COMPARATIVE MORPHOLOGICAL STUDY AND PHYLOGENY OF REPRESENTATIVES OF THE SUPERFAMILY CALYPTRAEOIDEA (INCLUDING HIPPONICOIDEA) (MOLLUSCA, CAENOGASTROPODA).

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Abstract –With the objective of testing the monophyly of the Calyptraeoidea and of searching for its ground plan, a detailed morphological analysis was conducted for the following species: a) Family Calyptraeidae, 1) *Bostrycapulus aculeatus* (Gmelin) (formerly *Crepidula*); 2) *Crepidula* aff. *plana* Say; 3) *C. protea* Orbigny (these from Brazil); 4) *C.* aff. *protea* (from Argentina) (published elsewhere); 5) *C. convexa* Say (from Venezuela); 6) *C. fornicata* (L.) (from Europe); 7) *Calyptraea centralis* (Conrad) (from Brazil); 8) *Crucibulum auricula* (Gmelin) (from Venezuela); 9) *Cr. quiriquinae* (Lesson) (from Chile); 10) *Trochita trochiformis* (Born) (from Chile); 11) *Sigapatella calyptraeformis* (Lam.) (from New Zealand, formerly Calyptraea); b) Family Hipponicidae, 12) *Hipponix costellatus* Carpenter (formerly *H. grayanus*); 13) *H. subrufus* (Lam.); 14) *H. incurvus* (Gmelin) (formerly *Capulus incurvatus*) (these 3 from NE Brazil); 15) *H. grayanus* Menke (from Mexico and Ecuador); 16) *H. leptus* n. sp. (N.E. Brazil); 17) *Sabia conica* (Schumacher); 18) *Malluvium devotus* (Hedley) (both Australia); 19) *Cheilea equestris* (L.) (N.E. Brazil); c) Family Capulidae, 20) *Capulus sycophanta* Garrard (Australia); d) Family Trichotropidae, 21) *Trichotropis cancellata* Hinds (W. USA); 22) *T. borealis* Broderip & Sowerby (N. Atlantic); 23) *T. sp*. (Alaska); e) Family Vanikoridae, 24) *Vanikoro sp*. (Australia). A phylogenetic analysis of 112 characters (177 states) from morphology of all systems and organs results in the following single most parsimonious tree: ((*Trichotropis cancellata* – *T. borealis*) (*Capulus sycophanta* (*Vanikoro sp* ((*Cheilea equestris* (*Sabia conica* (*Malluvium devotus* ((*Hipponix grayanus* – *H. leptus*) (*H. incurvus* (*H. costellatus* – *H. subrufus*)))))) (*Sigapatella calyptraeformis* (*Trochita trochiformis* (*Calyptraea centralis* ((*Crucibulum auricula* – *Cr. quiriquinae*) (*Bostrycapulus aculeatus* (*Crepidula argentina* (*C. convexa* (*C. fornicata* (*C.* aff. *plana* – *C. protea*)))))))))))). Length: 267, CI: 67, RI: 88. Outgroups from other caenogastropod superfamilies were used as well as some archaeogastropod groups. The main result is the monophyly of Calyptraeoidea supported by 27 synapomorphies with basal Caenogastropoda used as the outgroup (Cerithioidea, Hydrobioidea), and 21 synapomorphies when Stromboidea and Cypraeoidea were used as outgroups. Calyptraeoidea includes, successively along the tree, the following monophyletic families: Trichotropidae, Capulidae, Vanikoridae, Hipponicidae and Calyptraeidae. The hipponicid affinity of *Cheilea* is confirmed. Some taxonomic problems found in the sampled representatives (as mentioned above), were partially resolved.

Key words - *Caenogastropoda, Calyptraeoidea phylogeny, morphology, cladistic analysis, Hipponicoidea, Capuloidea.*

Resumo –Com o objetivo de testar a monofilia dos Calyptraeoidea e obter seu “plano básico”, um estudo morfológico detalhado é desenvolvido nas seguintes espécies: a) Família Calyptraeidae, 1) *Bostrycapulus aculeatus* (Gmelin) (previamente *Crepidula*); 2) *Crepidula* aff. *plana* Say; 3) *C. protea* Orbigny (todos do Brasil); 4) *C.* aff. *protea* (da Argentina) (publicada em outro artigo); 5) *C. convexa* Say (da Venezuela); 6) *C. fornicata* (L.) (da Europa); 7) *Calyptraea centralis* (Conrad) (do Brasil); 8) *Crucibulum auricula* (Gmelin) (da Venezuela); 9) *Cr. quiriquinae* (Lesson) (do Chile); 10) *Trochita trochiformis* (Born) (do Chile); 11) *Sigapatella calyptraeformis* (Lam.) (da Nova Zelândia, previamente Calyptraea); b) Família Hipponicidae, 12) *Hipponix costellatus* Carpenter (previamente *H. grayanus*); 13) *H. subrufus* (Lam.); 14) *H. incurvus* (Gmelin) (previamente *Capulus incurvatus*) (estes 3 do NE Brasil); 15) *H. grayanus* Menke (do México e Equador); 16) *H. leptus* n. sp. (N.E. Brasil); 17) *Sabia conica* (Schumacher); 18) *Malluvium devotus* (Hedley) (ambos da Austrália); 19) *Cheilea equestris* (L.) (N.E. Brasil); c) Família Capulidae, 20) *Capulus sycophanta* Garrard (Austrália); d) Família Trichotropidae, 21) *Trichotropis cancellata* Hinds (W. USA); 22) *T. borealis* Broderip & Sowerby (N. Atlântico); 23) *T. sp*. (Alaska); e) Família Vanikoridae, 24) *Vanikoro sp*. (Austrália). Uma análise filogenética fundamentada em 112 caracteres (177 estados) é realizada, baseada na morfologia de todos os órgãos e sistemas. A única árvore obtida é a seguinte: ((*Trichotropis cancellata* – *T. borealis*) (*Capulus sycophanta* (*Vanikoro sp* ((*Cheilea equestris* (*Sabia conica* (*Malluvium devotus* ((*Hipponix grayanus* – *H. leptus*) (*H. incurvus* (*H. costellatus* – *H. subrufus*)))))) (*Sigapatella calyptraeformis* (*Trochita trochiformis* (*Calyptraea centralis* ((*Crucibulum auricula* – *Cr. quiriquinae*) (*Bostrycapulus aculeatus* (*Crepidula argentina* (*C. convexa* (*C. fornicata* (*C.* aff. *plana* – *C. protea*)))))))))))). Passos: 267, IC: 67, IR: 88. como grupos externos são usados representantes de outras superfamílias de Caenogastropoda, assim como de outros grupos de arqueogastrópodes. Como resultados principais destacam-se a monofilia de Calyptraeoidea, suportada por 27 sinapomorfias se os grupos externos forem os Caenogastropoda basais (Cerithioidea, Hydrobioidea) e 21 sinapomorfias com Stromboidea e Cypraeoidea como grupos externos. Calyptraeoidea inclui sucessivamente ao longo da árvore as seguintes famílias monofiléticas: Trichotropidae, Capulidae, Vanikoridae, Hipponicidae e Calyptraeidae. A afinidade com Hipponicidae de *Cheilea* é confirmada, dentre alguns problemas taxonômicos encontrados nos representantes amostrados (como mencionados acima), foram parcialmente resolvidos.

Palavras-chave: *Caenogastropoda Calyptraeoidea filogenia morfologia análise cladística Hipponicoidea Capuloidea.*

CONTENTS

INTRODUCTION

The Calyptraeoidea (= Crepiduloidea) and the Hipponicoidea are very modified caenogastropods. They tend to modify their shells to a dorso-ventrally flattened, limpet or limpet-like morphology. They also tend to an almost sessile habit and to protandric hermaphroditism. The filter-feeding habit of the Calyptraeidae, in particular, has been the subject of some detailed studies of the movement of water and particles in the pallial cavity currents (Orton, 1912; Werner, 1953). Anatomical studies, however, are relatively scant in the literature (Kleinsteuber, 1913; Heath, 1916; Moritz, 1938, 1939; Ishiki, 1939; Coe, 1942; Werner & Grell, 1950; Werner, 1951, 1955), as are studies of the relationships within both superfamilies. The Capulidae, moreover, have enjoyed little taxonomical stability, and they have been considered to be in the Calyptraeoidea (Younge, 1962; Vaught, 1989), the Hipponicoidea (Abbott, 1974), as well as in the Capuloidea (Bandel & Riedel, 1994).

As part of a larger project on phylogenetic relationship of the order Caenogastropoda, at the superfamily level, three features of each superfamily has been examined: 1) their monophyly; 2) the separation from the other taxa; and 3) the ground plan. These three features can only be examined using phylogenetic analysis. Species representing the Superfamily Calyptraeoidea and Hipponicoidea were selected for detailed morphological study to form the base of a comparative cladistic analysis.

A previous phylogeny of the Calyptraeoidea had been presented by Bandel & Riedel (1994). Although the authors applied no orthodox methodology, 2 interesting trees were obtained by the intuitive method. In the first tree (fig. 5), the authors united in a single branch the Calyptraeidae and the Hipponicidae as Calyptraeoidea, supported by 2 synapomorphies: 1) teleoconch limpet-shaped and 2) breeding stalked egg capsules. In the second tree (fig. 6), of the Neomesogastropoda Bandel, 1991, the Calyptraeoidea appeared in a branch with the Capuloidea (grouping, according to authors, Capulidae plus Trichotropidae, on the basis of a shared echinospira larva). The branch Calyptraeoidea-Capuloidea is supported by the synapomorphy: facultative filter-feeding.

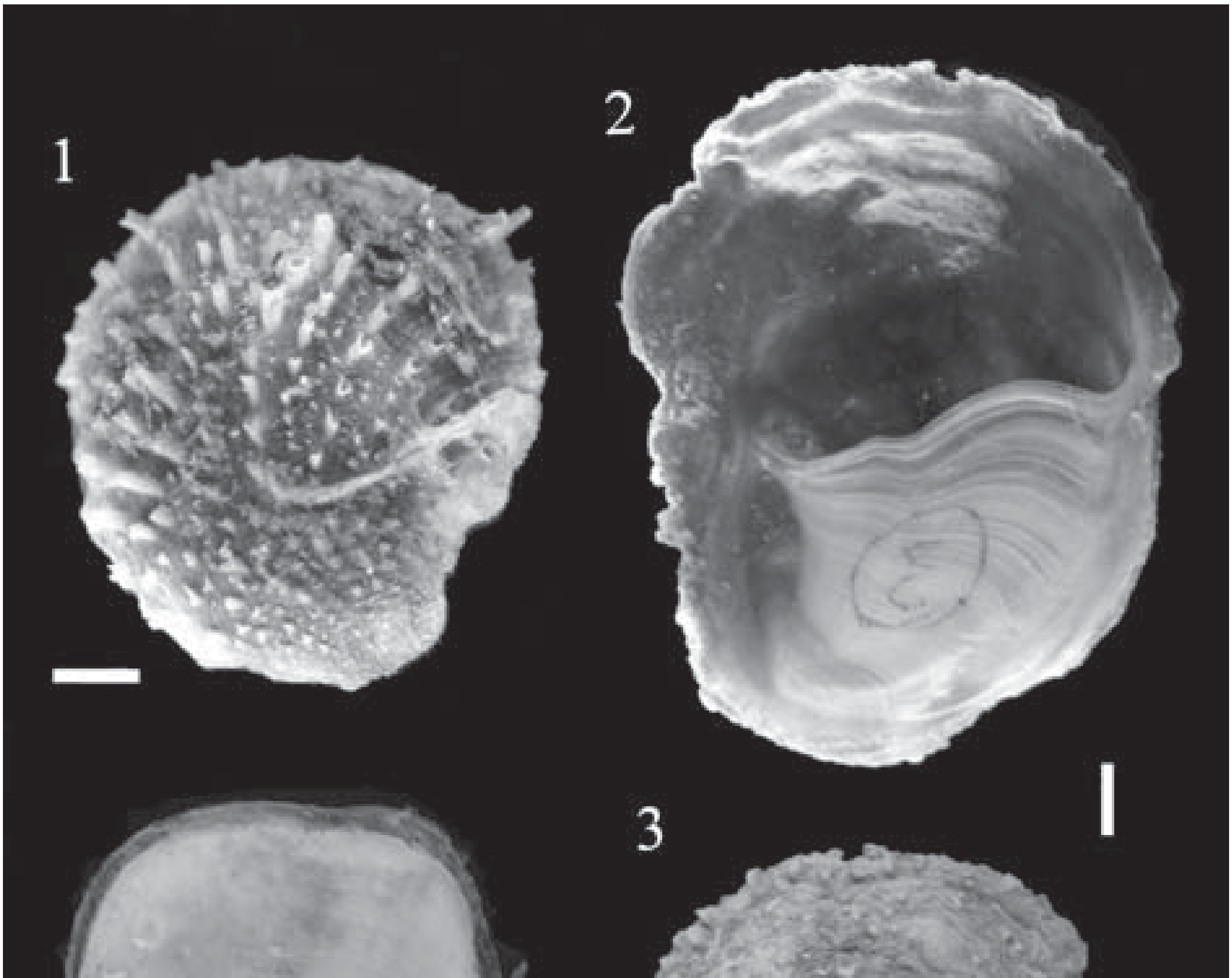
Hoagland (1977: 408-411, fig. 28) also gave a phylogenetic scenario for the group (except vanikorids and hipponicids). She stated that the family arose from a protandrous mesogastropod ancestor, with a gill modified for. The first branch led to the trichotropids in cold waters. The remainder is united by a shell flattened for sedentary life and lack of operculum. The basal taxon in this group is represented by *Trochita*, with a limpet-like foot and large shell aperture. From this taxon arose the capulid stock with high patelliform shell plus modification for proboscis feeding, and the remaining calyptraeids, sharing the increased whorl expansion rate. The so-called calyptraeid stock, with a patelliform shell that retains some remains of spiral coiling, is represented by *Calyptraea*, which has the septum modified into a curved plate. From this taxon, a branch marked by further modified shell and mantle growth gave risen to 2 branches: 1) *Crucibulum*, possessing curved septal plate fused into a cup and secondary external radial symmetry and 2) early *Crepidula* stock which were characterized by having an unwound columella with muscle still attached to it, asymmetric growth, and a flattened septum.

A new phylogenetic analysis is performed here, using an orthodox methodology to analyse holistic morphology of organs and structures never analyzed before.

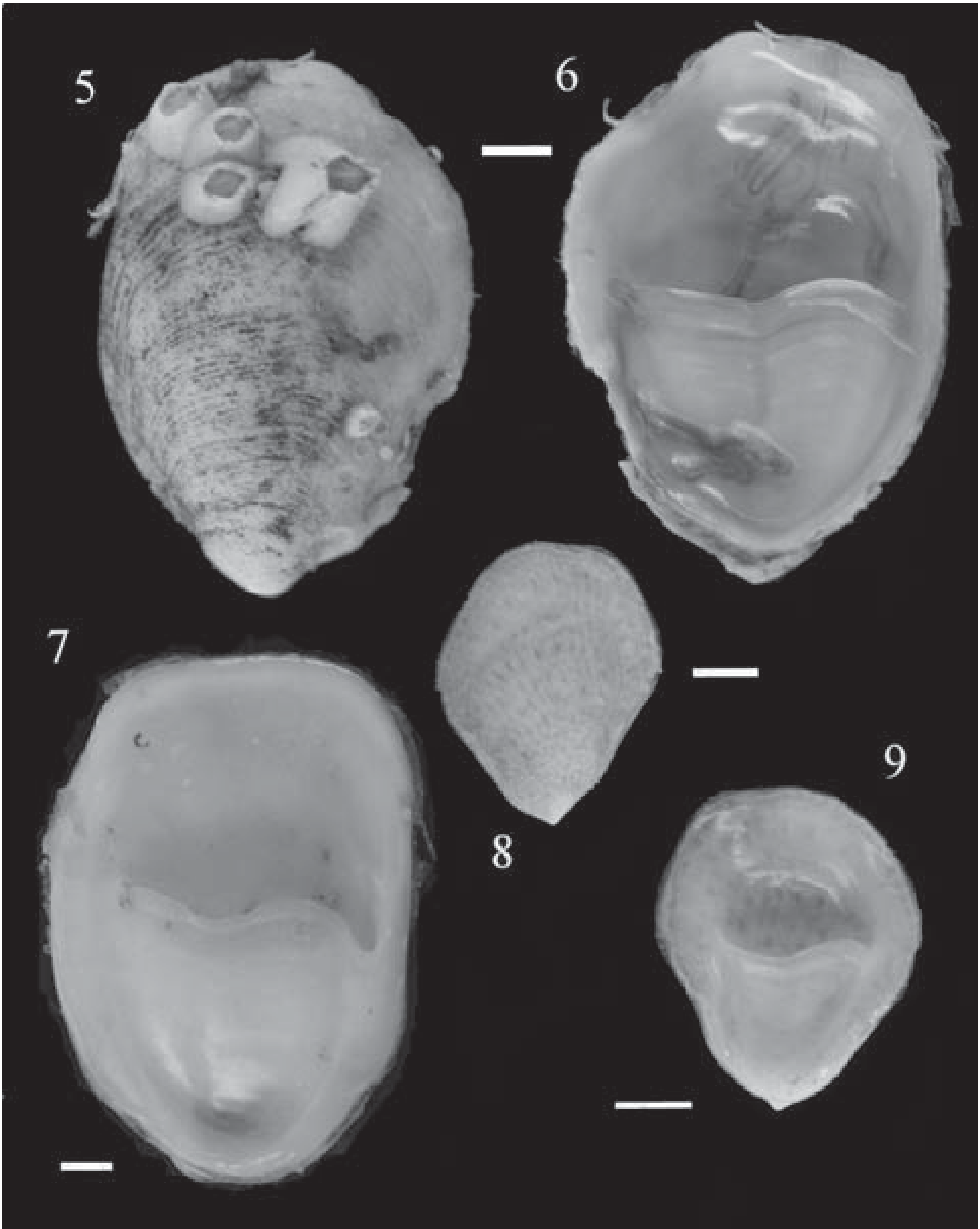
MATERIAL AND METHODS

Specimens examined for this study either belong to institutional collections or were collected especially for this study. The specimens were dissected using standard techniques, under a stereo-microscope, with the specimens immerse in water. Some organs such as the oviduct and foregut were processed using standard histological technique for serial sections of 5 µm with Mallory stain. Hard structures, such as shells, radulae and jaws were examined using SEM in the “Laboratório de Microscopia Eletrônica do Instituto de Biociências da Universidade de São Paulo” and in the MZSP. Some specimens were collected and examined alive in the laboratories of CEBIMar (Centro de Biologia Marinha, Universidade de São Paulo). The descriptive part of this paper provides a complete description of the first species. The remaining species are described in comparison to the first species and most of the similar features are omitted. This measure is adopted to decrease the length of this contribution, and for highlighting the informative characters. The same approach is adopted in the figures. A detailed list of specimens examined follows each species description.

The section of comparative morphology is organized as a phylogenetic analysis. The account of each character begins with an abbreviated descriptive sentence followed by plesiomorphic and derived conditions(s) and the CI and RI (consistency and retention indices, respectively) values for the character under the most parsimonious hypothesis. Following the apomorphic state(s), a list of terminal taxa with the apomorphic condition is presented. Hundreds of characters were examined but those that resulted autapomorphic, highly variable, or overlapping, were not



Figures 1-4, shells: **1**, *Bostrycapulus aculeatus*, dorsal view of a spiny specimen; **2**, same, ventral view; **3**, same, specimen with weak spines; **4**, *Crepidula* aff *plana*, dorsal view. Scales = 30 mm.



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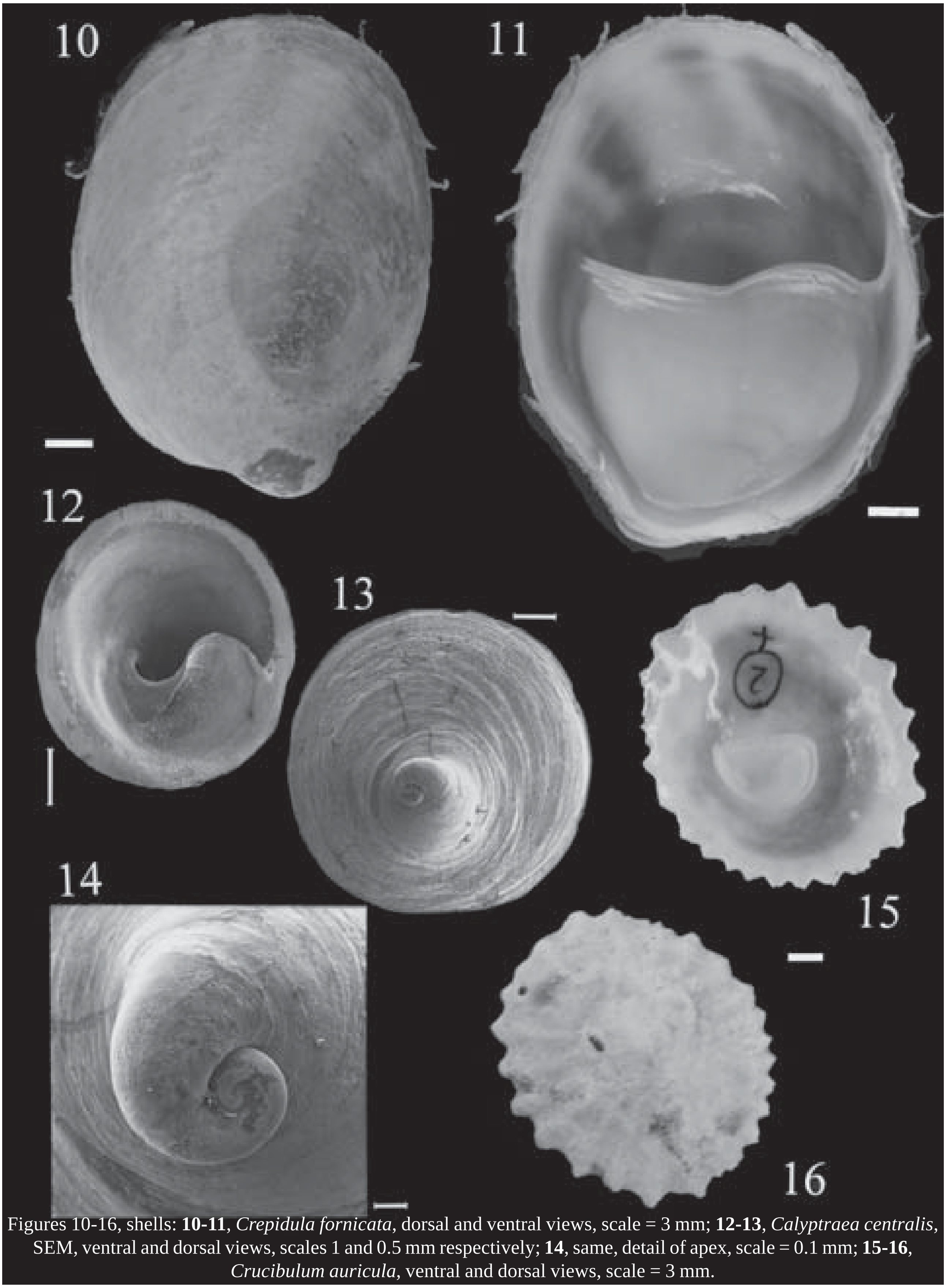

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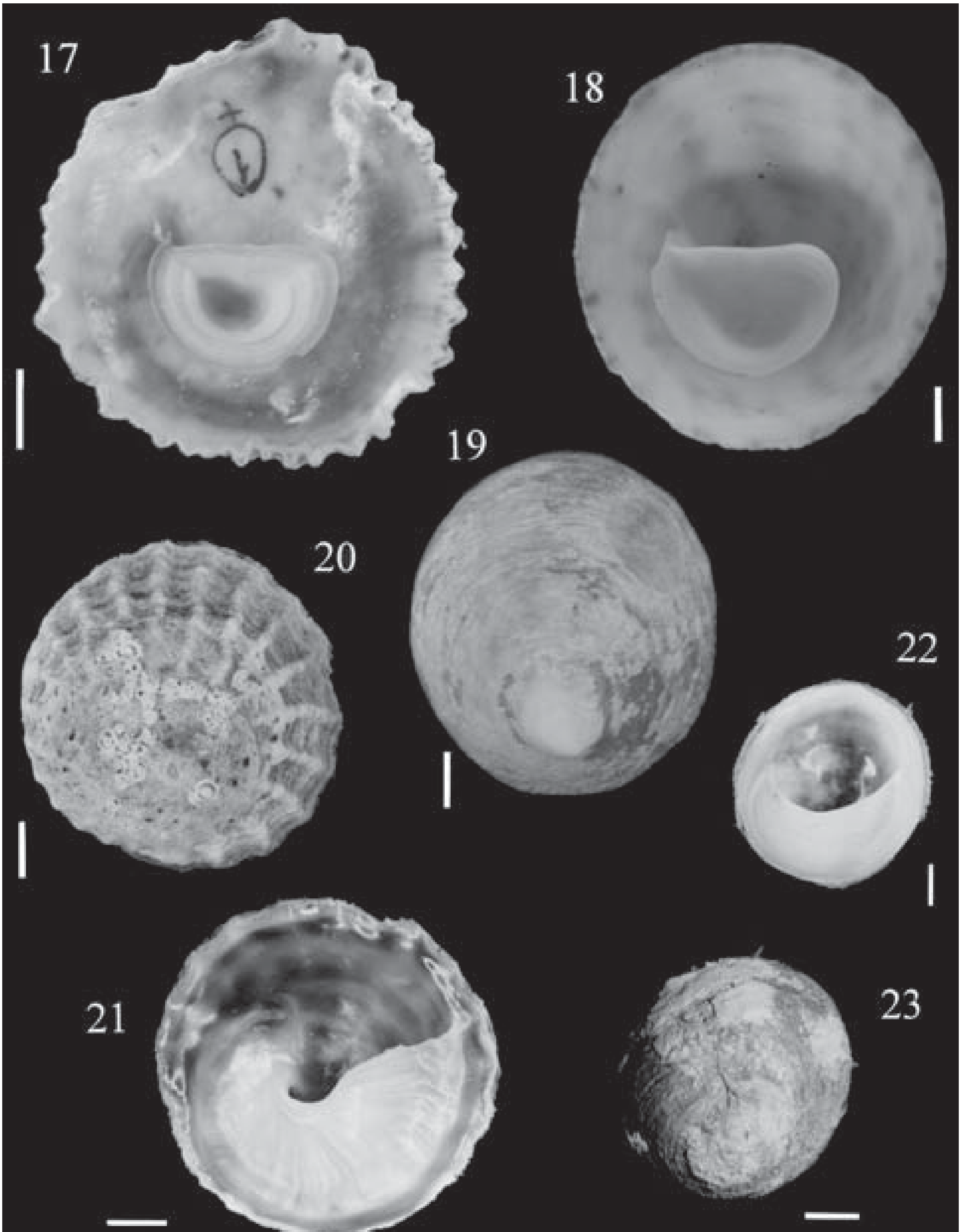

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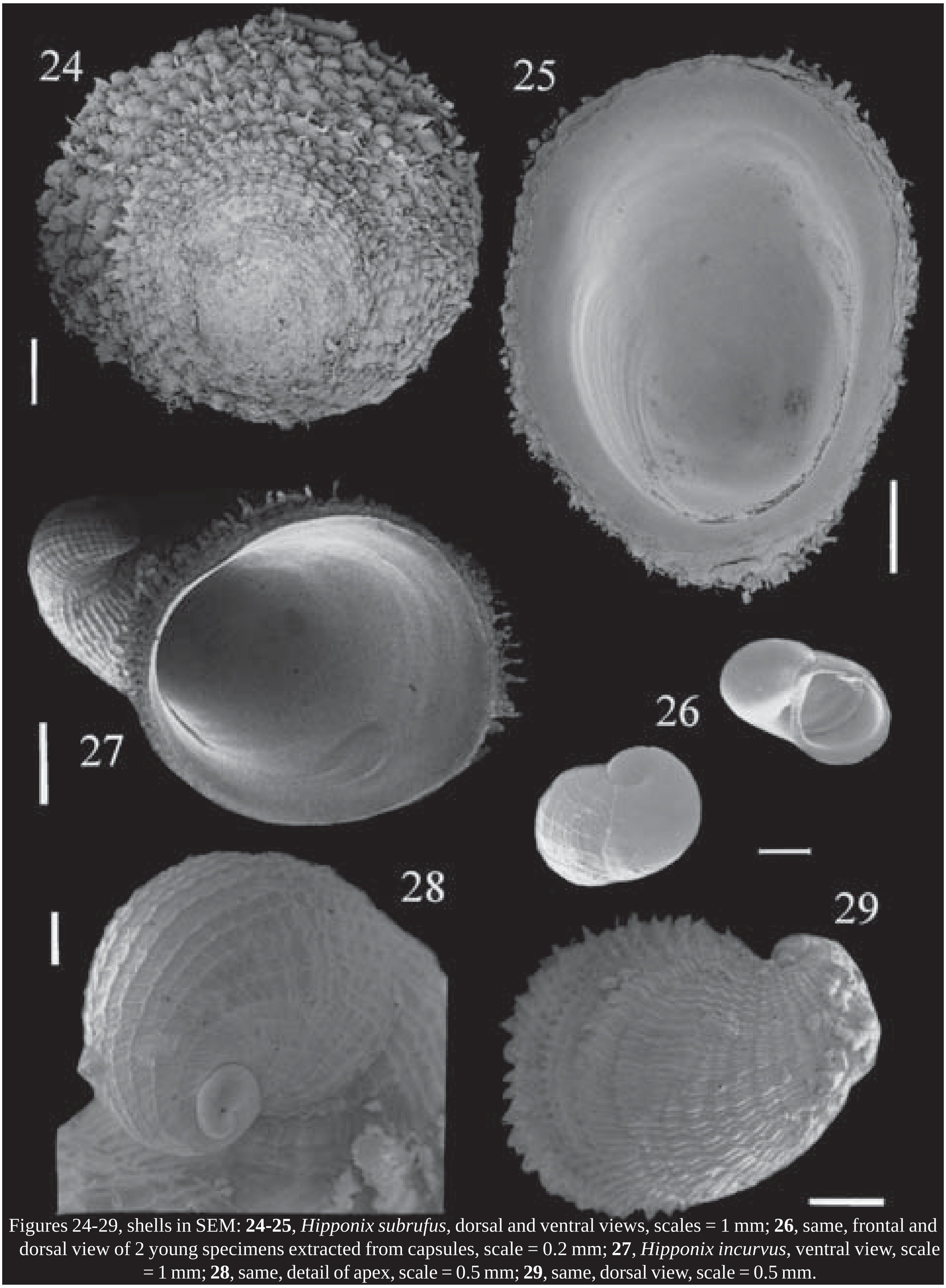

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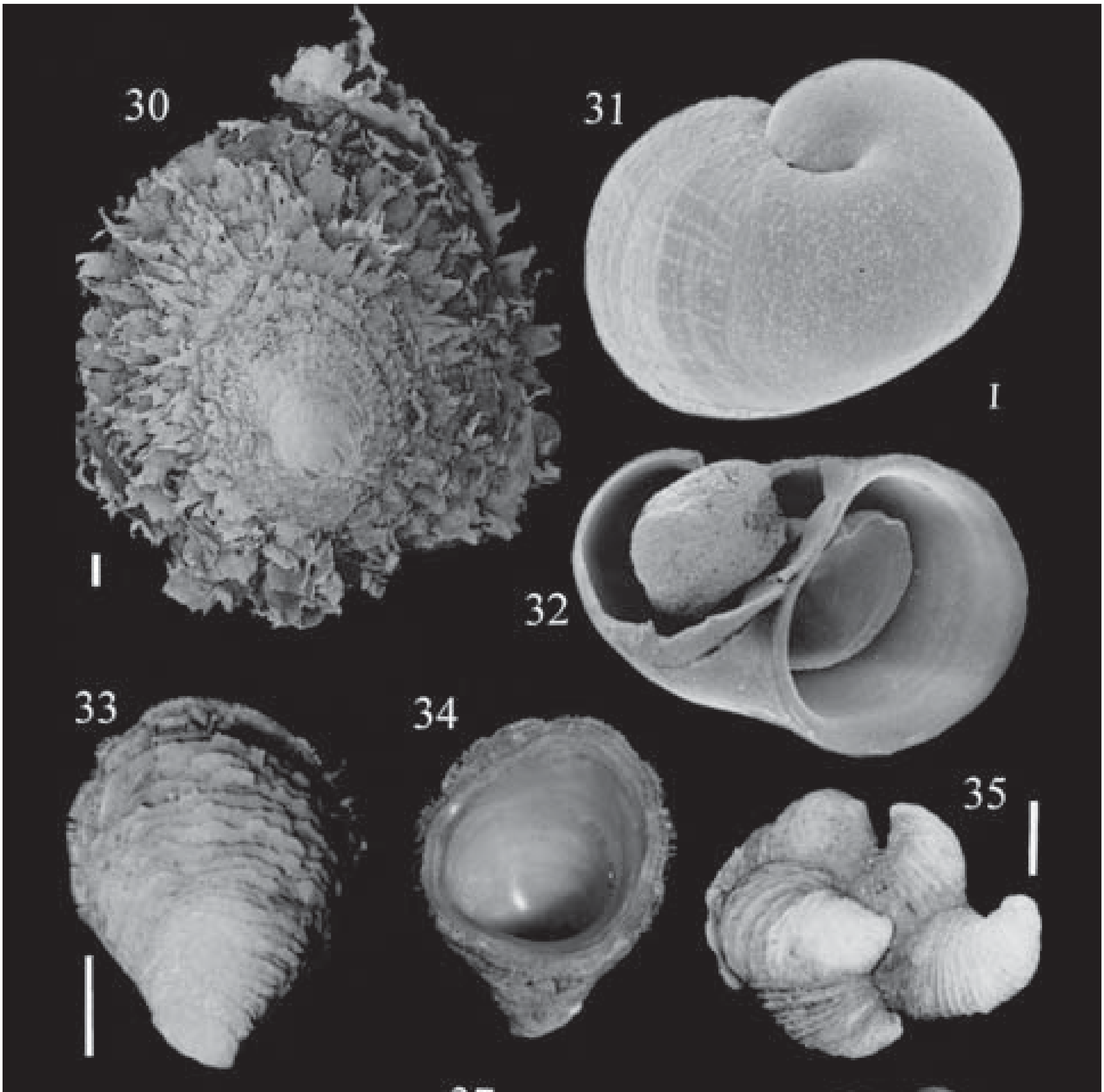

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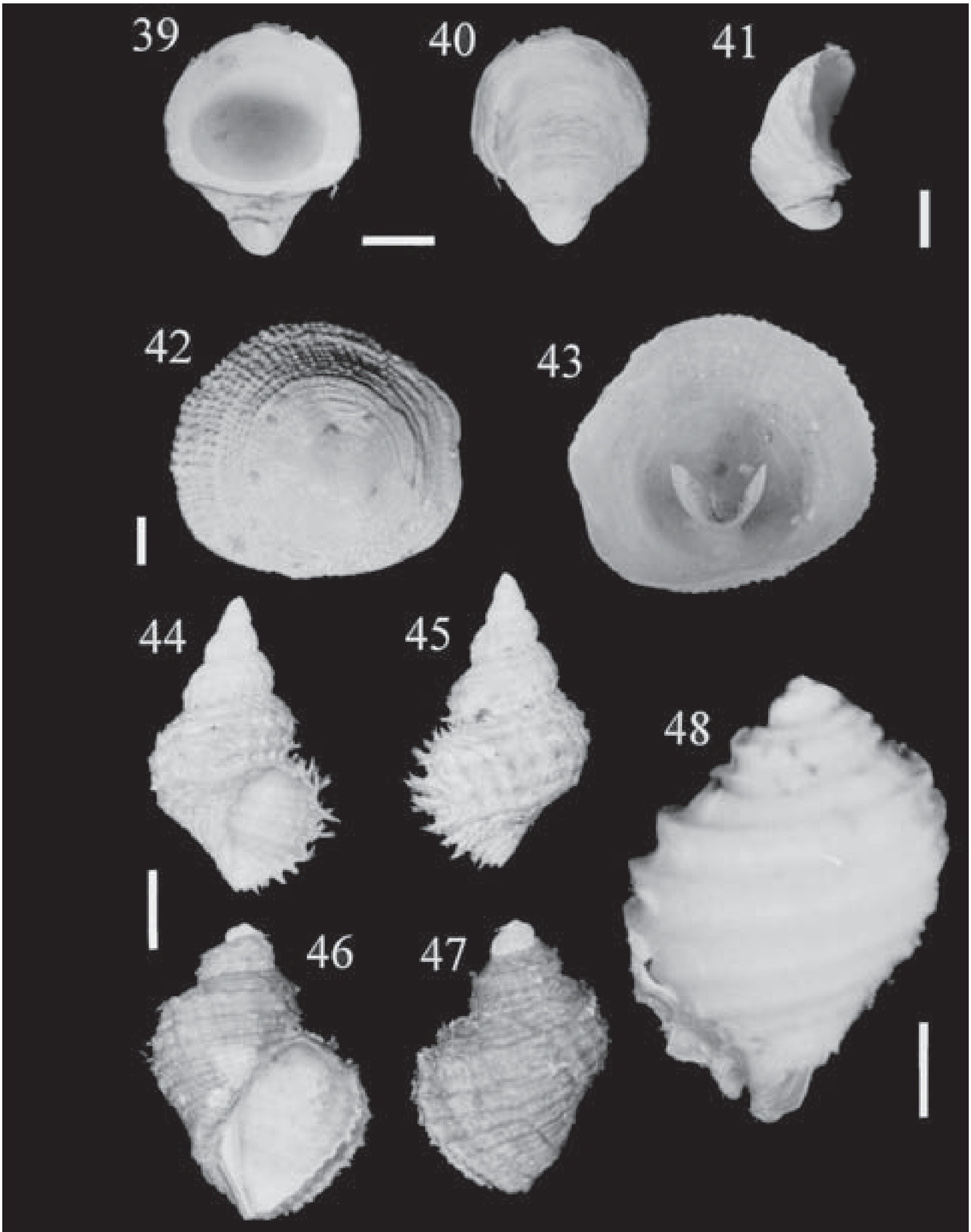

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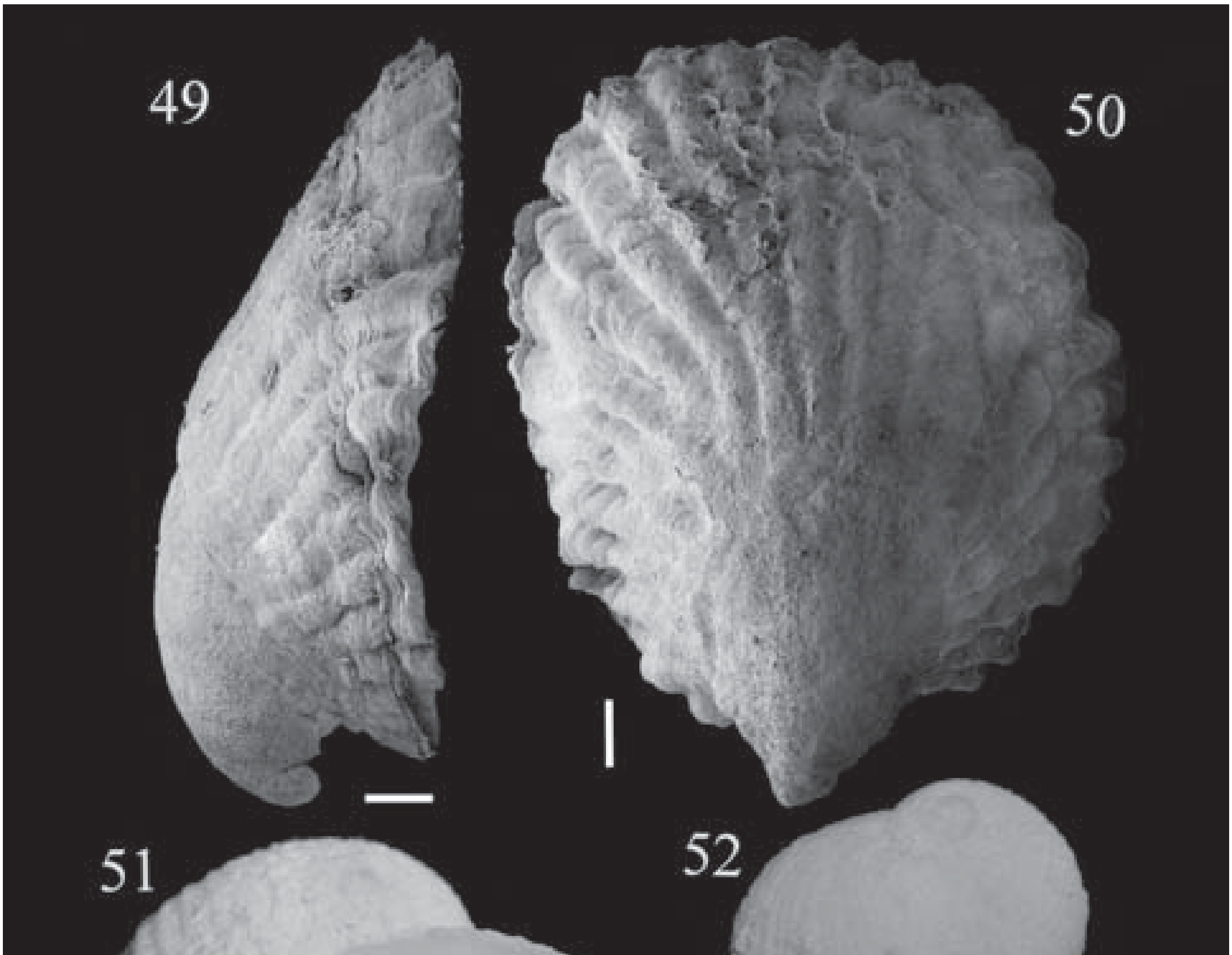

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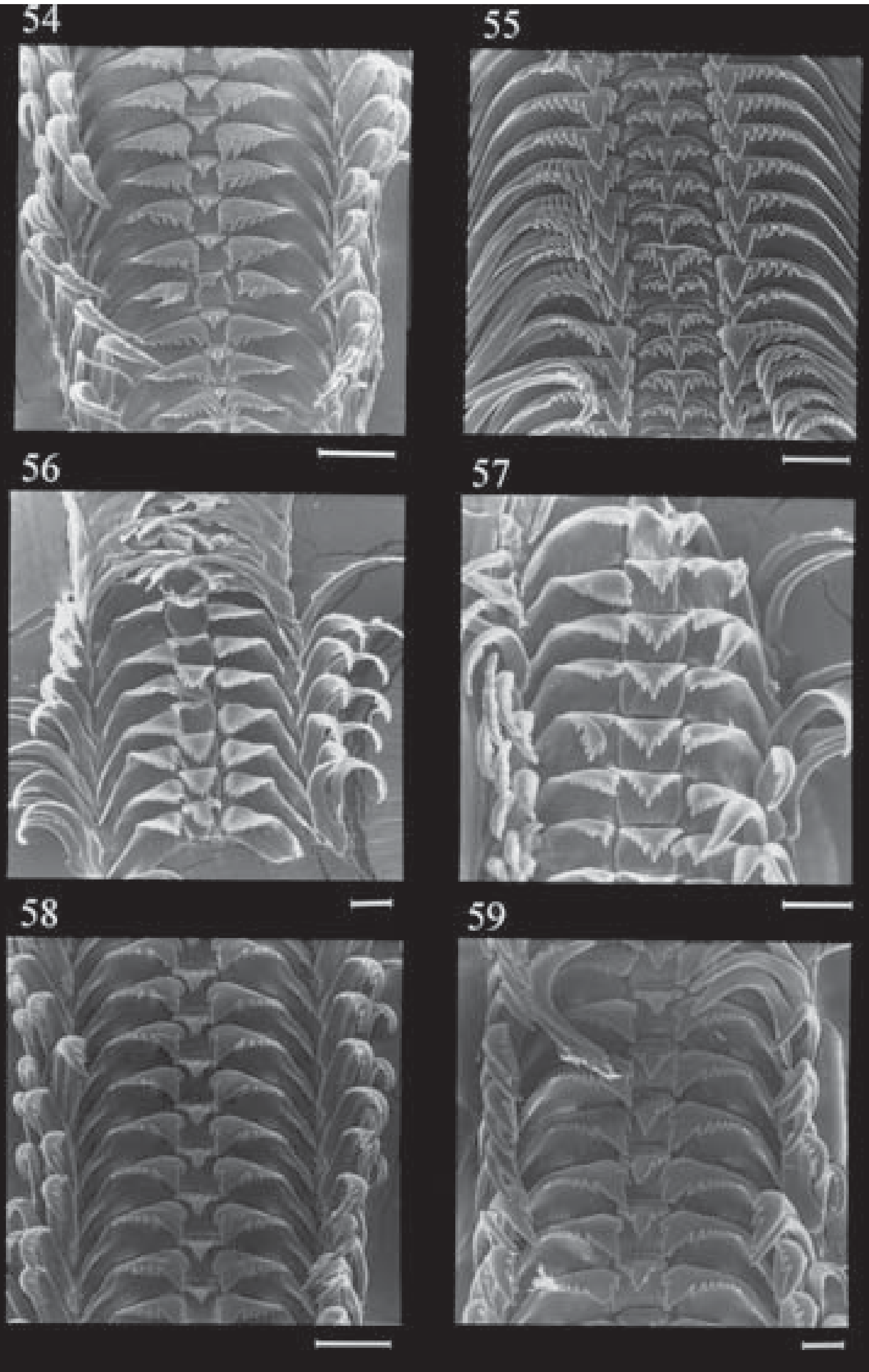

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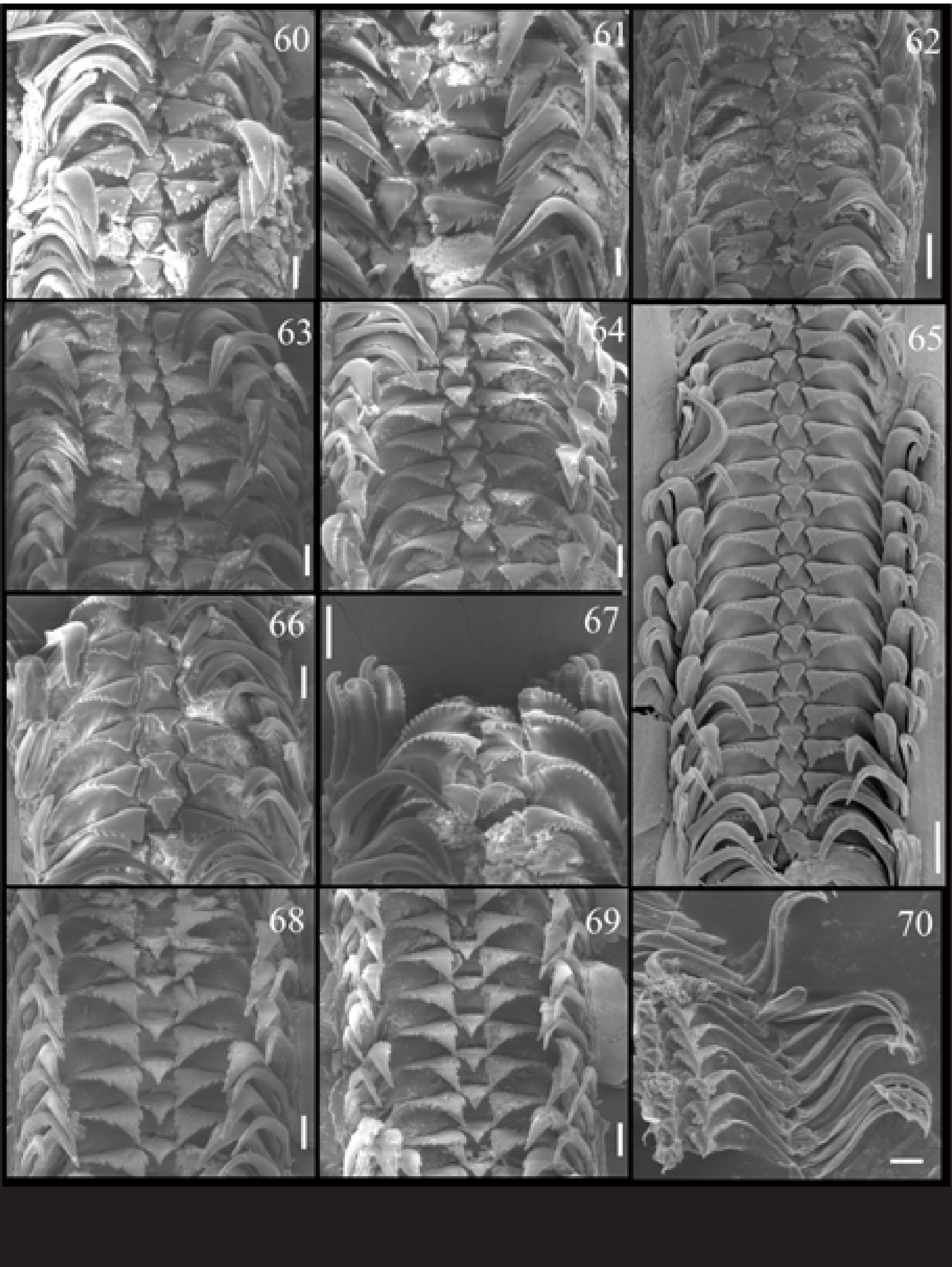

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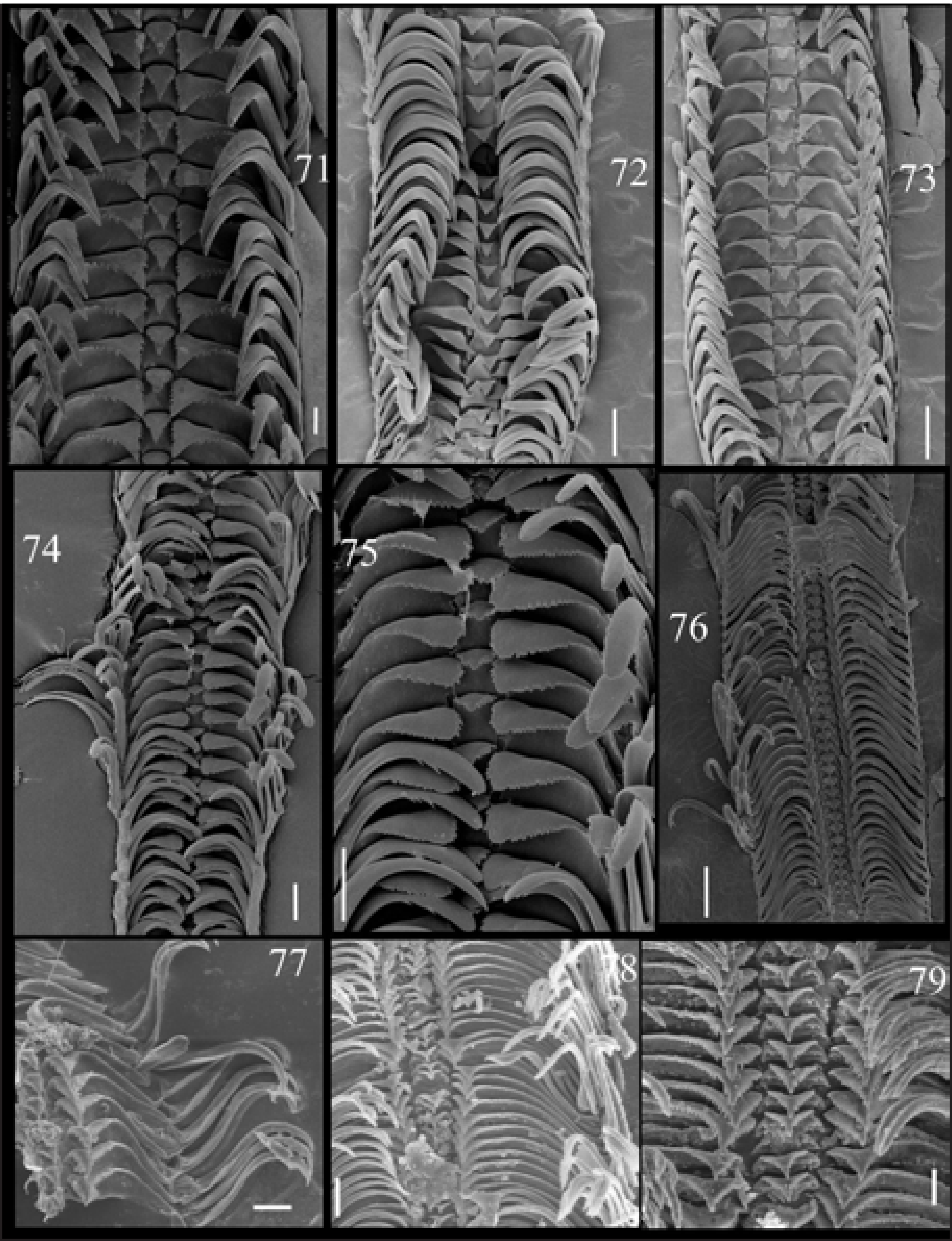

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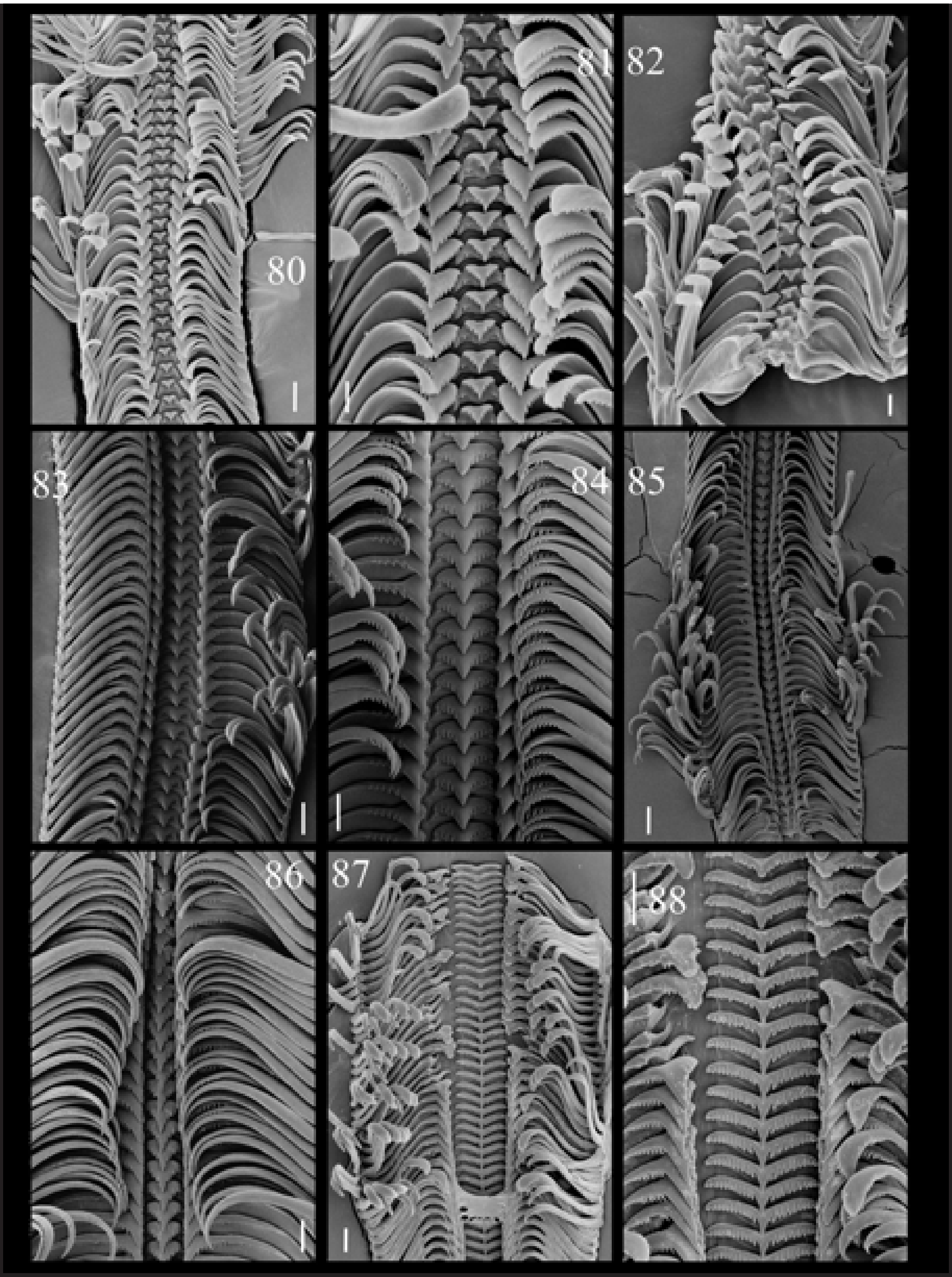

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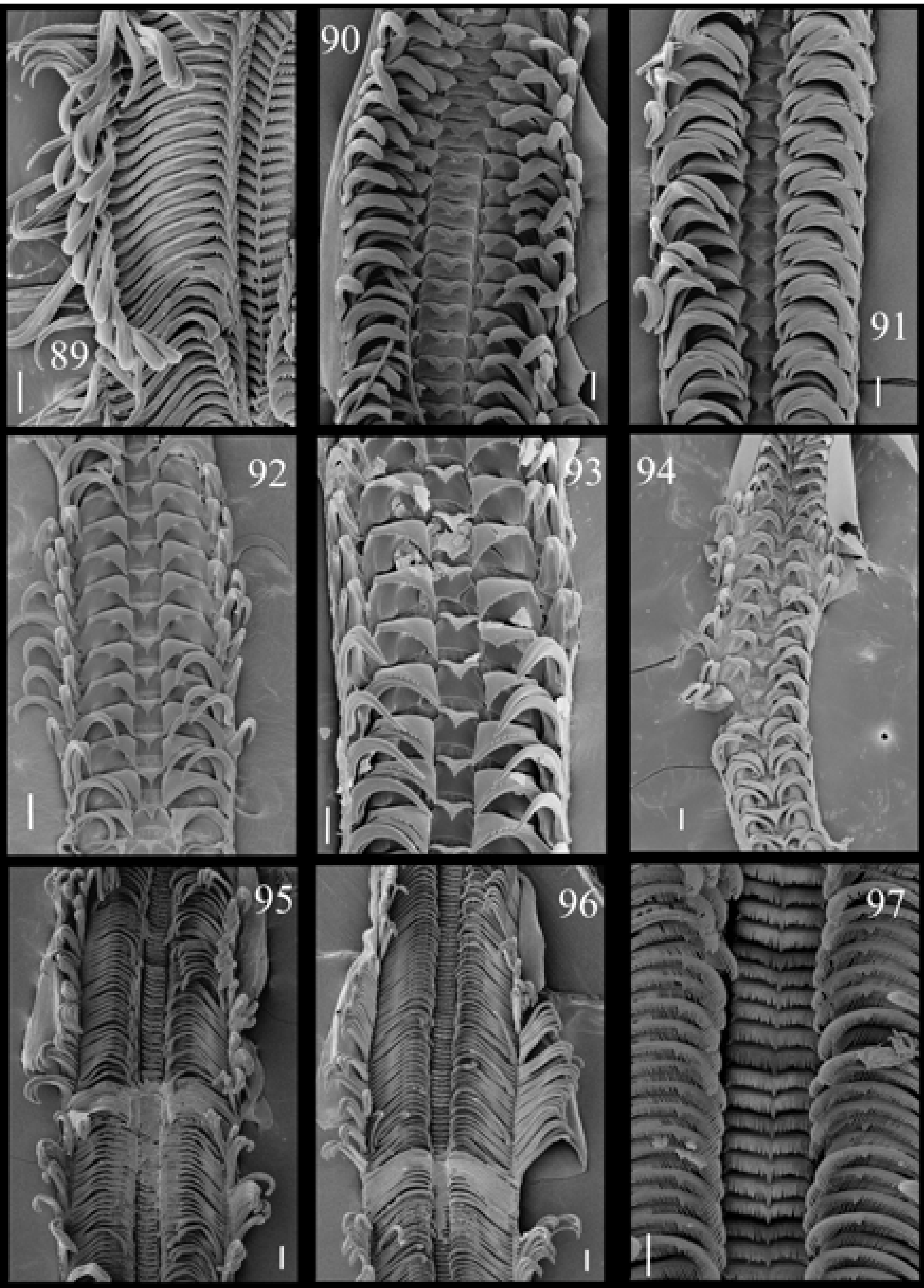

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included in the cladistic analysis. The remaining characters were organized in states, coded, polarized by outgroup comparison, and a cladistic analysis was performed.

The other Caenogastropoda already studied in this project were selected as outgroups. They are mainly the following: Cerithioidea (Simone, 2001); Littorinoidea - Hydrobioidea (Simone & Moracchioli, 1994; Simone 1995c, 1998); Stromboidea (Simone, in press); Cypraeoidea (Simone, submitted); Tonnoidea (Simone, 1995a); Muricoidea (Simone, 1995b on *Thala crassa*; Simone, 1996a on *Buccinanops* spp); Conoidea (Simone, 1999, on Terebridae). As more distant outgroups, some archaeogastropods were also analyzed (e.g., Simone, 1996b; 1997). In the discussion, some specific outgroup taxa are mentioned, based on my own observations or on data from the literature. In the matrix of characters (Fig. 436) only 2 taxa are shown, the ground plan of the Stromboidea and Cypraeoidea (Simone, in press and submitted, respectively). The ground plan of these superfamilies were chosen as being more representative, however, the final result is the same if the ground plan was substituted by anyone of the 49 (terminal) species present in those papers. Two analyses were performed, 1) with the ground plan of the Cerithioidea (Simone, 2001) and a pool of hydrobioidean and archaeogastropod characters as outgroups, which represents an “all zero” row in the data matrix (omitted); and 2) including the ground plan of the Stromboidea and Cypraeoidea operationally as part of the ingroup. The topology of the ingroup cladogram is the same in both analyzes. The distribution of synapomorphies and differences of the indices of both analyses are shown in the Fig. 438. Each character, state, and polarization is justified in the discussion section and, if necessary, a concise explanation is presented.

The discussion of each character is also based on the phylogenetic tree that was obtained (Figs. 437, 438). Although the matrix of characters (Fig. 436) and the subsequent tree (Figs. 437, 438) are shown only in the section following.

The synapomorphies of the ingroup, (superfamily autapomorphies) are preserved in the present paper, because they are the main concern as referred in the introduction. The ingroup autapomorphies are the basis to better establish a still imprecisely defined taxon. They confirm the internal position of some possible “outgroups” such as hipponicoideans and capuloideans. They can be used in the on-going phylogenetic study of the entire order Caenogastropoda as the ground plan of the superfamily (see, additionally, Yeates, 1992 and Pinna, 1996).

Some multistate characters are analyzed here with an additive (ordered) approach. In each case, the additive concept is justified in the discussion and is always based on the ontogeny or on the fact that each state is a clear modification of the preceding one. Additionally, each additive multistate character was also analyzed as non-additive, and any change in the result and/or indices are also reported.

The cladistic analysis was performed with the aid of the computer program “Tree Gardner 2.2” (Ramos, 1997), which works as an interface of Hennig86 (Farris, 1988). The algorithm “ie” was used (which search for all trees). The computer program PAUP was also used, mainly to obtain bootstrap support values for each node. Both programs presented the same result.

Abbreviations: **aa**, anterior aorta; **ab**, auricle region beyond ventricle connection; **ac**, anterior extremity of gill on mantle border; **ad**, adrectal sinus; **af,** afferent gill vessel; **ag**, albumen gland; **an**, anus; **au**, auricle; **bb**, bulged part of br; **bc**, bursa copulatrix; **bg**, buccal ganglion; **bm**, buccal mass; **bs**, blood sinus; **bv**, mantle blood vessel inserting in kidney; **cb**, glandular concavity where capsules attach; **cg**, capsule gland; **cm**, columellar muscle; **cp**, capsules; **cr**, crossing muscles; **cv**, ctenidial vein; **da**, aperture of duct to digestive gland; **dc**, dorsal chamber of buccal mass; **dd**, duct to digestive gland; **df**, dorsal fold of buccal mass; **dg**, digestive gland; **dm**, dorsal shell muscle; **dp**, posterior duct to digestive gland; **ea**, esophageal aperture; **en**, endostyle; **ep**, esophageal pouch; **es**, esophagus; **ey**, eye; **fd**, foot dorsal surface; **fg**, food groove; **fl**, female papilla; **fm**, foot retractor muscle; **fp**, female pore; **fs**, foot (mesopodium) sole; **ft**, foot; **ga**, parietal ganglion; **gc**, cerebral ganglion; **gd**, gonopericardial duct; **ge**, supra-esophageal ganglion; **gf**, gastric fold; **gi**, gill; **gp**, pedal ganglion; **gr**, gill thicker apical region of filament rod; **gs**, gastric shield; **hg**, hypobranchial gland; **hm**, head muscle; **ig**, ingesting gland; **in**, intestine; **ir**, insertion of m4 in “br”; **is**, insertion of m5 in radular sac; **iu**, “U”-shaped loop of intestine on pallial roof; **jw**, jaw; **kc**, kidney chamber; **kd**, dorsal lobe of kidney; **ki**, kidney; **km**, membrane between kidney and pallial cavity; **kv**, ventral lobe of kidney attached to intestine; **ll**, left lateral expansion (flap) of neck; **lm**, lateral shell muscle; m1 to m14, odontophore muscles; **ma**, accessory pair of muscles of jaws; **mb**, mantle border; **mc**, circular muscle (sphincter) of mouth; **mj**, muscles of jaws and mouth; **ml**, mantle region restricting pallial cavity; mo, mouth; **mr**, mantle reinforcement; **ne**, nephrostome; ng, nephridial gland; **nr**, nerve ring; **ns**, neck ventral surface; **oc**, odontophore cartilage; **od**, odontophore; **om**, odontophore superficial ventral membrane; op, operculum; **os**, osphradium; **ov**, pallial oviduct; **oy**, ovary; **pc**, pericardium; **pd**, penis sperm groove; **pe**, penis; **pf**, fold of pedal (mesopodium) sole; **pg**, pedal gland anterior furrow; **pi**, periostracum; **pp**, penis papilla; **pr**, propodium; **pt**, pallial sperm groove; **pv**, pallial cavity; **ra**, radula; **rl**, right lateral expansion (flap) of neck; **rm**, retractor muscle of snout; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **sa**, salivary gland aperture; **sc**, subradular cartilage; **sd**, salivary gland duct; **se**, shell septum or ventral plate; **sf**, satellite fold of osphradium; **sg**, salivary gland; **sh**, ventral surface of shell; **si**, siphon; **sm**, shell muscle; **sn**, snout-proboscis; **sp**, aperture of vas deferens into pallial cavity, **sr**, seminal receptacle; **ss**, style sac; **st**, stomach; **su**, septum between esophagus and odontophore; **sv**, seminal vesicle; **sy**, statocyst; **te**, cephalic tentacle; **tg**, integument; **tm**, net of transversal muscles of haemocoel; **tn**, tentacle nerve; **to**, tissue covering muddle region of radula before its in use part; **ts**, testis, **up**, union between both m5; **vc**, visceral connection with haemocoel; **vd**, vas deferens; **ve**, ventricle; **vg**, vaginal duct; **vm**, visceral mass; **vo**, visceral oviduct; **vs**, seminal receptacles.

Institutional abbreviations: 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; IOUSP, Instituto Oceanográfico da Universidade de São Paulo; LACM, Natural History Museum of Los Angeles County, California, USA; MORG, Museu Oceanográfico da Fundação Universidade de Rio Grande; MZSP, Museu de Zoologia da Universidade de São Paulo, Brazil; RMM, Redpath Museum, McGill University, Montreal, Canada; SMNH, Swedish Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.

Beyond the specimens of the species studied herein, some specimens of other species were also studied, however the material was not good enough for a detailed description. Though, these observations are sometimes included in the descriptions. The material of additional species is the following. *Capulus ungaricus* (Linné, 1767): USA, New Jersey, 39°14’42”N 72°47’18”W, USNM 829771, 1 specimen. *Hipponix pilosus* and *H. panamensis*: MEXICO; Jalisco, Bahia Bandeiras, Las Tres Marietas, 20°42’N 105°35’W, LACM 65-14.27 (part), 5 shells of each. H. cf. pilosus: no locality, RMM 5881, 3 shells. Some data extracted from Malacolog website was also used (Rosenberg, 1996), mainly on depth and distribution of the Western Atlantic species. Most of the data on Australian species (including synonymy and environmental data) may be credited to Peter Middelfart and Winston Ponder at AMS.

SYSTEMATICS

Family Calyptraeidae

Genus *Bostrycapulus* Olsson & Harbison, 1953
(Type species *Patella aculeata* Gmelin)

Bostrycapulus aculeatus (Gmelin, 1791)
(Figs. 1-3, 54, 98-118)

Synonymy in Hoagland (1977: 364). Complement:

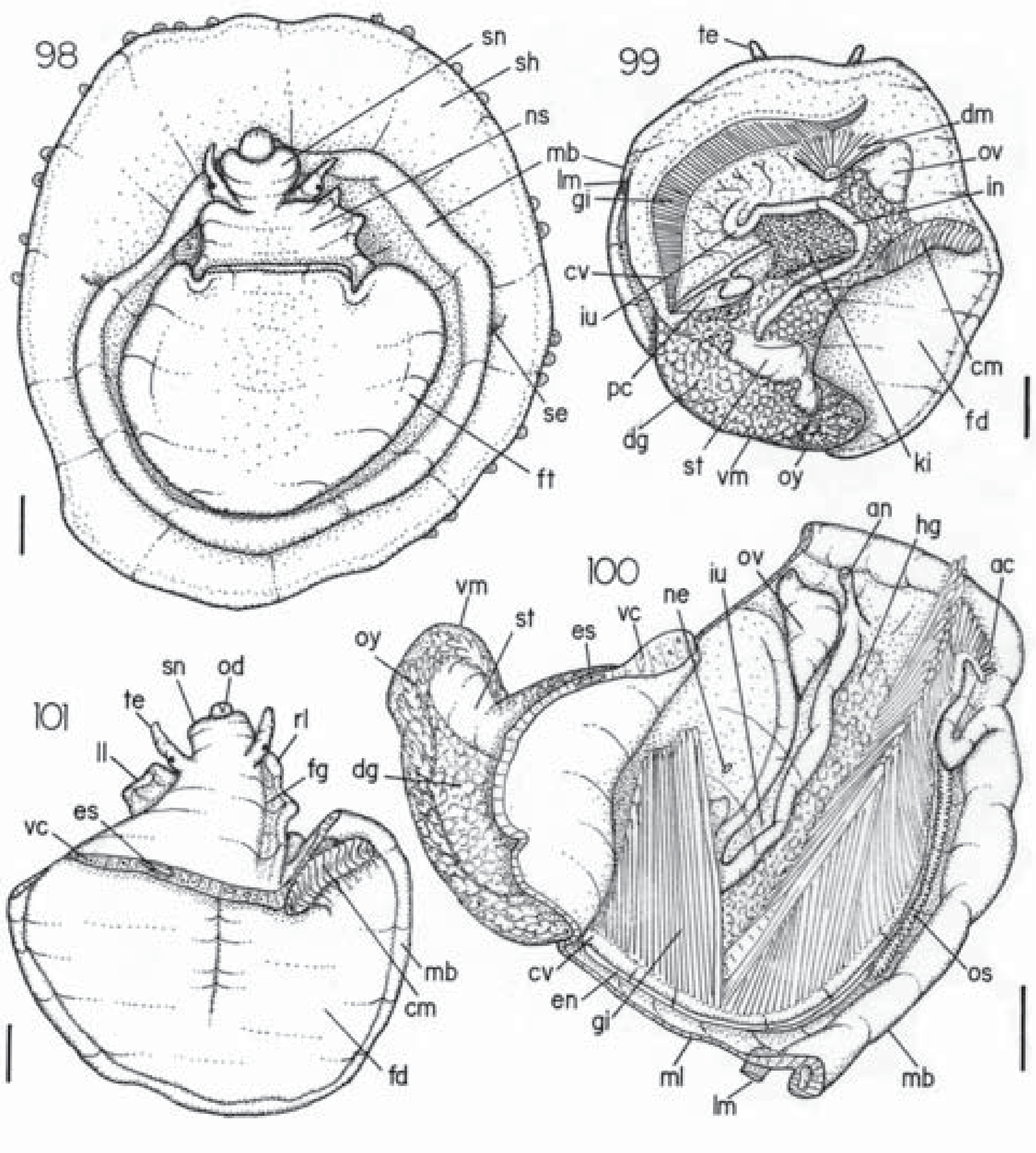
Crepidula aculeata: Morris, 1952: 100 (pl. 128); Abbott, 1954: 171 (pl. 21q); Warmke & Abbott, 1961: 86-87 (pl. 15, fig. i); Fretter & Graham, 1962: 376; Rios, 1970: 55; Keen, 1971: 458 (fig. 808); Rios, 1975: 64 (pl. 17, fig. 258); Hoagland, 1983b: 2, 6, 7; Hoagland, 1984: 607-621 (molecular); Rios, 1985: 59 (pl.21, fig. 266); Calvo, 1987: 97 (fig. 54); Jong & Coomans, 1988: 62; Poppe & Goto, 1991: 115; Rios, 1994: 71 (pl. 24, fig. 271); Merlano & Hegedus, 1994: 161 (pl. 50, fig. 587); Abbott & Morris, 1995: 180 (pl. 49).

Crepidula (Bostrycapulus) aculeata: Olsson & Harbison, 1953: 280; Oliveira et al., 1981: 112.

