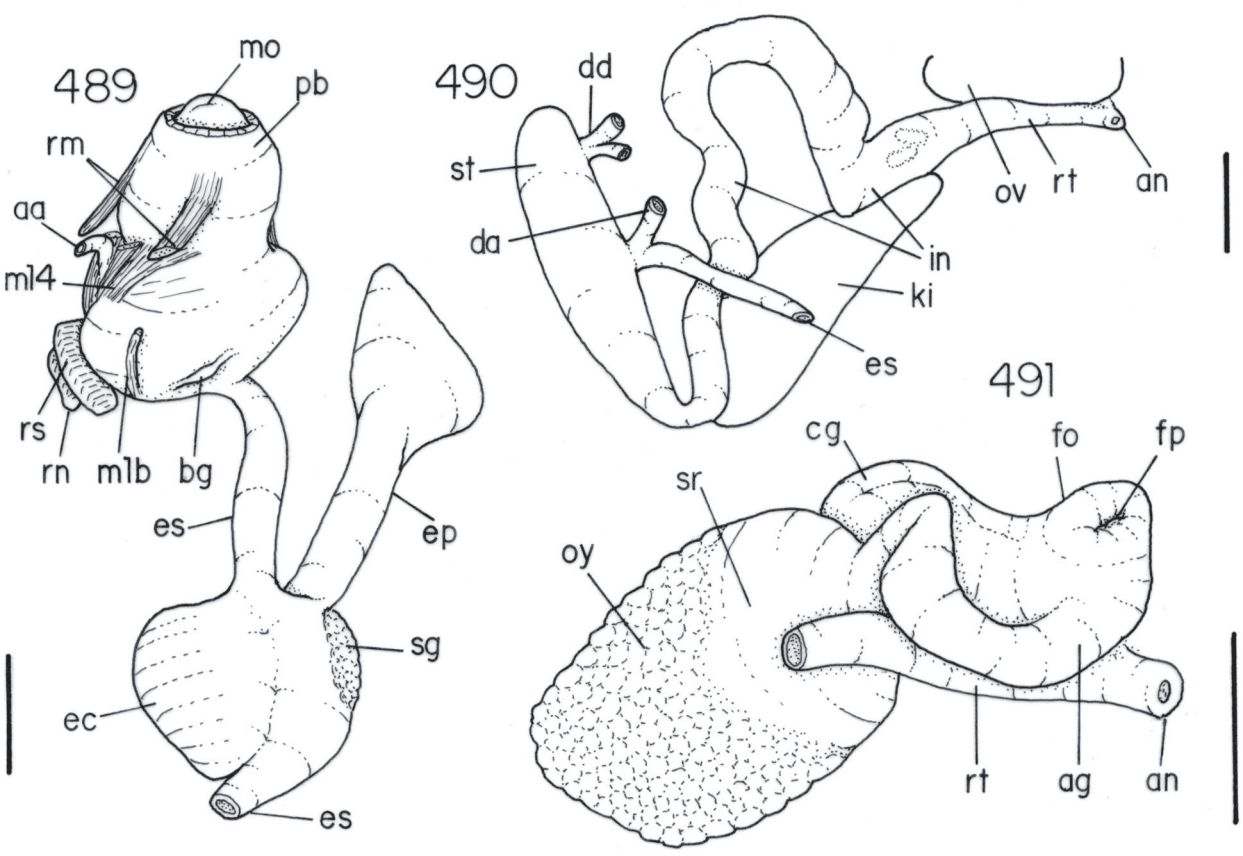
Shell (Figs. 66, 67). Similar in features to those of preceding *Lamellaria*, differing in being slightly longer laterally and shorter longitudinally.

Head-foot (Figs. 485, 486; color plate Figs. 25-27). Characters similar to those of *L. branca*, differing only by presence of pigmentation (of variable patterns) and by narrower anterior edge of foot. Left shell muscle separated into 2 bands, an anterior, smaller band inserted in anterior region of mantle border and siphon (and not in shell).

Mantle organs. Morphological attributes similar to those described for *L. branca*, distinctive or notable features following. Mantle covering entirely shell, dorsal surface with several well-spaced, small, simple papillae (Fig. 482). Mantle color variable among specimens, generally beige with sparse brown spots, sometimes orange, gray and other colors as base or spots. Anterior siphon well developed (Figs. 482, 485, 486). Pallial, radial, ventral muscle easily visible by transparency (Fig. 486). Most of mantle presenting 2 dense layers, external and internal (this touching shell), separated by a sponge-like conjunctive tissue (Fig. 485). Pallial cavity size and organizations closely similar to those of *L. branca*, except for following notes (Figs. 483, 485, 487). Osphradium proportionally larger, its filaments with rounded tip, right filaments larger and weakly scalloped. Gill filaments narrower and taller, curved towards right, rod narrow, tip pointed. Ctenidial vein narrow and with uniform width along its length (except in region of auricle insertion). Afferent gill vessel very narrow, running at some



Figs. 482-488, *Lamellaria mopsicolor* anatomy: **482,** whole dorsal view; **483,** pallial cavity roof and visceral mass just extracted from shell, dorsal view, siphon topology also shown; **484,** kidney opened longitudinally and some adjacent structures, ventral view; **485,** whole specimen with shell removed, dorsal view, mantle covering dorsal shell surface partially sectioned and deflected to right, pallial cavity roof and visceral mass deflected to left (both in ventral view); **486,** female, whole ventral view; **487,** pallial roof, transversal section in middle level osphradium; **488,** penis distal half, ventral view. Scales = 1 mm, except 488 = 0.25 mm.



Figs. 489-491, *Lamellaria mopsicolor* anatomy: **489,** foregut, lateral-left view; **490,** middle and distal digestive tubes, ventral view, seen as in situ; some adjacent structures also indicated; **491,** part of visceral and whole pallial female genital structures, ventral view, adjacent rectum and anus also shown. Scales = 1 mm.

distance at right from gill. Hypobranchial gland white, relatively tall, surface uniform.

Circulatory and excretory systems (Fig. 484). In general presenting same characters as those of preceding lamellariid, remarkable features following. Pericardium also part located exposed in posterior-left region of pallial cavity, dorsal to posterior third of gill, limited anteriorly with left shell muscle (Figs. 483, 485). Auricle connection to ctenidial vein sub terminal. Kidney narrow and relatively short. Nephridial gland small, restrict to wall between kidney and pericardium, bearing about 5 folds. Renal lobe single, large, triangular in section, posterior end connected to same of nephridial gland, attached only to dorsal surface of renal chambers, free from intestine or membrane between kidney and pallial cavity; surface presenting several irregular, transversal furrows.

Visceral mass (Figs. 483, 485). Same organization than that of *L. branca*. Digestive gland and gonad beige in color, gonad running in ventral surface of visceral whorls.

Digestive system (Figs. 489, 490). Foregut attributes similar to those of preceding lamellariid, with following remarkable features. Pleurembolic proboscis also short, jaws also large, possessing anterior-medial small projections. Furrowed portion of dorsal folds similar. Odontophore muscles: **m6a**, similar, as continuation of m6; **m7** pair very narrow; **m4** dorsal branch pair and **m11** connected to posterior region of odontophore cartilages. Buccal ganglia located close to median line. Radular sac little longer than buccal mass length. Radular teeth (Figs. 109, 110): similar characters to those of *L. branca*, differing in rachidian base having a concavity, and cut-edge narrower and sharper. Salivary gland smaller, clustering around middle esophagus. Anterior esophagus with a pair of relatively tall folds (continuation of buccal mass dorsal folds). Esophageal pouch (diverticle) very long, its basal 2/3 narrow as a duct, its distal 1/3 broader. Esophageal gland small located just posterior to nerve ring, color brown, with more transversal

septa. Middle esophagus with a pair of tall folds (continuation from those of anterior esophagus). Posterior esophagus narrow, without inner folds. Stomach large (Fig. 490), esophagus inserts in middle region of gastric anterior surface jointed with a narrow duct to digestive gland (located just at right). Another duct to digestive gland located also in anterior gastric surface in middle region between esophageal insertion and right stomach end, bifurcating in short distance. Gastric inner surface most smooth, with a single, low, narrow fold in ventral surface, from middle gastric region running towards intestine origin. Intestine originating in gastric left end, crosses slightly sinuous from left to right sides of visceral mass last whorl, contours a lobe of ovary, running towards left a distance equivalent to half of its preceding portion up to kidney chamber, where suddenly runs perpendicularly straightforward. Rectum replete of elliptical fecal pellets. Anus small, located posterior, at level of anterior third of gill (Fig. 485).

Genital system. **Male**. Adequate description in Marcus (1956: 14; pl. 3, fig. 16). Penis with basal 2/3 relatively narrow, distal third with a sub terminal broader region and a narrower, papilla-like tip (Figs. 488). Penis duct entirely tubular.

Female. Ovary running in ventral side of digestive gland and stomach (Figs. 483, 485), its anterior region, located in visceral last whorl, possessing a flat chamber (dorsal to intestine) (Fig. 491). This chamber suddenly narrows, becoming a thick walled, white, tubular albumen gland (Fig. 491). This tube twists in short distance and runs edging ventral surface of pallial oviduct. Capsule gland broad, short, and flat, located dorsal to albumen gland. Genital atrium relatively large, with thick walls, both capsule and albumen gland inserting directly in it. Genital pore broad, turned to right, at short distance from anus (Figs. 491).

Measurements of shells (in mm). MZSP 30684 (Shell only): 6.2 by 8.4.

Distribution. SE coast of Brazil.

Habitat. Under rocks, subtidal.

Material examined. BRAZIL; **São Paulo**; Ubatuba, Anchieta Island, MZSP 30683, 1♂; São Sebastião, Barequeçaba Beach, MZSP 30685, 1♀ (Simone col., 26/x/1996); Guarujá, Branca Beach, MZSP 30684, 1♀ (O. Domaneschi col., 11/6/1995). No data, MZSP 35008, 1 shell of Marcus' collection (probable type specimen).

Discussion. Marcus (1956) described *L. mopsicolor* as subspecies of *L. perspicua* (Linné). This data allowed Behrens (1980: 326) consider the originally Pacific *L. perspicua* as worldwide distributed. Based on the differences between *L. mopsicolor* and *L. perspicua* explored by Marcus (1956: 14), *L. mopsicolor* is herein considered in the specific rank, however it is obvious that Marcus did not consider the differences enough for this. The specific rank is here suggested up to further comparative studies. Fretter (1946) described the anatomy of *L. perspicua* and it differs greatly from the species here described. At least in the pallial oviduct (that paper, fig. 6), *L. perspicua* has a normal fashion (albumen and capsule glands in sequence) and seminal receptacles as several separated vesicles, what does not occur with *L. mopsicolor*.

Marcus (1956) did not designate types, neither type-locality. She examined specimens from Guaruja and Ilha Bela, São Paulo State, and from Cabo Frio, Rio de Janeiro State. No one specimen, which could be designed as lectotype, was found in the Marcus' collection, recently acquired by the MZSP. Most of the identified specimens of the ordinary MZSP collection, as *L. mopsicolor*, actually belong to *L. branca*. Initially it was difficult to identify which species actually could be regarded as Marcus' *L. mopsicolor*, because there were 2 species collected in the same geographic range, differing by the batimetry. The taxonomical problem was resolved, in favor to the shallow water species, with the Marcus (1956) good description.

A single shell was found in the Marcus' collection (color plate Figs. 25-27). This shell belonged maybe to a young specimen, since it is almost 1 whorl shorter than the larger lamellariids of above species. The shell has a label with Dr. Eveline Marcus calligraphy (color plate Fig. 28), with the original identification and nothing else. No locality or indication if the shell belongs to type series is provided. This young shell is perhaps a type-like specimen, and is included in this study and additional material examined. However a shell helps little in the differentiation between *L. branca* and *L. mopsiolor*.

N.B.: Another species similar to *L. mopsicolor*, but lacking pigment and with different characters of oviduct was examined. This species is not included in present study because a single, not well preserved specimen was available.

Material examined: URUGUAY; off Maldonado, 35º33'S 53º18'W, 58 m depth, MZSP 19498, 1♀ (GEDIP-RS, R.V. "W. Besnard", 12/viii/1972).

Lamellaria patagonica E.A. Smith, 1881

(Figs. 111-113, 492-507)

(Color plate Figs. 29-30)

Lamellaria patagonica E.A. Smith, 1881: 32-33 (pl. 4, figs) (loc: Trinidad Channel and Shell Bay, Patagonia); Marcus, 1956: 10; Rios, 1985: 62 (pl. 23, fig. 278); 1994: 79 (pl. 26, fig. 303).

Lamellaria fuegoensis Strebel, 1906: 145 (pl. 11, figs. 69a-c) (loc: Uschuaia).

Description

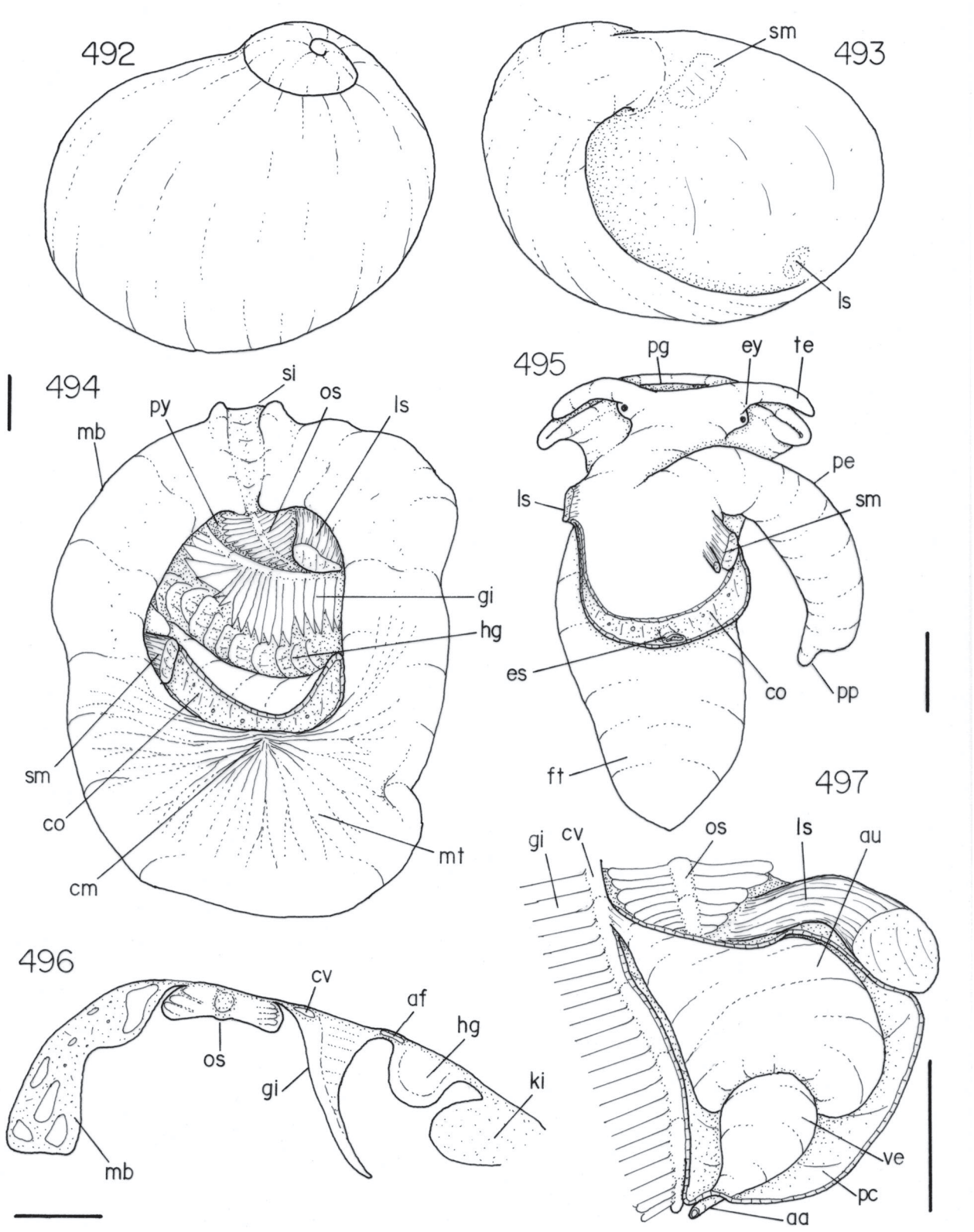
Shell (Figs. 492, 493; color plate Figs. 29-30). Similar features as those of preceding lamellariids, except in being more rounded and by inner lip almost covering columella. Muscular scars shown in Fig. 493.

Head-foot (Fig. 495). Characters similar to those described preceding lamellariids, including peduncled (socket-like) head, small ommatophore and broader anterior region of foot sole. Differs by proportionally broader head and by thick edge of pedal glands furrow. Pigmentation lacking.

