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COMPARATIVE MORPHOLOGICAL STUDY
OF REPRESENTATIVES OF THE THREE
FAMILIES OF STROMBOIDEA AND THE
XENOPHOROIDEA (MOLLUSCA,
CAENOGASTROPODA), WITH AN
ASSESSMENT OF THEIR PHYLOGENY

Luiz Ricardo L. Simone

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MUSEU DE ZOOLOGIA DA UNIVERSIDADE DE SÃO PAULO

CONTEÚDO

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COMPARATIVE MORPHOLOGICAL STUDY OF REPRESENTATIVES OF THE THREE FAMILIES OF STROMBOIDEA AND THE XENOPHOROIDEA (MOLLUSCA, CAENOGASTROPODA), WITH AN ASSESSMENT OF THEIR PHYLOGENY

LUIZ RICARDO L. SIMONE

ABSTRACT

A detailed comparative morphology of the following 21 species is made: 1) Strombidae: Strombus pugilis (Brazil), S. alatus (Florida, USA), S. gracilior (form Panama, Pacific coast), Eustrombus goliath (Brazil), E. gigas (Caribbean), Aliger costatus, A. gallus (northeastern Brazil), Tricornis raninus (Caribbean); Conomurex luhuanus, Canarium urceus, Lambis lambis, Terebellum terebellum (all Australia), Tibia insulaechorab (Pakistan); 2) Struthiolariidae: Struthiolaria papulosa (New Zealand), Tylospira scutulata (Australia); 3) Aporrhaidae: Cuphosolenus serresianus new comb., Aporrhais occidentalis and A. pespelicani (North Atlantic and Europe); 4) Xenophoridae: Onustus caribaeus and Xenophora conchyliophora (West Atlantic) and O. indicus (Australia). The three former families are usually considered members of the superfamily Stromboidea, while the Xenophoridae are included in their own superfamily Xenophoroidea. A phylogenetic (cladistic) analysis is undertaken, based on 102 characters (255 states); with some basal Caenogastropoda as the main outgroup. A single most parsimonious tree was obtained (length: 209, CI: 74; RI: 86) as follows: ((T. scutulata – S. papulosa) (C. serresianus ((A. occidentalis – A. pespelicani)((O. caribaeus – O. indicus) – X. conchyliophora)(T. terebellum (C. urceus (C. luhuanus (T. raninus (L. lambis (S. pugilis – S. alatus – S. gracilior)((E. goliath – E. gigas) (A. costatus – A. gallus)))))))))). According to this analysis, Stromboidea (including Xenophoridae) is a monophyletic superfamily supported by 42 synapomorphies, Xenophoridae and Strombidae are monophyletic, as well as Strombus, Aliger and Eustrombus are monophyletic genera; whereas Aporrhaidae and Aporrhais are paraphyletic taxa; the Xenophoridae are the sister taxon of the Strombidae. Lambis lambis is represented in a branch within species currently included in Strombus, thus some genera were revalidated (Eustrombus and Aliger) and subgenera require elevation to genera (Strombus s.s., Tricornis, Conomurex, Canarium).

Key Words. Mollusca; Gastropoda; Stromboidea; Xenophoroidea; Phylogeny; Morphology.

INTRODUCTION

The Stromboidea is considered in, most classifications, to comprise three families, Strombidae, Struthiolariidae and Aporrhaidae. Strombidae has a worldwide distribution and more than 70 species (Walls, 1980). The other two families are represented in the Recent faunas only by a few species, from restricted areas, although fossil records show they had wider distributions and were more diverse (Morton, 1951) in the past. The characters which unite these families are basically the fusiform shell (with expanded outer lip), and the foot with a sub-terminal, projecting operculum (Woodward, 1894).