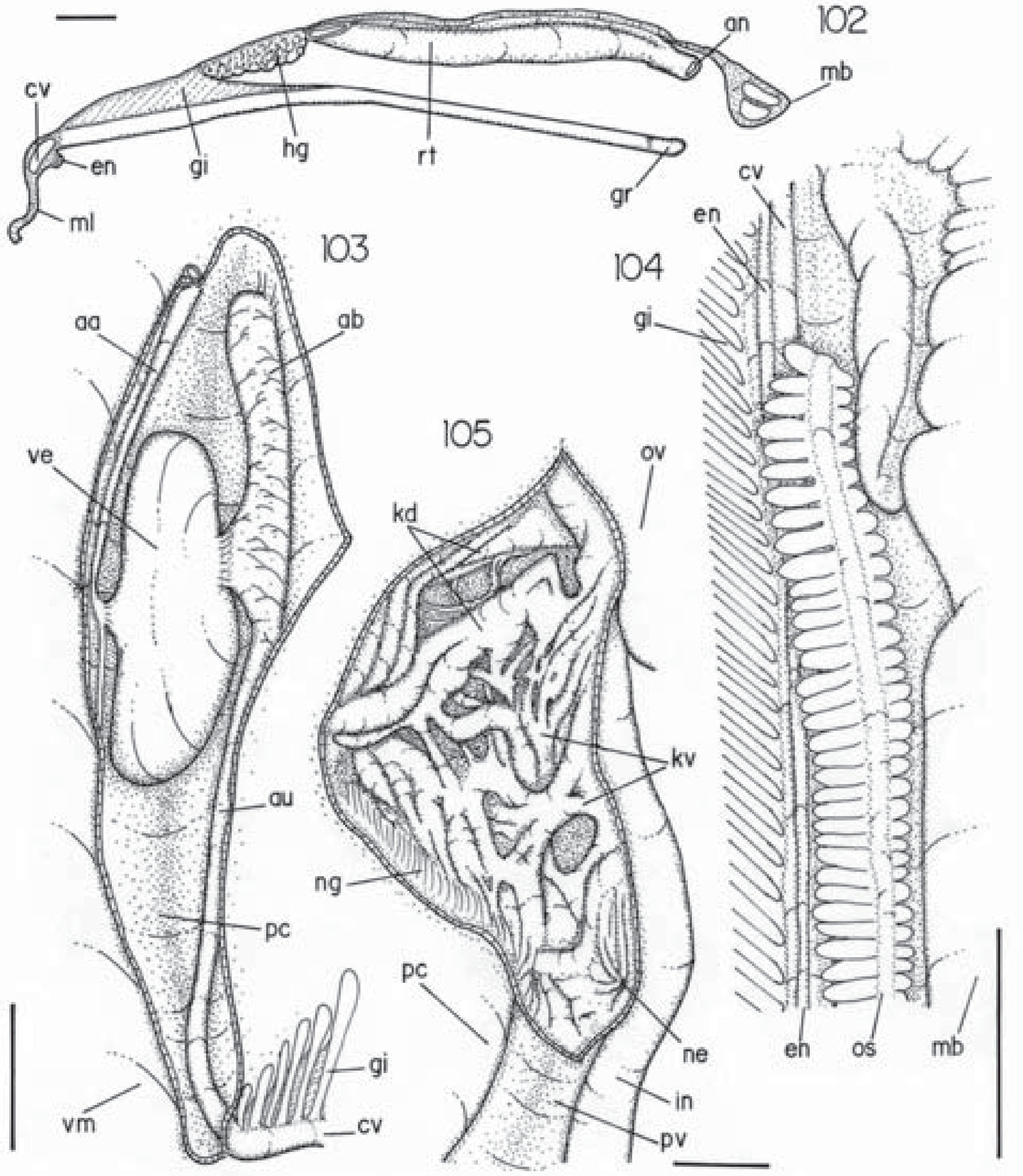
Description.

Shell (Figs. 1-3). Characteristic shell with dorsal surface covered by projected, scale-like spines; however spines presence, distribution and density very variable. Septum as seen in fig. 2. Other details in Hoagland (1977: 365).

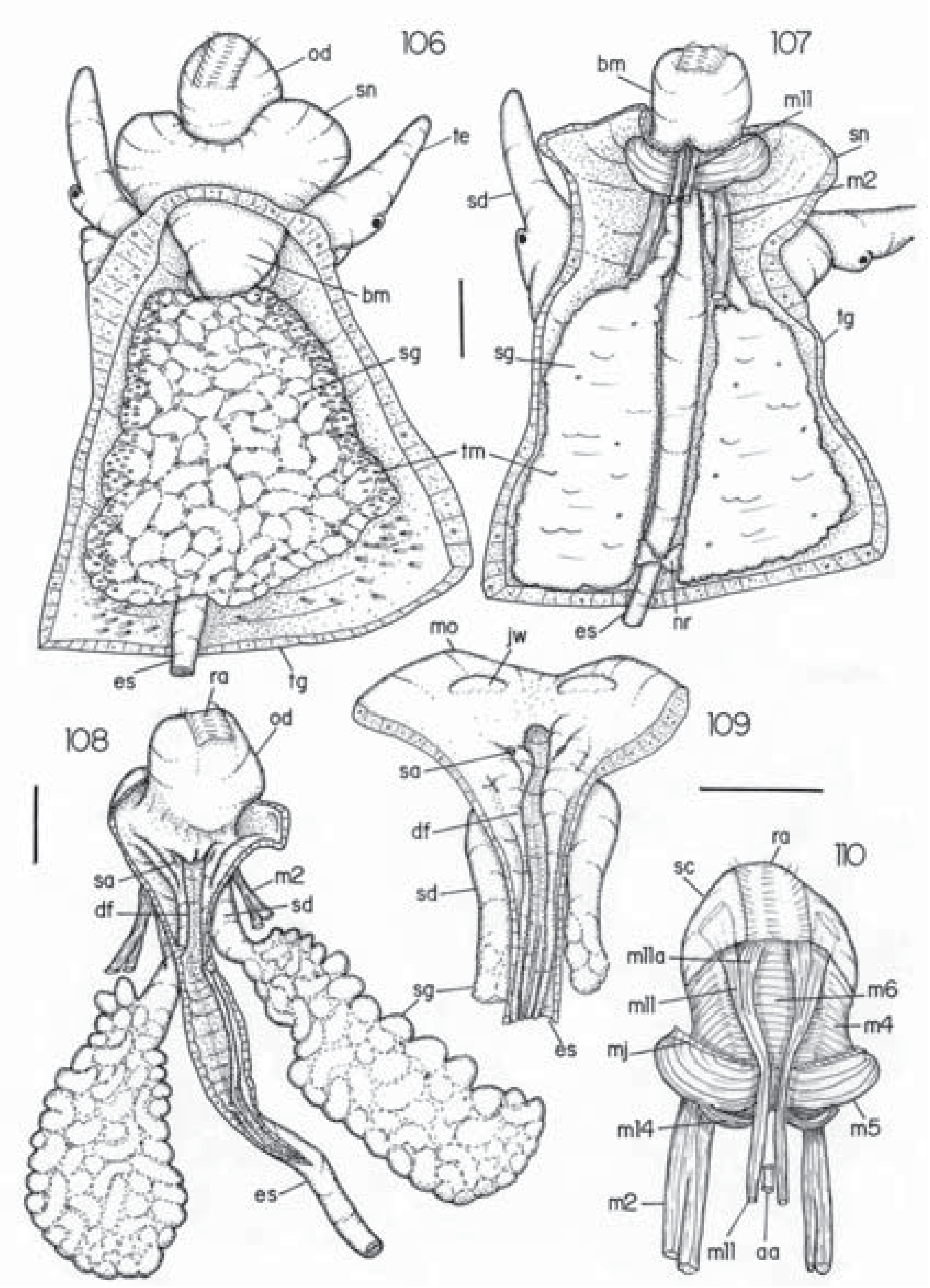
Head-foot (Figs. 98, 101, 106, 107). Head outstanding, preceded by long (about same length as foot), dorso-ventrally flattened, neck-like region (Figs. 98, 101). Snout-proboscis slightly short and cylindrical, with capacity of retraction and partial invagination of about half of this length within haemocoelic cavity (Figs. 106-108). Tentacles long, stubby, with basal half clearly broader than distal half. Eyes dark, located on small ommatophores half-way along tentacle’s lateral margin, just where they narrow. Neck-like region with pair of lateral, flattened lappets (nuchal lobes); left expansion narrower than right expansion; right expansion brings low food groove along its dorsal limit with head; sperm groove of males (described below) run externally along food groove (Fig. 101). Ventral surface of neck-like region forming additional, anterior sole, which also contacts substrate (Fig. 98). Foot very ample (occupies about ¾ of shell ventral surface), dorso-ventrally greatly flattened; shell septum as dorsal foot limit. Mantle fuses with dorsal surface of foot and protrudes beyond its borders. Furrow of pedal glands transversal, in anterior margin of foot; this anterior margin of foot covers ventrally posterior region of neck ventral surface (Fig. 98). Columellar muscle reduced, contours anterior border of shell septum, more concentrated at right (Fig. 101); in this right region keeps small scar in shell (Fig. 2). Inner haemocoel cavity narrow, running approximately in



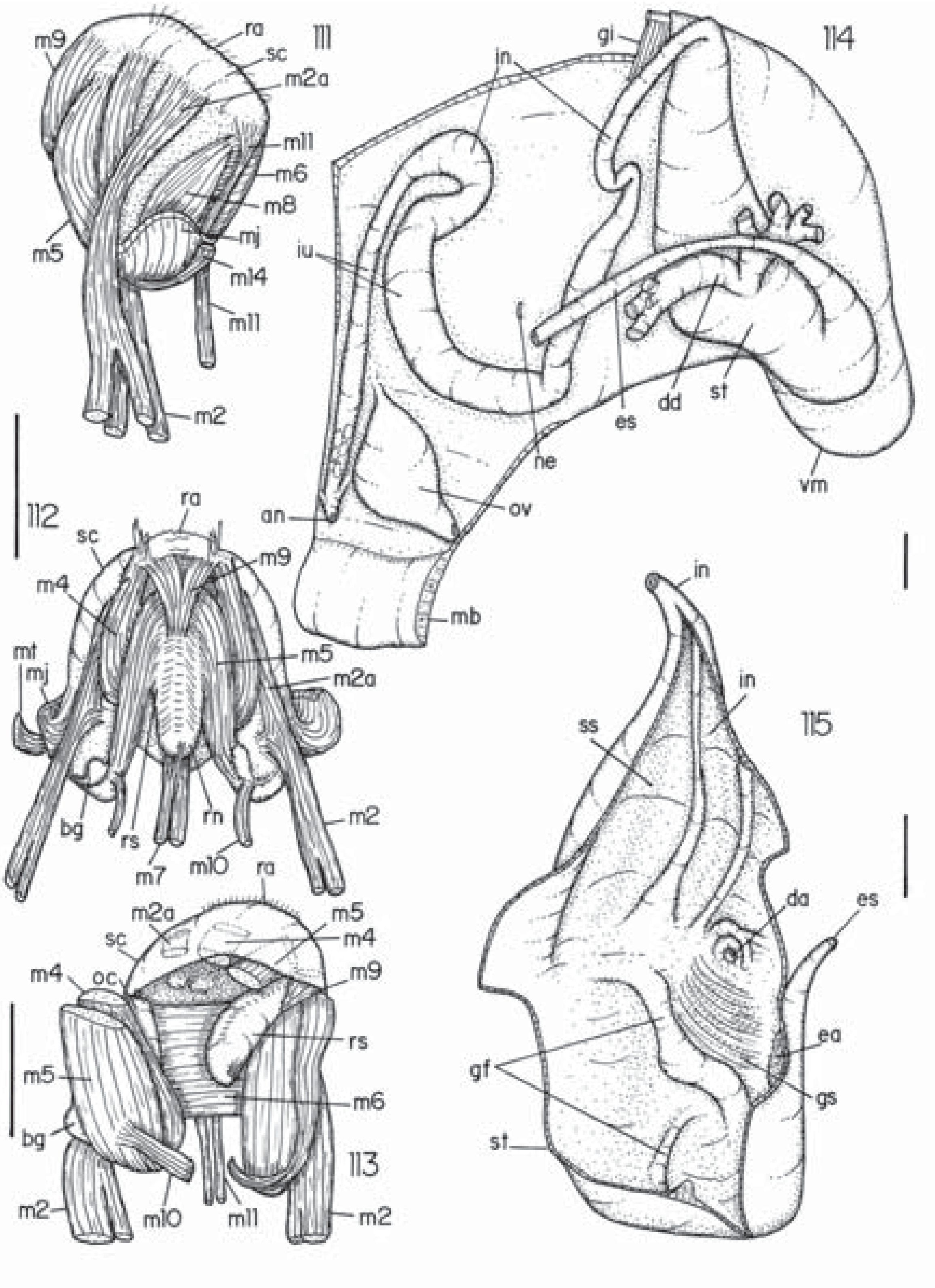
Figures 98-101, *Bostrycapulus aculeatus* anatomy: **98**, whole female, ventral view; **99**, female extracted from shell, dorsal view; **100**, pallial cavity and visceral mass, ventral view, anterior-ventral region of visceral mass deflected for exposure of whole pallial cavity; **101**, head-foot, female, dorsal view, visceral mass and pallial organs extracted. Scales = 2 mm.



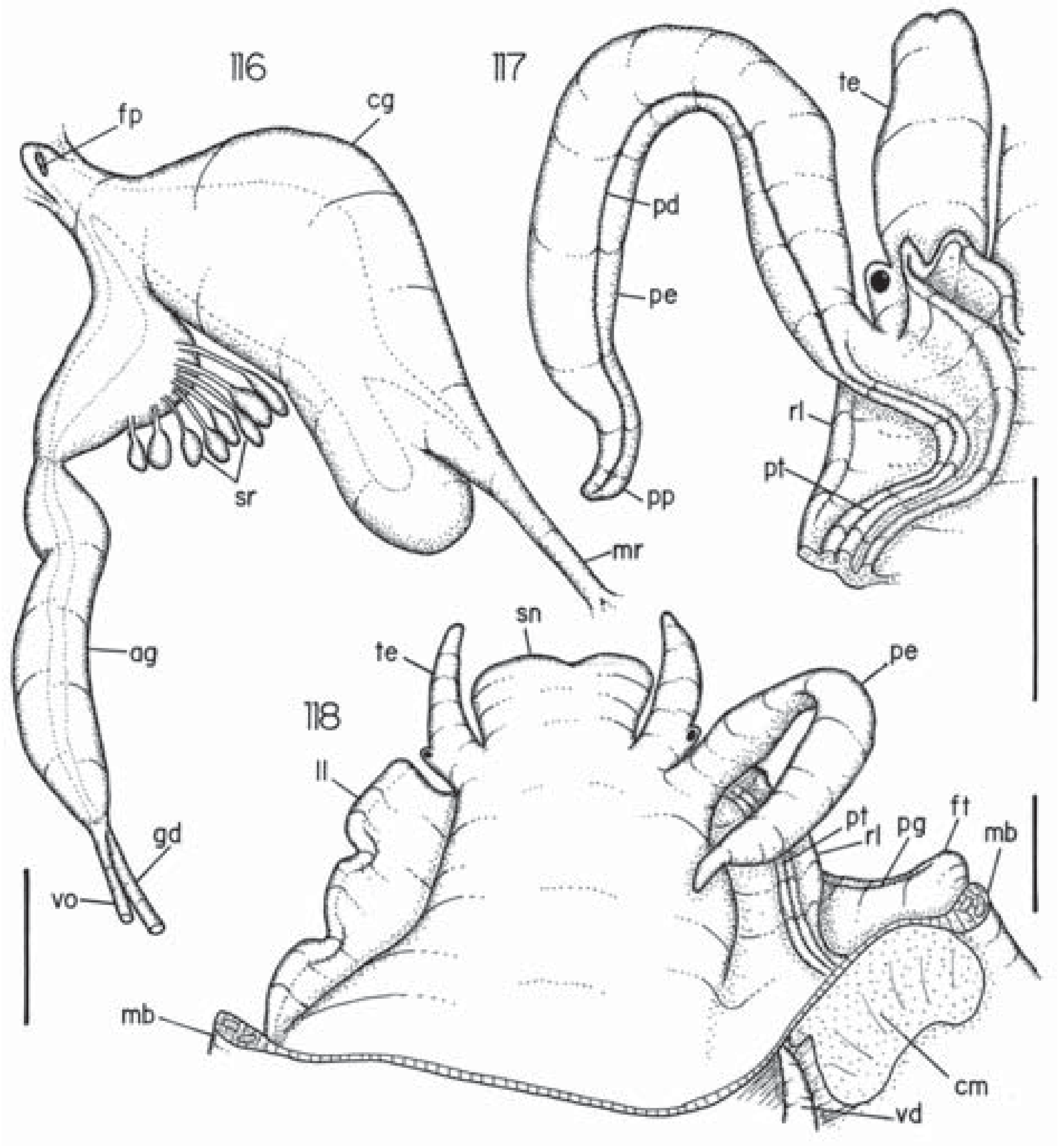
Figures 102-105, *Bostrycapulus aculeatus* anatomy: **102**, pallial cavity roof, transversal section in its middle portion, just parallel to rectum; **103**, pericardium, ventral view, ventral pericardium wall removed to show inner structures; **104**, pallial cavity, detail just in right region of osphradium; **105**, kidney and adjacent structures, ventral renal wall part removed and part deflected to right with inner surface exposed. Scales = 1 mm.



Figures 106-110, *Bostrycapulus aculeatus* anatomy: **106**, head and haemocoel, ventral view, foot and neck ventral surface removed; **107**, same, snout opened ventrally with its walls deflected, ventral portion of salivary glands and net of transversal muscles extracted for exposure of esophagus; **108**, foregut, ventral view, buccal mass and anterior esophagus opened longitudinally; **109**, dorsal wall of buccal mass, ventral view, odontophore and septum between it and esophagus removed; **110**; odontophore, dorsal view. Scales = 1 mm.



Figures 111-115, *Bostrycapulus aculeatus* anatomy: **111**, odontophore, lateral-left view; **112**, same, ventral view, most of muscles deflected laterally; **113**, same, right muscles (left in fig.) deflected to exposure of dorsal structures, radular sac and cartilage in lateral view; **114**, digestive tubes, ventral view, seen if all other structure were transparent, part of adjacent pallial cavity roof also shown; **115**, stomach, ventral view, inner surface exposed by a middle longitudinal incision. Scales = 1 mm.



Figures 116-118, *Bostrycapulus aculeatus* anatomy: **116**, pallial oviduct, ventral view; **117**, penis and adjacent structures of head-foot, ventral view; **118**, head-foot, anterior region of male, dorsal view, visceral mass and pallial organs removed. Scales = 1 mm.

center of neck region. Inner space almost all filled by salivary glands (described below) and great quantity of transversal, very slender muscular fibers; these fibers connect ventral surface of dorsal haemocoel wall with dorsal surface of its ventral wall, inclusive through salivary glands (Figs. 106, 107). No vestiges of operculum even in very young specimens.

Mantle organs (Figs. 99, 100, 102, 104). Mantle border very thick, slight hollow due to calibrous collar sinus (Fig. 102). Mantle border surrounds entire shell ventral margin, free in anterior half and attached to foot borders in posterior half. Mantle border without appendages, but entirely edged by series of minute repugnatorial glands; these glands are elliptical in form with a small duct turned externally; side by side with each other, sub-terminally in mantle edge (see fig. 164 of *C. fornicata*). Mantle border with special arrangement of folds in middle region of pallial cavity aperture, broad furrow beginning in gill anterior extremity, runs towards left and finishes about in right third part of osphradium level (Fig. 104). Dorsal shell muscle well developed (Fig. 99: dm), origin small, in about middle-right region of shell, just anterior to septum; fibers run anteriorly, fan-like, insertion in adjacent anterior region of dorsal surface of pallial cavity. Lateral shell muscle (Figs. 99, 100: lm) small, fan-like, located close to mantle border right side, just in region where pallial cavity penetrates shell septum chamber. Pallial cavity aperture occupies about 2/3 of anterior half of shell border turned to right (if shell compared with a clock, in dorsal view and with head occupying 12 hour, pallial aperture begins at 10 and finishes at 3 o'clock) (Fig. 98). Pallial cavity deep, broad, triangular, arched and dorso-ventrally flattened. Anterior extremity of pallial cavity slightly larger than its aperture because of closure at left and right extremities produced by fusion of mantle and foot. Gradually, pallial cavity narrows towards posterior, penetrating at left of visceral mass (described below); cavity length about 2/3 of total length of animal (Figs. 99, 100). Osphradium long, bipectinate, located between anterior half of gill and mantle border, occupying about middle region of pallial aperture somewhat perpendicular to longitudinal axis of animal body (Figs. 100, 104). Osphradium length little more than 1/3 of pallial aperture length, slightly flattened dorso-ventrally, attached to mantle separated from gill structures. Osphradium leaflets rounded, somewhat thick, right (posterior) leaflets longer than left (anterior) leaflets; right leaflets cover partially adjacent region of ctenidial vein (Fig. 104). Osphradium ganglion broad. Gill very large, its base somewhat narrow, edging anterior and left margin of pallial cavity almost its entire length; anterior gill extremity in right-anterior region of pallial cavity aperture, near to its right limit, on thick mantle border; gill posterior extremity in posterior end of pallial cavity (Fig. 100). Gill filaments triangular at their base, with very long, almost straight, stiff rod turned to right (Fig. 102); rods extend about twice length of their triangular, membranous base; these rods begin in ctenidial vein region, in left margin of cavity roof and touch food groove of head-foot in right margin of cavity floor; rod apex rounded and preceded by thicker region. Gill filaments connected to each other with cilia, mainly of their thicker apical region, maintained in somewhat firm position. Gill filaments longer in central gill region, shortening gradually in both extremities; gill anterior extremity, with short filaments, suddenly turns forwards, located on mantle border (Fig. 100). Ctenidial vein calibrous, with uniform width along its length. Endostyle well-developed (Figs. 100, 102: en), yellowish, somewhat narrow glandular ridge located in middle level of ventral surface of ctenidial vein all along its length. Hypobranchial gland whitish, slightly developed, with oblique superficial furrows; occupies surface between gill and visceral mass. About 1/3 of visceral mass encroaches in pallial cavity roof (Figs. 99, 100), occupying about 1/3 of this area in posterior-right region; pericardium and kidney posteriorly; a long intestinal loop, anus and pallial oviduct anteriorly (described below).

Visceral mass (Figs. 99, 100) A dorso-ventrally flattened cone introduced in shell chamber produced by septum (Fig. 2); this thin calcareous septum separates visceral mass from dorsal surface of foot. Left and anterior region of visceral mass region occupied by pallial cavity. Remaining regions of visceral mass with stomach as central structure, immediately surrounded by digestive gland (except in some ventral and dorsal areas). Gonad surrounds digestive gland externally. All structures described with more details below. Visceral mass still encroaches right-posterior region of pallial cavity roof as described above, and possesses another ventral flap in pallial cavity floor. Anterior extremity of visceral mass ventral flap just in shell septum anterior border, covering columellar muscle (Fig. 100).

Circulatory and excretory systems (Figs. 99, 103, 105). Pericardium very long, somewhat perpendicular to longitudinal axis of animal (Fig. 99); begins very narrow, just in posterior extremity of gill, in posterior-left end of pallial cavity; runs edging anterior margin of visceral mass part encroached in pallial roof, gradually enlarges; finishes in about middle level of this region of visceral mass, near to median line. Pericardium limits: 1) anterior and ventral the pallial cavity; 2) posterior the visceral mass (gonad generally); 3) dorsal the mantle and 4) right the kidney. Auricle thin walled and very long, runs all along pericardium length attached to its anterior and dorsal inner surfaces (Fig. 103); connects with ventricle approximately between its middle and right third parts; auricle has, then, broad portion beyond ventricle connection as blind sac (Fig. 103: ab). Ventricle elliptical, very muscular; its connection with auricle located about in middle region of its anterior surface; origin of aortas in opposite side. Anterior aorta broader and running towards opposite side than posterior aorta. Anterior aorta runs towards right, edging posterior inner pericardium surface; afterwards penetrates head haemocoel. Kidney well developed, occupying about half area of visceral mass within pallial cavity (Figs. 99-100). Kidney limits: 1) dorsal mantle; 2) ventral and lateral-left pallial cavity; 3) posterior-right visceral mass (gonad generally); 4) posterior-left pericardium; 5) anterior intestinal loop; 6) lateral-right intestine and oviduct (when present). Kidney mostly hollow, with pair of very irregular lobes (Fig. 105). Ventral lobe with about four transverse folds attached to right half of posterior renal wall. Dorsal lobe larger, occupying most of dorsal and lateral surfaces; bears several irregular, anastomozed folds; these folds in general towards adjacent intestinal loop, where there are several transversal folds; part also covers ventral surface around nephrostome. Nephridial gland in renal limit with pericardium, presents series of transversal, narrow folds connected with dorsal renal lobe (Fig. 105: ng). Nephrostome a very small slit in left region of ventral wall (Fig. 100).

Digestive system (Figs. 106-114). Snout-proboscis short and broad, with partial capacity of retraction inside haemocoel in small rhynchocoel (Figs. 106-108). Pair of narrow ventral proboscis retractor muscle immerse in proboscis wall. Mouth longitudinal, in center of anterior proboscis surface. Buccal mass very large, occupying most of proboscis inner space. Buccal mass with total protraction and invagination capacity. Jaw plates in dorsal wall of buccal mass, thin, broad laterally, short longitudinally (Fig. 109). Pair of dorsal folds broad and tall, begin posterior to jaws; dorsal chamber between both folds slight deep. Odontophore somewhat large, most of buccal mass volume. Odontophore muscles (Figs. 110-113): **m1**) jugal muscles, several very narrow muscles connecting buccal mass with adjacent wall of snout, more concentrated anteriorly around mouth; **m1a**) pair of dorsal protractor muscles, narrow, thin and superficial, origin in anterior-dorsal region of mouth, close to median line, insertion in posterior-dorsal-lateral region of odontophore; **m2**) pair of retractor muscle of buccal mass (retractor of pharynx), broad, origin in lateral-ventral region of haemocoel just posterior to snout, run towards anterior, insertion in lateral-posterior-dorsal region of odontophore cartilages; **m2a**) pair of dorsal tensor muscles of radula, continuation of m2 after insertion in cartilages, run towards anterior, insertion in subradular cartilage in middle region of its dorsal inner surface; **mt**) dorsal transversal muscle or ventral approximator muscle of cartilages, connects dorsally both posterior-dorsal-lateral surfaces of cartilages, lies between superficial membrane which covers odontophore and tissue on middle region of radula (to); **m4**) pair of median dorsal tensor muscle of radula, very large and thick, origin in ventral-middle-posterior region of odontophore cartilages, run towards medial, contours medial-ventral surface of cartilages, run on their dorsal surface, insertion in subradular cartilage dorsal-posterior-medial extremities; **m5**) pair of median radular tensor muscle, thick, origin in median-posterior-dorsal region of odontophore cartilages, just by side of m2 insertion and m2a origin, cover perpendicularly m4 middle region, run towards medial, insertion along radular sac on both sides (each m5 branch covers a side of radular sac, medially and dorsally); **m6**) horizontal muscle, very thin, unites anterior half of odontophore cartilages, inserting on their dorsal margin; **m7**) pair of ventral tensor muscle of radula, thin and narrow, origin in haemocoel ventral inner surface in level just posterior to buccal mass, close to median line, run towards anterior penetrating in membrane which covers ventral surface of odontophore, gradually increase like thin fan, insertion in median level of subradular cartilage ventral surface (not in its border); **m7a**) secondary medial branch of m5 inserted just in radula ventral border; **m8**) pair of strong muscles origin in posterior-dorsal-lateral region of odontophore cartilages just by side of insertion of m2, run attached to dorsal margin of odontophore cartilages, insert in their anterior-dorsal region close to horizontal muscle (m6); **m9**) pair of dorsal-medial tensor muscle of radula, broad and thin, origin along dorsal-median surface of radular sac (in its region internal to odontophore), cross to dorsal surface, insert in dorsal-ventral border of subradular cartilage; **mj**) jaws and peribuccal muscles, somewhat thick, surround lateral and dorsal wall of buccal mass, origin around mouth, insertion in middle level of lateral and dorsal wall of odontophore; **m11**) small impair muscle, origin in middle-ventral region of mouth, runs towards posterior in median line, insertion ventral in radula (within radular sac) like fan in region anterior to radular nucleus; **m14**) pair broad and thin, origin in posterior-dorsal region of odontophore, close to m2 and m5 origins, runs towards ventral and anterior, insertion in snout inner ventral surface in about middle level of odontophore; **to**) tissue covering middle region of radula within odontophore, in its dorsal surface. Radula short, little more than odontophore length.

Radula (Fig. 54): **rachidian** tooth tall, narrow, central cusp large and sharp pointed , secondary cusps vary from two to three pairs decreasing towards lateral, no basal cusps but pair of lateral reinforcements on its borders; **lateral tooth** broad, curved internally, with about eight triangular inner cusps, second cusp larger, apical, turned towards median, cusps decrease towards lateral, disappear about in middle region of tooth, remainder a slight thick border; **marginal teeth** long, curved, tall, pointed tip, about six cusps in their inner-apical margin; inner marginal tooth with about double width than outer marginal tooth. Pair of buccal ganglion large, close to each other near median line (Fig. 112), located between buccal mass and adjacent esophagus. Salivary glands very large, branched, occupy most of inner space of haemocoel, clustering around esophagus (Figs. 106-108). Several narrow transversal muscles unite internally dorsal and ventral surfaces of haemocoel, passing through salivary glands (tm). Salivary glands posterior limit close to visceral mass; neither pass through nerve ring. Ducts of salivary glands broad, run in dorsal surface of buccal mass, penetrate in adjacent buccal mass wall in very short distance, apertures small in anterior region of dorsal folds of buccal mass (Figs. 108, 109).

Esophagus (Figs. 107-109) narrow and long; anterior esophagus inner surface with pair of broad folds. Middle esophagus with pair of narrow folds (continuation from those of anterior esophagus) and slight broad glandular chamber. Posterior esophagus inner surface with only 4-5 longitudinal, narrow, similar sized folds. Stomach (Figs. 114, 115) slight conical, large, occupying about half of visceral mass size; esophagus inserts in left side of its posterior region, close to shell apex. Duct to digestive gland about in middle region of stomach ventral surface; highly branched. Stomach gradually narrowing towards anterior and left, arriving close to left-posterior extremity of pallial cavity. Stomach inner surface (Fig. 115) with pair of broad (laterally) and short (longitudinally) folds, both posterior to esophagus insertion and disposed slightly orthogonal to each other. Among a fold, esophagus insertion and digestive gland aperture a series of very narrow, transversal folds marking somewhat elliptical gastric shield. Anterior half of stomach with pair of slight tall, longitudinal folds; anterior region between both folds smaller than anterior region; former region as intestinal branch of stomach; broader (posterior) region as style sac, but without preserved crystalline style. Digestive gland pale brown in color, surrounds stomach except some areas in dorsal and ventral surfaces.

Intestine narrow and sinuous (Figs. 99, 100, 114); runs in anterior border of visceral mass from left to right, initially in its ventral region. Near median line it crosses to dorsal region and runs up to right-anterior extremity of visceral mass (Fig. 114). In this region it runs towards left and becomes broader, surrounds right and anterior border of kidney, suddenly runs towards right and runs parallel to preceding loop. Anus small, siphoned, located in right region of pallial cavity close to mantle border. Intestine distal loops replete of several somewhat small, elliptical fecal pellets.

Genital system. **Development**. Protandric hermaphrodite, most of small specimens, up to 9 mm, males. However some small specimens apparently develop to female without male phase. Other details in Hoagland (1983, 1986).

Male (Figs. 117, 118). Only small specimens are male (up to 6 or 7 mm). Testis orange in color, located in anterior region of visceral mass. Seminal vesicle convoluted, brown in color, located in anterior-right extremity of visceral mass, gradually narrows and becomes very slender tube that opens in right-posterior-ventral region of pallial cavity. A shallow groove runs from this aperture to penis base, in pallial floor near right margin of head. Sperm groove more clear and deep anteriorly. Penis long (about twice tentacle length), curved; suddenly narrows before tip producing papilla about half width of penis. Penis duct opened (groove), runs in middle region of penis ventral surface until papilla tip.

Female (Fig. 116). Ovary pale brown, surrounds digestive gland, more concentrated in anterior region of visceral mass. Visceral oviduct very narrow, runs from left to right in anterior border of visceral mass. Gonopericardial duct well-developed, slightly broader than visceral oviduct; origin in right-ventral extremity of pericardium, runs ventral to visceral glands encroached in pallial cavity, inserts in posterior extremity of pallial oviduct jointed with insertion of visceral oviduct. Pallial oviduct relatively small, located in right-anterior end of pallial cavity (Figs. 99-100). Albumen gland long, slight broad, whitish, walls thick glandular; located in anterior-right extremity of visceral mass. Capsule gland with two branches. First branch (cd1) as continuation of albumen gland, marked by constriction and sudden increase of its walls; in posterior surface of this branch of capsule gland, a series of about eight impair vesicular seminal receptacles, which increase towards anterior. Each vesicle with elliptical tip and long, slender, cylindrical duct. Second branch of capsule gland (cd2) very larger, a blind-sac with thick glandular, irregular walls; inner lumen broad, dorso-ventrally flattened. Both branches of capsule gland converge to genital pore located in right extremity of pallial cavity, close to mantle border and right of anus. Genital pore in form of small, short papilla. Other details in Hoagland (1986, fig. 3).

Nervous system. Similar as described for following species.

Habitat. Almost sessile, under rocks, corals and other hard substrates, from intertidal to 46 m depth.

Distribution. From North Carolina to Argentina. Is referred also as worldwide, certainly by anthropogenic dispersion.

Measurements of shells (in mm). MZSP 28672 ♀1, 23.3 by 6.2; ♀2, 21.9 by 5.4; MZSP 30812,♀, 28.0 by 6.7; MZSP 30814,♂, 9.1 by 4.2.

Material examined. SPAIN; **Alicante**, Alicante Harbor, Mediterranean Sea, 38 specimens, ANSP A10151 (04/iv/1981, Ex. K.E. Hoagland, H. Zibrowius). UNITED STATES OF AMERICA; **Hawaii**, Oahu, Honolulu Harbor, MZSP 29201, 10 specimens (ix/1997, R. DeFelice & S. Coles col., F. Moretzsohn leg.). BRAZIL; **Bahia**; Salvador; Ribeira beach, MZSP 28494, 5 specimens (Simone col., 24-25/ii/1997), Banco da Panela, 16-20 m depth, MZSP 28455, 10 specimens (Simone col., 26/ii/1997); **Rio de Janeiro**; Angra dos Reis, MZSP 30812, 12 specimens (sta. 132, 12/v/1966); **São Paulo**; Ubatuba, 23°25'S 44°52'W, 21 m depth, MZSP 30814, 11 specimens (sta. 27, o.t., 21/iv/1986), 23°45'S 45°00'W, 46 m depth, MZSP 30813, 14 specimens (sta. 11, 20/iv/1986); São Sebastião, Barequeçaba beach, MZSP 28608, 3 specimens (Simone col., 16/v/1997), MZSP 28672, 3 specimens (Simone col., 26/x/1996). AUSTRALIA; **New South Wales**, Sydney Harbor, 33º51'S 151º13'E, ANSP A11991, 13 specimens (28/i/1971, W.F. Ponder col.). R. V. W. Besnard sta. 414, 50 m depth, MORG 18033a, 1 female without spines (1/xi/1968).

Discussion. Specimens of *B. aculeatus* are extremely sedentary, as many other calyptraeids, they do not move to eat (they are filter feeders), for copulation (protandric hermaphrodites), nor to lay eggs (they brood). However, the species is distributed worldwide in the tropics (Hoagland, 1977: 365), and subtropics. To examine these apparently incongruent data, specimens from several parts of the species distribution were selected for comparative anatomical study. Despite some small differences, the separation of the samples in specific level was not possible, at least based on morphology. Having as base the Brazilian specimens, the specimens from Australia (ANSP A11991) generally have males possessing broader, longer and flattened penis; those from Hawaii (MZSP 29201) generally have "V"-shaped, concave shell septum border and shorter stomach; and those from Spain (ANSP A10151) generally have deeper shell without spines and some specimens possess narrow posterior duct to digestive gland from stomach. However no character was constant in all specimens of the lot, and these are thus regarded as examples of intraspecific variation. It is interesting to note that all specimens found in other places but Western Atlantic were found close to harbors, which suggests anthropogenic introduction. Several anomalies were found in some specimens from these localities. There were several functional females with long penises, the anterior duct to digestive gland in stomach present and a specimen (MZSP 29201) with a monopectinate osphradium.

B. aculeatus has natural affinity with the *Crepidula* species, and could be maintained in this genus, however, based on the quantity of morphological differences found and the availability of a generic taxon, the revalidation of *Bostrycapulus* is preferred. The authors of the genus (described as a subgenus of *Crepidula*), Olsson & Harbison (1953: 279-280), explored well the conchological attributes of *Bostrycapulus* among the remainder subgenera of *Crepidula*. The present study adds to the list of characters 1) the bipectinate osphradium, 2) the lack of posterior duct to digestive gland in stomach and 3) the different fashion of the pallial oviduct.

Genus *Crepidula* Lamarck, 1799
(Type: *Patella fornicata* Linné, 1758)

Crepidula aff. *plana*,1822

(Figs. 4, 7, 60-62, 119-140)

Synonymy part in Hoagland (1977: 389). Complement:

Crepidula plana: Hoagland, 1984: 607-621 (molecular) (part); Rios, 1985: 59 (pl. 21, fig. 267); 1994: 71 (pl. 24, fig. 272) [non Say, 1822].

Crepidula (Ianacus) plana: Rios, 1970: 56; 1975: 65 (pl. 17, fig. 260); Oliveira et al., 1981: 112 [non Say, 1822].

Description.

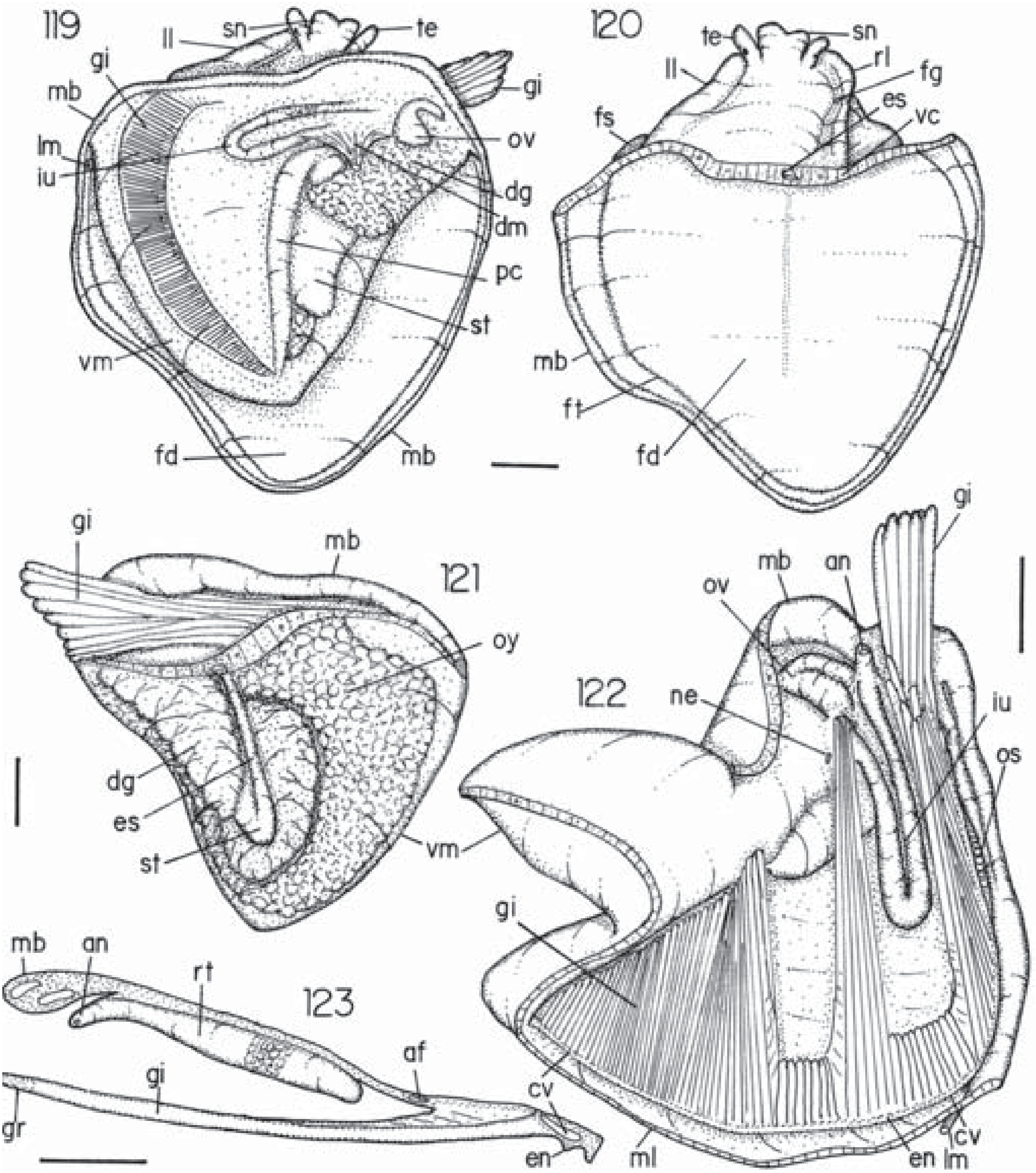
Shell (Figs. 4, 7). Color white, sculptured growth lines, plane to convex. Septum sometimes protrudes beyond ventral surface of shell. Other details similar to data of Hoagland (1977: 389, fig. 20).

Head-foot (Figs. 119, 120, 128). General characters very similar to those of preceding species, distinctive and notable features following. Foot region ventral to septum ampler (about twice head and neck areas) and thinner; clear longitudinal inner sinus runs in median line (Fig. 120). Head proportionally smaller, with less than ¼ of animal width. Tentacles without ommatophores; tip weakly bifid in retracted condition. Eyes dark, also located in about middle level of tentacles. Neck ventral surface, lappets and food groove also present. Columellar muscle smaller, very thin and narrow. Net of dorso-ventral muscles of haemocoel present, but united in two masses parallel to esophagus (fig. 128: tm), separated from salivary glands.

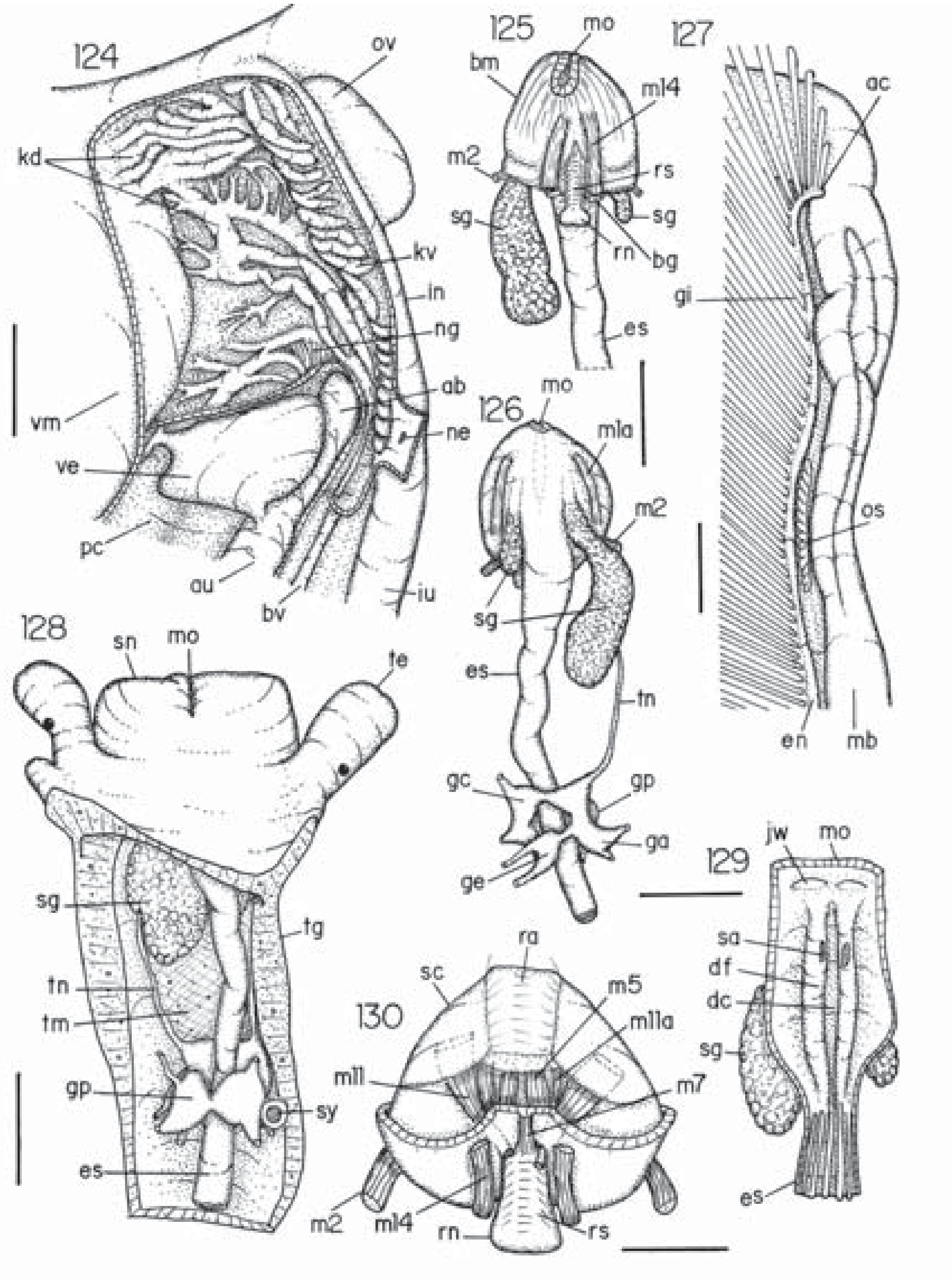
Mantle organs (Figs. 119, 122, 123, 127). Characters in general similar to those of preceding species, distinctive and notable characters following. Free mantle border broader, mainly those parts attached to foot sole. Repugnatorial glands also present. Dorsal shell muscle developed. Lateral shell muscle very narrow. Pallial cavity deeper, with about ¾ of animal length, its posterior limit close to posterior limit of visceral mass (Figs. 119, 122). Pallial aperture, if animal compared with a clock, begins at 10 and finishes at 2 o'clock. Special arrangement of folds of mantle edge in middle region of pallial cavity aperture shown in fig. 127. Osphradium very small (length about 1/8 of pallial cavity aperture width), situated about in middle level of pallial aperture parallel to mantle border (Figs. 122, 127). Osphradium monopectinate, with about 15 slight thick leaflets of rounded tip. Gill very large, similar to that of *B. aculeatus*, including long rod of filaments, thicker tip and slight narrow base. Gill anterior end on mantle border, weakly arched forwards, located between middle and right third parts of pallial aperture. Ctenidial vein and endostyle (Fig. 123) as in preceding species. Hypobranchial gland very thin, inconspicuous. About 1/3 of visceral mass encroaches in pallial cavity as in anterior species; some structure described below.

Visceral mass (Figs. 119, 121). Very similar characters to that of preceding species.

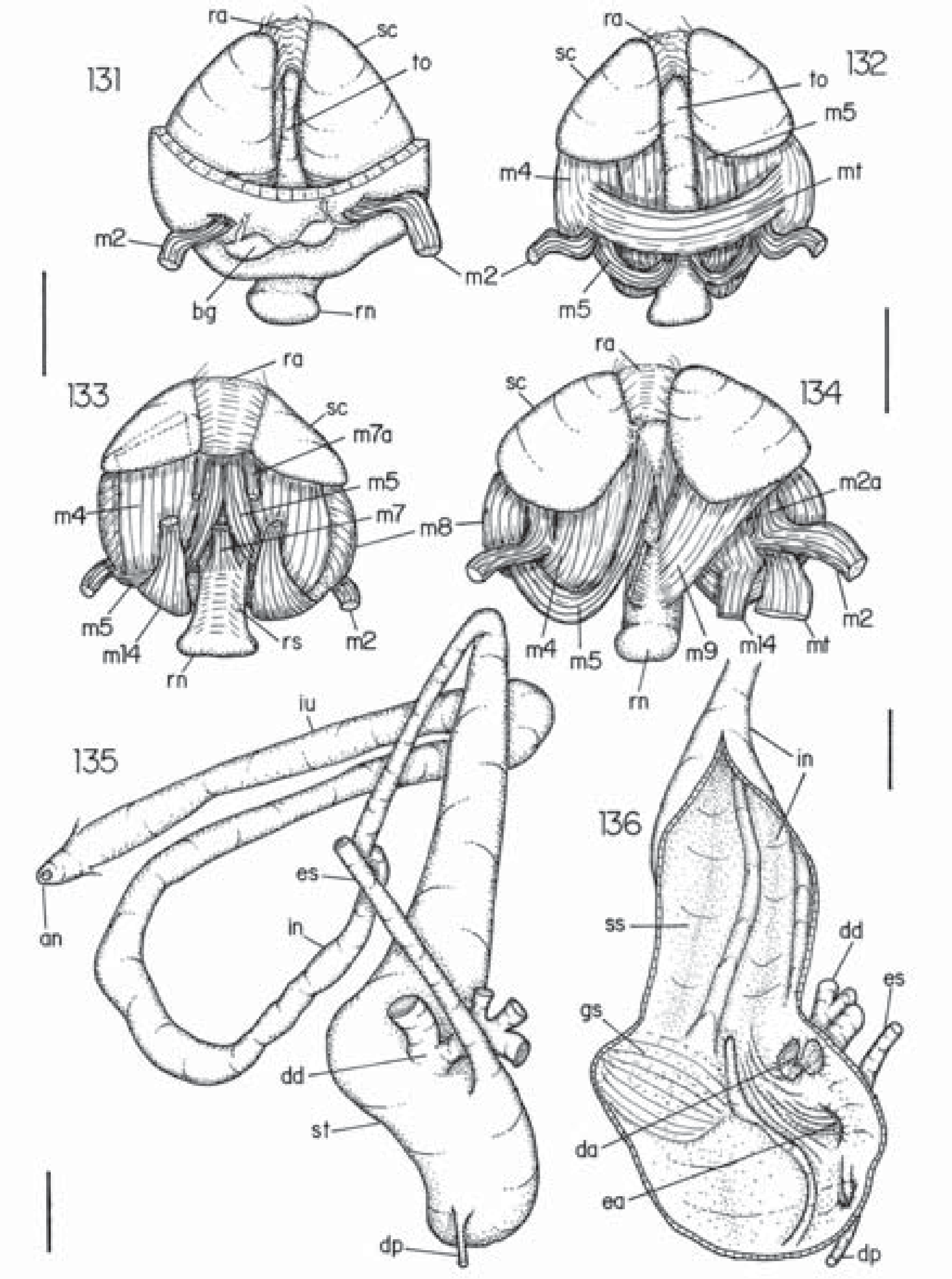
Circulatory and excretory systems (Fig. 124). Heart very similar to that of *B. aculeatus*, with very long auricle running anterior-left margin of visceral mass (encroaches on pallial cavity) and with its portion as blind-sac beyond ventricle. Kidney situation and limits similar to those of *B. aculeatus*. Inner renal tissue arrangement in two lobes, connected to each other. Ventral lobe covers posterior surface of rectum, bears many transverse, slight, tall, glandular folds. Dorsal lobe more concentrated at right, covers almost whole dorsal inner surface, bears some irregular, slight transverse, glandular folds. Nephridial gland small, bears several trans-



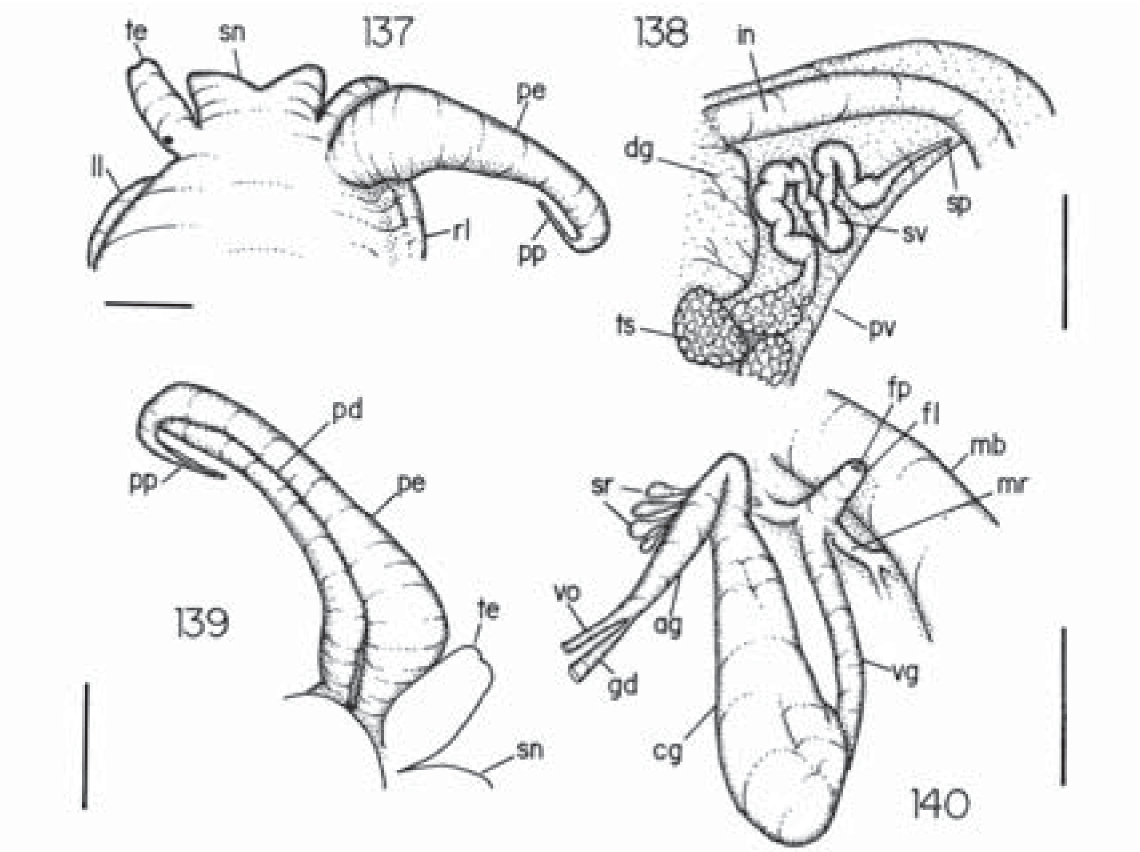
Figures 119-123, *Crepidula* aff *plana* anatomy: **119**, female extracted from shell, dorsal view; **120**, head-foot, female, dorsal view, visceral mass and pallial organs removed; **121**, visceral mass and pallial cavity extracted from head-foot, ventral view; **122**, same, ventral view, anterior-ventral region of visceral mass deflected to show pallial roof structures, some portions of gill filaments extracted to show strictures dorsal to them; **123**, pallial cavity roof, transversal section in its middle level, just parallel to rectum. Scales = 2 mm.



Figures 124-130, *Crepidula* aff *plana* anatomy: **124**, kidney and adjacent structures, including pericardium, ventral view, ventral wall of kidney and pericardium almost entirely extracted (except a small, deflected portion adjacent to nephrostome); **125**, buccal mass and adjacent esophagus, ventral view; **126**, same, dorsal view, nerve ring also shown; **127**, pallial cavity roof, ventral view, detail of anterior gill extremity and osphradium regions; **128**, head and haemocoel, ventral view, foot and neck ventral surface extracted; **129**, dorsal wall of buccal mass, ventral view, odontophore and septum between it and esophagus extracted; **130**, odontophore extracted, ventral view;. Scales = 1 mm, except 130 = 0.5 mm.



Figures 131-136, *Crepidula* aff *plana* anatomy: **131**, odontophore, dorsal view, **132**, same, part of superficial tissue extracted; **133**, same, ventral view; **134** same, dorsal view, some of muscles sectioned and deflected to show inner structures; **135**, digestive tubes seen if adjacent structures were transparent, ventral view; **136**, stomach, ventral view, its inner surface exposed by a middle longitudinal section. Scales 131-134 = 0.5 mm, 135-136 = 1 mm.



Figures 137-140, *Crepidula* aff *plana* anatomy: **137**, head of male, dorsal view, scale = 0.5 mm; **138**, right-anterior extremity of visceral mass of male, ventral view, scale = 0.25 mm; **139**, penis, ventral view, scale = 0.5 mm; **140**; pallial oviduct and adjacent mantle border, ventral view, scale = 1 mm.

verse, narrow folds, located in dorsal margin of membrane between kidney and heart chambers, more conspicuous anteriorly. Nephrostome a small slit in left-anterior region of membrane between kidney and pallial cavities, without inner folds close to it. A conspicuous vessel runs from middle region of mantle roof, lies between pericardium and pallial intestinal loop, inserts in left extremity of kidney.

Digestive system (Figs. 125, 126, 128-136). Buccal mass characters similar to those of *B. aculeatus*, with following distinctive or notable features. Dorsal chamber, limited by pair of dorsal folds of buccal mass, shallower (Fig. 129). Odontophore extrinsic and intrinsic muscles as described for preceding species (Figs. 130-134). Radula (Figs. 60-62) similar to that described for *B. aculeatus*, distinct features: rachidian tooth with broader central cusp, secondary cusps very small, from two to three pairs; lateral tooth with about 10 cusps, second cusp larger, apical and triangular; inner marginal tooth with about three times outer marginal width, about eight cusps in its inner, sub-apical margin and two cusps in outer margin (far from apex); outer marginal with two or three sharp cusps in its inner margin, slight far from tooth apex. Salivary glands much smaller, in form of pair of glandular sacs extending little more than same length of buccal mass (Figs. 125, 126, 129); right salivary gland larger than left one. Both salivary glands anterior and somewhat far from nerve ring. Salivary gland apertures in middle-anterior region of dorsal folds of buccal mass (Fig. 129). Esophagus narrow, its inner surface with four to six longitudinal, narrow folds along its whole length; visible glandular chambers absent (Figs. 128, 129).

Stomach (Figs. 135, 136) characters similar to those of preceding species but narrow. A posterior, narrow duct to digestive gland present, origin in posterior, inner gastric surface with differentiable sorting area of longitudinal, low folds lying from esophageal and anterior duct to digestive gland apertures, towards anterior, faint in area of intestine origin. Pair of slight tall, longitudinal folds present; shorter, begins just posterior to esophageal aperture, runs towards posterior, penetrating in posterior duct to digestive gland; other fold longer, runs between sorting areas and gastric shield towards posterior, surrounds posterior gastric wall. Gastric shield circular, with several, narrow, transversal folds, located just posterior to style sac origin. Anterior half of stomach, as in preceding species, tapers gradually towards anterior and left; its anterior surface also incompletely and asymmetrically divided by pair of tall folds into intestinal (narrower) and style sac (broader) portions. No style found. Digestive gland and intestine characters similar to those of *B. aculeatus*, except for presence of posterior duct to former and slender fashion of latter. Intestine (Fig. 135) replete with small, elliptical fecal pellets that begin to differentiate in intestinal loop preceding kidney. Intestinal loop exposed in pallial cavity, U-shaped, very long (Figs. 119, 122, 135). Anus siphoned, location as in *B. aculeatus*.

Genital system. **Development**. Protandric hermaphroditism. Up to 5 mm several specimens are immature males (i.e., with penis but glands incipient). From 4 to 7 mm mature males are found. Specimens larger than 6-7 mm are always mature females, but mature females 4-5 mm in length are also found. About 50% of minute specimens (up to 5 mm) have no penis, this maybe is indicative that about half of the specimens develop female organs without passing through male stage. Gould (1917) also found small specimens of *C. plana* without penis, called as “sexually inactive” specimens; that paper brings important data on *C. plana* development.

Male (Figs. 137-139). Shell of males generally brown spotted and more convex than same-sized females, but several exceptions exist. Male pallial cavity shorter, somewhat perpendicular to longitudinal axis. Testis white, only present in anterior region of visceral mass (remainder of visceral mass only occupied by stomach and digestive gland). Seminal vesicle located in right-anterior extremity of visceral mass, with about two irregular coils; its anterior region narrows and opens to pallial cavity floor as small papilla. Between this aperture and penis base a very shallow sperm groove; it runs on right surface of pallial floor (difficult to see in some males). Penis large, somewhat long, inserted just posterior to right cephalic tentacle. Penis basal region broad, narrows gradually distally. Apical papilla curved, very narrow and tapered. Penis groove runs about along central region of penis ventral surface until papilla tip.

Female (Fig. 140). Ovary, visceral oviduct and gonopericardial duct characters similar to those of *B. aculeatus*. Albumen gland slight narrow, elliptical, located in right-anterior extremity of visceral mass, exposed in ventral surface of pallial cavity. A series of generally four seminal receptacles inserts in posterior surface of albumen gland. Anterior extremity of albumen gland suddenly twists towards left and dorsally, inserting in capsule gland. Capsule gland exposed in right region of pallial cavity at right of anus, increases towards left, with thick, yellowish walls; its duct narrow, dorso-ventrally flattened. Left extremity of capsule gland rounded, with bind-end. Vaginal tube long and narrow, origin in anterior-left region of capsule gland, runs within mantle wall towards right, close mantle border suddenly ventrally and opens in tall papilla. This genital papilla presents two or three folded reinforcements of adjacent areas of mantle. Female genital pore very small, in papilla tip.

Central nervous system (Fig. 128). All ganglia large and close to each other around region of esophagus close to visceral mass. Sub- and supra-esophageal ganglia also close to nerve ring. Statocyst with single, large statolyth.

Habitat. Almost invariably within empty gastropod (bivalve sometimes) shells (or with hermit crab), from intertidal to 73 m depth.

Distribution. Southeast coast of Brazil (this distribution is still in analysis).

Measurements of shells (in mm). MZSP 30790,♀1, 27.5 by 4.6;♀3, 20.0 by 3.5; MZSP 30792,♂4.4 by 1.4.

Material examined. BRAZIL; **Bahia**; Salvador, Banco da Panela, 16-20 m depth, MZSP 28456, 5 specimens (Simone col., 26/ii/1997). **São Paulo**; Ubatuba (Integrated Project – IOUSP, R.V. Veliger II col.); 23°25’S 44°52’W, 21 m depth, MZSP 30803, 13 specimens (Sta. 27, 21/iv/1986); 23°29’S 44°52’W, 38 m depth, MZSP 30791, 1♂, MZSP 30798, 2 specimens (Sta. 8, 28/x/1985); 23°30’S 44°54’W, 42m depth, MZSP 30790, 5 specimens (Sta. 26, 21/iv/1986); 23°33’S 44°50.5’W, 43 m depth, MZSP 30799, 2♂(Sta. 7, 28/x/1985); 23°34’S 44°48’W, 44 m depth, MZSP 30801, 4 specimens (Sta. 17, 22/i/1986); 23°34’S 45°06’W, 21 m depth, MZSP 30802, 24 specimens (Sta. 12, 20/i/1986), 20 m depth, MZSP 30800, 1 specimen (Sta. 39, 21/x/1986); 23°34’S 45°07’W, 20 m depth, MZSP 30797, 2 specimens (Sta. 21, 18/iv/1986); 23°38’S 44°49’W, 47 m depth, MZSP 30795, 1♂(Sta. 16, 22/i/1986); 23°38’S 45°14’W, 16 m depth, MZSP 30805, 1 specimen (Sta. 42, 22/x/1986); 23°39’S 45°04’W, 36m depth, MZSP 30792, 2(Sta. 11, 20/i/1986); 23°44’S 45°00’W, 42 m depth, MZSP 30796, 2♀(Sta. 37, 21/x/1986); 23°44’S 45°15’W, 32 m depth, MZSP 30804, 10♀(sta. 5, 27/x/1985); 23°47’S 45°10’W, 35 m depth, MZSP 30793, 2 ♂ 1♀ (Sta. 14, 21/i/1986); off Ubatuba, MZSP 30794, 10 specimens. No loc., MZSP 30806, 100 specimens (Sta. FINEP 4576, v/1984).

Crepidula protea Orbigny, 1841

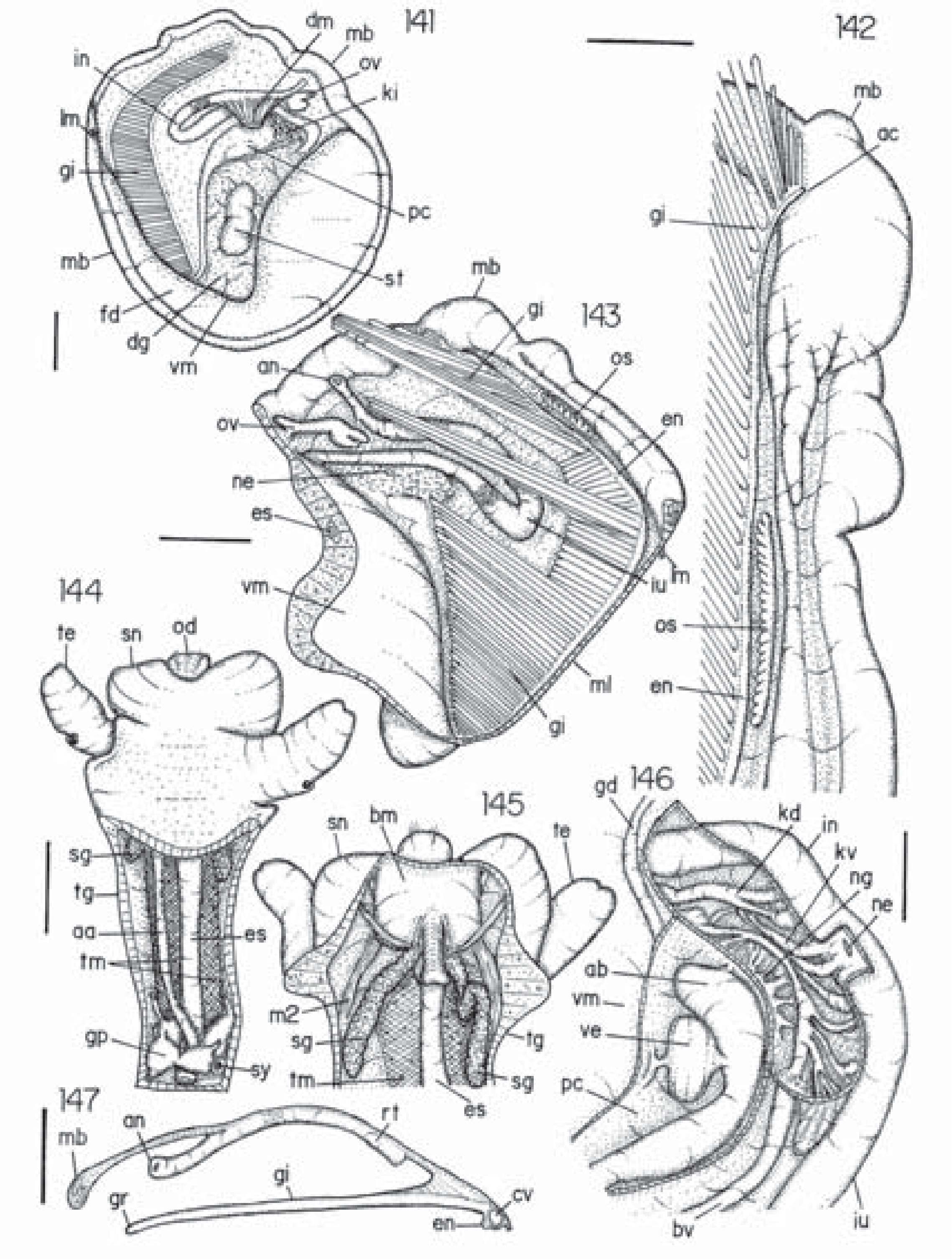
(Figs. 5, 6, 63, 64, 141-151)

Synonymy in Aguirre (1993: 26-28). Complement:

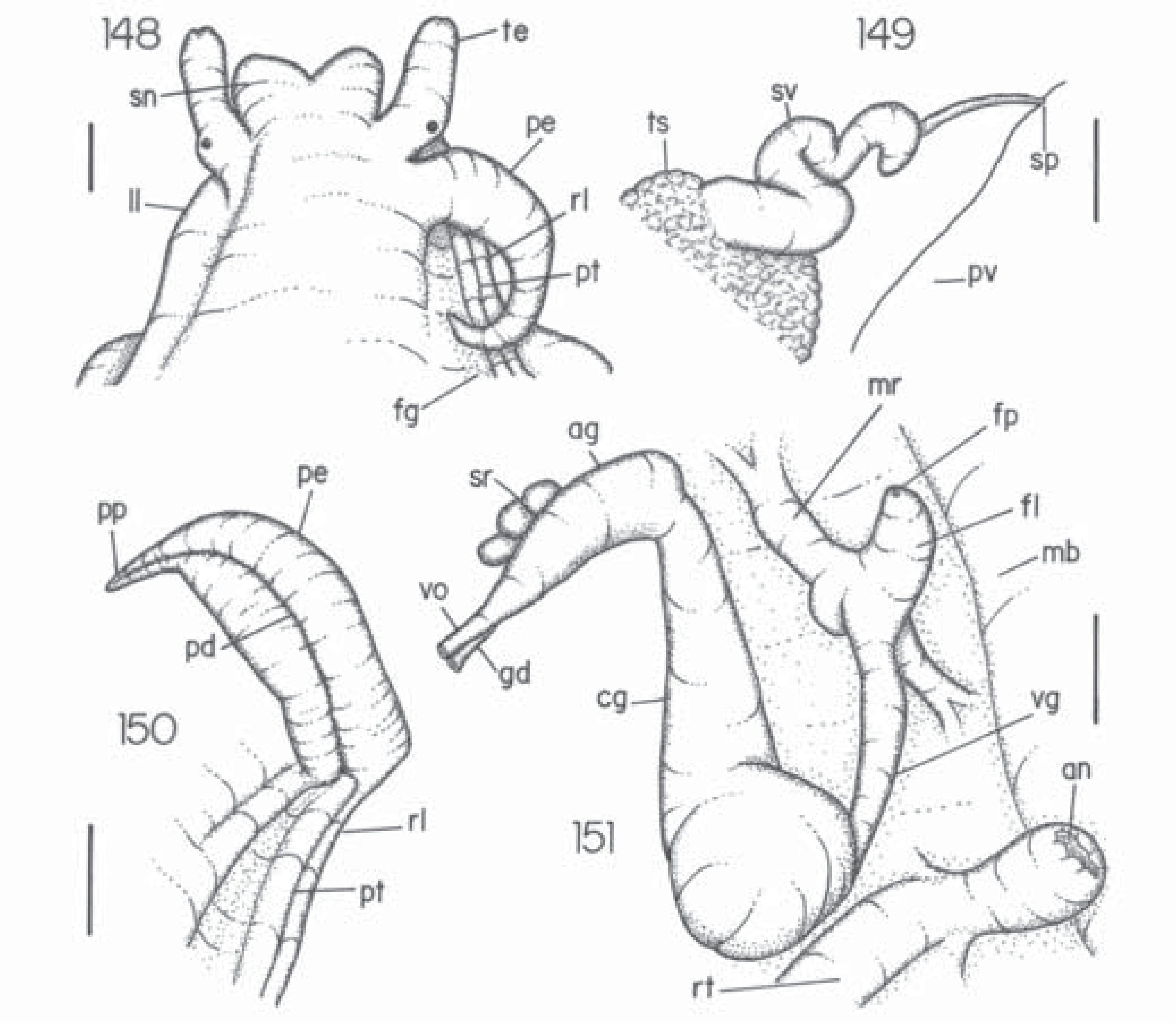
Crepidula protea: Warmke & Abbott, 1961: 87; Rios, 1970: 56 (pl. 11); 1975: 64 (pl. 17, fig. 259); Hoagland, 1977: 386, 388; Oliveira et al., 1981: 111-112; Hoagland, 1983a: 105-108 (fig. 1); Hoagland, 1984: 607-621 (molecular); Rios 1985: 60 (pl. 21, fig. 268); Calvo, 1987: 97, 99 (fig. 55); Aguirre, 1993: 26-28 (pl. 1, figs. 2-4, lectotype: BMNH 1454.12.4.573-4); Rios, 1994: 71 (pl. 24, fig. 273).

Description.

Shell (Figs. 5, 6). Relatively large (up to 40 mm), thin, planar to slightly convex. Color whitish beige to pale brown. Periostracum somewhat thick. Apex small, turned slightly to



Figures 141-147, *Crepidula protea* anatomy: **141**, female extracted from shell, dorsal view; **142**, pallial cavity roof, detail of anterior gill extremity and osphradium region, ventral view; **143**, visceral mass and pallial cavity roof, ventral view, anterior-ventral region of visceral mass deflected, some portions of gill with filaments extracted; **144**, head and haemocoel, ventral view, foot and neck ventral surface extracted; **145**, same, snout opened ventrally and its walls deflected; **146**, kidney, pericardium and adjacent structures, ventral view, ventral wall of kidney and pericardium extracted (except small portion deflected around nephrostome); **147**, pallial cavity roof, transversal section in its middle level, parallel to rectum. Scales 141, 143, 147 = 2 mm; 142, 144-146 = 1 mm.



Figures 148-151, *Crepidula protea* anatomy: **148**, head and neck, male, dorsal view; **149**, visceral mass, male, detail of its anterior–right extremity, ventral view; **150**, penis and adjacent structures of its base, ventral view; **151**, pallial oviduct and adjacent structures of mantle roof, ventral view. Scales = 0.5 mm.

right, at level of or above shell margin. Sculpture lacking except growth lines. Shell septum shallow, planar; sulcus at left; notch about in center of margin; covers about ½ of aperture area. Muscle scar very weak, close to right end of septum edge.

Shell similar to *C.* aff. *plana*, differs mainly in convex shape and in beige or reddish color (but several exceptions and overlap exist).

Head-foot (Figs. 141, 144, 148). Very similar characters to those of *C.* aff. *plana*, without notable differences. Presents inclusive bifid tip of retracted tentacles and eyes located in its middle-outer region.

Mantle organs (Figs. 141-143, 147). Mantle border, mantle cavity and aperture as described for *C.* aff. *plana*. Special arrangement of folds in middle regions of pallial cavity aperture shown in fig. 142. Pallial organ characters also similar to those described for *C.* aff. *plana*, including gill, osphradium monopectinate (with series of several tall, rounded leaflets), hypobranchial gland poorly developed and endostyle. Dorsal shell muscle present. Lateral shell muscle very narrow (Figs. 141, 143), even absent in about half of specimens.

Visceral mass (Fig. 141). As in preceding species.

Circulatory and excretory systems (Fig. 146). Pericardium and heart characters and limits similar to those of *C.* aff. *plana*. Kidney situation also similar to that of *C.* aff. *plana*. Inner renal tissue also similar to that of preceding species, but with fewer and stronger glandular folds. Separation between dorsal lobe (covering dorsal renal wall) and ventral lobe (covering posterior surface of adjacent intestine) less clear (Fig. 146). Nephridial gland more weakly developed, of similar location. Nephrostome free from inner glandular folds and pallial vessel insertion in left border of kidney, both similar to *C.* aff. *plana*.