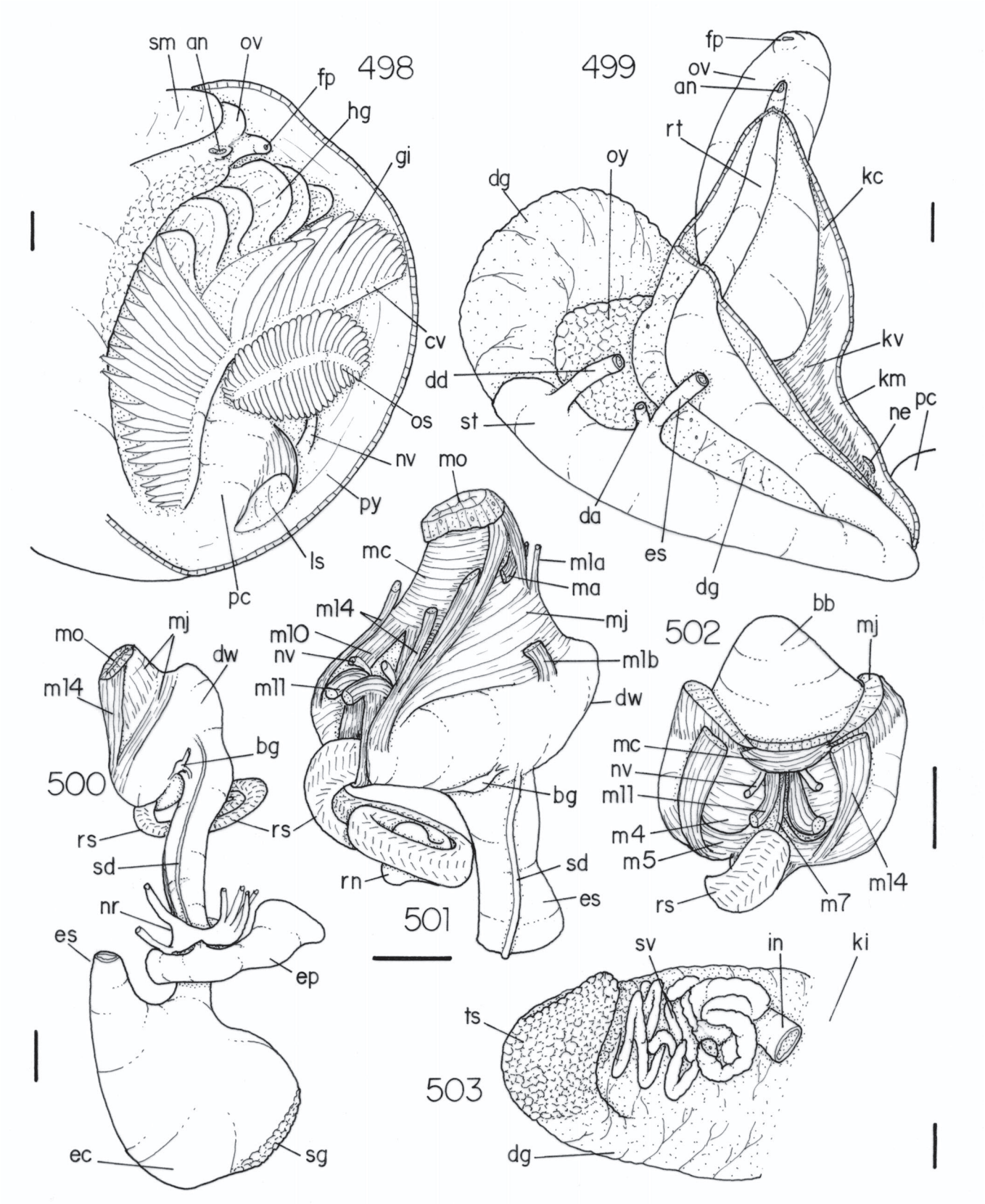
Mantle organs (Figs. 494, 496-498). Mantle attributes similar to those of preceding lamellariids, including extension (covering entire shell), peripheral thickness, anterior siphon, and pallial, posterior, ventral, radial muscle (Fig. 494). Differ in lacking papillae in outer-dorsal surface and in lacking pigments. Pallial cavity also with similar features as those of preceding lamellariids, distinctive or notable features following (Figs. 496, 498). Osphradium proportionally large, bipectinate, elliptical, slightly asymmetrical (fewer filaments at left); osphradium nerve on a low septum located transversally at middle level of osphradium left side. Osphradium filaments tip rounded, not projected, scalloped obliquely. Gill filaments slender and tall, tip sharp pointed, curved to right (Fig. 496). Ctenidial vein and afferent gill vessel of approximately same narrow width. Hypobranchial gland formed by several, successive, transversal, tall septa (Figs. 494, 496, 498), each one with rounded, thick edges, color white. Hypobranchial gland septa larger in center, gradually decreasing in both extremities, length somewhat same than that of gill. Between gill and rectum a space equivalent to that of gill base.

Circulatory and excretory systems. Heart and pericardium features (Fig. 497) similar to those of preceding lamellariids, including about half exposition in pallial cavity, part dorsal to gill posterior end, insertion of auricle about in middle level of ctenidial vein, and limit with left shell muscle. Renal features (Fig. 499) closer than those of *L. branca*, with renal lobe thin, constituted by series of transversal, anastomozed folds filling posterior half of dorsal renal chamber, connected to dorsal part of membrane between kidney and pallial cavity, not connected to intestine. Anterior half of renal chamber hollow, without renal tissue, compressed by gonoducts and rectum. Nephrostome close to posterior-left renal end, and close to renal lobe.

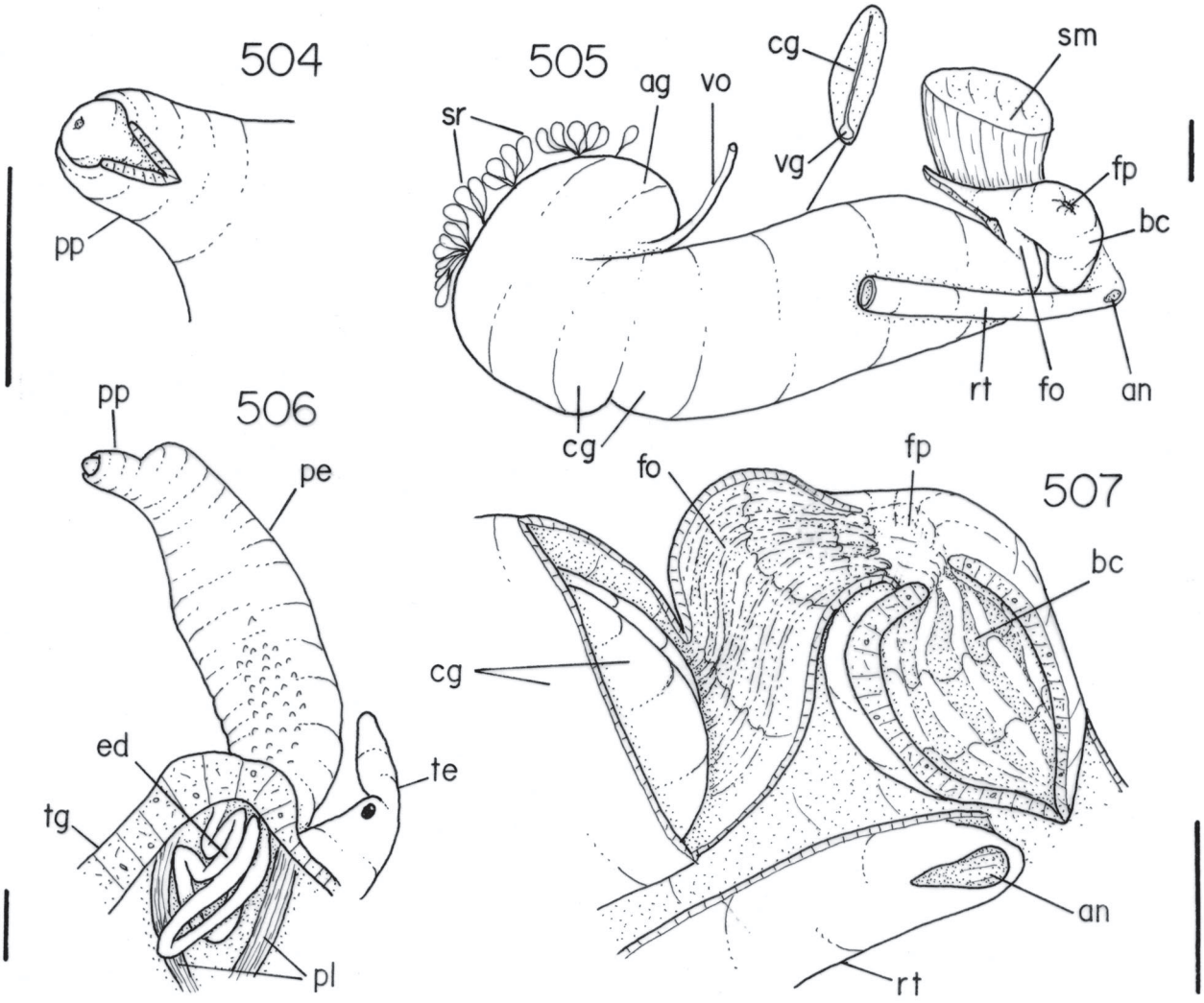
Digestive system (Figs. 499-502). Characters of foregut similar to those of preceding lamellariids, notable or distinctive features following (Figs. 500-502). Pair of dorsal folds of buccal mass also presenting furrowed portion, aperture of salivary gland located just anterior to furrowed portion, in middle level of each fold. Jaw plates with a small median projection. Odontophore and buccal mass muscles (Figs. 501, 502): **m1** concentrated in median line, along dorsal-anterior surface of oral tube; **m1b** pair present; **m2** pair absent; **ma**, pair of dilator (abductor) muscles of jaws, originating in lateral inner surface of proboscis, running a short distance, penetrating in mj fibers, inserting in outer surface of jaw plates; **m6a** as broad as m6, partially superpose on it; **m7** pair very narrow; **m7c**, pairs of very narrow fibers, originating on posterior-dorsal odontophore surface, running attached to local superficial membrane, inserting after short distance in dorsal surface of radular sac; **m10** pair short, originated from mc; **m11** pair with a membrane surrounding radular sac; **m14** pair close to median line. Radular sac with about double of odontophore



Figs. 492-497, *Lamellaria patagonica* anatomy: **492,** shell, dorsal view; **493,** same, frontal view; **494,** mantle covering ventral surface of shell, ventral view, head-foot removed pallial roof partially shown; **495,** head-foot, male, dorsal view; **496,** pallial roof, transversal section in middle level osphradium; **497,** pericardium and adjacent structures, ventral view, its ventral wall removed, left shell muscle partially deflected. Scales = 2 mm.



Figs. 498-503, *Lamellaria patagonica* anatomy: **498,** pallial cavity roof, female, ventral view; **499,** visceral mass anterior region and some adjacent pallial structures, ventral view, middle and distal digestive tubes shown as in situ, kidney opened longitudinally, with its pallial membrane deflected; **500,** foregut, lateral-left view, nerve ring also shown; **501,** buccal mass and adjacent esophagus, lateral-left view; **502,** odontophore, ventral view; **503,** visceral mass partially uncoiled, male, ventral view, only portion posterior to kidney shown. Scales = 1 mm.



Figs. 504-507, *Lamellaria patagonica* anatomy: **504,** penis, detail of terminal papilla with its outer protection partially sectioned; **505,** pallial oviduct, ventral view, some adjacent structures also shown, with a transversal section in indicated level; **506,** penis and its basal region, including adjacent haemocoel, ventral-slightly right view; **507,** pallial oviduct, ventral view, detail of its anterior end with most wall opened longitudinally, adjacent rectum and anus also shown. Scales = 1 mm.

length (Fig. 501). Radular teeth (Figs. 111-113) of similar attributes to preceding lamellariids, with following differences: rachidian flat and broader, lateral tooth tall, with a sharp pointed tip, cusps weak. Salivary glands small, cluster around middle esophagus. Salivary gland ducts running attached to anterior esophagus lateral surface, penetrate in dorsal wall just posterior to buccal mass. Anterior esophagus long, with a pair of longitudinal folds. Esophageal pouch just posterior to nerve ring (Fig. 500), bifurcates in short distance, with a branch longer, with tip broader. Esophageal gland, middle and posterior esophagus similar to those of *L. branca*. Stomach and intestine (Fig. 499) with close morphological attributes as those of *L. mopsicolor*, except for simple second duct to digestive gland (that far from esophageal insertion) and by less convolute intestine. Digestive gland pale beige. Anus simple, just anterior to kidney (Figs. 498, 499).

Genital system. **Male**. Testis pale beige, occupying first visceral whorls (Fig. 503). Seminal vesicle very convolute, extending at about half whorl in ventral surface of visceral last whorl; posterior loops narrower, becoming broad gradually (Fig. 503). Pallial vas deferens running immerse in pallial floor in its right-posterior region. Ejaculatory duct (in region of vas deferens preceding its penetration into

penis), with 3 loops as shown in Fig. 506. Penis large, broad, curve, dorso-ventrally flattened, thick (Figs. 495, 506). Penis base with some muscular reinforcements protruding in haemocoel (Fig. 506). Basal half penis ventral surface with several, very small, simple papilla. Penis duct entirely closed (tubular). Penis tip with a long, lateral and broad papilla; papilla tip protected by a preputial fold (Figs. 504, 506). Penis duct aperture in papilla tip.

Female. Visceral structures (Fig. 499) with characters similar to those of *L. branca*. Pallial oviduct large and broad, dorso-ventrally flattened, lying dorsal to kidney and rectum. Visceral oviduct very narrow, inserts in apex of albumen gland (Fig. 505). Albumen gland with about ¼ of remainder pallial oviduct, and located at right from its posterior end. Albumen gland running antero-posteriorly a short distance, where suddenly curves towards anterior, connecting with capsule gland (Fig. 505). Seminal receptacles as several, small, aligned vesicles located along posterior edge of albumen gland, groups of 5-7 adjacent vesicles unite their ducts and insert in albumen gland in single point. Capsule gland long, with thick walls. Vaginal groove running along capsule gland left edge. Capsule gland suddenly narrows anteriorly, its glandular laminas finish. Vaginal tube remains running from left to right, inner surface with some longitudinal, narrow folds, inserting close to female pore (Figs. 505, 507). Bursa copulatrix small, as a bind-sac, walls thick muscular, inner surface with some longitudinal, tall folds, aperture sphincter-like by side and anterior to vaginal aperture in genital pore. Genital pore in tip of a tall, broad papilla, situated turned to right close to right shell muscle and somewhat close to anus (Figs. 498, 505, 507).

Measurements of shells (in mm). MACN 24946, ♀ 4: 18.5 by 11.5 (total, no only shell).

Distribution. Rio Grande do Sul, Brazil to south Argentina and Malvinas Is.

Habitat. 16 to 75 m depth.

Material examined. ARGENTINA; **Terra del Fuego**; Paso Richmond, 4 m depth, MACN 24946, 1♂, 3♀.

Discussion. There is some confusion on the lamellariid systematics in all levels, however, Marcus (1986) made a comprehensive revision on the family genera, including a key. The 3 species studied here are *Lamellaria*, as they present 3 radular teeth per row and the male duct free in "visceral cavity". The latter character differentiates *Lamellaria* from *Coriocella* Blainville, 1824 on that key. However, it is not clear what exactly the character means, because little additional information is given. It is clear that visceral cavity may be the haemocoel, but the male duct (pallial vas deferens) of the 3 studied species is free only in its portion preceding penis base, being the remainder attached to the integument. This fact has particular importance in younger specimens, which the vas deferens still is not looping before its penis portion. In present level of knowledge, the attribution of *Lamellaria* to the 3 studied species appears adequate; however it is clear that further studies are necessary for defining better the differentiation between both genera with 3 teeth per row in radula. The study on *Coriocella nigra* (Blainville, 1824), type species of the genus, provided by Marcus (1986), revealed that it is close related to the present studied *Lamellaria*, differing mainly by the presence of pallial bosses.

Genus *Velutina* Fleming, 1821

(Type species *Bulla velutina* Müller)

Velutina velutina (Müller, 1776)

(Figs. 68, 69, 114, 115, 508-523)

(Color plate Fig. 33)

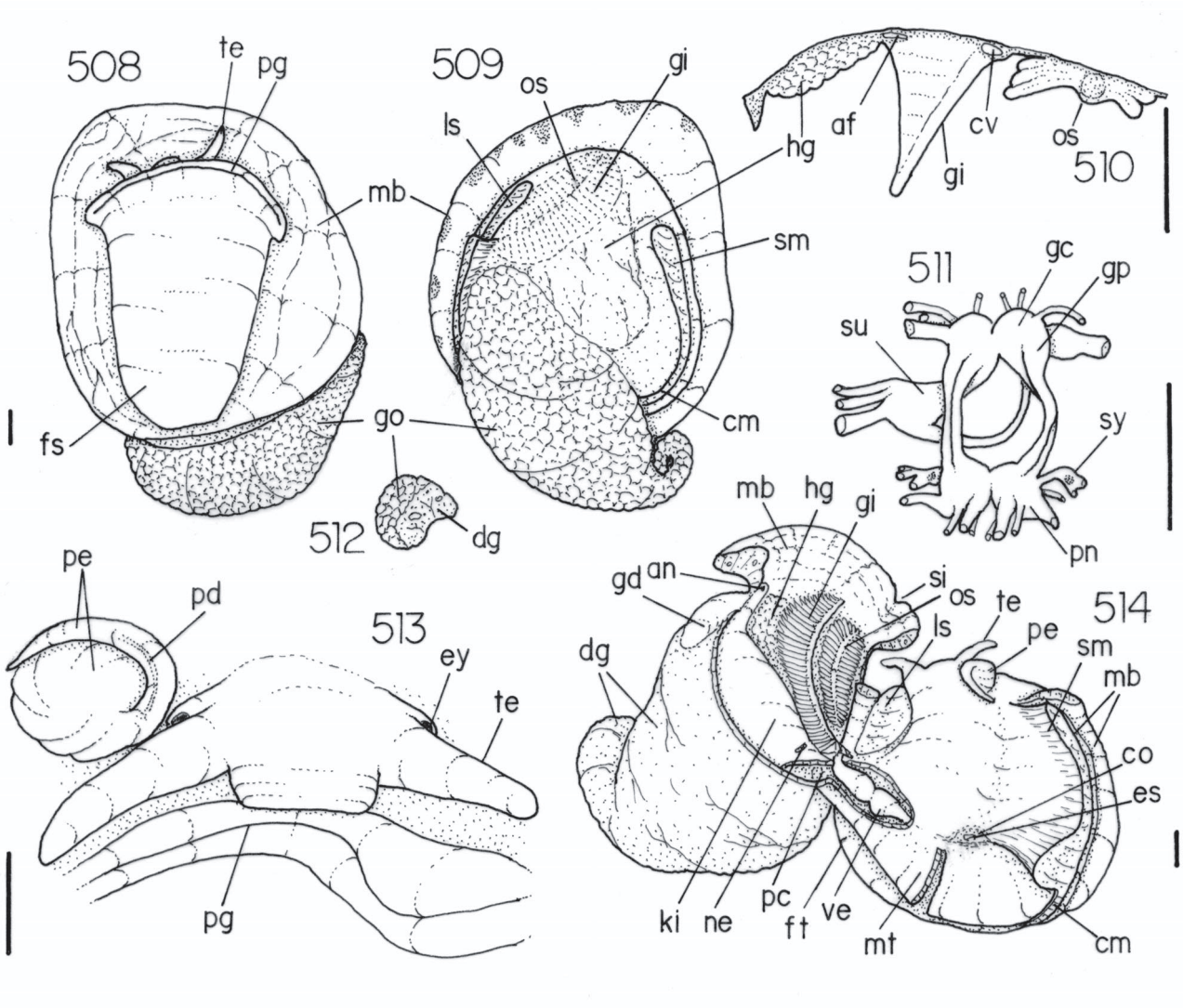
Synonymy in Rosenberg (1996). Remarks:

Bulla velutina Müller, 1776: 242 (loc: Denmark).

Velutina laevigata: Abbott, 1954: 175 (pl. 22, fig. n).

Velutina velutina: Fretter & Graham, 1962:54, 135, 242, 262, 350, 361, 381, 406, 407, 468, 555, 557, 643, 693 (figs. 128, 194C); Abbott, 1974: 146 (fig. 1602); Abbott & Dance, 1983: 83 (fig.); Trew, 1987a: 2.