Unlike most other Western Atlantic molluscs, the Strombidae, in particular, have few systematic problems, at least at species level. There are few and well-established species; the shell has several good diagnostic characters, reasonably different among them. Moreover, several revisionary papers on the group have been published (e.g., Clench & Abbott, 1941; Abbott, 1960; Matthews, 1967, 1980; Moscatelli, 1987). Practically, the only systematic problem at the species level is the "*S. pugilis* complex", which includes *S. pugilis* Linné, 1758 (type species of the genus), *S. alatus* Gmelin, 1790, and *S. nicaraguensis* Fluck, 1915. Some authors treat them as valid species (e.g., Dodge, 1956), and others as subspecies (e.g., Matthews, 1980; Rios, 1994).

Contrasting with their well-established taxonomy is the very scant anatomical knowledge. Most anatomical data on the strombids, with more than 70 species, are based on a few species, published in a few and older papers (e.g., Bouvier, 1887; Woodward, 1894; Risbec, 1927). There is no comparative study or phylogenetic analysis of the group, and most species are still placed in the single genus *Strombus* Linné, 1758.

The strombids are economically important as human food. They are consumed by fishermen in great quantities, mainly in the Caribbean (Muñoz *et al.*, 1987; Mulliken, 1996) and North Brazil. Although, in some localities they are cultivated (Ogawa & Corral, 1987; Ray & Stoner, 1995a; Wiedemeyer, 1998).

Interesting history, biological and paleontological features of the Strombidae, Struthiolariidae and Aporrhaidae had been provided by Morton (1997a, b).

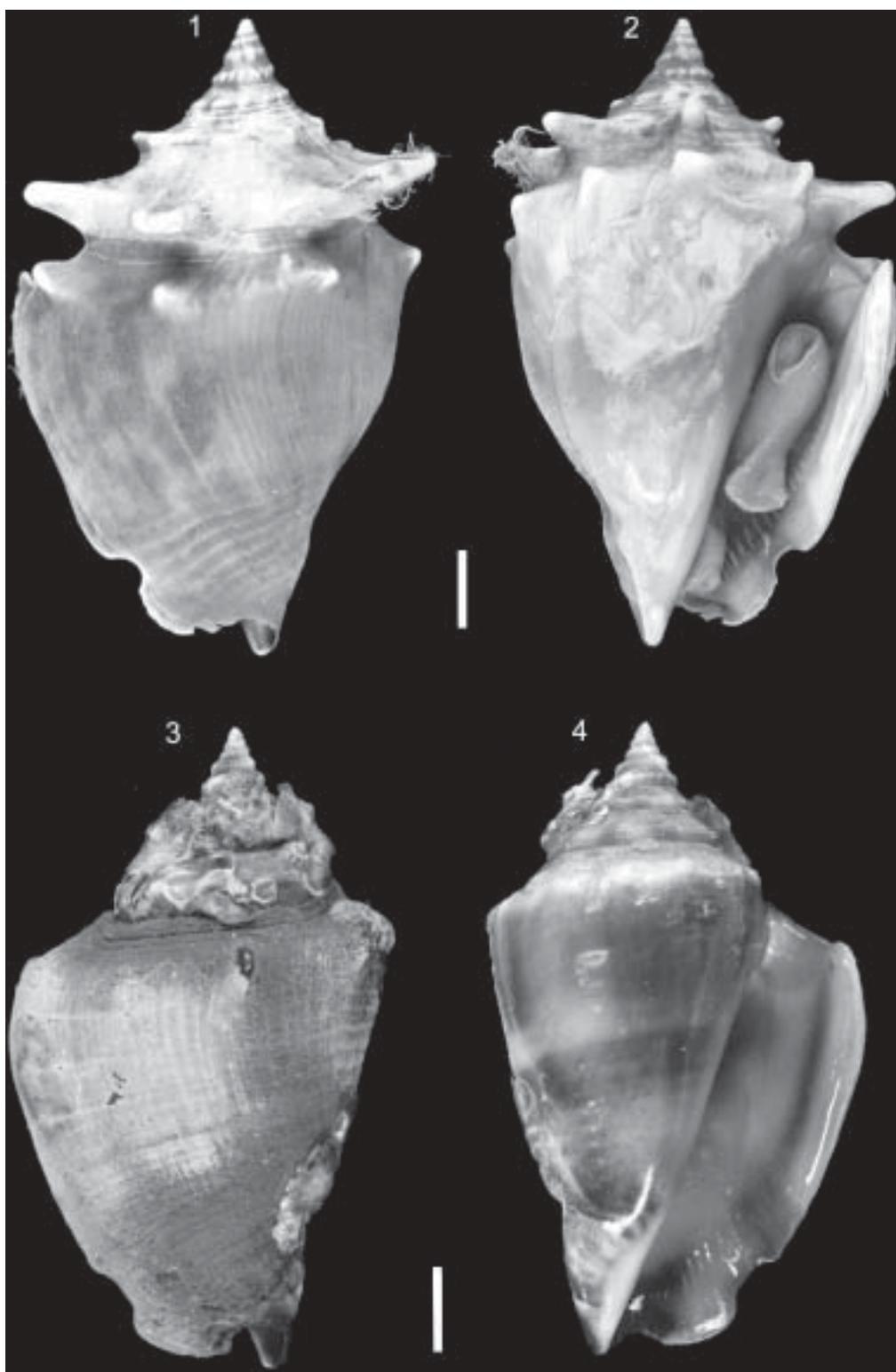
The Xenophoridae is represented in warm seas around the world by about 20 species, a taxon revised by Lambiotte (1979) and Ponder (1983). The latter paper presents a comprehensive historic account and comments of the systematic and morphological characters, including some anatomical data. The systematic relationships of the Xenophoridae have been problematic; they are included in the Stromboidea by some authors (e.g., Wenz, 1940; Walls, 1980), in the Calyptraeoidae (= Crepiduloidea) by others (e.g., Morton, 1958; Ponder, 1983), while others consider them in their own superfamily, Xenophoroidea (e.g., Boss, 1982).