Digestive system (Figs. 144, 145). Buccal mass characters as those described for *C.* aff. *plana*, included odontophore muscles. Radula characters (Figs. 63, 64) similar to those of *C.* aff. *plana*. Salivary glands practically symmetrical, slender, long, sometimes coiled, each one with about 1.5 times buccal mass length. Salivary glands separated from the net of transversal muscles of haemocoel. Entire esophagus with about eight narrow, longitudinal inner folds, one of them larger. No esophageal glandular chamber present. Stomach characters similar to those described for *C.* aff. *plana*, but with posterior duct to digestive gland broader and closer to esophageal insertion. Stomach inner surface also similar to that of anterior species, but possesses fold running in dorsal-posterior region, from esophagus insertion towards posterior, connects with long longitudinal fold of posterior gastric wall (this fold also present in *C.* aff. *plana*). Digestive gland, intestine loops and anus as in *C.* aff. *plana*.

Genital system. **Development**. It is dubious if *C. protea* is protandric hermaphrodite. Males are rarer than females both in minute and large specimens. There are mature males of small size (7.5-8.5 mm, MZSP PI-27) and of large size (12.5, 16.4 mm, MZSP PI-26). On the other hand, mature females with 5-6 mm are common.

Male (Figs. 148-150). Testis whitish, occupies anterior region of visceral mass. Seminal vesicle similar in location of *C.* aff. *plana*. Pallial floor sperm groove shallow (difficult to see in some specimens), more clearly close to penis. Penis origin just posterior to right tentacle. Penis broad, curved, of somewhat uniform width along its length. Penis tip with slender papilla, preceded by sudden penis construction. Penis groove runs in central region of penis ventral surface, up to papilla distal end.

Female (Fig. 151). Visceral and pallial organs characters very similar to those of *C.* aff. *plana*, inclusive 3-4 seminal receptacles in posterior surface of albumen gland and genital pore preceded by tall, outstanding papilla.

Habitat. On hard substrates, generally outside shells of other molluscs. From Intertidal to 125 m depth.

Distribution. From Cuba to Uruguay.

Measurements of shells (in mm). MZSP 30765,♀1, 23.4 by 6.5;♀2, 23.0 by 6.4; MZSP 30766,♂, 14.4 by 5.5.

Material examined. BRAZIL; **São Paulo**; Ubatuba (Integrated Project – IOUSP, R.V. Veliger II col.); 23°24’S 45°07’W, 20m depth, MZSP 30772, 12 specimens (Sta. 21, 18/iv/1986); 23°25’S 44°52’W, 21 m depth, MZSP 30767, 27 specimens (Sta. 27, 21/iv/1986), 18 m depth, MZSP 30785, 1 specimen (Sta. 18, 22/i/1986); 23°29’S 44°52’W, 38 m depth, MZSP 30775, 4 specimens (Sta. 8, 28/x/1985); 23°30’S 44°54’W, 42m depth, MZSP 30765, 21 specimens (Sta. 26, 21/iv/1986); 23°34’S 45°06’W, 21 m depth, MZSP 30776, 1 specimen, MZSP 30782, 9 specimens (Sta. 12, 20/i/1986), 20 m depth, MZSP 30781, 2 specimens (Sta. 39, 21/x/1986), 22 m depth, MZSP 30783, 6 specimens (Sta. 30, 09/vii/1986); 23°34’S 45°07’W, 20 m depth, MZSP 30777, 2 specimens (Sta. 21, 18/iv/1986); 23°38’S 45°14’W, 16 m depth, MZSP 30773, 5 specimens (Sta. 42, 22/x/1986); 23°39’S 45°04’W, 36m depth, MZSP 30769, 1♂(Sta. 11, 20/i/1986); 23°39’S 44°53’W, 45m depth. MZSP 30770, 1♂, MZSP 30787, 1 specimen (Sta. 25, 20/iv/1986); 23°39’S 45°04’W, 36 m depth, MZSP 30774, 3 specimens (sta. 11, 20/i/1986); 23°40’S 44°59’W, 35 m depth, MZSP 30766, 20 specimens (sta. 20, 20/iv/1986); 23°41’S 45°01’W, 35 m depth, MZSP 30779, 15 specimens (Sta. 38, 21/x/1986); 23°43’S 45°13’W, 20m depth, MZSP 30771, 1 specimen, MZSP 30786, 1 specimen (Sta. 15, 21/i/1986); 23°44’S 45°15’W, 32 m depth, MZSP 30768, 27 specimens, MZSP 30784, 12 specimens (sta. 5, 27/x/1985); 23°47’S 45°13’W, 36m depth, MZSP 30778, 1♂, MZSP 30780, 3 specimens (Sta. 23, 19/iv/1986); 23°49’S 44°39’W, 70 m depth, MZSP 30789, 17 specimens (Sta. 4852, 16/xii/1985); 24°13.1’S 44°45.2’W, 117m depth, MZSP 30788, 3 specimens, (Sta. 4951, 27/vii/1986);

MORG 18033, 3♂, 2♀(1/xi/1968, R.V. W. Besnard sta. 414, 50 m depth). No Loc., MZSP 30807, 22 specimens (Sta. FINEP 4576).

Discussion. It is difficult to separate *C.* aff. *plana* from *C. protea* based on anatomical characters. They are very similar and the differences described here may not be enough to justify specific separation. The shell differences are practically restricted to concave (*C.* aff. *plana*) or convex (*C. protea*) shape (*C. protea* is, in general, more richly pigmented too). Although the shell form is greatly influenced by adaptations to the substrate in sessile animals. If the animal is living in the inner region of an empty gastropod shell, it becomes concave (*C.* aff. *plana*), if living in the outer surface of the same, the specimen becomes convex and more richly pigmented. On the other hand, the differences of the development are perhaps the key for a specific separation, because *C.* aff. *plana* is, practically without doubt, a protandric hermaphrodite, while *C. protea* may not be (see above). Thus, both groups are recognized as species herein, but it is clear that further studies can change this concept. Anyway, if both are really separate species, they are indubitably very close related ones.

Hoagland (1983a) provides an additional argument for specific separation between *C. protea* and *C.* aff. *plana*, based on the composition of the egg capsule and the number of embryos (*C.* aff. *plana* about 2000, while *C. protea* about 5500). However, there is a doubt in such species Hoagland actually studied, and this matter is still in analysis.

Crepidula argentina

A different species with virtually identical shell attributes to *C. protea* was studied, based on samples collected from northern Argentina. The species has been described in another paper: Simone, Pastorino & Penchaszadeh (2000), but it is included in the data matrix of the present study.

Crepidula convexa Say, 1822

(Figs. 8, 9, 66, 67, 152-159)

Synonymy in Hoagland (1977: 369). Complement:

Crepidula glauca: Warmke & Abbott, 1961: 87 (pl. 15, fig. l); Bandel, 1976: 264 (figs 20, 21); Bandel & Riedel, 1994: 341 (pl. 7, fig. 6).

Crepidula convexa form *glauca:* Abbott, 1954: 171; Jong & Coomans, 1988: 62; Merlano & Hegedus, 1994: 161.

Crepidula convexa: Hoagland, 1977: 369-370.

Description.

Shell (Figs. 8, 9). Characteristic shell concave, low, color white with several, slightly uniformly aligned, circular, dark brown spots (Fig. 8), more concentrated in oldest regions of shell. Although altogether white shells are common, as well as greatly compressed ones, resembling *C.* aff. *plana*. Other details in Hoagland (1977: 370).

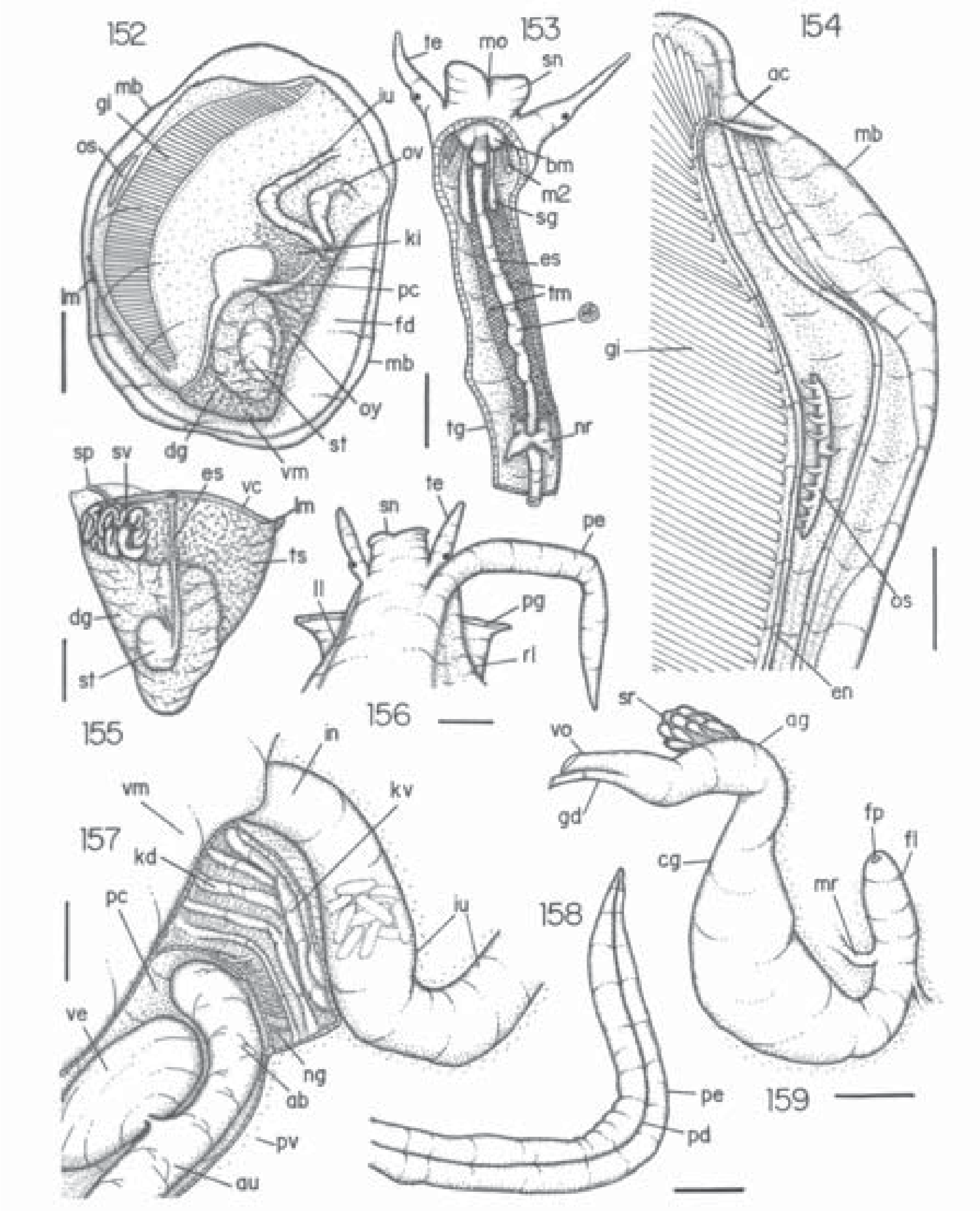
Head-foot (Figs. 153, 156). Very similar characters to *C.* aff. *plana*, neck region proportionally longer. Tentacles with basal half clearly broader than distal half, narrowing just distal to eyes. Tentacles tip not bifid, but no specimen with tentacles greatly contracted was examined. Anterior margin of foot with pair of lateral projections, clearer in smaller specimens. Haemocoel very narrow; inner net of transversal muscles well-developed, separated from salivary glands.

Mantle organs (Figs. 152, 154). Mantle border, as in preceding species, with repugnatorial glands. Arrangement of folds in middle region of pallial aperture shown in fig. 154. Pallial cavity broad and also deep; pallial aperture, if compared with a clock, begins at 9 and finishes at 3 o'clock. Arrangement of pallial organs very similar to that described for *C.* aff. *plana*, including a very thin inconspicuous hypobranchial gland. Osphradium monopectinate, distinct in having few leaflets separated from each other, tall and filiform. Anterior end of gill on mantle border, turned forward, possessing fold as continuation of ctenidial vein. Intestinal loop preceding anus not as long, V-shaped. Dorsal shell muscle absent. Lateral shell muscle narrow and small.

Visceral mass (Figs. 152, 155). Similar to those of preceding species, but proportionally smaller.

Circulatory and excretory systems (Fig. 157). Heart characters as described for preceding species. Kidney relatively small, limits similar to those of anterior *Crepidula* species. Dorsal renal lobe with some oblique folds slight far with each other, covering inner surface of dorsal renal wall. Ventral renal lobe connected with posterior surface of adjacent intestine, two or three tall folds, disposed in same direction as intestine. Nephrostome a small slit in anterior-left surface of membrane between kidney and pallial cavity, without inner glandular folds close to it. Nephridial gland some transversal small folds along dorsal region of membrane between kidney and pericardium. No pallial vessel inserted in left extremity of kidney.

Digestive system (Figs. 153, 155, 157). Buccal mass characters very similar to those described for *C.* aff. *plana*. Radula (Figs. 66, 67) also similar to that of *C.* aff. *plana*, rachidian tooth with central, large, triangular cusp and about four pairs of secondary, small cusps; lateral tooth with about 10 cusps, third cusp larger, apical, triangular; inner marginal tooth about three times outer marginal tooth width, flattened, about nine small, sub-terminal cusps in inner margin and two cusps in outer margin slight far from apex; outer marginal tooth slender, about three cusps in its inner margin.



Figures 152-159, *Crepidula convexa* anatomy: **152**, female extracted from shell, dorsal view, scale = 2 mm; **153**, head and haemocoel, ventral view, foot and neck ventral surface extracted, with a detail of a transversal section of indicated level of esophagus, scale = 1 mm; **154**, pallial cavity roof, ventral view, detail of region between anterior extremity of gill and osphradium, scale = 1 mm; **155**, visceral mass isolated, male, ventral view, scale = 0.5 mm; **156**, head and neck, male, dorsal view, scale = 0.5 mm; **157**, kidney, pericardium and adjacent structures, ventral view, ventral wall of both fully extracted, scale = 0.5 mm; **158**, penis, detail of its middle and apical regions, scale = 0.25 mm; **159**, pallial oviduct, ventral view, scale = 0.5 mm.

Salivary gland slender and long (Fig. 153); right gland longer than left one; both not mixed with net of transversal muscles. Esophagus very narrow and long. Inner surface with four longitudinal, glandular folds. Stomach as described for *C.* aff. *plana*, but posterior duct to digestive gland stay turned to left (instead turned to posterior). Inner gastric surface with deep and relatively ample gastric shield. Intestine loops similar to those of *C.* aff. *plana*, except that loop in pallial cavity roof, which is shorter and ampler (U-shaped) (Fig. 157). Anus siphoned, close mantle border right region.

Genital system. **Development**. Apparently protandric hermaphrodite, with most small specimen males, but small specimens without penis are common. Transition male-female around 4-5 mm. Other details of development and egg capsules see Bandel (1976: 264, fig. 20, 21).

Male (Figs. 155, 156, 158). Testis white, located in anterior-left region of visceral mass. Seminal vesicle large, highly convolute. Aperture to pallial cavity, similar to those of preceding species, preceded by narrow, almost straight papilla. Between this aperture and penis base a shallow sperm groove running in floor of pallial cavity right region. Penis origin just posterior to right tentacle. Penis very long (about same length as head-foot) and curved; width uniform along its length; distal end tapers, without clear papilla. Penis groove runs in center of penis ventral surface, until tip.

Female (Fig. 159). Ovary, visceral oviduct and gonopericardial duct characters as described for *C.* aff. *plana*. Pallial oviduct also similar to that of *C.* aff. *plana*, but with many vesicles (seminal receptacles) inserted in posterior region of albumen gland, all surrounded by secondary, transparent membrane. Vaginal tube shorter and broader. Genital pore preceded by very tall papilla with reinforcements from adjacent areas of mantle. All examined females present vestigial penis, very smaller compared to those of males.

Central nervous system. Similar to those of preceding species (Fig. 153).

Habitat. Subtidal, on other gastropods shells, up to 11 m depth.

Distribution. Northwestern Atlantic.

Measurements of shells (in mm). MZSP 30810,♀1, 13.3 by 2.7;♀3, 8.8 by 2.0;♂ 2, 4.3 by 1.0.

Material examined. VENEZUELA; **Isla Margarita** (Simone col.); Isla de Coche, La Uva, MZSP 30809, 50 specimens (6/ii/1995); El Yaque, MZSP 30810, 40 specimens (28/i/1996); Porlamar, Playa Bella Vista, MZSP 30811, 5 specimens (2/ii/1995).

Discussion. *C. convexa* has a shell and inner anatomy similar to those of *C.* aff. *plana* and *C. protea*. It differs mainly in the absence of a dorsal shell muscle; in the osphradium having fewer, filiform and tall leaflets; a proportionally smaller visceral mass; the absence of a developed pallial vessel inserting in left extremity of kidney; salivary glands longer; posterior duct to digestive gland turned to left (maybe induced by small size of visceral mass); pallial intestinal loop shorter, U-shaped; male seminal vesicle intensely more convolute (several coils); and by more quantity of vesicles of pallial oviduct.

Hoagland (1977: 370) considered *C. convexa* synonym of *C. glauca* Say, 1822. The name *C. convexa* is preferred here because of the arguments in favor to validity of C. convexa given by Hoagland. However, the question is still controversy, as Warmke & Abbott (1961) e.g., consider both species valid. Collin (2002) has referred further in favor to the name *C. convexa* over *C. glauca*, and that paper must be consulted for a further discussion of the taxonomy of this species. In a personal communication, Collin pointed out the possibility of the sample examined here may be not of *C. convexa*, since, by her concept, the species that does not range south of Georgia.

Crepidula fornicata (Linné, 1758)

(Figs. 10, 11, 71, 72, 160-164)

Synonymy in Hoagland (1977:375). Complement:

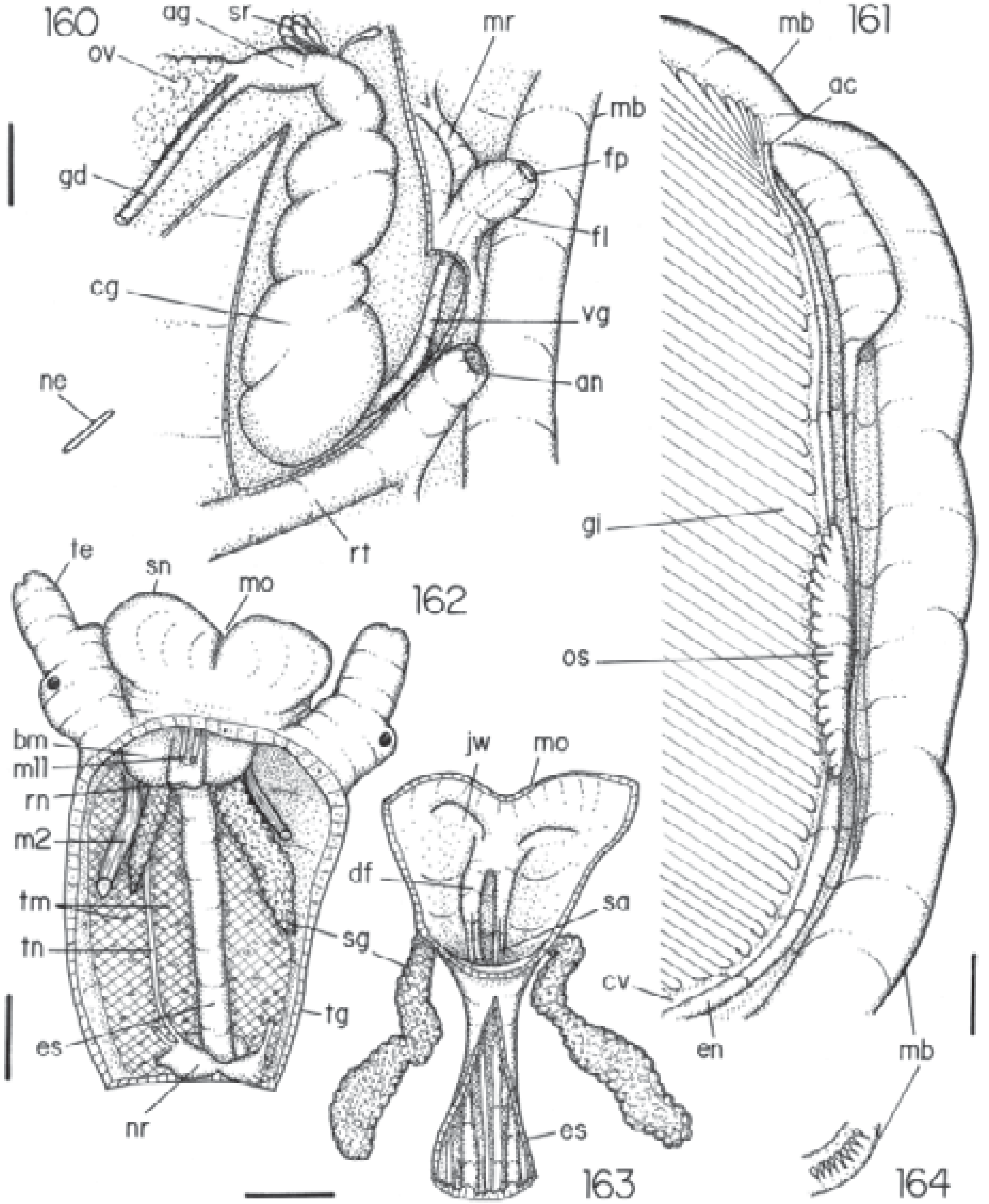
Crepidula fornicata: Olsson & Harbison, 1953: 277; Abbott, 1954: 170 (pl. 21m); Fretter & Graham, 1962: 70, 106, 107, 111, 115, 204, 220, 225, 254, 262, 315, 338, 374, 404, 454, 505, 643, 660 (figs. 39a, 41, 58, 59, 61-63, 121a, 185, 197, 212, 218b, 221, 236); Rios, 1975: 65; Oliveira et al., 1981: 110-111; Hoagland, 1983b: 4, 6; Hoagland, 1984: 607-621 (molecular); Taylor & Miller, 1989: 230 (figs. 7, 8); Poppe & Goto, 1991: 114 (pl. 15, figs. 18-19); Bandel & Riedel, 1994: 340-341; Abbott & Morris, 1995: 181 (pl. 49).

Description.

Shell (Figs. 10, 11). Relatively large (up to 60 mm), sculptured only by growth lines, highly convex. Other details in Hoagland (1977: 375-376, fig. 11).

Head-Foot (Fig. 162). Similar to those of preceding *Crepidula* species, distinctive and notable features following. Foot sole muscles more powerful. Dark brown pigmented mainly in dorsal regions of head and ventral region between foot and mantle attached to it. Repugnatorial glands as described for preceding species, along mantle border, but Fretter & Graham (1962, fig. 58) show specimens with this gland reunited in some tufts. Tentacles with bifid apex in retracted condition. Basal half of tentacles (up to eyes) clearly broader than distal half. Haemocoel broad, almost all filled by net of transversal, very narrow muscular fibers (do not pass through salivary glands). Other details in Fretter & Graham (1962, fig. 58).

Mantle organs (Figs. 161, 164). In general similar to those of preceding species, with following distinctive or interesting features. Inner surface of pallial cavity pigmented by black or dark brown. Distribution of pallial structures as



Figures 160-164, *Crepidula fornicata* anatomy: **160**, pallial oviduct and adjacent structures of pallial roof, ventral view, ventral recover of mantle extracted; **161**, pallial cavity roof, ventral view, detail of region between anterior extremity of gill and osphradium; **162**, head and haemocoel, ventral view, foot and neck ventral surface extracted; **163**, dorsal wall of buccal mass, ventral view, odontophore extracted, esophagus partially opened longitudinally; **164**, detail of mantle border, in its posterior-right region. Scales = 1 mm.

shown by Fretter & Graham (1962: 102, fig. 58) but in examined specimens the posterior end of cavity is more anterior. Special arrangement of folds in mantle border shown in fig. 161. Osphradium slightly small (about 1/5 of pallial cavity aperture, monopectinate, tall. Osphradium filaments thick, short, semi-spherical. Osphradium dorsal insertion close to ctenidial vein. Gill similar to preceding species, also located in mantle border, but with anterior extremity almost straight and far from osphradium. Endostyle narrow and slightly tall. Other details see Werner (1953: 260-314, figs 1-3, 6-8, 12-14, 16, 18-20, 22-27), Fretter & Graham (1962, fig. 61), Taylor & Miller (1989: 230 for osphradium).

Visceral mass. Similar to that described for *B. aculeatus*. Fretter & Graham (1962, fig. 58) show a dorsal view of visceral mass, the examined specimens only differ by presenting very larger ovary.

Circulatory and excretory systems. Heart and pericardium as described for preceding species. Kidney also similar to those of anterior species, with following notable characters: color pale cream; ventral lobe, attached to intestine, with several irregular folds; dorsal lobe with some longitudinal folds running almost entire kidney length; nephridial gland small, some transversal folds in dorsal region of pericardium membrane; nephrostome proportionally ample, slit-like, located about in center of membrane between kidney and pallial cavity, closer to ventral lobe, without inner folds close to it. Vessel as that of *C.* aff. *plana*.

Digestive system (Figs. 162, 163). Buccal mass, odontophore extrinsic and intrinsic muscles similar to those described for *B. aculeatus*. Dorsal wall of buccal mass with dorsal, inner folds narrow and close to median line; aperture of salivary glands on these folds, but posterior, near posterior level of buccal mass and very long antero-posteriorly. Radula similar to those of preceding species, main features: rachidian tooth narrow, with five to seven cusps, central cusp very larger, triangular; lateral tooth broad, with 11 to 12 cusps, fourth cusp very larger, triangular, terminal; inner marginal tooth with about double of outer marginal tooth width, inner marginal with six cusps in inner margin, outer marginal lacking cusps or wit up to 2 cusps in inner margin far from tip. Salivary glands long and narrow, about 1.5 times buccal mass length. Esophagus with about 6-7 longitudinal, narrow folds; in anterior region two of these folds larger, gradually decrease and become similar to others in posterior esophagus. Stomach similar to those of *C.* aff. *plana*, possessing posterior duct to digestive gland; after short distance this duct bifurcates in T-fashion, with an anterior and a posterior branch (Other details in Orton, 1922; Mackintosh, 1925). Stomach inner surface with pair of low folds running from esophageal insertion towards posterior, fuse with each other in posterior gastric region and become single taller fold that surrounds posterior gastric surface and runs towards anterior, finishes between both folds that separate style sac from intestine; other slight tall fold edges at right esophageal and both ducts to digestive gland apertures. Intestinal loops, rectum and anus as described for preceding species. Other details in Haller (1892), Graham (1939: 97-101, 2 figs.).

Genital system. **Development** and **male**. My observations verify and do not add to previous descriptions (e.g., Werner, 1953; 1955; Fretter & Graham, 1962: 358, fig. 185).

Female (Fig. 160). Ovary similar in location to those of preceding species. Visceral oviduct very short, inserting in albumen gland close to insertion of very long gonopericardial duct. Albumen gland almost indistinct from capsule gland, only weakly slender and smaller. Several vesicles united in outer region of albumen gland, inserted in it close with each other. Capsule gland a long, conic, thick glandular tube, runs towards left ant slight anterior immerse in mantle wall. Vaginal tube narrow, origins in anterior-left region of capsule gland, runs towards anterior and right also immerse in mantle wall up to genital pore. Genital pore small, preceded by tall papilla similar to that of *C.* aff. *plana*.

Central nervous system. See Graham (1954, fig. 4A).

Habitat. On hard substrates, intertidal to 49 m depth.

Distribution. NW Atlantic; originally from Gulf of St. Lawrence to Texas, now also in north coast of Europe and Mediterranean.

Measurements of shells (in mm). MZSP 30808, ♀ 1, 30.4 by 10.0; ♀ 2, 29.3 by 10.7.

Material examined. GERMANY; Amrum Island, MZSP 30808, 2 ♀ (L. Fornelis col., 23/vi/1960).

Genus *Calyptraea* Lamarck, 1799

(Type species: *Patella chinensis* Linné, 1758)

Calyptraea centralis (Conrad, 1841)

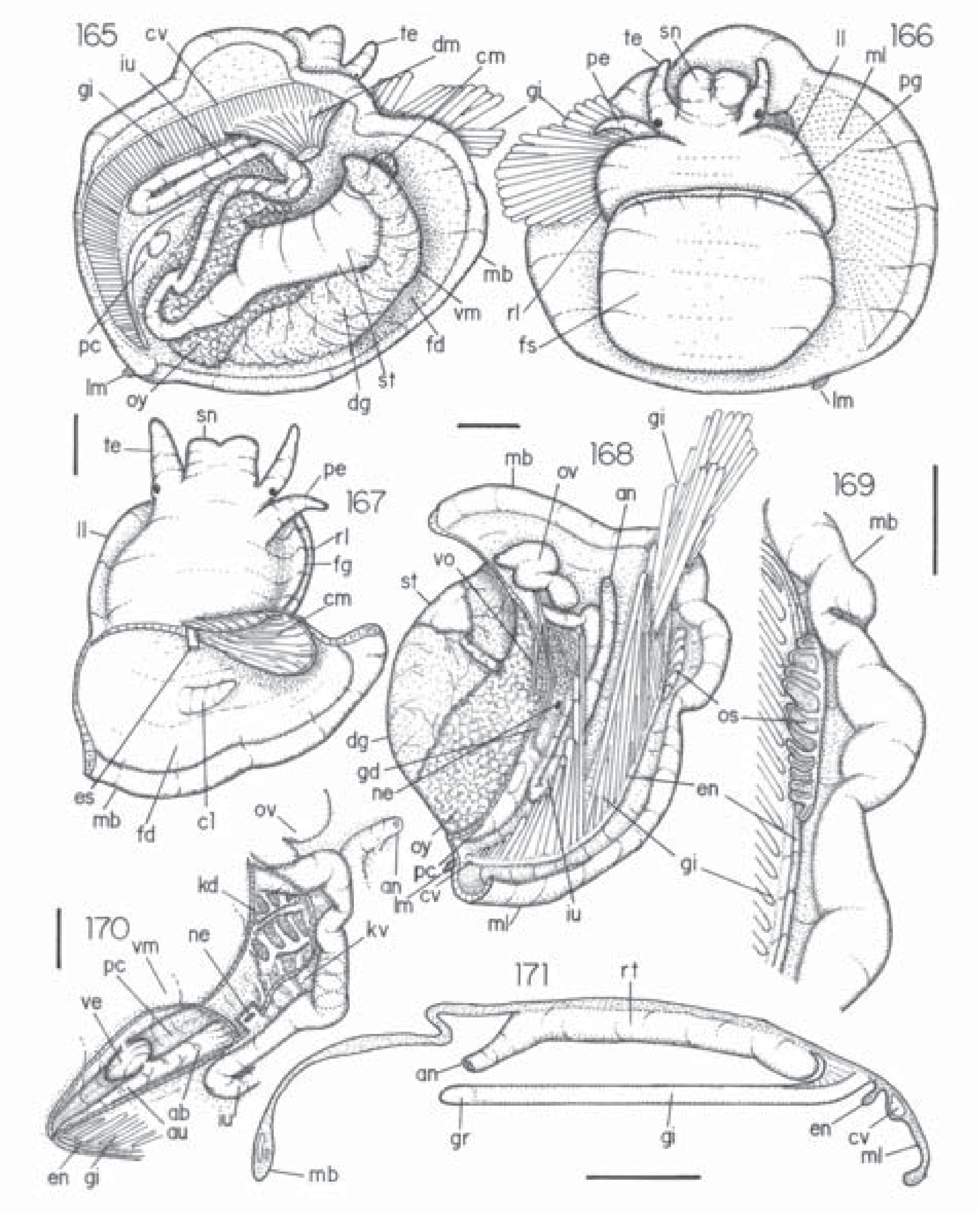
(Figs. 12-14, 56, 57, 165-184)

Synonymy in Olsson & Harbison, 1953: 277. Complement:

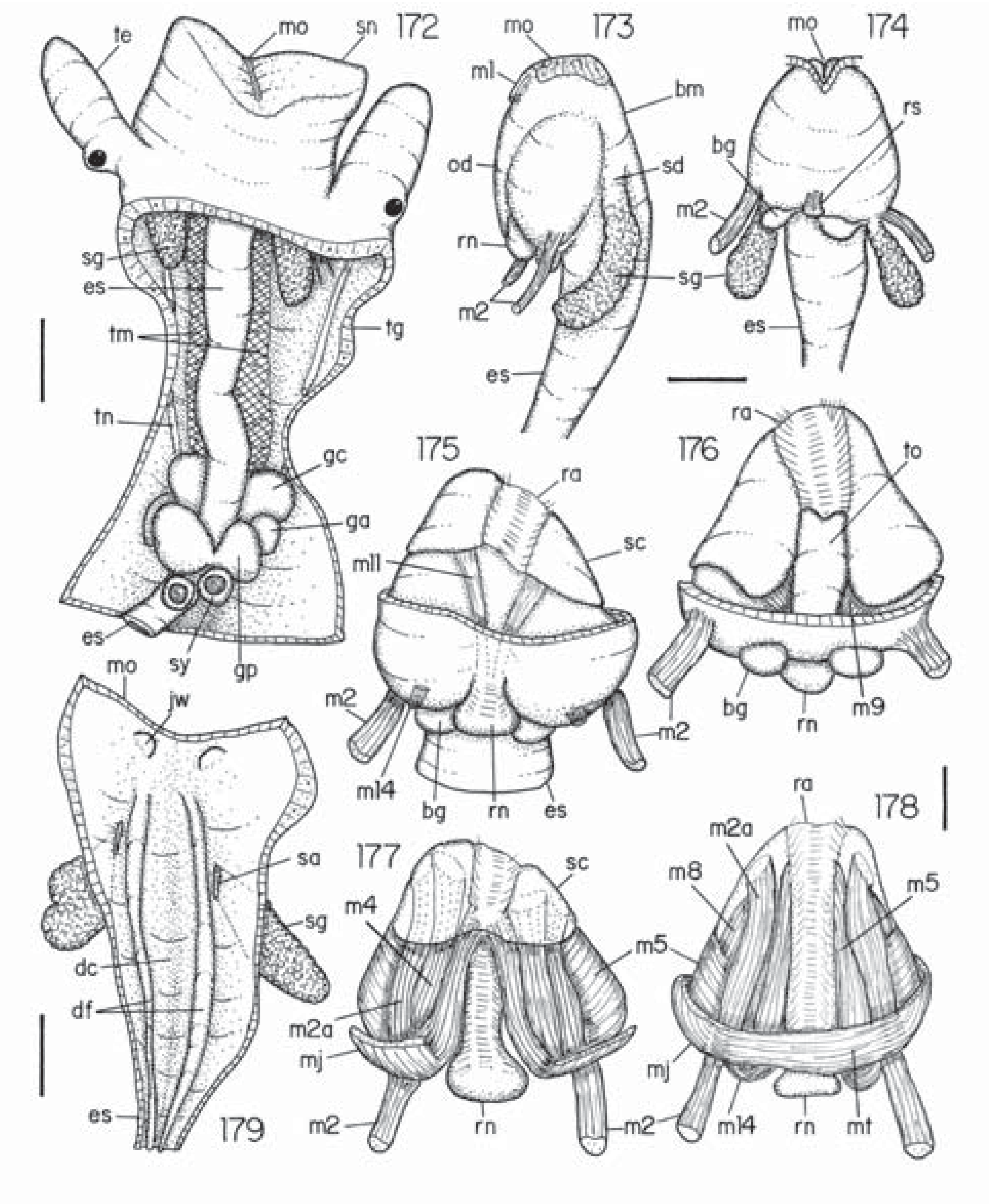
Calyptraea centralis: Abbott, 1954: 169 (pl. 20, fig. l); Warmke & Abbott, 1961: 86 (pl. 15, fig. o); Rios, 1970: 55; 1975: 64 (pl. 17, fig. 256); Bandel, 1976: 263 (fig. 19); Oliveira et al., 1981: 109; Rios, 1985: 58 (pl. 21, fig. 262); Jong & Coomans, 1988: 62; Rios, 1994: 71 (pl. 24, fig. 275); Merlano & Hegedus, 1994: 160 (pl. 50, fig. 582); Bandel & Riedel, 1994: 339; Abbott & Morris, 1995: 179 (pl. 45).

Description.

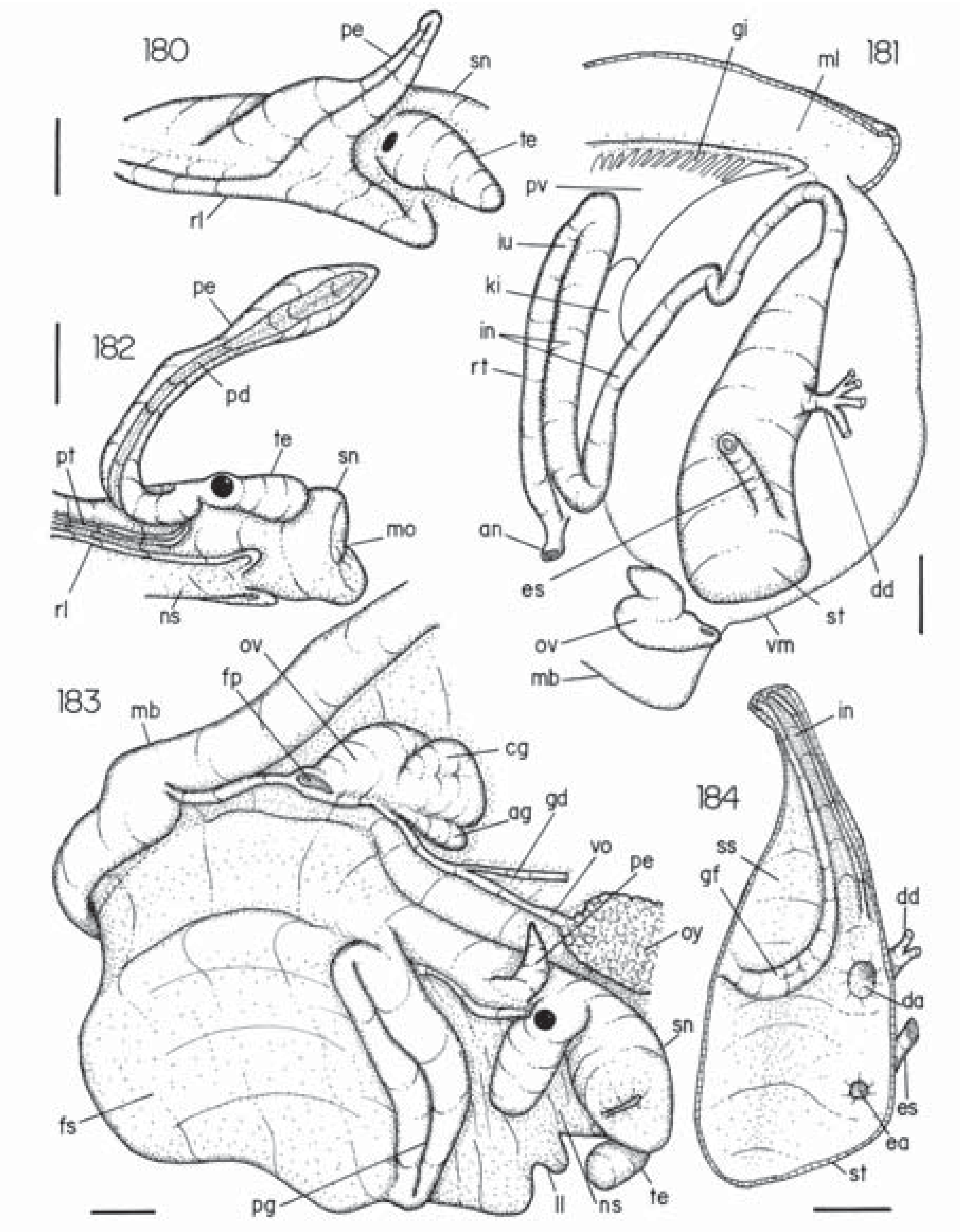
Shell (Figs. 12-14). Of small size (up to 5 mm), circular, conic, with somewhat spiral septum in center and right of ventral surface (Fig. 13). Apex small, sub-central, with about



Figures 165-171, *Calyptraea centralis* anatomy: **165**, female extracted from shell, dorsal view; **166**, same, ventral view; **167**, head-foot, dorsal view, visceral mass and pallial organs extracted; **168**, visceral mass and pallial organs, ventral view; **169**, pallial cavity roof, detail of osphradium region; **170**, kidney and pericardium, ventral view ventral wall of both extracted except a small portion around nephrostome; **171**, pallial cavity roof, transversal section in its middle region, parallel to rectum. Scales = 0.5 mm. Lettering: **c1**, mantle projection adjacent to shell umbilicus.



Figures 172-179, *Calyptraea centralis* anatomy: **172**, head and haemocoel, ventral view, foot and neck ventral surface extracted; **173**, buccal mass and adjacent esophagus, lateral-left view; **174**, same, dorsal view; **175**, odontophore, ventral view; **176**, same, dorsal view; **177**, odontophore, ventral view, superficial membrane and muscles removed; **178**, same, dorsal view; **179**, dorsal wall of buccal mass, ventral view, odontophore and septum between it and esophagus extracted, esophagus also opened longitudinally. Scales 172, 179 = 0.25 mm; 173-178 = 0.1 mm.



Figures 180-184, *Calyptraea centralis* anatomy: **180**, head of female, lateral-right view, showing vestigial penis present in all females, scale = 0.2 mm; **181**, digestive ducts, ventral view, seen if other structures were transparent, scale = 0.4 mm; **182**, head of male, lateral-right view, scale = 0.1 mm; **183**, head-foot and mantle cavity roof, female, lateral-right view, mantle deflected upwards to expose pallial oviduct, scale = 0.2 mm; **184**, stomach, ventral view, inner surface exposed by an longitudinal incision, scale = 0.4 mm.

2 whorls (Fig. 14). Other details in Abbott (1974: 139).

Head-foot (Figs. 166, 167, 172, 180, 182, 183). Head and neck regions somewhat similar to those of preceding *Crepidula* species, including neck ventral surface and flaps, but shorter; penis present in all specimens behind right tentacle, shorter in females. Pair of retractor muscles of snout present. Tentacles slender, without ommatophores. Eyes located slight over outer region of tentacles base. Foot also similar to that of *Crepidula*, with planar, dorso-ventrally flattened sole compressed by shell septum; anterior margin of this sole covers ventrally small area of neck ventral surface. Pedal glands furrow in anterior margin of foot sole. Mantle, as in *Crepidula*, attached to dorsal surface of foot sole and extending beyond its posterior and lateral borders. A tall, pointed and flat projection adjacent to shell umbilicus located about in center of dorsal foot surface (Fig. 167). Columellar muscle similar located as those of *Crepidula*, but larger, in form of semi-cone turned to right; inserts in border of shell septum and adjacent regions of shell inner surface and inner surface of septum.

Mantle organs (Figs. 165, 168, 169, 171). Mantle border very broad, including region surrounding foot; in region of mantle aperture a special arrangement of folds but not so complex as in *Crepidula* spp. Dorsal shell muscle present, very similar to those of *Crepidula*, proportionally larger; origin in region of shell inner surface anterior and weakly at right of shell septum; its fibers spread like fan towards anterior for a short distance and insert in dorsal surface of mantle just anterior to the gill (Fig. 165). Lateral shell muscle small and narrow, located in posterior end of pallial cavity. Pallial cavity conical and curved, begins just inside shell septum, suddenly increases towards anterior and right. Pallial aperture proportionally small, if animal compared with a clock, this aperture begins at 11 and finishes at 4 o'clock; left region of pallial cavity closed by mantle septum, restricting pallial aperture to condition described above. Osphradium slightly small (length about 1/5 of pallial cavity width), located parallel to mantle border about in central region of pallial aperture. Osphradium monopectinate, bearing some tall, flattened leaflets with rounded tip (Fig. 169). Gill similar to those of *Crepidula*, occupying most of inner pallial space, inserts all along left and anterior pallial margins. Gill filaments also similar to those of *Crepidula*, with very long (Figs. 168, 171), rigid rod, maintained firmly in position by cilia, mainly of the apical region. Gill rods do not originate directly from ctenidial vein, but slightly more internal, edging it. Endostyle narrow and tall, runs between ctenidial vein and gill along anterior border of gill (Fig. 171). Gill posterior end just in posterior end of cavity; gill anterior end in central region of pallial aperture, on mantle border, somewhat far from osphradium. Visceral mass, as in *Crepidula*, encroaching right-posterior region of pallial cavity roof and a flap ventral, as cavity floor (respective organs described below).

Visceral mass (Figs. 165, 168, 181). Somewhat conic, curved; differs from those of *Crepidula* in being turned anteriorly (Fig. 165). Large stomach as central structure. Gonad fills anterior region. Digestive gland surrounds posterior and ventral surfaces of stomach up to distal apex of visceral mass. As described above, about 1/3 of visceral mass encroaches pallial cavity roof; kidney and pericardium as more anterior structures (both described below).

Circulatory and excretory systems (Figs. 168, 170). Pericardium located in visceral mass partly encroached in pallial roof, in its left-anterior border, transversally long. Auricle narrow and long (but not so long as those of *Crepidula*); its connection with ventricle almost in central region of its posterior surface, possessing broader portion beyond it as blind-sac (similar to *Crepidula*). Kidney in anterior-right region of visceral mass, edged anteriorly by intestinal loop, dorso-ventrally flattened. Renal tissue almost all massive, dorsal and ventral (connected to intestine) lobes largely connected with each other, some irregular, pinned, hollow regions present. Nephrostome a small slit located in anterior-left region of membrane between kidney and pallial cavity.

Digestive system (Figs. 172-179, 181, 184). Buccal mass similar to those of *Crepidula* spp. Dorsal wall of buccal mass inner surface with pair of low folds and very small jaw plates. Aperture of salivary glands somewhat large slit, located in outer side of dorsal folds, in middle level of buccal mass. Odontophore muscles similar to those of *Crepidula*, but with **m7** shorter and inserted in border of subradular cartilage (Figs. 173-178). Radula (Figs. 56-57): rachidian tooth broad, about 11 cusps, central cusp somewhat similar to secondary cusps, cusps gradually decreasing towards lateral; lateral tooth curved inwards, with about 14 sharp cusps, third to fifth cusp slightly larger and apical; marginal teeth similar to each other, long, tall, slender, with about 12 sharp, sub-terminal cusps in inner edge; outer marginal weakly narrower than inner marginal tooth. Pair of buccal ganglia large, located close to median line (Figs. 173-176). Esophagus slender and long, anterior inner surface with pair of folds as continuation from those of dorsal wall of buccal mass (Fig. 179); this pair of folds gradually diminish in posterior esophagus, where four to six additional, longitudinal similar sized folds gradually appear. Stomach slightly conical and large (Figs. 165, 181). Esophagus inserts in ventral-posterior region of stomach. Duct to digestive gland single and large, located in middle level of posterior gastric surface. Inner gastric surface (Fig. 184) only with pair of longitudinal folds separating intestinal and style sac branches (grooves) of anterior stomach half; this pair of folds surrounds posterior limit of style sac and connect with each other on opposite side. Intestinal groove of stomach much narrower than style sac one. No style present. Digestive gland brown in color. Intestine appears after gradual constriction of style sac, suddenly crosses sinuously from left to right regions of anterior visceral mass through gonad and digestive gland (Fig. 181); in right extremity of visceral mass encroached in pallial cavity suddenly towards left, edging anterior border of kidney, part exposed in pallial cavity; close to gill newly towards right, running parallel to its preceding loop up to anus. This last intestinal loop stays as anterior margin of visceral mass. Anus small, siphoned, located in right region of pallial cavity near to pallial oviduct base.

Genital system. **Development**. Protandric hermaphrodite, with all smaller specimens male (however, few small specimens were available). Egg capsules and spawn see Bandel (1976: 263, fig. 19).

Male (Fig. 182). Testis and seminal vesicle similar located as those of *Crepidula* spp. Seminal vesicle white, with up to two coils, opens into pallial cavity right-posterior region by small papilla. Pallial sperm groove, from this papilla to penis base, shallow and narrow, clearer anteriorly. Penis very long (about three times head length), its basal two-thirds narrow, of uniformly width; its distal 1/3 broader, elliptical, spoon-like. Penis spermatic groove slight broad, mainly on apical region.

Female (Figs. 168, 180, 183). Ovary larger than testis, color pale beige (in fixed animals), located also in anterior region of visceral mass. Visceral oviduct slightly short. Gonopericardial duct similar to those of *Crepidula*, except that connects with visceral oviduct at some distance from pallial oviduct. Pallial oviduct somewhat small, located in right extremity of pallial cavity, close to mantle border (Figs. 168, 183). Albumen gland small, elliptical, sac-like, only connected with vaginal tube in its anterior extremity; right surface of this gland connected to capsule gland. Capsule gland as larger structure, broad, elliptical, thick glandular walled; its lumen broad, dorso-ventrally flattened, connected with vaginal groove. Vaginal groove anterior extremity amply opened (female pore), connected to mantle. From genital pore a fold runs towards posterior and inserts in mantle border. Most females possess small penis about half sized as those of males (Figs. 167, 180).

Central nervous system (Fig. 172). Similar to those of *Crepidula* species, with ganglia proportionally large, close with each other. Located posterior in haemocoel far from buccal mass.

Habitat. On hard substrates, from 5 to 101 m depth.

Distribution. From North Carolina, USA, to Uruguay.

Measurements of shells (in mm). MZSP 30843,♂, 3.6 by 1.6; MZSP 30845,♂, 4.5 by 2.0; MZSP 30846, ♀, 7.4 by 3.0;♀, 6.6 by 2.9.

Material examined. BRAZIL; **São Paulo**; Ubatuba (Integrated Project – IOUSP, R.V. Veliger II col.); 23°30'S 44°54'W, 42m depth, MZSP 30841, 2♂(Sta. 26, 21/iv/1986); 23°24'S 45°07'W, 20m depth, MZSP 30823, 6 specimens (Sta. 21, 18/iv/1986); 23°34'S 44°48'S, 44m depth, MZSP 30825, 4 specimens (Sta. 17, 22/i/1986); 23°36.2'S 44°39.5'W, 50m depth, MZSP 30826, 22 specimens (Sta. 4946, 26/vii/1986); 23°39'S 45°04'W, 36m depth, MZSP 30839, 8 specimens (Sta. 11, 20/i/1986); 23°39'S 45°16'W, 16m depth, MZSP 30836, 1♂(Sta. 24, 18/iv/1986); 23°39'S 44°53'W, 45m depth. MZSP 30838, 1♂(sta. 25, 20/iv/1986); 23°41'S 45°15'W, 17m depth, MZSP 30840, 1♂(Sta. 33, 10/vii/1986); 23°43'S 45°13'W, 20m depth, MZSP 30828, 2 specimens (Sta. 15, 21/i/1986); 23°45'S 44°57'W, 48m depth, MZSP 30837, 1♂(Sta. 28, 9/vii/1986); 23°45'S 45°00'W, 46m depth, MZSP 30842, 1♂(Sta. 19, 20/iv/1986); 23°46'S 45°09'W, 35m depth, MZSP 30843,3 ♂, 2♀ (Sta. 32, 10/vii/1986); 23°47'S 45°10'W, 35m depth, MZSP 30821, 1a MZSP 30835, 2 specimens (Sta. 14, 21/i/1986); 23°47'S 45°13'W, 36m depth, MZSP 30845, 1♂(Sta. 23, 19/iv/1986); 23°47'S 45°58'W, 47m depth, MZSP 30835, 5 specimens (Sta. 4854, 17/xii/1985); 23°47'S 44°58.2'W, 50m depth, MZSP 30831, 6 specimens (Sta. 4949, 27/vii/1986); 23°49'S 44°39.4'S, 77m depth, MZSP 30822, 4 specimens (Sta. 4947, 26/vii/1986); 23°50'S 45°10'W, 40m depth, MZSP 30829, 3 specimens (Sta. 22, 19/iv/1986); 24°08'S 45°01'W, 76m depth, MZSP 30833, 1 specimen (Sta. 4858, 18/xii/1985); 24°08.5'S 45°01.5'W, 79 m depth, MZSP 30824, 2 specimens (Sta. 4953, 28/vii/1986); 24°13.1'S 44°45.2'W, 117m depth, MZSP 30827, 14 specimens, MZSP 30832, 9 specimens (Sta. 4951, 27/vii/1986); 24°22'S 44°54'W, 102m depth, MZSP 30830, 1 specimen (Sta. 4859, 18/xii/1985); 24°22'S 44°54.5'W, 101m depth, MZSP 30844, 3 specimens (Sta. 4954, 29/vii/1986); Anchieta Island, MZSP 30840, 24 specimens (28/ii/1962).

Discussion. *Ca. centralis* is very similar to the type species of the genus, *Ca. chinensis* (Linné). Giese (1915) studied the genital system of this species. *Ca. centralis* differs from *Ca. chinensis* by simple fashion of penis tip (lacking the special fold and papilla) and by lacking seminal receptacle in pallial oviduct (Giese, 1915, pl. 8, figs 1a, b).

Genus *Crucibulum* Schumacher, 1817

(Type species: *C. rugosa-costatum* Schumacher = *Patella auricula* Gmelin, 1791)

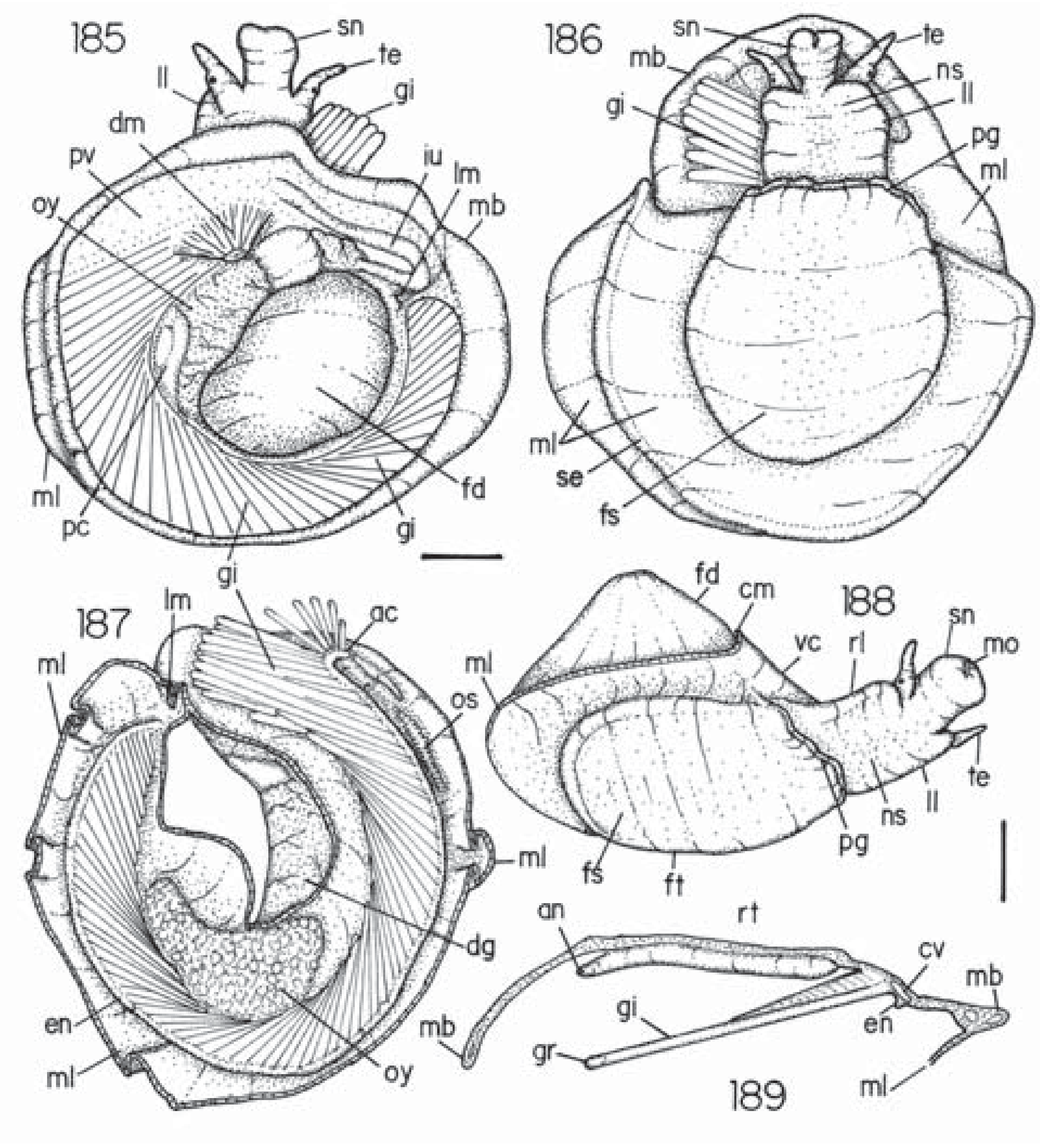
Crucibulum auricula (Gmelin, 1791)

(Figs. 15-17, 58, 59, 185-206)

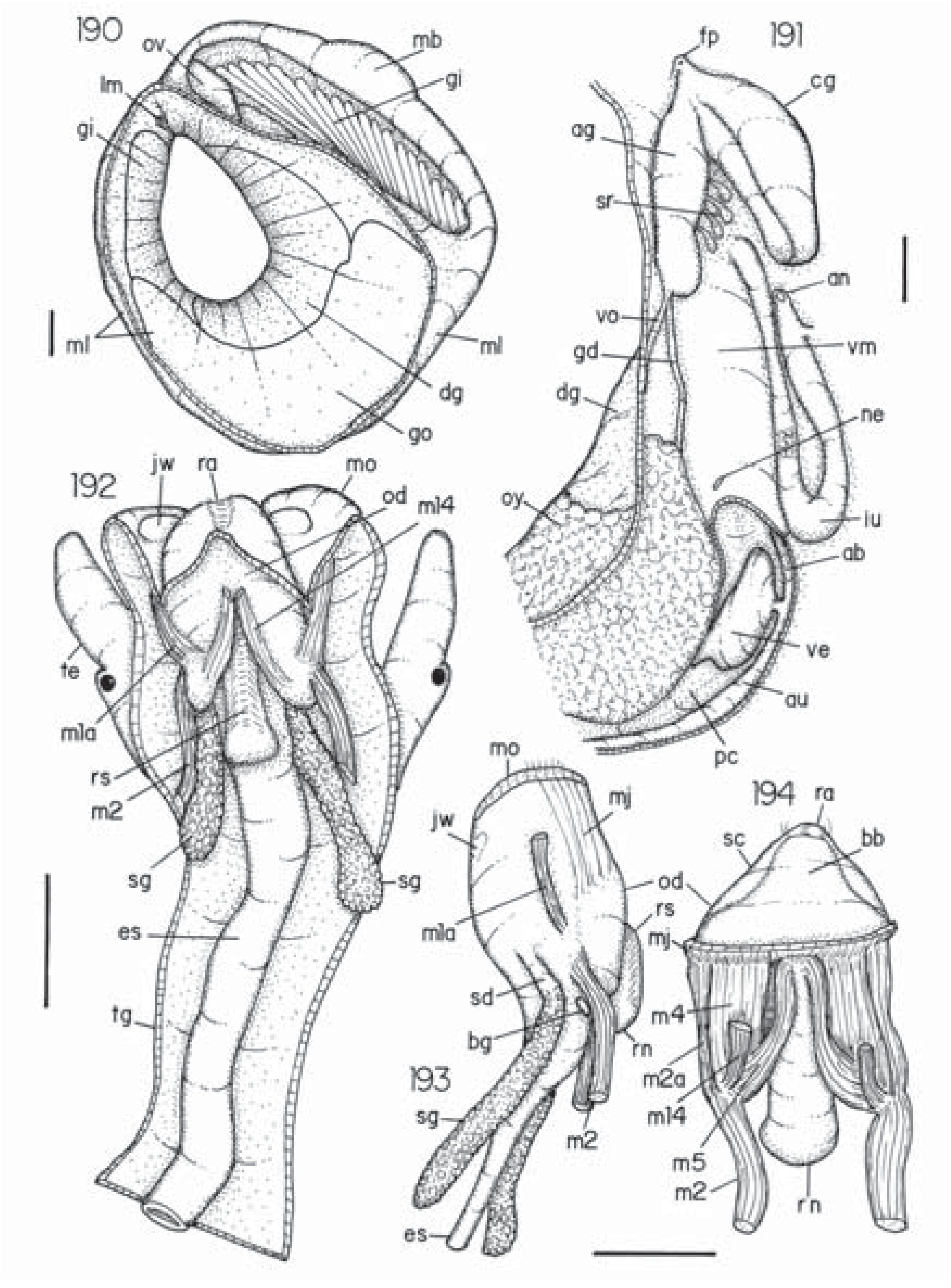
Patella auricula Gmelin, 1791: 3694.

Calyptraea (Calypeopsis) auriculata: Orbigny, 1845: 461.

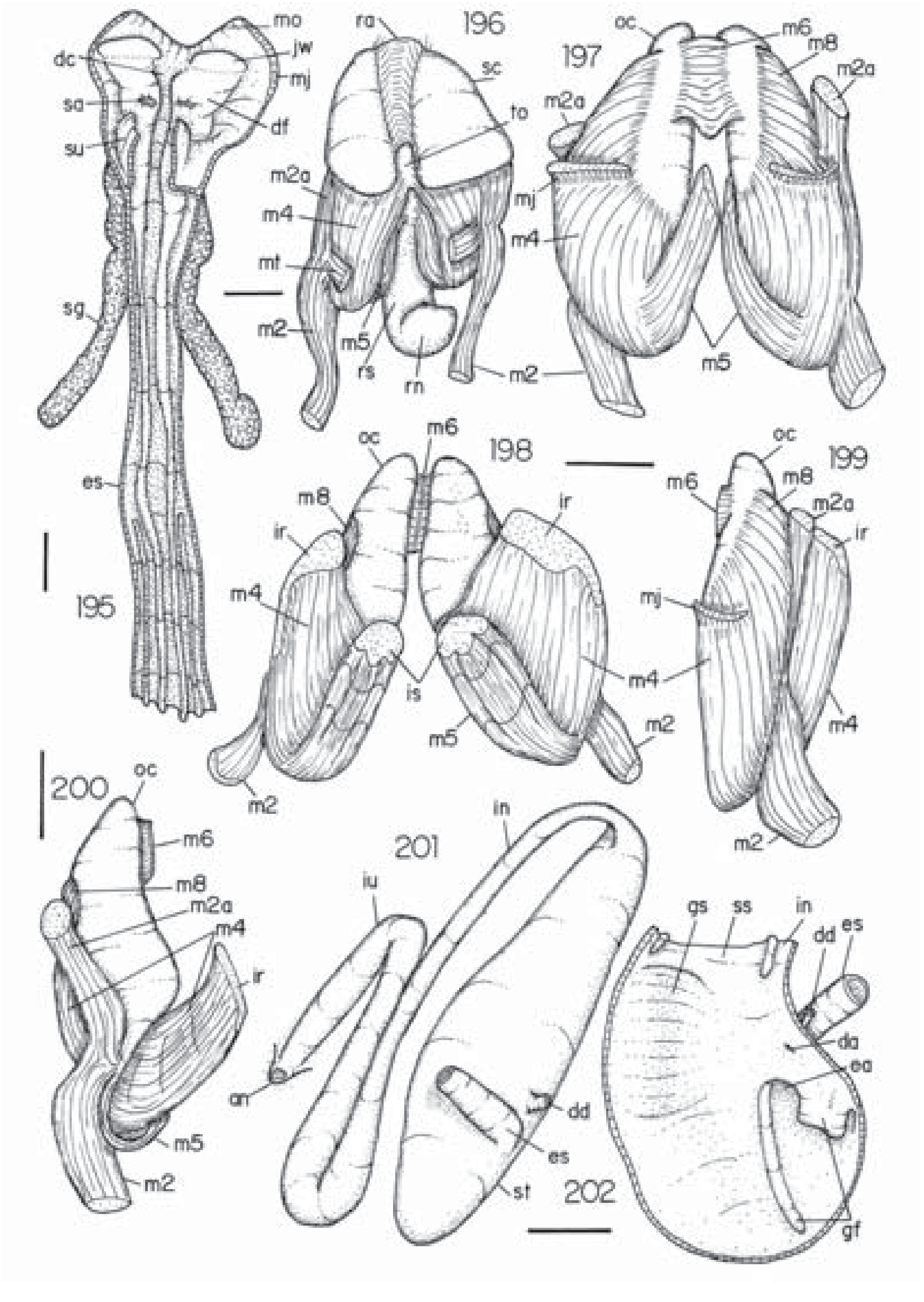
Crucibulum auricula: Abbott, 1954: 169 (pl. 21s); Warmke & Abbott, 1961: 86 (pl. 15, fig. n); Rios, 1970: 55; 1975: 65 (pl. 17, fig. 263); Bandel, 1976: 263; Rios, 1985: 59 (pl. 21, fig. 264); Penchaszadeh, 1985: 237; Jong & Coomans, 1988:62; Rios, 1994: 71 (pl. 24, fig. 275); Merlano & Hegedus, 1994: 160 (pl. 50, fig. 584); Abbott & Morris, 1995: 180 (pl. 49).



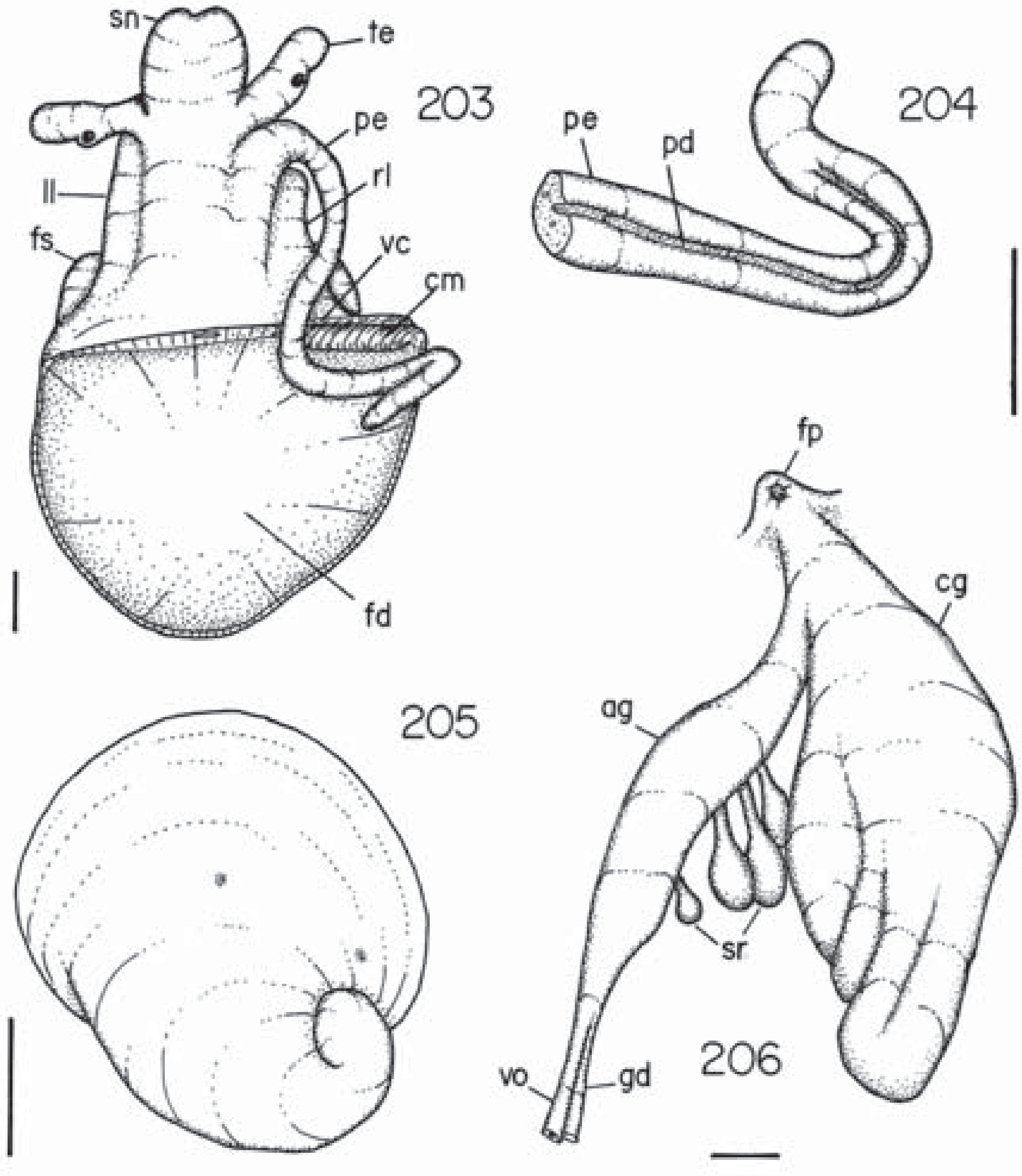
Figures 185-189, *Crucibulum auricula* anatomy: **185**, female extracted from shell, dorsal view; **186**, same, ventral view; **187**, visceral mass and pallial cavity roof, ventral view, mantle sectioned ventrally to expose inner structures; **188**, head-foot, lateral-right view, visceral mass and pallial organs extracted; **189**, pallial cavity roof, transversal section of its middle region, parallel to rectum. Scales = 2 mm.



Figures 190-194, *Crucibulum auricula* anatomy: **190**, pallial cavity and visceral mass, ventral view, seen as just extracted from head-foot; **191**, anterior region of visceral mass and pallial oviduct, ventral view, ventral wall of pericardium removed; **192**, head and haemocoel, ventral view, foot and neck ventral surface extracted, net of transversal muscles not drawn; **193**, buccal mass and adjacent esophagus, lateral-right view; **194**, odontophore, ventral view. Scales = 1 mm.



Figures 195-202, *Crucibulum auricula* anatomy: **195**, dorsal wall of buccal mass and esophagus opened longitudinally, ventral view; **196**, odontophore, dorsal view, superficial layer of membrane and muscles removed; **197**, same, ventral view, only more internal muscles exposed cartilages partially deflected; **198**, same, dorsal view; **199**, same, right side only, ventral view; **200**, same, dorsal-inner view, most of muscles deflected externally; **201**, digestive tubes seen if remainder structures were transparent, ventral view; **202**, stomach, ventral view, inner surface exposed by a longitudinal incision. Scales = 0.5 mm, except 201-202 = 1 mm.



Figures 203-206, *Crucibulum auricula* anatomy: **203**, head-foot of male, dorsal view; **204**, detail of apical region of penis; **205**, young specimens found within capsules attached to neck ventral surface; **206**, pallial oviduct, ventral view. Scales = 0.5 mm, except 205 = 0.25 mm.

Crucibulum auriculum: Bandel & Riedel, 1994: 342-343 (pl. 7, fig. 9-10).

Description.

Shell (Figs. 15-17). Limpet-like, conical, low, with strong radial ridges. Ventral shelly septum conical, inserted about in center of ventral shell surface (Figs. 15, 17). Anterior margin of ventral plate slightly straight; its right region shorter than left one. Other details in Orbigny (1845).

Head-foot (Figs. 186, 188, 192, 203). Head and neck regions similar to those of *Crepidula* spp, including neck ventral surface and lateral flaps. Tentacles stubby, long, without ommatophores; basal half clearly broader than distal half. Eyes located in middle-outer region of tentacles. Haemocoel long and narrow, transverse muscular fibers scanty. Foot sole planar, its anterior margin covering short area of neck's ventral surface, and possessing furrow of pedal gland. Foot dorsal surface very tall, conic, with rounded tip, solid-muscular (Fig. 188); this region fits inside shell septum. Posterior and lateral edges of foot sole connected to mantle (surrounding shell ventral plate border); anterior edge connected to visceral mass (also surrounding anterior border of shell septum). Columellar muscle (or muscle attached to anterior shell septum edge) very thin, almost missing, some transversal muscular fibers in anterior edge of shell ventral plate, more clear at right. Columellar muscle weakly proportionally larger in small specimens (Fig. 203).

Mantle organs (Figs. 185-187, 189, 190). Mantle covers entire ventral surface of shell and also presents another region from shell margin to border of its ventral plate, restricting pallial cavity. Mantle, in shell ventral plate border, inserts in lateral and posterior region between foot sole and its dorsal surface; very thin mantle portion also covers dorsal surface of foot, which secretes ventral surface of shell ventral plate. Dorsal shell muscle present, inserts just anterior to shell septum, close median line; its fibers spread like fan for a short distance and connect in adjacent region of mantle (Fig. 185). Lateral shell muscle small, located in shallow furrow between posterior and anterior ends of pallial cavity (Figs. 185-187, 190: lm). Pallial aperture relatively small (Fig. 190), if animal is compared to a clock, it begins at 12 and finishes at 2 o'clock. Pallial cavity occupies space between shell ventral surface and dorsal surface of the septum (except a portion at right side occupied by visceral mass); in larger specimens, pallial cavity "posterior" end touches anterior end, becoming almost complete ring (there is no communication between both extremities), separated by shallow furrow (Figs. 187, 190). In smaller specimens a larger space between both extremities of pallial cavity. Osphradium long, bipectinate, parallel to mantle border, occupying left half of pallial aperture. Osphradium leaflets slightly thick. Gill very large, continues all along circular pallial cavity. Gill anterior extremity on mantle border, located near right border of pallial aperture. A slight tall fold begins in gill anterior extremity, runs on mantle border towards left, and finishes close right extremity of osphradium (Fig. 187). Ctenidial vein edges outer margin of gill and pallial cavity, with uniform width along its length. Endostyle narrow, running in ventral surface of ctenidial vein (Fig. 189); its anterior and posterior end just close to those of gill. Gill filaments similar to those described for *Crepidula* spp., with tall, rigid straight rod; apical region of rod thicker, connected with same region of neighbor filaments by cilia. Posterior and middle gill filaments almost of same length, in anterior region they gradually lengthen; close to anterior extremity they suddenly become short, with gill axis turned forward. Between gill and shell ventral plate (in posterior 1/3) and between gill and visceral mass (in anterior 2/3 of pallial cavity length) very narrow space without detectable hypobranchial gland.