Velutina (Velutina) velutina: Colikov & Gulbin, 1990: 109, 120, 127 (figs. 5, 6).



Figs. 508-514, *Velutina velutina* anatomy: **508,** whole ventral view, specimen extracted from shell; **509,** same, dorsal view; **510,** pallial roof, transversal section in middle level osphradium; **511,** central nervous system, dorsal view; **512,** transversal section in penultimate whorl of visceral mass; **513,** detail of head region, frontal view; **514,** whole specimen in dorsal view, with pallial roof and visceral mass partially sectioned and deflected to left (this in ventral view), pericardium opened, a transversal section in mantle region covering ventral-posterior shell surface also shown. Scales = 2 mm.

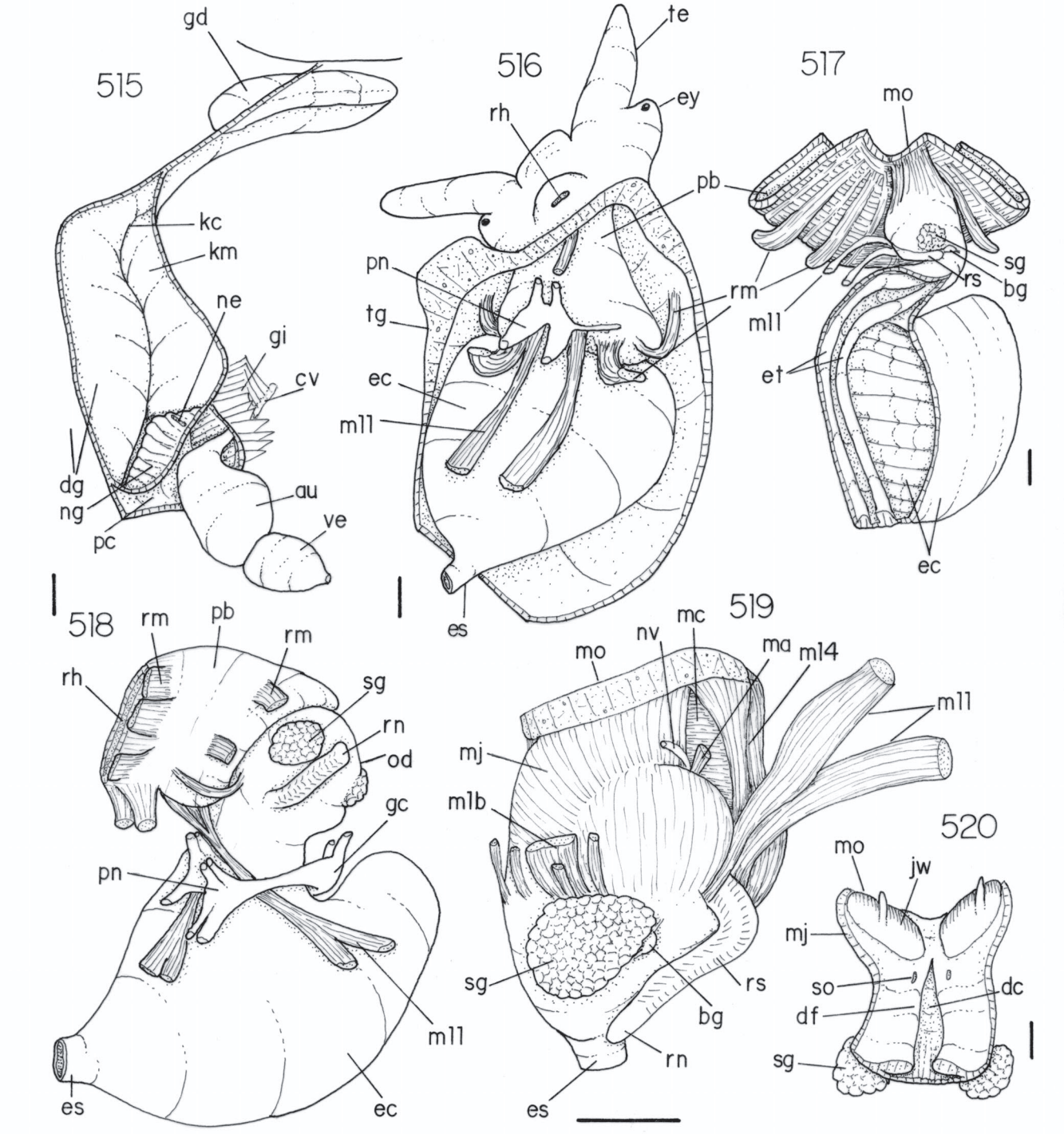
Description

Shell (Figs. 68, 69, color plate Fig. 33). Very thin, auriculiform, brown-transparent. Spire small, of 3 concave whorls. More details in Abbott (1974: 146).

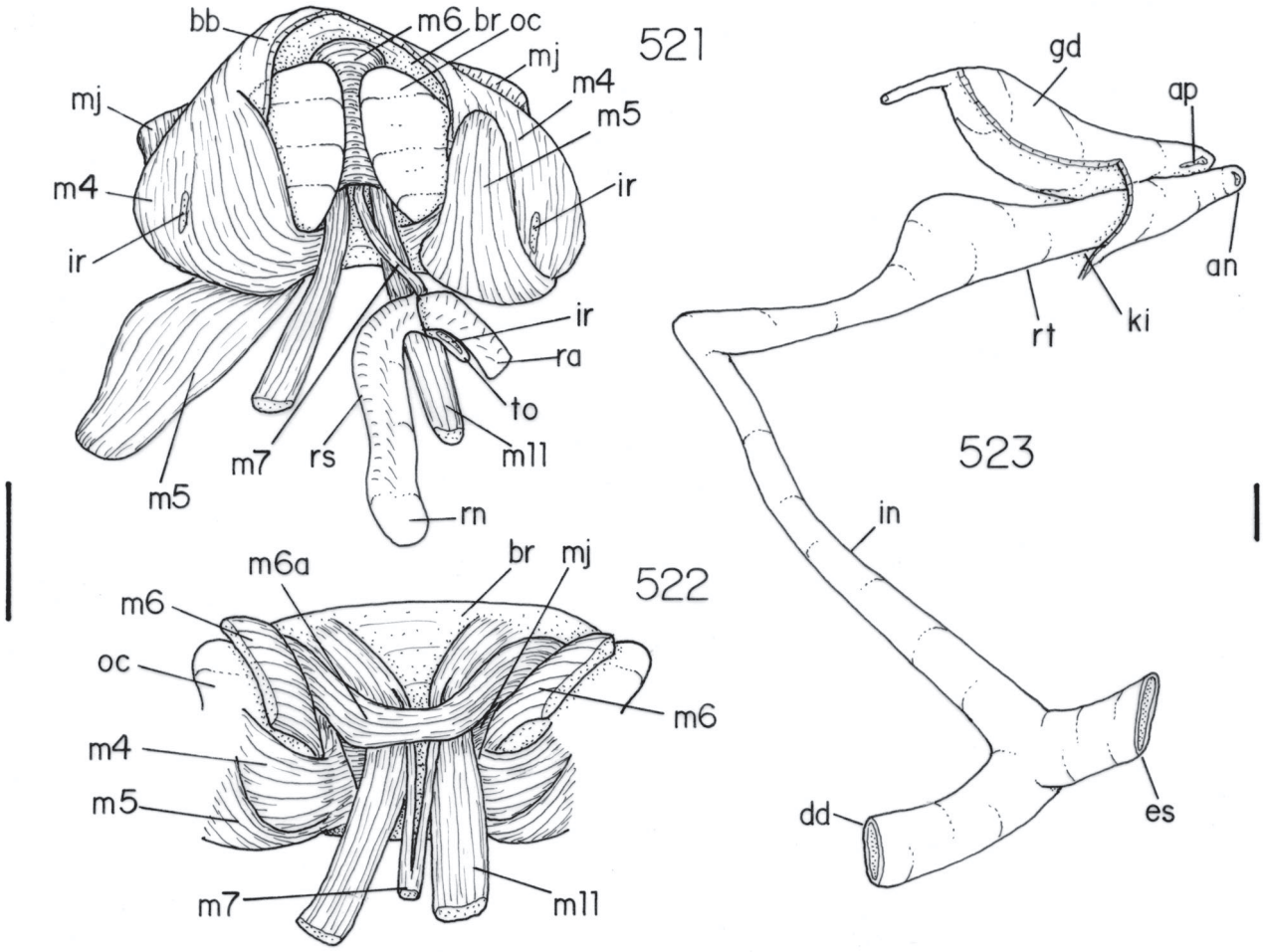
Head-foot (Figs. 508, 513, 514, 516). Head somewhat peduncled (socket-like), tentacles stubby; inter-tentacular membrane between both tentacles short and flat (Figs. 513, 516). Eyes small, on small ommatophores, located slightly over outer tentacles base. Rhynchostome a small pore located posterior and ventral to inter-tentacular membrane. Foot with about half area than that of remainder ventral animal surface. Foot sole broader anteriorly (Fig. 508), foot anterior margin arched, with furrow of pedal glands, slightly projected in both sides. Foot posterior end rounded. Columellar muscle modified in a horseshoe shell muscle (Figs. 509, 514), both anterior extremities broader (left extremity broader), remainder narrow, except for a broader region in right-posterior region. Posterior-dorsal surface of foot with a concavity supporting ventral portion of shell, separated by a broad flap of mantle (Fig. 514). Haemocoel broad, weakly curved towards right (Fig. 516). Penis present in all specimens (described below).

Mantle organs (Figs. 509, 510, 514). Mantle border double-folded (Figs. 508, 509, 514), an inner fold simpler, restricted to shell edge and connected shortly to shell muscle. Outer fold very thicker,

with irregular furrows, in part covering outer shell surface; pigmented by a series of semicircular, dark brown spots along edge. Siphon an anterior notch of outer mantle fold (Fig. 514). Pallial cavity of about half whorl (Figs. 509, 514), organization somewhat similar to those of Lamellaria. Osphradium bipectinate, large, elliptical. Osphradium filaments scalloped (Fig. 510), left filaments fewer and smaller than right filaments, outer half of each filament not attached to mantle and projected externally. Between osphradium and gill a narrow area. Gill extending little beyond osphradium length (anterior and porteriorly), weakly curved, area about half of that of pallial cavity. Gill filaments tall, edges almost straight, rods extending little beyond membranous portion, tip slightly pointed (Fig. 510). Gill posterior end on pallial floor. Ctenidial vein and afferent gill vessel with about same width. Between gill and visceral organs a narrow posterior



Figs. 515-520, *Velutina velutina* anatomy: **515,** kidney and pericardium region, kidney opened longitudinally, only pallial portion of pericardium shown, posterior gill end deflected, heart still connected to ctenidial vein; **516,** head and haemocoel, ventral view, foot and shell muscles removed, proboscis retracted; **517,** foregut, lateral-left view, esophagus opened longitudinally; **518,** same, proboscis removed, nerve ring also shown; **519,** buccal mass, lateral-right view; **520,** same, detail of its dorsal wall, ventral view. Scales = 1 mm.



Figs. 521-523, *Velutina velutina* anatomy: **521,** odontophore, ventral view, radula removed and deflected posteriorly (only partially shown), both cartilages deflected, right m5 (left in fig.) also deflected; **522,** same, detail of median region with m6 sectioned; **523,** middle and distal digestive tubes, ventral view, shown as in situ, adjacent pallial gonoduct also shown. Scales = 1 mm.

space and a broader anterior space. Hypobranchial gland thick, tall, white, surface uniform, located compressed just between gill and visceral structures.

Circulatory and excretory systems. Pericardium located in posterior-left region of pallial cavity floor (Fig.514). Connection auricle-ctenidial vein sub terminal, at short distance from gill posterior end (Fig. 515). Auricle at left from ventricle. Kidney narrow and flat (Fig. 515), situated slightly oblique, compressed between visceral mass and pallial cavity. Nephridial gland tall, narrow, triangular in section, with several transversal, irregular folds, restricted to membrane between kidney and pericardium. Renal lobe single, flat, located along membrane between kidney and pallial cavity, part covering nephrostome. Remainder renal space a hollow and flat chamber. Nephrostome a small slit close to pericardium.

Visceral mass (Figs. 509, 512, 514). Conical, palcispiral (about 2 whorls), not involute. Hermaphroditic gonad beige in color, lying in dorsal and external surface of each whorl. Digestive gland pale brown, lying in ventral and inner region of each whorl. Digestive tubes narrow, running in anterior half whorl. Kidney as visceral anterior limit, occupying posterior and right region of pallial cavity.

Digestive system (Figs. 516-523). Proboscis pleurembolic, short, broad (Figs. 516-518); inner layer of longitudinal muscles separated in bands, being proboscis retractor muscle (**rm**) some of ventral bands; middle layer of circular muscles; integument as outer layer. Oral tube relatively broad and long (about ¾ of buccal mass length) (Fig. 517), mostly constituted by jaw muscles (**mj**) and buccal sphincter (**mc**). Jaw plates large, thick, anterior cut edge with perpendicular striae; an outstanding, pointed projection located in middle region of each jaw plate cut edge, turned anteriorly. Pair of dorsal folds of buccal mass broad, smooth (without furrowed portion) (Fig. 520); between both a relatively deep dorsal chamber with inner surface covered by low longitudinal folds. Salivary gland ducts open in anterior-median end of dorsal folds, just posterior to jaws (Fig. 520). Odontophore muscles somewhat similar to those of

Lamellaria, with following remarkable features (Figs. 519, 521, 522): **m1b** pair broad; **ma** pair (jaw abductors) present; **m5** pair broad but thinner; **m6** with about 2/3 of cartilages length; **m6a** narrow, arched, running dorsal to m6; **m7** pair very narrow, originated from median-anterior edge of m4 dorsal branch; **M14** pair present. Buccal ganglia just in septum between esophagus and odontophore, close to median line. Radular sac with about double length than odontophore. Radular teeth (Figs. 114, 115): rachidian tooth broad, 5-7 stubby cusps, central cusp 2-3 times larger than neighbor cusps, tooth's lateral edges concave; lateral tooth almost as broad as rachidian, weakly curved inwards, 4-5 stubby cusps, second cusp terminal and about double sized than remainder cusps; inner and outer marginal teeth similar with each other, hook-like, tall, curved, base slightly flat, tip sharp pointed, no secondary cusps. Salivary glands as 2 small masses, one in each side than buccal mass lateral-posterior surface (Fig. 519). Salivary ducts running entirely immerse in dorsal wall by a short distance, open as above described. Anterior esophagus relatively short, inner surface with only an air of tall longitudinal folds. Middle esophagus long, also with a pair of longitudinal folds (continuations from those of anterior esophagus). Esophageal gland large (Fig. 517), deep, with about 10 thick septa filling it entirely, color clear beige. Posterior esophagus long and narrow, inner surface lacking folds or sometimes with some weak longitudinal folds. Duct to digestive gland broad (almost as large as terminal esophageal region). Stomach inconspicuous, a single sudden curve at right from duct to digestive gland (Fig. 523). Intestine running transversally towards right, without clear separation with stomach, immerse in digestive gland. In region close to right surface of visceral mass, intestine suddenly curves and runs straight forward, crossing transversally kidney (Fig. 523). Intestine mostly narrow, except for a short portion crossing kidney. Anus siphoned (Figs. 514, 523), close to right region of mantle border.

Genital system. Simultaneous hermaphrodite, most of visceral and pallial structures described by Fretter & Graham (1962: 373, fig. 194C). Pallial structure complex, possessing male and female glands. Penis relatively small, located at right from right tentacle of all specimens (Figs. 513, 514); basal region very broad, sessile; distal region narrow, slender, pointed, may be retracted inside broader basal portion. Penis duct entirely closed (tubular), narrow, simple (not coiled) up to penis tip.

Central nervous system (Figs. 511, 518). Similar features to remainder cypraeoideans, with following distinctions. Connectives among pedal ganglia and remainder 2 pairs of ganglia shorter. Subesophageal ganglion large, almost of same size of each nerve ring ganglia. Statocysts small, immerse in a secondary ganglia located in lateral region of pedal ganglia.

Measurements of shells (in mm). LACM 68-74 1: 25.4 by 18.0; 2: 22.4 by 16.1 (shell only).

Distribution. Western and Eastern North Atlantic.

Habitat. Intertidal to 120 m depth.

Material examined. UNITED STATES OF AMERICA; **Washington**; Washington Co. 20 km SE of Block Island "Deep Hole", 48-55.5 m, DMNH 044547, 1 specimen (R/V North Wind, 19/x/1960); **British Columbia**; Hecate Strait, Ethelda Bay, 52º58.2'N 129º31.2'W, LACM 68-74, 6 specimens (D.B. Quayle & F.R. Bernard leg., 22/x/1968).

Velutina sp.

(Figs. 524-529)

N.B.: a single young specimen of a dubious (unidentified or *V. velutina* immature) species was also available for study, then the description is very limited and this species is not included in phylogenetic analysis. However the interesting data described down are important for discussion.

Description.

Shell (Figs. 524, 525). Sculpture several narrow, spiral threads. Protoconch smooth, of 1 whorl. Spire small, clear, semi-spherical, located in right side. Aperture very ample, almost circular. Inner lip sigmoid, simple. Outer lip projected, without teeth.