As part of a project of comparative morphology and phylogenetic analysis of the Caenogastropoda superfamilies, 13 species were selected to represent the family Strombidae, 2 Australian species for Struthiolariidae, 3 northern Atlantic species for Aporrhaidae and 3 species for Xenophoridae (2 from the Western Atlantic and 1 from Australia). The objectives were: 1) to establish the morphological species-level characters, looking for characters which could be useful for future systematic (mainly supra-specific) revisions; 2) to investigate anatomical characters, including and beyond the shell, testing their relevance in comparative and phylogenetic studies; and 3) most especially to understand the morphological ground plan of the superfamilies and to test their monophyly. Although this study is undoubtedly a step towards a phylogenetic classification for the stromboideans, a broader study on the phylogeny of the Stromboidea has been planned for the future.

Several examined species have been changed from their more commonly accepted genus, mainly based on the final phylogenetic analysis. However, the new generic allocations are mentioned in the whole paper, and the justifications are presented both in the description and phylogenetic sections.

MATERIAL AND METHODS

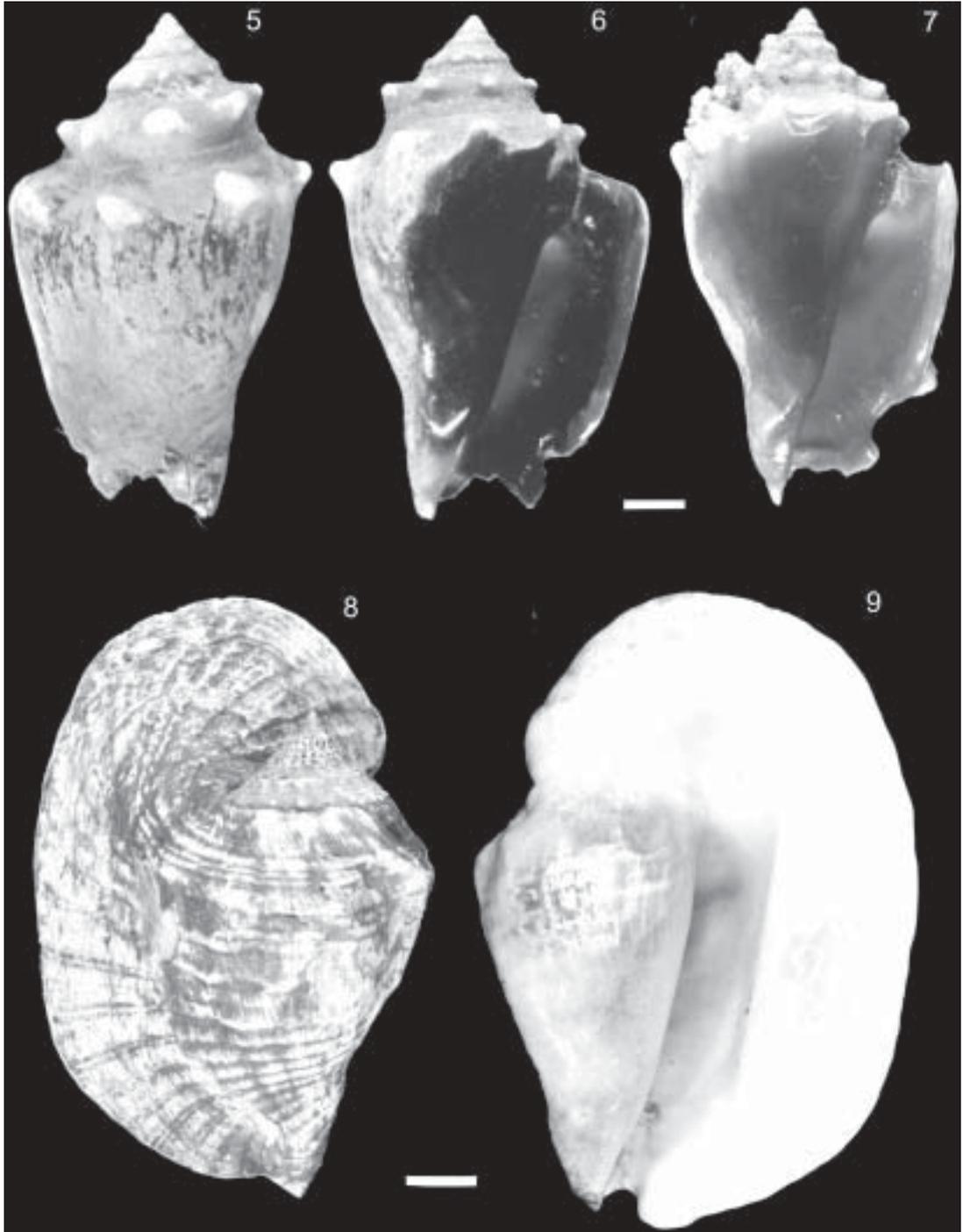
A list of specimens examined and dissected for each species follows each description. Most of the specimens belong to institutional collections (listed below), while others were collected especially for this study.