Visceral mass (Figs. 187, 190, 191). Surrounds left and posterior regions of outer surface of shell septum. If compared to a clock, begins at 3 and finishes at 8 o'clock, broader in its median region. Large stomach as central structure. Digestive gland surrounds stomach, mainly in its ventral and posterior surfaces. Gonad occupies anterior region, mainly close to region where visceral mass connects with head-foot. Pericardium, last intestinal loop and pallial oviduct as outer limits of visceral mass.

Circulatory and excretory systems (Fig. 191). Pericardium extremely narrow and long, begins in posterior end of pallial cavity, contours posterior region of gill, runs edging inner margin of pallial cavity posterior region, also outer margin of visceral mass up to opposite side of pallial cavity, in this final region pericardium enlarges. Auricle very narrow and long, with same length as pericardium; in its final portion stay external to ventricle. Ventricle elliptical, thick walled, connected not in auricle end, but before it, having portion of auricle beyond ventricle connection as blind-sac. Approximately in opposite side of ventricle connection, origin of anterior and posterior aortas, similar to *Crepidula* spp. Kidney very small, dorso-ventrally flattened, almost all solid-glandular; located just in right border of pericardium, compressed dorsally by digestive gland. Nephrostome a small slit in left region of membrane between kidney and pallial cavity.

Digestive system (Figs. 192-202). Buccal mass characters similar to those of *Crepidula* spp, differences or notable features following. Jaw plates broad, slightly thicker. Pair of dorsal inner folds of buccal mass broad, between both a shallow groove (Fig. 195). Aperture of salivary glands slightly ample, transversal, located posterior, almost at level of septum that separates esophageal from odontophoric part of buccal mass. Odontophore muscles (Figs. 193-200) very similar to those described for *Crepidula*, except for smaller and thinner horizontal muscle (**m6**) and **m14**, and space separating insertions of m6 from m8 and m4. Radula (Figs. 58, 59) similar to those of *Crepidula* spp.; rachidian tooth with five to seven triangular cusps, central cusp about double size of neighboring cusps; lateral tooth with eight to 10 triangular cusps, second or third cusp larger and apical (about three times neighboring cusp width), lateral half of tooth edge smooth, somewhat thick; marginal teeth long, tall, slender, apex sharp and curved, about five sub-terminal, triangular cusps in inner edge; outer marginal tooth more flattened and about twice broader than inner marginal tooth. Salivary glands narrow and long, with about same length as buccal mass (Figs. 192, 195). Esophagus narrow and long. Anterior esophagus with pair of broad longitudinal folds as continuation of those of dorsal buccal mass wall. Posterior esophagus with four or five similar sized longitudinal folds, two of them are continuation (but narrower) of those from anterior esophagus. Stomach large, long, slightly elliptical (Figs. 201, 202). Esophagus inserts in inner-ventral surface of stomach. Duct to digestive gland narrow, single, located near to esophageal insertion, slightly closer to intestinal portion of stomach. Stomach inner surface (Fig. 202) with tall, transversal and narrow fold located just ventral to esophageal insertion; other low and long folds runs from dorsal region of esophageal aperture towards posterior, in blind-sac portion of stomach suddenly faint. Gastric shield ample, circular, thin, located in opposite side of esophageal aperture just posterior region to style sac. A pair of low, longitudinal folds separate intestinal from style sac branches of stomach, similar to those described for preceding species; intestinal branch very narrower. Intestinal loops simpler to those of *Crepidula* spp. (Figs. 191, 201); after steep end of style sac, intestine suddenly runs anteriorly parallel to stomach axis, at level of end of stomach, suddenly turns towards posterior and runs parallel, external and close to its preceding loop along about half of its length, where suddenly turns towards anterior; this final loop runs parallel, external and close to preceding loop for about 2/3 of its length, up to anus. Several small, elliptical fecal pellets fill intestinal lumen. Anus small, siphoned, located in pallial oviduct base, in right extremity of pallial cavity (Fig. 191).

Genital system. **Development**. Protandric hermaphrodite, with all examined small specimens male (but few small specimens were available). Some specimens present one or two spherical capsules weakly attached to neck ventral surface, within each capsule about 15 young specimens in same developmental stage, without operculum (Fig. 205). Other details of capsules in Bandel (1976: 263).

Male (Figs. 203, 204). Testis very small, situated in posterior-ventral region of visceral mass, from which very narrow sperm duct runs towards anterior. Seminal vesicle with several coils, color clear beige, located almost on opposite side than testis, in anterior extremity of visceral mass, opens to pallial cavity in middle level of right surface of pallial floor. Pallial sperm groove very shallow, difficult to see. Penis very long (about same length as that of head-foot), coiled within pallial cavity. Penis origin just posterior to right tentacle. Penis with uniform width along its length, tip rounded. Penis sperm groove run in central region of penis ventral surface, finished at some distance from tip.

Female (Fig. 206). Ovary large, color cream, occupies anterior and ventral regions of visceral mass (Figs. 185, 190, 191). Visceral oviduct runs on visceral mass ventral surface towards anterior and right. Gonopericardial duct long, narrow, runs from right extremity of pericardium towards right, joining with oviduct where it inserts in albumen gland. Albumen gland long, thick walled, duct central, slight broad. Series of four seminal receptacles inserts in anterior surface of albumen gland, central vesicles larger. Capsule gland large (about twice albumen gland size), walls very thick, irregular, glandular. Capsule gland lumen broad, dorso-ventrally flattened, as blind-sac. Both lumen of albumen and capsule glands unite with each other anteriorly forming short vaginal tube. Genital pore small, in tip of small papilla.

Habitat. On hard substrates, mainly shells of other molluscs, from intertidal to 79 m depth.

Distribution. From North Carolina, USA, to Paraíba, Brazil.

Measurements of shells (in mm). MZSP 30818, ♀1, 6.6 by 27.8;♀2, 6.8 by 26.2;♀5, 7.1 by 24.7; MZSP 30819,♀4, 6.7 by 25.4.

Material examined. VENEZUELA; **Isla Margarita** (Simone col.); Between Ponta Mosquito and Isla Coche, MZSP 30818, 3♂, 8♀ (6/ii/1995); Pedro Gonzales, Playa Puerto Cruz, MZSP 30819, 4♀(4/ii/1995); Porlamar, Guaraguao Bay, Playa Bella Vista, MZSP 30820, 3♂, 3♀ (2/ii/1995).

Crucibulum quiriquinae (Lesson, 1830)

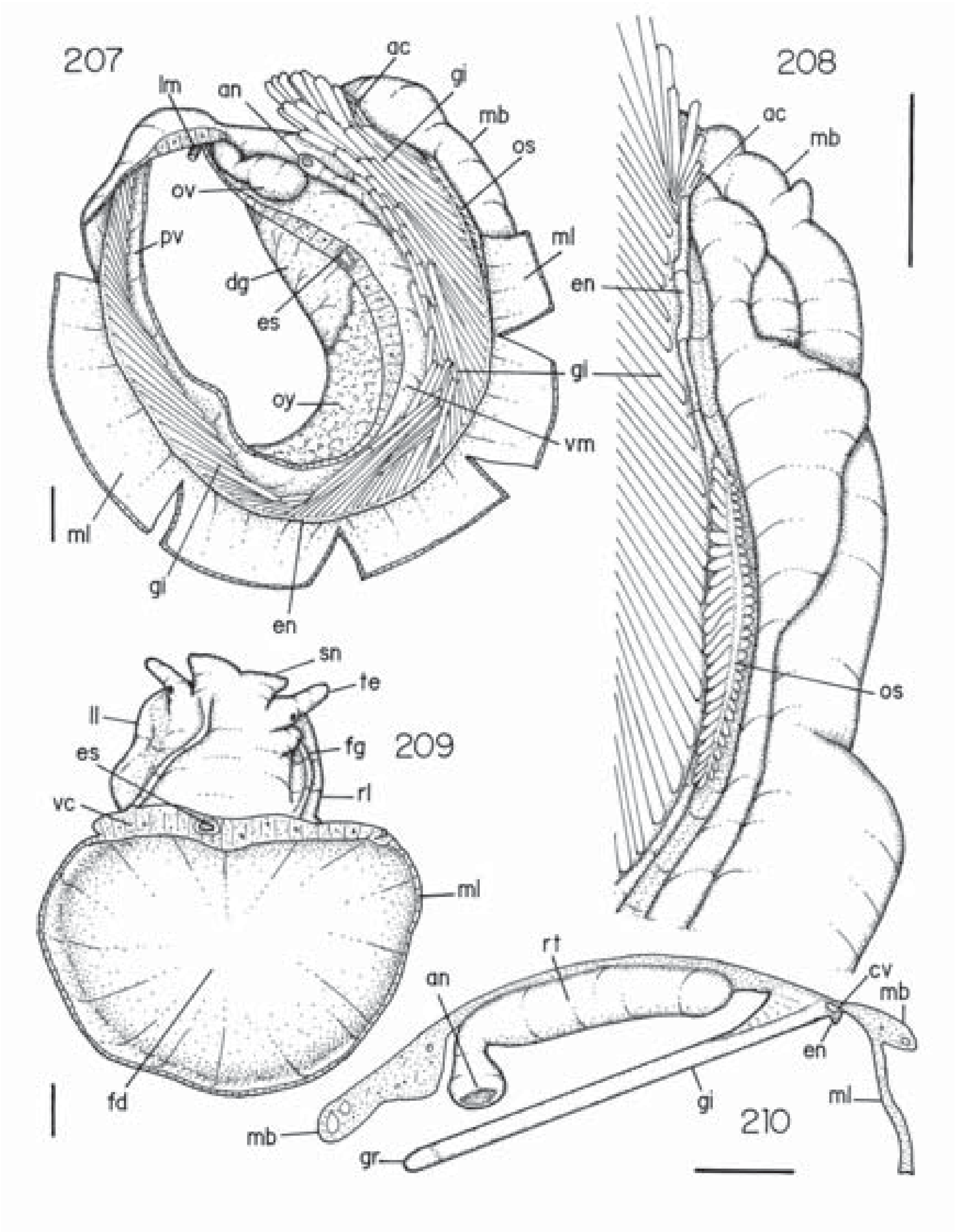
(Figs. 18, 19, 68, 69, 207-226)

Crucibulum quiriquinae: Keen, 1971: 463; Véliz et al., 2001: 527-533 (fig. 2a-e, 3a-c).

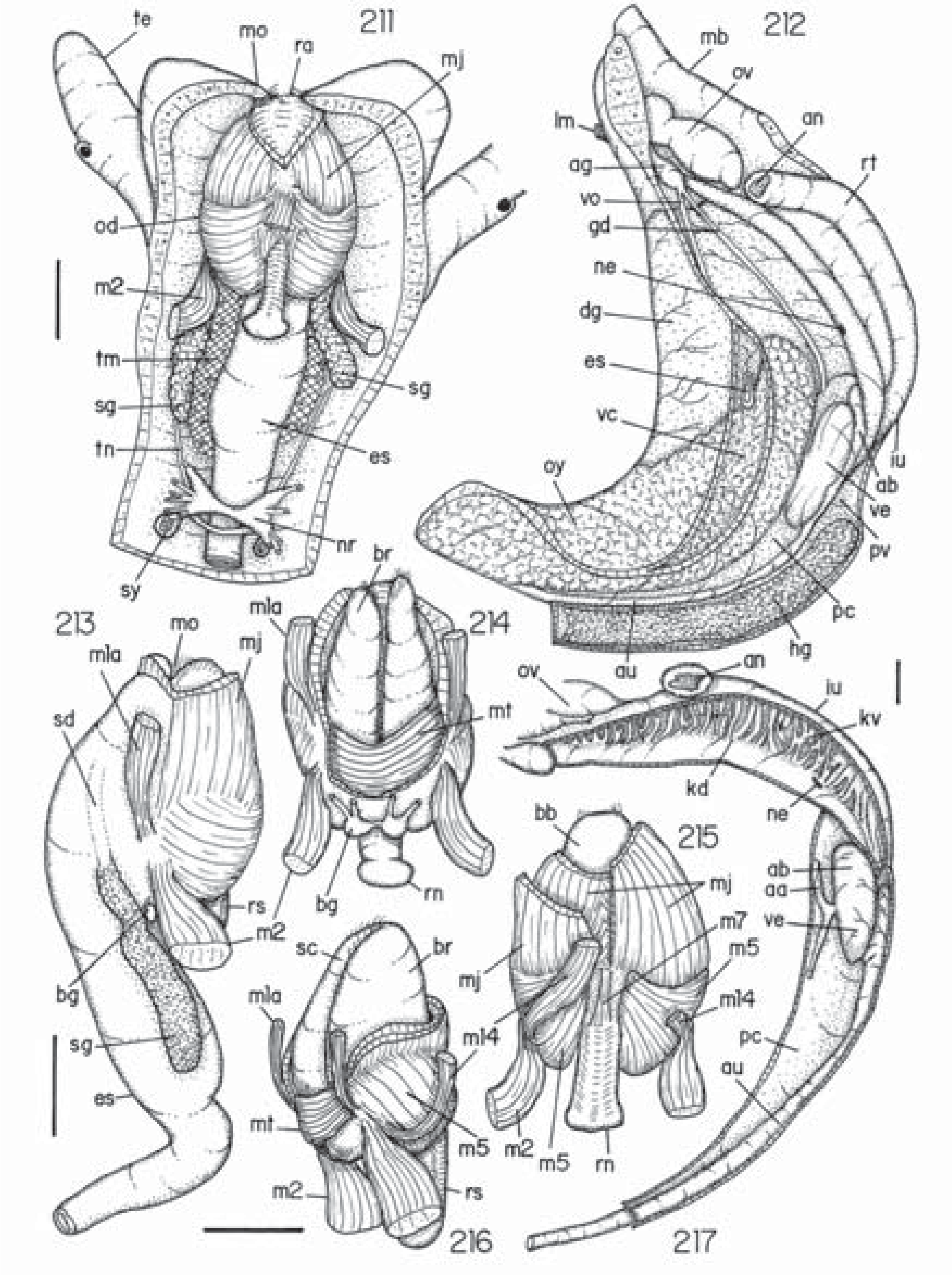
Description.

Shell (Figs. 18, 19). Similar to that of *C. auricula*, but larger (up to 35 mm) and taller. Sculpture several radial, low ribs. Shell ventral plate also similar to *C. auricula*. Other details in Keen (1971) and Véliz et al. (2001).

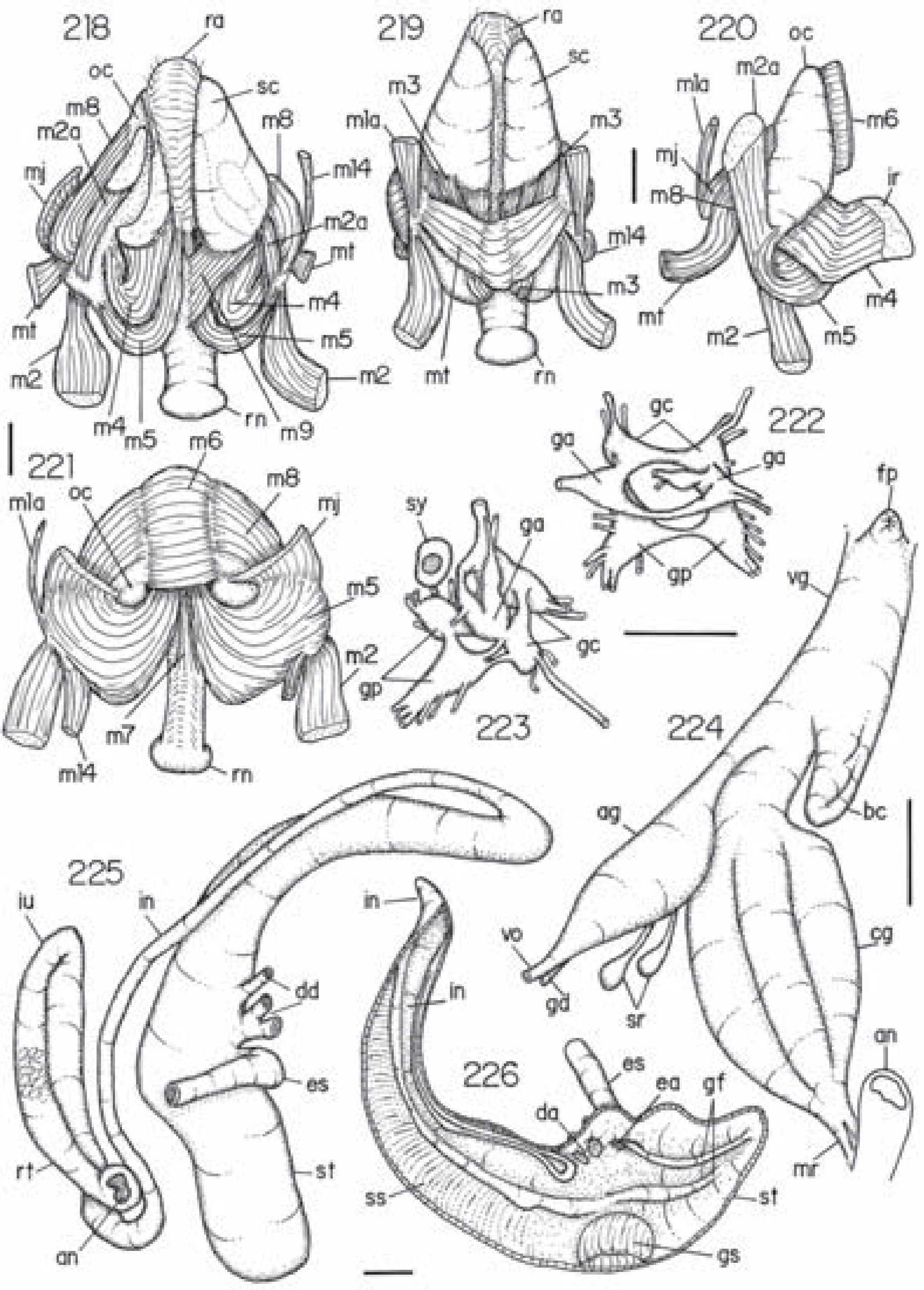
Head-foot (Figs. 209, 211). Very similar to that of *C. auricula*, including neck ventral surface and tall, conic, solid foot. Distinctive features following. A tall fold runs in left surface of pallial floor and dorsal surface of head, from posterior to anterior, suddenly faint in snout base. Tentacles with small ommatophores in its middle-outer region. Haemocoel with net of transverse muscle small, but differ-



Figures 207-210, *Crucibulum quiriquinae* anatomy: **207**, pallial cavity roof, ventral view, mantle sectioned in ventral surface for exposition of inner structures; **208**, same, detail of region between anterior extremity of gill and osphradium; **209**, head-foot, female, dorsal view, that longitudinal fold of right side of head present in all examined specimens; **210**, pallial cavity roof, transversal section of its middle region, parallel to rectum. Scales = 2 mm.



Figures 211-217, *Crucibulum quiriquinae* anatomy: **211**, head and haemocoel, ventral view, foot and neck ventral surface extracted, snout opened longitudinally; **212**, whole view of visceral mass and adjacent anterior region of pallial cavity, ventral view, heart seen by transparency; **213**, buccal mass and adjacent esophagus, lateral-right view; **214**, odontophore, dorsal view; **215**, same, ventral view, mj not symmetrically extracted; **216**, same, lateral-right view; **217**, kidney and pericardium, ventral view, ventral wall of pericardium extracted, ventral wall of kidney sectioned longitudinally and deflected downwards. Scales = 1 mm.



Figures 218-226, *Crucibulum quiriquinae* anatomy: **218**, odontophore, dorsal view, superficial membrane and muscles removed, most of muscles deflected, part of left side of subradular cartilage also removed (only insertions of muscles preserved), mt sectioned and deflected; **219**, same, before section of mt and sc; **220**, same, only left structures, most of muscles deflected for cartilage exposure; **221**, same, dorsal view, most of muscles deflected; **222**, nerve ring, ventral view; **223**, same, lateral-right view, only one statocyst shown; **224**, pallial oviduct, ventral view, anus also shown; **225**, digestive tubes, ventral view, seen if remainder structures were transparent, **226**, stomach opened longitudinally, ventral view. Scales = 1 mm.

entiable; not passing through salivary gland (Fig. 211).

Mantle organs (Figs. 207, 208, 210, 212). Mantle border characters similar to those of *C. auricula*, inclusive restriction of lateral and posterior regions of pallial cavity. Mantle border more complex in region of mantle aperture, with folds shown in fig. 208. Arrangement and characters of pallial organs similar to those of *C. auricula*. Osphradium bipectinate, located in left half of pallial aperture. Osphradium leaflets slight thick, anterior filaments shorter than posterior ones. Gill anterior extremity on mantle border, almost straight, far from osphradium. Endostyle tall, on ventral surface of ctenidial vein (Fig. 210). Hypobranchial gland more developed, runs as low ridge in anterior area between gill and visceral mass.

Visceral mass (Figs. 207, 212). Similar to that of *C. auricula*.

Circulatory and excretory systems (Figs. 212, 217). Pericardium and heart characters similar to those of *C. auricula*, with extremely long auricle, but ventricle located more anteriorly. Kidney larger and more complex than that of *C. auricula*. Inner renal space almost entirely filled by several irregular, glandular folds, no clear separation in lobes. Kidney stays compressed between gonad and adjacent intestinal loop. Ventral membrane that separates kidney from pallial cavity almost entirely free from glandular folds. Nephrostome a small slit in posterior (left) region of this membrane.

Digestive system (Figs. 211, 213-215, 218-221, 225, 226). Buccal mass characters (Figs. 211, 213) similar to those of *C. auricula*, except that dorsal wall inner surface presents aperture of salivary glands more anterior (closer to jaws) and longitudinal disposed. Buccal mass and odontophore muscles also similar to those of *Crepidula* spp and *C. auricula* (Figs. 211-215, 218-221), but with stronger muscles; **m6** (horizontal muscle) broader and thicker, with insertion closer to m8 and m4 origins; **m3** pair of small muscles, origin in posterior-medial region of odontophore, runs dorsally covered by mt, inserts on subradular membrane dorsal margin; **mj** thicker, with two muscular layers. Radula (Figs. 68, 69) similar to that of *C. auricula*; rachidian tooth with five to seven triangular cusps, central cusp with about three times width of neighboring cusps; lateral tooth with about seven cusps, second or third cusp apical and very large (more than three times width of neighboring cusps); marginal teeth with long, sharp apical region without cusps, three or four sharp cusps located in inner edge, on base of tooth apex (about in 2/3 of their length). Esophageal characters as those of *C. auricula*. Stomach location similar to that of *C. auricula*. Stomach characters, however, differs by (Figs. 225, 226): stomach form much longer and more slender, esophagus and two or three ducts to digestive gland connect about in middle region of gastric posterior surface (esophagus at right) close with each other. Stomach inner surface with pair of parallel folds in dorsal surface of gastric bind-sac portion, one of them originates in esophageal aperture. Gastric shield proportionally small, just in beginning of style sac portion of stomach. Intestinal and style sac branches of stomach long — about twice of remainder gastric regions length. Both branches separated from each other by pair of longitudinal folds, dorsal fold tall, ventral fold double and slender, both components of ventral folds connects close to digestive gland ducts as small ring, distally (in level where style sac finishes) fused to each other. Style sac with series of low transversal folds covered by chitin. Intestinal loops similar to those of *C. auricula* (Fig. 225), but with first portion (running parallel to stomach) much longer and more slender. Last intestinal loops replete with small, elliptical fecal pellets. Anus broad, siphoned, close to pallial oviduct base (Figs. 207, 212).

Genital system (Fig. 224). Only females examined. Ovary concentrated in anterior-left region of visceral mass, where it connects with head-foot (Figs. 207, 212). Visceral oviduct and gonopericardial duct similar to those of *C. auricula*, both very long and slender. Pallial oviduct characters also similar to those of *C. auricula*, differing by: fewer seminal receptacles connected to albumen gland (only two); vaginal tube very longer (extends after connection of albumen and capsule glands), has secondary diverticulum located in its posterior region turned towards capsule gland. Genital pore small, in apex of small papilla.

Nervous system (Figs. 211, 222, 223). Similar to those of *Crepidula* spp. In having large, concentrated ganglia. Differs in having additional ventral connective contouring esophagus, just posterior to connective of pedal ganglia. This additional connective apparently connects both parietal ganglia, but further studies are still necessary.

Habitat. See Véliz et al. (2001).

Distribution. South Peru to Chile.

Measurements of shells (in mm). MZSP 30817,♀1, 16.4 by 30.5;♀2, 22.0 by 32.9.

Material examined. CHILE, MZSP 30817, 3♀.

Discussion. Véliz et al. (2001) have pointed out that in Chile there are 2 species identifiable as *C. quiriquinae*. The shells of the specimens examined here are similar to their called “population I”, typical for the species.

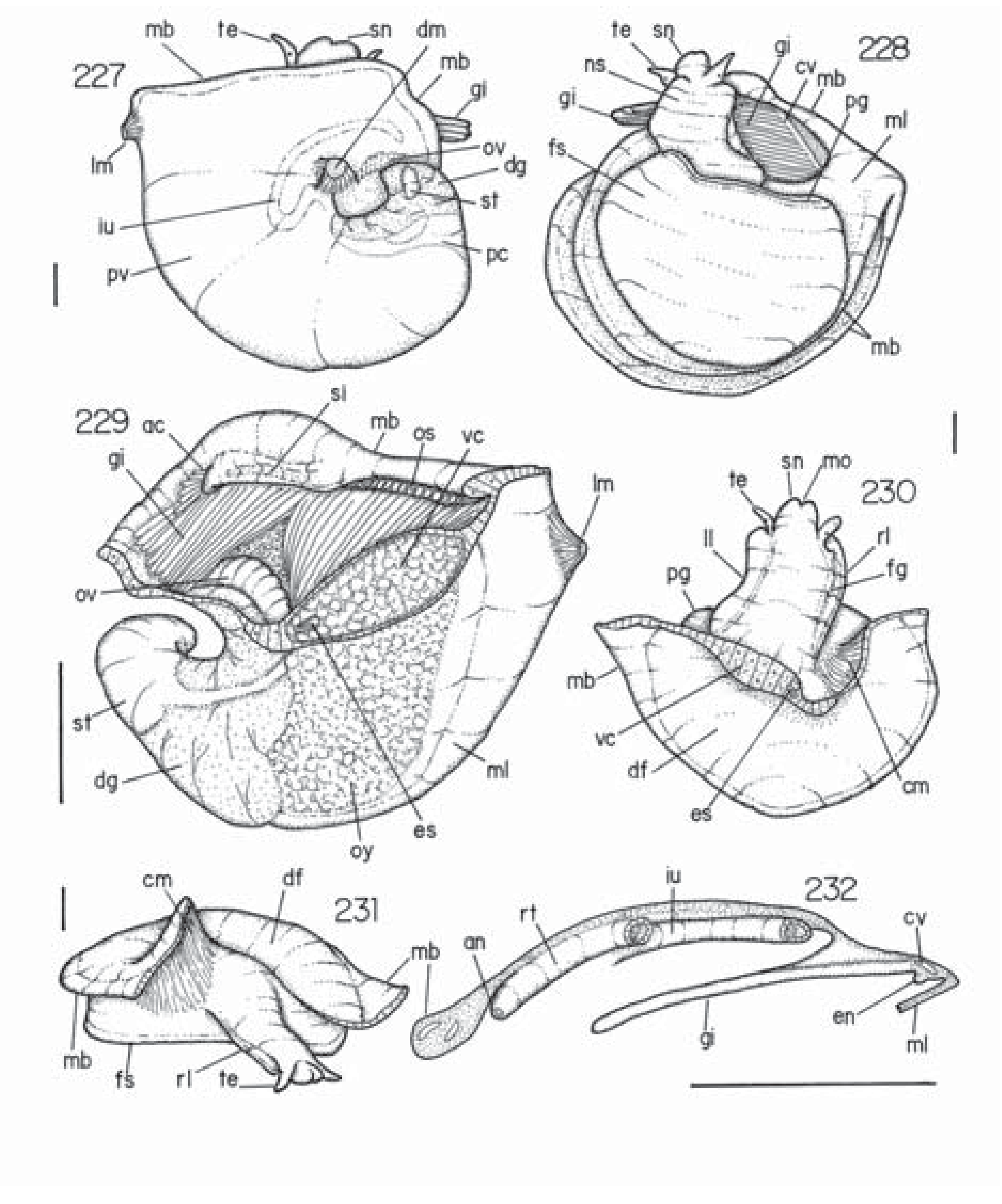
Genus *Trochita* Schumacher, 1817

(Type species: *Patella trochiformis* Born)

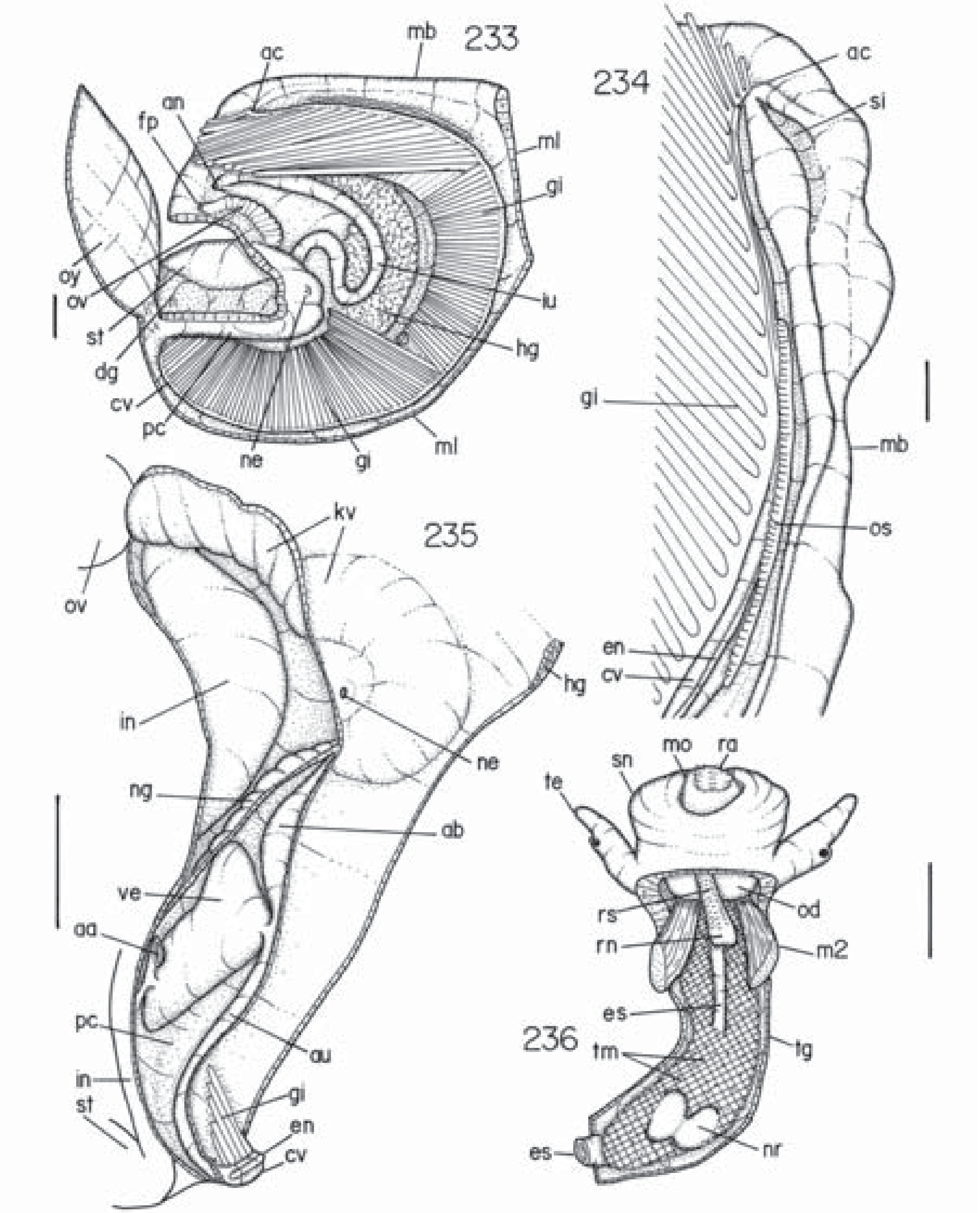
Trochita trochiformis (Born, 1778)

(Figs. 20, 21, 72, 73, 227-251)

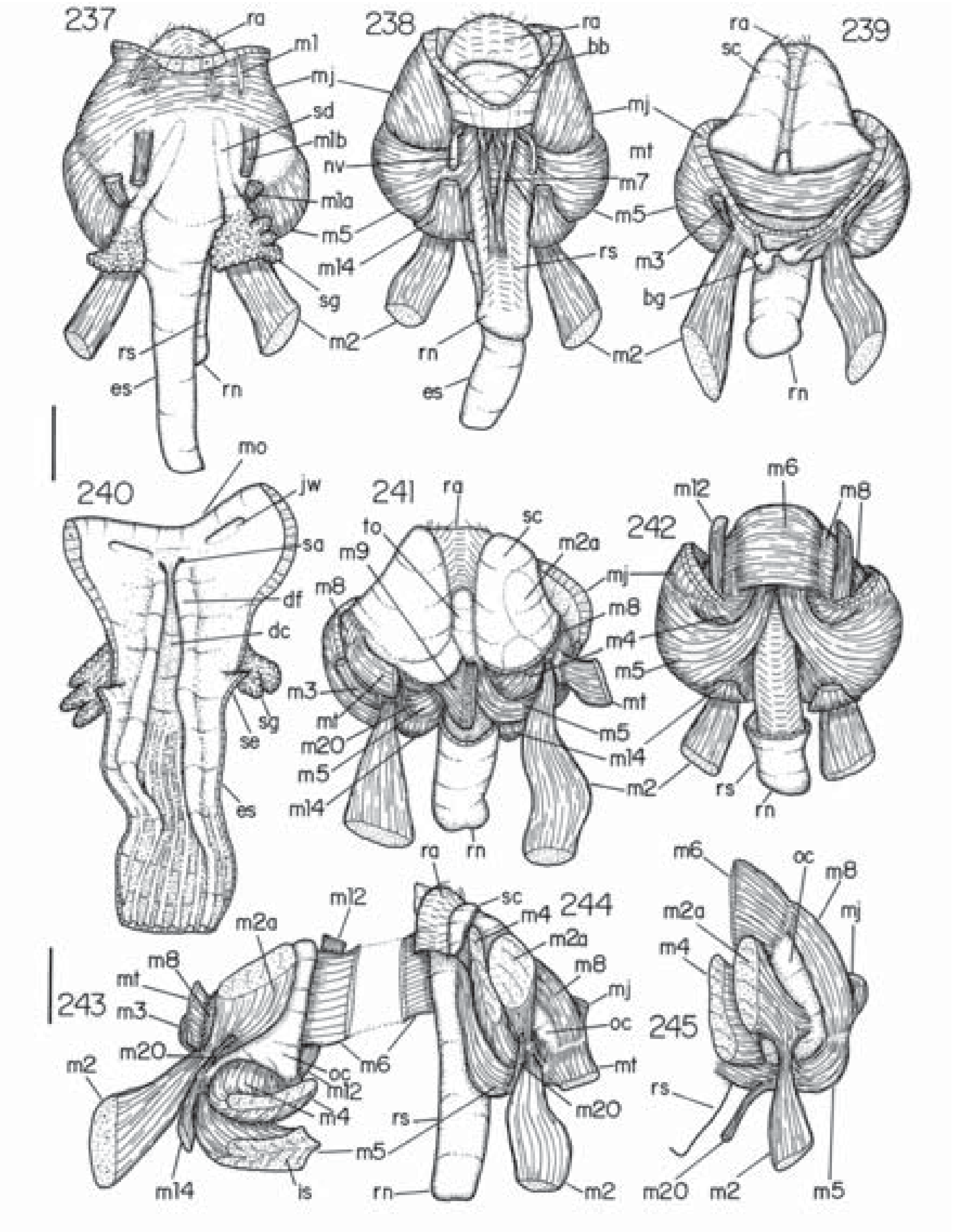
Ancient synonymy in Orbigny (1846: 461). Complement:



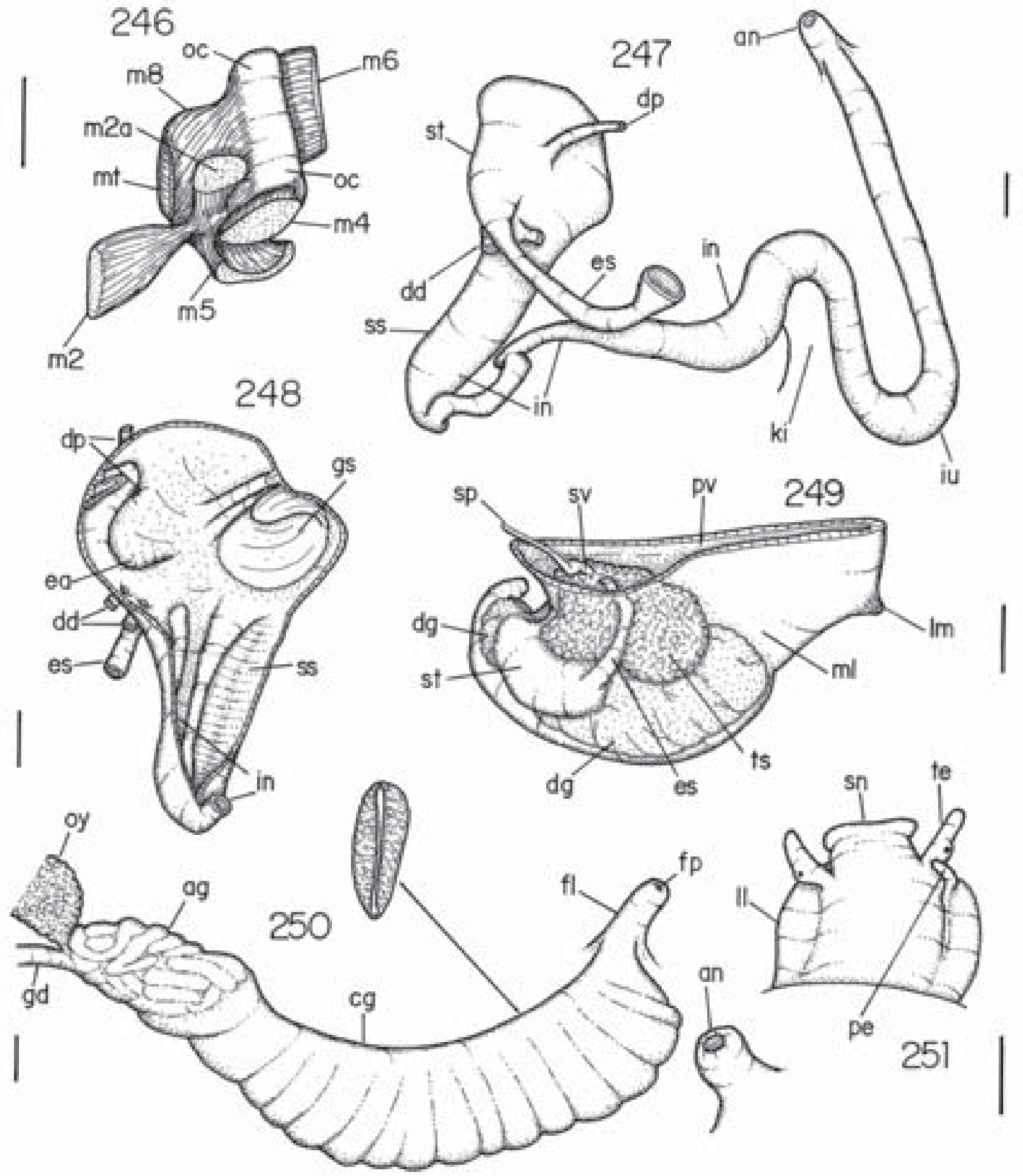
Figures. 227-232, *Trochita trochiformis* anatomy: **227**, whole view of a female extracted from shell, dorsal view; **228**, same, ventral view; **229**, pallial cavity and visceral mass, ventral view, head-foot extracted; **230**, head-foot, dorsal view; **231**, same, frontal view; **232**, pallial cavity roof, transversal section tangential to rectum. Scales = 5 mm.



Figures. 233-236, *Trochita trochiformis* anatomy: **233**, pallial cavity, ventral-inner view, visceral mass lying in floor of this cavity deflected to left, some gill filaments in central gill region removed; **234**, same, detail of the osphradium and gill anterior end; **235**, kidney and pericardium, ventral view, both sectioned longitudinally with inner structures exposed, adjacent surface of pallial cavity roof also shown; **236**, head and haemocoel, ventral view, foot removed. Scales = 2 mm, except 233 = 5 mm.



Figures. 237-245, *Trochita trochiformis* buccal mass: **237**, buccal mass, dorsal view; **238**, same, ventral view; 239 same, dorsal view, dorsal wall of buccal mass extracted; **240**, dorsal wall of buccal mass, ventral-inner view, anterior esophagus opened longitudinally; **241**, odontophore, dorsal view, mt and m9 sectioned and deflected in right side; **242**, same, ventral view, superficial membrane removed; **243**, same, dorsal view, left half only, most muscles deflected; **244**, same, right side only, most muscles in situ; **245**, same, ventral view, right side only, most muscles in situ. Scales = 1 mm.



Figures. 246-251, *Trochita trochiformis* anatomy: **246**, odontophore, dorsal view, left half only, several muscles sectioned close to their base; **247**, middle and distal digestive tubes, ventral view, seen in situ if remainder structure were transparent; **248**, stomach, ventral view, opened by means of a longitudinal incision along its ventral side, inner surface exposed; **249**, visceral mass, male, ventral view, posterior part of pallial cavity also shown; **250**, pallial oviduct, ventral view, anterior portion of visceral structures, anus, and a transversal section in indicated level also shown; **251**, head and neck, male, dorsal view. Scales = 1 mm.

Calyptraea (Trochatella) trochiformis: Orbigny, 1846: 464-642 (pl. 59, fig. 3).

Calyptraea (Trochita) trochiformis: Keen, 1971: 456 (fig. 804).

Trochita trochiformis: Abbott, 1974: 143.

Description

Shell (Figs. 20, 21). Slightly trochiform, conical, low, up to 4 whorls with almost straight profile. Spire paucispiral occupying about half of shell area. Sculpture several radial and irregular ridges. Periphery of shell septum extending little beyond whorls limit (similar to *Xenophora* species). Columella present, sinuous. Ventral surface of whorls almost straight. No umbilicus. Other details in Keen (1971: 456).

Head-foot (Figs. 228, 230, 231, 236, 251). Head and neck regions similar to those of preceding species, with slight retractile snout, neck ventral surface, lateral lappets and shallow food groove. A low, narrow fold runs longitudinally along left-dorsal side of most specimens. Foot a broad cylindrical muscular mass, ventral surface plane; dorsal surface spiral, increasing right-anteriorly. Columellar muscle well-developed, tall, triangular (Figs. 230, 231), located approximately at middle of foot right side; attached along shell columella. Dorsal surface of foot covered by thin layer of mantle, which extends, slightly thickened, little beyond dorsal foot margins. Sloped between this dorsal foot margin and foot sole a considerable distance, longer in columellar muscle region. Anterior margin of foot short, flap-like, possessing transversal furrow of pedal glands, extends anteriorly covered by basal portion of neck ventral surface as in preceding species.

Mantle organs (Figs. 227-229, 232-234). Mantle border slight thick, edges entire foot sole and also shell aperture; in left side restricts pallial aperture. If compared to a clock, pallial aperture begins about at 11 and finishes at 2 o'clock. Special arrangement of folds in middle-dorsal region of pallial aperture (Fig. 234). Dorsal shell muscle broad, located near columellar muscle, dislocated more anteriorly and medially. Lateral shell muscle slightly small, located in left-anterior extremity of pallial cavity external wall, just posterior to mantle border; connects this region of mantle to inner surface of left extremity of shell aperture (Figs. 227, 229). Pallial cavity very deep, slightly triangular and curved. Anterior region broad, larger than pallial aperture; gradually narrows towards posterior and left, penetrating through visceral mass by about 8/10 of whorl. Osphradium monopectinate, long, narrow; located compressed between gill and mantle border (Fig. 234) at about 2/3 of pallial aperture. Osphradium filaments slightly broad, rounded, small; situated edging tip. Gill very large, similar to those of preceding species. Anterior extremity on mantle border turned forwards in right region of pallial aperture. Gill filaments as described for other calyptraeids. Hypobranchial gland well-developed, mainly in anterior half of pallial cavity region between gill and visceral mass (Fig. 233), also extends, very thin, to neighboring areas. Visceral mass organs bulging into pallial cavity described below.

Visceral mass (Figs. 227, 229, 233, 249). With about ¾ whorl within shell spire, triangular, curved, with posterior extremity turned anteriorly and to left. Its anterior region divided, due to pallial cavity, into two portions: ventral and dorsal (Figs. 229, 233). Ventral portion flattened, broad and long (about 2/3 of pallial cavity length), situated between pallial cavity and shell ventral wall, becoming most of pallial cavity floor; constituted almost only by gonad and small portion of digestive gland at its posterior limit. Dorsal portion encroaching on pallial cavity roof, similar to those of *Crepidula* and *Calyptraea*. Except "U"-shaped intestinal loop, this is sigmoid and amply exposed in pallial cavity roof.

Circulatory and excretory systems (Fig. 235). Heart characters and location similar to those of *Crepidula* species, but shorter. Auricle also long and tubular, with blind-sac portion beyond ventricle connection. Kidney yellowish, with two lobes. Ventral lobe broad and tall, with shallow transversal folds, attached to intestine only in its broader right region. Dorsal lobe smaller, extends by pallial cavity roof as circular mass surrounding nephrostome, radial folded. Intestine runs along kidney, almost free from its lobes except at its right-anterior limit (as above described), however, there is very thin glandular renal tissue covering its ventral surface. Nephridial gland slight large, with transversal folds, covers almost entire membrane between kidney and pericardium chambers. Nephrostome a small slit in center of membrane between kidney and pallial cavity.

Digestive system (Figs. 236-248). Foregut characters similar to those of preceding species (Fig. 236). Buccal mass very large, its dorsal wall with two pairs of outstanding jugal muscles (Fig. 237): **m1a)** similar to those of preceding species but more developed, origin in dorsal wall of snout posterior to mouth, inserts deeply in odontophore lateral-ventral region close to m2 insertion; **m1b)** origin in posterior-dorsal inner surface of snout, insertion in middle region of buccal mass dorsal wall; **mj)** thick in ventral region and separated into two branches, very thin in dorsal region. Inner surface of buccal mass dorsal wall with pair of broad folds and shallow dorsal chamber (Fig. 240). Jaws very thin, broad and short. Odontophore muscles (Figs. 237-239, 241-246) similar to those of preceding species, with following distinctive or notable features: **m2a)** broader and shorter, insertion not direct in cartilages, but in m4, slightly dislocated from insertion of m2, i.e., does not look to be a continuation of m2 as in preceding species; **mt)** inserted in m8 and not in m4; **m4)** thinner, origin in outer surface of cartilages and only in small portion of their median-inner surface, origin amply connected with m8 and m2a, contours posterior border of cartilages, towards medial and anterior, inserts in subradular cartilage close to radula; **m5)** also inserts in ventral and dorsal sides of radular sac in each side, cover m4 pair in their entire posterior surface; **m8)** much broader, connected with cartilages in their lateral border, amply connected with m4 from which is difficult separated; **m9)** present, **m14)** pair lateral located; **m20)** small and narrow pair, origin in m5 just where it inserts in m4 and cartilage (in ventral-median region of odontophore), inserts in subradular cartilage in middle region of its posterior border. Odontophore cartilages slightly thin and narrow. Radula slightly long – about twice odontophore length. Radular teeth similar to preceding calyptraeids (Figs. 72, 73), with following remarks: rachidian tooth narrow, lacking cusps; lateral tooth with about double rachidian width, lacking cusps or with about 8 weak and small cusps in outer edge; inner marginal tooth tall, curved, tip pointed, with about 5 weak subterminal cusps in both sides; outer marginal tooth similar to inner marginal tooth but with about half of its width, tip sharp pointed, lacking cusps. Salivary glands two small, amorphous masses just in posterior and dorsal regions of buccal mass (Fig. 237); in short distance their ducts penetrates in dorsal wall and run towards anterior; open after considerable distance, in dorsal folds anterior limit. Buccal ganglion pair small, close median line (Fig. 239). Esophagus narrow and long. Esophageal inner surface with six to eight longitudinal, narrow, similar sized folds, being two of them narrow continuations of dorsal folds of buccal mass (Fig. 240). Stomach large, occupies most of visceral mass posterior space (Figs. 229, 233, 249). Stomach form slight conical-irregular, long, similar to those of preceding species (Figs. 247, 248). One to two (close located) anterior ducts and slight broad posterior duct to digestive gland. Style sac and intestine amply connected with each other, separated only by pair of folds. Stomach inner surface with pair of parallel folds beginning from esophageal and anterior duct to digestive gland apertures, edge posterior limit of gastric shield, gradually faint in approximately opposite side of esophageal aperture; in their middle region covers posterior duct to digestive gland. Gastric shield slight large, rounded, located just posterior to style sac. Digestive gland pale brown, slight small, covers some portions of stomach and posterior region of gonad. Intestine narrow and sinuous after end of style sac (Figs. 233, 247), crosses gradually from ventral to dorsal region of visceral mass, becoming slightly broader; cross through kidney and exits to pallial cavity. In pallial cavity roof presents two slight ample loops. Rectum cross from left to right sides up to right-anterior extremity of pallial cavity. Anus siphoned, close to mantle border.

Genital system. **Development**. Protandric hermaphrodite, with males smaller than 14 mm. Some large specimens present several balloon-like egg capsules connected by mucus in neck ventral surface, like other examined calyptraeids.

Male (Figs. 249, 251). Visceral structures somewhat similar to those of preceding calyptraeids, testis yellowish, located in anterior region of visceral mass. Seminal vesicle small, with single, weak zigzag; in short distance narrows and becomes long and slender vas deferens, runs towards right. Between aperture of vas deferens and penis a shallow, almost straight furrow. Penis very small and simple, (about half of tentacles length); tip rounded, lacking papilla. Penis groove running along central region of ventral surface up to penis tip.

Female (Fig. 250). Ovary orange, mainly located in ventral-anterior portion of visceral mass encroaching pallial cavity (Fig. 229). Connects with pallial oviduct in its right-anterior border by very short duct. Long gonopericardial duct, similar to those of preceding species also inserts in this position. Posterior-ventral limit of pallial oviduct is a large sac with irregular, narrow, white glandular folds. Remainder of pallial oviduct long, tubular, thick glandular. Albumen gland a short posterior portion, beige in color. Capsule gland long, white, with series of slightly regular spaced, deep, transverse furrows converging on right border, where vaginal furrow runs. A slightly long vaginal tube anterior to capsule gland in form of tall papilla. Papilla tip possesses genital pore, slightly far from anus.

Habitat. Sedentary on hard substrates.

Distribution. From Ecuador to Chile.

Measurements of shells (in mm). LACM 75-15,♀, 12.6 by 29.4; LACM 75-41,♀(larger), 24.5 by 50.0; LACM 75-14 ,♂3, 4.2 by 14.7.

Material examined. CHILE. **Antofagasta**; Antofagasta, *Aulacomya* beds NW of Mejillones, 23º02;S 70º31'W, 10-30 m depth, LACM 75-21, 1♀(J.H. McLean; Sebens & Suchanek col., 11/x/1975, sta. 12); *Piura* beds at south end of the city, 23º42'S 70º27'W, LACM 75-15, 2 ♂,2♀(J.H. McLean & J. Tomicia leg., 5-6/x/1975, sta. 6). **Tarapaca**; Cumbres Borascosas (S. of Iquique), 20º42'S 70º11.5'W, LACM 75-14, 1♂2 ♀(J.H.McLean leg.; sta. 5; 3/x/1975, intertidal). **Chiloe**; Gulf of Corcovado, W. of Isla Talcon, Pomalin, 42º42'S 72º52'W, LACM 75-41, 8 dry specimens (J.M. McLean leg.; sta. 31; 4-6/xi/1975; intertidal)

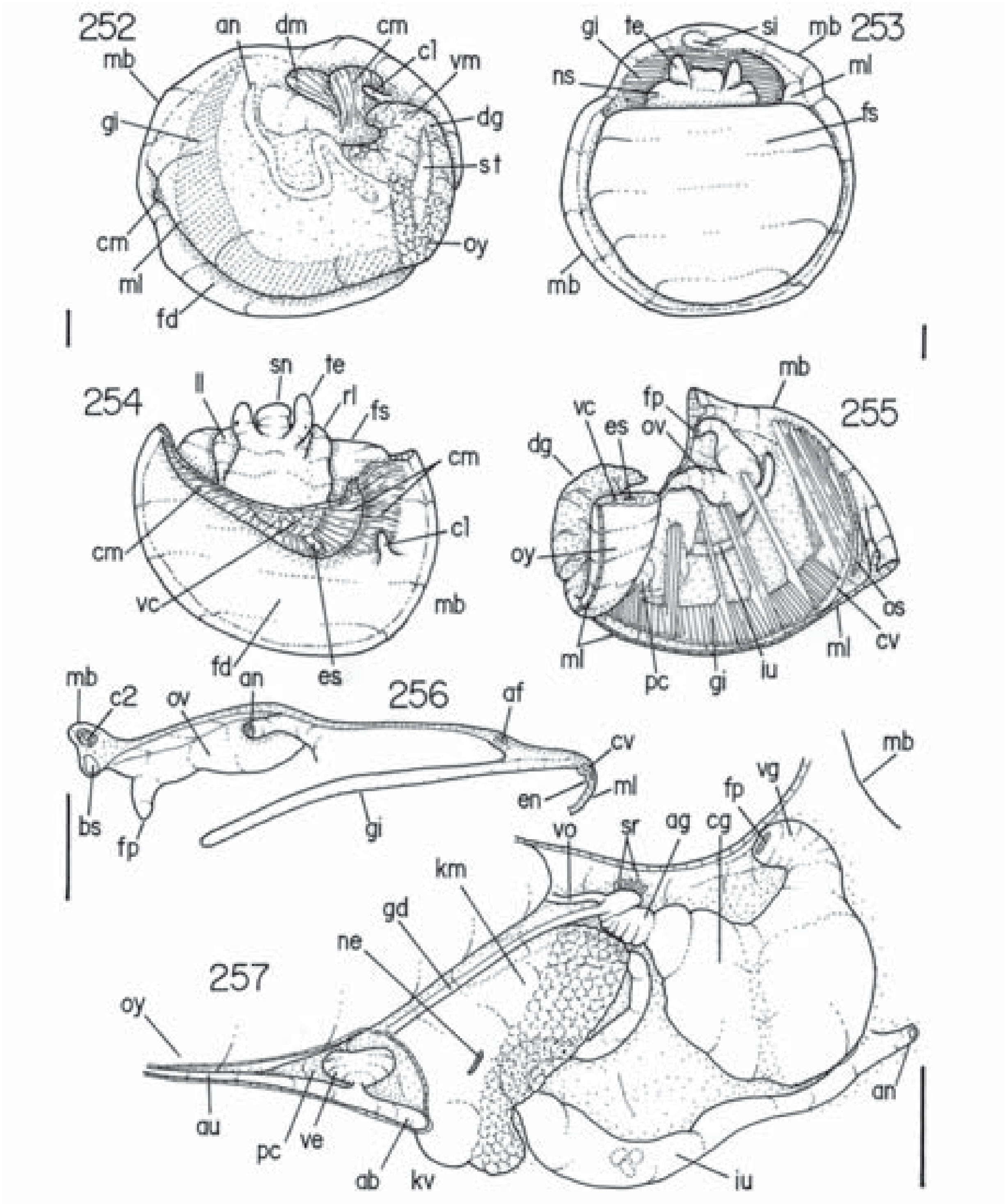
Genus *Sigapatella* Lesson, 1830

(Type species: *Calyptraea novozelandiae* Lesson, 1830)

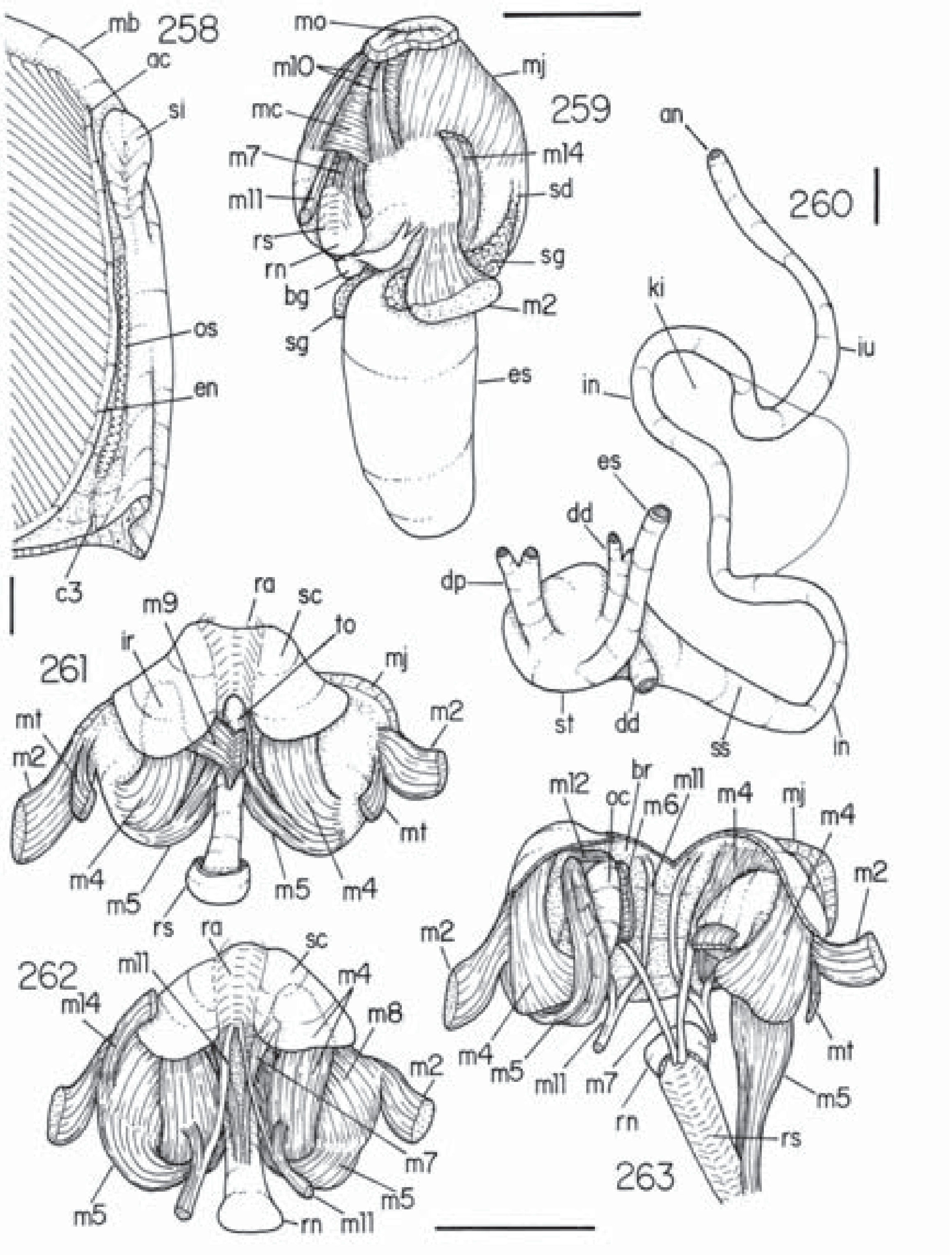
Sigapatella calyptraeformis (Lamarck, 1822)

(Figs. 22, 23, 74, 75, 252-263)

Synonymy see Pritchard & Gatliff (1900: 199), Hedley (1913: 288). Complement and remarkable data:



Figures. 525-257, *Sigapatella calyptraeformis* anatomy: **252**, female extracted from shell, whole dorsal view; **253**, same, ventral view; **254**, head-foot, dorsal view; **255**, pallial cavity, ventral-inner view, visceral mass lying in floor of this cavity deflected to left, some gill filaments in several gill regions removed; **256**, pallial cavity roof, transversal section tangential to rectum; **257**, right and posterior regions of pallial cavity roof, ventral-inner view, ventral wall of pericardium removed, some renal structures seen by transparency. Scales = 2 mm. Lettering: **c1**, projection of mantle adjacent to shell umbilicus; **c2**, repugnatorial gland.



Figures. 258-263, *Sigapatella calyptraeformis* anatomy: **258**, pallial cavity, ventral-inner view, detail if its anterior region; **259**, buccal mass and anterior esophagus, ventral-lateral-left view; **260**, middle and distal digestive tubes, ventral view, seen in situ if remainder structure were transparent; **261**, odontophore, dorsal view, mt and m9 sectioned and deflected in right side; **262**, same, ventral view, central region partially opened showing inner structures; **263**, same, completely open, m6 sectioned, left m5 (right in fig.) shown still connected to radular sac, left cartilage deflected showing structures dorsal to it. Scales = 1 mm. Lettering: **c3**, osphradium nerve.

Trochus calyptraeformis Lamarck, 1822: 12.

Crepidula tomentosa Quoy & Gaimard, 1835: 419 (pl. 72, figs 1-5).

Trochita calyptraeformis: Tenison-Woods, 1879: 38.

Calyptraea calyptraformis: Pritchard & Gatliff, 1900: 199; Wells & Bryce, 1985: 58.

Calyptraea tomentosa: Tate & May, 1901: 376.

Sigapatella calyptraeformis: Smith, 1915: 83; May, 1921: 57; 1923 (pl. 26, fig. 17); McMichael, 1960: 68; Garrard, 1961: 11; Macpherson & Gabriel, 1962: 130 (fig 155); Oliveira et al., 1981: 113; Wilson, 1993: 163 (pl. 22, figs. 12a, b).

Description.

Shell (Figs. 22-23). Similar characters to those of *Trochita,* with spire, columella and ventral surface concave. Differs by narrow and deep umbilicus lying by side of columella. Other details in above references.

Hear-foot (Figs. 253, 254). Very similar characters to those of preceding calyptraeid species, including long neck, neck lobes, neck ventral surface and propodium projected and flat. Posterior half of foot similar to those of *Crepidula* in being flattened and plane. Columellar muscle large, slightly spiral; thick, right side broad and tall, inserts in columella at about half whorl; gradually narrows towards center and left, becomes thin, lying ventral margin of shell aperture. Left extremity of this region of columellar muscle connects with inner surface of shell aperture and may be homologous to lateral shell muscle. A narrow and tall pallial fold just posterior to columellar muscle right side, inserted in dorsal surface of foot, inserted inside umbilicus. Dorsal muscle absent. Transverse net of muscles of haemocoel well-developed.

Mantle organs (Figs. 252, 255-258). Mantle border thick, with tall fold in left extremity of pallial aperture restricting it (Fig. 258). Another tall fold just anterior to gill end, siphon-like, faint at left, tall, projected and semi-circular at right. Pallial cavity similar to those of remaining calyptraeids, deep, conic and slightly flat. Osphradium bipectinate, long and narrow, length little more than 1/3 of pallial cavity aperture (Figs. 255, 258). Osphradium leaflets thick and small, anterior leaflets shorter than posterior leaflets. Right osphradium end just at base of a siphon-like fold. Gill and endostyle features similar to those of *Trochita* (Fig. 256). Hypobranchial gland very thin, inconspicuous. Visceral part encroaching right region of pallial cavity long and flat, each organ described below.

Visceral mass (Figs. 252, 255). With characters similar to those of *Trochita,* including ventral region as floor of pallial cavity filled by orange gonad.

Circulatory and excretory systems (Fig. 257). Heart attributes similar to those of preceding calyptraeids, auricle very long and slender, with broad portion beyond ventricle connection. Pericardium triangular, located posterior to kidney, ventricle located at right. Kidney large, somewhat rectangular and dorso-ventrally flattened; presents 2 regions: anterior region solid-glandular, pale beige, with tissue connected to dorsal and ventral walls and also local intestinal loops; posterior region mostly hollow, white, with several inner folds in dorsal wall connected to tissue of anterior region. Nephrostome a small slit located in middle-anterior level of posterior kidney (hollow) region. Nephridial gland inconspicuous.

Digestive system (Figs. 259-263). Buccal mass characters similar to those of preceding calyptraeids (Figs. 259, 261-263), distinctive or notable features following. **Mj** thick and broad, almost half of buccal mass volume; **mc** and **m10** pair thin, m10 as ventral part of mc; **m1a** absent; **m2a** pair not differentiated; **m4 m5** and **m9** similar; **m6** narrow and very thin; **m7** pair narrow and long, origin in dorsal branch of m4 anterior-median edge, runs towards posterior attached to subradular membrane, insertion inside of radular sac close to radular nucleus; **m8**, thick and broad cover outer surface of cartilages; **m11** pair narrow, origin in ventral inner surface of haemocoel just posterior to buccal mass, run towards dorsal, penetrate in odontophore jointed with radular sac, short branch connects with adjacent region of m4, after run attached to subradular membrane up to its anterior-median region; **m12** pair small and short, origin in anterior extremity of odontophore cartilages, insertion in subradular cartilage lateral-anterior surface; **m14** pair similar, but laterally located. Radular sac short (not extended beyond odontophore) and narrow. Radular teeth (Figs. 74, 75): rachidian tooth narrow, with about 9 small, slightly irregular cusps; lateral tooth broad (about 4 times broader than rachidian), curved inwards, tip slightly rounded, cusps small and irregular, about 4 in inner edge and 18 in outer edge; inner and outer marginal teeth similar with each other (outer marginal weakly narrower), curved, tip rounded several very small cusps in inner edge, 2 to 5 long cusps in outer edge (cusps far from distal end). Buccal ganglia large, located close to median line (Fig. 259). Salivary glands short, slender, curved towards ventral, edging buccal mass posterior surface (Fig. 259). Dorsal wall of buccal mass inner surface and esophagus with similar characters as those of preceding species, inner folds tall and with irregular surface. Stomach slightly spherical, esophagus inserts in posterior-left region (Fig. 260). Ducts to digestive gland large, double, located on each side of esophageal insertion in gastric ventral surface. Posterior duct towards right, anterior duct with T-fashion. Intestine-style sac narrow and long; after stomach, narrows gradually towards anterior and left, amply connected to each other, separated by pair of longitudinal folds. Gastric inner surface smooth, without special folds. Intestine, after style sac end, narrow (Fig. 260), runs sinuously towards right initially immersed in digestive gland, contours posterior, right and part of anterior kidney edges, possesses weak loop inside kidney before its exit to pallial cavity roof. Rectum simply curved, running at some distance from right edge of pallial cavity. Anus narrow, siphoned (Figs. 255, 257).

Genital system (Figs. 255, 257). Only females examined, but some of them present vestigial penis just posterior to right cephalic tentacle. Ovary orange, located in anterior region of visceral mass mainly in its ventral portion. Visceral oviduct narrow, runs in right-dorsal-posterior region of visceral mass encroached in pallial cavity. Gonopericardial duct very long, inserts in albumen gland by side of oviduct. Albumen gland small, curved, transverse folded, as posterior region of pallial oviduct. A series of 5-6 vesicular seminal receptacles along dorsal surface of albumen gland. Capsule gland large, ample, lobed, curved, dorso-ventrally flattened. Vaginal tube thick, curved towards posterior and right, origin in right-anterior edge of capsule gland. Genital pore a small slit turned posteriorly, low fold extends beyond genital pore towards posterior.

Central nervous system. Similar characters as those of *Crepidula*, except for longer located subesophageal ganglion and smaller statocysts.

Measurements of shells (in mm). AMS 353086 ♀2: 12.6 by 18.8;♀3: 14.8 by 23.9.

Distribution. NSW to Fremantle (Bass Strait, Central E coast, G. Aust. Bight, Lower E coast, Lower W coast, S Gulfs coast, SW coast, Tas. coast) (Wilson, 1993).

Habitat. Hard substrates (stones and in dead shells), with mussels and epizoic red algae; up to 200 m depth.

Material examined. NEW ZEALAND; East of Vire Point, Perseverance Harbor, Campbell Island 52º33'S 169º10'E, 15 m depth, AMS 353086, 3♀(sta. 38661, 12/ii/1980).

Discussion. There are several characters of the preceding calyptraeids absent in *S. calyptraeformis*, such as the dorsal shell muscle, the lateral shell muscle, the reduction of the columellar muscle, odontophore muscle m2a, etc. These data and the trochoid fashion of the shell do not support a relationship with the species of the genera *Calyptraea* and *Trochita*. The present suggestive generic attribution is based on shell similarities with the fossil type species and the close geographic occurrence, as well as above mentioned differences from species of *Calyptraea* and *Trochita*, in such further informations are given in discussion section. [On *Calyptraea*, *C. centralis* is very similar to the type species: *C. chinensis* (see above), and on *Trochita* the type species was examined.]

Family Hipponicidae

Genus *Hipponix* Defrance, 1819

(Type species: *Patella cornucopiae* Lamarck, 1802)

Hipponix costellatus Carpenter, 1856 (revalidated)

(Figs. 49, 50, 55, 264-283)

Hipponyx ?barbatus, var. *costellatus* Carpenter, 1856: 4 [loc. ? Ad insulas Maris Caribbaei].

?*Hipponyx (Amalthea) effodiens* Carpenter, 1856: 5 [loc. Ad insulas Maris Caribbaei].

Hipponyx grayanus: Lopes & Alvarenga, 1955: 168-169 (non Menke, 1853.).

Siphonaria sp: Rios, 1970: 140 (pl. 49).

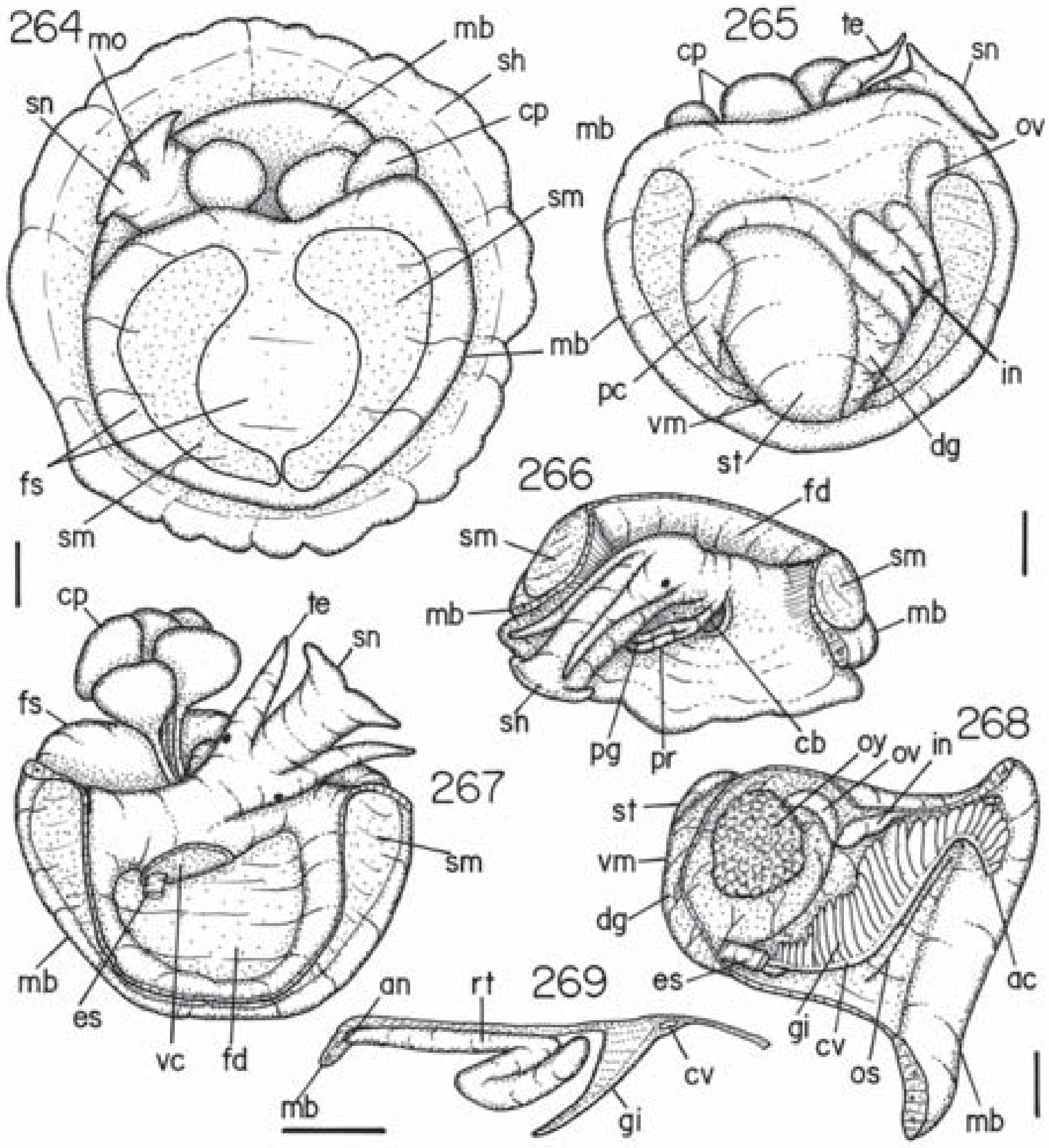
Hipponix grayanus: Matthews & Kempf, 1970: 23; Rios, 1975: 62 (pl. 17, fig. 249); 1985: 56 (pl. 20, fig. 253); Leal, 1991: 89 (pl. 14, fig. E-F); Rios, 1994: 69 (pl.24, fig. 266) (non Menke, 1853.).

Diagnosis. Western Atlantic species with shell sculptured by broad radial ridges, of somewhat uniform width. Osphradium very narrow, almost a line. Penis with narrow and long papilla in tip. Pallial oviduct with single and broad bursa copulatrix located between ovary and albumen gland, gonopericardial duct absent.