Head-foot (Figs. 526-528). Broad towards lateral, slightly short towards antero-posterior (Figs. 526, 527). Head outstanding. Cephalic tentacles stubby, without ommatophores. Eyes dark, small, lo-

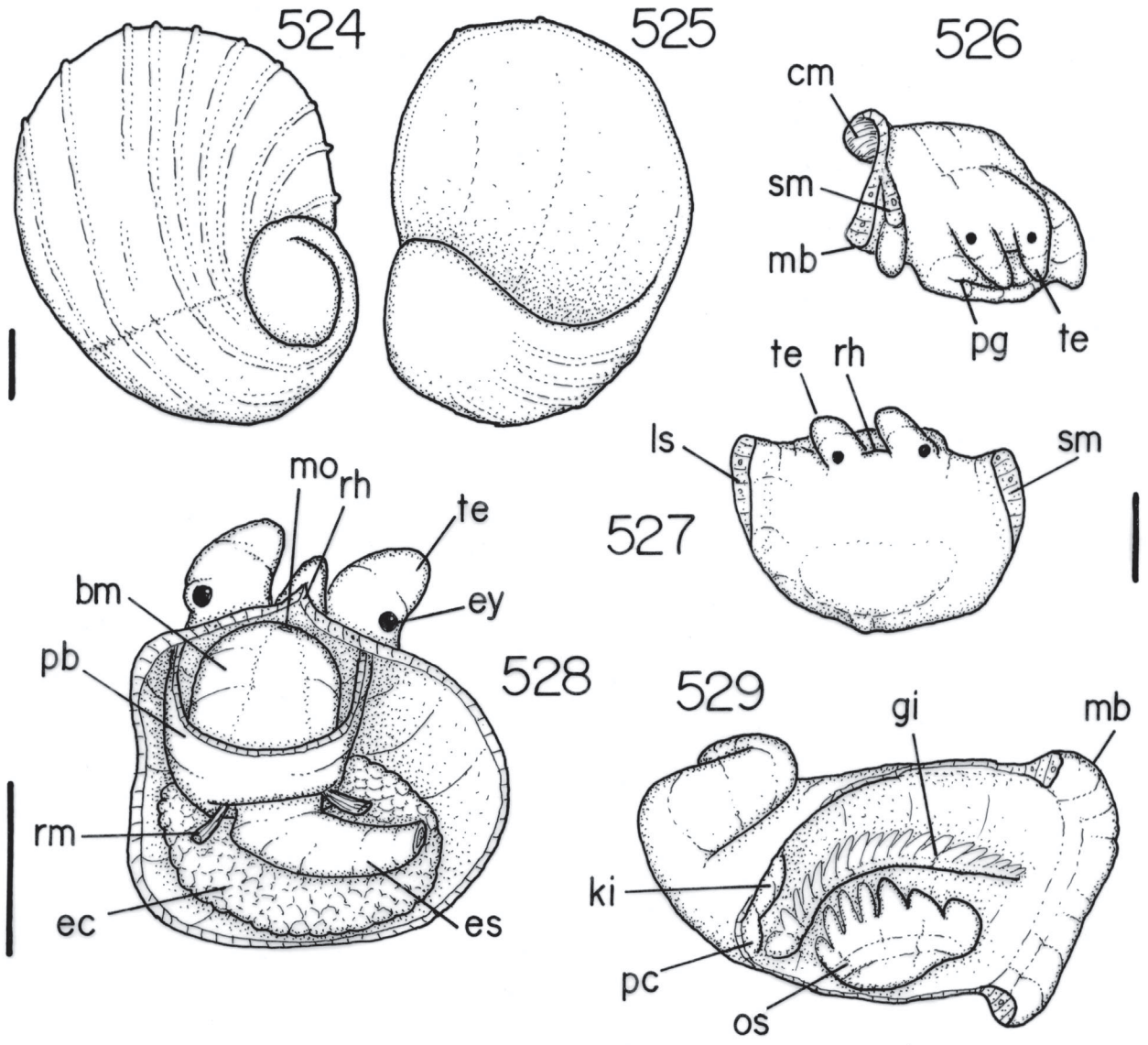
cated in tentacles base. Anterior furrow of pedal glands with thick edges. Columellar muscle broad, of half whorl. Haemocoel broad, almost circular, connection with haemocoel between posterior and right regions (Fig. 528).

Mantle organs (Fig. 529). Mantle border thick, without appendages or siphon, restricted to inner aperture edges. Osphradium flattened, somewhat elliptical and bipectinate; osphradium ganglion running along central region; in left side a single, long, flat filament; in right side about 7 irregular sized, thick filaments (anterior filaments broader). Gill long, narrow, surrounding right osphradium margin. Gill filaments few, tall, triangular. Pericardium proportionally small, located in posterior gill end.

Digestive system (Fig. 528). Proboscis of pleurembolic type, short. Rhynchodeal wall thin, semi-transparent. Buccal mass part of proboscis broad, with almost same length of rhynchodeal part. Pair of retractor muscles narrow, located in lateral region of proboscis. Esophageal gland large, occupies most of posterior haemocoel half. Remainder esophagus simple, without gland.

Measurements of shells (in mm). 1.3 by 1.1.

Material examined. UNITED STATES OF AMERICA. **Massachusetts**; Georges Bank, 40º39'30"N 67º43'18"W, USNM 840786, 1♀ (Battelle/Whoifoir MMS col., sta. 05-22, Eastward RV, 6/vii/1981).



Figs. 524-529, *Velutina* sp. anatomy: **524,** shell, dorsal view; **525,** same, frontal view; **526,** head-foot, frontal view; **527,** same, dorsal view; **528,** head and haemocoel, ventral view, foot and shell muscles removed, proboscis retracted and partially dissected; **529,** pallial cavity roof and visceral mass, ventral view. Scales = 0.25 mm.

DISCUSSION OF CHARACTERS

The following section of comparative morphology is organized as a phylogenetic analysis, the presentation of each character begins with an abbreviated descriptive sentences followed by plesiomorphic and derived conditions(s); it also included 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.

The remaining Caenogastropoda studied up to the present in this project were selected as outgroups. They are mainly the following: Cerithioidea (Simone, in press b); Littorinoidea (Simone, 1998); Hydrobioidea (Simone & Moracchioli, 1994; Simone 1995a); 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, on Terebridae). Some archaeogastropods were also analyzed as more distant outgroups(e.g., Simone, 1996a; 1997). In the following discussion, some specific outgroup taxa are mentioned, based on personal observations or on literature data. On the other hand, in the table of characters, except for the Stromboidea ground plan, no other specific taxon is shown. Each character, state and polarization, is justified in the present section, and, when necessary, a concise discussion is also conferred. Although, at the present discussion, the cladogram obtained as final result is considered, i.e., the allocation and optimization of some character states are discussed, the cladogram is only presented in the next section.

Three parameters considered here are known as polemic, and some authors do not accept them. The **first** is the use of the ingroup synapomorphies (those that support node 1, or the cypraeoidean "autapomorphies" in the present case). They are used herein because they are just the main goal of this study, since it is still lacking a phylogenetic definition for the superfamily. This definition, as referred in the Introduction, is essential for a larger project about the Caenogastropoda phylogeny. Moreover, there are authors who further discuss (favorably) the problem (e.g., Yeates, 1992). The **second** is to consider some multistate characters as additive (ordered). A multistate character is considered as ordered when the ontogeny supports it, or, sometimes, by comparison, i.e., the states are clearly a modification of the preceding one. For those multistate characters considered as additive, further explanation is presented in the discussion of each character. Furthermore, a parallel analysis considering it as non-additive was performed and the changes in the result are reported. The **third** is the arbitrary choice of an optimization in the cladogram presented herein (Fig 530) in those (few) cases in which more than 1 optimization is equally parsimonious. It is possible to apply the heuristic options ACCTRAN (assume that convergence is more likely than reversion) or DELTRAN (vice-versa) in PAUP program, which would produce 2 trees with the same topology, a duality that is avoided here. In cases in which more than 1 optimization is possible, all of them are reported in the discussion of each character, but only 1 is presented in fig. 530.

Some terms used in the following discussion merit explanation: the word archaeogastropod is used in its traditional sense, but it is recognized as a paraphyletic taxon. The term "basal" caenogastropods refers to those taxa that are generally 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 usually refers to Tonnoidea and Neogastropoda. Where "examined species" or "all species" is mentioned, only the ingroup species are included.

Shell

1. Form: 0= fusiform; 1= involute, with apex visible (pediculariids, triviids, ovulids, cypraeids); 2= involute, with inlaid apex (ovulids, **except** *Jenneria*) (CI= 66; RI= 90; additive).

The so-called involute shell is that type in which each whorl covers most of the precedent one. This conformation produces an inlaid spire, which is generally hardly visible, and a bilateral-like fashion. In most ovulids, the involute condition is more developed, with virtually total absence of a visible spire. The additive optimization is based on the ontogeny, in which the very young specimens of the ovulids (being state 2 an adult) have state 1.

2. Situation: 0= external; 1= covered by mantle (all species **except** pediculariids); 2= internal (*Lamellaria* spp) (CI= 66; RI= 83; additive).

Other tendency of the ingroup species is to cover the shell with the mantle. Most species have functionally an internal shell, which is exposed only when the animal is disturbed. This tendency has its apogee in the lamellariids, of which the *Lamellaria* have a permanently covered internal shell, with the mantle lobes entirely fused. This kind of evolution, the limacization, is very uncommon among the prosobranchs, and there is almost no parallel among the caenogastropods.

The plesiomorphic condition of the pediculariids probably resulted from a reversion. This is evident in the young specimens, which apparently present a functional internal shell (Fig. 54).

3. Outer lip: 0= thin, cut-edge; 1= thick, smooth (*Hespererato, S. uniplicata; C. acicularis, P. intermedium, Cyphoma* spp); 2= thick, with teeth (triviids, *Jenneria, Ovula, Calpurnus*, cypraeids) (CI= 50; RI= 90; additive).

Some of the younger specimens of the pediculariids present a thick outer lip (Fig. 54), which is lost in more mature specimens (Figs. 50-53, 55, 57, 58). This fact raises some doubts, whether pediculariids have state 0 or 1. The latter condition is adopted herein, but the matter is still considered as open. The additive condition is based on the ontogeny, as when the outer lip becoming thick in the species possessing state 2, it has an initial lacking teeth condition.

4. Outer surface: 0= opaque smooth periostracum; 1= glossy (*Hespererato*, ovulids **except** *Jenneria*, cypraeids); 2= opaque, sculptured (triviids, *Jenneria*) (CI= 66; RI= 90; not additive).

5. Transversal reinforcement in middle level: 0= absent; 1= present (*C. signatum, C. gibbosum*) (CI= 100; RI= 100).

6. Siphonal canal: 0= absent; 1= present (all species **except** lamellariids) (CI= 100; RI= 100).

7. Anal canal: 0= absent; 1= present (pediculariids, triviids, ovulids, cypraeids) (CI= 50; RI= 80).

The anal canal is another important feature of the ingroup species, it is equivalent in size and located in the opposite side of the incurrent siphon canal. Although present in most ingroup species, the anal canal is particularly long in several ovulids (e.g., *Volva* Röding, 1798). The siphon and anal canals have been referred by Kay (1996) as anterior and posterior channels, respectively.

8. Anal canal fold; 0= absent; 1= present in columella (*S. uniplicata, Ovula, P. intermedium*); 2= present as part of inner lip teeth (*E. acicularis*, *E. spurca*) (CI= 50; RI= 33; not additive).

9. Aperture: 0= anterior-right; 1= totally at right (all species **except** lamellariids) (CI= 100; RI= 100).

Another consequence of the involute condition is the lateralization of the aperture. The aperture is normally inferior-right in most shelled gastropods, but entirely at right in most ingroup species. The shell lateralization produces some changes in the inner anatomy commented in some of the following paragraphs.

10. Ventral outstanding calcareous band: 0= absent; 1= present (*E. acicularis, E. spurca, M. moneta, M. annulus, R. caputserpentis*) (CI= 50; RI= 75).

In the apomorphic state, present only in adult shell, the transversal section of the shell changes from circular to somewhat triangular fashion. The calcareous marginal band can also be called as marginal callus.

11. Adult ventral region fitting in substrate: 0= no; 1= yes (pediculariids) (CI= 100; RI= 100).

The condition found in the pediculariids is apparently derived from the normal cypraeoidean fash-

ion, because the young specimens possess a shell that looks like the eratoids and triviids. After a certain stage, including the one with thickening outer lip, the shell borders grow up and extend beyond, towards the ventral region, fitting the animal to the substrate. This condition is common in sessile gastropods such as calyptraeids and acmaeids.

12. Flat central region of dorsal surface; 0= absent; 1= present (*M. moneta, M. annulus*) (CI= 100; RI= 100).

The shell of most cypraeoideans is apparently developed to work as a protective box, the animal, after passing through the narrow aperture, remains protected from aggressors inside it. Besides its narrow condition, transversal teeth sometimes reinforce the aperture.

Several shell characters were searched, however most of them, but the ones above mentioned, were autapomorphic in the present sample and were not considered.

Head-Foot

13. Form: 0= somewhat spherical; 1= long antero-posteriorly (compressed laterally) (all species **except** lamellariids) (CI= 100; RI= 100).

This character is directly connected to the narrow shell aperture condition, which almost produces a bilateral symmetrical shell fashion.

14. Tentacles position: 0= dorsal or lateral to snout; 1= ventral-lateral to snout (cypraeids, ovulids) (CI= 100; RI= 100).

The ventral disposition of the cephalic tentacles appears to be indicative of the up-side-down mode of life of the animals. In most cases apparently reflects adaptation to living among rocky substrates.

15. Eyes location: 0= slightly over tentacles base; 1= about in middle region of tentacles (cypraeids, ovulids, triviids, eratoid) (CI= 100; RI= 100).

The normal fashion of the cephalic tentacles of the caenogastropod is the eyes located in their outer surface, slightly over the tentacles' base. However, in the above mentioned species this tendency is even more developed, with the eyes approximately located in the middle level of the tentacles' length.

16. Ommatophore: 0= absent; 1= present (all species **except** pediculariids) (CI= 50; RI= 75).

The ommatophore is herein defined as a small stalk of the eyes, which keeps them slightly distant from the main tentacle axis (e.g., Fig. 121). This character has 2 equally parsimonious optimizations: as cypraeoidean synapomorphy with reversion in node 6 (pediculariids) or convergence between node 2 (lamellariids) and node 9, the first hypothesis is represented in the cladogram.

17. Right accessory muscle of columellar muscle: 0= absent; 1= entirely connected to columellar muscle (cypraeids); 2: part as an isolated muscle (cypraeids **except** *R. caputserpentis*) (CI= 100; RI= 100; additive).

The obtained tree clearly shows the above-suggested additive polarization of the accessory muscle of the columellar muscle, or pallial muscle. In most ingroup specimens it is only a superior-right region of the columellar muscle, a result of the morphological adaptation for the involute shelled fashion. In the cypraeids, however, this region of columellar muscle is outstanding in the basal taxon (state 1), and entirely separated (a true pallial muscle) in the remainder branches (e.g., Figs. 116, 144, 231: pm).

18. Anterior projection of nuchal region of head: 0= absent; 1= present (all species **except** lamellariids) (CI= 100; RI= 100).

This muscular projection of the head is expanded forwards, with distal region anterior to the head (e.g., Figs. 119, 144, 245: ar). This projection fits inside the columellar region of the shell, in a special cavity at the left of the siphon, and it appears to be another adaptation to the involute shell fashion.

19. Posterior projection in opposite side of anterior projection above cited: 0= absent; 1= present (*S. uniplicata, C. acicularis, P. intermedium, Cyphoma* spp) (CI= 50; RI= 75).

This projection is analogous to the anterior projection (character 18), but projected towards the opposite side (e.g., Figs. 289, 307, 368). Probably it is the result of the hyper-involute shell condition of the above ovulids.

20. Neck region: 0= inlaid; 1= long (pediculariids) (CI= 100; RI= 100).

The extraordinarily long neck condition of the pediculariids is remarkable (e.g., Fig. 447), and projects the head forwards, beyond the anterior edge of the foot. Inner anatomical modification is also noted, mainly in the esophageal length. Some of them are also analyzed below.

21. Propodium anterior-dorsal transversal folds: 0= absent; 1= present (*S. uniplicata, C. acicularis, P. intermedium, Cyphoma* spp) (CI= 50; RI=75).

The transversal folds are somewhat uniformly sized and restrict to the propodium (surface of the foot dorsal to the pedal glands furrow). In some species there is a differentiated coloration on each fold, similar to the remainder foot dorsal surface and mantle lobes (e.g., Fig. 307). According to the cladogram, these folds are a convergence between ovulid nodes 15 and 18.

22. Columellar muscle: 0= spiral, more than one whorl; 1= only one flap turned towards posterior, about half whorl (all species **except** lamellariids); 2= similar, but turned inwards (ovulids **except** *Jenneria*) (CI= 100; RI= 100; additive).

The columellar muscle fashion is also closely connected to adaptations to the involute shell. This feature is still more developed in the hyper-involute ovulid node 14 (state 2). The additive condition is based on the ontogeny, since the very young specimens of the ovulids possess a state 1 fashion.

23. Columellar muscle form: 0= a single flattened flap; 1= horseshoe shaped (*Velutina*); 2= separated into a pair (left and right shell muscles) (*Lamellaria* spp) (CI= 100; RI= 100; not additive).

Although not considered as additive, the tree showed that possibly the almost double condition of *Lamellaria* (e.g., Figs. 461, 485, 495: is + sm) might be derived from the horseshoe condition present in *Velutina* (Figs. 509, 514). In *Lamellaria*, a thin muscular layer connects both shell muscles, crossing the ventral region of the connection between the haemocoel and the visceral mass. This region can be homologous to the middle region of *Velutina* muscle, which may be homologous to the middle region of the normal columellar muscle. This evolutionary trend suggests that the thicker lateral portions of the *Velutina* shell muscle and both shell muscles of *Lamellaria* may be homologous to the edges of normal fashioned columellar muscle.

24. Proboscis retractor muscles: 0= absent; 1= present, mainly in ventral surface (all species) (CI= 100; RI= 100).

One (e.g., Fig. 159) or more (e.g., Fig. 469) pairs of proboscis retractor muscles are present in all ingroup species. These muscles are part of the characters indicative of a proboscis, rather than a snout. Further comments on proboscis features are presented in the digestive system section.

25. Haemocoel connection with visceral mass: 0= posterior; 1= lateral-left (all species **except** lamellariids) (CI= 100; RI= 100).

The haemocoel connection with visceral mass, which is usually posterior in the gastropods, is lateral-left in most ingroup species (e.g., Fig. 282). This feature is maybe another adaptation to the involute shell fashion.

26. Operculum: 0= present; 1= absent (all species) (CI= 100; RI= 100).

This character obviously refers to the adult stage and is revealed as one of the ingroup

synapomorphy.

Mantle organs

27. Mantle border: 0= not extending beyond shell aperture; 1= extending beyond shell aperture (all species **except** pediculariids) (CI= 50; RI= 75).

The mantle extending beyond the shell aperture, formed by left and right mantle lobes (e.g., color plate Figs. 9, 19, 22), has been long known as a cypraeoidean feature. The covering of the shell by the mantle produces its glossy surface.

In the cladogram, 2 equal parsimonious optimizations are possible: 1) cypraeoidean synapomorphy with reversion in node 6 (pediculariids); or 2) convergence of node 2 (lamellariids) with node 9. The reversion in pediculariids (first and preferred hypothesis) is based on the condition of their young, in which the shell is probably covered by the mantle.

28. Mantle border dorsal fusion: 0= absent; 1= present (*Lamellaria* spp) (CI= 100; RI= 100).

In most species, both mantle lobes can be retracted inside the shell upon any disturbance. This is not possible for the *Lamellaria* species, which permanently fused the mantle around the shell (e.g., Fig. 485). However, some other lamellariids, e.g., *Marsenina* Gray, 1850, present a small aperture in which a very small portion of the shell is exposed (Marcus, 1986).

29. Outer surface of mantle border: 0= smooth; 1= with papillae (*L. mopsicolor, Jenneria, S. uniplicata, C. acicularis, Ovula*, cypraeids) (CI= 33; RI= 85).

30. Pallial papillae type: 0= absent; 1= simple and short (*L. mopsicolor, C. acicularis, Ovula, L. cinerea*); 2= simple and tall (*S. uniplicata, P. arabicula, C. tigris*); 3= some branched (*Jenneria, R. caputserpentis, P. robertsi, L. lynx, E. acicularis, E. spurca, M. moneta, M. annulus*); 4= simple, broad, base narrower (*M. zebra, M. cervinetta*) (CI= 44; RI= 61; not additive).

31. Type of pallial papillae branches: 0= absent; 1= alternate (*R. caputserpentis, P. robertsi, E. acicularis, E. spurca, M. moneta, M. annulus*); 2= brush-like (all branches in papilla apex) (*Jenneria, L. lynx*); ?= papilla resulted only by contraction of muscles, disappearing when mantle is retracted (CI= 40; RI= 50; not additive).

32. Uniform distribution of small and low papillae: 0= absent; 1= present (*L. cinerea, P. robertsi, P. arabicula*) (CI= 50; RI= 50).

33. Outstanding (larger) papillae: 0= absent; 1= closer to inner lobe region and far from outer edge (*M. zebra, M. cervinetta, E. acicularis, E. spurca, C. tigris, M. annulus, M. moneta, R. caputserpentis*); 2= aligned transversally (*C. lynx*); 3= randomly distributed throughout mantle, among smaller papillae (*P. robertsi, P. arabicula*) (CI= 75; RI= 87; not additive).

34. Coloration of exposed part of mantle: 0= clear or diffuse dark spots sometimes coalescent; 1= alternate dark and pale bands (*M. moneta, M. annulus*); 2= ample rings (*C. gibbosum*); 3= small rings (*Calpurnus*); 4= dichotomic bands (*P. intermedium*, *C. signatum*) (CI= 100; RI= 100; not additive).

The state of *Calpurnus verrucosus* may be equally parsimoniously considered as a synapomorphy of node 17 or an autapomorphy of the species; the first hypothesis is represented in Fig. 530.

35. Left-ventral region of mantle border: 0= narrow; 1= very ample, as a lobe (all species) (CI= 100; RI= 100).

The mantle border has further functions besides merely secreting the shell, it is an important region

for bearing receptors and for another interactions with the environment. In the case of most cypraeoideans, the normal fashion during the activity is the extended mantle, thus the mantle usually has more importance than the shell in interacting them with the substrate, in protecting the animal against predators, etc. Due to this additional important feature, the cypraeoidean mantle also presents highly valuable structures for comparative studies, as shown in the above characters (29-35). They were used in helping species separation (e.g., Schilder, 1936: 100-103; Kay, 1960b: 279, 1964). Burgess (1985) even presented a nomenclature to the different kinds of cypraeid papillae. The papillae, in particular, present all sorts of adaptations, most of them were not explored herein because of their autapomorphic condition, however they should be very important in a deeper study of the group. Although weak mantle papillae are present in some lamellariids and triviids, only those present in the ovulids and cypraeids are considered herein, as they are tall and complex. In the examined living triviids (Figs. 408, 409; color plates Figs. 19-21) there are functional papillae that disappear in the disturbance by contraction. The mantle papillae appeared in node 12, and interestingly was lost (as a reversion according to the tree) in the ovulid node 18 (*Pseudocyphoma* plus *Cyphoma*). Other ovulids lacking mantle papillae have been reported in the literature, e.g., *Kuroshivolva shingoi* Azuma & Cate, 1971 (figs. 22, 23). Gosliner & Liltved (1987) have shown that apparently some triviids have well-developed mantle papillae.

36. Developed siphon (outstanding from mantle border): 0= absent; 1= present (all species **except** lamellariids); 2= with papillae in border (cypraeids) (CI= 100; RI= 100; additive).

The siphon of the mantle is herein designed for those secondary folds protruded and separated from the mantle border (e.g., Figs. 146, 154: si). Although mostly short, all ingroup species possess a developed siphon, however eratoids, as also pointed out by Fretter (1951), have a long siphon (Fig. 416). The siphon has also a muscular root originated from the head-foot musculature. The additive condition of the apomorphic states is based on the comparison, as state 2 is clearly a modification of state 1.

37. Anal siphon: 0= absent; 1= present (ovulids, cypraeids) (CI= 100; RI= 100).

Although most cypraeoideans present an anal siphon in the shell, this only appears as a fold differentiated from the mantle border of ovulids and cypraeids (e.g., Figs. 116, 146: as). The anal siphon apparently evolved similarly, but in the opposite side, to the incurrent siphon.

38. Osphradium: 0= ridge-like; 1= bipectinate (all species); 2= with three branches (ovulids, cypraeids) (CI= 100; RI= 100; additive).

The bipectinate condition of the osphradium is clearly a remarkable feature of the "higher" caenogastropods, being an adaptation to increasing the surface of this sensory organ. In the case of the ovulids and cypraeids (node 12) there is an outstanding feature – the three-branched osphradium (e.g., Figs. 116, 175, 308: os). This kind of osphradium has 3 branches running somewhat equidistant from each other, one branch is turned towards the anterior end, another towards the posterior end and another towards the right branch. Observing the osphradia of the other species from the base of the tree and also the position of the osphradium nerve, it is possible to conclude that the anterior and posterior branches of the 3-branched osphradium are homologous to the normal osphradium (with single axis). The right branch is a new acquisition of the taxa after node 12 (cypraeids and ovulids).

Although the name "tripectinate" of the cypraeid osphradium fashion is presented in the literature, this nomenclature is not followed here, because the cypraeid osphradium, as above mentioned, is actually a bipectinate with 3 branches (as also noted Rocha *et al*., 1994), and has been referred as 'trifid' (Schilder, 1936; Kay, 1960b), 'tripartite' (Ghiselin & Wilson, 1966), 'triradiate' (Taylor & Miller, 1989). A relation between the osphradium size and the quantity of suspension on the water was reported in the cypraeid literature (e.g., Azevedo, 1989). Details of the osphradium leaflets cilia ultrastructure of a cypraeid are found in Taylor & Miller (1989).

39. Osphradium filaments: 0= rounded tip; 1= sharp projected tip (*L. branca, Jenneria*, cypraeids **except** *R. caputserpentis*) (CI= 33; RI= 83).

40. Osphradium filament tip: 0= attached to mantle; 1= projected from mantle (all species **except** *Hespererato, C. acicularis*) (CI= 33; RI= 0).

41. Osphradium monopectinate condition: 0= absent; 1= partial (pediculariids); 2= total (*Pedicularia* sp1) (CI= 100; RI= 100; additive).

The monopectinate condition is derived from the bipectinate one, as it is shown in the above sequence and in the position of the species in the tree. A partial monopectinate condition is herein defined as an osphradium with posterior and anterior parts bipectinate and monopectinate, respectively (e.g., Figs. 443, 448, 454). It seems to be the intermediary step for a true monopectinate condition (Fig. 429).

The monopectinate osphradium condition appears to be connected to the process of body miniaturization. There is a parallel phenomenon in other caenogastropods; these miniaturized species present the monopectinate condition, as, e.g., calyptraeids (Simone, submitted), columbellids (deMaintenon, 1999), and cerithioideans (Simone, in press b). Within the cypraeoideans, this rule appears to be followed, as the pediculariids present a small size.

42. Scalloped osphradium filaments: 0= absent; 1= present (*Velutina, L. patagonica*, triviids) (CI= 33; RI= 33).

The scalloped filament seems to be an additional adaptation for increasing the organ surface (e.g., Fig. 412). It is equally parsimonious to consider, in the case of lamellariids, the state 1 as a family synapomorphy with a reversion in node 4, or a convergence between *Velutina* and *L. patagonica*; the first hypothesis is represented in the cladogram (Fig. 530).

43. Distance between osphradium and anterior region of gill: 0= close; 1= slightly separated (all species **except** lamellariids) (CI= 100; RI= 100).

44. Distance between osphradium and posterior region of gill: 0= close; 1= slightly separated (*Ovula, Calpurnus, P. intermedium, Cyphoma* spp, *L. cinerea, M. zebra, M. cervinetta*); 2= very far (pediculariids) (CI= 40; RI= 78; additive).

The osphradium normally surrounds the left margin of the gill or the ctenidial vein in most outgroups, and, then, it is considered as the plesiomorphic condition.

45. Gill form: 0= slightly straight; 1= curved (concavity left) (all species **except** lamellariids) (CI= 100; RI= 100).

The peculiar curved form of most cypraeoidean gills (e.g., Fig. 116: gi) has also been pointed out as a distinction by previous authors (e.g., Schilder, 1936; Kay, 1960b).

46. Posterior half of gill: 0= far from visceral mass; 1= lying close to visceral mass (all examined species) (CI= 100; RI= 100).

47. Hypobranchial gland: 0= only a glandular mass; 1= with several transversal septa from mantle (ovulids, cypraeids) (CI= 100; RI= 100).

Transversal septa of the mantle, as a reinforcement of the gland, are not normally found even in thick hypobranchial glands. In the case of the above taxa, the mantle septa run through the glandular tissue (e.g., Figs. 118, 158) and generally have the ventral edge exposed, mainly in the right side. They end at some distance from the base of the gill.

Visceral mass

48. Position: 0= almost entirely posterior to pallial cavity; 1= encroaching right region of pallial cavity roof (all species **except** lamellariids) (CI= 100; RI= 100).

The derived condition is normally found in species in which the aperture becoming more lateral.

The aperture and the mantle cavity migrate towards the right, causing a displacement of the visceral mass to the anterior region, which becomes oblique and partially encroaches the pallial cavity right region (e.g., Fig. 116). A parallel evolution is found in other lateral apertured shell groups, such as stromboideans (Simone, in press c), and neogastropods (e.g., marginellids and olivids, personal observation).

Circulatory and excretory systems

49. Pericardium position: 0= entirely posterior to gill; 1= broad part dorsal to posterior region of gill (all species); 2= narrow part dorsal to posterior gill region (ovulids, cypraeids) (CI= 100; RI= 100; additive).

50. Auricle connection with ctenidial vein: 0= posterior to gill, as an isolated vessel; 1= anterior from posterior extremity of gill, with a short portion of ctenidial vein as a bind-tube (all species); 2= almost at middle level of gill (*Lamellaria* spp) (CI= 100; RI= 100; additive).

51. Auricle form: 0= obese; 1= long, somewhat narrow, running through mantle up to ctenidial vein (ovulids, cypraeids) (CI= 100; RI= 100).

Characters 49-51 are related to the lateralization of the aperture, as explained in character 48. This morphological phenomenon results in an encroachment of the visceral mass at the pallial cavity right region, including pericardium and heart, which is dislocated from the posterior part of the gill to its dorsum (character 49). However, the auricle obviously remains connected to the ctenidial vein, but this connection is also dislocated towards the anterior region (character 50) and, as consequence, a short posterior portion of this vein (posterior to the auricle connection) becoming a blind tube with inverted flow (e.g., Figs. 117, 145). Particularly in *Lamellaria* spp, this state is more developed, in which the auricle-ctenidial vein connection is located almost in the middle region of the gill (e.g., Figs. 467, 497). Here, this condition is separated in another state. The auricle of the ovulids and cypraeids, in particular, has the singular form described in character 51, with its region running dorsal to gill, looking like a somewhat narrow tube. The 3 states of characters 49 and 50 are considered as additive because of ontogeny, since the previous states are present in the few early young specimens examined, however, nothing changes in the result if these characters are considered as non-additive.

52. Kidney: 0= most solid-glandular; 1= most hollow (all species) (CI= 100; RI= 100).

53. Kidney position: 0= transversal; 1= oblique (all species) (CI= 100; RI= 100).

54. Kidney form: 0= triangular or rhomboid; 1= long and narrow (all species) (CI= 100; RI= 100).

The derived states of characters 53 and 54 are also part of the modifications for the shell aperture lateralization, as commented in the preceding characters. The kidney of the ingroup species becomes positioned obliquely, compressed between the visceral glands (digestive and gonad) and the pallial cavity (e.g., Figs. 117, 145), resulting in a long and flat fashion.

55. Kidney lobes: 0= 2; 1= 1 (dorsal) (all species) (CI= 100; RI= 100).

56. Nephridial gland: 0= slightly small, narrow, triangular in section; 1= with a lobe slightly large, massive, with a well-developed vessel in its center (ovulids, cypraeids) (CI= 100; RI= 100).

The caenogastropod normal fashion of double-lobed kidney is apomorphicly lost in the ingroup (character 55). However, the ovulids and cypraeids (node 12) possess a kidney with apparently 2 lobes (e.g., Figs. 117, 145, 291: kv+nl). This shape is because of the great development of the nephridial gland (character 56), one of the synapomorphies that support this node. Although most species present a simply broad gland in the anterior region, the enlargement of the nephridial gland has the form of a separated lobe, connected to the gland only in its anterior region, in some species.

57. Nephrostome: 0= simple 1= inner region protected at right by nephridial gland vessel (ovulids **except** *C. signatum*, cypraeids) (CI= 50; RI= 91).

A portion of the nephridial gland, with a conspicuous branch of the afferent renal vessel, coming from the haemocoel, covers the right region of the nephrostome (e.g., Fig. 117), and this state is one of the synapomorphies of node 12. However, according to the interpretation of the cladogram, it is reversed in *C. signatum*.

58. Intestinal loop crossing through kidney chamber: 0= longitudinal; 1= transversal (lamellariids) (CI= 100; RI= 100).

As a rule, the intestine runs along the kidney length in most ingroup and outgroup species (e.g., Fig. 117), however, in the lamellariids, the intestine is only present in the anterior region of the kidney, crossing it transversally (e.g., Fig. 490).

Digestive system

59. Pleurembolic proboscis: 0= absent; 1= short (all species); 2= long (lamellariids, pediculariids, eratoid) (CI= 66; RI= 87; additive).

The proboscis of the cypraeoideans has been referred to as absent (e.g., Ghiselin & Wilson, 1966) or of the acrembolic type. However, the species of the basal branches of the cladogram possess a proboscis of true pleurembolic fashion (e.g., Figs. 420, 470, 518). The structure is particularly long in the eratoid, resembling the neogastropod proboscis. However, the sampled ovulid and cypraeid species present a short proboscis (e.g., Figs. 119, 220), with an inconspicuous buccal mass portion bulging into the rhynchodeal cavity when the proboscis is retracted. This fashion is somewhat similar to the acrembolic type of proboscis. Fretter (1951) described the proboscis of some cypraeoideans, and designated them as of the pleurembolic type. She also pointed out the differences in length among the species, and even described *Simnia patula* (Pennant) (ovulid) as lacking proboscis (pg. 18). Kay (1960a:179) also designates the cypraeid proboscis as of the pleurembolic type.

The present character is divided into 3 additive states with absence of proboscis in an extremity and a long fashioned proboscis in the other extremity , having the short proboscis as the intermediary. According to the obtained tree, the long fashion of pleurembolic proboscis (state 2) appeared in node 1, with a notable reversion to state 1 (short proboscis) in node 10. Nevertheless, the buccal mass portion of the proboscis only becomes inconspicuous in node 12 (after triviids).

Anyway, under a tenuous nebula of uncertainty, all cypraeoidean proboscises are herein considered as pertaining to the pleurembolic type.

60. Jaws: 0= two separated plates; 1= two plates connected with each other, with a median hook (*Lamellaria* spp); 2= a uniform chitinous thin plate (cypraeids); 3= with a middle anterior spine (*Velutina*) (CI= 100; RI= 100; not additive).

61. Jaw thickness: 0= thick; 1= thin (pediculariids, ovulids, cypraeids) (CI= 50; RI= 85).

The pair of jaw plates has a particular importance in the cypraeoideans as analyzed in characters 60 and 61. It becomes notably thin in the species encompassed by nodes 6 and 12, becoming a simple chitin-like membrane in the cypraeids (node 20).

62. Oral tube: 0= very short; 1= slightly long (about 1/3 of remainder buccal mass length) (all species) (CI= 100; RI= 100).

The oral tube connects the buccal mass with the mouth, and normally is somewhat long in the proboscis-bearing gastropods. In the cypraeoideans, the pairs of muscles m10 and m14 lie as a ventral reinforcement of the oral tube, while the pair mj lies on its ventral and lateral regions (e.g., Figs. 122, 124, 149).

63. Buccal special glands opening in anterior-ventral region of oral tube: 0= absent, 1= single (*Ovula*); 2= 2 pairs (*P. intermedium, Cyphoma* spp) (CI= 100; RI= 100; not additive).

64. Paired buccal glands: 0= absent; 1= larger hollow gland (*P. intermedium, C. signatum*); 2= larger solid-glandular gland (*C. gibbosum*) (CI= 100; RI= 100; not additive).

These herein called buccal glands (characters 63, 64) are notable examples of the molluscan morphological plasticity, since they arise where apparently there is nothing in the relative species. Although the presence of a single gland is an *Ovula* autapomorphy (Fig. 333), the presence of 2 pairs is a notable synapomorphy of the ovulid node 18 (e.g., Figs. 292, 293, 313, 326).

The buccal glands look similar to the accessory salivary glands of some, not closely related, neogastropods, inclusive in their insertion in the ventral region of the oral tube. Sometimes the accessory salivary gland is odd (resembling the *Ovula* gland), as, e.g., in the marginellids and mitrids.

The function and structural constitution of the buccal glands are interesting goals for further investigations. The single gland of the *Ovula* was reported by Vayssière (1923), and the 2 pairs of gland (in the case, for *C. gibbosum*) by Ghiselin & Wilson (1966). In the latter, the authors suggest a relation of such gland with the coelenterates diet, and additionally a possible homology to the sublingual glands if *Theodoxus* (see Whitaker, 1951: 23), a nerithimorph. However, a similar gland is not found in the remainder ovulids. Fretter (1951) described odd glandular diverticulum for *Erato voluta* (Montagu), but, different from the gland presently described, the glandular diverticulum opens in the anterior esophagus.

65. Separation between odontophore and esophagus: 0= posterior; 1= middle-dorsal (lamellariids, pediculariids, ovulids) (CI= 33; RI= 86).

Most archaeogastropods possess the buccal mass fashion looking like the state 1 of this character (e.g., Figs. 314, 327), however, the present polarization is based on the basal caenogastropods, which possess the state 0, considered herein as plesiomorphic into the group.

According to the obtained cladogram, 2 equally parsimonious optimizations are possible: 1) cypraeoidean synapomorphy, reversion in node 9, reappearing in node 13 (ovulids) or 2) convergence among node 2 (lamellariids), node 6 (pediculariids) and node 13 (ovulids), the first hypothesis is shown in Fig. 530.