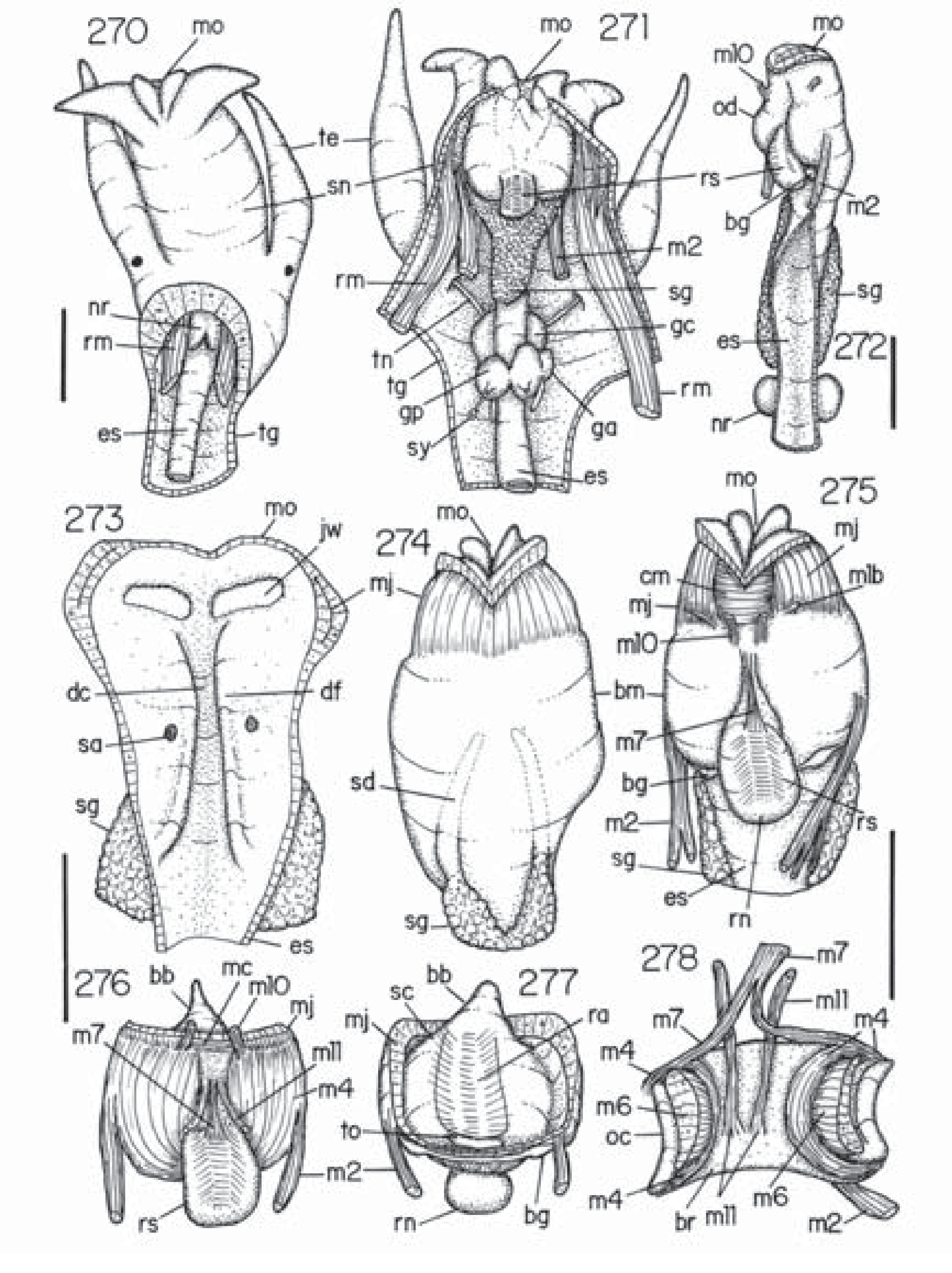
Description.

Shell (Figs. 49, 50). Limpet-like, conical, apex turned posteriorly about in median line. Protoconch see Leal (1991: 89-90, pl. 14, figs. E, F). Sculpture thick, slight irregular, radial ridges; greatly eroded apex. Inner surface glossy; shell muscle scar horseshoe shaped (concavity turned forward), symmetrical, extremities broader.

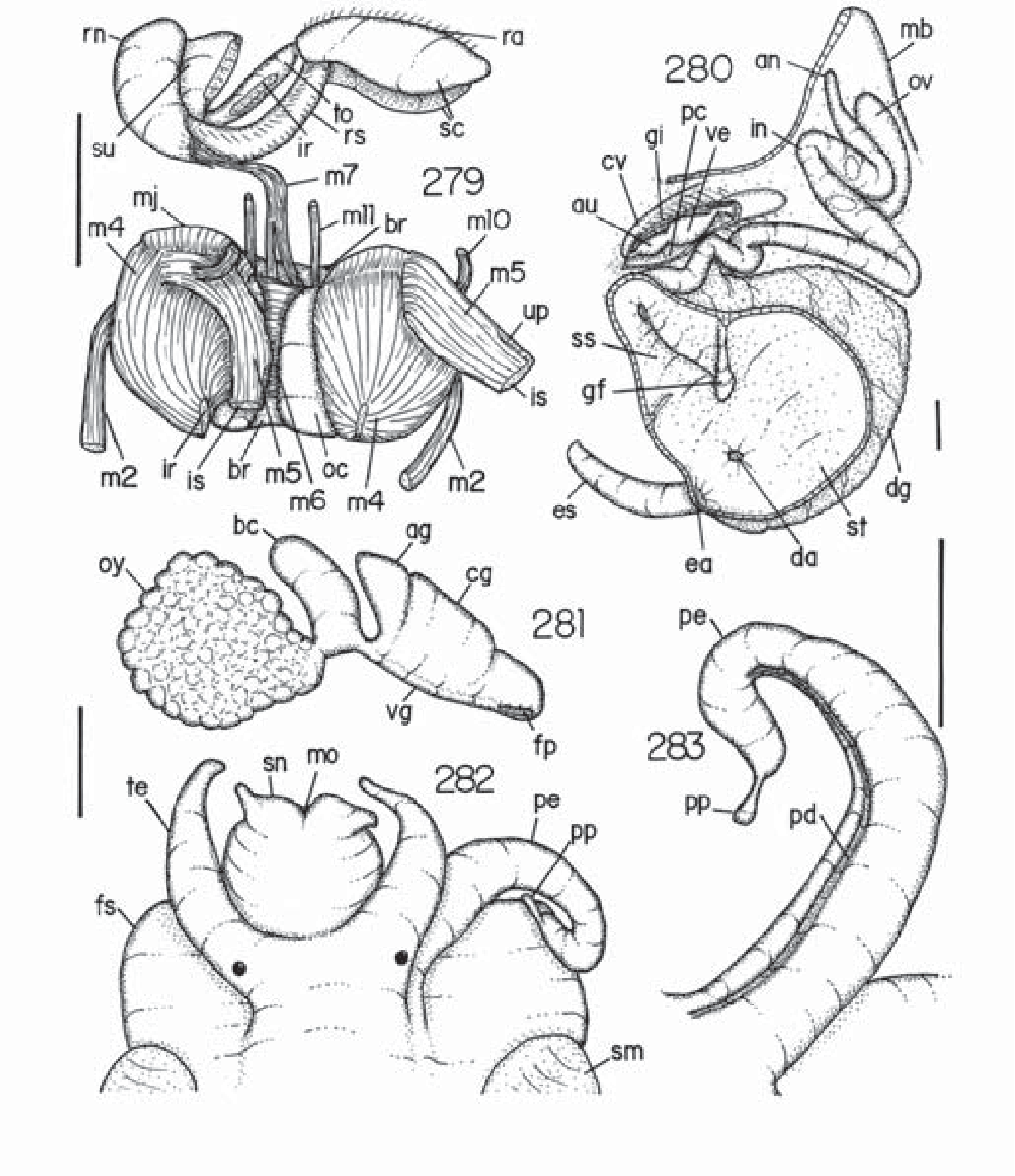
Head-foot (Figs. 264-267, 270, 271, 282). Head outstanding, somewhat large (about 2/3 of foot length and ¼ of its width), with long snout and tentacles. Tentacles stubby, tapering gradually, without ommatophores. Eyes small, located on outer side of tentacle base. Snout-proboscis cylindrical long (about ½ of foot length), anterior margin slight plane, bifid, with pair of lateral, sharp, short projections. Snout-proboscis with some capacity of retraction within haemocoel. Proboscis haemocoel spacious, inner surface with two pairs of retractor muscles located on its lateral surface, run longitudinally (Figs. 270, 271); both originate in ventral and lateral inner surface of haemocoel at level just posterior to snout, run towards anterior, attached to inner snout surface, inserted in anterior snout wall close to mouth, where diminishes gradually in several branches. Propodium inserted just in ventral margin of snout base, dorso-ventrally flattened, planar, margins rounded; length about ½-1/3 of that of proboscis (Figs. 266, 267). Transversal furrow of pedal glands in anterior margin of propodium. Foot with plane sole, center very thin and transparent, borders very



Figures 264-269, *Hipponix costellatus* anatomy: **264**, female, whole ventral view, note localization of capsules (cp); **265**, same extracted from shell, dorsal view; **266**, head-foot, female, frontal view, head turned to right (left in fig), capsules removed; **267**, same, dorsal view, visceral mass and pallial organs removed, capsules preserved in situ; **268**, visceral mass and pallial cavity roof, ventral view; **269**, pallial cavity roof, transversal section in its middle region, just parallel to rectum (gill filament is not so aligned as shown). Scales = 1 mm.



Figures 270-278, *Hipponix costellatus* anatomy: **270**, head and haemocoel, ventral view, foot included propodium removed; **271**, same, snout opened ventrally, its walls deflected; **272**, buccal mass and esophagus, ventral, slight lateral-left view, esophagus opened longitudinally; **273**, dorsal wall of buccal mass, ventral view, odontophore and its septum with esophagus removed; **274**, buccal mass, dorsal view; **275**, same, ventral view; **276**, odontophore, ventral view; **277**, same, dorsal view; **278**, same, ventral view, detail of its central region with m6 sectioned and deflected, inner (ventral) surface of br exposed. Scales = 1 mm.



Figures 279-283, *Hipponix costellatus* anatomy: **279**, odontophore, ventral view, most of muscles deflected, radula and subradular cartilage extracted and deflected upwards; **280**, visceral mass, intestine (seen if remainder structures were transparent) and pericardium, dorsal view, dorsal wall of stomach and pericardium removed, part of adjacent mantle also shown; **281**, ovary and pallial oviduct, ventral view; **282**, anterior region of head-foot of male, dorsal view; **283**, penis, ventral view. Scales = 0.5 mm.

thick in stirrup form (straight region anterior). Shell muscle horseshoe shaped, very broad anteriorly and narrow posteriorly (Figs. 264-267); this muscle, which may be modification of columellar muscle, is main component of thicker region of foot; origin in shell, about mid way between its center and border (except anterior quarter), runs almost straight ventrally; insertion in foot sole in similar, but broader fashion than its scar in shell; a separation of shell muscle in posterior region, close to median line. Shell muscle insertion seen ventrally through transparency of foot sole (Fig. 264). Pair of large head muscles in straight thick anterior margin of foot. Both head muscle originate from broader region of shell muscle and also from adjacent region of foot sole, run medially and anteriorly; insertion along head wall and snout retractor muscles. Some very narrow muscle fibers cross from a side to another (left and right) and from dorsal to ventral just anterior to head muscles. Foot sole extends, as plane flap, beyond thicker anterior margin produced by shell and head muscles, presents about ½ of length of remainder posterior foot sole. Between propodium and anterior projection of foot sole, close median line, a small glandular concavity present in females, where brood capsules stalks attach.

Mantle organs (Figs. 265, 268, 269). Mantle border thick and broad, connected with shell muscle in lateral and posterior regions; no appendages. Pallial cavity shallow — about half of visceral mass length. Osphradium ridge-like, long, extremely narrow, somewhat parallel to mantle border (closer in right extremity). Gill slightly small, but with length longer than cavity width. Gill anterior extremity on middle of mantle border right region, turned to left. After mantle border gill curves and runs towards left and posterior up to posterior-left extremity of pallial cavity. Gill filaments slight tall, triangular, apex sharp turned posteriorly; taller filaments in middle of gill, gradually decrease towards extremities. Hypobranchial gland not detectable.

Visceral mass (Figs. 265, 268, 280). Almost spherical, encased in concavity between thick borders of foot sole (shell and head muscles) and shell apical (central) part. In ventral view it is seen through thin central foot region. Large stomach dorsally; small gonad as ventral structure; digestive gland compressed between both. Connection with haemocoel in middle portion of anterior thick foot border, in its posterior-median surface. Visceral mass organs dislocated anteriorly, compressing and encroaching on pallial cavity, some organs such as pericardium stay dorsal to pallial cavity posterior half.

Circulatory and excretory systems (Fig. 280). Pericardium of considerable size; located dorsal to pallial cavity just dorsal to posterior end of gill. Ctenidial vein almost in its posterior end, connects with small, elliptical auricle. Ventricle posterior and right of auricle. Aorta after very short distance divides into anterior and posterior aortas, anterior one running anteriorly close esophagus. Kidney very small, dorso-ventrally flattened, solid-glandular, located just at right from pericardium. Nephrostome a very small slit at right, removed from kidney. Kidney and nephrostome located in pallial roof.

Digestive system (Figs. 271-280). Mouth longitudinal, located in middle of plane, anterior surface of proboscis. Buccal mass just posterior to mouth, occupying about half of snout length. Odontophore muscles (Figs. 271-279): **mj**) jaws and peri-buccal muscles, originate around mouth wall, insertion in anterior margin of odontophore (except small ventral portion) and in dorsal wall of buccal mass close to jaws; **mc**) constrictor of mouth or mouth sphincter, several circular fibers running around mouth internally to mj; **m1**) several very small muscles connecting buccal mass with adjacent regions of snout inner surface, more concentrated anteriorly (jugal muscles); **m1b**) the single pair of outstanding jugal muscles, originate in snout ventral-lateral surface, run towards medial, insertion in middle-anterior-ventral region of odontophore just in ventral insertion of mj; **m2**) large pair of retractor muscles of buccal mass (retractor of pharynx), originate in lateral-inner surface of middle level of haemocoel (between both **rm** – retractor muscle of snout), runs towards anterior, insertion in lateral-posterior region of odontophore surface close to limit between odontophore and esophageal parts of buccal mass; **to**) elliptical conjunctive tissue on middle region of radular ribbon, just before its exposed portion; **m4**) large pair of ventral-posterior tensor muscle of radula, origin in dorsal-outer surface of odontophore cartilages, their fibers contour outer-ventral border of these cartilages up to opposite side, insertion in small region of “to” lateral surface; **br**) subradular membrane, thin but strong, covers inner (ventral) surface of subradular cartilage, inserts in both sides of dorsal surface of m4; **bb**) bulged anterior region of “br” just anterior to radula end; **m5**) pair of dorsal-posterior tensor muscle of radula, origin on m4 ventral-anterior surface, runs towards medial and posterior, inserts in radula just dorsal to m4 insertion in “to”; **m6**) horizontal muscle, somewhat thick, connects both anterior-dorsal margins of odontophore cartilages; **m7**) narrow pair, origin in m4 anterior margin, just at insertion of “br”, runs medially between both cartilages, after short distance entrance in radular sac, insertion in radular sac ventral surface a short distance from its nucleus; **m10**) small pair of ventral protractor muscle of odontophore, origin in anterior-ventral inner surface of snout, close mouth, runs towards posterior short distance, insertion in ventral-anterior surface of odontophore; **m11**) narrow and long pair, origin in “br” inner posterior surface, run anteriorly attached to br, contour anterior-middle region of odontophore close to m7, insertion in adjacent region of snout inner ventral surface. Buccal ganglion located laterally, close to m2 insertion (Figs. 272, 275); their connectives cross between radular nucleus and adjacent ventral wall of odontophore. Radula somewhat short, little more than buccal mass length. Radula (Fig. 55): rachidian tooth broad and short, seven to nine cusps on cutting edge, central cusp about double the size of neighboring cusps, no basal cusps but small, sharp, low, lateral projection present in each side; lateral tooth very broad – more than twice rachidian width, about eight triangular cusps, third or fourth cusp larger (about double width of neighbor), apical, turned internally and forward, cusps gradually decrease laterally by about 1/3 of tooth cut-edge length (remainder smooth); inner and outer marginal teeth similar to each other, long, tall, slender, slightly flattened, about five sharp, sub-terminal cusps in each side of curved apical region, tip sharp pointed. Jaws two broad plates in anterior dorsal wall of buccal mass (Fig. 273). Pair of dorsal folds of buccal mass broad, begin just posterior to each jaw, their medial border outstanding; between both a shallow dorsal chamber with smooth surface. Aperture of salivary glands circular, in middle level of dorsal folds, at some distance from their medial border. Salivary glands small, cluster around esophagus anterior to nerve ring. Salivary ducts only visible anteriorly, on dorsal-posterior surface of buccal mass, penetrate local wall and run some distance towards anterior (Fig. 274) and open as described above. Esophagus narrow and long; its inner surface single, without glands or folds (Fig. 272). Stomach large, almost spherical, occupying most of visceral mass (Figs. 265, 280). Esophagus runs in ventral gastric surface and inserts in middle region of its posterior border. Ducts to digestive gland single, narrow, originate anterior to esophageal aperture. Most of gastric inner surface uniformly smooth (Fig. 280). Style sac and intestine origin on left gastric side, both almost completely separated from each other, except on short basal portion. No style observed. A somewhat tall transversal fold surrounds style sac aperture, broader close to intestine origin. Stomach filled with mucus and gravel. Intestine narrow, after detaches from style sac, crosses from left to right side of visceral mass anterior and partly immersed in digestive gland, left portion of this loop slight sinuous (Fig. 280). After this first portion, intestine has other three almost straight portions marked by almost 180º turn; each portion about half of precedent portion. Last intestinal loop in pallial roof, several large, elliptical fecal pellets aligned along them. Anus small weakly siphoned, located in right extremity of pallial cavity, close to mantle border (Figs. 268, 280).

Genital system. **Development**. Protandric hermaphrodite, with all small specimens male (but not many small specimens were available). Some females had up to five egg capsules in space ventral to head and dorsal to anterior projection of foot sole (Fig. 267), color yellow. Each capsule broad, slight rounded and flattened, with basal stalk of approximately same length as its broad part. These stalk stay connected to mother's body just in concavity between propodium and anterior projection of foot sole (Fig. 266: cb).

Male (Figs. 282, 283). Testis small, located in center of the ventral surface of the visceral mass, color pale cream. Visceral vas deferens narrow, runs from testis to right-posterior region of pallial cavity, where opens. Seminal vesicle not differentiable. Pallial sperm groove very shallow, difficult to see. Penis base inserted in ventral region of right cephalic tentacle (and not dorsal or posterior to it). Penis somewhat long, about 1.5 times head length, narrows gradually up to rounded tip. A small papilla located on lateral region of penis tip; papilla tip blunt, base slender. Few males lack this papilla. Penis groove slight shallow, ends at some distance of penis tip (about 1/6 before).

Female (Fig. 281). Ovary similar located as testis, color pale orange. At very short distance from ovary, oviduct suddenly expands and become hollow diverticulum (bursa copulatrix?), turned posteriorly. Visceral oviduct connects also after very short distance from this diverticulum in pallial oviduct. Pallial oviduct small, located in right region of pallial cavity slightly ventral to rectum and posterior to anus. Albumen gland small, triangular, color whitish. Capsule gland larger, most of pallial oviduct length; posterior surface connected with albumen gland; wall thick glandular, yellowish. Capsule gland gradually narrows approaching rounded anterior extremity. Genital pore on left side of this anterior extremity, longitudinal and narrow.

Nervous system (Fig. 271). Large ganglia close to each other around esophagus, far, very posterior from buccal mass. Statocyst very small, with single statolyth.

Habitat. Generally on shells of other gastropods, intertidal to 54 m depth.

Distribution. Brazil, from Ceará to Bahia, including ocean islands.

Measurements of shells (in mm). MZSP 28498, ♀1, 4.7 by 9.8;♀5, 5.0 by 7.9;♀4, 1.8 by 3.3.

Material examined. WEST INDIES; BMNH 1865.11.30.26 (photo of a shell identified as *Amalthea effodiens*). BRAZIL; **Bahia**; Salvador (Simone col.), Ribeira Beach, MZSP 32146, 1♀; Banco da Panela, 16-20m depth, MZSP 28457, 2♀ (26/ii/1997); Ribeira Beach, MZSP 28498, 2♂, 6♀(24-26/ii/1997); Itapuã Beach, MZSP 28449, 1♂(23-27/ii/1997).

Discussion. *H. costellatus* was previously considered to be an Atlantic occurrence of *H. grayanus*. The analysis of the differences of the inner morphology, explored below, from the Pacific samples of *H. grayanus*, revealed the specific separation. Then, the supposed junior synonym previously described for the Atlantic was revalidated. *H. effodiens*, also described from the Atlantic, was considered a synonym of *H. antiquatus* (e.g., Rosenberg, 1996). However, the original description shows clearly that the shell is sculptured with radial, broad threads instead of concentric scales, characteristic of *H. antiquatus*. These data allow that *H. effodiens* may be a *H. costellatus* synonym. Carpenter's species were never figured and the single descriptions available are the brief original ones. A search for the type specimens was made in the BMNH and Redpath Museum, McGill

University, Montreal, Canada (RMM) (depository of Carpenter's collection), but they were not found. Two lots of shells sent from that Museum identified as *H. costellatus* were actually of another species. A shell identified as *Amalthea effodiens* is in the BMNH. Photos of this specimen were sent and revealed close similarity with the shells of the specimens examined in this study.

H. costellatus was originally described as a variety of *H. barbatus* (Sowerby, 1835). This species, according to Keen (1971), is a synonym of *H. pilosus* (Deshayes, 1832), which inhabits the Pacific Ocean. Carpenter (1956) described *H. costellatus* based on a single specimen with dubious provenance, stating that the exterior surface is similar to *H. grayanus* (and the "base" is of *H. barbatus*). *H. effodiens* was described in the same paper, characterized by tall radiating furrows. Despite the enveloping nebula of uncertainties, the name *H. costellatus* was preferred because of page precedence and also because it has been referred to as *H. grayanus* synonym (e.g., Rios, 1994). However further studies are still necessary.

Hipponix subrufus (Lamarck, 1822)
(Figs. 24-26, 70, 77, 284-293)

Ancient synonymy in Carpenter (1856: 4). Complement:

Hipponix subrufus: Leal, 1991: 90 (pl. 14, fig. G); Rios, 1994: 69 (pl. 24, fig. 267).

Hipponix subrufus subrufus: Abbott, 1954: 166; Warmke & Abbott, 1961: 85 (pl. 15, fig. g); Rios, 1970: 53; Abbott, 1974: 135; Rios, 1975: 62 (pl. 17; fig. 250); 1985: 56 (pl. 20, fig. 254); Calvo, 1987: 95 (fig. 52); Jong & Coomans, 1988: 61; Merlano & Hegedus, 1994: 159.

Description.

Shell (Figs. 24-26). Similar to that of preceding species, but with sculpture more delicate and complex: several rows of small nodules organized in irregular radial lines (Figs. 24, 25). Protoconch (Fig. 26) see Leal (1991: 90). Other details in Abbott (1974: 135).

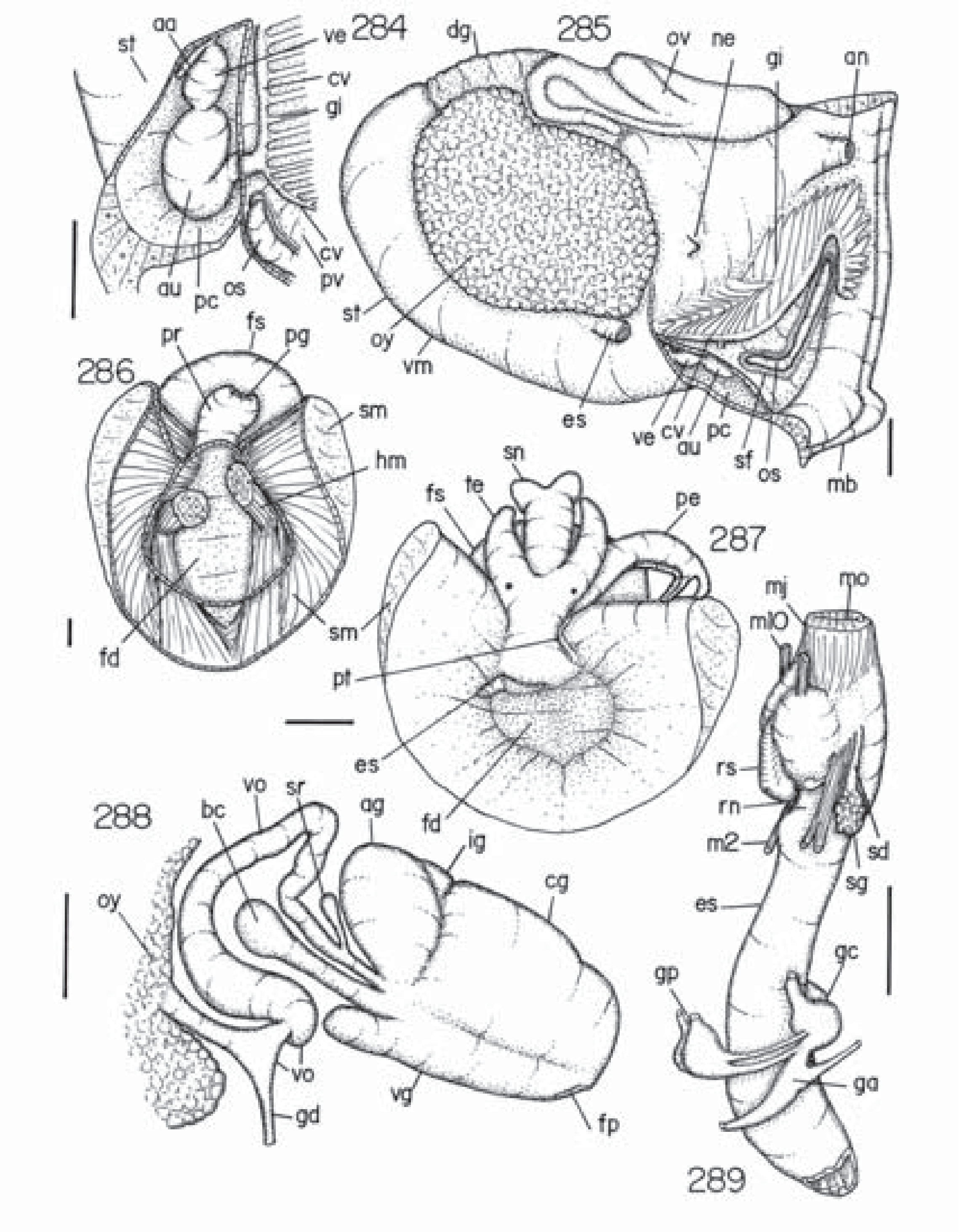
Head-foot (Figs. 286, 287, 293). Very similar to *H. costellatus*, including head, propodium and muscle arrangements. Differs only in head muscle pair, which have independent origin in foot sole from shell muscle (Fig. 286); several muscle fibers, run as thin layer from origin of head muscles posteriorly and laterally, spreading superficially on foot sole and shell muscle medial-posterior side.

Mantle organs (Figs. 284, 285, 292). Characters very similar to those of *H. costellatus*. Distinctive or notable features following. Osphradium much broader, also ridge-like, strongly angled between its middle and left thirds. Narrow satellite fold surrounding entire osphradium. Gill similar located, inclusive curved anterior extremity on mantle border. Gill filaments tall and sharp, with undulated membrane and long, straight rod.

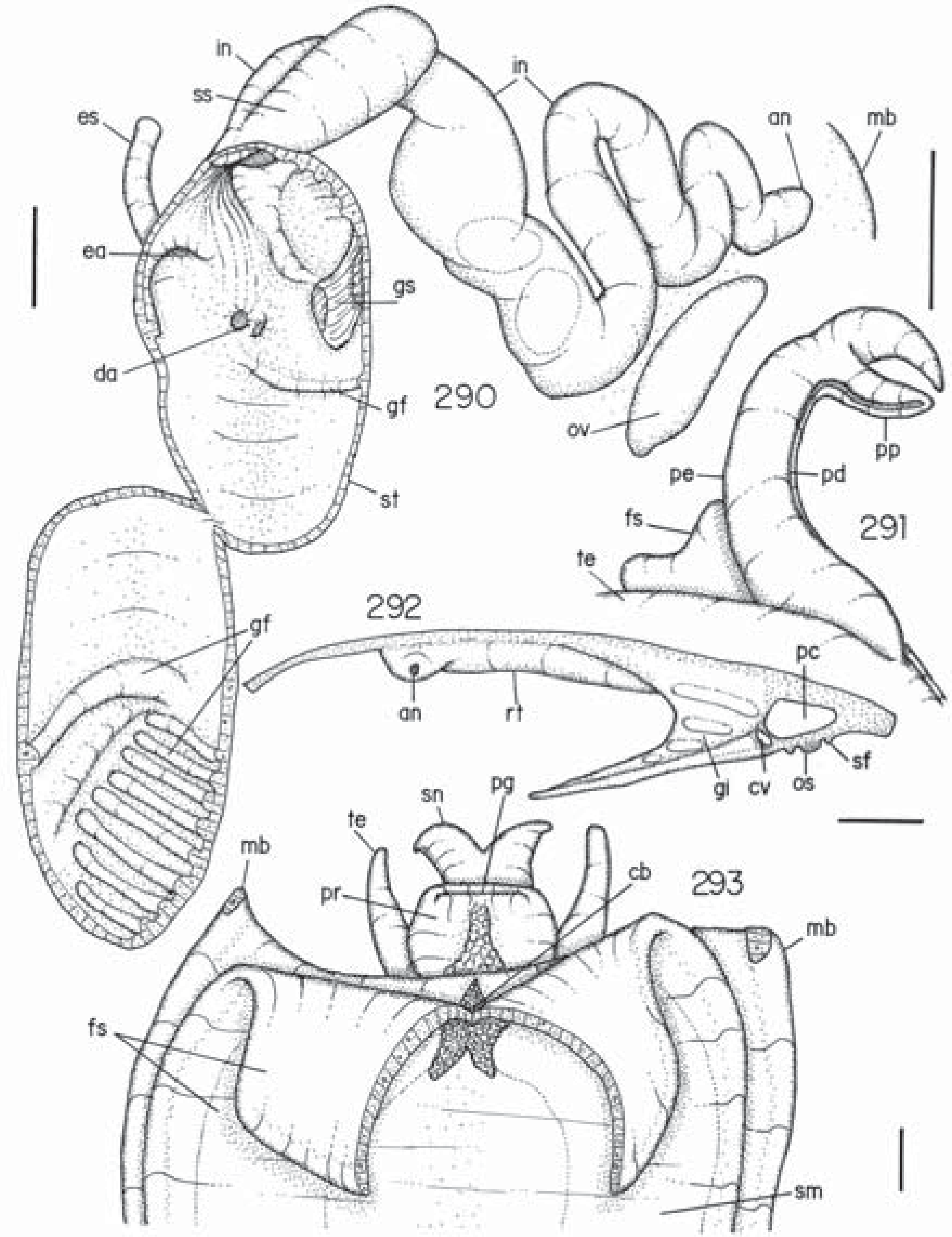
Visceral mass (Fig. 285). Characters as those described for *H. costellatus*.

Circulatory and excretory systems (Fig. 284). Heart similar to that of *H. costellatus*, but slightly more anterior, almost close to mantle border, located dorsal to gill and osphradium. Auricle connected to ctenidial vein before its posterior extremity, i.e., there is portion of ctenidial vein beyond auricle connection as blind-sac and with current contrary to normal fashion. Auricle also presents portion anterior to its connection with ctenidial vein. Kidney, as in *H. costellatus*, very small, solid, compressed between visceral mass organs and pallial cavity. Nephrostome a small slit on a weak papilla, slightly away and at right from kidney.

Digestive system (Figs. 289, 290). Buccal mass characters very similar to those described for *H. costellatus*, except for stronger m2 and m10 (Fig. 289). Radula similar to that of preceding species (Figs. 70, 77), but with sharper and longer cusps on teeth; rachidian tooth with about 11 cusps, central cusp about double neighboring cusps; lateral tooth with about 14 cusps, third or four cusp apical, larger, several times larger than neighboring cusps; marginal teeth with sub-terminal series of about nine pairs of cusps. Salivary glands in form of two small, irregular spheres just dorsal to m2 pair; their ducts run as described for preceding species. Esophagus broader than that of *H. costellatus*; its inner surface with pair of low, longitudinal folds, not continuation of those from dorsal wall of buccal mass, but separated by short smooth distance from those, just posterior to buccal mass level. Stomach site and size similar to those of preceding species. Stomach inner surface weakly more complex (Fig. 290): its right half uniformly smooth; differentiable sorting area in dorsal-left region, possessing some transversal folds; other transversal fold begins just at left from esophageal aperture, runs ventrally by posterior gastric wall until close to sorting area, where fades; some longitudinal, low folds edge intestinal origin, some of them run up to origin of ducts to digestive gland; other transverse, low fold in ventral wall at right to these ducts. Gastric shield well-developed, located at some distance form style sac aperture, in middle of anterior gastric wall. Ducts to digestive gland double, very close with each other, located in middle region of ventral gastric wall. Style sac almost completely separated from intestine, only united with it in its basal region; style sac with about half of gastric length and width; its inner surface yellow, iridescent. Intestine origins in ventral region of style sac base. Intestinal loops similar to those described for *H. costellatus* (Fig. 290), except in being broader and in having additional loop up to anus. Fecal pellets and anus as those of *H. costellatus*.



Figures 284-289, *Hipponix subrufus* anatomy: **284**, anterior-left extremity of visceral mass (dorsal to gill) and adjacent surface of pallial cavity roof, ventral view, ventral wall of pericardium removed; **285**, visceral mass and pallial cavity roof, ventral view; **286**, foot and shell muscle, dorsal view, head removed; **287**, head-foot of male, dorsal view, visceral mass and pallial structures removed; **288**, pallial oviduct and part of visceral female organs, ventral view; **289**, buccal mass, esophagus and nerve ring, lateral-left view. Scales = 0.5 mm.



Figures 290-293, *Hipponix subrufus* anatomy: **290**, digestive tubes, dorsal view, seen if remainder structures were transparent, dorsal wall of stomach part removed and deflected inwards, localization of pallial oviduct and mantle border also shown; **291**, penis and adjacent structures of its base, dorsal view; **292**, pallial cavity roof, transversal section of its middle region just parallel to rectum (gill filament is not so aligned as shown); **293**; anterior region of head-foot of female, anterior part of foot sole sectioned in median line and deflected inwards to shown brood glandular concavity (cb), part of pedal gland also shown (by transparency) in propodium. Scales = 0.5 mm.

Genital system. **Development**. Protandric hermaphrodite as preceding species, apparently all small specimens are male, but few were available.

Male (Figs. 287, 291). Visceral and pallial organs characters similar to those of *H. costellatus*, inclusive ventral implantation of penis, but pallial sperm duct is clearer. Penis differs in tip, which has tall, sub-terminal papilla preceded by shallow constriction. Papilla very tall in some species, almost of same size as remaining distal region of penis (without sperm groove), while other specimens this papilla is smaller. Penis sperm groove slightly shallow, runs up to papilla tip at its proximal face.

Female (Figs. 288, 293). Characters similar to those of *H. costellatus*, distinctive and notable features following. From ovary, a broad and thin walled tube runs anterior, after a short distance connects with very narrow gonopericardial duct or ligament. After this insertion, visceral oviduct runs posterior and walls thicken ; it contours to right margin of visceral mass anterior extremity slight sinuously. Small seminal receptacle inserts on visceral oviduct a short distance from its insertion on albumen gland. Bursa copulatrix also inserts in pallial oviduct just to left of visceral oviduct insertion. Albumen gland elliptical, orange, connected to vaginal duct on left side. Between albumen and capsule glands a narrow, white, thin walled region that could be ingesting gland. Vaginal tube possesses posterior diverticulum covering left side of bursa insertion. Capsule gland large, pale orange, occupies about 1/3 of pallial oviduct length. Albumen and capsule gland lumen with large opening to vaginal duct. Genital pore a narrow slit of pallial oviduct anterior end, turned to left. Brood in glandular concavity between propodium base and anterior projection of foot sole similar to that of *H. costellatus* (Fig. 293); its glandular tissue between shell muscles insertion.

Habitat. Hard substrates, mainly dead coral, intertidal to 21 m depth.

Distribution. North Carolina, USA, to Bahia, Brazil.

Measurements of shells (in mm). MZSP 30816;♀3, 5.4 by 9.8;♂2.9 by 6.4.

Material examined. WEST INDIES; RMM 5880, 3 shells (identified as *H. costellatus*). BRAZIL; **Pernambuco**; Fernando de Noronha Archipelago (Simone & Souza Jr. col., vii/1999); Atalaia Beach, MZSP 31150, 21 specimens (day 18); Conceição Beach, MZSP 31406, 1♂, 4 shells; Buraco da Raquel, MZSP 31134, 1♀, 8 shells, MZSP 31121, 12 specimens (day 19); Porto Beach, MZSP 31201, 1♂, 9♀, 14 shells (day 17), MZSP 31188, 2 shells (day 17), MZSP 32144, 20 shells, several protoconchs (day 20); Ponta da Sapata, 21 m depth, MZSP 31321, 5 shells (day 18); Rata Island, Buraco do Inferno, MZSP 30955, 11♀, 1 shell, MZSP 32096, 1♀(day 19), Cagarras, MZSP 30964, 1 shell (day 21); **Bahia**; Abrolhos Islands, MZSP 30816, 6♂, 8♀(L.Pinni Nt. col., v/1958).

Hipponix incurvus (Gmelin, 1791)
(Figs. 27-29, 78, 79, 294-308)

Synonymy in Leal (1991: 92). Complement:

Patella incurva Gmelin in Linné, 1791: 3715.

Capulus (Krebsia) incurvatus: Abbott, 1954: 168 (err.).

Capulus incurvatus: Rios, 1970: 55; 1975: 63 (pl. 17, fig. 255); Oliveira et al, 1981: 109; Rios, 1985: 58 (pl. 21, fig. 261); Leal, 1991: 92-93 (pl. 14, fig. K); Rios, 1994: 72 (pl. 24, fig. 277); Merlano & Hegedus, 1994: 161 (pl. 50, fig. 590); Abbott & Morris, 1995: 178 (pl. 49).

Capulus incurvus: Rosenberg, 1996.

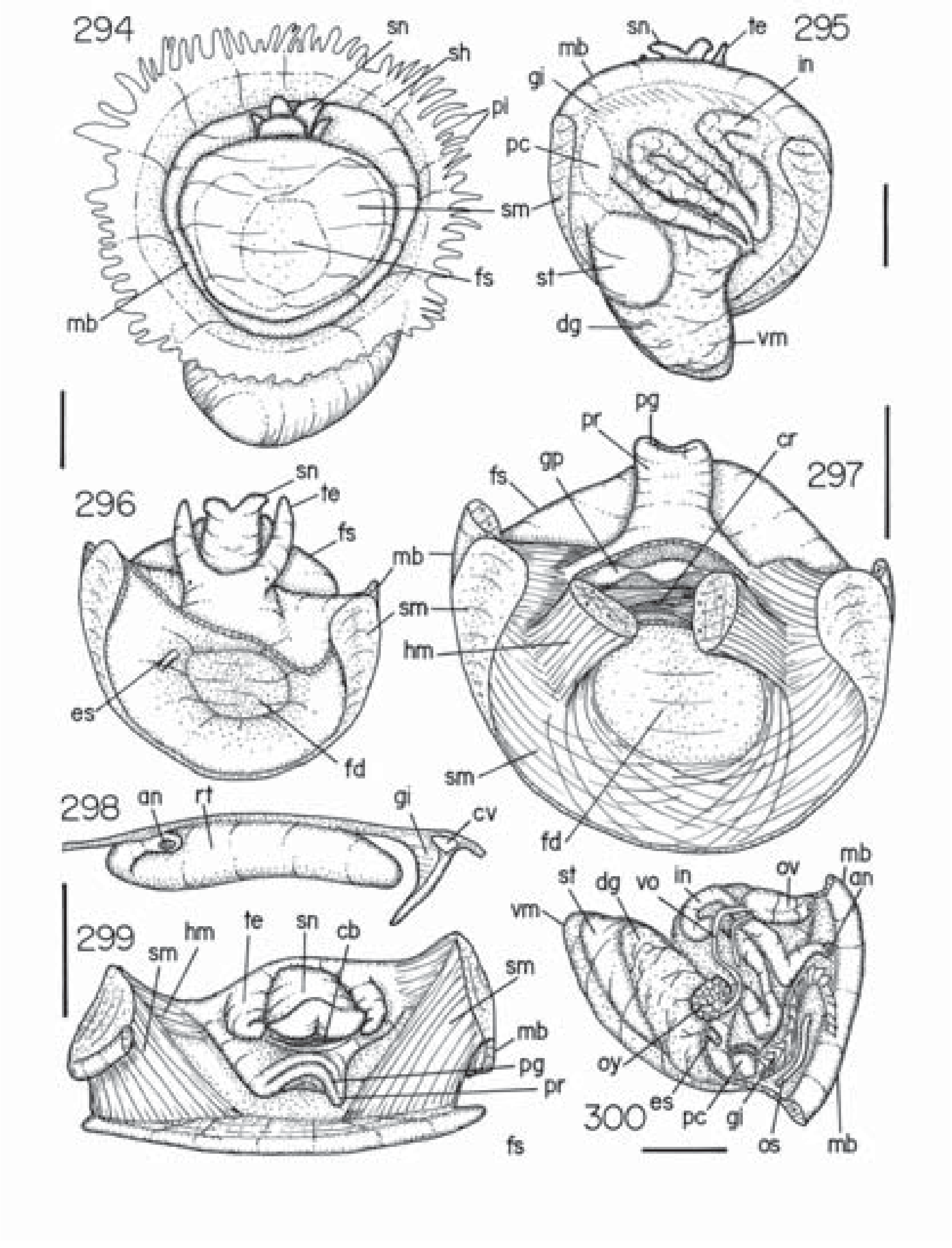
Description.

Shell (Figs. 27-29). Similar to preceding *Hipponix* spp, but deeper, slight spiral apex, asymmetrical. Protoconch (Fig. 28) see Leal (1991). Sculpture several spiral ribs, some larger; strong undulations in older shell areas. Periostracum present, mainly near shell borders, possesses several, irregular projections. Muscle scar also similar to those species, but closer to shell border. Other details in Abbott (1974: 137).

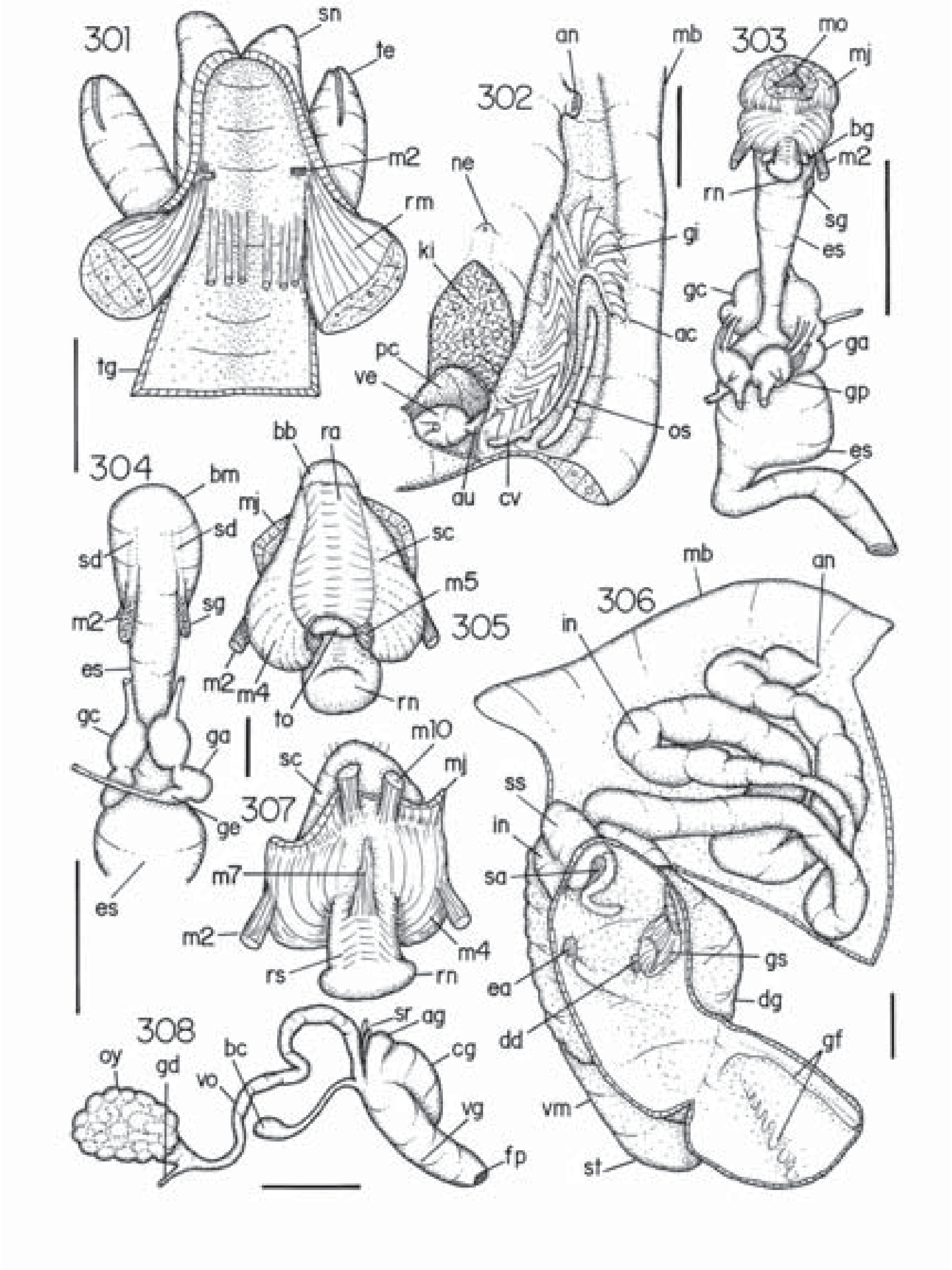
Head-foot (Figs. 294-297, 299, 301). Characters very similar to those of *Hipponix* species, including propodium, anterior projection of foot sole, shell and head muscles. Distinctive features following. Head muscles origin in inner-anterior surface of shell muscle and not from foot sole. Crossed muscles: pair of muscles crossing just anterior to head muscles (Fig. 297); anterior muscle connects ventral surface of left head muscle with foot sole adjacent to base of right head muscle; posterior crossed muscle inverted in connections. Tentacles with shallow longitudinal furrow in apex, running a short distance to ventral surface. Eyes minute, almost vestigial, located in outer region of tentacles base. Snout haemocoel ample, with pair of very broad retractor muscles with origin and insertions as those of *Hipponix* spp. Other additional, narrow retractor muscles detectable in dorsal inner surface of snout base, about three pairs, originating in lateral regions of foot.

Mantle organs (Figs. 295, 298, 300, 302). Characters very similar to those of *Hipponix* spp, very shallow, dislocated anteriorly by visceral mass. Osphradium ridge-like, broad, without satellite fold. Gill small, anterior region also curved, on mantle border. Gill filaments narrow, sharp, not so tall.

Visceral mass (Figs. 295, 300). Components and situation of organs as described for *Hipponix* spp, differing only in taller form. Its ventral surface also stays encased in foot concavity.



Figures 294-300, *Hipponix incurvus* anatomy: **294**, female, whole ventral view; **295**, same extracted from shell, dorsal view; **296** head-foot, female, dorsal view, visceral mass and pallial organs removed; **297**; foot and shell muscle, dorsal view, head removed; **298**, pallial cavity roof, transversal section of its middle region just parallel to rectum (gill filament is not so aligned as shown); **299**, head-foot of female, frontal view; **300**, visceral mass and pallial cavity roof, ventral view. Scales = 1 mm.



Figures 301-308, *Hipponix incurvus* anatomy: **301**, head and haemocoel, ventral view, snout opened longitudinally, foregut removed; **302**, pallial cavity roof and anterior extremity of visceral mass, ventral view, ventral-lateral-left wall of pericardium removed; **303**, buccal mass, esophagus and nerve ring, ventral view; **304**, same, dorsal view; **305**, odontophore, dorsal view; **306**, visceral mass and intestine (seen if remainder structures were transparent), dorsal wall of stomach part removed and deflected inwards, mantle border also shown; **307**, odontophore, ventral view; **308**, Ovary, visceral and pallial oviducts, ventral view. Scales = 0.5 mm, except 305, 307 = 0.1 mm.

Circulatory and excretory systems (Figs. 300, 302). Pericardium and heart characters similar to those of *Hipponix* spp., located part dorsal to posterior gill region. Auricle connection with ctenidial vein not at end of gill as in *H. subrufus*, presenting posterior portion of ctenidial vein as blind-tube. Kidney characters as those described for *Hipponix*, including solid, flattened tissue, and papillate nephrostome.

Digestive system (Figs. 303-307). Buccal mass characters similar to those of *Hipponix* spp, including jaws, dorsal wall folds and odontophore muscles (Figs. 303-305, 307). Salivary glands a pair of small, long, narrow masses extending somewhat posterior to buccal mass. Salivary ducts immersed in dorsal wall of buccal mass, pigmented (pale brown), open in pair of dorsal folds near their anterior region. Radula similar to those of *Hipponix* spp. (Figs. 78, 79), but with wider lateral and marginal teeth (about five times rachidian width); rachidian tooth with about 11 cusps, central cusp more than three times neighboring cusps width, a pair of small, triangular, basal cusps; lateral tooth with about 22 cusps, generally eighth cusp apical, larger (more than three times neighboring cusp width), turned forward; marginal teeth with sub-terminal series of about 12 cusps in each side. Esophagus narrow anterior to nerve ring, without inner folds; after nerve ring suddenly expands as crop; no detectable inner glands or folds. Stomach characters similar to those of *H. subrufus* (Fig. 306), except for dorsal sorting area narrow, running transversally in middle level of dorsal gastric surface; a pair of ventral folds, right fold broad, run from esophageal aperture towards anterior where faint; left folds narrow, runs from esophageal aperture to duct to digestive gland. Some specimens with transverse fold separating gastric shield from intestinal aperture. Digestive gland single, located in middle region of ventral gastric wall. Style sac somewhat small (about ¼ of stomach length and width) and almost half separated from intestine, only very shortly connected in its basal region. Intestine origins ventral to style sac base, much more complexly looped than preceding *Hipponix* spp., its several loops shown in fig 306. Fecal pellets similar to those of anterior species. Anus small, siphoned, located in right extremity of pallial cavity close to mantle border, far from gill.

Genital system. Only females examined (Fig. 308). Ovary slight small, located in ventral region of visceral mass as in *Hipponix* species. Visceral oviduct, after short distance from ovary, connects to very narrow gonopericardial duct or ligament. Visceral oviduct runs slightly sinuously towards right and anterior, inserting in base of albumen gland. A pair of very small seminal vesicles insert in visceral oviduct just on right surface of its insertion. Bursa copulatrix small, with long duct, inserts in left side of visceral oviduct insertion. Albumen gland small, elliptical, separated from capsule gland by constriction. Capsule gland large (most of pallial oviduct), somewhat flattened, its duct broad and flattened, amply connected to vaginal duct. Genital pore a small slit in pallial oviduct anterior end, turned anteriorly. Female MZSP 28996 presents capsules very similar to those of *H. costellatus*, inserted in glandular concavity of propodium (Fig. 299), but with very smaller and more abundant capsules.

Nervous system (Figs. 303, 304). Similar to those of preceding *Hipponix* spp.

Habitat. On hard substrates, mainly coral, intertidal to 525 m depth.

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

Measurements of shells (in mm). MZSP 31132,♀,4.5 by 9.6; MZSP 30981,♀, 5.0 by 11.8.

Material examined. BRAZIL; **Pernambuco**; Fernando de Noronha Archipelago (Simone & Souza Jr. col., vii/1999); Porto Beach, MZSP 31227, 1 shell (day 17), MZSP 32145, 2 protoconchs (day 20); Buraco da Raquel, MZSP 31132, 1♀, 7 shells, capsules (day 19); Atalaia Beach, MZSP 31047, 2 shells (day 18); Rata Island, Buraco do Inferno, MZSP 30981, 7♀, 2 shells (day 19). Porto de Galinas, Central Beach, MZSP 31350, 1♀(C. Magenta col., vii/1999). **Bahia**; Abrolhos Island MZSP 30815, 3 specimens (L. Pinni col., v/ 1958); MZSP 28996, 1♀(Moura, Fancini & Sazima col., 9-15/i/1998).

Hipponix grayanus Menke, 1853

(Figs 30-32, 76, 309-318)

Ancient synonymy in Carpenter (1856: 4). Complement:

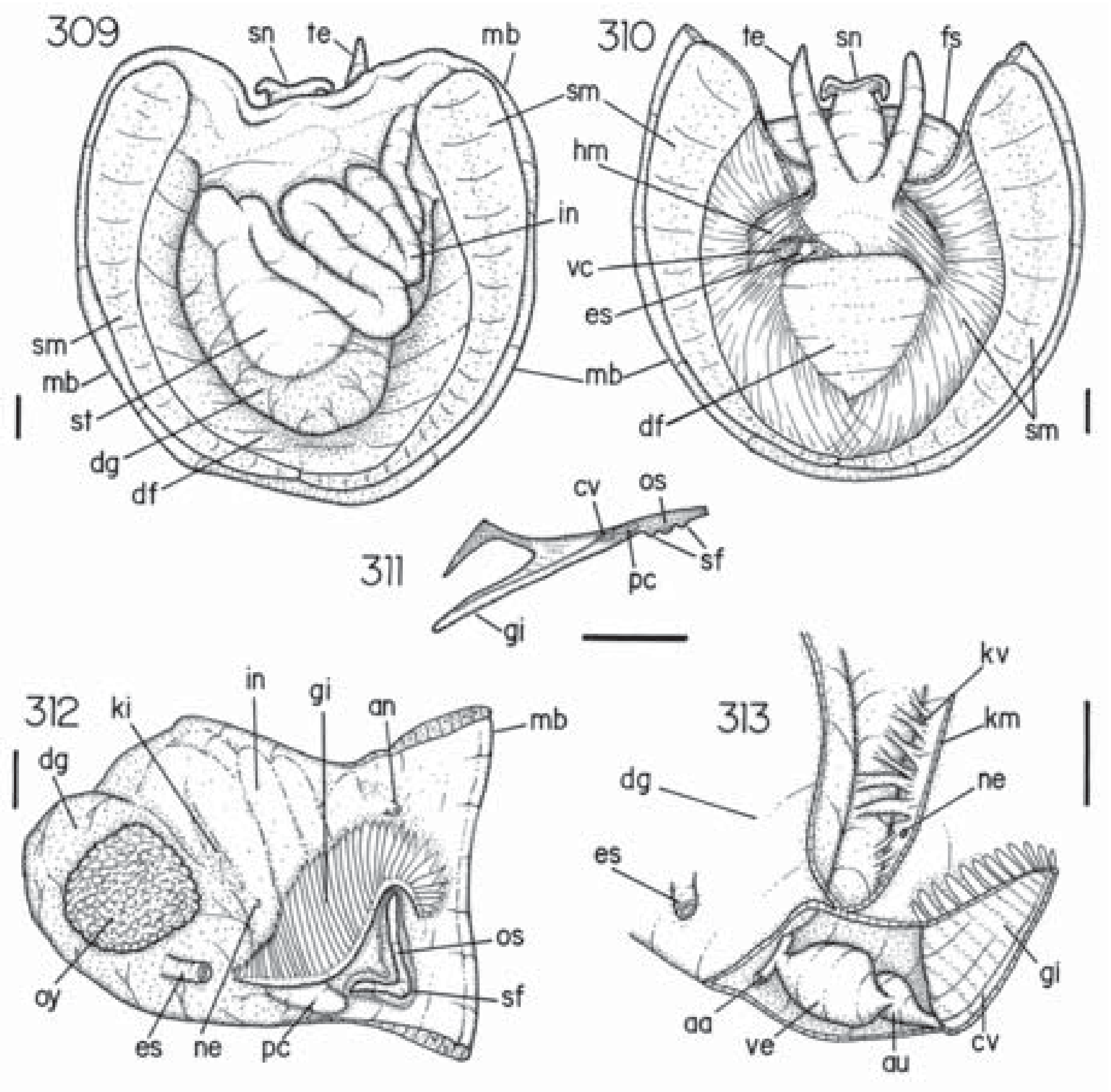
Hipponyx radiata Gray in Sowerby, 1835 (pre-occupied name by Quoy & Gaimard, 1824).

Hipponyx grayanus Menke, 1853: 79.

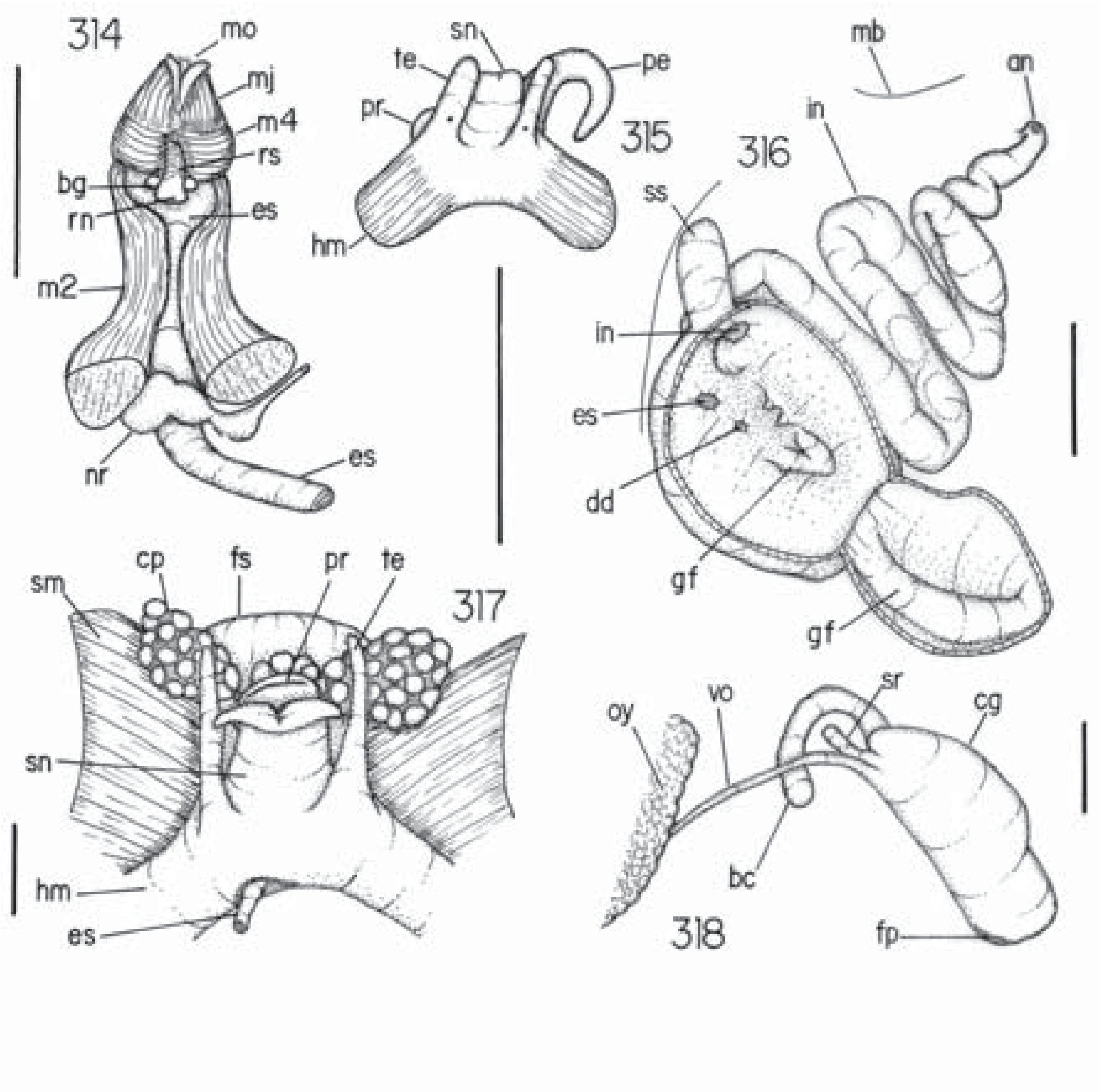
Hipponix grayanus: Keen, 1971: 453 (fig. 765).

Shell (Figs. 30-32). Similar to *H. costellatus* and *H. subrufus*, with radial threads and some nodules (Fig. 30). Periostracum slight developed, mainly near shell border, with projected scales. Other details in Carpenter (1856: 4) and Keen (1971: 453). Young specimens (seen inside capsules) (Figs. 31, 32) protoconch with single whorl, outer surface smooth, without sculpture, umbilicus narrow. First teleoconch portion with sparse, irregular, spiral lines.

Head-foot (Figs. 310. 315. 317). Very similar to preceding *Hipponix* species. Following distinctive features. Eyes very small, almost vestigial, located in inner surface of tentacles base, close to snout. Head muscles strong, origin separated from shell muscle. Shell muscle more lateral, somewhat far from visceral sac. Foot sole and ventral surface of shell muscle attached to ventral calcareous, several-layered plate (all specimens present foot sole extracted, except if part of ventral plate was also removed). Propodium and ven-



Figures 309-313, *Hipponix grayanus* anatomy: **309**, Female extracted from shell, dorsal view; **310**, head-foot, female, dorsal view; **311**, pallial cavity roof, transversal section in its middle level; **312**, pallial cavity and visceral mass, ventral view; **313**, same, detail of left transition between both, kidney opened longitudinally, ventral wall of pericardium, with gill, sectioned and deflected to right. Scales = 0.5 mm.



Figures 314-318, *Hipponix grayanus* anatomy: **314**, buccal mass, anterior esophagus and adjacent structures, ventral view; **315**, head of male, dorsal view, re-hydrated specimen; **316**, middle and distal ducts of digestive system, dorsal view, seen in situ if remainder structures were transparent; **317**, head and adjacent structures, female, dorsal view; **318**, part of visceral and pallial female genital structures, ventral view. Scales = 1 mm.

tral brood concavity also present. Young specimens with operculum very thin, palcispiral, almost circular.

Mantle organs (Figs. 311, 312). Mantle border characters and disposition of pallial organs similar to those of preceding *Hipponix* species. Mantle border thick and broad. Osphradium ridge-like, broad, with narrow satellite fold all around it. Gill somewhat large (occupying about half of cavity area). Gill filaments with broad base and tall, slender, sharp tip; most of them pointing posteriorly. Anterior gill extremity curved to left, on mantle border.

Visceral mass (Figs. 309, 312). Similar characters to those of other *Hipponix* species, also very dislocated anteriorly, encroaching on posterior half of pallial cavity roof.

Circulatory and excretory systems (Fig. 313). Heart characters and location similar to those of preceding *Hipponix* species, but slightly more dislocated to the anterior (Figs. 312, 313), located almost entirely dorsal to gill. Ctenidial vein connects with auricle almost in its middle region, having long posterior portion of this vessel beyond this connection, probably this part of vein has contrary direction of circulation (in relation to other gastropods) postero-anterior. Kidney a deep hollow chamber compressed between visceral mass (stomach and digestive gland) and first intestinal loop. Renal tissue very scant, only some transverse folds in its ventral region, connecting anterior border of membrane between kidney and pallial cavity with adjacent intestinal loop, at right from nephrostome. Nephridial gland smaller, at left from nephrostome, close to pericardium. Nephrostome a small slit in left region of membrane exposed in pallial cavity.

Digestive system (Figs. 314, 316). Buccal mass characters very similar to those of preceding *Hipponix* species, inclusive anterior insertion of m7. Differs only by very larger m2 pair size (although very narrow in their insertion). Salivary glands cluster around esophagus anterior to nerve ring. Esophagus narrow, inner surface with some longitudinal folds. Stomach, as in preceding *Hipponix* species, large, occupying most of visceral mass space. Stomach inner surface almost entirely smooth (Fig. 316); in ventral surface three small folds in central region, right fold larger and slightly triangular; esophageal aperture small, located in posterior-left region of ventral gastric surface, aperture of duct to digestive gland between esophageal aperture and larger gastric fold; intestine and style sac origin in left gastric region. Style sac slightly short, cylindrical, almost entirely separated from intestine. A rounded fold separates style sac aperture from that of intestine. Intestine originates just posterior to style sac, contouring it ventrally, becomes broad and runs along anterior surface of stomach. Intestine has about six to seven gradually decreasing loops towards anterior, up to anus (Fig. 316).

Genital system. **Development**. Suggestive protandric hermaphroditism, most of small specimens males. Brood strategy similar to those of preceding hipponicids (Fig. 317) about 3 large capsules containing about 30 young, 1-whorl shelled specimens. Capsule rods connected to glandular brood concavity of foot.

Male (Fig. 315). The examined males were dry and rehydrated for examination. The analysis is, therefore limited. Visceral structures look similar to those of preceding hipponicids. Penis small, curve, originated ventral to head, apex simple, somewhat rounded.

Female (Figs. 317, 318)**.** Ovary and visceral oviduct characters similar to those of preceding hipponicids. Gonopericardial duct not found. Visceral oviduct narrow, almost straight, oblique, inserts in pallial oviduct at its posterior-left end. Seminal receptacle small, narrow, sac-like, located just at side of visceral oviduct insertion. Bursa copulatrix long (little shorter than pallial oviduct length) slightly narrow, width somewhat uniform along its length, distal end rounded, weakly broad. Bursa insertion in posterior-right end of pallial oviduct. Remainder pallial oviduct a single glandular mass without clear separations between albumen and capsule glands; inner lumen broad and flat. Genital pore a simple, longitudinal slit, located in anterior-left end. Glandular concavity between propodium and foot sole similar to those of preceding hipponicids.

Habitat. Rocky, intertidal to 9 m depth.

Distribution. Mexico to Ecuador.

Measurements of shells (in mm). LACM 75-8.3, ♀, 8.0 by 15.5; LACM 66-114.17, 8.2 by 15.6.

Material examined. MEXICO; **Jalisco**; Bahia Banderas, Las Tres Marietas, 20°42’N 105°32’W, 5-9 m depth, LACM 65-14.27, 11 dry specimens (J.H. McLean, C. Miller leg.; R/V Gringa; 20-21/iii/1965). COSTA RICA; **Puntarenas**, Gulfo de Niceya, between Isla Tolinga and Isla Alcatraz, 3-5 m depth, LACM 75-8.3, 4 dry specimens (C.C. Swift leg.; 2/v/1975). ECUADOR; **Manabi**; off Isla La Plata, 18 m depth, 1°15.4’S 81°05.3’W, LACM 33-23.6, 1♀(R/V Velero III; AHF 23-33; 22/i/1933); **Guayas**; N side of Santa Elena Peninsula, E of Salinas, 2°11.47’S 80°56.52’W, 9 m depth, LACM 66-114.17, 15 dry specimens (R/V Anton Brunn, sta. 6670; 8/v/1966).

Discussion. *H. grayanus* differs from *H. costellatus* mainly in that 1) eyes are very reduced, almost absent; 2) osphradium is broader; 3) presence of satellite fold around osphradium; 4) broader gill with longer and slender filaments; 5) kidney tissue is scanty; 6) heart more anterior, with connection auricle-ctenidial vein almost in middle level of gill; 7) broader m2; 8) stomach with different arrangement of folds and insertions; 8) intestine longer and more convolute; 9) penis without apical papilla; 10) bursa copulatrix longer and more slender; 11) accessory vesicle between bursa and visceral oviduct insertions.

One of the more remarkable differences between *H.*

grayanus and *H. costellatus* is that the former has a capacity of forming a ventral plate of several calcareous layers. The shell muscle, in fact, becomes attached to this plate apparently without capacity of detachment. These features are not observed in Brazilian species of *Hipponix (H. costellatus, H. subrufus*), which are not attached to substrate to the same degree, and possess thinner ventral plate. The ventral calcareous plate is even called “ventral valve”, while the shell is called “dorsal valve”, in ancient literature (e.g., Sowerby, 1835). Other Pacific species, *H. antiquatus*, also has a ventral calcareous plate (Yonge, 1953).

Hipponix leptus new species

(Figs. 33-35, 80-82, 319-328)

Hipponyx antiquatus: Lopes & Alvarenga, 1955: 168.

Hipponix antiquatus: Abbott, 1954: 166 (part); Warmke & Abbott, 1961: 84 (pl. 15, fig. h); Rios, 1970: 53; Cauquoin, 1970: 138; Vermeij, 1972: 91; Abbott, 1974: 135 (part); Rios, 1975: 62 (pl. 17, fig. 247); 1985: 55 (pl. 20, fig. 252); Leal, 1991: 88-89 (pl. 14, figs. C, D); Rios, 1994: 69 (pl. 24, fig. 265) (*non* Linné, 1767).

Types **Holotype**: MZSP 32259 D (from type locality). **Paratypes**: BRAZIL; **Pernambuco**; Fernando de Noronha Archipelago (Simone & Souza Jr. Col., vii/1999); Buraco da Raquel, MZSP 31041, 45 specimens (day 22); Porto Beach, MZSP 31208, 1D(with capsules), 2 shells (day 17), MZSP 31248, 1 shell, MZSP 32143, 5 protoconchs (day 20); Atalaia Beach, MZSP 31151, 2D, 3 shells (day 18); Ponta da Sapata, 21 m depth, MZSP 31322, 1 shell (day 18); Caieira Beach, MZSP 31022, 3Ú, 17D, 1 shell (day 23); Rata Island, Buraco do Inferno, 10 m depth, MZSP 31077, 1Ú, 9D, 4 shells (day 19).

Type locality: BRAZIL; **Pernambuco**; Fernando de Noronha Archipelago, Caieira Bay, 03º50’30”S 32º24’10”W.

Diagnosis Western Atlantic species with shell, sculptured by concentric, irregular scales. Eyes very reduced, but present. Anterior lateral projections of snout. Gill relatively large. Penis distal third bifid.

Description.

Shell (Figs. 33-35). Of medium size (up to 25 mm), patelliform, flat to tall and slightly coiled. Color pale cream to pale brown. Protoconch, as described by Leal (1991), of 1 whorl, smooth, central to sub-terminal-posterior located. Sculpture strong concentric scales, irregularly sized and disposed; sometimes very small and weak radial striae between scales. Inner surface smooth, glossy, pale brown. Muscle scar horseshoe shaped (concavity anterior), broad anteriorly, very narrow posteriorly; runs about in middle region between apex and shell border.

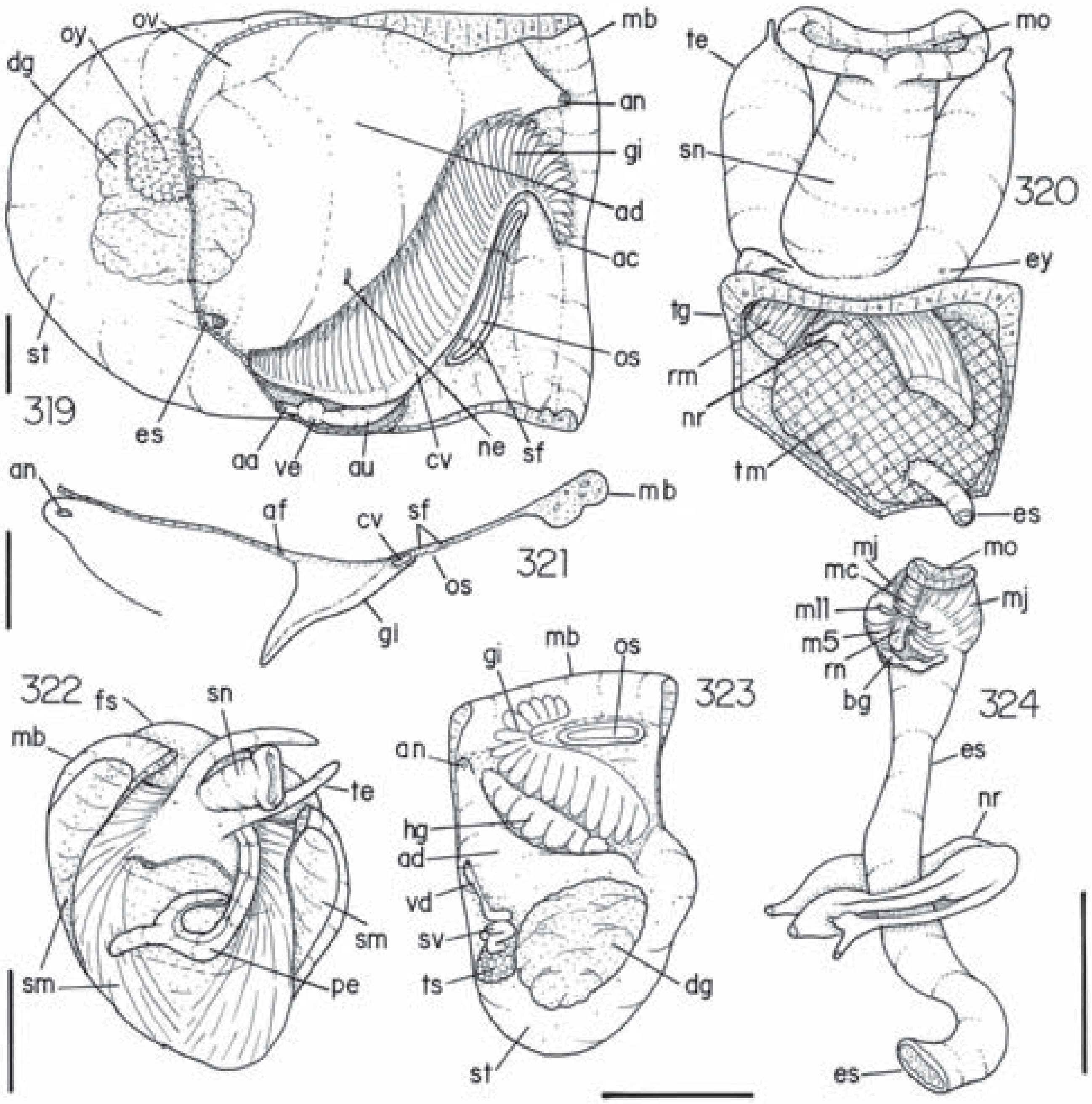
Head-foot (Figs. 320, 322). Characters similar to those of *H. costellatus*, included separation between head and shell muscles. Eyes very reduced, deeply located in integument. Snout-proboscis anterior surface with pair of broad, ample lappets projected in both sides; both projections form anterior concavity with mouth in center. Head muscle pair originates in foot sole, very close to shell muscle inner edge, in its middle level. Shell muscle separated posteriorly, close to median line. Haemocoel short and broad, inner space almost wholly filled by net of transversal muscles.