66. M1a: 0= inconspicuous; 1= developed (all species) (CI= 100; RI= 100).

The m1a is a pair of jugal muscles connecting the dorsal-anterior region of the buccal mass with the adjacent region of the haemocoel (e.g., Fig. 125). It is a notable synapomorphy of the ingroup.

67. Mc: 0= a single band; 1= two bands (*M. zebra, M. cervinetta*) (CI= 100; RI= 100).

The mc, or buccal sphincter, is apomorphically duplicated in the above species (e.g., Figs. 127, 130), being a notable synapomorphy that assists in the support of node 27.

68. Mj originating: 0= only in odontophore cartilages; 1= also forming a muscular plate in median-anterior region of odontophore, between its cartilages (all species) (CI= 100; RI= 100).

The mj pair is normally very thick in the cypraeoideans. Its (posterior) origin, which is usually simple in the odontophore cartilages, is more complex in the ingroup species. The mj origin has the form of a marked muscular plate, as a platform separated from remainder odontophoric structures (except for its lateral connection with the cartilages) (e.g., Figs. 133, 384). Apparently, this muscular platform apparently also works as a reinforcement of the origin of m4 pair. The virtual cavity formed between the mj plate and the remainder odontophoric structures is developed by *J. pustulata* for storing the older portion of the radula in a secondary, distal sac (e.g., Figs. 381, 384).

69. M2: 0= broad, running separated from esophagus; 1= narrow, running attached along esophagus (all

species, **except** following); 2= absent (*Velutina, L. patagonica, L. mopsicolor, S. uniplicata, C. acicularis, P. intermedium*) (CI= 33; RI= 33; additive).

70. M11: 0= absent; 1= present (all species); 2= with insertion surrounding ventral region of radular sac base (*P. robertsi, P. arabicula, L. cinerea, M. zebra, M. cervinetta*) (CI= 50; RI= 50; additive).

The m2, or retractor pair of the buccal mass (character 69), is normally well-developed in caenogastropods occupying a lateral location. In the ingroup, however, it is usually modified in a pair of narrow and long muscles located laterally (m2), running attached to the anterior esophagus, and another pair close to the median line (m2/m11) (e.g., Figs. 125, 126). Additionally, it has a muscular flap surrounding the radular sac. M11 is a narrow pair of muscles in the basal caenogastropods (character 70), and the most probable is that it has an additional component derived from the m2 pair in the ingroup. This explains their additional insertion in the radular sac and in the posterior surface of the odontophore, which is absent in the outgroups. Despite the possible derivation from m2, the pair of muscles is only indicated as m11 in the figures.

71. M3: 0= absent or a very thin layer immerse in ventral membrane evolving odontophore; 1= well-developed muscle (*S. uniplicata, C. acicularis, Ovula, Calpurnus, C. signatum, C. gibbosum; L. cinerea, L. lynx, C. tigris, M. zebra, M. cervinetta, E. acicularis, E. spurca, M. moneta, M. annulus*) (CI= 33; RI= 85).

The m3 pair is broad and very thin (e.g., Fig. 126), and is clearly a specialization of the membrane that covers the ventral and lateral surfaces of the odontophore, which becomes muscular. This pair of muscles is a remarkable synapomorphy of nodes 14 and 23, as a convergence.

72. M4: 0= originating in mj more lateral; 1= originating in mj along median line (all species) (CI= 100; RI= 100).

73. M4 ventral branch: 0= connected to dorsal branch; 1= separated anteriorly (ovulids, cypraeids) (CI= 100; RI= 100).

The m4 pair is the largest muscle of the caenogastropod odontophore, surrounding most of the pairs of cartilages (e.g., Fig. 150). In the ingroup, the 2 modifications explored in characters 72 and 73 were detected, in relation to the normal fashion of the basal caenogastropods, supporting respectively nodes 1 and 12.

74. M5 form: 0= thin and long; 1= very broad and slight short (*L. mopsicolor, L. branca*, eratoid, triviids, ovulids, cypraeids) (CI= 50; RI= 83).

75. M5 medial union with its pair: 0= absent; 1= present (triviids, ovulids, cypraeids) (CI= 100; RI= 100).

76. M5 inserting in radular sac: 0= small, almost in a point; 1= large, along a considerable portion of radular sac (all species) (CI= 100; RI= 100).

The m5 pair is also a large muscle with an apparent antagonistic function to m4, as a tensor of the exposed portion of the radula (e.g., Figs. 133, 150). Based on the basal caenogastropods, only the 3 modifications analyzed in characters 74-76 were detected.

77. M6: 0= single; 1= double (m6 plus m6a) (all species) (CI= 100; RI= 100).

78. M6a type: 0= absent; 1= similar sized to m6 (*Lamellaria* spp, *Hespererato*); 2= m6 and m6a narrow (pediculariids, ovulids, cypraeids); 3= m6a dorsal to m6 (*Velutina*, triviids) (CI= 60; RI= 60; not additive).

79. M6a connection with adjacent ventral surface of mj platform: 0= absent; 1= present (triviids, cypraeids **except** *R. caputserpentis*) (CI= 50; RI= 91).

M6 (characters 77-79), or horizontal muscle, is a single muscle uniting both odontophore cartilages. The duplication of m6 into m6 and m6a is one of the outstanding synapomorphies of the Cypraeoidea (node 1) (e.g., Figs. 132, 150, 181). The form and localization of m6a, however, present variations, as explored in character 78, being, sometimes, dorsal to m6 (state 3). Additionally, the m6a becomes attached, along median line, to the muscular platform formed by mj in the cypraeids after node 21.

80. M7: 0= originating in median border of ventral m4 branch; 1= originating in anterior border of ventral m4 branch (triviids, *M. zebra, M. cervinetta*); 2= absent (*Pedicularia* sp1, ovulids, cypraeids **except** preceding species) (CI= 50; RI= 81; not additive).

M7 is a pair of small and narrow muscles originated from the dorsal and medial edges of m4 and inserted in the radular sac (e.g., Fig. 127). Based on the m7 of basal caenogastropods, the above polarization of the 3 states is suggested.

After node 10, 2 equally parsimonious optimizations are possible: 1) a synapomorphy of node 10, state 2 appearing in node 12, and a reversion to state 1 in node 27; or 2) state 2 as synapomorphy in node 12, with state 1 appearing convergently in node 11 (triviids) and node 27. The first hypothesis is showed in the cladogram.

81. M7a (originating among m4 fibers): 0= absent; 1= present (ovulids **except** *Jenneria*) (CI= 100; RI= 100).

M7a is a pair of small muscles originated in the medial-posterior region of each cartilage and inserted into radular sac, admirably passing through the fibers of m4 (e.g., Figs. 300, 339). Although with a function similar to m7, m7a is probably not a modification of that muscle, but an interesting new acquisition helping in the support of the ovulid node 14. However, both muscles were not found occurring together.

82. M10: 0= narrow and thin; 1= broad and thick (all species) (CI= 100; RI= 100).

83. M11 muscular connection with m4 dorsal branch: 0= absent; 1= present (all species) (CI= 100; RI= 100).

Characters 82 and 83 are polarized according to the fashion of the basal caenogastropods, and resulted as ingroup synapomorphies.

84. M12: 0= absent; 1= present (cypraeids **except** *L. lynx, E. spurca*) (CI= 33; RI= 77).

M12 is a pair of narrow and somewhat long muscles originated in the outer-anterior surface of the cartilages and inserted in the inner surface of m4, running posteriorly and covering the origin of mj (e.g., Fig. 137). This muscle is a notable cypraeid synapomorphy (node 20), with a reversion in both species mentioned.

The architaenioglossans and the cerithioideans also present a muscle called m12 in previous papers (Simone, 2001; in press b), but with different attributes, such as being shorter and with insertions in the subradular membrane. Certainly, these are not muscles homologous to those of the cypraeoideans.

85. M14: 0= absent; 1= present (all species) (CI= 100; RI= 100).

M14 is a pair of muscles with apparently a function similar to m10, i.e., protractor of buccal mass. It differs from the m10, from which m14 covers ventrally, because it is more posteriorly inserted (e.g., Figs. 126, 127). The m14 insertion is close to the median line, surrounding the entrance of the radular sac in the odontophore, which is additionally covered by the m3.

86. Radula length: 0= short (about same length than buccal mass length); 1= long (two or three

times it) (ovulids, cypraeids **except** *R. caputserpentis, P. robertsi, P. arabicula*) (CI= 50; RI= 92).

The radula length polarization is mainly based on the state found in most basal caenogastropods. From this point of view, the state 1 resulted as a convergence between node 13 (ovulids) and cypraeid node 23.

87. Radular nucleus form: 0= simple; 1= broad, almost bifid (ovulids **except** *Jenneria*) (CI= 100; RI= 100).

The singular fashion of the radular nucleus (e.g., Fig. 337), outstandingly broad and somewhat bifid, is one of the synapomorphies supporting the ovulid node 14.

88. Rachidian: 0= with several cusps; 1= with 3 cusps (*Calpurnus, P. intermedium, Cyphoma* spp, cypraeids) (CI= 50; RI= 93).

89. Lateral tooth: 0= with several cusps; 1= with 3 cusps (*Calpurnus*, cypraeids); 2= lacking cusps (*P. intermedium, Cyphoma* spp); 3= divided into 2 teeth (*Jenneria*) (CI= 75; RI= 92).

It is equally parsimonious to consider the state 1 in ovulids as a synapomorphy in node 17 or an autapomorphy of *Calpurnus verrucosus*, the first hypothesis is represented in the cladogram.

90. Inner and outer marginal tooth: 0= with about 5-10 cusps; 1= with 3 cusps (cypraeids); 2= with several cusps (ovulids **except** *Jenneria*); 3= lacking cusps (*Hespererato*); 4= with 2 cusps (triviids); 5= marginal teeth absent (*Lamellaria* spp) (CI= 100; RI= 100; not additive).

91. Inner and outer marginal form: 0= flat, spoon-like; 1= pointed (all species **except** *Lamellaria* spp and ovulids); 2= brush-like (ovulids) (CI= 100; RI= 100; not additive).

92. Inner and outer marginal teeth shape: 0= different from lateral tooth; 1= similar to lateral tooth (cypraeids) (CI= 100; RI= 100).

93. Lateral and marginal teeth: 0= simply curved; 1= sigmoid (*L. mopsicolor, L. branca, C. tigris, M. zebra, M. cervinetta, E. acicularis, E. spurca, M. moneta, M. annulus*) (CI= 50; RI= 87).

The characters of the radula have succeeded the shell in importance and systematic application (e.g., Schilder, 1936: 94-98; Kay, 1960b: 279-281; Bandel, 1984). This fact is partially reflected in the publication of a massive radula atlas for most cypraeids (Bradner & Kay, 1996). In this scenario, several radular characters of the ingroup were selected (Figs.70-115), however, most of them resulted autapomorphic, with the exception of the above ones (88 to 93). The polarization of these characters is mainly based on the basal caenogastropods.

94. Dorsal inner folds of buccal mass: 0= simple; 1= with oblique secondary furrows in their anterior, broader region (lamellariids, cypraeids, ovulids **except** *Jenneria*); 2= with oblique glandular folds (*E. acicularis, E. spurca*) (CI= 50; RI= 70; additive).

The presence of oblique furrows in the dorsal folds of the buccal mass is one of the node 12 synapomorphies (e.g., Figs. 124, 162:ff), with a notable convergence in node 2. Particularly, the species comprised by node 29 present a specialization of state 1, the reason for the 3 states being considered as additive. The function of those oblique furrows is an interesting goal for further investigations.

95. Salivary glands: 0= large (almost of same size of esophageal gland); 1= very small (*P. intermedium, Cyphoma* spp., pediculariids **except** *P. sp1*); 2= separated into 2 masses (*Velutina*) (CI= 66; RI= 80; not additive).

State 1, according to the obtained cladogram, resulted in a convergence between pediculariid node 7 and ovulid node 18. In the latter, the reduction of the salivary glands is maybe connected to the appearance of the glands of the buccal tube.

96. Esophageal pouches: 0= absent; 1= single and short (*C. tigris*); 2= single and long (*Lamellaria* spp); 3= a pair (*L. cinerea,* ovulids **except** *Jenneria*) (CI= 75; RI= 88; not additive).

From the above states of the esophageal pouches, the only one that supports a node is state 2, as one of the lamellariid node 3 synapomorphies (e.g., Figs. 473, 489: ep).

97. Esophageal gland: 0= absent; 1= present, with some transversal septa (about 10) (all species **except** *Pedicularia* sp.2); 2= present, with much transversal septa (triviids, ovulids, cypraeids) (CI= 66; RI= 90; additive).

98. Esophageal gland form: 0= along esophagus; 1= restrict to an elliptical sac (all species) (CI= 100; RI= 100).

The esophageal gland (characters 97, 98) is a ventral structure in the form of a broad diverticle and filled by transversal, glandular septa (e.g., Figs. 124, 162: ec). Although it is regarded as an ingroup synapomorphy, a similarly fashioned esophageal gland is found in naticoideans and tonnoideans. The homology of those esophageal glands, as well as of those with the neogastropod gland of Leiblein, has been investigated in the present project.

Although *Pedicularia* sp.2 lacks a well-developed esophageal gland, some transversal folds indicative of an homologous local are detectable, and then it is regarded as possessing the gland in character 98.

In character 97, the states are considered as additive because of ontogeny, as a gland with few septa precedes the gland with many of them in young specimens. However, the topology of the obtained cladogram does not change if the character is regarded as non-additive, except for RI, which changes to 88.

99. Esophagus: 0= narrow, slightly thick walled; 1= broad, very thin walled (triviids, ovulids, cypraeids) (CI= 100; RI= 100).

This character in state 1 helps with the node 10 support and excludes the broad esophageal gland. The esophagus itself, in state 1, presents a broad and thin walled fashion (e.g., Fig. 149), somewhat different from the outgroups.

100. Stomach: 0= with inner folds and sorting areas; 1= with smooth inner surface (all species) (CI= 100; RI= 100).

101. Style sac: 0= conspicuous; 1= inconspicuous (all species) (CI= 100; RI= 100).

Although several species of cypraeoideans have not been reported as carnivores, they possess a relatively simple midgut. The stomach (characters 100, 101), in particular, is a simple, broad curve of the digestive tube, marked only by the ducts to the digestive gland, lacking any clear separation with the neighboring regions of the esophagus and intestine (e.g., Figs. 139, 167, 284: st). This fashion resembles the stomach of predator higher caenogastropods, such as tonnoideans and neogastropods. Fretter (1951), who studied samples of eratoid, triviids and ovulids, described them as carnivores living on sessile colonial animals; she also described some behavioral activities.

102. Inner surface of duct to anterior digestive gland lobe: 0= simple; 1= several transversal septa (*R. caputserpentis, C. tigris, M. zebra, M. cervinetta, E. spurca*) (CI= 33; RI= 50).

The duct to the digestive gland closer to the intestine is normally broad and protruded in the ingroup species, several times larger than the portion of the duct closer to the esophagus (e.g., Fig. 139). The structure has been referred as caecum by some authors (e.g., Kay, 1960b: 281). Additionally, some species present enigmatic transversal septa in the duct, in their proximal region (e.g., Figs. 139, 183: dd). This state resulted as a cypraeid node 27 synapomorphy, with a notable convergence with *R. caputserpentis*

and *E. spurca*.

103. Duct to anterior digestive gland lobe originating: 0= slight far from esophageal insertion and intestine origin; 1= just between esophageal insertion and intestine origin (*L. branca,* triviids, cypraeids, ovulids **except** *Jenneria*).

The fashion described in state 1 (e.g., Fig. 139) is maybe due to the simplification of the stomach. According to the obtained cladogram, it is one of the node 10 synapomorphies, with a convergence in *L. branca* and a reversion in *Jenneria*.

104. Intestine: 0= narrow (at least in region near its origin); 1= wholly broad (cypraeids) (CI= 100; RI= 100).

105. Intestinal loops in visceral mass: 0= several; 1= single (all species) (CI= 100; RI= 100).

106. Intestinal loops in pallial roof region: 0= none, i.e., almost straight; 1= a sigmoid loop (ovulids **except** *Jenneria*); 2= several (*Ovula, P. intermedium, Cyphoma* spp) (CI= 66; RI= 88; additive).

The intestinal characters (104-106) also show a tendency to simplification among the ingroup representatives, as also seen in the stomach, which are only expected in truly carnivore caenogastropods (e.g., most neogastropods). On the other hand, in the ovulids, which normally eat coelenterates, the intestine has loops in the pallial roof region (e.g., Figs. 303, 328), which increases in complexity towards the more derived clades in the tree. State 1 appeared in node 14, while state 2 is a convergence between *Ovula* and node 18. As state 2 is a modification of state 1, they are regarded as additive, however, the cladogram topology is the same if they are considered as non-additive, with a single change in the RI (= 80).

Genital system

Male

107. Seminal vesicle position in visceral mass: 0= middle; 1= lateral-left (triviids, ovulids, cypraeids) (CI= 100; RI= 100).

The state 1 of this character, which helps in the support of node 10, may also have connection to the lateralization of the shell aperture.

108. Vas deferens region anterior to seminal vesicle: 0= short, turned forward, terminal (in relation to seminal vesicle mass); 1= long, oblique, sub-terminal (ovulids, cypraeids) (CI= 100; RI= 100).

State 1 is one of the synapomorphies of node 12 and is connected with the presence, in the taxa located after this node, of a portion of the visceral mass projected to the left side of the pallial cavity posterior region. This visceral projection is filled with the seminal vesicle in the mature males, in which coils lie anterior to the portion that runs to the pallial cavity (e.g., Figs. 116, 221, 272: sv). This fashion is clearly represented by Rau (1934, fig. 15).

109. Closed pallial prostate: 0= absent; 1= present (*Velutina, L. mopsicolor, L. branca, Hespererato, N. pediculus, Ovula*); 2= inside triangular sinus (*E. acicularis, E. spurca*) (CI= 33; RI= 33; not additive).

The prostate gland is herein regarded as a differentiated glandular closed (tubular) portion of the pallial vas deferens (e.g., Fig. 405: pt), which otherwise is a glandular, thick edged furrow.

The state 1 of this character is distributed throughout the cladogram, the single node supported by it is node 2, with a reversion in *L. patagonica*. However, state 2 helps in the support of node 29 (genus *Erosaria*).

110. Location of aperture of vas deferens into sperm groove of pallial floor: 0= in right margin; 1= almost

in middle region (all species) (CI= 100; RI= 100).

State 1 (e.g., Fig. 188: ap) is a step towards the total closure of the pallial vas deferens, becoming a complete tube. At least almost half of its posterior region is one of the ingroup synapomorphies.

111. Form of aperture of vas deferens into sperm groove of pallial floor: 0= a simple papilla; 1= preceded by a triangular attachment of mantle in head-foot surface (triviids, ovulids, cypraeids) (CI= 100; RI= 100).

The triangular, hollow region in the middle-posterior portion of the pallial floor has the columellar muscle as a ventral surface, and is a simple blood sinus in the basal ingroup species. However, in the taxa located in node 10 and above, the vas deferens runs through this space, opening just anterior to it (e.g., Fig. 119: rr).

112. Pallial vas deferens: 0= an opened groove; 1= closed (a tube) (*Velutina, S. uniplicata, Cymbula acicularis*); 2= a duct with a loop free in haemocoel close to penis base (*Lamellaria* spp) (CI= 66; RI= 85; additive).

The pallial vas deferens becomes entirely closed (tubular) (state 1) in the taxa united by nodes 2 and 15 (e.g., Fig. 371), as a convergence. State 2, moreover, is one of the synapomorphies of the genus *Lamellaria* (node 3) (e.g., Fig. 480). This character is considered as additive because of its ontogeny, since the young *Lamellaria* males have the vas deferens entirely immerse in the integument, having a free loop inside the haemocoel only in their maturity. The topology of the cladogram does not change if the character is considered as non-additive, the only change is in RI = 75.

113. Penis duct: 0= a groove; 1= a duct (closed) (lamellariids, *Hespererato, S. uniplicata, C. acicularis*) (CI= 33; RI= 66).

114. Differentiated broad and flat basal region of penis: 0= absent; 1= present (*Ovula, Calpurnus, P. intermedium, Cyphoma* spp) (CI= 100; RI= 100).

115. Penis papilla: 0= absent; 1= present (*Lamellaria* spp, *S. uniplicata, C. acicularis*) (CI= 50; RI= 75).

The penis' characters 113-115 are the only ones suitable for supporting nodes. Character 113 (state 1) helps in the support of nodes 2, 15 and the eratoid convergences. Character 114 helps in the support of ovulid node 14, and is notable because of the form of the penis, with a triangular, flat base and a long, slender and cylindrical distal region (e.g., Figs. 289, 315). Character 115, a penis papilla, helps in the support of nodes 3 (genus *Lamellaria*) and 15, by convergence. Most of the remainder species have a simple-fashioned penis, except for *Jenneria*. This species has a claviform penis with a spiral groove, ending in a pointed, sub terminal projection (Fig. 385). The *Jenneria* characters were not presently explored, as they would result as autapomorphies.

Female

116. Ovary anterior limit: 0= posterior to isolated visceral oviduct; 1= anterior to it (pediculariids, eratoid, triviids, ovulids, cypraeids) (CI= 100; RI= 100).

The state 1 of this character (e.g., Fig. 154) is maybe another consequence of the lateralization of the shell aperture, and, differently from the seminal vesicle of the males (which supports the node 10), it helps in the support of a basal node (5).

117. Gonopericardial duct: 0= present; 1= absent (all species **except** *L. branca* and triviids) (CI= 33; RI= 33).

The presence of a gonopericardial duct is herein regarded as plesiomorphic. Based on this interpretation, the structure loss occurs in node 1 as an ingroup synapomorphy. However, 2 reversions were detected, in *Lamellaria branca* (Fig. 481: gr) and in node 11 (triviids) (e.g., Fig. 407: gr).

118. Pallial oviduct: 0= opened (a groove); 1= totally closed (a tube) (all species) (CI= 100; RI= 100).

The opened pallial oviduct (as a thick edged groove) is regarded as plesiomorphic because of its presence in the cerithioideans and in some stromboideans. However, it is closed (a glandular tube) in several other caenogastropod superfamilies. With these facts, both polarizations are plausible. The present polarization is, then, suggestive, but it is possible that further analyses can bring new insights to the matter.

119. Bursa copulatrix glandular wall: 0= absent; 1= attached to capsule gland (ovulids **except** *Jenneria*); 2= posterior, to capsule gland (*Jenneria*) (CI= 100; RI= 100; not additive).

The normal fashion of the bursa copulatrix is a sac with muscular walls, scarcely glandular (e.g., Fig. 141). However, in the species above mentioned, the structure is almost as glandular as the remainder pallial oviduct, being a distinct feature (e.g., Figs. 306, 319). State 1 supports the ovulid node 14, while state 2 is a *Jenneria* autapomorphy (Figs. 386, 387). However, the glandular condition itself could be regarded as an ovulid synapomorphy. Ghiselin & Wilson (1966) already detected the ovulid fashion of the pallial oviduct, as somewhat bifid. They called the 2 portions as 'proximal' (posterior, herein called bursa) and 'distal' lobe.

120. Scanty glandular bursa copulatrix form: 0= a simple sac; 1= "U"-shaped, with inner folds (*M. zebra, M. cervinetta*); 2= a multi, uniform-digital sac (*L. cinerea*); 3= very long, with broad distal end (*E. spurca*); 4= with dorsal duct (*M. moneta, M. annulus*); 5= glandular mass of several tubes (*C. tigris*); 6= irregular digital sac (*L. lynx*); 7= with 3 branches (*R. caputserpentis*); 8= a muscular sac (*T. oryza*); 9= inserted in anterior region (*P. robertsi*); ?= absent or richly glandular (CI= 100; RI= 100; not additive).

121. Bursa copulatrix position in pallial oviduct: 0= anterior; 1= middle (*M. zebra, M. cervinetta*); 2= posterior (*P. decussata, T. oryza*, ovulids, *R. caputserpentis, L. cinerea, L. lynx, C. tigris, E. acicularis, M. moneta, M. annulus*) (CI= 50; RI= 75; not additive).

122. Bursa copulatrix large, muscular, attached by a duct directly to capsule gland: 0= absent or other condition; 1= present (*Pedicularia decussata, P. californica*) (CI= 100; RI= 100).

Although plesiomorphicly scantly glandular in non-ovulid species, the bursa copulatrix form and location of the cypraeoideans are important sources of characters for individualizing subgroups of the taxon. These features, however, have been little explored in the literature. Nevertheless, most states of the bursa character 120 resulted in autapomorphies in the present sample.

123. Seminal receptacle: 0= absent; 1= several acina in a single sac (*M. annulus*); 2= long and narrow (single or multiple) (triviids); 3= connected to bursa copulatrix (*P. intermedium, Cyphoma* spp); 4= several along albumen gland (*L. patagonica*) (CI= 100; RI= 100; not additive).

The long and narrow fashion of the seminal receptacles (state 2) (e.g., Fig. 407) appears to be a triviid character, as also shown by Fretter (1946, fig. 5).

124. Vaginal groove inside pallial oviduct: 0= simple; 1= with some longitudinal folds, separated from capsule gland by an outstanding fold (*M. moneta, M. annulus*) (CI= 100; RI= 100).

125. Capsule gland: 0= as a continuous increment of pallial oviduct; 1= separated by a narrow portion

(*E. acicularis; E. spurca*) (CI= 100; RI= 100).

126. Anterior chamber close to female pore: 0= absent; 1= present (*L. cinerea, C. tigris, L. lynx*) (CI= 50; RI= 50).

127. Bursa copulatrix posterior-dorsal located, connected to capsule gland by a duct: 0= absent; 1= present (*M. zebra; M. cervinetta, L. cinerea; L. lynx, P. robertsi; M. moneta, C. tigris*) (CI= 33; RI= 71).

128. Female genital pore: 0= a simple aperture; 1= a papilla (all species **except** eratoid and triviids) (CI= 33; RI= 33).

129. Female genital pore: 0= free from pallial floor; 1= preceded by a tubular region attached to pallial floor (pediculariids, eratoid, triviids, ovulids, cypraeids) (CI= 100; RI= 100).

The characters of the pallial oviduct (118-129), as well as several other characters that were excluded because of the autapomorphic condition, show the importance of the structure in comparative studies of the cypraeoideans. However, those here (excluded) autapomorphic features could certainly serve as a basis for some taxa in a further sample. The part of the pallial oviduct running in the floor of the pallial cavity, with the genital pore closer to the head in the form of a low and blunt papilla (characters 128-129) is a distinction in most ingroup species (e.g., Fig. 447).

It is important to emphasize that the features of the pallial oviduct were little investigated herein, and most of the nomenclature presented is based on comparisons and topology. It is likely that further studies on the histology and physiology can change the concept. Furthermore, it is interesting to note that very different pallial oviduct features were found among species with male penis uniformity. This fact shows the puzzled condition of the oviduct attributes, which must be investigated. Gosliner & Liltved (1987) explored several oviduct attributes to define some African triviid species, and also noted the uniformity of the male features. Additional discussion on the cypraeoidean genital system is found in Kay (1960b: 282-283), Ghiselin & Wilson (1966: 136-140).

130. Brood pouch in foot with an aperture in sole: 0= absent; 1= present (pediculariids) (CI= 100; RI= 100).

The brood pouch immersed in the female foot of the pediculariids appears to be reported here for the first time, although, on the pediculariids, Boss (1982: 1008) reported that "the eggs are evidently deposited in an ovisac, ...". When filled with embryos, the brood pouch protrudes in the right region behind the head, bulging into the integument (e.g., Figs. 428, 447, 453). The aperture is narrow and surprisingly located in the anterior surface of the foot sole, slightly dislocated to the right (e.g., Fig. 431: ba). This outstanding feature resulted as one of the pediculariid (node 6) synapomorphies and appeared somewhat similar amongst these species. The pediculariid brood pouch bears about a hundred embryos or young specimens (with 1 whorl) apparently in the same stage of development. Slightly similar, analogous head-foot located brood pouches are found in the cerithioideans (Thiaridae and Planaxidae), but the aperture in those taxa is close to that of the pallial oviduct, in the right-dorsal surface of the head-foot, on the pallial floor.

Central nervous system

131. Buccal ganglia: 0= close median line; 1= lateral (all species) (CI= 100; RI= 100).

132. Sub-esophageal ganglion: 0= far from nerve ring; 1= close to nerve ring (all species) (CI= 100; RI= 100).

The nerve ring of the cypraeoideans has both cerebral and pleural ganglia forming almost a single mass, difficult to be individualized (e.g., Fig. 185). However, both foot ganglia are located far from the

remainder ganglia, and connected to them through long connectives. Except for this, the ingroup nerve ring is somewhat concentrated, as expressed by character 132. Another distinctive feature of the cypraeoidean nerve ring is that it looks obliquely positioned, with pedal ganglia closer to the right and the remainder ones, closer to the left side of the haemocoel (e.g., Figs. 121, 123).

The cypraeoidean nerve ring has been reported as possessing a very long pair of posterior prolongations of the pedal ganglia (e.g., Shaw, 1909, fig. 3; Schilder, 1936: 103). However, this fashion was not observed in the several examined species, which were supposedly to possess it, and was not presently considered. Similar approach is applicated by Gosliner & Liltved (1985).

Table I. Matrix of the characters of the Cypraeoidea and 2 outgroups. Outgroup represents the basal caenogastropods (Cerithioidea, Rissooidea), Stromboidea is the second outgroup.

Taxon \character	1				2				3				4				5				6				
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	6	
Outgroup	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	0	
Stromboidea	00100	10000	00000	10000	00010	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	01000	00000	00000	00000	00000	00000	00000	0	
M. zebra	11210	11010	00111	12100	01011	11014	00101	21211	00111	11121	11111	11012	11000	1											
M. cervinetta	11210	11010	00111	12100	01011	11014	00101	21211	00111	11121	11111	11012	11000	1											
L. cinerea	11210	11010	00111	12100	01011	11011	01001	21211	00111	11121	11111	11012	11000	1											
E. acicularis	11210	11211	00111	12100	01011	11013	10101	21211	00101	11121	11111	11012	11000	1											
E.spurca	11210	11211	00111	12100	01011	11013	10101	21211	00101	11121	11111	11012	11000	1											
L.lynx	11210	11010	00111	12100	01011	11013	20201	21211	00101	11121	11111	11012	11000	1											
M.moneta	11210	11011	01111	12100	01011	11013	10111	21211	00101	11121	11111	11012	11000	1											
M.annulus	11210	11011	01111	12100	01011	11013	10111	21211	00101	11121	11111	11012	11000	1											
C.tigris	11210	11010	00111	12100	01011	11012	00101	21211	00101	11121	11111	11012	11000	1											
R.caputserpentis	11210	11011	00111	11100	01011	11013	10101	21201	00101	11121	11111	11012	11000	1											
M.robertsi	11210	11010	00111	12100	01011	11013	11301	21211	00101	11121	11111	11012	11000	1											
M.arabicula	11210	11010	00111	12100	01011	11012	01301	21211	00101	11121	11111	11012	11000	1											
N.pediculus	11220	11010	00101	10100	01011	11000	?0001	10101	01101	10111	01111	00010	01000	1											
T.orysa	11220	11010	00101	10100	01011	11000	?0001	10101	01101	10111	01111	00010	01000	1											
H.maugeriae	01110	10010	00101	10100	01011	11000	?0001	10100	00101	10111	01111	00020	01000	1											
C.signatum	21111	11010	00111	10110	12011	11000	?0041	11201	00111	11121	11111	10010	11211	1											
C.gibbosum	21111	11010	00111	10110	12011	11000	?0021	11201	00111	11121	11111	11010	11221	1											
P.intermedium	21110	11110	00111	10110	12011	11000	?0041	11201	00111	11121	11111	11010	11211	1											
O.ovum	21210	11110	00111	10100	02011	11011	00001	11201	00111	11121	11111	11010	11101	1											
S.inuplicata	21110	11110	00111	10110	12011	11012	00001	11201	00101	11121	11111	11010	11001	1											
C.acicularia	21110	11010	00111	10110	12011	11011	00001	11200	00101	11121	11111	11010	11001	1											
Calpurnus	21210	11010	00111	10100	02011	11000	?0031	11201	00111	11121	11111	11010	11001	1											
Jenneria	11220	11010	00111	10100	01011	11013	20001	11211	00101	11121	11111	11010	11001	1											
Velutina	01000	00000	00000	10000	00110	11000	?0001	00101	01000	10011	01111	00123	01001	1											
P.decussata	10000	11010	10100	00101	01011	10000	00001	10101	10121	10111	01111	00020	11001	1											
P.californica	10000	11010	10100	00101	01011	10000	?0001	10101	10121	10111	01111	00020	11001	1											
P. sp1	10000	11010	10100	00101	01011	10000	?0001	10101	20121	10111	01111	00020	11001	1											
P. sp2	10000	11010	10100	00101	01011	10000	?0001	10101	10121	10111	01111	00020	11001	1											
L.patagonica	02000	00000	00000	10000	00210	11100	00001	00101	01000	10012	01111	00121	01001	1											
L.mopsicolor	02000	00000	00000	10000	00210	11111	00001	00101	00000	10012	01111	00121	01001	1											
L.branca	02000	00000	00000	10000	00210	11100	?0001	00111	00000	10012	01111	00121	01001	1											

Taxon \character	6	7	8				9				10				11				12				13		
	7890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12			
Outgroup	0000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00			
Stromboidea	0000	00000	00000	00000	00000	10000	00000	00001	00000	00000	01100	00000	00000	00											
M. zebra	1112	11111	11211	01111	10111	11110	02111	11111	01101	10000	11101	10000	01110	11											
M. cervinetta	1112	11111	11211	01111	10111	11110	02111	11111	01101	10000	11101	10000	01110	11											
L. cinerea	0112	11111	11212	01111	10111	11010	32111	10111	01101	10000	11102	20000	11110	11											
E. acicularis	0111	11111	11212	01111	10111	11120	02111	10111	01121	10000	1110?	20001	00110	11											
E.spurca	0111	11111	11212	01101	10111	11120	02111	11111	01121	10000	11103	?0001	00110	11											
L.lynx	0111	11111	11212	01101	10111	11010	02111	10111	01101	10000	11106	20000	11110	11											
M.moneta	0111	11111	11212	01111	10111	11110	02111	10111	01101	10000	11104	20010	01110	11											
M.annulus	0111	11111	11212	01111	10111	11110	02111	10111	01101	10000	11104	20110	00110	11											
C.tigris	0111	11111	11212	01111	10111	11110	12111	11111	01101	10000	11105	20000	11110	11											
R.caputserpentis	0111	01111	11202	01111	00111	11010	02111	11111	01101	10000	11107	20000	01110	11											
M.robertsi	0112	01111	11212	01111	00111	11010	02111	10111	01101	10000	11109	00000	01110	11											
M.arabicula	0112	01111	11212	01111	00111	11010	02111	10111	01101	10000	1110?	?0?00	0???0	11											
N.pediculus	0111	01011	11311	01101	00004	10000	02111	10101	01011	10000	1010?	?0200	00010	11											
T.orysa	0111	01011	11311	01101	00004	10000	02111	10101	010?1	10000	10108	20200	00010	11											
H.maugeriae	0111	01010	11100	01101	00003	10000	01101	10001	00011	00100	1110?	?0000	00010	11											
C.signatum	0111	11111	11202	11101	11122	20011	32111	10101	21101	10010	1111?	20300	00110	11											
C.gibbosum	0111	11111	11202	11101	11122	20011	32111	10101	21101	10010	1111?	20300	00110	11											
P.intermedium	0121	01111	11202	11101	11122	20011	32111	10101	21101	10010	1111?	20300	00110	11											
O.ovum	0121	11111	11202	11101	11002	20010	32111	10101	21111	10010	1111?	20000	00110	11											
S.inuplicata	0121	11111	11202	11101	11002	20010	32111	10101	11101	11101	1111?	20000	00110	11											
C.acicularia	0121	11111	11202	11101	11002	20010	32111	10101	11101	11101	1111?	20000	00110	11											
Calpurnus	0111	11111	11202	11101	11112	20010	32111	10101	11101	10010	1111?	20000	00110	11											
Jenneria	0111	01111	11202	01101	10030	20000	02111	10001	01101	10000	1112?	20000	00110	11											
Velutina	0121	01000	11300	01101	00000	10012	01101	10001	00011	01100	0110?	?0000	00100	11											
P.decussata	0111	01000	11200	01101	00000	10001	01101	10001	0????	?000?	1110?	21000	00111	11											
P.californica	0111	01000	11200	01101	00000	10001	01101	10001	00001	00000	11100	01000	00111	11											
P. sp1	0111	01000	11202	01101	00000	10000	01101	10001	0????	???0?	1110?	00000	00111	11											
P. sp2	0111	01000	11200	01101	00000	10001	00101	10001	00???	00000	1110?	00000	00111	11											
L.patagonica	0121	01000	11100	01101	00005	??010	21101	10001	0000?	?2101	0110?	00400	00100	11											
L.mopsicolor	0121	01010	11100	01101	00005	??110	21101	10001	0001?	?2101	01100	00000	00100	11											
L.branca	0111	01010	11100	01101	00005	??110	21101	10101	0001?	?2101	00100	00000	00100	11											