Mantle organs (Figs. 319, 321, 323). Features also similar to those of preceding *Hipponix* species; characteristic attributes following. Mantle border thick, simple. Osphradium long, broad, little longer than 1/3 of gill length, situated slightly oblique. Osphradium satellite fold well developed, surrounds entire osphradium ganglion. Gill large (about half of pallial cavity area), sigmoid, anterior extremity curved and located on mantle border. Gill filaments tall, triangular, curved towards right, tip pointed. Hypobranchial gland thin and inconspicuous in larger individuals but thicker and transversally folded in younger ones.

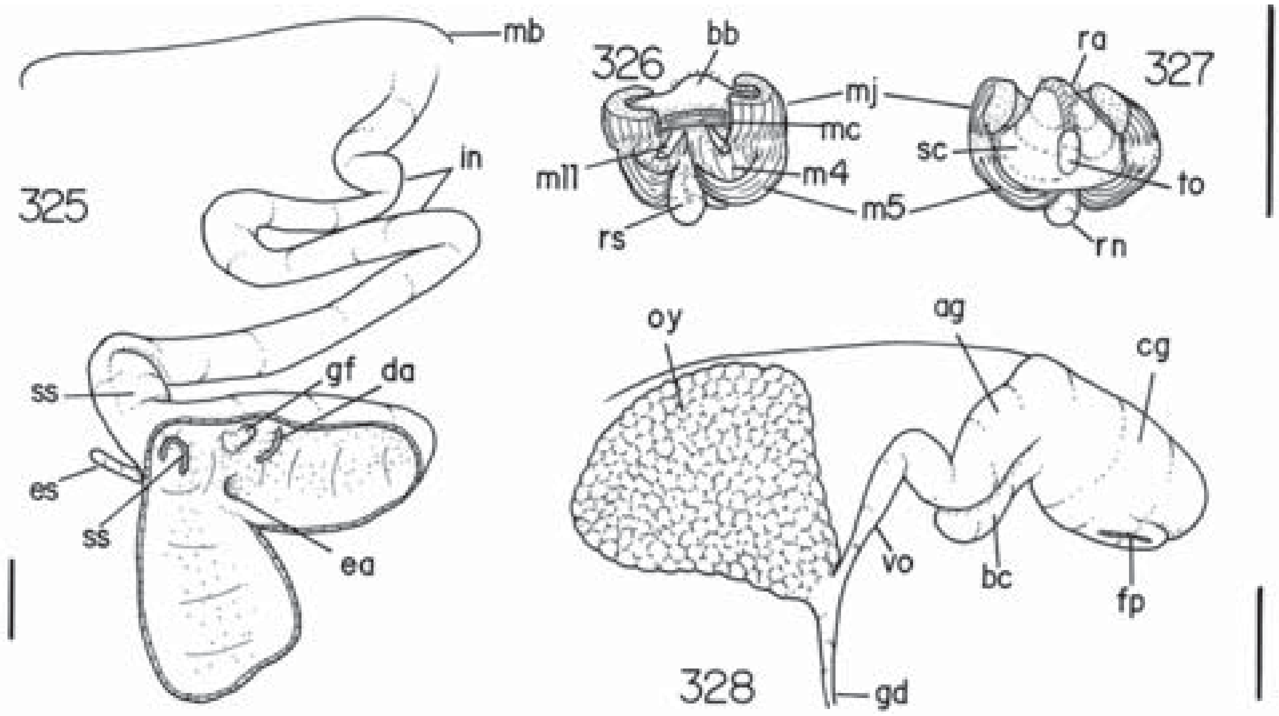
Visceral mass (Figs. 319, 323). Organization similar to that of preceding *Hipponix* species. Stomach large as posterior structure. Digestive gland and gonad proportionally small, ventral, slightly central. Digestive gland color greenish pale brown, gonad color pale beige.

Circulatory and excretory systems (Fig. 319). Characters somewhat similar to those of *H. grayanus*, with following remarks. Heart proportionally small, entirely located dorsal to posterior half of gill, small part exposed in pallial cavity at left from this gill region. Pericardium posterior limit attached to gastric style sac. Kidney chamber deep and flat, compressed between visceral mass and first intestinal loops. Renal tissue only in ventral (pallial) surface, thin, surface uniform, posterior to nephrostome. Nephrostome a very small slit located in left-posterior region of visceral mass encroaches pallial cavity.

Digestive system (Figs. 324-327). Snout-proboscis with differentiated expanded anterior region described above. Buccal mass reduced, length less than ¼ of that of proboscis. Jaw plates lacking. Odontophore very small (e.g., 0.35 mm in animal with 10 mm shell length). Odontophore muscles (Figs. 326-327) with organization similar to those of preceding hipponicids, remarkable features following: **m2** pair absent; **m5** pair thick, insertion covering considerable portion of radular sac, similar to calyptraeid fashion; **m11** pair relatively broad, originate in adjacent region of haemocoel ventral surface. Radular teeth somewhat similar to preceding hipponicids, remarkable features following (Figs. 80-82): rachidian tooth slightly triangular, with 7 to 9 small cusps, central cusps pointed, about 3 times larger than neighbor



Figures 319-324, *Hipponix leptus* anatomy: **319**, pallial cavity and visceral mass, female, ventral view; **320**, head and haemocoel, female, ventral view, foot removed, a vestigial penis still present in base of right tentacle (left in fig.); **321**, pallial cavity roof, transversal section tangent to rectum; **322**, head-foot of male, dorsal view; **323**, pallial cavity and visceral mass, male, ventral view; **324**, buccal mass, anterior esophagus and nerve ring shown in situ, ventral-slightly lateral-left view. Scales = 1 mm.



Figures 235-328, *Hipponix leptus* anatomy: **325**, middle and distal digestive tubes, dorsal view, seen in situ if remainder structures were transparent, dorsal gastric wall sectioned and deflected to left; **326**, odontophore, ventral view; **327**, same, dorsal view; **328**, female genital organs, ventral view. Scales 7, 10= 1 mm, 8-9 = 0.5 mm.

cusps; lateral tooth with about 3 times rachidian tooth width, with 7 to 9 small cusps in inner edge and 10 to 12 cusps in outer edge, tip pointed, turned forwards; inner lateral tooth tall, narrow, tip broad (spoon-like), with about 20 very small, terminal cusps; outer marginal similar to inner marginal tooth, weakly narrower. Salivary glands reduced. Buccal ganglion pair close to median line. Anterior esophagus broad, inner surface covered by several irregular longitudinal folds, each fold slightly broad and glandular. After nerve ring, esophageal inner folds gradually become narrower and uniformly longitudinal. Stomach very large (about half of visceral mass volume) (Fig. 325). Esophageal aperture small, in mid-posterior region of gastric ventral surface. Duct to digestive gland broad, single, located at same level as esophageal aperture, anterior and slightly right of it. Gastric shield small, located just to right of duct to digestive gland aperture on ventral gastric surface. A ventral, transverse, gastric fold, low and broad, edging at left gastric shield and esophageal aperture. Other small gastric fold peduncled, somewhat spherical, located at right of duct to digestive gland aperture and posterior to gastric shield. Aperture of intestine and style sac in left gastric end, connected with each other. Style sac with about 1/3 of remainder stomach length, entirely connected with intestine, inner space compressed by tall and broad longitudinal fold. Intestine broad, performing about 3 successively smaller zigzags towards right up to anus (Fig. 325). Anus a slightly tall papilla, locates in right-anterior region of pallial cavity.

Genital system. **Development**. Not all small specimens are male, about 50% of them only. No large males, suggesting protandric hermaphroditism. Largest male examined 11 mm long. Some rare females, with well developed pallial oviduct, retain penis. Capsules brooded as in preceding hipponicids.

Male (Figs. 322, 323). Testis very small, located in mid-right region of visceral ventral surface. Seminal vesicle with about 4 irregular loops, located just anterior to testis. Seminal vesicle suddenly narrows and becomes long and straight vas deferens, it runs distance equivalent to vesicle length on pallial cavity floor (edging its right border) and opens. From this aperture to penis base weak sperm groove. Penis, as preceding hipponicids, originated ventrally to snout and right cephalic tentacle. Penis relatively narrow and long (about ¾ of foot length). Penis distal third bifid, right branch flat and solid, left branch similar, but with penis furrow running all along it at almost up to its tip. Tip of both penis branches rounded.

Female (Fig. 328). Organization of structures similar to that of preceding hipponicids, distinctive or notable features following. Ovary relatively small, from its left-anterior region visceral oviduct origins. Gonopericardial duct begins in this same region and runs obliquely. Visceral oviduct gradually becomes thick and broad, runs towards anterior and right with weak zigzag. Albumen gland probably located in broader portion of visceral oviduct. Seminal receptacle a broad sac located by side of albumen gland, connects to capsule gland by narrower duct just anterior and at left than albumen gland connection. Capsule gland somewhat small, elliptical, thick and simple. Glandular concavity between propodium and mesopodium as those of preceding hipponicids

Central nervous system (Fig. 324). Of hipponicid fashion, large, relatively concentrated ganglia.

Measurements of shells (in mm). Holotype ♀= 7.4 by 18.7; MZSP 31041 ♀1= 7.6 by 15.5; ♂2= 5.3 by 12.9; ♀4= 10.5 by 18.0; MZSP 31022 ♂2= 5.9 by 11.0; MZSP 31077 ♂= 2.8 by 6.5.

Distribution. For the moment confined to Fernando de Noronha Archipelago, however probably occurs in entire Western Atlantic range of "*H. antiquatus*", from Florida, USA to Espírito Santo, Brazil.

Habitat. On hard substrate, mainly in hidden surface of rocks and reefs, subtidal up to 21 m depth. Supposedly microphagus, however a specimen (MZSP 31041-D1) had a crab cheliped inside esophagus occupying most of haemocoel volume.

Material examined. Types only.

Etymology. The specific epithet refers to the shell sculpture, from the Greek *leptos*, which means "like scale of peel".

Discussion. Up to now, *H. leptus* was considered a Western Atlantic occurrence of *H. antiquatus* (Linné, 1767) from tropical Pacific coast of North, Central and South Americas. However, the Western Atlantic specimens differ in several aspects from *H. antiquatus* as described anatomically by Yonge (1953, 1960), showing that this appears to be another case of misidentification based on similarities of shell features (which are very variable). *H. leptus* differs from Pacific *H. antiquatus* in having the foot less attached to ventral calcareous plate, ventral calcareous plate thinner, anterior region of snout-proboscis broader and ampler, eyes less developed, osphradium broader and with satellite fold, gastric style sac more developed, and inner gastric folds present. On the other hand, both species apparently present similarities not only in shell characters, but also in penis morphology (Yonge, 1960, fig. 1) and in the reduced size of the buccal mass. Bandel & Riedel (1994: 334, fig. 2) showed a protoconch with spiral threads for *H. antiquatus* from Yucatan, Mexico; this kind of protoconch sculpture is not observed in examined specimens.

According to G. Rosenberg (person. communication) there are some doubts about the actual locality of the type material of *H. antiquatus*. With the shell characters helping little, and the anatomical study by Yonge (1953, 1960) based on Pacific specimens, the designation of the Pacific population as *H. antiquatus* appears to be coherent.

H. leptus presents a series of distinctive features if compared with the other studied hipponicids, such as: ample anterior region of snout, small size of heart and buccal mass, absence of m2 (pair of retractor of buccal mass), m1a and of jaws, reduction of salivary glands, short portion of oviduct between ovary and gonopericardial duct, and pallial oviduct features.

Genus *Sabia* Gray, 1847

(Type species: *Amalthea conica* Schumacher)

Sabia conica (Schumacher, 1817)

(Figs. 36-38, 83, 84, 329-342)

Synonymy see Hedley (1902: 600); Ludbrook (1957: 49) remarks and complement:

Amathea conica Schumacher, 1817: 181 (pl. 21, fig. 4) [holotype ZMUC 181, no. 1071, no locality; designed Tasmania afterwards by Ludbrook (1957)].

Patella australis Lamarck, 1819: 335 [Type locality: New Holland = Australia].

Hipponix conicus: Laws, 1970: 115-121 (figs. 1-9).

Description.

Shell (Figs. 36-38). Similar to preceding hipponicids. Color white. Periostracum brown. Sculptured only by growth lines and broad radial threads. Apex slightly weak and tall. Other details in Knudsen (1991).

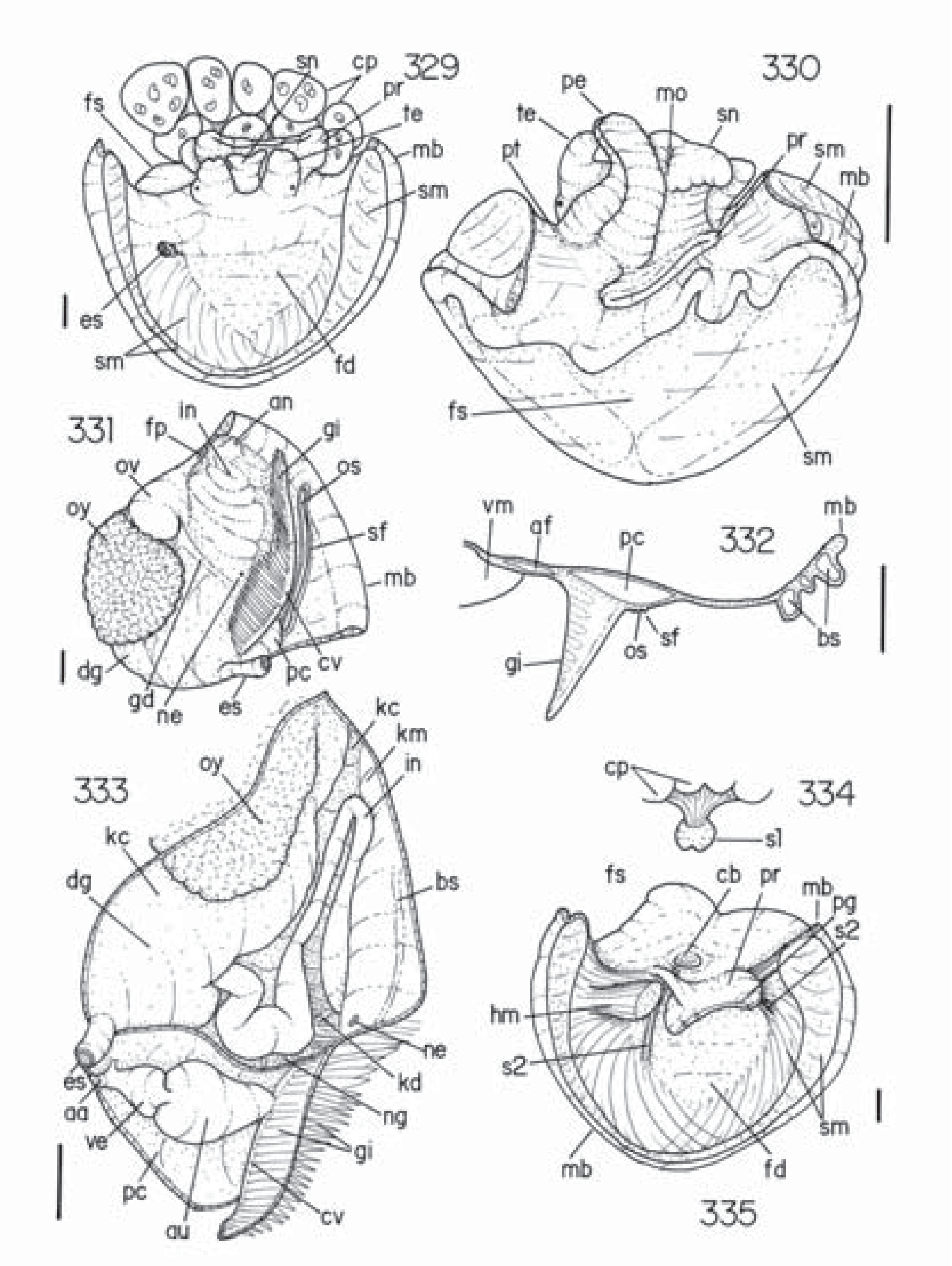
Head-foot (Figs. 329, 330, 335). Characters similar to those of preceding hipponicids, with following notable or distinctive features. Head broad and slightly inlaid. Snout narrow, weakly bifid in anterior margin. Tentacles broad, stubby, tip somewhat bifid and pigmented by black. Foot and shell muscles as those of preceding hipponicid species; pair of head muscles origin in inner-anterior surface of shell muscle. Propodium with broader distal edge than its base. Propodium distal edge with pedal gland furrow and about 1/3 of foot width. Brood glandular concavity present, described below. A pair of narrow muscles origins in inner-ventral edge of shell muscles, run towards anterior, inserts around brood glandular concavity (Fig. 335: s2), right muscle more oblique than left muscle. Pedal sole free from ventral calcareous plate. Haemocoel narrow and strongly curved towards left, inner space filled by transversal net of muscle fibers similar to those of calyptraeids.

Mantle organs (Figs. 331, 332). Mantle border thick and simple. Pallial cavity short, greatly compressed by visceral sac, with organization similar to those of preceding hipponicids. Osphradium ridge-like, slightly oblique, very long (little shorter than gill), anterior end on mantle border close to gill; between osphradium posterior end and mantle border considerable distance. Osphradium satellite fold present, narrow, surrounds entire osphradium. Gill weakly sigmoid, occupying about 1/3 of pallial cavity area. Gill filaments tall, triangular, tip pointed. Afferent gill vessel very broad. Pericardium part dorsal to posterior region of gill.

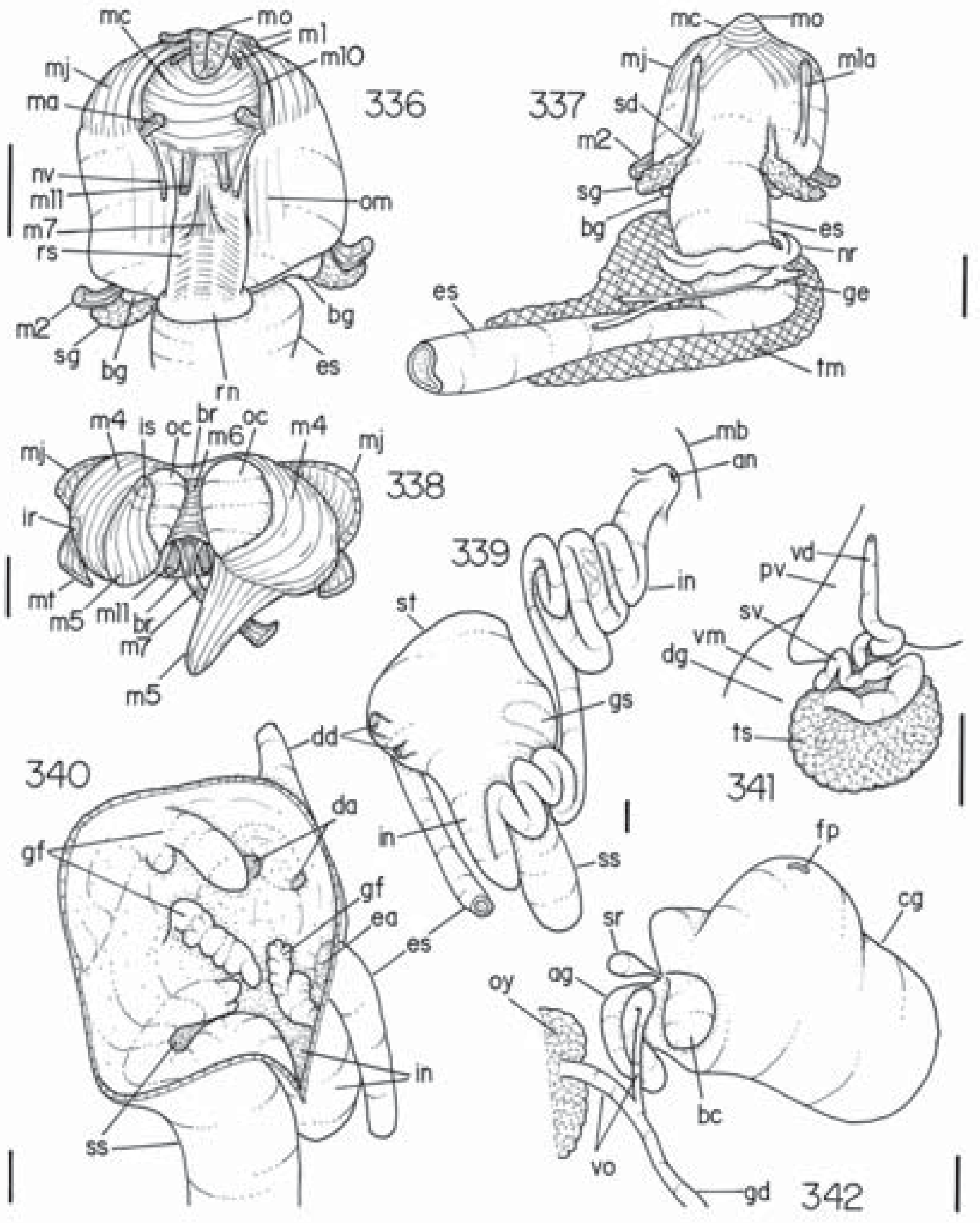
Visceral mass (Fig. 331). Of similar organization as those of preceding hipponicids.

Circulatory and excretory systems (Fig. 333). Heart relatively large, located partly dorsal to gill posterior region extending little beyond gill left margin. Auricle anterior-right, connected to ctenidial vein between middle and posterior 1/3 of gill length. Kidney mostly hollow, deep, greatly compressed between visceral mass and pallial intestinal loops. Renal tissue very scant, only some narrow, irregular glandular folds in dorsal and anterior surfaces between intestinal loop. A single, sigmoid intestinal loop running in dorsal surface. Nephridial gland reduced. Nephrostome a small slit close to pericardium, in membrane between kidney and pallial cavities.

Digestive system (Figs. 336-340). Buccal mass and odontophore features similar to those of preceding hipponicids, characteristic attributes following. Dorsal folds of buccal mass slightly tall in region posterior to jaws, aperture of salivary glands very small. Odontophore muscles (Figs. 336-338): **m1a** pair present; **ma**, pair of accessory muscles of jaws, origin in ventral-median surface of haemocoel, adjacent to odontophore, run towards dorsal, penetrate between mc and m10 jointed with odontophore nerve pair, insertion along inner surface of mj and jaw plates; **m2** pair narrow; **mt** present, very thin; **mc** broad and thin; **m7** pair origin in medial edge of m4 dorsal branch, attached to subradular membrane, insertion inside radular sac close to nucleus; **m8**, **m2a** absent; **m10** pair as median-ventral part of mj. Radular sac short and broad. Radular teeth similar to preceding hipponicids (Figs. 83, 84), remarks following: rachidian tooth with 9 cusps, central cusp about 3 times larger than secondary cusps; lateral tooth very broad (more than 3 times broader than rachidian), with about 11 cusps, generally 6th cusp much larger and terminal; inner and outer marginal teeth similar to each other, tall, narrow, with 5 to 8 sub-terminal cusps on each side. Salivary glands very small, located in posterior-dorsal region of buccal mass, violet. Buccal ganglia small, located laterally, close to m2 insertion. Anterior esophagus broad, suddenly narrows and curves towards left in region posterior to nerve ring. Esophagus with about 12 longitudinal, tall inner folds. Stomach very large and ample. Esophageal insertion in middle level of posterior gastric wall. Ducts to digestive gland double, narrow, located close with each other and close to esophageal aperture. Intestinal origin at right from esophageal aperture. Style sac origin just anterior to that of intestine. Stomach inner



Figures 329-335, *Sabia conica* anatomy: **329**, head-foot, female, dorsal view, egg capsules still connected; **330**, same, male, frontal – slightly ventral view, propodium and mesopodium deflected downwards; **331**, pallial cavity and visceral mass, female, ventral view; **332**, pallial cavity roof, transversal section in its middle portion; **333**, region between pallial cavity and visceral mass, ventral view, kidney opened longitudinally, its ventral wall deflected to right, ventral surface of pericardium (with gill) sectioned and also deflected to right; **334**, basal portion of egg capsules extracted from glandular brood concavity shown in fig. 335; **335**, foot, female, dorsal view, head extracted, propodium deflected exposing glandular brood concavity (cb). Scales = 2 mm. Lettering: **s1**, calcareous base for attachment of egg capsules rods in cb; **s2**, muscle of cb.



Figures 336-342, *Sabia conica* anatomy: **336**, buccal mass, ventral view; **337**, buccal mass and anterior esophagus, dorsal view, part of net of transversal muscles also shown; **338**, odontophore, ventral view, both cartilages deflected, left m5 (right in fig.) deflected; **339**, middle and distal digestive tubes, ventral view, seen if remainder structures were transparent; **340**, stomach, dorsal view, inner surface exposed by means of a longitudinal, dorsal incision; **341**, detail of right side of transition pallial cavity-visceral mass, male, ventral view, evidence to genital organs; **342**, visceral and pallial female genital structures, ventral view, ovary only partially shown. Scales = 1 mm.

surface with several folds (Fig. 340): transversal, tall, irregular fold separates esophageal aperture from intestine origin, another similar fashioned fold located in opposite (ventral) gastric wall; tall smooth fold incompletely surrounds style sac aperture, almost closing it. A broad, smooth, bifid fold just ventral to the ducts to digestive gland, with slight expansion towards ventral wall as limit of gastric shield. Intestine and style sac almost entirely separated from each other, united only in short proximal portion. Style sac narrow, with width about 1/3 that of stomach and length about ½. Intestine intensely coiled in 2 regions: ventral to style sac and in pallial cavity, inside adrectal sinus as shown in fig. 339. Anus siphoned, close to mantle edge.

Genital system. **Development**. Apparent protandric hermaphroditism, all small specimens males and larger specimens females. Females with about 8 large capsules containing about 100 young specimens (with 1 whorl), each bears thin, paucispiral operculum and are separated from the others by transparent membranes. Capsules connected to brood concavity by relatively short stalk (Fig. 329), a broad calcareous node, produced and attached to concavity (Fig. 334). Other details in Laws (1970).

Male (Figs. 330, 341). Testis pale beige, small, located in ventral and lateral-right regions of visceral sac. Seminal vesicle coiled, thick, just posterior to pallial cavity right-posterior margin. Seminal vesicle broad, gradually narrows up to straight and long papilla in such tip vas deferens opens in pallial floor. Sperm groove shallow, runs on right side of pallial cavity floor up to penis base. Penis located in ventral-right side of snout, base broad, narrowing gradually. Penis length little longer than snout. Penis groove runs along middle region of penis ventral surface. Penis tip flat, rounded, with groove running in lateral edge. Other details in Laws (1970).

Female (Figs. 334, 335, 342). Ovary similar located as testis (of males), but larger, its anterior edge close to posterior limit of pallial cavity. Visceral oviduct very narrow, running slightly beyond ovary. Gonopericardial duct long and narrow. Visceral oviduct V-shaped in gonopericardial duct region. In pallial cavity, oviduct gradually increases in zigzag fashion. After zigzag, pallial oviduct suddenly expands in amorphous glandular mass lying dorsal to intestinal loops (albumen gland?). Seminal receptacle a small vesicle preceding oviduct expansion, connected to oviduct right side by narrow duct. Bursa copulatrix similar to seminal receptacle but larger, flattened, located ventral, attached to adjacent oviduct wall; bursa duct short, inserted close to that of receptacle. No apparent separation between albumen and capsule glands. Genital pore a small slit located in middle region of oviduct right side, on elevation. Brood concavity similar to those of preceding hipponicids but ampler.

Central nervous system (Fig. 337). Nerve ring with small ganglia posterior, far removed from buccal mass, supra and subesophageal ganglia close to nerve ring. Remainder characters similar to those of preceding hipponicids.

Measurements of shells (in mm). AMS 353011: 1♀) 14.4 by 27.0; 2 ♀) 15.8 by 24.8; 3 ♂) 6.0 by 10.4; 4 ♂) 7.5 by 15.7.

Distribution. Bass Strait, Central W coast, G. Aust. Bight, Lower W coast, NE coast, S Gulfs coast, SW coast, Tas. coast.

Habitat. On hard substrates, up to 200 m depth.

Material examined. AUSTRALIA; **West Australia**; Woodman Point, Cockburn Sound, 32º08'S 115º44'E, AMS 353083, 1♂, 3♀(sta. 815B, W.F. & J.M. Ponder col., 12/xii/1971); **Tasmania**; Green Cape, Maria Island, 42º 43'S 148º01'E, 5 m depth, AMS 353011, 4♂, 4♀(sta. 38616, W. F. Ponder & D.C. Wolfe col., 26/iii/1970).

Discussion. According to information given by P. Middelfart and W. F. Ponder (AMS), there are considerable systematic confusion to the validity of the specific name. There is no type locality for the taxon, and Lamarck's description is very brief. Some authors have the view that *Hipponyx australis* Quoy & Gaimard (1835: 434) is a subsequent reference of *A. conica* (e.g., Ludbrook, 1957), while others have the opinion that this is a different species (e.g., Hedley, 1902: 600). One of the latest revisions of the taxon considered *A. conica* as the available name as this taxon (Ludbrook, 1957), this approach is adopted here.

Genus *Malluvium* Melvill, 1906

(Type species: *Capulus lissus* E.A. Smith)

Malluvium devotus (Hedley, 1904)

(Figs. 39-41, 85, 86, 343-357)

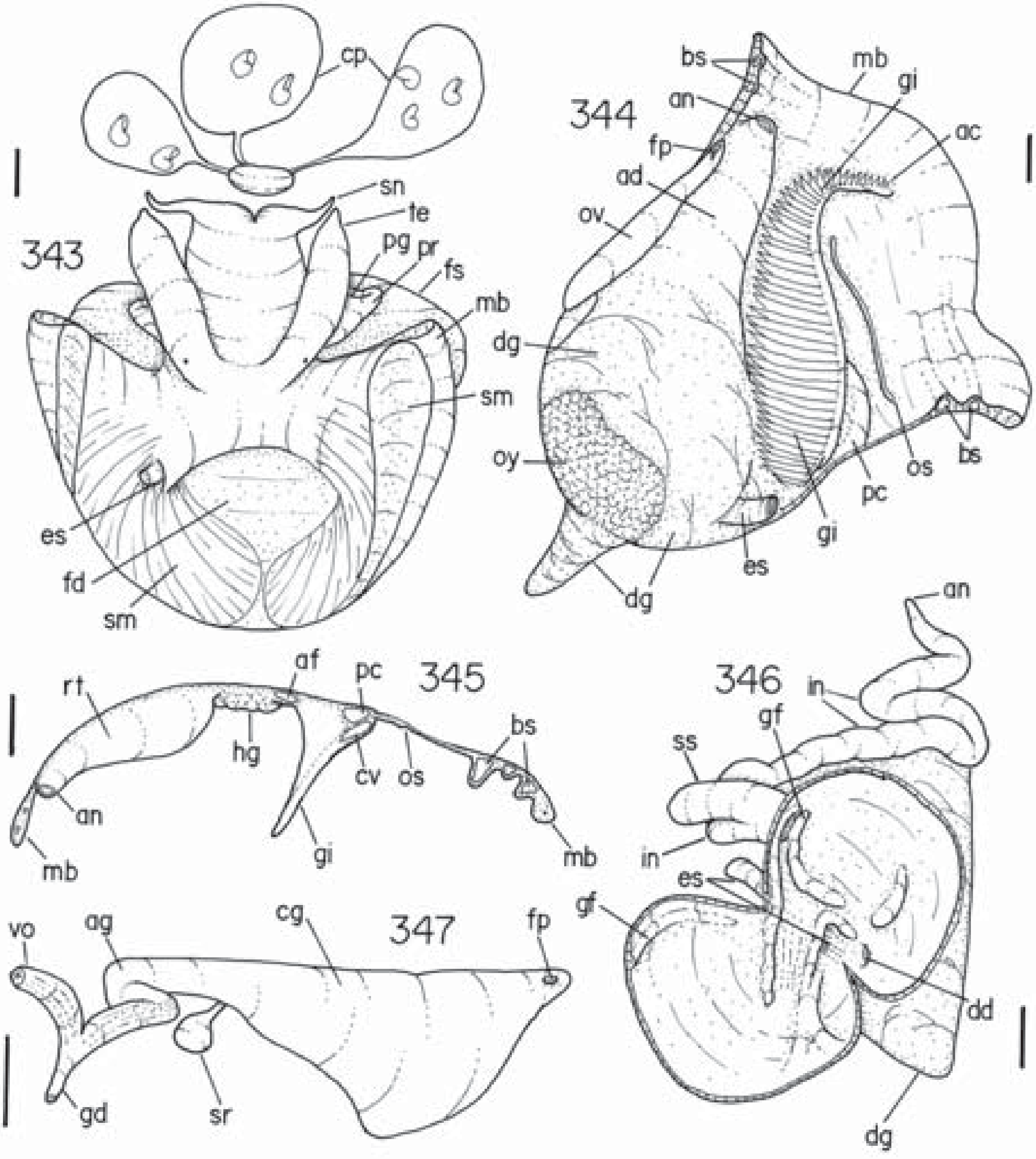
Capulus devotus Hedley, 1904: 190 (pl. 8, figs 15, 16) [holotype AMS; Type locality: Sixteen miles east of Wollongong, NSW, in 100 fathoms]; 1905: 41; Hedley & Petterd, 1906: 213; Hedley, 1907: 285; Hedley & May, 1908: 110; Gatliff & Gabriel, 1913; 75; Hedley, 1918: M57; May, 1921: 58; 1923: fig. 20; Thiele, 1930: 580; Garrard, 1961: 12; Macpherson & Gabriel, 1962: 130.

Malluvium devotus: Wilson, 1993: 165 (fig.).

Description.

Shell (Figs. 39-41). Characters similar to those of preceding hipponicids, but taller and curved posterior. Sculpture concentric low scales. Other details in Hedley (1904: 190).

Head-foot (Figs. 37, 343). Similar features as those of



Figures 343-347, *Malluvium devotus* anatomy: **343**, head-foot, female, dorsal view, egg capsules extracted from glandular brood concavity; **344**, pallial cavity and visceral mass, ventral view; **345**, pallial cavity, transversal section tangent to rectum; **346**, middle and distal digestive tubes and part of digestive gland, dorsal view, intestine shown in situ if remainder structures were transparent, dorsal wall of stomach partially extracted and deflected downwards; **347**, middle and anterior (pallial) oviduct, ventral view. Scales = 1 mm.

preceding hipponicid species, notable or differentiable attributes following. Head proportionally larger, width about half of that of foot. Tentacles broad, tip pointed. Eyes very small, vestigial. Anterior margin of snout with pair of long lateral projections. Foot sole free from ventral calcareous plate. Propodium large, broad, with distal edge broader than its base. Glandular concavity for brooding present. No vestige of crossed muscles.

Mantle organs (Figs. 344, 345). Characters also similar to those of preceding hipponicids, differences following. Mantle border thick, with broad inner collar blood vessels. Osphradium ridge-like, very narrow, length about 2/3 of that of gill. Gill sigmoid, occupying about 1/3 of pallial cavity area; anterior extremity slender. Gill filaments tall, triangular, tip pointed. Hypobranchial gland low. Pallial cavity very compressed by visceral mass (details below).

Visceral mass (Figs. 344, 346). Similar attributes as those of preceding hipponicids, except in being taller, having apex turned posteriorly and having amore posteriorly located gonad.

Circulatory and excretory systems (Fig. 344). Heart and pericardium characters similar to those of other hipponicids, but more anterior, located dorsal to posterior half of gill, part exposed in left-anterior side of gill margin. Kidney very similar to that described for *H. grayanus*.

Digestive system (Fig. 346). Buccal mass characters very similar to those described for *H. costellatus*, with short radular sac, differs by narrower **m2** and by presence of **mt** (similar to those of calyptraeids but thinner). Radular teeth: rachidian tooth narrow, with about 9 cusps, central cusp about 3 times larger than neighbors; lateral and both marginal approximately of same length; lateral tooth broad (about 4 times broader than rachidian), about 8 sub-terminal, small cusps in outer edge; both marginal teeth similar with each other, tip pointed, from 5 to 9 small, subterminal cusps in both sides. Esophagus with 4-5 narrow, longitudinal, inner folds not uniform in size. Stomach very large and broad, insertion of esophagus on posterior-left side, protected dorsally by transverse gastric fold. Duct to digestive gland single, located close to esophageal aperture, slightly posterior. Another short, ventral gastric fold anterior to duct to digestive gland. A pair of long gastric folds on each side of fold dorsal to esophageal aperture, run along lateral-right gastric wall in direction to intestine-style sac aperture. Style sac about half of stomach width and length, with distal half separated from intestine. Intestine origins ventral to style sac, after separated runs ventrally to style sac and after edges anterior gastric wall. Intestine, in pallial cavity, with 2 successive smaller loops. Anus small, slightly siphoned.

Genital system (Fig. 347). Only females examined, however one of them has narrow vestigial penis ventral to head of normal hipponicid fashion. Ovary orange, occupies posterior region of visceral sac. Visceral oviduct slightly broad, runs on right side of visceral sac ventral surface. Gonopericardial duct narrow, long, inserted in visceral oviduct just before pallial cavity. In region of gonopericardial duct insertion, oviduct possesses some inner longitudinal folds and V-fashion. Pallial oviduct narrow and sigmoid in posterior region, gradually increases in single, large glandular mass (albumen plus capsule gland). In level about 2/3 of pallial oviduct length, it narrows up to small, papilla-like genital pore. Seminal receptacle vesicular, single, located in left region of posterior end of pallial oviduct; its duct narrow and somewhat long. Brood glandular concavity similar to those of preceding hipponicids, however it secrets larger calcareous node for anchoring capsules (Fig. 343). Generally 3-4 capsules with about 20 young specimens (of 1 whorl), each specimen separated by transparent membranes. Capsules fashion similar to those of remainder hipponicids, with relatively long basal stalk.

Measurements of shells (in mm). AMS 353123: 1) 8.6 by 18.2; 2) 9.4 by 18.7.

Distribution. Australia; Bass Strait, Central E coast, G. Aust. Bight, Lower E coast, S Gulfs coast, SW coast, Tasmania coast.

Habitat. Continental shelf, continental slope; mostly attached to the inner lip of dead *Sassia kampyla* (Watson, 1883) (cf Garrard, 1961), up to 200 m depth

Material examined. AUSTRALIA; **New South Wales**; between Port Staphens & the Hawkesbrury, 33º15’S 151º45’E, 366-411 m depth, AMS 353123, 4♀(sta. 38487, R.V. “Kapala”, prawn trawl, 17-21/vii/1972).

Genus *Cheilea* Modeer, 1793

(Type species: *Patella equestris* Linné)

Cheilea equestris (Linné, 1758)

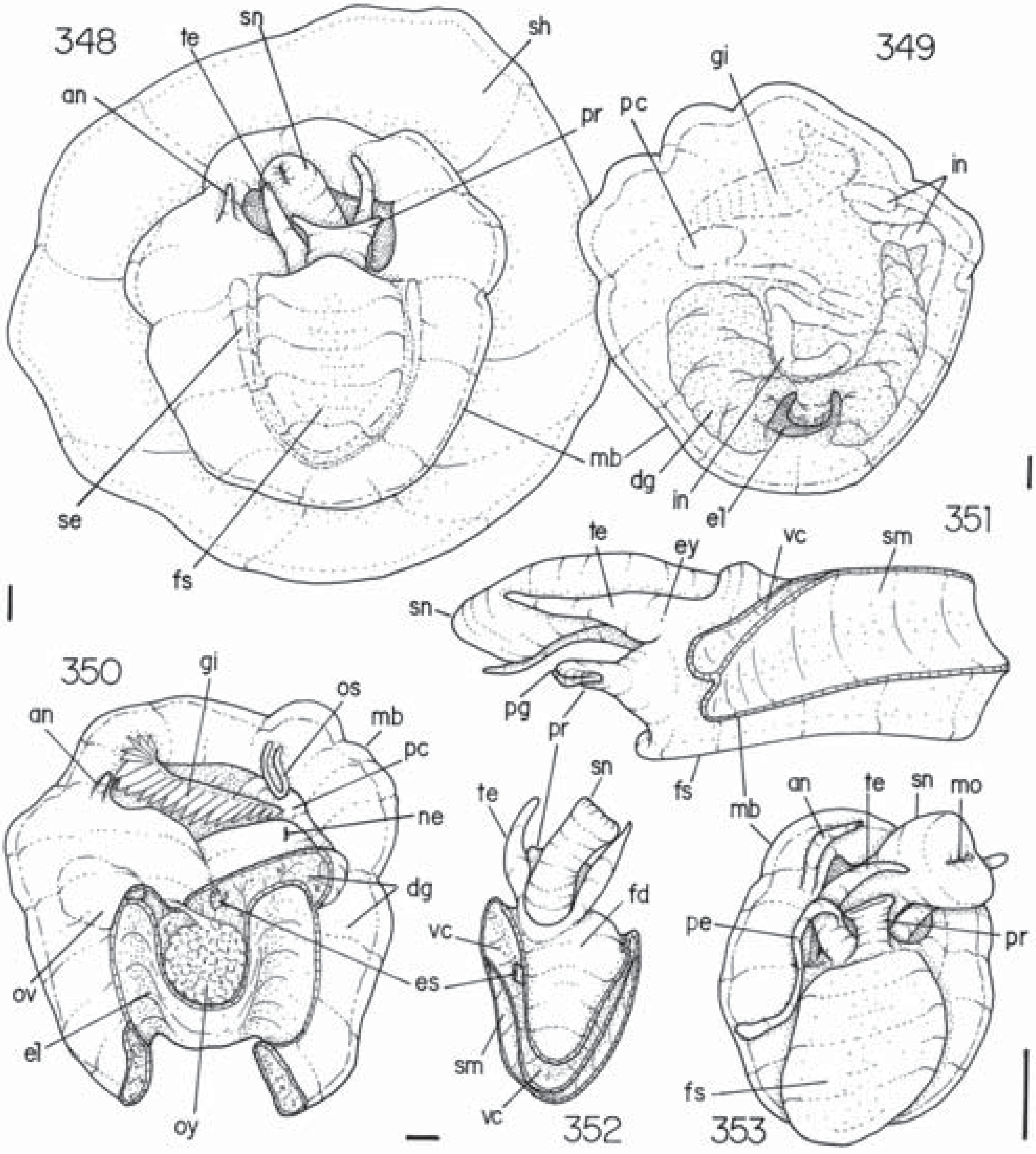
(Figs. 42, 43, 87-89, 348-369)

Synonymy in Leal (1991: 91). Complement:

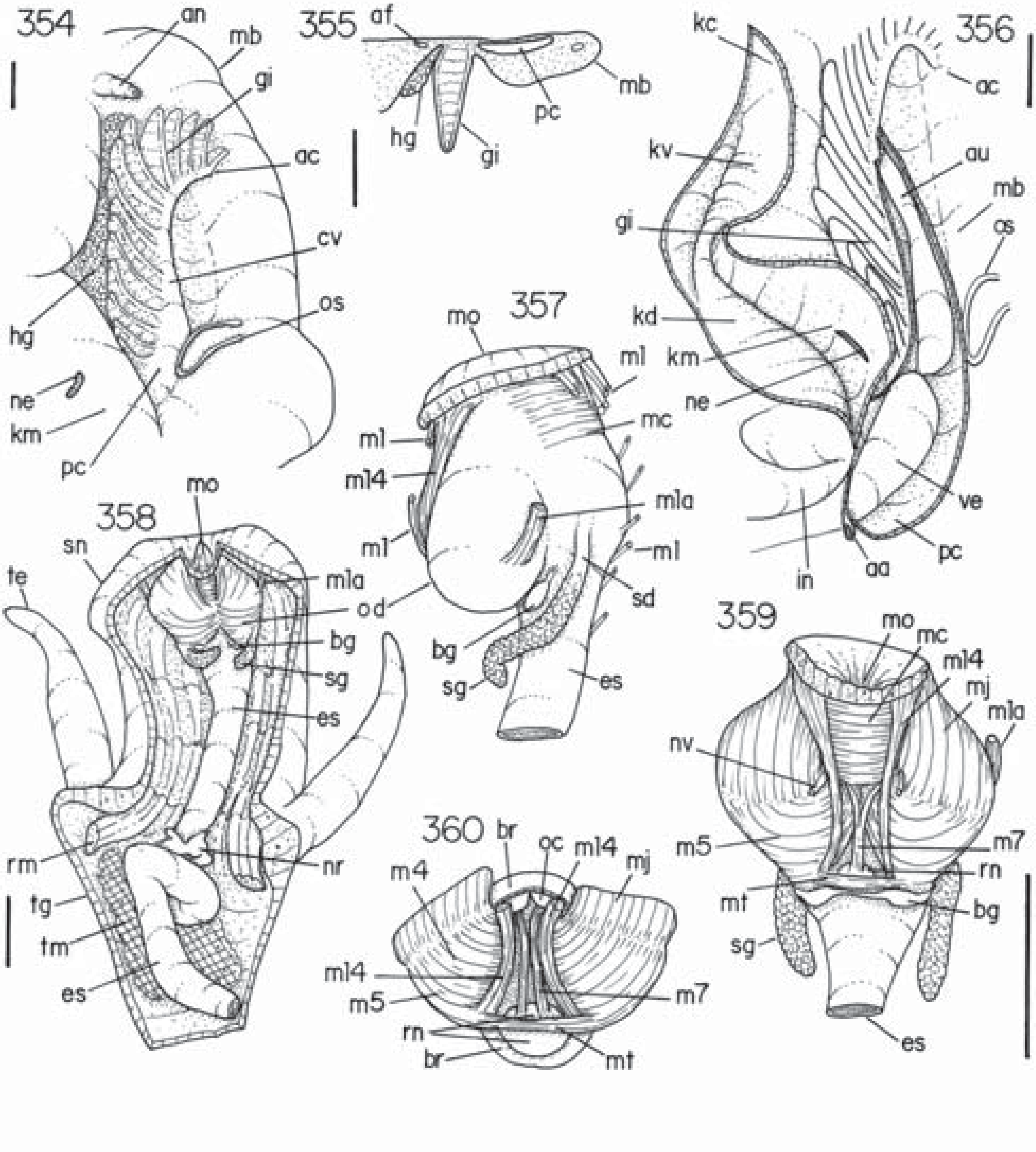
Cheilea equestris: Abbott, 1954: 165 (pl. 21p); Rios, 1970: 53; 1975: 64 (pl. 17, fig. 257); Calvo, 1987: 95 (fig. 53); Rios 1994: 70 (pl. 24, fig. 269); Bandel & Riedel, 1994: 336 (fig. 4, pl. 6, fig. 1).

Description.

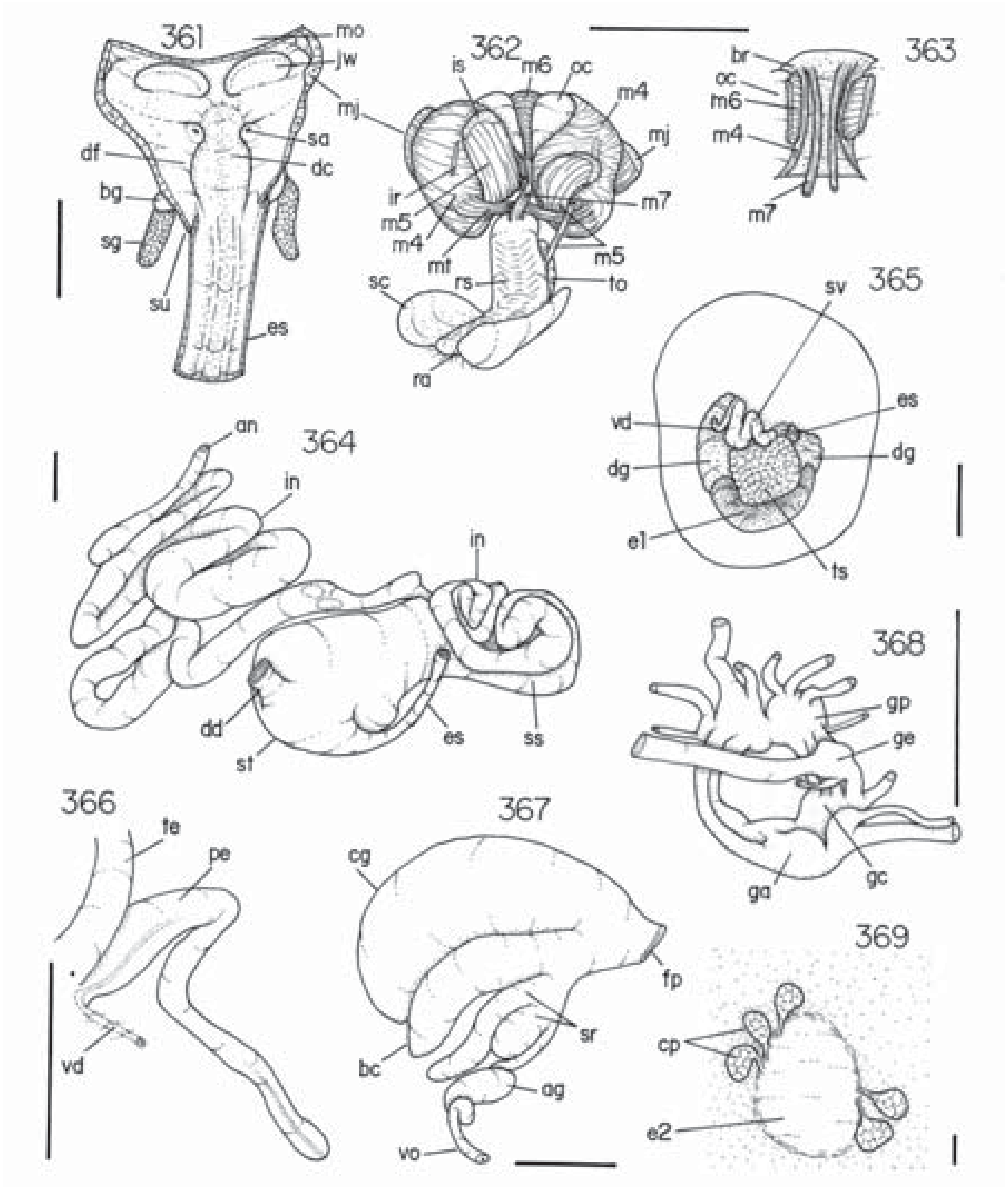
Shell (Figs. 42, 43, 348). Limpet-like, with well-developed ventral plate. Sculpture several radial ribs, of uniform size, periodically interrupted by small nodes, aligned concentrically. Outer surface irregularly undulated. Inner surface without apparent muscle scars. Protoconch described by Leal (1991, pl. 14, fig. H). Shell ventral plate incompletely conical (opened anteriorly), situated obliquely, from shell apex to posterior. Other details in Abbott (1974: 139-140).



Figures 348-353, *Cheilea equestris* anatomy: **348**, female, whole ventral view, shell septum edges seen by transparency; **349**, same extracted from shell, dorsal view; **350**, pallial cavity and visceral mass, ventral view, portion posterior to shell ventral plate sectioned and deflected; **351**, head-foot, female, lateral-left view; **352**, same, dorsal view; **353**, male, lateral-right slightly ventral view, whole specimen extracted from shell, penis pulled outside. Scales = 1 mm. Lettering: **e1**, space let by shell ventral plate in visceral mass.



Figures 354-360, *Cheilea equestris* anatomy: **354**, pallial cavity roof, ventral-inner view; **355**, same, transversal section in its middle region; **356**, same, detail of left border with visceral mass, ventral view, kidney and pericardium opened longitudinally, their inner structures exposed; **357**, buccal mass and part of anterior esophagus, lateral-left view; **358**, head and haemocoel, ventral view, foot extracted, snout-proboscis opened by a longitudinal, ventral incision; **359**, buccal mass, ventral view; **360**, odontophore, ventral, slightly posterior view. Scales = 1 mm.



Figures 361-369, *Cheilea equestris* anatomy: **361**, dorsal wall of buccal mass and anterior esophagus, ventral view, odontophore extracted, esophagus opened longitudinally; **362**, odontophore, ventral view, radula and subradular cartilage deflected downwards, left m5 (right in fig.) also deflected; **363**, same, detail of its median region after longitudinal section of m6; **364**, middle and distal digestive tubes, ventral view, shown in situ if remainder structures were transparent, 2 fecal pellets shown; **365**, middle region of visceral mass, male, ventral view; **366**, penis and adjacent head structures, dorsal view; **367**, pallial and short part of visceral oviduct, ventral view; **368**, nerve ring, ventral view; **369**, substrate of an extracted specimen, its ventral calcareous plate and some egg capsules still attached. Scales = 1 mm. Lettering: **e1**, space let by shell ventral plate in visceral mass; **e2**, ventral calcareous “valve”, secreted by foot on hard substrate.

Head-foot (Figs. 348, 351-353, 358). Head and anterior fashion of foot similar to those of preceding hipponicids. Snout-proboscis very long and broad, anterior end simple (not expanded nor bifurcated). Eyes very reduced. Propodium similar to those of hipponicids, with small expansions in both anterior sides. Between propodium and head no glandular concavity. Foot (mesopodium) sole small, restricted inside shell ventral plate. Foot very thick, solid and small, also restricted to ventral half of shell ventral plate inner space. No columellar muscle or shell muscle, attachment only in outer surface of foot with inner surface of shell ventral plate (Figs. 351, 352: sm). Dorsal foot surface planar, outer margin edged by connection with visceral mass (Figs. 351, 352: vc). Haemocoel narrow, posterior half (posterior to proboscis) filled with net of transverse muscles. Proboscis retractor muscle pair well developed, origin and insertion lateral, each runs along inner surface of proboscis in 3-4 slightly tall longitudinal bands. Head muscle pair immersed in integument, covering proboscis retractor muscle.

Mantle organs (Figs. 349, 350, 354-356). Mantle located on lateral and posterior surface of foot ventral region, contours very thin anterior and ventral edges of shell ventral plate, and after suddenly becomes thicker. Mantle border slightly thick in posterior half and very thick in anterior half. Pallial cavity arrangement of structures and size similar to those of preceding hipponicids, greatly compressed by visceral mass. Osphradium oblique, anterior portion located on mantle border. Only low and narrow satellite fold of osphradium present, interrupted anteriorly. Inner surface of area surrounded by osphradium fold apparently lacking any structure, i.e., an osphradium ganglion. Gill relatively small and oblique, anterior region curved, located on mantle border. Gill filaments tall and narrow, apex slightly rounded and almost central. Between gill and visceral mass encroached inside pallial cavity a very narrow area filled by hypobranchial gland. Hypobranchial gland grayish-beige, somewhat tall, compressed by neighbor structures. Anus preceded by very tall, papilla-like portion, very long in some specimens.

Visceral mass (Figs. 349, 350, 365). Entirely surrounding shell ventral plate, internally and externally. Inner shell ventral plate portion of visceral mass located on dorsal surface of foot, connected to it along its borders. Remaining visceral mass surrounds anterior edge of shell ventral plate and its entire outer surface, covering it completely. Gonad located as ventral structure inside shell ventral plate, on foot. Digestive gland fills remaining space, except central region, occupied by stomach and adjacent intestinal loops. Visceral mass encroaches in pallial cavity similarly to remainder hipponicids.

Circulatory and excretory systems (Fig. 356). Heart characters somewhat similar to those of preceding hipponicids, located dorsal to gill posterior half and part exposed in pallial cavity. Auricle connected to ctenidial vein about in its center, with long (posterior) portion as blind sac of inverted flow. Kidney also similar to those of preceding hipponicids, distinctive attributes following. Renal chamber deep and very compressed between anterior region of visceral mass and adrectal sinus. Renal tissue very thin, surface smooth, covers posterior surface of left side and anterior surface of left side, in this some transversal folds. Nephrostome a relatively large slit far from any other inner structure; located in left region of kidney chamber.

Digestive system (Figs. 357-364). Buccal mass and odontophore organization somewhat similar to those of preceding hipponicids, interesting features follows (Figs. 357-363). Jaw plates well-developed, slightly elliptical, median and anterior cut edges. Dorsal folds broad and low, possessing tall and broad pair of anterior papillae in aperture of salivary glands (Fig. 361). Dorsal chamber (between both dorsal folds) shallow and broad, surface smooth. Odontophore muscles: **m1**, relatively concentrated along median line, in both sides (ventral and dorsal), particularly crowd in anterior-dorsal edge; **m1a** pair present, similar to calyptraeids; **m2** pair absent; **mc** and **mj** thick; **m7** pair narrow, origin in subradular membrane bulged part (bb), run attached to it separated from m4, insertion in radular sac, close to radular nucleus; **mt,** present, somewhat narrow, similar to calyptraeids; **m10** pair not distinguishable, maybe mixed wit mj; **m14** pair close to median line, narrow, origin in ventral-inner surface of mouth, run on ventral surface of odontophore towards posterior, insertion in m4 pair covered by mt. Radular teeth somewhat similar to preceding hipponicids, remarkable features following (Figs. 87-89): rachidian tooth very broad and short, with about 15 to 19 small, pointed cusps, central cusp about 3 times larger than neighboring cusps; lateral tooth about 2 times broader than rachidian tooth, with 4 to 5 broad cusps on inner edge and 7 to 9 narrow, pointed cusps on outer edge, apex broadly pointed and tall, turned forward; inner marginal tooth tall, narrow, tip flat, rounded (spoon-like), with about 10 very small, terminal cusps; outer marginal tooth similar to inner marginal tooth, but with pointed tip and with 4 to 5 very small, subterminal cusps. Salivary glands small, sac-like, long, located separated from each other just posterior to odontophore. Salivary ducts penetrate dorsal wall of buccal mass in its posterior-dorsal region, open as described above. Pair of buccal ganglia lateral located, covered by salivary glands. Anterior esophagus relatively broad, inner surface with pair of longitudinal, low folds located on dorsal side. Middle esophagus coiled just posterior to nerve ring, inner surface covered by about 20 very narrow longitudinal folds. Stomach large (Fig. 364), transversally in center of visceral mass, anterior to shell ventral plate. Esophagus crosses ventral surface of stomach transversally and inserts in its posterior-right surface. Duct to digestive gland single, broad, located in ventral-right gastric surface. Style sac completely connected to intestine, weakly separated from each other. Gastric inner surface mostly smooth, pair of folds separates esophageal from duct from digestive gland apertures, each fold slightly tall and broad, left fold shorter, straight, right fold longer, curved. Gastric shield thin, located in opposed side of esophageal aperture. Intestine with 2 coiled regions, separated by weakly sigmoid loop, region just after style sac, located in its ventral surface; other region located in adrectal sinus of pallial cavity roof. Form of intestinal loops in Fig. 364. Anus, as described above, long siphoned, located in anterior-right region of pallial cavity (Figs. 348, 350, 353. 354).

Genital system. **Development**. Apparently protandric hermaphrodite, most of small specimens, up to 6 mm, males. Specimens larger than 11 mm long always mature females. Brood strategy differs from those of preceding hipponicids, because it lacks brood concavity which holds capsule stalks. Capsules, although similar in shape to those of remainder hipponicids, stay with stalks attached to substrate, in periphery of ventral calcareous plate (Fig. 369), protected by shell.

Male (Figs. 353, 365, 366). Testis pale cream in color, located in center of visceral mass inside shell ventral plate. Seminal vesicle small, intensely coiled, located in anterior region of testis more concentrated at right. In posterior-right region of pallial cavity, seminal vesicle gradually narrows. Pallial vas deferens runs attached to right surface of pallial floor very narrow and entirely closed (tubular); runs almost straight up to posterior region of right cephalic tentacle base, penetrating into penis base. Penis long, basal 1/3 broader and flat, narrowing gradually; distal 2/3 narrow, flat, of uniform width along its length. Penis tip weakly broader, rounded. Penis duct entirely closed (tubular), very narrow and simple (not coiled), opens in center of penis tip.

Female (Fig. 367). Ovary pale beige, similarly located as testis of males. Visceral oviduct narrow, origin in ovary anterior edge, runs obliquely towards anterior and right. Region of visceral oviduct preceding pallial cavity coiled, its walls gradually increasing forming narrow albumen gland, newly narrow in region preceding its connection with pallial oviduct. Pair of seminal receptacles slightly broad, sac-like, located in posterior surface of albumen gland insertion. First receptacle smaller, almost spherical. Second receptacle long and narrower. Bursa copulatrix follows both receptacles, size about half of that of capsule gland, connected to it at short distance from genital pore. Capsule gland elliptical, large (about 1/5 of pallial cavity volume), located in posterior-right region of pallial cavity. Capsule gland inner lumen flat, walls thick-glandular, whitish. Capsule gland inserts by side of bursa copulatrix in short vaginal atrium. Female genital pore simple, slit-like, located about in mid- region of pallial cavity right edge. No brood concavity between head and propodium.

Central nervous system (Figs. 368). Characters similar to those of preceding species, relatively large ganglia, concentrated far posterior from buccal mass. Sub- and supra esophageal ganglia close to cerebral ganglia.

Measurements of shells (in mm). MZSP 31152♀1, 9.4 by 22.6; ♀2, 7.4 by 17.5; MZSP 31974,♂1, 2.5 by 5.6;♂2, 3.0 by 5.4; ♀5.6 by 1.0.

Distribution. North Carolina, USA, to Espírito Santo, Brazil, also reported to Indo-Pacific (see comments below).

Habitat. On hard substrates, mainly in hidden surface of rocks and reefs, subtidal.

Material examined. BRAZIL; **Pernambuco**; Fernando de Noronha Archipelago (Simone & Souza Jr. Col., vii/1999); Atalaia Beach, MZSP 31152, 6♀ (day 18); Conceição Beach, MZSP 31411, 2 shells; Ponta da Sapata, 21 m depth, MZSP 31323, 1 shell (day 18); Meio Beach, 4-6 m depth, 1 shell (day 22); Porto Beach, MZSP 31184, 1♂, 1 shell (day 17), MZSP 31240, 2♀(day 20); Buraco da Raquel, MZSP 31124, 9 specimens (day 19); Between Meio Island and Rata Island, 10 m depth MZSP 30991, 1♂, 1♀(day 21); Buraco do Inferno, Rata Island, 10 m depth, MZSP 31974, 3♂, 3♀(day 19).

Discussion. *C. equestris*, described as *Patella* by Linné (1758), has a type locality in the Indian Ocean. Normally it is regarded that the species occurs worldwide in all tropical regions of the 3 Oceans (Leal, 1991; Rios, 1994). However, it is quite possible that the present sense of *C. equestris*, actually encompasses several species. If confirmed, the Brazilian material should be described as a new species. Leal (1991: 92) found an undescribed species in Abrolhos Reef complex, which surely is not the species sampled herein. Under the above remarks, a conservative approach is adopted here, and the sample studied was identified as *C. equestris*. This is due to lack of comparative material from others regions, as well as lack of previous studies.

The genus *Cheilea*, according to the literature, is considered both Calyptraeidae (e.g., Abbott, 1974; Leal, 1991) and Hipponicidae (e.g., Rios, 1994). *C. equestris* is the type species of the genus. Based on the material studied herein, the close relationship with the hipponicids is clear. The arrangement of the anterior region of head-foot is clearly of hipponicid type, differing only by lack of brood glandular concavity. Several characters of the digestive system also corroborate the hipponicid nature of *Cheilea*, such as the arrangement of the odontophore muscles and the presence of a single duct to digestive gland in stomach. The arrangement of the pallial cavity is also hipponicid-like, greatly compressed by the visceral mass. The origin of the penis, basal in head, is also a hipponicid attribute. The confusion may be due to the superficial similarity of the *Cheilea* shell with that of *Crucibulum*, as seen here, a true calyptraeid (Owen, 1835; this study). However, the central shell ventral plate differs considerably. In *Crucibulum*, it is a whole cone (Figs. 15, 17, 18), while is an incomplete cone in *Cheilea* (Fig. 43). Furthermore, the arrangement of the structures around the shell ventral plate is completely different. In *Crucibulum*, the foot wholly fills the inner region of the shell ventral plate, and the visceral mass stays in its left side. In *Cheilea*, the inner region of the ventral plate is also filled by visceral structures (including gonad).

Family Capulidae

Genus *Capulus* Montfort, 1810

(Type species: *Patella ungarica* Linné, 1767)

Capulus sycophanta Garrard, 1961

(Figs. 90, 91, 370-387)

Capulus sycophanta Garrard, 1961: 12 (pl. 2. figs 1a, b) [holotype AM C.63342; Type locality: trawled in 25 fathoms in Keppel Bay]; Wilson, 1993: 165 (pl. 22, figs 6a, b); Beesley, Ross & Wells, 1998: 774.

Description.

Shell. Not examined, for shell characters see Garrard (1961: 12), Wilson (1993: 165).

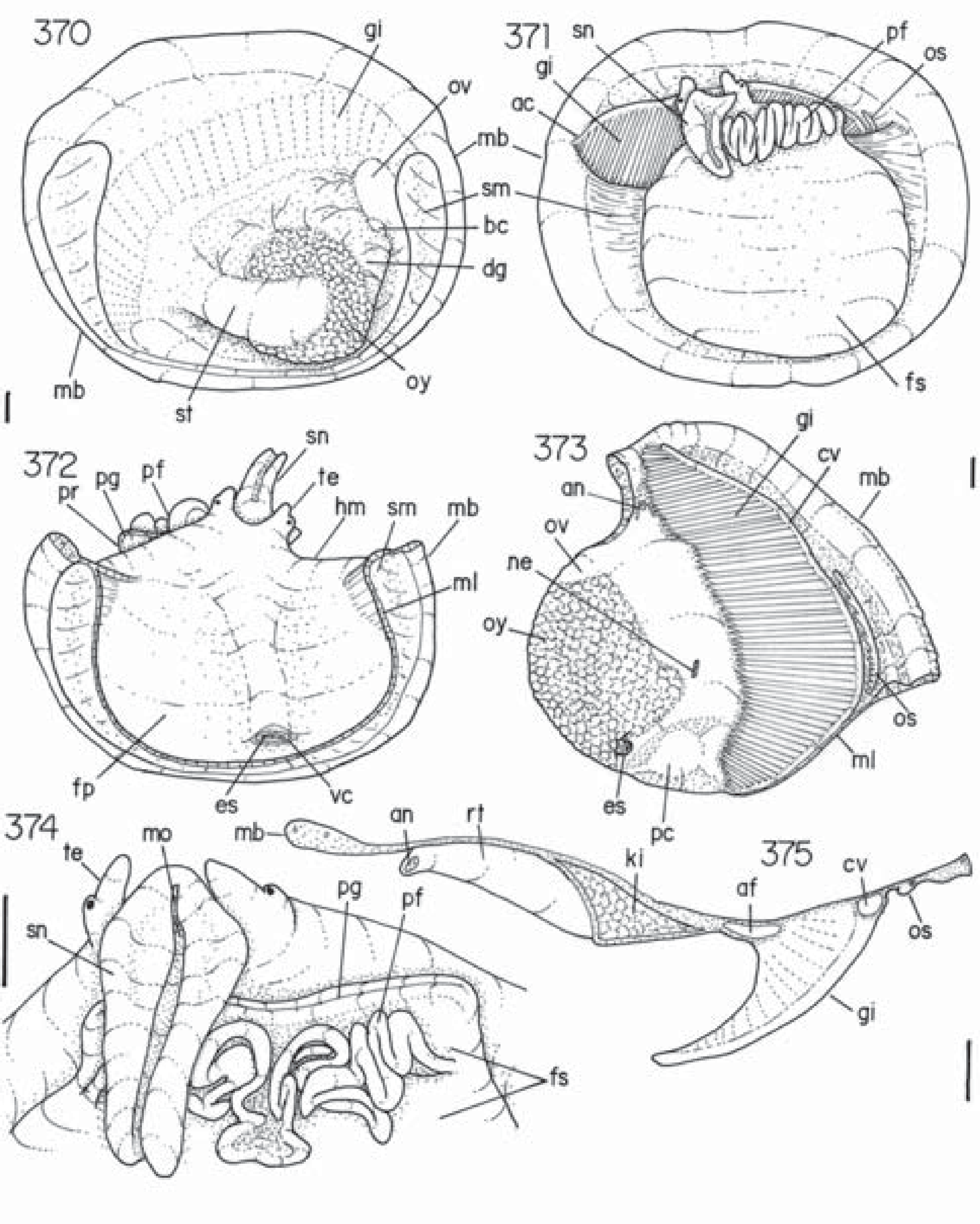
Head-foot (Figs. 371, 372, 374, 378). Form somewhat similar to those of hipponicids. Distinctive and notable features following. Head relatively small, projected forwards. Snout with very long ventral projection, extending about 1/3 length of foot, narrowing gradually. Snout projection distal end rounded, central notched; broad furrow runs along its dorsal surface. Mouth a longitudinal slit located in proximal end of furrow. Tentacles short, stubby. Eyes on small and short protuberances of middle-outer side of tentacles. Tentacles relatively far from each other. Foot sole planar, sub-rounded. Anterior foot sole edge straight, with transversal furrow of pedal glands. A very ample pedal fold present, inserted parallel to anterior foot edge and at some distance from that. Pedal fold edge very coiled, extending amply ventral and anterior to foot if straighted. Shell muscle similar to those of hipponicids in having horseshoe-attachment to shell, with broad anterior ends, narrowing towards median line. Although also convex, differs from hipponicids by thick central region of foot and by more developed connection between dorsal margin of shell muscle and visceral sac. No projected propodium or glandular concavity for brooding. Haemocoel broad in anterior half and narrow in posterior half, most filled by transversal net of muscular fibers. Head muscles thin, immersed in haemocoel wall.

Mantle organs (Figs. 370, 371, 373, 375, 376). Mantle border thick, smooth, except for some undulations in both lateral extremities. Both extremities very muscular, left extremity with additional muscular fold. Pallial cavity slightly triangular, occupying about half animal's length. Osphradium close and parallel to mantle border, in left region of cavity. Osphradium long, monopectinate, length about 1/3 of pallial cavity aperture. Osphradium leaflets narrow, distributed along posterior side of osphradium ganglion attached to adjacent mantle surface, most of them positioned obliquely turned to virtual point close to anterior-left region of osphradium (Fig. 376). Gill very large, occupies about half of pallial cavity area, curved, mostly parallel to mantle border. Anterior gill end on mantle border, close to its right extremity. Gill posterior end close to pallial cavity posterior limit. Gill leaflets triangular, tall, curved. Afferent gill vessel broad. Hypobranchial gland inconspicuous. Visceral mass encroaches by about 1/3 of pallial cavity area, in posterior-right region, each organ described below.

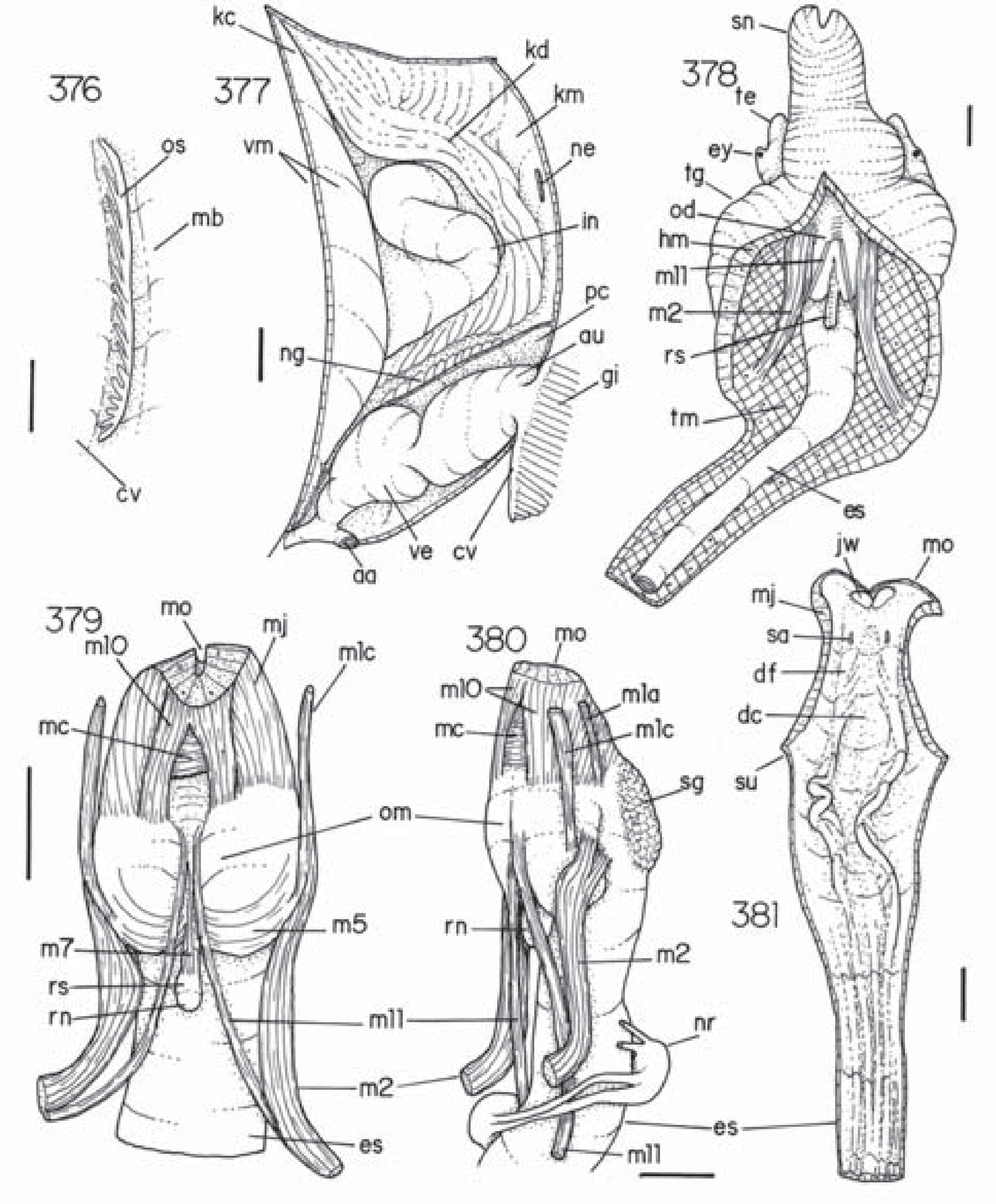
Visceral mass (Figs. 370, 373). Somewhat similar characters to those of hipponicids, sac-like, spherical, partially attached to dorsal surface of head-foot concavity. Gonad pale brown, occupies ventral-posterior region, running to posterior-dorsal region surrounding stomach. Digestive gland also pale brown, located in remaining regions of visceral mass around stomach, anterior to gonad. Pericardium and kidney as anterior limits of visceral mass in mantle roof.

Circulatory and excretory systems (Figs. 373, 377). Heart relatively large, located in left region of visceral mass, part dorsal to gill's posterior end. Auricle connection with ctenidial vein sub-terminal, with small part of ctenidial vein posterior to this connection. Ventricle posterior to auricle. Kidney large, trapezoid, dorso-ventrally flattened, located at central and right limits of visceral mass in pallial roof. Ventral and posterior inner renal surfaces without glands. Nephridial gland narrow, thin, triangular in section, located in dorsal region of membrane between kidney and pericardium. Intestine with small loop inside kidney chamber central-posterior region free from renal tissue. Renal lobes a single massive, solid, folded mass fulfilling dorsal and anterior renal chamber around intestine. Nephrostome a small slit in middle-anterior region of membrane between kidney and pallial cavity.

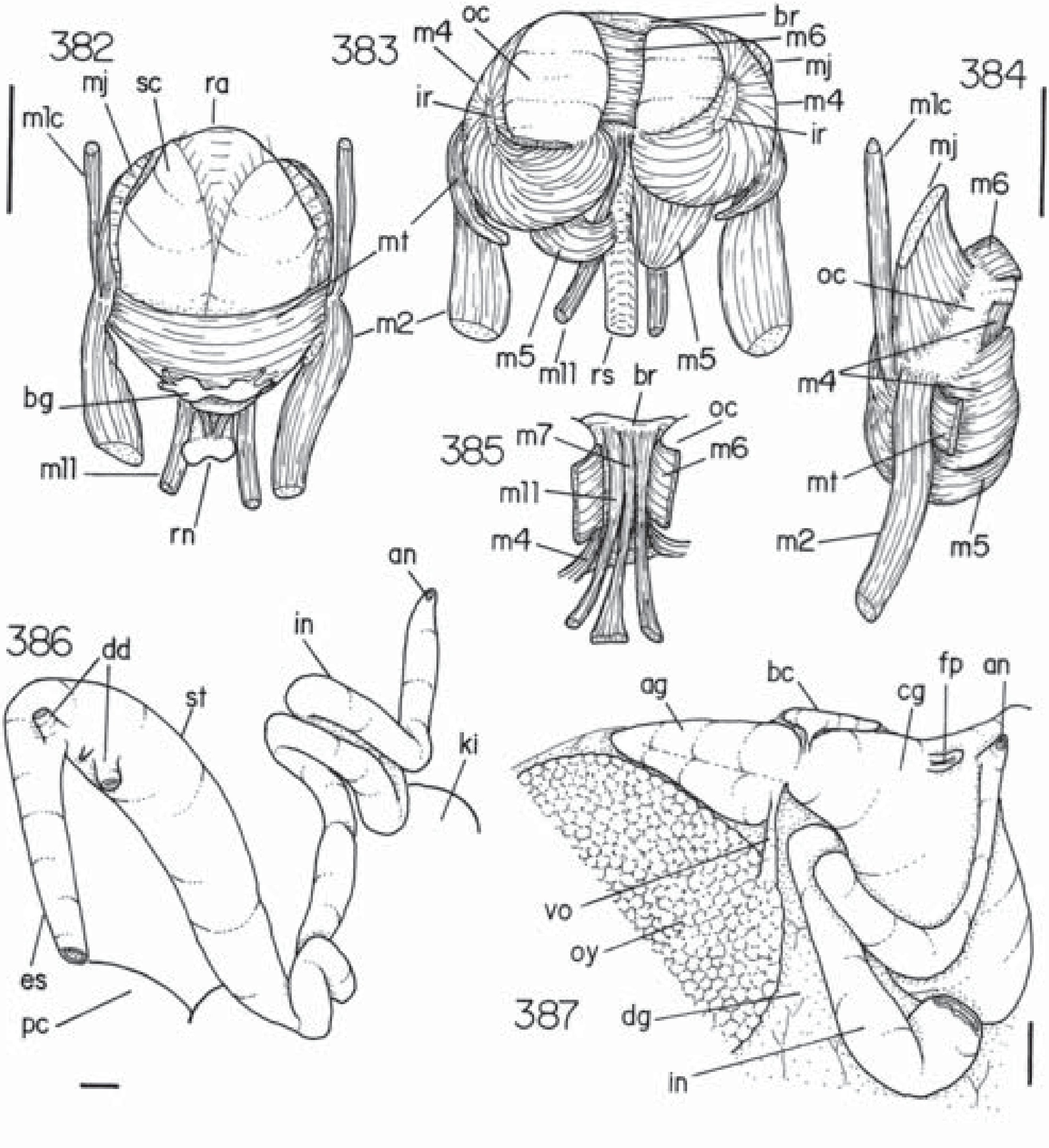
Digestive system (Figs. 378-386). Buccal mass just posterior to mouth, extending beyond snout. Snout base with partial capacity of retraction inside haemocoel. Snout retractor muscles thin, ventral attached to haemocoel ventral wall. Jaw plates small and thin. Buccal mass and odontophore muscles (in comparison with those of calyptraeids) (Figs. 379, 380, 382-385): m1a pair present, thin; m1c pair similar to m1a but located ventrally, insertion close to those of m2; m2 pair long, broad and thick, insertion partly in outer surface of buccal mass dorsal wall and mostly in mj; mj pair long and slightly thin; mt and mc similar but thin; m2a absent; m4 pair short end extremely thick (about half of odontophore volume), origin in posterior surface of cartilages, insertion in tissue on radula (to) and adjacent



Figures 370-375, *Capulus sycophanta* anatomy: **370**, female extracted from shell, whole dorsal view; **371**, same, ventral view; **372**, head-foot, female, dorsal view; **373**, pallial cavity and visceral mass, ventral view; **374**, head and anterior region of foot, frontal-slightly ventral view; **375**, pallial cavity, transversal section tangent to rectum. Scales = 2 mm.



Figures 376-381, *Capulus sycophanta* anatomy: **376**, detail of osphradium and adjacent surface of mantle, ventral view; **377**, detail of left transition pallial cavity-visceral mass, ventral view, kidney and pericardium opened longitudinally, with their inner surfaces shown; **378**, head and haemocoel, ventral view, foot extracted; **379**, buccal mass and anterior esophagus, ventral view; **380**, same, lateral-left, slightly ventral view; **381**, dorsal wall of buccal mass and anterior esophagus, ventral view, odontophore extracted, esophagus opened longitudinally. Scales = 1 mm.



Figures 382-387, *Capulus sycophanta* anatomy: **382**, odontophore, dorsal view; **383**, same, ventral view, radula partially removed and deflected, both cartilages deflected, only right m5 (left in fig.) still connected to radular sac; **384**, left half of odontophore, dorsal view, most muscles deflected; **385**, odontophore, detail of median region after longitudinal section of m6; **386**, middle and distal digestive tubes, ventral view, seen in situ if remainder structures were transparent, topology of some neighbor structures also indicated; **387**, visceral and pallial female genital organs and adjacent structures, ventral view, ovary only partially shown. Scales = 1 mm.

region of radular sac, narrow part of m4 pair also attached to subradular membrane (br) parallel to cartilages; m5 pair short and thin, origin on m4 posterior-outer surface, run somewhat perpendicular to m4 covering them, insertion in radular sac just ventral to m4 insertion; m6 short and thin; m7 very thin, single, origin on inner surface of subradular membrane on median line, insertion inside radular sac posterior region; m8 and m9 absent; m10 pair thin; m11 pair narrow and very long origin in posterior-ventral region of haemocoel inner surface, runs anteriorly passing through nerve ring, after running parallel to m2, penetrates odontophore by side of radular sac, insertion in subradular membrane in each side of m7. Dorsal wall of buccal mass inner surface with pair of tall folds located posterior to jaws (Fig. 381). Radular sac short and narrow. Radular teeth (Figs. 90, 91): rachidian tooth broad, with about 15 cusps in cut-edge, central cusp much broader than neighboring cusps; lateral tooth a little broader than rachidian, tip pointed, 2 cusps on inner and about 7 cusps on outer edge; inner and outer marginal teeth similar with each other (outer weakly narrower), tip pointed, 1-2 subterminal, small cusps. Salivary gland aperture in middle of anterior end of dorsal folds. Salivary glands very small totally immersed in outer surface of buccal mass dorsal wall (Fig. 380). Anterior esophagus with pair of tall longitudinal folds (Fig. 381). Middle and posterior esophagus with about 8 longitudinal, low, narrow folds being 2 of them continuation from those of dorsal wall of buccal mass and from anterior esophagus. Stomach narrow and long, located longitudinally in middle region of visceral mass (Fig. 386). Esophageal insertion in posterior region of stomach. Ducts to digestive gland originate just anterior to insertion of esophagus, generally 3 ducts, with middle duct very narrow. No clear style sac. Stomach narrows close to kidney middle-posterior region. Intestine, after stomach, with small loop (Fig. 386), then runs transversally edging posterior edge of renal chamber. After renal chamber intestine possesses 2 large loops compressed with each other in pallial cavity roof. After loops rectum runs straightforward. Anus small, papilla-like, close to right extremity of mantle border.

Genital system (Fig. 387). Only females examined. Visceral oviduct short and narrow, connects ventral-anterior region of ovary with anterior end of albumen gland. Albumen gland conic, located posterior to remainder pallial oviduct inside visceral mass. Bursa copulatrix small, dorsal, connected by narrow duct in opposite side to insertion of visceral oviduct. Capsule gland large, blind-sac, walls thick, located in pallial roof surrounded by intestinal loops. Genital pore a small papilla just posterior to anus.

Central nervous system (Fig. 380). Somewhat similar to those of preceding species, but with pedal ganglia far from cerebral-pleural ganglia (connectives long and narrow). Nerve ring located very posterior to buccal mass and far from salivary glands.

Distribution. Probably occurs north of the type locality in Keppel Bay (Wilson, 1993), Australia.

Habitat. In scallop beds, subtidal; attached to shells of ***Amusium balloti*** Bernardi (cf Garrard, 1961).

Material examined. AUSTRALIA; Queensland; 60 km NE of Yeppoon, 20º50'S 151º11'E, 46-55 m depth, AMS 07348, 3♀without shells (sta. 1774C; T. Nielson col., 1969-1970, trawled).

Family Trichotropidae

Genus *Trichotropis* Broderip & Sowerby, 1829

(Type species: *Turbo bicarinatus* Sowerby)

Trichotropis cancellata Hinds, 1843

(Figs. 44-45, 92, 388-413)

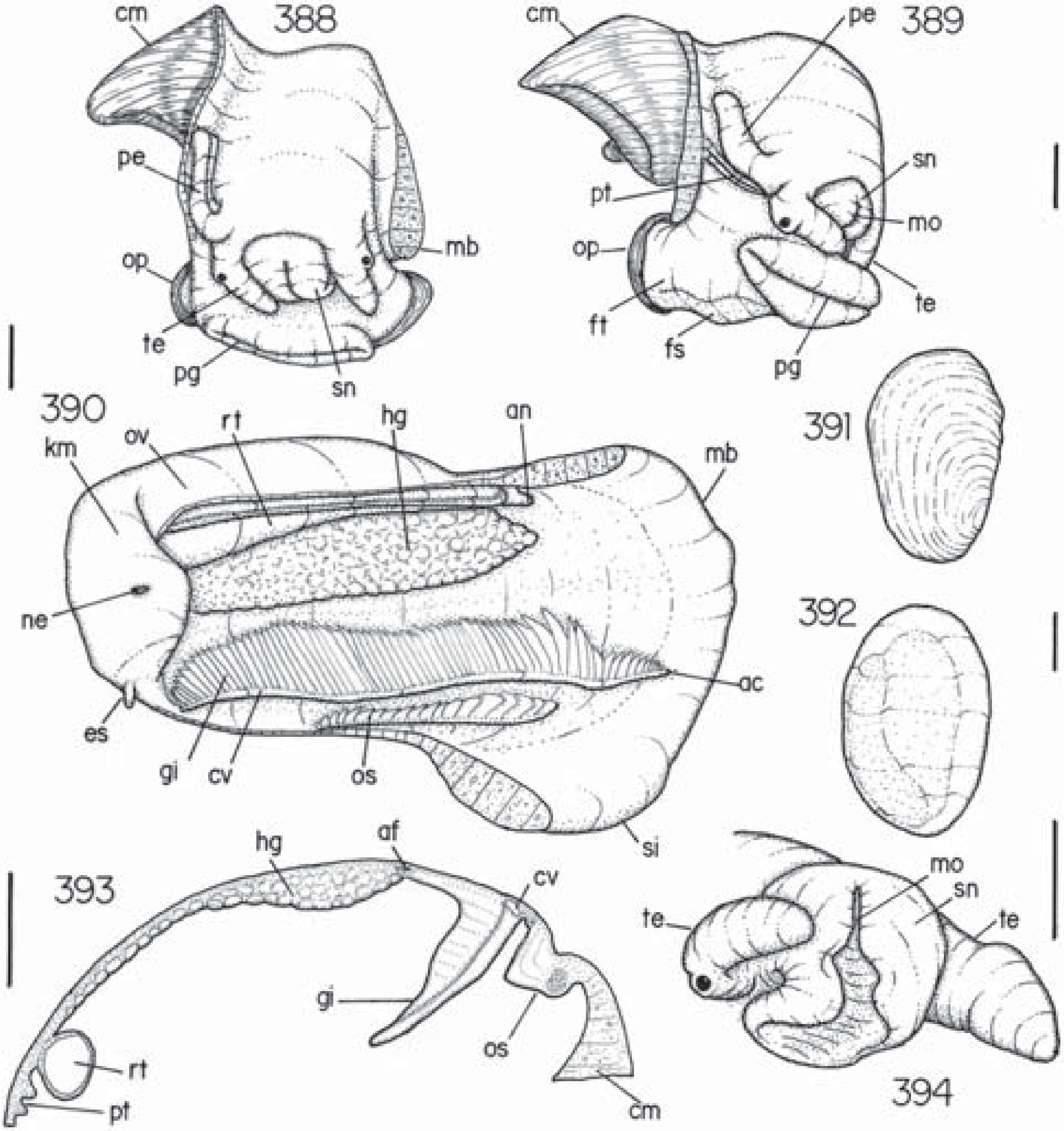
Trichotropis cancellata: Abbott, 1954: 167-168 (pl. 24b); Yonge, 1962: 160-179 (figs. 1-10); Pernet & Kohn, 1998: 349-355 (figs. 1-3).

Trichotropis (Turritopis) cancellata: Abbott, 1974: 138 (fig. 1519).

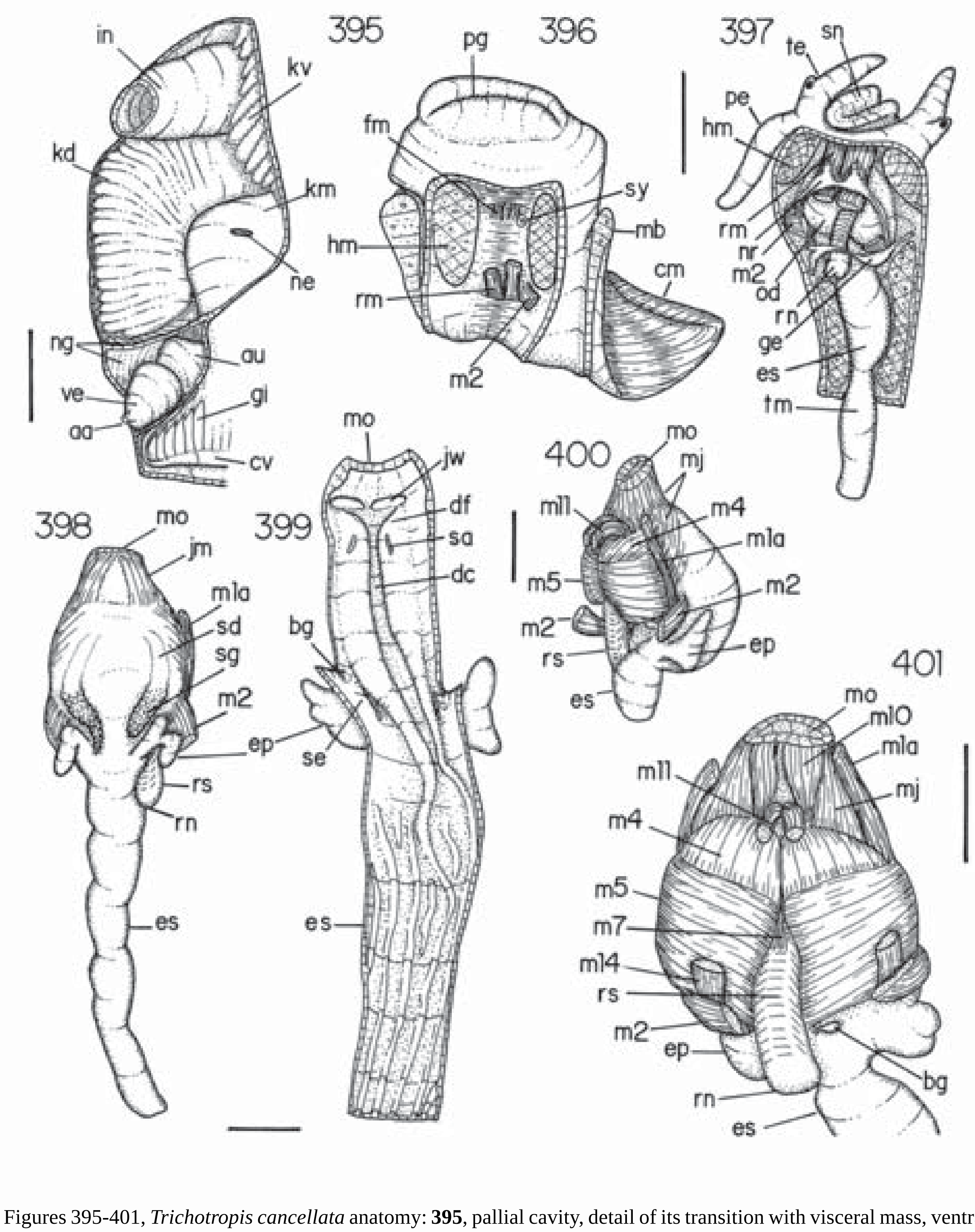
Description.

Shell (Figs. 44, 45). Spire tall, multispiral, conic. Whorls convex. Sculpture spiral and axial ridges, both predominating. Periostracum clear brown with projections coincident with axial ridges. Aperture simple, rounded. Other details in Yonge (1962: 161-162, figs. 1-2).

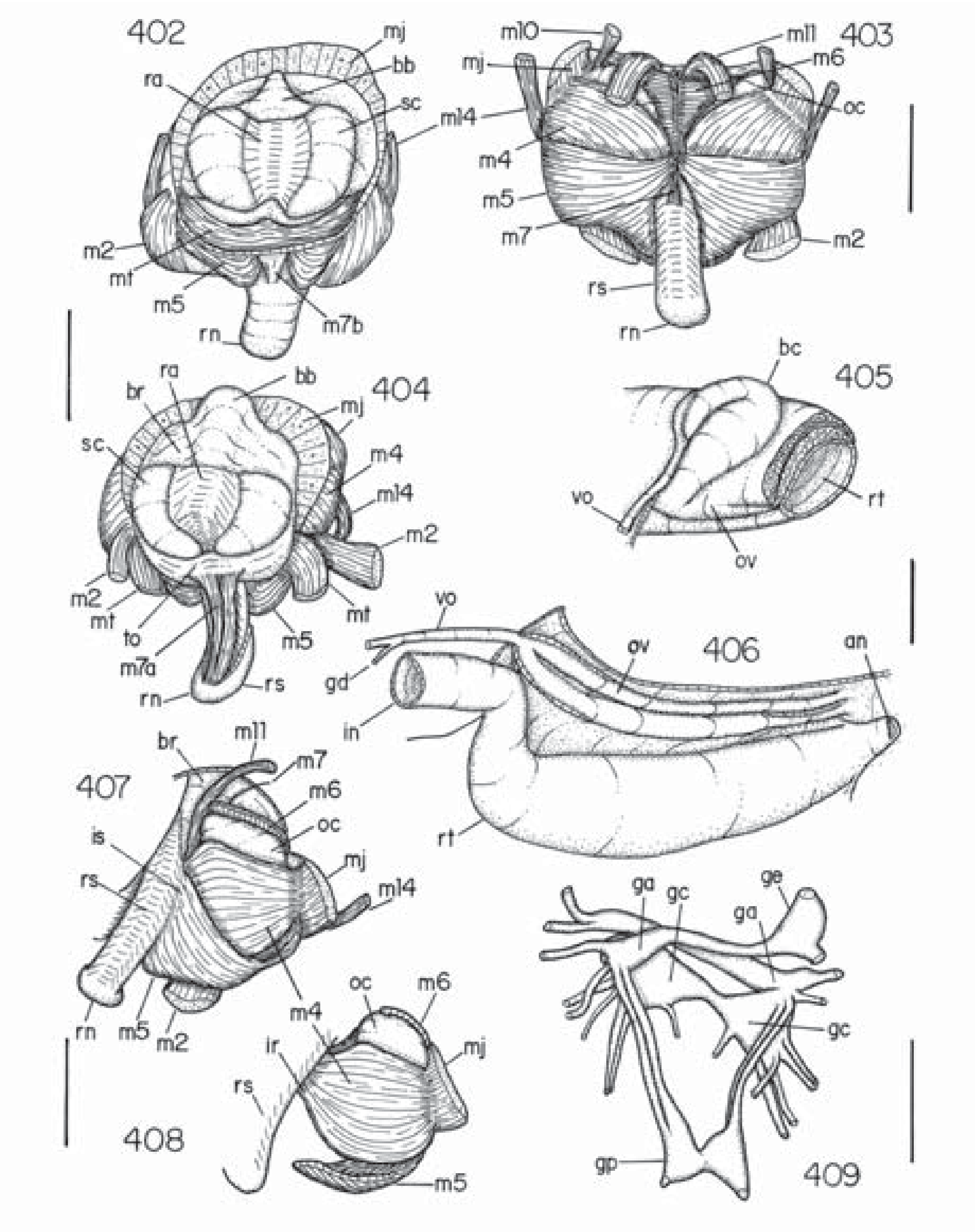
Head-foot (Figs. 388, 389, 394, 396, 397). Head outstanding, large, broad. Tentacles stubby, ommatophores very small, approximately on middle level of outer surface. Eyes dark, relatively small. Snout with partial capacity of retraction within haemocoel. Snout anterior margin modified by slightly long and flattened projection, directed ventrally and posteriorly; this projection with broad furrow in its dorsal surface, furrow narrows up to mouth; undulated folds edging this furrow. Snout base with partial capacity of retraction inside haemocoel. Mouth longitudinal, small, located closer to dorsal region of anterior snout surface. Foot somewhat large, very similar to normal fashion of caenogastropods. Opercular pad sub-terminal. Sole planar, relatively small. Anterior furrow of pedal gland well-developed, at some distance from snout base, edged by very thick borders. Columellar muscle also similar to normal fashion of caenogastropods, of about 1.5 whorls. All examined specimens, including females, have penis (described below). A pair of head muscles present, very broad, origin in lateral regions of foot, run towards posterior, inserts along head integument. Pair of foot retractor muscles small, origin on anterior-ventral region of haemocoel, run towards anterior,



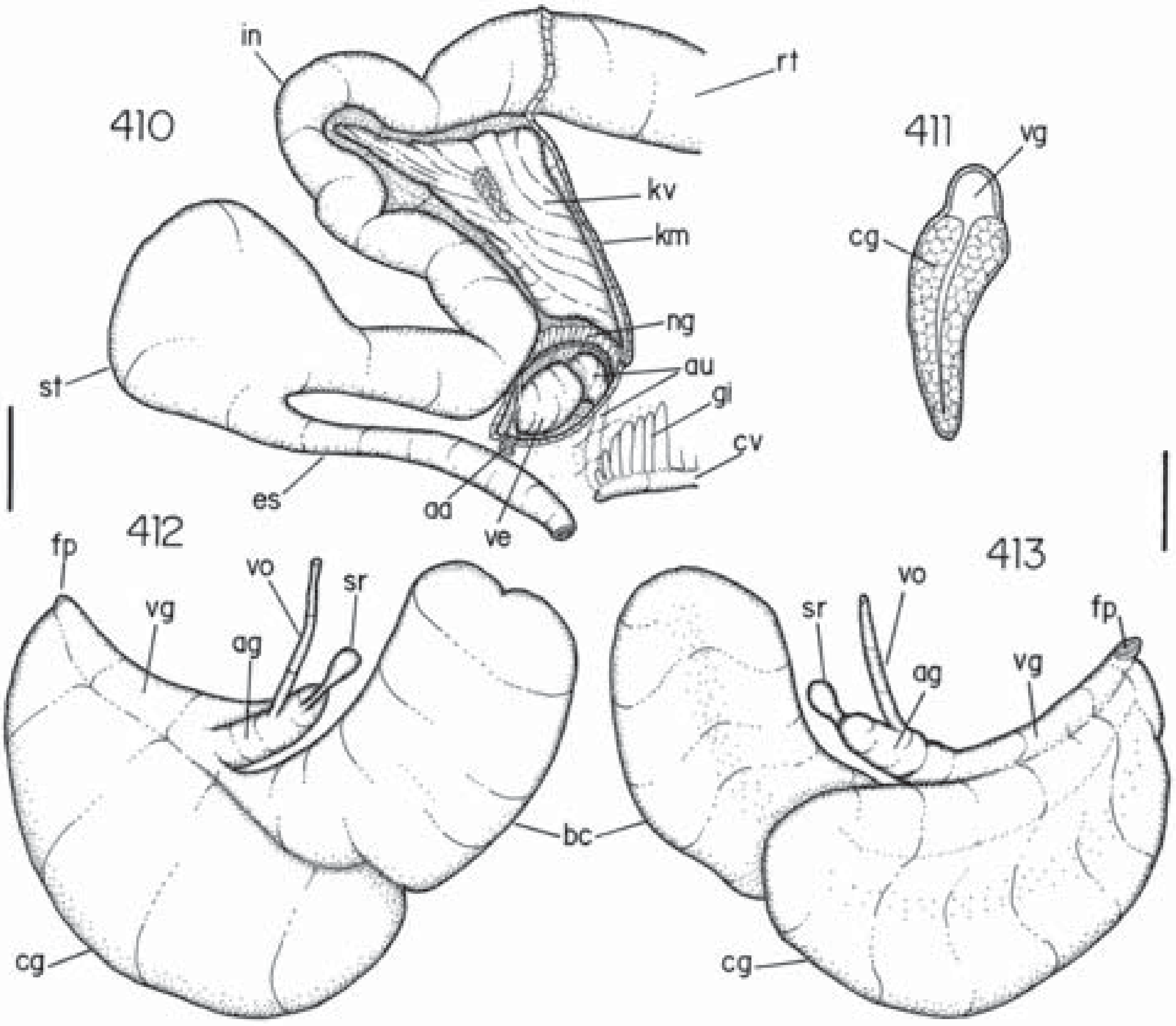
Figures 388-394, *Trichotropis cancellata* anatomy: **388**, head-foot, female (despite the penis), frontal-dorsal view; **389**, same, lateral-right view; **390**, pallial cavity roof, ventral-inner view; **391** operculum, outer view; **392**, same, inner view; **393**, pallial cavity roof, transversal section through middle level of osphradium; **394**, head, frontal-slightly ventral view. Scales = 1 mm.



Figures 395-401, *Trichotropis cancellata* anatomy: **395**, pallial cavity, detail of its transition with visceral mass, ventral view, kidney and pericardium opened longitudinally, their inner structures exposed; **396**, foot and columellar muscle, former in dorsal view, head and dorsal wall of haemocoel removed; **397**, head and haemocoel, ventral view, foot removed (complement of fig. 9); **398**, buccal mass and anterior esophagus, dorsal view; **399**, dorsal wall of buccal mass and anterior esophagus, ventral view, odontophore removed, esophagus opened longitudinally; **400**, buccal mass and adjacent esophagus region, lateral-left view; **401**, same, ventral view. Scales = 1 mm.



Figures 402-409, *Trichotropis cancellata* anatomy: **402**, odontophore, dorsal view; **403**, same, ventral view, its superficial membrane removed; **404**, same, dorsal view, posterior muscles and membrane sectioned and deflected; **405**, posterior end of pallial oviduct, dorsal view; **406**, right margin of pallial cavity roof, female, ventral-inner view **407**, left half of odontophore, ventral view, m5 weakly deflected showing structures covered by it; **408**, same, m5 totally deflected; **409**, nerve ring, dorsal view. Scales = 1 mm.



Figures 410-413, *Trichotropis cancellata* anatomy: **410**, middle digestive tube and adjacent reno-pericardial structures, ventral view, shown if remainder structures were transparent, ventral wall of pericardium removed; **411**, pallial oviduct, transversal section in its middle region; **412**, same, whole dorsal view; **413** same, whole ventral view. Scales = 1 mm.

insertion in anterior margin of foot, mainly in region of pedal gland furrow. Pair of retractor muscles of proboscis slightly large, origin in ventral-middle region of haemocoel close to median line, insertion in ventral and lateral surface of proboscis. Other details in Yonge (1962: 163-164, figs. 2-3).

Operculum (Figs. 391, 392). Corneus, elliptical, thin. Occupies entire aperture. Nucleus excentric, located close to outer-inferior margin. Outer surface with concentric undulations. Scar narrow, edging inner margin.

Mantle organs (Figs. 390, 393, 406). Mantle border thick, simple, without projections, siphon or pigment. Pallial cavity of about 1 whorl. Osphradium relatively large (about half of gill length), monopectinate, long. Osphradium posterior region edging left margin of cavity; anterior region parallel to mantle border. Osphradium filaments slightly triangular, tip rounded, located only on right side of osphradium ganglion. A low glandular ridge detectable between gill and osphradium. Gill large (length approximately same as that of cavity) and long. Gill filaments tall, base broad, irregularly narrow up to slender tip. Ctenidial vein slightly narrow, in base of rods. Rod extends little beyond membranous part of filament. Anterior region of gill on mantle border. Between gill and rectum a broad space (almost 3 times broader than gill area). Hypobranchial gland greenish, slightly tall, presenting small glandular chambers, occupies most of area between gill and rectum. Rectum somewhat narrow, edging right margin of cavity at about 4/5 of its length. Anus siphoned, short, at some distance from mantle border. Gonoducts running ventral and at right from rectum at almost its entire length, more details below. Other details in Yonge (1962:165-167, figs. 2-5).

Excretory and circulatory systems (Figs. 395, 410). Heart relatively small, located right of posterior gill end. Auricle triangular, with anterior surface connected to anterior margin of pericardium. Ctenidial vein contours posterior limit of pallial cavity and inserts in left region of auricle. Kidney large, occupies most of anterior limit of visceral mass. Dorsal lobe flattened, with several transverse, not uniform furrows, occupying most of dorsal surface of kidney chamber. Ventral lobe smaller, more concentrated in right region of kidney chamber partly connected to intestine. Both lobes connected to each other in middle and right regions. An intestinal loop edges posterior limit of kidney. Nephrostome a small slit approximately in middle region of membrane between kidney and pallial cavity, neither adjacent glandular folds nor vessels.

Visceral mass. Very similar characters to normal fashion of caenogastropods, with gonad in peri-columellar region and digestive gland occupying remainder space. Stomach restricted to first whorl of visceral mass, which is 2 whorls more posterior to it. Other details in Yonge (1962: 163, fig. 4).

Digestive system (Figs. 397-404, 407, 408, 410). Buccal mass large, about half of haemocoel volume. Oral tube well-developed, thick, muscular. Pair of jaw plates thin, laterally broad, short in length. Pair of dorsal folds very broad, aperture of salivary glands long, large, in middle of anterior region of these folds (Fig. 399). Dorsal chamber somewhat deep, inner surface smooth. Odontophore muscles slightly similar to those of *Crepidula* spp., distinctive or notable features following (Figs. 398, 400-404, 407, 408): **m1**) no differentiated pair detectable; **mj**) thick and long, immersed in oral tube, absent in ventral region, occupied by m10; **m2**) as in *Crepidula*; **m2a**) absent; **m4**) pair broad, slightly thin, surround posterior region of cartilages, insert in lateral and dorsal surface of middle region of radular sac; **m5**) pair of equivalent size as m4, origin in dorsal, lateral surface of odontophore, surround externally m4, insert in radular sac just posterior to m4 insertion; **m6**) horizontal muscle, relatively thin; **mt**) present, similar to those of calyptraeids; **m7**) pair extremely thin and narrow, only some fibers, originate in subradular membrane inner-anterior surface, contour m6 towards ventral and posterior, insertion in radular sac ventral-median surface at some distance from nucleus; **m7b**) pair slightly broad, origin in dorsal-median surface of mt, runs towards posterior within radular sac, insertion in dorsal surface of radula anterior to radular nucleus; **m8**) pair absent as differentiated muscles, maybe part of ventral m4 region connected to cartilages; **m9**) absent; **m10**) pair well developed, as ventral part of oral tube; **m11**) long pair, insertion in bulged part of subradular membrane (bb) somewhat thin, contour anterior region of odontophore towards ventral and after posterior through m10 pair, origin in ventral inner surface of haemocoel, close to median line, in adjacent posterior region of odontophore; **m14**) pair present, but thin and located laterally, origin in anterior-lateral-inner surface of proboscis, runs towards posterior, insertion in lateral-posterior region of odontophore surface. Radular teeth (Fig. 92): rachidian tooth narrow, cut edge pointed, with about 3-4 weak, subterminal cusps in each side; lateral tooth with about twice rachidian width, tip pointed, curved inwards, cusps lacking; inner and outer marginal teeth similar with each other (outer weakly narrower than inner tooth), tall, curved, tip sharp pointed (hook-like), cusps lacking. Salivary glands very small (Fig. 398), rarely extending beyond odontophore level, slender, most attached to dorsal surface of buccal mass. Salivary ducts run immerse in dorsal wall of buccal mass and open as described above. Pair of pouches small, thin-walled, in form of irregular and expanded diverticles located in both sides of esophagus just posterior to buccal mass. Esophagus slightly narrow and long; anterior esophagus with only pair of folds (continuation from those of buccal mass); gradually secondary folds appear in middle esophagus, both folds continuation of those of anterior esophagus taller (Fig. 399); posterior esophagus with 5 to 8 similar sized, low, longitudinal folds. Other details in Yonge (1962: 167-168).

Stomach (Fig. 410) large, broad, occupying about half volume of first whorl of visceral mass. Esophagus and intestine connecting stomach in anterior side, side-by-side (esophagus left). Duct to digestive gland not examined (all specimens damaged in region) but sufficiently described by Yonge (1962: 168, fig. 6), with style sac connected to intestine and 2 ducts to digestive gland. Gastric shield with transverse low folds, located in dorsal surface. Intestine simple, without differentiable style sac. Intestine in “S” form, contouring posterior margin of kidney (Fig. 410). Rectum and anus (Fig. 406) described above.

Genital system. **Male** (Figs. 388, 389). (Examined specimen slightly immature.) Seminal vesicle and prostate absent. Pallial sperm groove runs in pallial floor from right-anterior region to penis base. Penis sub-cylindrical (somewhat flattened), slightly short. Penis origin just posterior to right tentacle. Penis tip rounded. Penis groove runs at lateral margin up to penis tip.

Female (Figs. 405, 406, 411-413). Visceral oviduct narrow, inserts on right-ventral region of albumen gland. Pallial oviduct large, with about 2/3 of pallial cavity length; runs at right margin of cavity dorsal to rectum. Albumen gland white, small, cylindrical, located in right-posterior region of pallial oviduct. Seminal receptacle small, spherical, connected to posterior-dorsal surface of albumen gland by narrow duct. Vaginal tube runs anterior to albumen gland edging right surface of pallial oviduct. Capsule gland large, broad, dorso-ventrally flattened, opened to vaginal tube along its right margin. Capsule gland with thick, yellowish glandular walls. Bursa copulatrix large (almost same size as capsule gland in some specimens), broad, dorso-ventrally flattened; expands posterior to pallial oviduct sometimes encroaching dorsal surface of kidney. Bursa anterior region runs dorsal to posterior region of capsule gland, gradually narrows up to slender duct. Bursa duct connects with vaginal tube dorsal-left surface, in level between middle and posterior third parts. Bursa wall relatively thick glandular, yellowish. Female pore a small papilla on anterior end of vaginal tube; a pair of small folds extends beyond female pore on right margin of pallial cavity. Penis similar to those of males present in all females. Other details of genital system in Yonge (1962: 170-174, fig. 7).

Central nervous system (Figs. 409). Nerve ring similar to those of *Crepidula* spp., but weakly less concentrated and located more anterior (posterior to buccal mass). Sub- and supra-esophageal ganglia located slightly near to nerve ring, connected by short connective with parietal ganglia.

Habitat. On muddy and rocky bottoms, other details in Yonge (1962: 175-177, figs. 9, 10).

Distribution. Bering Sea to Oregon, USA.

Measurements of shells (in mm). USNM 857615: 10.8 by 6.8.

Material examined. UNITED STATES OF AMERICA; **Alaska**; Seldovia, Outside Beach, BMNH, 1 female (D.G. Reid leg., 6/viii/1988); **Washington**; San Juan Island; off Friday Harbor Marine Lab, 15-17 m depth, USNM 857615, 1♂, 4♀, 2 shells (G. Rosenberg col.; 13/viii/1983); 5.5 m depth, USNM 857628, 1♂(24/iv/1987).

Trichotropis borealis Broderip & Sowerby, 1829

(Figs. 46, 47, 93, 414-419)

Synonymy in Rosenberg, 1996. Complement:

Trichotropis borealis: Graham, 1954: 129-143 (figs. 1-2); Abbott, 1954: 167 (pl. 24d); Fretter & Graham, 1962: 54, 62, 152, 153, 157, 232, 262, 310, 316, 369, 377, 628, 643, 688 (fig. 95); Abbott & Morris, 1995: 178.

Trichotropis (Ariadnaria) borealis: Abbott, 1974: 138 (fig. 1518).

Description.

Shell (Figs. 46, 47). Similar to that of *T. cancellata*, except for ampler aperture and lower spiral ribs. Other details in Abbott (1974: 138).

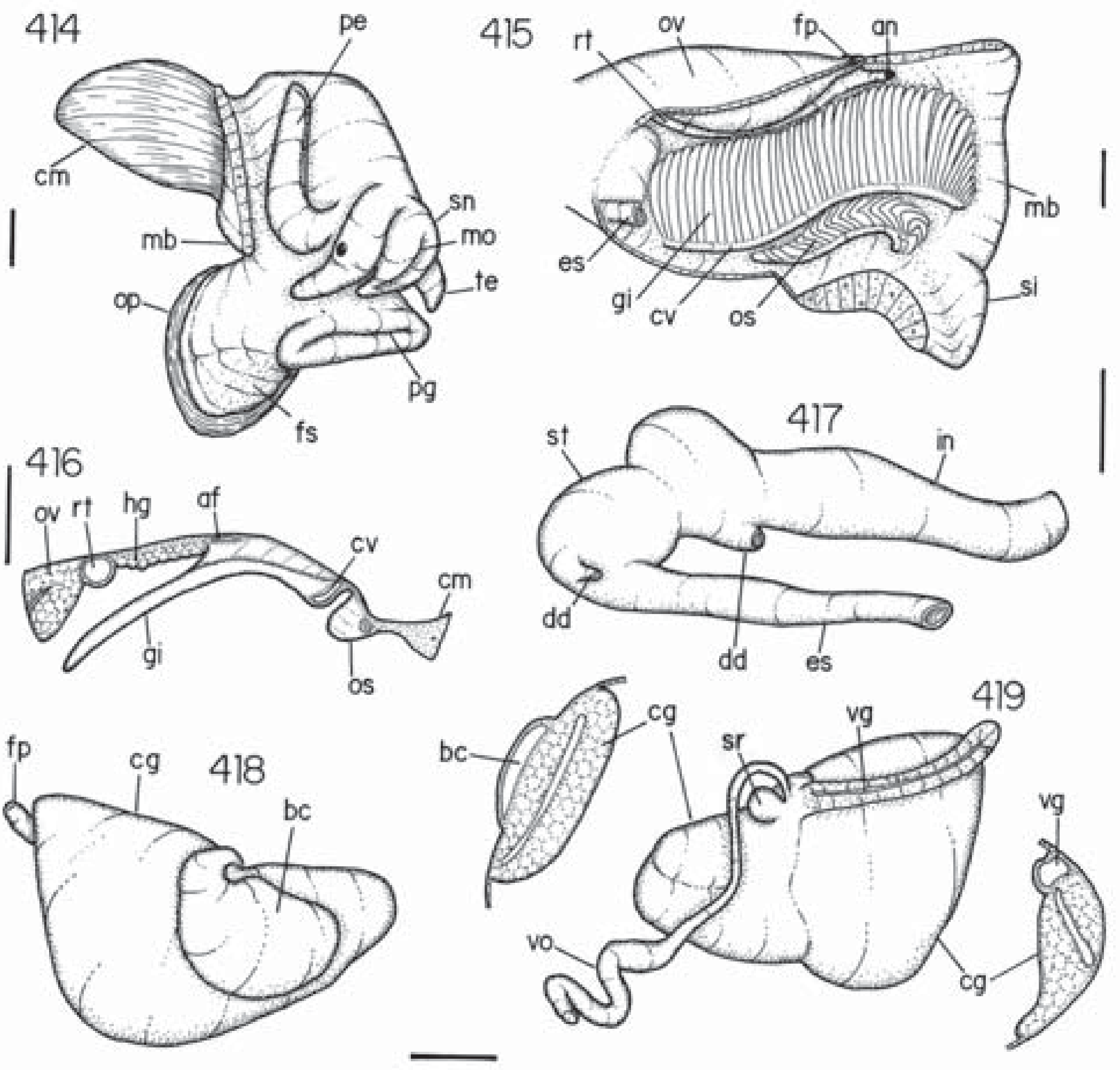
Head-foot and **operculum** (Fig. 414). Characters similar to those of *T. cancellata*, inclusive snout projection, small ommatophore, thick borders surrounding pedal glands furrow and operculum location. A pair of shallow furrow separating sole from dorsal region of foot present. Penis present in all specimens, inclusive females. Other details in Graham (1954, fig. 1); Fretter & Graham (1962: 157, fig. 95).

Mantle organs (Figs. 415, 416). Similar features of those of *T. cancellata*. Distinctive and notable features following. Siphon more developed and slightly differentiated form mantle border. Osphradium monopectinate, also with filaments only at right of osphradial ganglion. Gill filaments with longer and narrower tip, constituted only by rod.

Circulatory and excretory systems. Very similar in characters to those of *T. cancellata*, except for slightly larger size of heart and pericardium.

Visceral mass. Similar to that of preceding species as well as of normal fashion of caenogastropods, but short (about 1.5 whorls).

Digestive system (Fig. 417). Characters of buccal mass similar to those of *T. cancellata*, included large pair of retractor muscles of proboscis, **m7b** present and **m14** laterally located. Radular teeth also very similar to those of preceding trichotropid species, with following remarks: rachidian tooth with 9 to 13 small cusps, central cusps about twice larger than neighbor cusps; lateral cusp about 1.5 times broader than rachidian tooth, 0 to 2 small cusps in inner margin and 4 to 8 small cusps in outer margin, apex broadly



Figures 414-419, *Trichotropis borealis* anatomy: **414**, head-foot, female (despite penis), lateral-right view; **415**, pallial cavity roof, ventral-inner view; **416**, same, transversal section through middle region of osphradium; **417**, middle digestive tubes, ventral view, seen in situ if remainder structures were transparent; **418**, pallial oviduct, dorsal view; **419**; same, ventral view, part of visceral oviduct and transversal sections in 2 indicated levels also shown. Scales = 1 mm.

pointed; inner marginal tooth with about double width of outer marginal tooth, both lacking cusps. Salivary glands also small, but slightly longer than that of preceding species. Esophageal features similar to those of *T. cancellata*, including pair of pouches and distribution of inner folds, but, as noted by Yonge (1962), glandular tissue poorly developed. Stomach slender, "U"-shaped; 2 ducts to digestive gland; anterior duct small, narrow, located just posterior to esophageal insertion in stomach; posterior duct broader, located on left surface of intestinal origin in stomach. Inner surface of stomach and intestinal loops characters similar to those of *T. cancellata*, except for longer region of intestine between stomach and kidney.

Genital system. **Male** (Fig. 414). Characters very similar to those of *T. cancellata*, except for slightly longer penis, which narrows gradually up to slightly sharper tip.

Female (Figs. 418, 419). Characters similar to those of *T. cancellata*. Distinctive or notable features following. Visceral oviduct posterior region convolute, reminiscent of male seminal vesicle. Albumen gland not so distinct, immersed in remaining pallial oviduct. Seminal receptacle spherical, located just posterior to insertion of visceral oviduct in pallial oviduct. Vaginal tube runs in pallial cavity floor, edging its right margin. Capsule gland large, very thick walls; occupies most of pallial oviduct at about 2/3 of cavity length. Bursa copulatrix smaller than that of preceding species, also located dorsal to capsule gland, slightly elliptical, narrows gradually in anterior region, curves towards posterior by short distance, connect with vaginal tube posterior extremity just anterior and to right of insertion of visceral oviduct.

Habitat. Deep waters, from 2 to 192 m depth.

Distribution. Arctic North Atlantic.

Measurements of shells (in mm). AMNH 2433: 18.4 by 11.4.

Material examined. SWEDISH; **Hvita**; On Solowetskij, SMNH 865, 2♀(Knipowitsch col., 1894). DENMARK; Greenland; Etah, AMNH 2433, 1♀(M.C. Tanquary col., 7/x/1914, Crocker Land Expedition). GREENLAND; **Etah**; AMNH 2433, 1♀ (M.C. Tanquary; Crocker Land Expedition, 7/ix/1914). UNITED STATED OF AMERICA; **Georges** Bank, Northern slope, 41°34´N 68°59´W, 117 m depth, USNM 847722, 1♂, (MMS/BLM col.; sta. 40; xi/1977).

Trichotropis sp.

(Fig. 48)

A single specimen of a un-identified species was available for study, from which an anterior part of the animal was extracted. Although the study was not enough for a detailed anatomy, it revealed some interesting data .

Shell (Fig. 48). Similar to *T. borealis*, but only sculptured by strong, uniform spiral ridges, 7 in last whorl. Aperture ampler.

Head-foot and **operculum**. Very similar to those of preceding *Trichotropis*. Tentacles longer (about 5 times snout length). A small ommatophore present.

Mantle cavity. Very similar characters to *T. borealis*, inclusive more developed siphon. Gill of intermediate size between those of *T. borealis* and *T. cancellata*.

Digestive system. Buccal mass and esophagus characters very similar to those of *Trichotropis* spp., including pair of esophageal pouches and small salivary gland (almost entirely immersed in dorsal wall of buccal mass). Origin of **m2**, **rm** and **m11** pairs singular in being all united in single muscular block. Radular teeth characters similar to those of *T. cancellata*, with following remarks: rachidian tooth with 2 to 5 small pairs of subterminal cusps; lateral tooth narrower (about same width as rachidian), with 5 to 7 small cusps on outer edge.

Genital system. **Female**. No detailed examination of genital organs, but the total absence of penis in examined female is a notable feature, because all females of both preceding *Trichotropis* species have a penis very similar to those of males. Yonge (1962: 169) already pointed out the "large penis invariably present in all but the very smallest animals" in *T. cancellata*.

Measurements of shells (in mm): 10.5 by 8.2.

Material examined. UNITED STATED OF AMERICA; **Alaska**; N. E. off St. Lawrence Island, 64°35´06"N 168°00´06"W, 27 m depth, USNM 836919, 1♀(sta. 269 LGL Ecological Res. Asso., 24/vii/1982).

Family Vanikoridae

Genus *Vanikoro* Quoy & Gaimard, 1832

(Type species: *Sigaretus cancellata* Chemnitz)

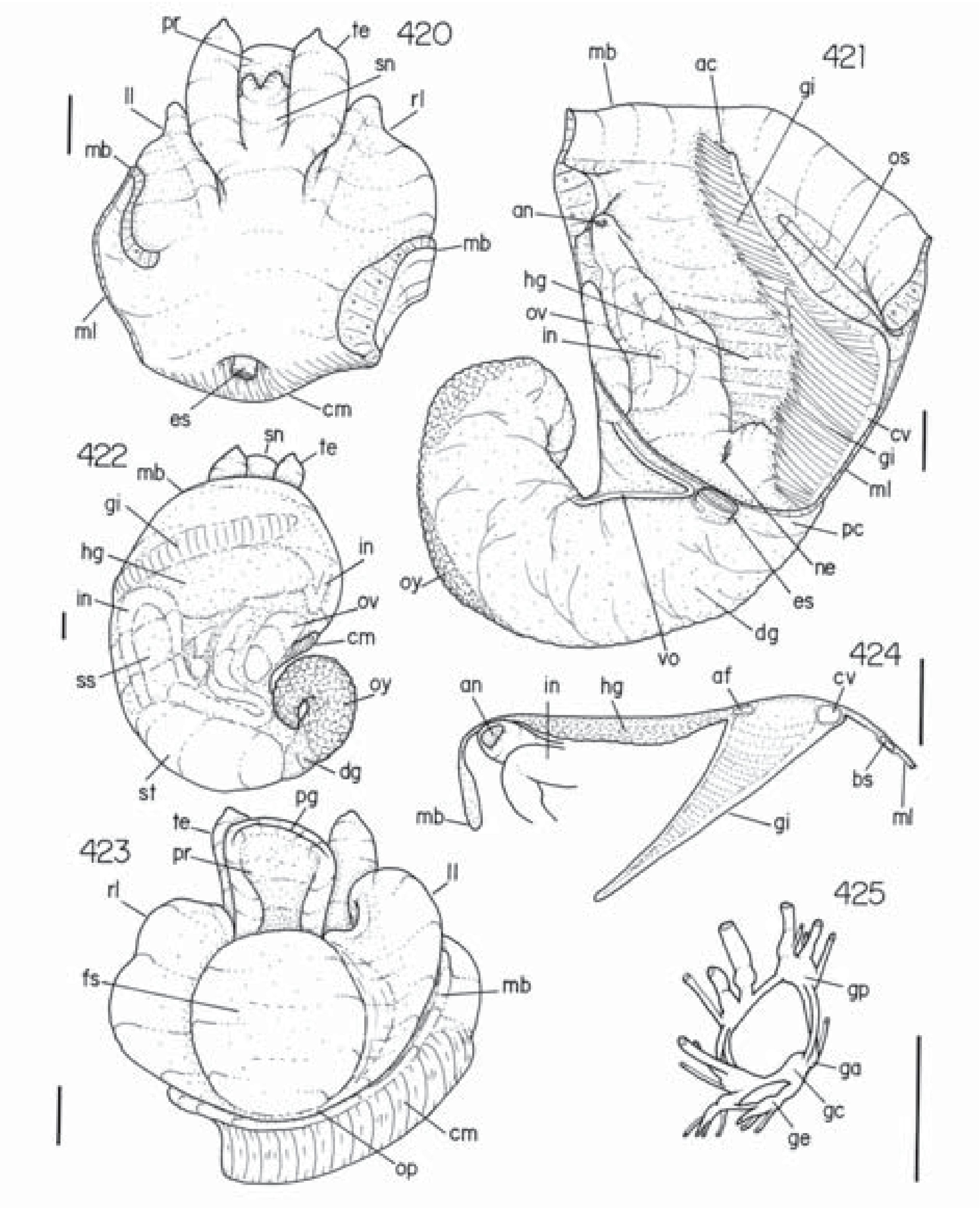
Vanikoro sp.

(Figs. 51-53, 95-97, 420-435)

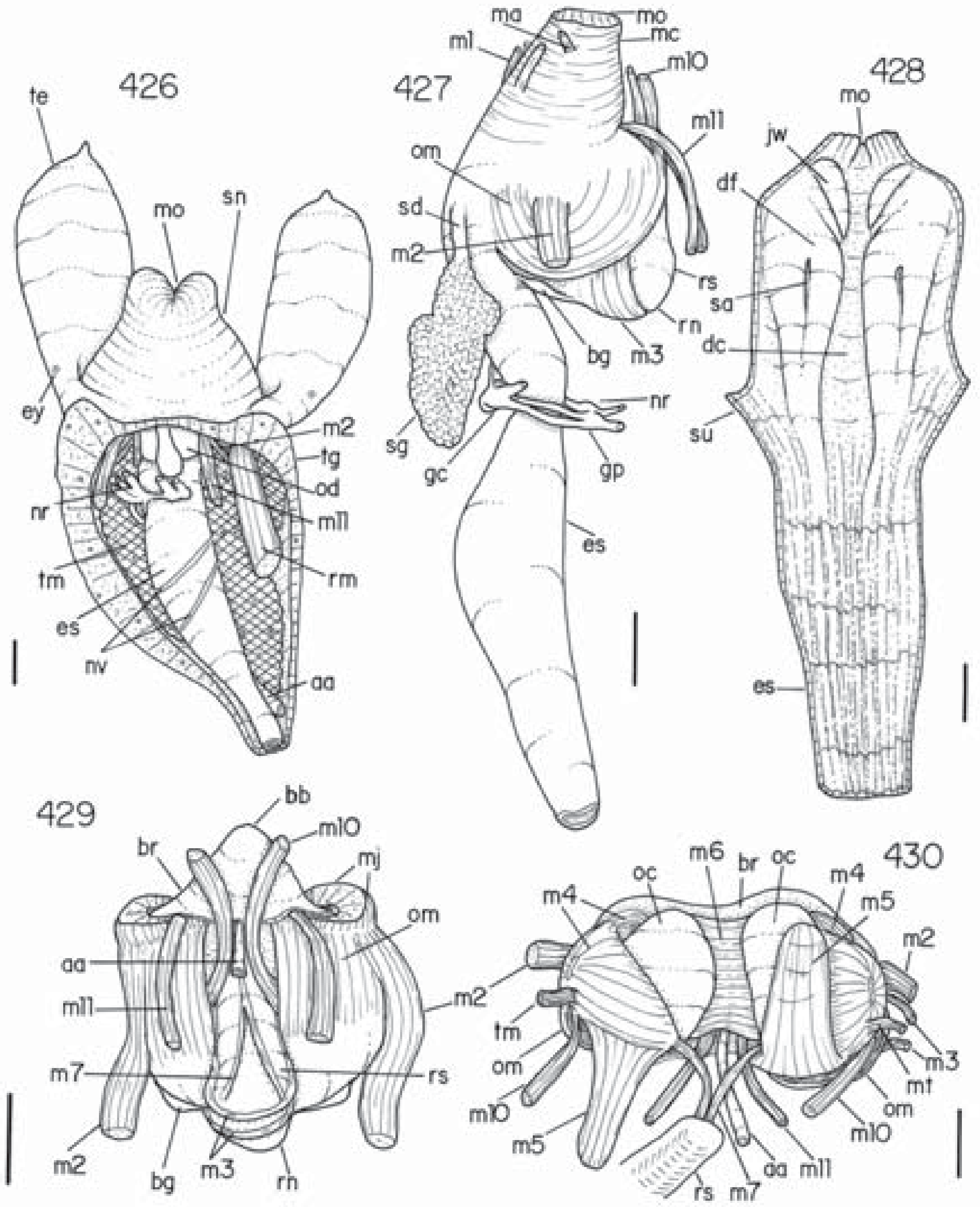
Description

Shell (Figs. 51-53). Large, thick walled, white, globose, spiral. Spire well-developed, with about half size of body whorl. Sculpture oblique, axial undulations and narrow, uniform, weak spiral threads, with 4-5 very weaker threads and many microscopic striae in between. Aperture round, ample, strongly opisthocline (Fig. 53), lips thick. Umbilicus very narrow.

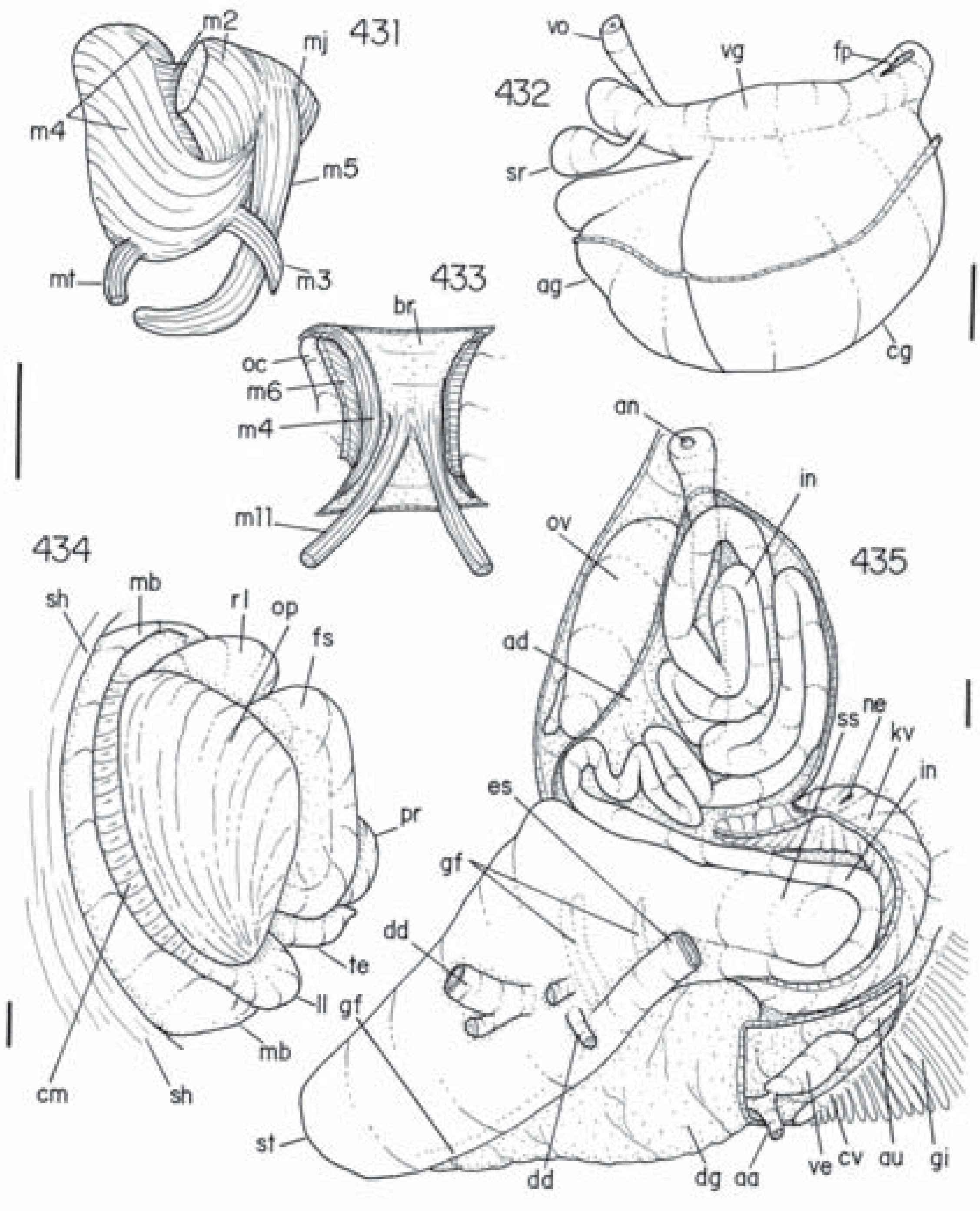
Head-foot (Figs. 420, 423, 426, 434). Head large, peduncled, socket-like. Snout small and conic. Snout anterior end bilobed, with several transversal furrows. Tentacles very large and flattened, base narrow and thick, located on each side of snout, suddenly becomes broad and flat; close to distal end suddenly narrow; tentacle tips small, pointed. Eyes very small, dark, slightly far from surface (seen by transparence of the integument). A pair of large and ample nuchal



Figures 420-425, *Vanikoro* sp. anatomy: **420**, head-foot, female, dorsal view; **421**, pallial cavity roof and visceral mass, ventral view; **422**, female, whole specimens extracted from shell, dorsal view; **423**, head-foot, ventral view, specimen without operculum, but with its usual position indicated; **424**, pallial cavity roof, transversal section tangential to rectum; **425**, nerve ring, ventral view. Scales = 2 mm.



Figures 426-430, *Vanikoro* sp. anatomy: **426**, head and haemocoel, ventral view, foot removed; **427**, buccal mass and anterior esophagus, lateral-right view; **428**, dorsal wall of buccal mass and anterior esophagus, ventral view, odontophore removed, esophagus opened longitudinally; **429**, odontophore, ventral view; **430**, same, both cartilages deflected, radular sac removed downwards, right m5 (left in fig.) also deflected. Scales = 1 mm.



Figures 431-435, *Vanikoro* sp. anatomy: **431**, odontophore left half, lateral-left view, m2 sectioned close to its base, m5 deflected; **432**, pallial oviduct, ventral view, rectum removed (indicated by dotted line); **433**, odontophore, ventral view, detail of median region after longitudinal section of m6; **434**, head-foot, posterior-opercular view; **435**, middle and distal digestive tubes, ventral view, adjacent reno-pericardial area and pallial cavity also shown, ventral wall of pericardium and adrectal sinus removed, kidney chamber sectioned along its ventral edge, its ventral-anterior wall deflected. Scales = 1 mm.

lobes somewhat similar to those of calyptraeids, but thicker and broader. Nuchal lobes as lateral folds inserted along both sides of head-foot, anterior edges straight and thicker, located forward in each side from head. Foot small and cylindrical, circular in section. Propodium similar to those of hipponicids, long and flat, with pedal glands furrow in distal edge. No glandular concavity. Propodium located between foot sole and head. Columellar muscle very thick and short, about ¼ whorl. Haemocoel elliptical, filled with net of transverse muscle fibers as most of preceding species. Pair of lateral-ventral snout retractor muscles large.

Operculum (Fig. 434). Present in single specimen, very thin, yellow, edges irregular. Nucleus terminal. Sculpture radial. Partially occupies aperture.

Mantle organs (Figs. 421, 422, 424). Mantle border thick and simple, without folds. Left and right extremities thick muscular, possessing secondary muscular folds. Pallial cavity slightly deep (about 1 whorl). Osphradium long and narrow, ridge-like, length about half that of pallial cavity aperture; located just posterior and parallel to mantle border, in its left extremity. Gill very large, occupying about half of pallial cavity area. Gill anterior end on mantle border, located slightly at right of its middle region. Gill posterior end close to posterior limit of pallial cavity. Gill leaflets very tall, triangular, with rods on both sides (left rod broader), almost straight (weakly turned to right). Ctenidial vein narrow. Endostyle absent. Afferent gill vessel narrow, runs inside gill's right edge. Hypobranchial gland thick, whitish, located between gill and visceral organs, more developed in posterior half of pallial cavity where possesses some transversal folds. Part of visceral mass encroaches on pallial cavity roof, each organ described below.

Visceral mass (Figs. 421, 422). Characters similar o those of trichotropids, with about 3 whorls. Stomach very large, occupying last visceral whorl. Gonad cream in color, located in dorsal and peri-columellar regions of each whorl. Digestive gland pale brown, in ventral side of each visceral whorl. Gonad and digestive gland also cover stomach.

Circulatory and excretory systems (Figs. 421, 435). Heart relatively small, located at left-posterior limit of pallial cavity, partly dorsal to posterior gill region. Auricle small, anterior, connected to ctenidial vein before its posterior 1/3. Posterior 1/3 of ctenidial vein as blind-sac. Kidney narrow and curved, located in middle region of pallial cavity posterior limit. Renal tissue a single tall solid mass, triangular in section, transversly folded, contouring gastric style sac and adjacent intestine but not attached to them. Nephrostome a small transverse slit in right region of membrane between kidney and pallial cavity.

Digestive system (Figs. 426-431, 433, 435). Buccal mass large, mostly located inside snout. Snout-proboscis with partial capacity of retraction inside haemocoel by powerful snout retractor muscles. Jaw plates narrow, oblique (Fig. 428). Buccal mass and odontophore muscles (in comparison to those of calyptraeids) (Figs. 427-431, 433): **mc** thin and broad, forming slightly long and conic oral tube; **m1** no par differentiated except some small anterior pairs close to median line; **ma**, pair of lateral dilator muscles, small and narrow, origin in lateral inner surface of peribuccal wall, penetrate in mj fibers, insertion in region of jaws; **m2** pair similar; **m2a** absent; **m3** pair of transversal, narrow muscles surrounding radular sac region penetrating odontophore; **m4** pair similar to those of hipponicids, but with thicker dorsal portion attached to cartilages and adjacent subradular membrane (br), after this region m4 contour m2 insertion; **m5** pair similar to those of hipponicids, thin, long, originating from m4; **m6** thin and long, with about same length than cartilages; **m7** small, origin in subradular membrane anterior region, close to median line, in 2 branches, in short distance unite with each other and run in single band, insertion inside radular sac. Dorsal wall of buccal mass with pair of broad and low folds, with jaws as their inner-anterior protection. Aperture of salivary glands longitudinal slits, in middle region of dorsal folds in shallow furrows. Salivary glands 2 amorphous masses just posterior to buccal mass (Fig. 427), not passing through nerve ring. Radular sac short. Radular teeth (Figs. 95-97) somewhat similar to those of hipponicids: rachidian teeth broad, central cusp pointed, a lot of (about 25 pairs) of secondary cusps, long, small and very slender; lateral tooth about 4 times broader than rachidian, low; outer and inner lateral teeth with about same length as lateral tooth, but tall and slender; lateral and both marginal teeth with series of several small, long and slender cusps in median region of outer edges. Esophagus narrow, with about 8-10 inner longitudinal, low folds. Stomach (Fig. 435) very large, esophageal insertion in its middle-left region. Ducts to digestive gland just posterior to esophageal insertion, in gastric ventral surface. Gastric inner surface mostly smooth, pair of narrow, low folds run along left surface up to esophageal insertion; another pair situated somewhat perpendicular to preceding pair, separating esophageal insertion from style sac aperture; another tall transverse fold in intestinal origin. Style sac slightly long, anterior, with about half of stomach length and width. Intestine narrow, completely separated from style sac but attached to it at about its proximal half length, both with single wall. After this distance intestine and style sac separate from each other. Intestine contours style sac and anterior gastric wall, after possesses several loops in ample pallial adrectal sinus as shown in fig. 435. Anus a short and broad papilla at some distance from mantle border.

Genital system. Only females examined (Fig. 432). Visceral oviduct very narrow, runs on columella up to central region of pallial cavity posterior edge; in this region suddenly curves right and runs to right-posterior limit of this cavity. Visceral oviduct inserts sub-terminally in cylindrical vaginal tube. Seminal receptacle vesicular and slightly large, inserts in opposite side to visceral oviduct insertion. Albumen and capsule glands a single flattened mass, with thick glandular walls, part located dorsal to adrectal sinus. Albumen gland connection with vaginal tube narrow. Capsule gland amply connected to vaginal tube. Vaginal tube extends posterior to insertion of visceral oviduct as bind-sac and lies along right margin of oviduct up to genital pore. Genital pore a longitudinal slit turned to right.

Central nervous system (Fig. 425). Nerve ring characters similar to those of preceding species, localized far removed from buccal mass. Ganglia slightly small, pedal ganglia separated from other 2 pairs. Subesophageal ganglion close to nerve ring with additional bridge dorsal to esophagus.

Measurements of shells (in mm). AMS 353090: 1) 22.6 by 25.4; 2) 19.9 by 21.1; 3) 20.7 by 23.7.

Habitat. Under coral.

Material examined. VANUATU; Bay of Lenakel, Tonna Island, 19º32'S 169º16'E, AMS 353095, 1♀(W. F. Ponder col., 1966). AUSTRALIA; **Queensland**; Heron Island, Capricorn Group, 23º27'S 151º55'E, AMS 353090, 3 ♀(A. Warén & C. Lamb col., 23/viii/1985).

Note: Some of data discussed in preceding section are also based on other papers on other species, which complement some information unavailable in studied sample, such as male attributes (Récluz, 1845; Berg, 1896; Warén & Bouchet, 1988). Some characters of the head-foot were confirmed as present in other species. The penis is inserted behind right tentacles as usual (Berg, 1896: pl. 2, figs. 2, 6), with closed penis duct.

DISCUSSION OF CHARACTERS

Some terms used in the following discussion merit some explanation. The word "archaeogastropod" is used in traditional sense, but it is recognized as a paraphyletic taxon. The term "basal" caenogastropods refers to those taxa which generally are in the beginning of the mesogastropods in most catalogues (e.g., Abbott, 1974; Rios, 1994), in particular the Cerithioidea, Littorinoidea and Hydrobioidea. The term "higher" caenogastropods in general refers to Tonnoidea and Neogastropoda. Where mentioned "examined species" only the ingroup species are included. The following generic abbreviations are used: *C. = Crepidula*; *Ca. = Calyptraea*; *Cp. = Capulus*; *Cr. = Crucibulum; T. = Trochita; Tr. = Trichotropis*.

Shell

1. Form: 0= fusiform or globose; 1= patelliform (limpet) (*H. costellatus, H. subrufus, H. grayanus H. leptus, Sabia, Capulus*); 2= patelliform-like, with a ventral calcareous plate (*Cheilea*, calyptraeids, **except** *Trochita, S. calyptraeformis*); 3= patelliform-like, with long, slight spiral apex (*H. incurvus, Malluvium*); 4= trochiform-like (*Trochita trochiformis, S. calyptraeformis*) (CI: 57; RI: 70; not additive).

The shell of the calyptraeids has been considered to be patelliform (limpet-like). However, the limpet-like condition is a single cone, in which the muscles coming from the foot insert firmly in the shell ventral surface. This condition is not found in the calyptraeids, as seen by the presence of any sort of shelly septum, and also by the absence of strong muscles connecting the animal in this shell (see comments on muscles below). This condition reflects the small muscular scars in the ventral shell surface of those species.

On the other hand, the hipponicids and capulids show a true limpet-like condition, which, according to the obtained tree, is a convergence in both groups. However, in some species as *H. incurvus* and *Malluvium* spp, the shell is longer and still spiral. A "true" plesiomorphic coiled shell is only shown, in present sample, by *Trichotropis* and *Vanikoro*. The shell condition of *Trochita trochiformis* and *S. calyptraeformis* is referred to here as "trochiform" due its similarity with the shell of the trochids (Vetigastropoda), however some differences from the true trochiform condition are found. In fact, *T. trochiformis* and *S. calyptraeformis* shells resembles the shell of the Xenophoridae (Stromboidea), differing by reduced spire and by the absence of foreign objects attached to it.

2. Shelly septum: 0= absent or a true columella; 1= a planar septum (*B. aculeatus, Crepidula* spp.); 2= a spiral septum (*Calyptraea centralis*); 3= a cone (*Crucibulum* spp.) 4= a semi-cone (*Cheilea*) (CI: 100; RI: 100; not additive).

The ventral calcareous plate of the some calyptraeids apparently is a different sort of modification of the columellar part of the shell. In part, this is suggested analyzing the insertion of the small columellar muscle of these animals in the ventral plate border. Analyzing the present sample of calyptraeids, it is possible to imagine a derivation of the septa of the *Crepidula* and of the *Crucibulum* from the irregular septum present in *Calyptraea*, which can be derived from the weak spire of *Trochita* and *S. calyptraeformis*. However, this sort of analysis can not be done "a priori", thus the three septal states are presently regarded as homologous, but independently derived. But the obtained tree corroborates this suggestion of evolution of the calyptraeid shell septum.

Taylor & Smythe (1985) paid special attention to the shell umbilicus for differentiation in the *Trochita* species. *S. calyptraeformis* and *Ca. centralis* possess a narrow umbilicus, including adjacent mantle projection inserted in dorsal foot surface (which secretes the umbilicus inner surface). *T. trochiformis* lacks umbilicus. This character was not considered here mainly because of the dubious polarization.

3. Periostracum: 0= glabrous; 1= pillose, i.e., with hair

(all species) (CI: 100; RI: 100)

4. Protoconch position in dorsal view: 0= central or near center; 1= posterior. (*B. aculeatus, Crepidula spp., H. incurvus, Malluvium, Cp. sycophanta*) (CI: 25; RI: 62).

5. Spire: 0=tall; 1= weak (*T. trochiformis, S. calyptraeformis, H. incurvus, Malluvium*); 2= absent (remainder species **except** *Trichotropis* spp. and *Vanikoro*) (CI: 33; RI: 33; not additive).

A true spire, i.e., a spiral tube filled by visceral mass, is found in *Trochita*, *S. calyptraeformis*, *Vanikoro* and *Trichotropis*, however it is low (except trichotropids). In the other species a small spire is sometimes clear, mainly in young specimens, but empty. The other species of *Hipponix*, beyond *H. incurvus*, sometimes have very tall and somewhat coiled specimens, although a rare condition.

Head-foot

6. Operculum (in adult form): 0= present; 1= absent (all examined species **except** *Trichotropis* spp. and *Vanikoro*) (CI: 50; RI: 66).

An operculum is not present in very young specimens extracted from egg capsules of the calyptraeids. Maybe this structure is missing early in development. Neither in some embryological studies on calyptraeids an operculum is mentioned (Moritz, 1939, on *C. adunca* Sowerby), while other developmental studies on calyptraeids (e.g., Werner, 1955; Collin, 2000, 2001) opercula are mentioned. On the other hand, a paucispiral operculum is found in young specimens of hipponicids [e.g., *H. subrufus* (Fig. 26), *Sabia conica* and *H. grayanus* (Fig. 32)] capsules. In *Vanikoro* sp. some specimens have operculum, while others do not. There are, however, species where an operculum is always present (Warén & Bouchet, 1988). The obtained tree clearly shows this calyptraeoidean tendency to lose the operculum. It is present in basal trichotropids and absent in species after node 5, with *Vanikoro* as intermediary.

7. Anterior region of foot, marked by a transversal furrow of pedal glands: 0= as exploratory part; 1= covered by neck ventral surface (calyptraeids); 2= in distal margin of a propodium (hipponicids, *Vanikoro*) (CI: 100; RI: 100; not additive).

The homology of anterior end of the caenogastropod foot sole is clearly shown by the transverse furrow of pedal glands. Its analysis allows any structural modification of this region of foot, as in the cases of examined species. In the calyptraeids, e.g., allows that probably the ventral surface of the neck is not a modification of the foot, but a new functional acquisition of the head.