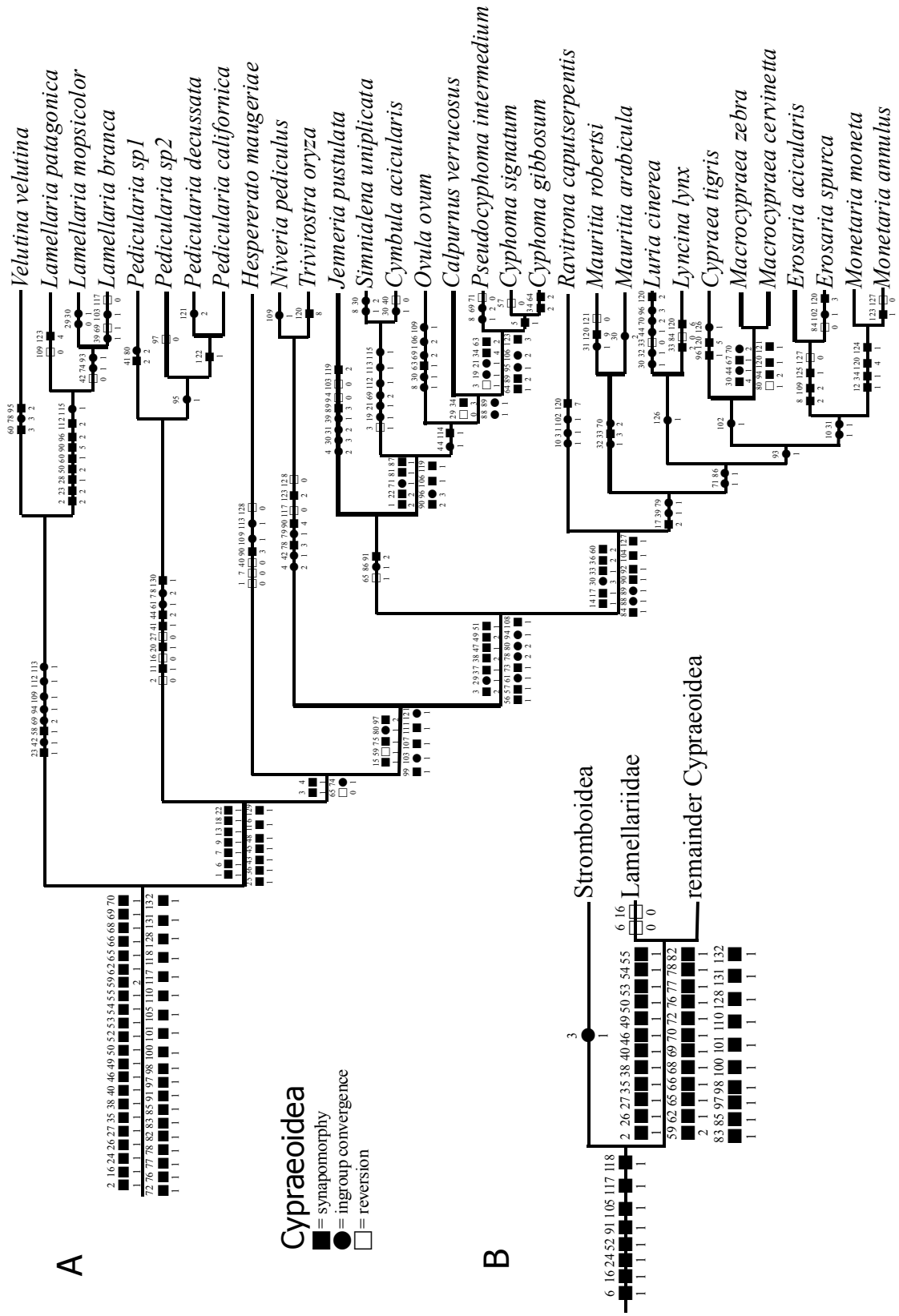


Fig. **530**. Cypraeoidea single obtained tree, with synapomorphies of each node indicated (black square: non-homoplastic synapomorphy; black circle: ingroup convergence; hollow square: reversion), number above of each symbol indicates character; below of it indicates the state. **A**, tree with basal caenogastropods (Cerithioidea and Rissooidea) as outgroups (not represented); length: 279, CI: 69, RI: 88. **B**, same, with the inclusion of the Stromboidea ground plan; 'Lamellariidae' represents the second node, included its synapomorphies, in the Fig. A; 'remainder Cypraeoidea' represents the other nodes of the Fig. A; length: 281, CI: 68, RI: 89. Outgroups not shown in both cladograms.

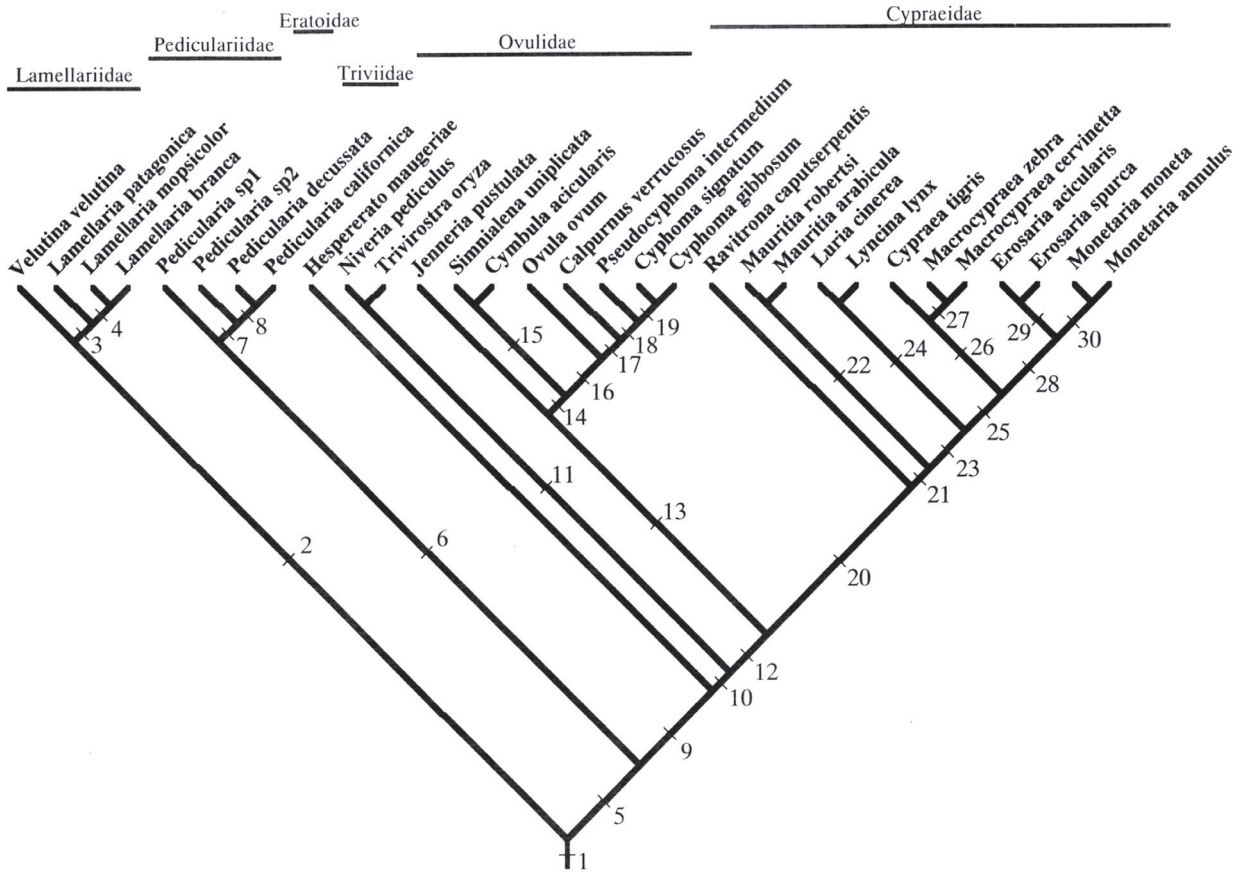


Fig. **531**. Cypraeoidea single obtained cladogram, with each node numbered. Above the cladogram there is the indication of the families (the horizontal line corresponds to the terminal shaft of the tree).

DISCUSSION OF THE CLADOGRAM

(Table I; Figs 530-531)

The superfamily Cypraeoidea (**node 1**) resulted in a monophyletic taxon, supported by 41 morphological synapomorphies in an analysis with Cerithioidea and Rissooidea as outgroups (Fig. 530A), and by 34 synapomorphies with the inclusion of the ground plan of the Stromboidea (Fig. 530B). The taxon unites 6 monophyletic families (and possibly a seventh: Pseudossaculidae, presently lacking in the sample studied). Lamellariidae, which has been referred to a proper superfamily –Lamellarioidea –, can be perfectly regarded as part of the cypraeoideans. Obviously, there is a possibility of calling node 2 Lamellarioidea, keeping Cypraeoidea for the taxa above node 5. However, another unnamed epithet, which could be avoided, must be designed for showing the identity of both groups. Then, it is preferably that all those 6 families be designated as Cypraeoidea.

Among the synapomorphies supporting the monophyly of the Cypraeoidea, the most distinctive are: the shell covered by the mantle, i.e., functionally internal (character 2); the lost operculum (26); the great development of mantle lobes (27); a part of the pericardium located dorsal to the gill (49); sub terminal connection between auricle and ctenidial vein (50); the kidney form long (53, 54); the short pleurembolic proboscis (59); mj of odontophore forming a muscular plate (68); m2 and m11 narrow, located close to the median line (69, 70); the duplication of m6 (horizontal muscle) into m6 and m6a (77, 78); the m14 pair (85); esophageal gland sac-like, with transversal, glandular septa (97, 98); simplification of the stomach (100, 101); and the papilla-like condition of the female genital pore (128).

Node 2 represents the Lamellariidae family, supported by 8 synapomorphies, of which, the out-

standing ones are: the almost separation of the columellar muscle into a pair (23); the intestine crossing through the kidney transversally (58); the loss of m2 (69); the closed pallial prostate (109); the closure of the pallial vas deferens (112) and of the penis duct (113). The first lamellariid branch is the *Velutina*, with the remainder ones comprised by **node 3** in the genus *Lamellaria*. This node is supported by 9 synapomorphies, among which the most notable ones are: the fully internal location of the shell (2); the entire separation of the columellar muscle into a pair (23); the mantle border entirely fused (28); the connection of the auricle almost in the middle region of the ctenidial vein (50); median hook in the jaws (60); the lack of the radular marginal teeth (90); the long esophageal pouches (96); and the free haemocoelic loop of the ejaculatory duct (112). The gap between the 2 present samples of the lamellariids, the *Velutina* and the *Lamellaria,* is clear. Although samples of another genera were not available, it is possible that both assemblages actually be considered as separate families (see Colikov & Gulbin, 1990), or both could be extremes of a somewhat continuous evolutionary trend of a single taxon. It is known, at least regarding the fusion of the mantle border, that there are lamellariine genera which still present a vestige of separation, such as an orifice (e.g., *Coriocella* Blainville, 1824). Additional morphological information about the lamellariines and diagnostic characters are found in Marcus (1986). Among the 3 sampled species of the genus *Lamellaria*, the 2 Brazilian species, *L. mopsicolor* and *L. branca* resulted closer (**node 4**) than the Argentine one (*L. patagonica*), sharing 3 synapomorphies.

Node 5 unites the remainder cypraeoideans, except the lamellariids. The node is supported by 14 synapomorphies, the most remarkable ones are: the involute shell form (character 1); the anal canal (7); the lateralization of the shell aperture (9); the incurrent siphon separated from the mantle border (36); and the anterior region of the pallial oviduct running in the pallial floor (129).

Node 6 is the branch that follows and represents the pediculariids. It is supported by 10 synapomorphies, from which the most notable ones are: reversion to the functional external shell (2); expansions of the shell fitting on the substratum (11); very long neck region (20); partial monopectinate osphradium (41); and brood pouch of the females (130). The 4 sampled species are successively disposed afterwards, with the remainder 2 nodes supported by 1 synapomorphy each, ending with node 8 uniting *Pedicularia decussata* and *P. californica* as sister species.

Node 9 is the pediculariid sister taxon, and is supported by 4 synapomorphies, as the complexity of the shell outer lip (3); glossy shell outer surface (4); anterior separation between odontophore and esophagus (65); and the broad and short form of the odontophore muscle m5. The following branch is *Hespererato maugeriae*, representing the Eratoidae. From the 7 autapomorphies of this species, some are expected to be characters of the family, but additional species need to be studied.

Node 10 gathers the triviids, ovulids and cypraeids in one taxon, supported by 10 synapomorphies. The most distinctive ones are: the reversion of the proboscis to a short condition, with weak buccal mass, resembling the acrembolic proboscis (59); the increasing number of septa of the esophageal gland (97); the duct to digestive gland located exactly between the esophagus and the intestine (103); the lateral-left location of the male seminal vesicle (107); and the tendency of the bursa copulatrix of being more posteriorly positioned (121).

The following branch represents the triviids (**node 11**) supported by 8 synapomorphies, being notable ones the following: sculpture in the shell outer surface (4); scalloped osphradium filaments (42); the connection of m6a with the adjacent muscular platform formed by mj (79); reversion to the presence of the gonopericardial duct (117); and the long and narrow form of the female seminal receptacle (123). Most authors consider the triviids and the eratoids as a single taxon (e.g., Schilder, 1968; Rios, 1994), however, the results obtained herein do not support this concept, because it resulted in a paraphyletic taxon located between nodes 9 and 12. However, both groups have several species, and some of them are difficult to determine to which one they belong. It is possible that, with more species studied in more details, a new insight arises to the question.

Node 12 unites the cypraeids and the ovulids as sister taxa, and is supported by 15 synapomorphies, of which, the outstanding ones are: the papillae in the outer surface of the mantle lobes (29); the anal siphon in the mantle border (37); the tri-radiate condition of the osphradium (38); the transversal mantle septa

through the hypobranchial gland (47); a long and narrow portion of the auricle running dorsal to the gill (51); lobe-like nephridial gland (56); reduction of m6 and m6a (78); loss of m7 (80); and oblique furrows of the dorsal folds of the buccal mass (94).

The Ovulidae (**node 13**) is supported by 3 synapomorphies, which single outstanding feature is the brush-like inner and outer marginal teeth of the radula (91). The low number of synapomorphies supporting the node are unusual if compared with the remainder basal nodes. If the radular characters 86 and 91 were removed, nodes 13 and 20 would collapse, appearing a trichotomy representing the *Jenneria*, the remainder ovulids and the cypraeids. Thus, except for the radula, there is no other detectable strong source of characters uniting *Jenneria* with ovulids, and it is possible that further analyses could bring *Jenneria* to a proper family, as sister taxon of the ovulids plus cypraeids. **Node 14** unites the remainder sampled ovulids, and is supported by 9 synapomorphies, of which the most remarkable ones are: highly convolute shell, lacking entirely a visible apex (character 1); odontophore muscle m3 (71); m7a, a pair of small odontophore muscles running through the fibers of m4 (81); almost bifid radular nucleus (87); radular marginal teeth with many cusps (90); a pair of esophageal pouches (96); the pallial loops of the intestine (106); and the glandular condition of the bursa copulatrix (119).

The remainder nodes of the ovulids show a closer condition of the *S. uniplicata* and *Cymbula acicularis*, which were considered as belonging to the same genus, *Simnia* Risso, 1826, by some authors (e.g., Rios, 1994). **Node 15**, which groups the *Simnia*-like sampled species, is supported by 7 synapomorphies and is the second ovulid branch. The remainder branches include successively *Ovula, Calpurnus, Pseudocyphoma* and both *Cyphoma* species. Further comments and history of the ovulids are found in Cate (1973) and Rosenberg (1992).

Node 20 represents the Cypraeidae family, supported by 13 synapomorphies, of which the most remarkable ones are: right accessory muscle of the columellar muscle (17); branched pallial papillae (30); papillae at the siphon edges (36); the loss of the jaw plates (60); the odontophore muscle m12 (85); the radular rachidian, lateral and marginal teeth with 3 cusps each (88-90); and the dorsal condition of the bursa copulatrix, possessing a narrow and long duct (127).

Despite the somewhat uniform anatomical attributes of the cypraeids, an organization of the 12 sampled species was obtained, including the type species of the genus *Cypraea* (*C. tigris*). Some authors still consider this genus as the only genus of the family (e.g., Rios, 1994), while others consider several genera and subgenera. In the present study the genera are considered as, and all of them resulted, monophyletic taxa. Although a first step towards a better organization of the family is presented herein, there are more than 250 species of cypraeids and certainly further studies are still necessary. Meyer (1998 plus personal communication) performed molecular analyses on the cypraeids and some outgroups (cypraeoideans and others). Most of the results he obtained are still unpublished, therefore, unavailable for public discussion. His analysis is on 16S and COI mitochondrial DNA of more species than those sampled herein, most of the results he obtained are compatible with those presented herein, except for the location of the *R. caputserpentis,* which has always resulted in a sister taxon of the branch *M. moneta – M. annulus*. This point of view agrees with some authors that consider *R. caputserpentis* in the same taxon of the other 2 species (e.g., Bradner & Kay, 1996; Lorenz & Hubert, 2000), while in the present study, *R. caputserpentis* resulted in the basal cypraeid branch, far from the *Monetaria* species. Gosliner & Liltved (1985, fig. 35) also presented a phylogeny with 4 terminal taxa, based on 6 characters. The tree presented herein has 2 branches, 1 with Cypraeidae-Ovulidae, and another with Triviidae-Lamellariidae.

Specimens of Sacculidae were not available for study. According to the literature data on *Sacculus* (Hirase, 1926), there are characters in common with the cypraoideans, such as 1) body entirely surrounded by mantle (except for a small dorsal slit); 2) well-developed proboscis; 3) taenioglossate radula; 4) bipectinate osphradium; 5) middle esophagus with an unpaired folded dilatation (pouch). Sacculidae is the only cypraeoidean family not sampled herein.

CONCLUSIONS

1) The superfamily Cypraeoidea is a monophyletic taxon, supported by 34 morphological synapomorphies.
2) According to the obtained cladogram, the superfamily encompasses the following monophyletic families along the tree: Lamellariidae, Pediculariidae, Eratoidae, Triviidae, Ovulidae and Cypraeidae (each family is the sister taxon of the group of the following listed families). Sacculidae is still *incertae sedis*.
3) The analysis of all systems and organs is suitable for comparative studies, supporting the phylogenetic and taxonomic approaches.

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