The anterior foot structure of hipponicids and *Vanikoro* is called propodium following the literature nomenclature (e.g., Yonge, 1953). However this propodium is not homologous to the propodium of higher gastropods as, e.g., olivids and naticids, because it does not contain the pedal gland furrow. The hipponicid and the *Vanikoro* propodia are, in fact, a flattened stalk for the pedal gland furrow. Collin (person. com.) suggested the name “pseudopropodium” for this structure.

The undulated, tall fold of the *Capulus* is unique in present sample, resulting in an autapomorphy. This fold is inserted at short distance of anterior edge of foot sole, apparently not homologous to any structure of the remainder species. McLean & Andrade (1982: 8-9) mentioned and figured (figs. 16, 19) the presence of a similar foot fold in *Capulus ungaricoides* (Orbigny, 1941), they called it a brood sac.

8. Posterior region of foot: 0= robust, almost cylindrical; 1= plane, flattened (*B. aculeatus, Crepidula* spp, *Ca. Centralis, S. calyptraeformis*); 2= conic, massive (*Crucibulum* spp.); 3= concave (hipponicids, *Cp. sycophanta*) (CI: 60; RI: 84; not additive).

The feet of the most examined species are much modified, little resembling those of the other gastropods. In the *Bostrycapulus, Crepidula, Calyptraea* and *S. calyptraeformis*, the foot is dorso-ventrally flattened, compressed between the shell septum and the substrate. Something similar is found in *Crucibulum*, but the dorsal foot surface is a slight tall, solid cone (also compressed between shell ventral plate and the substrate). On the other hand, the foot of the *Hipponix* and *Capulus* is completely different, thin in the center and thick in the borders. Part of this thickness is due to the shell and head muscles. The foot of these species stays compressed between the visceral mass and the substrate. In *Cheilea*, a similar conformation of remainder hipponicids is present, however greatly compacted by the shell ventral septum. Although the center of the *Cheilea* foot is thick, it was regarded as having the same muscular fashion of the family Hipponicidae, because the muscular arrangement is similar. Other details of *Cheilea* foot muscles are, on the other hand, considered. In the case of *H. grayanus* the foot sole is attached to the ventral calcareous plate (connected to the substrate, as a ventral “valve”). This condition indicates that *H. grayanus*, and maybe other Pacific species like *H. antiquatus* (L.) (Yonge, 1953, 1960), have lost the capacity to crawl. Yonge (1953) showed in fig. 1b the ventral valve secreted by the ventral surface of foot, has muscle scars. As discussed in the preceding section, the Atlantic hipponicids also secreted a ventral calcareous plate, but it is thinner, and they retain some crawling capacity.

9. Head muscles: 0= absent; 1= developed, immersed in integument (*Trichotropis* spp., *Vanikoro, Ca.*

sycophanta); 2= as a distinct muscle (hipponicids, capulid); 3= of independent origin in relation to shell muscle (*H. subrufus, H. grayanus, H. leptus*) (CI: 60; RI: 77; not additive).

The head muscles are a strong pair that connects laterally the head with the foot sole and/or medial-ventral region of shell muscle. This pair of muscles may be a modification of the muscular tissue of the haemocoel lateral walls present in other gastropods. The head muscles have also been referred to as retractor muscle of head (Yonge, 1953).

10. Pair of crossing muscles anterior to head muscles: 0= absent; 1= incipient (*H. grayanus, H. costellatus, H. subrufus, H. leptus*); 2= large, well developed (*H. incurvus*) (CI: 100; RI: 100; not additive).

This pair of muscles is very clear in *H. incurvus*, and resembles the cruciform muscles of the mantle border of some bivalves (Veneroidea). The homology of the crossing muscles with muscles of other gastropods is unclear. Maybe a key for this is in a more detailed analysis of the incipient muscles in the homologous region of the other *Hipponix* and in additional species of the group. According to the tree, the *H. incurvus* muscles may be derived from those of the remaining hipponicids of node 9.

11. Planar neck ventral surface: 0= absent; 1= present (calyptraeids) (CI: 100; RI: 100).

12. Neck lateral flattened lappets: 0= absent; 1= present (calyptraeids, *Vanikoro*) (CI: 50; RI: 90).

The ventral surface of the neck region of the calyptraeid head could even be called “sole”, but, as discussed above, it probably is not homologue to any foot sole region. This name could be used because this structure has also capacity of to adhere to the substrate (observed in some live specimens of *B. aculeatus*). On the other hand, this observation was not confirmed in other species. The neck region has also a pair of lateral, asymmetric expansions, neck lappets, with slightly thicker margins. Both the ventral surface and the lappets are used by the calyptraeids as a brood chamber. Fretter & Graham (1962) called the lappets of *C. fornicata* “neck lobes”, and those structure of calyptraeids are convergent with vanikorids (see also Warén & Bouchet, 1988).

13. Tentacles tip: 0= sharp or rounded; 1= weakly bifid in retracted condition (*C.* aff. *plana, C. protea, C. fornicata*); 2= with a longitudinal, ventral furrow (*H. incurvus*); 3= broad and flat (*Vanikoro*) (CI: 100; RI: 100; not additive).

14. Eyes location: 0= weakly over tentacle base; 1= middle level of tentacles (calyptraeids); 2= reduced (*H. grayanus, H. leptus, Cheilea, Malluvium, Vanikoro*) (CI: 50; RI: 81; not additive).

The eyes located slightly over tentacles base, and not at the base, is characteristic of the caenogastropods, and is regarded here as plesiomorphic for the ingroup. However, some species , possess eyes almost in the middle level of the tentacle. *H. grayanus* no only has a reduced pair of eyes, but also they are located in inner surface of the tentacles, turned to snout. Details of calyptraeid eye anatomy are found in Kleinsteuber (1913, fig. T).

15. Snout-proboscis anterior region: 0= rounded, almost plane; 1= with a pair of lateral projections (*H. incurvus, Sabia*); 2= lateral projections long (remainder hipponicids **except** *Cheilea*); 3= long ventral projection (*Cp. sycophanta, Trichotropis* spp) (CI: 60; RI: 71; not additive).

The snout of *Trichotropis* and *Capulus* is very different from other gastropods, with a long, flattened projection on its ventral anterior border. This projection probably collects the food coming from the gill and conduces it to the mouth. No clear difference was found between the *Trichotropis* and *Capulus* snouts. According to the obtained tree, it is equally parsimonious to regard the state 3 snout fashion as calyptraeoidean synapomorphy, with a reversion in the node 4, or independent origin (convergence) in both groups (node 2 and *Capulus*). The first hypothesis is preferred herein. The kind of snout shape of *Capulus* was also shown by McLean & Andrade (1982: 8, *C. ungaricoides*), which pointed out the possible boring in its bivalve host shell. Pernet & Kohn (1998) have referred this kind of snout as “pseudoproboscis”. In that study, the authors demonstrated the kleptoparasitism of *T. cancellata* on suspension-feeding polychaetes, during which the animal uses the proboscis to capture food from the worm’s feeding crown.

16. Snout retraction within haemocoel: 0= none; 1= partial, due retractor muscles (all examined species) (CI: 100; RI: 100).

17. Retractor muscles of snout: 0= none; 1= a pair (all examined species); 2= more than a pair (*H. costellatus, H. subrufus, H. incurvus*) (CI: 100; RI: 100; additive).

The condition of the snout of the calyptraeids, hipponicids, capulids, vanikorid and trichotropids is intermediary between a true snout and a pleurembolic proboscis. This fact is due to the presence of developed ventral retractor muscles and a partial capacity of retraction within the haemocoel, observed in living and in fixed specimens. This condition differs from the normal snout, observed in the archaeogastropods and in the basal caenogastropods. On the other hand, the retraction capacity and the space within the haemocoel available for its retraction are poor compared with those species that present an undiscussible proboscis (higher caenogastropods). Further study is necessary to determinate if the ingroup condition is intermediate or if it is due to the reduction of a previously long proboscis. The snout of the hipponicids has been referred to as a proboscis (Yonge, 1953; Fretter & Graham, 1962). The ventral pair of retractor muscles usually has the same origin of the head muscles and runs partially immersed in them. The additive condition of this character is based on the ontogeny, because all very young specimens possess a single pair of retractor muscles. The analysis considering it as non-additive character resulted in the same tree and indices.

18. Columellar muscle: 0= spiral; 1= much reduced (*B. aculeatus*, *Crepidula spp*, *Crucibulum spp*., *Cheilea*); 2= a shell muscle (hipponicids **except** *Cheilea*, *Capulus*) (CI: 50; RI: 84; not additive).

The state 2 is apparently of independent origin in 2 branches: *Capulus* and node 7. However, as commented above, *Cheilea* presents a head-foot musculature arrangement somewhat similar to the remaining hipponicids.

19. Dorsal shell muscle: 0= absent; 1= as a flat anterior expansion of the columellar muscle (*S. calyptraeformis*); 2= distinct, close to columellar muscle (*T. trochiformis*); 3= far from columellar muscle (other calyptraeids **except** *C. convexa*) (CI: 50; RI: 87; additive).

The dorsal shell muscle is described in more detailed for *B. aculeatus*. The additive condition of this character in based on the ontogeny, which shows some weak muscle fibers remaining connecting the dorsal muscle to the columellar muscle in the young specimens. Coding this character as non-additive the resulted tree is the same, the indices change to CI: 75 and RI: 85. The steps also change (from 6 to 4) because of the reversion (state 3 to 0) in *C. convexa*.

20. Lateral shell muscle on right: 0= absent; 1= present connected to columellar muscle (*S. calyptraeformis*, *Trochita*, *Ca. centralis*); 2= as an isolated muscle (*B. aculeatus*, *Crepidula spp*, *Crucibulum spp*) (additive) (CI: 100: RI: 100).

Like the shell, the muscular system that connects the animal with its shell is much modified in the examined species. In the case of the capulids and most hipponicids, the typical limped muscle attachment is found: a U-shaped, strong shell muscle. In the calyptraeids, however, there are few small muscles functioning in this way — the very small columellar muscle, the lateral muscle and the dorsal muscle. The calyptraeid columellar muscle is very thin, more notable at the right edge of shell septum. The dorsal muscle is single, fan-like, located in the anterior region of animal, close to the median line. *C. convexa*, however, is apparently missing this muscle. Observing the calyptraeids and their position on the tree, it is possible to see that the dorsal and the lateral shell muscles are derived from the columellar muscle extremities. The condition shown by *S. calyptraeformis* and *Trochita* represent the more plesiomorphic one, with both muscles still connected to columellar muscle. The lateral muscle is to the left end and the dorsal muscle to the right-dorsal end of the columellar muscle. In the remainder calyptraeids, the columellar muscle becomes thin (generally edging the anterior border of shell septum only), with the other 2 muscles remaining a little thicker. The dorsal shell muscle migrates dorsally in taxa after node 15, becoming independent of columellar muscle. *C. adunca*, present a pair of shell muscles connected to each other by a thin shelf (Moritz, 1938, fig. 6, as shell muscle). Nothing similar was found in examined specimens, but Hoagland (1977) pointed out that some species have two muscle scars (species group V), that may represents another sort of modification. *Trochita dhofarensis* Taylor & Smythe (1985, fig. 4) apparently lacks both dorsal and lateral shell muscles, and have a thick columellar muscle, which may represents the most plesiomorphic state in the family. The dorsal shell muscle was detected in *Crepidula* (as *Janacus*) by Kleinsteuber (1913, fig. G). He called it the shell muscle, but it was not pointed out in also studied *Trochita* or *Calyptraea* (figs E-F).

21. Net of transverse muscles in haemocoel: 0= absent; 1= present (calyptraeids, trichotropids, *Vanikoro*, *H. leptus*, *H. grayanus*, *Cheilea*, *Sabia*, *Malluvium*); 2= greatly developed, passing through salivary glands (*B. aculeatus*) (CI: 66; RI: 66; additive).

The “net” of transversal muscles is in fact more than simply a series of muscular fibers, but also a mass of diffuse connective tissue. This mass in part fills the haemocoel space around the esophagus and is more developed in calyptraeid species, mainly in *B. aculeatus*. It is possible that the development of these muscles could be connected to the hydrostatic pressure of an unusually long neck. The net of muscles reverted in hipponicids of the node 11.

The additive optimization is based on the comparison, since the *B. aculeatus* condition appears to be an increment of the state 1. Nothing changes in the result if the character is considered as not additive.

22. Food groove: 0= absent; 1= present (calyptraeids) (CI: 100; RI: 100).

The food groove is a shallow furrow of the pallial cavity floor that receives the particles collected by the gill, and transports them by cilia to the mouth (Werner, 1955). The food groove is also found in some other filter-feeding gastropods, such as turritellids, vermetids (both Cerithioidea) and struthiolariids (Stromboidea) (Simone, 2001, in press). Although similar in location and in function, the food groove of the calyptraeids is different in being edged by low folds and to disappear anteriorly at some distance from the mouth. These differences probably do not allow homoplasy. The filter-feeding *Trichotropis* does not present an anatomic food groove, but an analogous ciliate current is present (Yonge, 1962, Pernet & Kohn, 1998).

23. Connection between head-foot and visceral mass: 0= posterior; 1= turned towards left (hipponicids, calyptraeids) (CI: 100; RI: 100).

The condition 1 is clearly shown as the esophagus strongly curves left in the above species, as it crosses from the haemocoel to the visceral mass, passing through diaphragm-like septum.

Pallial organs

24. Mantle fusion with posterior-dorsal surface of foot: 0= absent; 1= present (all examined species **except** *Trichotropis* spp.) (CI: 100; RI: 100).

In the case of the calyptraeids the mantle border is fused no only with border of the foot, but also with its dorsal surface. This part of the mantle secretes the ventral-right surface of the shell of *S. calyptraeformis* and *Trochita* and the shell septum of the remaining species. The species of the hipponicids, vanikorids and capulids also have this type of mantle border-foot, but it is not just in the foot border. This fusion is slightly over the plane of foot sole, closer to shell muscle ventral margin.

25. Repugnatorial glands along mantle border: 0= absent; 1= present (*B. aculeatus*, *Crepidula* spp., *Capulus*, *Ca. calyptraeformis*) (CI: 33; RI: 71).

Fretter & Graham (1962, fig. 58) show the repugnatorial glands reunited in some areas of the mantle border of *C. fornicata*. This sort of distribution was not observed in this study, in the specimens of *C. fornicata* (species shown in that figure). The repugnatorial glands are not easily seen, they are very small and almost transparent. They are distributed side-by-side uniformly all along mantle border of the *Crepidula* species in the present sample, however it is possible that they also occur in the species of the other genera, maybe less developed and only detectable by thin sections. Anyway their greater development is a character of those calyptraeids.

There is a strong possibility that more of the examined calyptraeoideans possess the repugnatorial glands, being a probable synapomorphy of a clade, but this is not possible to verify at this time without microscopic examination. Only those species which these glands seen in the dissection were considered to possess the repugnatorial glands.

26. Mantle border with special arrangement of folds between gill anterior extremity and osphradium: 0= absent (smooth); 1= present (calyptraeids) (CI: 100; RI: 100).

Special attention was paid to the arrangement of the folds in anterior edge of the mantle, just in the pallial cavity aperture. The arrangement of folds apparently is indicative of an incipient siphonal canal, because the folds in general converge to the gill and osphradium anterior extremities. The siphon folds in mantle border of *C. fornicata* was called food-pouch by Orton (1912, fig. 4). A weak siphon in mantle border is found in trichotropids.

27. Mantle border restricting mantle cavity: 0= absent; 1= present in lateral regions (calyptraeids); 2= present in lateral and anterior regions (*Crucibulum* spp.) (CI: 100; RI: 100; additive).

This character is considered additive because the states vary only in degree, having *Crucibulum* spp. the most modified fashion. Nothing changes (tree or indices) if the character is considered not additive.

28. Mantle cavity length: 0= about half of animal length; 1= more than 2/3 of animal length (calyptraeids); 2= less than ¼ of animal length (hipponicids) (CI: 100; RI: 100; not additive).

The compression of the pallial cavity by the visceral structures is also noted by Yonge (1953), “causing displacement dorsally of the anus and ctenidium”.

29. Mantle cavity form: 0= conic; 1= almost a complete ring (*Crucibulum* spp.) (CI: 100; RI: 100).

As is general the case in limpet gastropods, the pallial cavity is ample, without restrictions beyond those of the head-foot structures. However in the calyptraeids the mantle reduces the pallial cavity aperture, closing the lateral regions of this cavity (characters 27, 28), i.e., a membranous part of the mantle connected between the foot and the shell borders restricts the cavity (**ml** in figures). This closure is more developed in the *Crucibulum* species where the pallial cavity is a curved, almost ring-like tube (the posterior extremity, which in these animals is turned anteriorly, is not opened, but so a blind-sac).

The area of the pallial cavity is obviously ampler in filter-feeding species such as the calyptraeids, because of the increase of the gill. The contrary situation is found in the hipponicids, with much reduced pallial cavities, compressed by the visceral mass (other data are discussed below).

30. Osphradium type: 0= ridge-like; 1= pectinate (calyptraeids, trichotropids, *Cp. sycophanta*) (CI: 33; RI: 77).

31. Osphradium position: 0= very oblique, almost perpendicular to mantle border; 1= slight oblique, but almost parallel to mantle border (all species); 2= parallel to mantle border (calyptraeids) (CI: 100; RI: 100; additive).

The three states of this character are apparently degrees of a same trend. This is confirmed in the tree, and nothing changes even if it is considered as non-additive.

32. Osphradium size: 0= large, about ½ of mantle aperture length or more; 1= small, less than ¼ of this distance (*C.* aff. *plana, C. protea, C. convexa, C. fornicata, C. argentina*) (CI: 100; RI: 100).

33. Ridge-like osphradium form: 0= broad and long; 1= very narrow (*H. costellatus, Malluvium*); 2= with satellite folds around it (*H. subrufus, H. grayanus, H. leptus, Sabia*); 3= only satellite fold present (*Cheilea*) (CI: 60; RI: 50; not additive).

34. Pectinate osphradium form: 0= not pectinate; 1= bipectinate (calyptraeids **except** following); 2= monopectinate, with filaments in tip (*C.* aff. *plana, C. protea, C. convexa, C. fornicata, C. protea, Ca. centralis, T. trochiformis*); 3= monopectinate, with triangular filaments in right side (*Trichotropis* spp., *Ca. sycophanta*) (CI: 50; RI: 72; not additive).

35. Osphradium leaflets form: 0= absent; 1= thick (calyptraeids); 2= slender and tall (*C. convexa*); 3= triangular, in right side of osphradium ganglion, attached to mantle roof (*Trichotropis* spp., *Ca. sycophanta*) (CI: 75; RI: 90; not additive).

The ridge-like type of osphradium, found in the basal Caenogastropoda, is regarded as plesiomorphic. The pectinate type of osphradium is a structural adaptation to increase the surface of this sensory organ. Pectinate osphradia are found in the architaenioglossans and in several groups of caenogastropods, such as some cerithioideans, stromboideans, and all higher groups. The homology of the state "pectinate osphradium" among the different groups is still unclear, but almost certainty it developed several times independently. Two types of pectinate osphradia are normally found: the bipectinate osphradium and the monopectinate one. The monopectinate osphradium is in general found in the miniaturized members of the normally bipectinate taxa. The calyptraeids also follow this rule. However *C. fornicata* is a large species possessing a monopectinate osphradium. Taylor & Miller (1989: 230) studied details of the osphradium of *C. fornicata*, and is an important paper for further description of the cilia. In that paper, the authors state that most *C. fornicata* have ordinary monopectinate osphradium, however, some specimens possess 2-3 leaflets on the left side (their fig. 7), and suggested that the structure is reduced from a bilamellar condition. Monopectinate osphradia are also present in *C. adunca* (Moritz, 1938), and other *Crepidula* species.

Both conditions (mono- and bipectinate) occur in some genera. In the case of *Calyptraea*, a bipectinate osphradium is found in *C. chinensis* (Werner, 1953, figs 4, 17) and the monopectinate in *C. centralis* (this study). Kleinsteuber (1913, fig. V) showed a broad bipectinate osphradium, with somewhat large anterior (right) filaments that gradually decrease towards posterior (left) in *Calyptraea*.

Satellite folds around osphradium are probably glandular and of unknown function. Similar folds are also (homoplastic) found in some cerithioideans and stromboideans (Simone, 2001, in press). However satellite folds were never observed in pectinate osphradia. An osphradium satellite fold of another hipponicid, *Hipponix australis* (Lamarck, 1819) was shown by Knudsen (1991, fig. 3b).

The osphradium of *Trichotropis*, although also of monopectinate condition, is singular in having triangular filaments attached to the osphradium ganglion, and also extending towards the right, attached to the adjacent mantle area. Something similar occurs in *Capulus*.

According to obtained tree, 3 equally parsimonious optimizations of the pectinate condition are possible: 1) a synapomorphy of the calyptraeoideans and independent reversions to ridge-like condition in *Vanikoro* and in hipponicids (node 6); 2) a synapomorphy of the ingroup, reversion in node 4, reappearing in calyptraeids (node 13); 3) independent (convergent) acquisitions of trichotropids (node 2), capulids and calyptraeids (node 13). The first hypothesis is preferred herein.

The several osphradium characters shown herein agree with the suggestion of high systematic value of this organ by Brown & Olivares (1996) for the calyptraeids.

36. Gill size: 0= about half of pallial cavity roof area; 1= very large (most of that area) (calyptraeids) (CI: 100; RI: 100).

37. Gill position: 0= longitudinal in pallial cavity; 1= transversal, part parallel to mantle border (all examined species) (CI: 100; RI: 100).

38. Gill anterior extremity form: 0= straight; 1= curved forwards and left (all examined species **except** *Trichotropis* spp and *Ca. sycophanta*) (CI: 100; RI: 100).

39. Gill anterior extremity location: 0= posterior to mantle border; 1= on mantle border (all examined species) (CI: 100; RI: 100).

40. Gill filament rods: 0= same size than membranous part of filaments; 1= extending little beyond membranous part of filaments (all species); 2= very long, two or three times longer than membranous part of filaments (calyptraeids) (CI: 100; RI: 100, additive).

The additive condition of this character is based on the ontogeny, observing the gill filaments that are formed in its anterior region. The not additive optimization nothing changes in the tree or in the indices.

41. Gill filaments: 0= free from each other; 1= connected with each other by cilia (calyptraeids) (CI: 100; RI: 100).

The gill of the calyptraeids is modified because of its additional filtration function, the modifications include elongation of the filaments and adaptations to they stay firmly in position (increase of rods, fixative cilia, etc.). The opposite is found in the hipponicids, which have proportionally small gills. On the other hand, some states in common are found in all ingroup species if compared with the normal gill fashion of the caenogastropods, such as the gill position and its anterior extremity (on the mantle border and turned forwards). Details on the structure and ciliation of gill filaments of *C. fornicata* is shown by Orton (1912, figs. 5-6).

42. Hypobranchial gland: 0= thick, large, with chambers and tall folds; 1= low, of almost uniform surface (all examined species); 2= very thin, inconspicuous (*B. aculeatus, Crepidula spp*, hipponicids **except** *Cheilea*, *Cp. sycophanta*, *S. calyptraeformis*) (CI: 40; RI: 66; additive).

Contrasting with the increased gill of the calyptraeids, their hypobranchial gland is reduced, it is at least detectable in some species, while in others it is inconspicuous. In the same way, the hipponicids also present the same tendency.

The additive optimization of the states of this character is due to suspicion they are part of a single evolutionary trend. If it is performed as not additive, the same tree is obtained, with same CI and steps, the RI changes to 62.

43. Endostyle: 0= absent; 1= present (calyptraeids) (CI: 100; RI: 100).

In the filter feeding *Trichotropis*, no endostyle was found, however a series of low, oblique glandular folds is present between the gill and the left margin of pallial cavity. These folds maybe can be homologue to endostyle.

44. Endostyle location: 0= absent; 1= ventral to ctenidial vein (calyptraeids); 2= between ctenidial vein and gill (*Ca. centralis*) (CI: 100; RI: 100; not additive).

The endostyle (name giving as an analogy with those of the Cephalochordata) is a glandular ridge in left margin of the gill, running parallel and close to ctenidial vein. A surprisingly similar endostyle is found in the other filter-feeding caenogastropods, as turritellids (Cerithioidea) and struthiolariids (Stromboidea). These multiple occurrence is regarded as convergence because of the extra necessity of mucus in the gill of those animals, which collect particles. Although this character was considered as non- additive, the disposition of its states in the tree shows that it may be additive. Using an additive optimization changes nothing in the tree or indices.

Circulatory system

45. Pericardium location: 0= anterior-left region of visceral mass; 1= exposed in pallial cavity roof, almost in its center (calyptraeids); 2= dorsal to posterior end of pallial cavity (hipponicids, capulid, *Vanikoro*) (CI: 100; RI: 100; not additive).

46. Auricle end: 0= in ventricle connection; 1= with a portion beyond (at right) ventricle connection as a bind-sac (calyptraeids) (CI: 100; RI: 100).

47. Auricle form: 0= somewhat spherical; 1= short, attached to anterior inner surface of pericardium (all species); 2= same, but very long, tubular (calyptraeids) (CI: 100; RI: 100, additive).

The uncommon form of the calyptraeid auricle, with a portion beyond the ventricle connection as a blind-sac, is also shown by Moritz (1938, fig. 5) for *C. adunca*. Kleinsteuber (1913) described other details of the circulatory system.

This character is considered as additive by the comparative method, because each state appears to be a modification of the preceding one. However, nothing changes in the results if the optimization is changed to not additive.

The expansion of the auricle beyond the ventricle and its connection to the anterior surface of the pericardium is possibly due to an aperture between auricle and nephridial gland, normally found in the higher caenogastropods. This type of aperture is difficult to see in the dissections, and serial sections of the region were not performed herein.

48. Posterior region of ctenidial vein between gill and auricle: 0= long; 1= very short (all examined species **except** *Trichotropis* spp.) (CI: 100; RI: 100).

49. Ctenidial vein connection with auricle: 0= in posterior end of gill; 1= sub-terminal in gill, with a portion of the ctenidial vein beyond this connection as a blind sac (hipponicids, capulid, *Vanikoro*) (CI: 50; RI: 88).

Maybe due to the modification of the body form of the ingroup species, the pericardium is also modified if compared with the normal fashion of the gastropods. In the calyptraeids the pericardium is very long and narrow, the ventricle remains in the center of the body (close to median line), far away from the gill's posterior end. Running the entirety of this distance is a very long and narrow auricle. Interestingly, the calyptraeid auricle has another uncommon character: a portion beyond ventricle connection as a blind sac.

Moreover, the pericardium of the hipponicids and capulids has also an uncommon location: dorsal to the gill's posterior end. This location is possibly due to the posterior compression of the visceral mass. The connection of the ctenidial vein with the auricle, which in the calyptraeids contours the posterior gill end, is unique in the hipponicids, vanikorids and capulids. In both, the connection is subterminal, i.e., at some distance of the posterior gill end, in a T-fashion. A short portion of the ctenidial vein is, then, a bind-tube, with an inverted blood circulation. This condition is clearer in *H. grayanus* and *Cheilea*.

50. Vessel in pallial roof insertion in left margin of kidney: 0= absent (or inconspicuous); 1= slightly perpendicular to kidney (*C.* aff. *plana*, *C. protea*, *C. fornicata*); 2= edging rectum (*C. argentina*) (CI: 100; RI: 100; not additive).

Excretory system

51. Kidney tissue: 0= massive; 1= two lobes (calyptraeids, trichotropids, *Cp. sycophanta*); 2= a chamber between visceral mass and first intestine loops (*H. grayanus*, *H. leptus*, *Cheilea*, *Vanikoro*, *Sabia*, *Malluvium*) (CI: 50; RI: 75, not additive).

52. Kidney form: 0= rhomboid; 1= dorso-ventrally flattened (*H. costellatus*, *H. subrufus*, *H. incurvus*); 2= slender and very long (*Crucibulum* spp.) (CI: 100; RI: 100; not additive).

53. Nephridial gland: 0= present; 1= reduced (calyptraeids, hipponicids) (CI: 100; RI: 100).

54. Nephrostome: 0= isolated in membrane between kidney and pallial cavity; 1= with adjacent inner glandular folds (*B. aculeatus*, *Vanikoro*); 2= far removed from renal chamber (*H. costellatus*, *H. subrufus*) (CI: 66; RI: 50; not additive).

The kidney of the ingroup species is small, almost reduced. It is still more reduced in the hipponicids, in which the kidney is only a small, flattened glandular mass in a flat, hollow chamber. The reduction in part precludes the characterization of the organ, but in the calyptraeids, the normal fashion of the caenogastropods is still noted (a pair of lobes, nephridial gland, etc.), the same does not occur in the species of the hipponicids. Anyway, the reduction *per se* is a valuable character.

Visceral mass

55. Size: 0= of moderate size (about 1/3 of animal volume); 1= small (calyptraeids **except** *T. trochiformis*, *Ca. calyptraeformis*) (CI: 100; RI: 100).

56. Form: 0= spiral; 1= triangular (turned posteriorly) (*B. aculeatus*, *Crepidula* spp.); 2= long and fusiform (*Crucibulum* spp.); 3= sac-like (hipponicids, capulid); 4= triangular (turned forward) (*Ca. centralis*, *S. calyptraeformis*, *T. trochiformis*) (CI: 80; RI: 90; not additive).

The visceral mass form and size are closely related with the morphological modification of the body plan of these animals. In the calyptraeids, the visceral mass moulds within (in *B. aculeatus*, *Crepidula* and *Calyptraea*) or around (in *Crucibulum*) the shell septum. In the other two families (state 3), the visceral mass is molded by the foot dorsal concavity, from which it is weakly attached.

57. Kidney and pericardium: 0= occupying most of visceral anterior edge; 1= occupying about half of visceral anterior edge (*Vanikoro*, hipponicids, calyptraeids) (CI: 100; RI: 100).

Digestive system

58. Modified m1: 0= absent; 1= m1a (towards anterior) (calyptraeids **except** *S. calyptraeformis*, *Cheilea*, *Sabia*, *Malluvium*, *Trichotropis* spp., *Capulus*); 2= m1a + m1b (this towards posterior) (*T. trochiformis*) (CI: 40; RI: 57, additive).

The m1b is a *T. trochiformis* autapomorphy. The additive optimization is merely because of the presence of the m1a in this species, however nothing changes if the character not coded as additive.

59. M2a: 0= absent; 1= present (calyptraeids **except** *S. calyptraeformis*) (CI: 100; RI: 100).

60. Mt: 0= absent; 1= present (all examined species **except** *Hipponix* spp) (CI: 50; RI: 80).

61. M3: 0= absent; 1= present (*Crucibulum* spp.) (CI:

100; RI: 100).

62. M4 form: 0= very broad, surrounding cartilages; 1= narrow, contouring cartilages posterior surface (calyptraeids) (CI: 100; RI: 100).

63. M4 insertion (beyond br): 0= only in “to” (tissue preceding exposed portion of radula); 1= also in subradular cartilage (calyptraeids, *Cheilea*, trichotropids, *Ca. sycophanta*) (CI: 33; RI: 75).

64. M5 insertion: 0= only in dorsal side of radula; 1= in lateral side of radula, encroaching both sides (dorsal and ventral) (calyptraeids, *Trichotropis* spp.) (CI: 50; RI: 90).

65. M7 origin: 0= of middle region of m4 median-ventral surface; 1= in anterior margin of m4 (hipponicids **except** *Cheilea*); 2= extremely narrow (*Trichotropis* spp.); 3= origin from bulged region of subradular membrane (br) (*Cheilea*, *Ca. sycophanta*, *Vanikoro*) (CI: 75; RI: 88, not additive).

66. M7 accessory muscles: 0= absent; 1= m7a (*B. aculeatus*); 2= m7b (in dorsal surface) (*Trichotropis* spp.) (CI: 100; RI: 100, not additive).

67. M6: 0= thick, 1= thin (calyptraeids) (CI: 100; RI: 100).

68. M8: 0= absent; 1= present (calyptraeids) (CI: 100; RI: 100).

69. M9: 0= absent; 1= present (calyptraeids) (CI: 100; RI: 100).

70. M10 size: 0= large; 1= small (hipponicids **except** *H. incurvus*); 2= absent (calyptraeids **except** *B. aculeatus, S. calyptraeformis*); 3= immersed in mj (trichotropids, *Vanikoro*, *Cp. sycophanta*, *S. calyptraeformis*) (CI: 50; RI: 75, not additive).

71. M12: 0= absent; 1= present (*C.* aff. *plana*, *C. protea*, *S. calyptraeformis*) (CI: 50; RI: 50).

72. M14: 0= absent; 1= lateral (*T. trochiformis, S. calyptraeformis*); 2= ventral (remainder calyptraeids, *Cheilea*) (CI: 100; RI: 100).

The odontophore is an important structure for comparative studies and for obtaining characters. As shown above, the odontophore muscle characters easily separate the calyptraeids from remaining groups. However, analyzing the position of the taxa on the cladogram, it is possible to suggest some evolutionary trends. The massive m4 pair, present in basal caenogastropods having dorsal and ventral branches surrounding the pair of odontophore cartilages, modified in the following aspects: 1) the pair of dorsal branches divided, a part give origin to pair m2a (in node 14), becoming a continuation of the m2; other part originated the pair m8 (in node 13); 2) the pair of ventral branches becoming attached directly to the subradular membrane, condition absent both basal caenogastropods and basal calyptraeoideans.

The m5 pair is inserted in a short portion of radular sac in basal caenogastropods, but in trichotropids and calyptraeids there is a modification to an ampler inserted condition, surrounding both sides of radular sac.

The m9 and the mt are new acquisitions of the calyptraeoideans, absent in some hipponicids (node 9 – a reversion).

The m14 pair is also a new feature of the calyptraeids. It is laterally located in both basal taxa (*S. calyptraeformis*, *Trochita*) and ventral in remaining taxa (after node 15). A surprisingly similar m14 occurs in *Cheilea*.

It is interesting to observe that some hipponicids reverted some odontophore muscles to a condition similar to those of basal caenogastropods, becoming similar to those. This in part can be explained by the tendency for reduction of this organ.

73. Rachidian basal-lateral cusp: 0= absent; 1= present (*Hipponix* spp.) (CI: 100; RI: 100).

74. Rachidian form: 0= almost a square; 1= long antero-posteriorly (calyptraeids); 2= broad (hipponicids, *Cp. sycophanta*, *Vanikoro*) ((CI: 100; RI: 100; not additive).

75. Rachidian central cusp: 0= clearly larger than neighbor cusps; 1= almost of same size than neighbor cusps (*Hipponix* spp, *Calyptraea centralis*) (CI: 50; RI: 80).

76. Lateral tooth width: 0= about same as rachidian; 1= more than twice rachidian (all species **except** trichotropids and *Cp. sycophanta*) (CI: 100; RI: 100).

77. Lateral tooth tip: 0= turned inwards; 1= turned forwards (*Hipponix* spp, *Malluvium*) (CI: 100; RI: 100).

78. Inner and outer marginal teeth tip: 0= blunt; 1= pointed (all species) (CI: 100; RI: 100).

79. Inner and outer marginal teeth tip: 0= with cusps;

1= without cusps (trichotropids) (CI: 100; RI: 100).

80. Inner and outer marginal teeth length: 0= little more than rachidian width; 1= more than twice rachidian width (all species **except** trichotropids, *Cp. sycophanta*); 2= more than 4 times rachidian width (*Hipponix* spp, *Malluvium*) (CI: 100; RI: 100; additive).

The additive optimization is based on the comparison among the states, appearing to be the same tendency of increment of the marginal teeth. However, the result is the same if the analysis is performed as not additive.

81. Inner and outer marginal teeth cusps: 0= in both sides of tip; 1= only in tip inner margin (calyptraeids **except** *S. calyptraeformis*) (CI: 100; RI: 100).

The polarization of the radular characters is mainly based on Cerithioidea, Hydrobioidea and Stromboidea features. The radula importance in calyptraeoidean comparative studies was explored by Bandel & Riedel (1994). Several features of radula were searched, but, except for those above, they are autapomorphic or inconclusive.

82. Salivary glands: 0= passing through nerve ring; 1= anterior to nerve ring (all examined species) (CI: 100; RI: 100).

83. Salivary glands form: 0= a single mass clustering around esophagus; 1= separated into two masses (all examined species **except** *H. costellatus* and *H. grayanus*) (CI: 33; RI: 0).

84. Salivary glands size: 0= large, occupying more than half of haemocoel volume; 1= very small (all examined species **except** *B. aculeatus*) (CI: 50; RI: 0).

The ingroup state, having salivary glands, that do not pass through the nerve ring, is extraordinary. This state is regarded as synapomorphy of the neogastropods. On the other hand, salivary glands anterior to nerve ring in the mesogastropod grade are rare, but have been observed in some Cerithioideans (Simone, 2001, a species of Pleuroceridae) and in the Strombidae (Simone, in press), as well as in all ingroup species, even those with very large glands (*B. aculeatus*). Possibly, the whole anterior condition of the ingroup salivary glands is due to the elongation of the anterior esophagus, the result of adaptations for protracting the snout (almost a true proboscis, see discussion above) and, additionally in the calyptraeids, the elongation of the neck.

Another clear tendency of the ingroup species is to reduce the salivary glands. Except in *B. aculeatus*, all remainder examined species have a pair of very small glands, generally not long enough to forming a mass clustering around esophagus. In *Trichotropis* the salivary glands are so small that are only visible in their posterior extremity, close to the posterior region of buccal mass, where a short portion detaches from local wall. Practically the entire salivary glands of this taxon are immerse in the dorsal wall of the buccal mass. The salivary gland of *H. leptus* is extremely reduced, almost absent, maybe due to buccal mass reduction.

85. Esophagus inner surface: 0= with folds and glands; 1= only with folds (all examined species **except** following); 2= smooth (*H. costellatus*, *Cheilea*); 3= with a pair of pouches (*Trichotropis* spp.) (CI: 75; RI: 50; not additive)

This character is better compared to the archaeogastropods, in which the esophagus is normally rich in glands and special chambers. However several basal caenogastropods have glandular ridges in the esophagus, which are regarded as plesiomorphic.

86. Ducts to digestive gland (in stomach): 0= 2 (or more) of equivalent size; 1= 2, posterior reduced (*Crepidula spp*, *Malluvium*); 2= 1 (*B. aculeatus*, *Ca. centralis*, *Crucibulum* spp., *Hipponix* spp., *Cheilea*) (CI: 40; RI: 75, not additive).

The plesiomorphic condition of the caenogastropod stomach is with a pair of ducts to the digestive gland. However reduction to a single duct and even reversion to a pair was observed (convergently) in the cerithioideans (Simone, 2001). The Californian *Crepidula adunca* also presents a pair of ducts to digestive gland (Moritz, 1938).

Although this character was analyzed as non- additive, an additive optimization is also intuitive, because the 3 states appear to be a single evolutionary trend. If this character is considered additive, the resultant tree is the same, but the number of steps changes from 5 to 7, and the indices to CI: 28, RI: 68.

87. Style sac and intestine: 0= amply connected with each other; 1= almost entirely separated (hipponicids **except** *H. leptus* and *Cheilea*, *Vanikoro*) (CI: 33; RI: 66).

The style sac amply connected to intestine is the plesiomorphic character, found in the archaeogastropods, basal caenogastropods and even in the other mollusc groups (i.e., Bivalvia). On the other hand, the tendency to separate both structures, until their complete separation (only communicated by stomach – this case is not found in the ingroup species, which have a very short portion still united), is found in the cerithioideans and in the stromboideans (Simone, 2001, in press). The Californian *Hipponix antiquatus* (L.) apparently have the style sac fused with the intestine (Yonge, 1953).

No examined specimens presented a crystalline style within style sac, however it was found in *C. adunca* (Moritz, 1938) and *H. antiquatus* (cf. Yonge, 1953). The absence in the examined specimens can be a fixation artifact.

88. Intestinal loops: 0= several; 1= few (up to three) (trichotropids, calyptraeids, *H. costellatus, H. subrufus*) (CI: 33; RI: 75).

Several intestinal loops are found, in general, in herbivorous and microphagous gastropods, and therefore in most archaeogastropods and some basal caenogastropods. It is regarded as plesiomorphic. Although the ingroup species have considerable intestine length, only basal hipponicids possesses a similar plesiomorphic, several-looped fashion.

89. Intestinal loop, "U"-shaped, preceding rectum, exposed in pallial cavity roof: 0= absent (or within visceral mass); 1= present (calyptraeids **except** *T. trochiformis, S. calyptraeformis*); 2= ample (*C. convexa*) (CI: 100; RI: 100; additive).

The described, U-shaped, intestinal loop is an interesting character of the calyptraeids, unique in being almost all exposed in pallial cavity roof. The posterior surface of its initial portion is connected to the kidney, but the intestine extends beyond the renal limit. In *C. convexa,* this intestinal loop is also developed, but weakly shorter and forming a more open angle (about 70-80º). *Trochita* and *Trichotropis* also possess the homologous region of the intestine, but part is immersed in intestinal tissue and part exposed in the pallial cavity. The different kind of intestinal loops among *Trochita, Calyptraea* and *Crepidula* was also pointed out by Kleinsteuber (1913, figs. T-V).

The additive optimization is merely suggestive, because the state 2 appears to be a modification of the state 1. However, nothing changes in the result if this character is considered not additive.

90. Intestinal loop anterior to kidney: 0= absent; 1= present (all species **except** trichotropids) (CI: 100; RI: 100).

In general, the intestine runs straightforward after kidney chamber (normal rectum), but in most ingroup species there are one or more loops anterior to kidney. This state, however, is apparently absent in *Hipponix australis* (Lamarck, 1819) (sic Knudsen, 1991, fig. 2).

91. Anus position in females: 0= close genital pore; 1= far from it (hipponicids, *S. calyptraeformis*) (CI: 50; RI: 87).

Genital system

Development

92. Reproduction type: 0= gonochoristic; 1= protandric hermaphroditism (all examined species **except** *C. protea*) (CI: 50; RI: 0).

As discussed previously the differences in development are the main character used for the concept on *C. protea* and *C.* aff. *plana* remains as separated species. This datum, as well the development of all ingroup species, merits further studies, because the available material is not adequate for this sort of evaluation. As stated above, several small specimens of calyptraeids have no penis, and probably evolve to female without the male phase. Anyway, the hermaphroditism is not the rule among the caenogastropods, and indubitably it is a derived condition.

Some studies on the development of calyptraeids, from eggs to female phase, are found in literature (Conklin, 1897; Gould, 1917 on *C.* aff. *plana*; Coe 1936, 1938a, 1948; Collin, 2000). The present data are based on these studies.

93. Spawning: 0= outside of body, in substrate; 1= in shell cavity, protected by neck ventral surface; (calyptraeids) 2= in shell cavity protected by and connected to propodium (hipponicids **except**, *Cheilea*) (CI: 100; RI: 100; not additive).

The ingroup species developed singular methods for brooding the egg capsules in two different ways protected by the mother shell. Several specimens were examined with the capsules still attached, but this character was not confirmed in all species. The states were inferred to all species (beyond those without examined brooding specimens) based on literature (e.g., Bandel, 1976) or due to the presence of the morphological structures females use for protecting the capsules~~,~~. All calyptraeid and hipponicid egg capsules seen in this study and shown in the literature (e.g., Hoagland, 1986: 177, fig. 5) are virtually identical in shape, looking like a "balloon". The development of the embryos, however, is quite variable, as some species present free swimming larva, while other are of direct development (Gallardo, 1977; Hoagland & Coe, 1982).

94. Gonad position in visceral mass: 0= along columellar surface; 1= concentrated in anterior and ventral regions (calyptraeids); 2= somewhat in center of ventral region (hipponicids); 3= without precise localization (*Capulus*) (CI: 100; RI: 100; not additive).

This character is also influenced by the modification of the body plan of these animals.

Male

95. Seminal vesicle: 0= in central-anterior region of visceral mass ventral surface; 1= in right-anterior extremity

of visceral mass (calyptraeids, *H. leptus*, *Cheilea*, *Sabia*); 2= absent (remainder hipponicids) (CI: 66; RI: 83; not additive).

The seminal vesicle is a differentiated, thick glandular region of the visceral vas deferens, present in most caenogastropods. In the ingroup species, the location of this structure is modified in the calyptraeids, while it is missing as differentiable organ in most hipponicids.

96. Penis origin: 0= by side or posterior to right tentacle; 1= ventral to it (hipponicids) (CI: 100; RI: 100).

Although no male of *Vanikoro* and *Capulus* was examined, the data by Berg (1896) and by Giese (1915) (respectively) show the normal origin of the penis behind right cephalic tentacle.

97. Penis with papilla on tip: 0= absent; 1= present (*B. aculeatus, C.* aff. *plana, C. protea, C. argentina, H. costellatus, H. subrufus*) (CI: 25; RI: 40).

The papilla of the hipponicids penis is quite variable among specimens of a single species. That of *H. costellatus* is absent in some specimens, however, perhaps due its fragility, it could be lost during fixation. The penis papilla of *H. subrufus*, on the other hand, is very large in some specimens, while not so large in others, but always present. The Californian *H. antiquatus* also possesses a papillate penis (Yonge, 1960, fig. 1) similar to that of *H. subrufus* and *H. leptus*. Brown & Olivares (1996) already suggested the presence of penis papillae as valuable systematic feature for the calyptraeids.

98. Distal end of penis sperm groove: 0= extends to distal tip of penis; 1= slight far from penis tip (*Cr. auricula, H. costellatus, H. subrufus*) (CI: 50; RI: 50).

99. Pallial vas deferens and penis duct: 0= opened (a groove); 1= closed (a tube) (*Cheilea, Vanikoro*) (CI: 50; RI: 0).

According to the tree, *Cheilea equestris* and *Vanikoro* (see also Berg, 1896) are convergent in the closure of the male pallial gonoducts, from a groove to a tube.

Female

100. Seminal receptacles in albumen gland: 0= absent; 1= present (all examined species **except** *H. costellatus, H. grayanus, H. leptus, Cheilea, Trichotropis* spp.); 2= reunited in a sac (*C. convexa*); 3= modified in irregular ridges (*T. trochiformis*) (CI: 50; RI: 50; not additive).

Gould (1917: 11) called the small vesicles seminal receptacles (nomenclature followed here), but they may represent additional secretory organs. Although considered apomorphic due to their absence in most of the outgroups, something similar is found in the xenophorids (Stromboidea) and in tonnids (Tonnoidea). Tthe structures in tonnids are paired. The structure of *Trochita* is immersed in the albumen gland as a coiled glandular tube. It may be homologous to the others, but it was considered here as analogous.

101. Albumen gland location: 0= in pallial cavity, posterior to capsule gland; 1= edging visceral mass, at side of capsule gland (*B. aculeatus, Crepidula spp, Crucibulum spp.*) (CI: 100; RI: 100).

102. Glandular concavity in propodium base for capsules attachment: 0= absent; 1= present (hipponicids **except** *Cheilea*) (CI: 100; RI: 100).

Cheilea was the single hipponicid without this structure. The egg capsules are similar in form, but unlike those of the remaining members of the family, where the capsules stalks connected to the concavity, the *Cheilea* capsules are attached to the borders of the ventral calcareous plate (fig. 369).

103. Capsule gland: 0= continuation of pallial oviduct; 1= a blind sac (*B. aculeatus, Ca. centralis, Crucibulum* spp.); 2= similar, but with vaginal tube in its base (*Crepidula* spp.) (CI: 100; RI: 100; additive).

The additive optimization is based on the similarity between states 1 and 2, which appear to be a successive modification. However the results (tree and indices) are the same if this character is treated as additive.

104. Bursa copulatrix: 0= present; 1= missing (calyptraeids **except** *Cr. quiriquinae, Cp. sycophanta, Malluvium, T. borealis*) (CI: 20; RI: 63).

105. Vaginal tube: 0= very short (extending little beyond capsule gland); 1= very long (*Crepidula spp, Cr. quiriquinae*); 2= arched towards posterior (*S. calyptraeformis*) (CI: 66; RI: 80; not additive).

106. Genital pore: 0= a slit; 1= a small papilla (calyptraeids **except** *S. calyptraeformis*); 2= a tall papilla (*C.* aff. *plana, C. protea, C. convexa, C. fornicata*) (CI: 100; RI: 100; additive).

The pallial oviduct is normally a source of characters valuable for comparative study in caenogastropods, both in species and at higher levels. In the hipponicids, the pallial oviduct is large and different in each species. In the calyptraeids it is very small and similar in some species. Except for the species listed above in the state 2, most calyptraeid pallial oviduct is unique in being "V"-shaped, with the female pore located at the vertex. In the species listed in state 2 the pallial oviduct is similar, but there is a long and slender vaginal tube beginning atthe base of the capsule gland. However, it is not difficult to realize that one may be derived from the other. Another apparent kind of modification of the pallial oviduct, closer to the basal condition, is present in *Crepidula walshi* Reeve (Yipp, 1983, fig. 4), this may represents another evolutionary branch for the genus. Examples of some calyptraeid pallial oviducts, and comparative comments, are also found in Kleinsteuber (1913, fig. W).

Some structures and glands are named herein based on their aspect and topology, but surely further studies are necessary to confirm their function. The pallial oviduct, as a whole, had been referred singly as "uterus" in ancient literature (e.g., Kleinsteuber, 1913; Gould, 1917), but the nomenclature has been uniform with more recent papers (e.g., Yipp, 1983) that includes histological studies. Hoagland (1986) performed a comparative study of calyptraeid anatomy and function of the pallial oviduct, and figured the structure of *Crepidula lessoni* (Broderip), *C.* cf *convexa* and *C. aculeata*. Although the pictures are too schematic to be used here in detail, the data are incorporated to present study. In that study, the albumen gland is called the posterior pallial oviduct, the capsule gland as medial pallial oviduct, and the vaginal tube as anterior one. The presence of the gonopericardial duct and several vesicular seminal receptacles is clear in all species.

The character 106 is considered to be additive because state 2 appears to be a modification (increasing) of state 1. However, nothing changes if it is considered as non-additive.

107. Closure of the pallial oviduct: 0= opened (a furrow); 1= closed (a tube) (all species) (CI: 100; RI: 100).

Central nervous system

108. Position: 0= just posterior to buccal mass; 1= very posterior, far removed from buccal mass (all examined species **except** *Trichotropis* spp.) (CI: 100; RI: 100).

109. Ganglia proportional size and location: 0= small, far from each other; 1= large, close with each other (calyptraeids, hipponicids) (CI: 100; RI: 100).

110. Buccal ganglia position: 0= close to median line; 1= lateral in odontophore, close to m2 insertion (hipponicids **except** *Cheilea* and *H. leptus*, *Trichotropis* spp., *Vanikoro*) (CI: 25; RI: 62).

111. Additional ventral connective between both parietal ganglia: 0= absent; 1= present (*Crucibulum auricula*) (CI: 100; RI: 100).

The available material was not good enough for detailed studies of the central nervous system, which in general needs special fixation. On the other hand, the structure is normally conservative at superfamily or family levels. However, some interesting aspects of the main ganglia were obtained and used herein. The buccal ganglia state is polarized based on basal caenogastropods, but a similar tendency for lateral located ganglia is also found in the cerithioideans (Simone, 2001).

Except for *Trichotropis*, the remaining ingroup species have a relatively concentrated nerve ring relatively with proportionally large ganglia, unexpected in sedentary animals. In part the microphagy, and consequently the limited necessity for esophagus expansion can explain this.

Details of the central nervous system, its main nerves and ganglia are found in Kleinsteuber (1913, figs. N, Q), Heath (1916), Moritz (1938, fig. 4) (these both for *C. adunca*); Graham (1954, fig. 4 for *Capulus ungaricus* and *C. fornicata*), from which the examined species are very similar.

Larval type

112. Echinospira larva: 0= absent; 1= present (capulids, trichotropids) (CI: 50; RI: 50).

Despite the importance (Collin, 1997a) for species-level systematics, no larval character was scored in present material, because of total impossibility. However, the echinospira larva was strongly recommended to be included in present study by Riedel (personal communication). For this inclusion, the data of Bandel & Riedel (1994) was used, who pointed out this kind of larva for the capulids and trichotropids.

According to the present study, 2 equal parsimonious optimizations are possible: 1) a calyptraeoidean synapomorphy with reversion in node 4; 2) convergence trichotropids and capulids. The second hypothesis is preferred here. Additional data on larval characters are found in Collin (1997b).

CLADISTIC ANALYSIS

Figure 436. Matrix of characters of the Calyptraeoidea sample studied herein, with 2 outgroups included in last rows. A basal caenogastropod sample, operationally an all-zero row, is omitted.

DISCUSSION OF THE CLADOGRAM AND THE TAXONOMY

		1		**2**		**3**		**4**		**5**		
	12345	**67890**	**12345**	**67890**	**12345**	**67890**	**12345**	**67890**	**12345**	**67890**	**12345**	**6**
Bacule	21112	11100	11010	11132	21111	11101	20?11	11112	11111	12100	10111	1
Cplana	21112	11100	11110	11132	11111	11101	21?21	11112	12111	12101	10101	1
Cprote	21112	11100	11110	11132	11111	11101	21?21	11112	12111	12101	10101	1
Carge	21112	11100	11010	11132	11111	11101	21?21	11112	12111	12102	10101	1
Cconve	21112	11100	11010	11102	11111	11101	21?22	11112	12111	12100	10101	1
Cforni	21112	11100	11110	11132	11111	11101	21?21	11112	12111	12101	10101	1
Calypt	22102	11100	11010	11031	11110	11101	20?21	11112	11121	12100	10101	4
Cruaur	23102	11200	11010	11132	11110	12111	20?11	11112	11111	12100	12101	2
Cruqui	23102	11200	11010	11132	11110	12111	20?11	11112	11111	12100	12101	2
Trochi	40101	11000	11010	11021	11110	11101	20?21	11112	11111	12100	10100	4
Scalyp	40101	11100	11010	11011	11111	11101	20?11	11112	12111	12100	10100	4
Hcoste	10102	12321	00002	12200	00110	00200	10100	01111	02002	01110	01120	3
Hsubru	10102	12331	00002	12200	00110	00200	10200	01111	02002	01110	01120	3
Hincur	30111	12322	00201	12200	00110	00200	10000	01111	02002	01110	01100	3
Hgray	10102	12331	00022	11200	10110	00200	10200	01111	02002	01110	20100	3
Hlept	10102	12331	00022	11200	10110	00200	10200	01111	02002	01110	20100	3
Sabia	10102	12320	00001	11200	10110	00200	10200	01111	02002	01110	20100	3
Malluv	30111	12320	00022	11200	10110	00200	10100	01111	02002	01110	20100	3
Cheile	24102	12020	00020	11100	10110	00200	10300	01111	01002	01110	20100	3
Capusy	10112	10310	00003	11200	10011	00001	10033	01011	02002	01110	10000	3
Tcanc	00100	00010	00003	11000	10000	00001	10033	01011	01000	01000	10000	0
Tborea	00100	00010	00003	11000	10000	00001	10033	01011	01000	01000	10000	0
Vanik	00100	02010	01320	11000	10010	00000	10000	01111	01002	01110	20010	0
Stromb	00000	00000	00000	01000	00000	00000	00000	00000	00000	00100	10000	0
Cyprae	00000	00000	00000	11000	00000	00001	00010	00000	00000	00110	10000	0

Figure 436. Matrix of characters of the Calyptraeoidea sample studied herein, with 2 outgroups included in last rows. A basal caenogastropod sample, operationally an all-zero row, is omitted.

	5 6		**7**		**8**		**9**		**10**		**11**	
	7890	**12345**	**67890**	**12345**	**67890**	**12345**	**67890**	**12345**	**67890**	**12345**	**67890**	**12**
Bacule	1111	01110	11110	02010	10101	11101	20111	01111	01001	10110	11110	00
Cplana	1111	01110	01112	12010	10101	11111	10111	01111	01001	10211	21110	00
Cprote	1111	01110	01112	12010	10101	11111	10111	00111	01001	10211	21110	00
Carge	1111	01110	01112	02010	10101	11111	10111	01111	01001	10211	11110	00
Cconve	1111	01110	01112	02010	10101	11111	10121	01111	00002	10211	21110	00
Cforni	1111	01110	01112	02010	10101	11111	10111	01111	00001	10211	21110	00
Calypt	1111	01110	01112	02011	10101	11111	20111	01111	00001	00110	11110	00
Cruaur	1111	11110	01112	02010	10101	11111	20111	01111	00101	10110	11110	?0
Cruqui	1111	11110	01112	02010	10101	11111	20111	01111	0??01	10101	11110	10
Trochi	1211	01110	01112	01010	10101	11111	00101	0111?	0??03	00010	11110	00
Scalyp	1001	01110	01113	11010	10101	01111	00101	1111?	00?01	00002	01110	00
Hcoste	1000	00001	00001	00121	11102	01012	21101	11222	11100	01000	01111	00
Hsubru	1000	00001	00001	00121	11102	01111	21101	11222	11101	01000	01111	00
Hincur	1000	00001	00000	00121	11102	01111	21001	11222	1??01	01000	01111	00
Hgray	1000	00001	00001	00121	11102	01011	21001	11222	10000	01000	01111	00
Hlept	1000	00001	00001	00121	11102	01111	20001	11221	10000	01000	01110	00
Sabia	1101	00001	00003	00020	10101	01111	01001	11221	10001	01000	01111	00
Malluv	1101	00001	00001	00020	11102	01111	11001	11222	10?01	01010	01111	00
Cheile	1101	00103	00001	00020	10101	01112	20001	11021	10010	00000	01110	00
Capusy	0101	00103	00003	00020	00100	01111	00001	0103?	0?001	00010	01100	01
Tcanc	0101	00112	20003	00000	00110	01113	00100	01000	00000	00000	01001	01
Tborea	0101	00112	20003	00000	00110	01113	00100	01000	00000	00010	01001	01
Vanik	1001	00003	00003	00020	10101	01111	01001	0100?	0?011	00000	01101	00
Stromb	0000	00000	00000	00000	00100	00001	00100	00000	00000	00000	01000	00
Cyprae	0000	00000	00000	00000	00100	00000	00100	00000	00000	00000	01000	00

Abbreviations: **Bacule**, *Bostrycapulus aculeatus*; **Cplana**, *Crepidula* `aff` *plana*; **Cprote**, *C. protea*; **Carge**, *C. argentina*; **Cconve**, *C. convexa*; **Cforni**, *C. fornicata*; **Calypt**, *Calyptraea centralis*; **Cruaur**, *Crucibulum auricula*; **Cruqui**, *Crucibulum quiriquinae*; **Trochi**, *Trochita trochiformis*; **Scalyp**, *Sigapatella calyptraeformis*; **Hcoste**, *Hipponix costellatus*; **Hsubru**, *H. subrufus*; **Hincur**, *H. incurvus*; **Hgray**, *H. grayanus*; **Hlept**, *H. leptus*; **Sabia**, *Sabia conica*; **Malluv**, *Malluvium devotus*; **Cheile**, *Cheilea equestris*; **Capusy**, *Capulus sycophanta*, **Tcanc**, *Trichotropis cancellata*; **Tborea**, *T. borealis*; **Vanik**, *Vanikoro* sp.; **Stromb**, Stromboidea ground plan; **Cyprae**, Cypraeoidea ground plan.

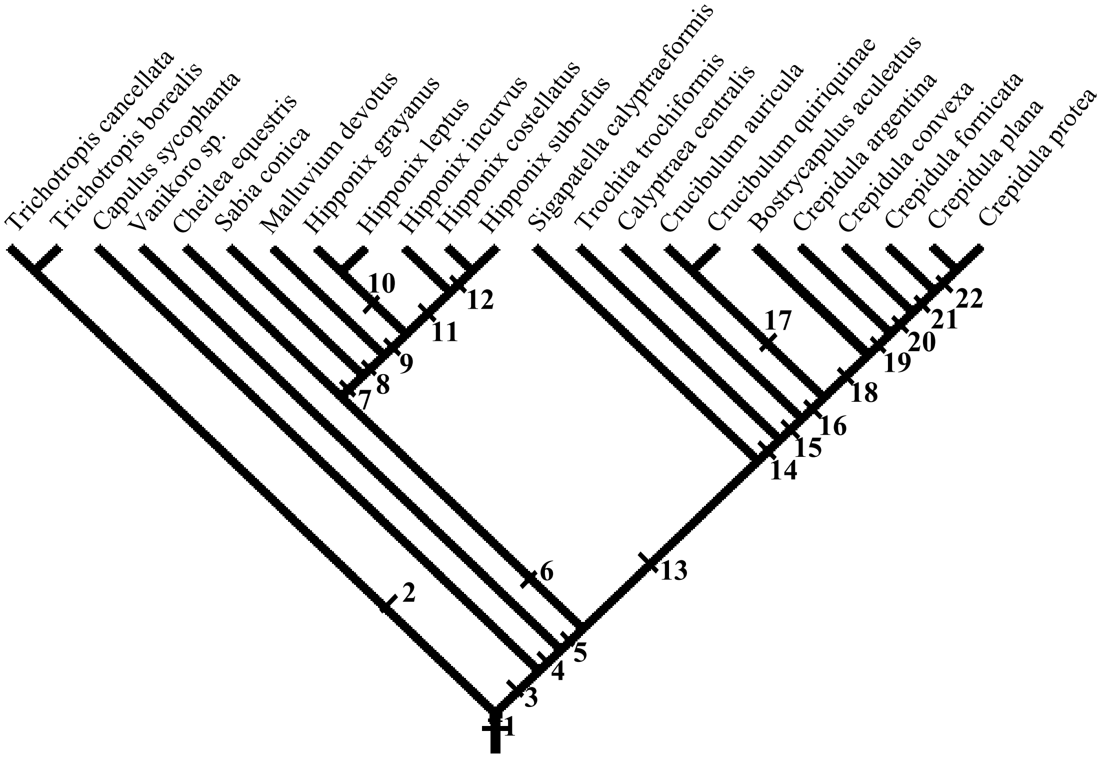


Figure 437: Single most parsimonious tree with numbered nodes. Length 267; CI 67; RI 88.

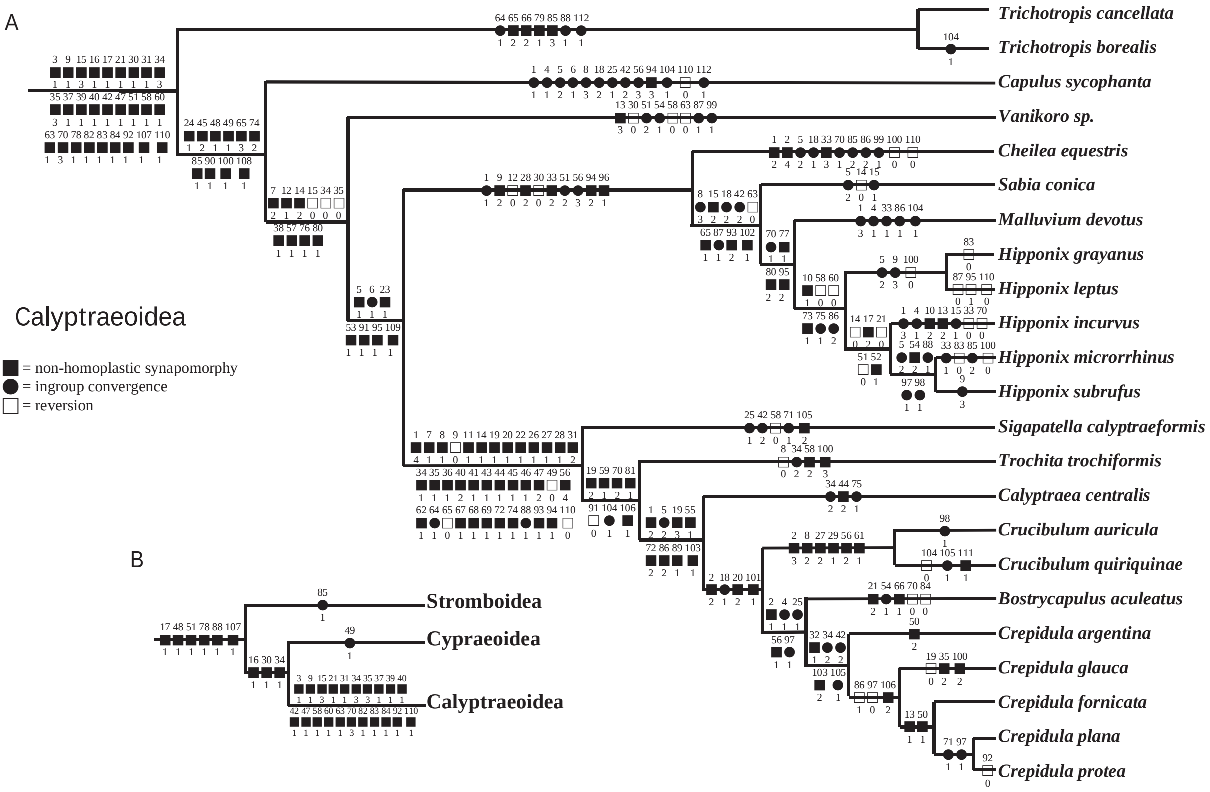


Figure 438: **A**, Single most parsimonious tree with the synapomorphies of each node shown. Length 265; CI 67; RI 88, archaeogastropods, Cerithioidea and Hydrobioidea as outgroups. **B**, same, with the addition of 2 outgroups as part of ingroup (Cypraeoidea and Stromboidea ground plans. Calyptraeoidea represent the tree A except the node # 1. Length 272; CI 65; RI 89. Black square = non homoplastic synapomorphy; black circle = ingroup convergence; white square = reversion; number upper = character; number below = state.

(Figs 436 - 438)

The Calyptraeoidea, Hipponicoidea and Capuloidea appear to be a single taxon – Calyptraeoidea – supported by 27 synapomorphies (node 1) if the outgroups were the archaeogastropods, Cerithioidean and Hydrobioidea (Fig. 438A); and 21 synapomorphies if the Stromboidea and the Cypraeoidea ground plans were included in the ingroup (Fig. 438B). Another analysis considering all characters as not additive was performed and the obtained tree is absolutely the same. The parameters are length: 265, CI: 67, RI: 87. According to P. Bouchet (personal communication), the name Calyptraeidae has priority over Crepidulidae (and respective superfamily names) based on the following: the name Crepidulidae was established (as Crepiduladae) by Fleming (1822: 494). The name Calyptraeidae was established (in the vernacular form “les Calyptacées”) by Lamarck (1809: 321). Children (1823: 227) first latinized it (as Calyptraciana). The name Calyptraeidae was never credited to Children, but to Lamarck, having priority over Crepidulidae according to ICZN article 11.7.2. Calyptraeidae was first raised to superfamily (as Calyptraeacea) by Thiele (1925: 88) (name also mentioned by Troschel, 1861: 188), the same only happened to Crepidulidae (as Crepidulacea) in Abbott (1974: 138). Hipponicidae was introduced by Troschel, 1861 and Capulidae by Fleming, 1822. The presented result in part clarifies an apparent confusion refering to the inter-relationship of these taxa (see introduction) and gives a basis for understanding its identity.

The first branch of the Calyptraeoidea tree is the trichotropids (node 2), which share 7 synapomorphies. The basal position of the trichotropids was expected because of their shell shape and the presence of an operculum-. This position was also suggested by Hoagland (1977).

The following branch (node 3), supported by 10 synapomorphies, represents the remaining calyptraeids except the trichotropids. This node is marked by the beginning of shell modification, and adaptations of the inner anatomy reflecting shell modification, such as restriction of the pallial cavity by the mantle (character 24), the position of the reno-pericardial structures (chs. 45, 48), intestinal loops (ch. 90), position of nerve ring (ch. 108), etc.

Capulus sycophanta has 13 autapomorphies, most (11) being convergent states, mainly with the hipponicids. Several of these convergences (characters 1 to 18) are clearly due to patelliform, limpet shell shape adaptations, sometimes also shared even with outgroups limpet representatives (e.g., patellids, acmaeids, cocculinids), as, e.g., the horseshoe-shaped shell muscle.

The following branch (node 4), supported by 10 synapomorphies, is mainly characterized by the modification of the head-foot (chs. 7, 14). The *Vanikoro* sp, representing the family Vanikoridae Gray, 1840, is the sister-group of the hipponicids and calyptraeids (node 5), and in the present analysis it appears with 8 autapomorphies. Further comments on the family Vanikoridae are found in Warén & Bouchet (1988).

Node 5 unites the Hipponicidae and the Calyptraeidae supported by 7 synapomorphies. This group is mainly characterized by the reduction of the spire (ch. 5), of the operculum (ch. 6), and posterior position of the nerve ring (109).

Node 6 represents the family Hipponicidae, united by 10 synapomorphies, which includes *Cheilea* as the basal branch, followed by *Sabia*, and after that by *Malluvium*. The genus *Hipponix*, with Pacific and Atlantic representatives, is monophyletic, supported by 6 synapomorphies (node 9).

Node 13 representing the family Calyptraeidae is very well supported by 37 synapomorphies. *S. calyptraeformis* is the first branch of the calyptraeids, followed by *Trochita trochiformis* (node 14) and *Calyptraea centralis* (node 15). *S. calyptraeformis* has been considered to belong to both *Trochita* and *Calyptraea*, which, as commented in preceding sections, is not consistent with my results. This is the reason why I attributed it to *Sigapatella*-, opinion shared with other authors (e.g., Garrard, 1961; Macpherson & Gabriel, 1962; Wilson, 1993). Although, there are 5 species in the genus *Trochita* (Taylor & Smythe, 1985), which are united by shared plesiomorphies (see, e.g., data by Rehder, 1943), such as spiral shell. It is possible that the spiral shelled calyptraeids may represent paraphyletic grades of basal taxa. However, there is not enough anatomical information in the literature to resolve this question.

Node 16 groups the non-spiral shelled calyptraeids, supported by 4 synapomorphies. The *Crucibulum* is monophyletic, indicated by 6 synapomorphies, while its sister group is a clade with the species represented after node 18 (with 5 synapomorphies). This clade groups the previously considered *Crepidula* species. *B. aculeatus*, as mentioned in the description section, is separated from the *Crepidula* by its own characters and on the presence of an available genus name. The genus *Crepidula* (node 19) is supported by 5 synapomorphies.

The tree obtained in the present study is not to be regarded as “the phylogeny of the superfamily Calyptraeoidea”, but as another step in that direction. The informations extracted from the tree mostly agree with the present knowledge and taxonomy of the group, but there are a few polemic points. The presented result is, however, considered enough for interpreting the heterogeneous sample as belonging to the same biological unit called Calyptraeoidea, with a group of defining characters known (node 1). This ground plan can be interpreted as definitive of the group and can be used to understand the relationships of the group with other closely related superfamilies.

Bremer support and Bootstrapping were used to de-

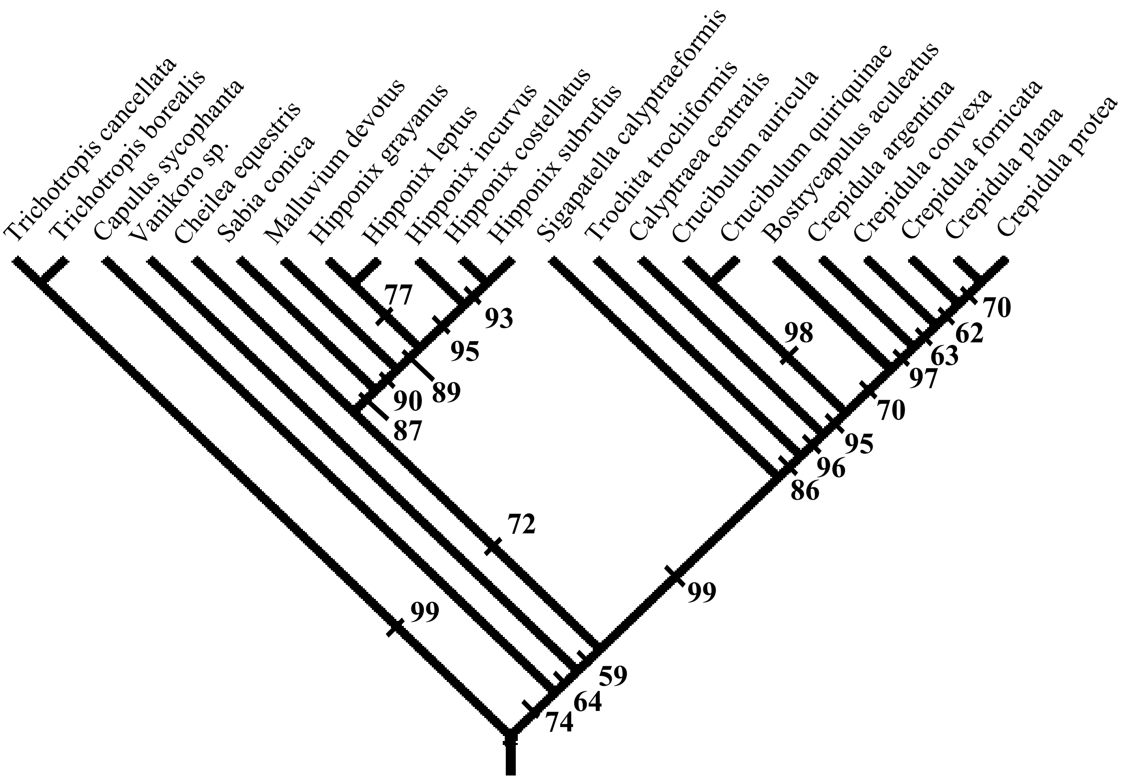


Fig. 439, obtained cladogram showing bootstrap support of each node, based on 500 replicates each with 10 random additions of a heuristic search.

termine how well supported the different nodes were. Only nodes 1 and 13 had a Bremer index of 1 while the other nodes all collapsed. This result is maybe due to the high degree of homoplasies and to the relatively few characters in the dataset. It is possible that the Bremer index is more suitable for molecular analyses that normally encompass several hundred characters. A more informative result was obtained from the bootstrap analysis. (Fig. 439). Any node with over 70% support is considered to be well-supported. In this point of view, most nodes of obtained cladogram are well supported, having only 3 nodes between 60 and 70% (nodes 4, 20 and 21).

CONCLUSIONS

The Calyptraeoidea is a monophyletic taxon and groups the families Trichotropidae, Capulidae, Vanikoridae, Hipponicidae and Calyptraeidae.

Its ground plan is known (node 1), and includes 21 synapomorphies.

Characters of all systems and organs are valuable for comparative studies and for phylogenetic analyses.

Some taxonomic changes were necessary for the taxonomy to reflect the possible phylogenetic relationships, such as to consider *Cheilea* a hipponicid, and the attribution of *Sigapatella* to *S. calyptraeformis*.

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