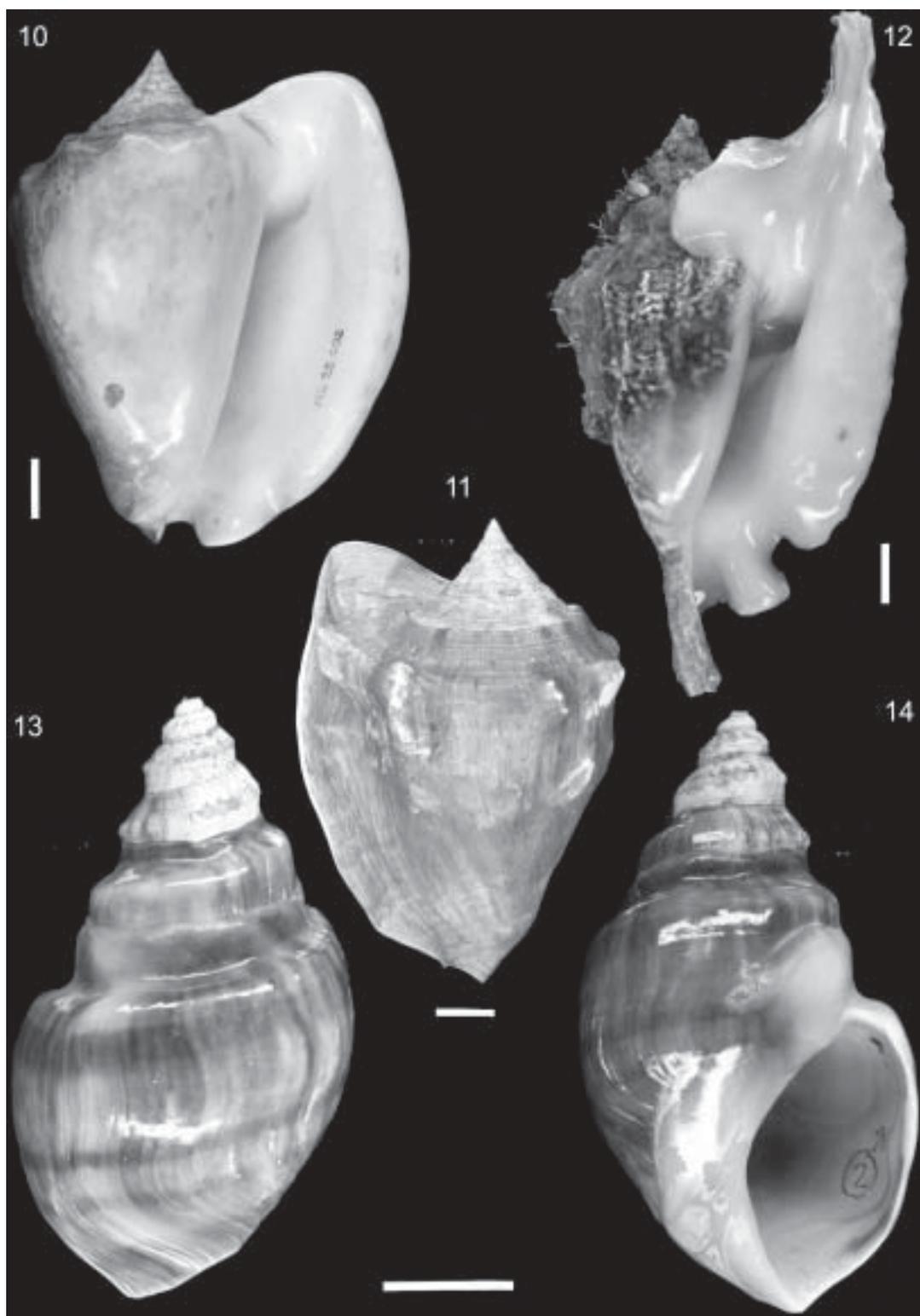
Figures 1-4. *Strombus pugilis* shell. 1-2. Dorsal and ventral views of a specimen of typical form, with subsutural spines well-developed (MZSP 28735, Ubatuba, SP); 3-4. Dorsal and ventral view of a specimen from Salvador, BA (MZSP 28477) without developed spines. Scales = 10 mm.

The specimens were dissected by standard techniques, with the specimens examined using a stereomicroscope. The material was immersed in

70% ethanol or 4% formalin. The fixative is necessary during the dissection, and not water, due the secretion of the hypobranchial gland. If a specimen



Figures 5-9. Shells. 5-6. *Strombus alatus*, dorsal and ventral views, specimen with the typical black pigment in aperture; 7. *S. alatus*, specimen with red pigment in aperture, similar to that of *S. pugilis* (see Figs. 3-4) (Sanibel Is., Florida, MZSP 28808), scale = 10 mm; 8-9. *E. goliath*, dorsal and ventral views (MZSP 25012, Pernambuco), scale = 40 mm.



Figures 10-14. Shells. 10-11. *Aliger costatus*, ventral and dorsal views (MZSP 25002, Pernambuco), scale = 20 mm; 12. *A. gallus*, ventral view (MZSP 28560, Salvador, BA), scale = 10 mm; 13-14. *Tylospira scutulata*, dorsal and ventral views (AMS 28627, Australia, despite the symbol, is a female), scale = 10 mm.

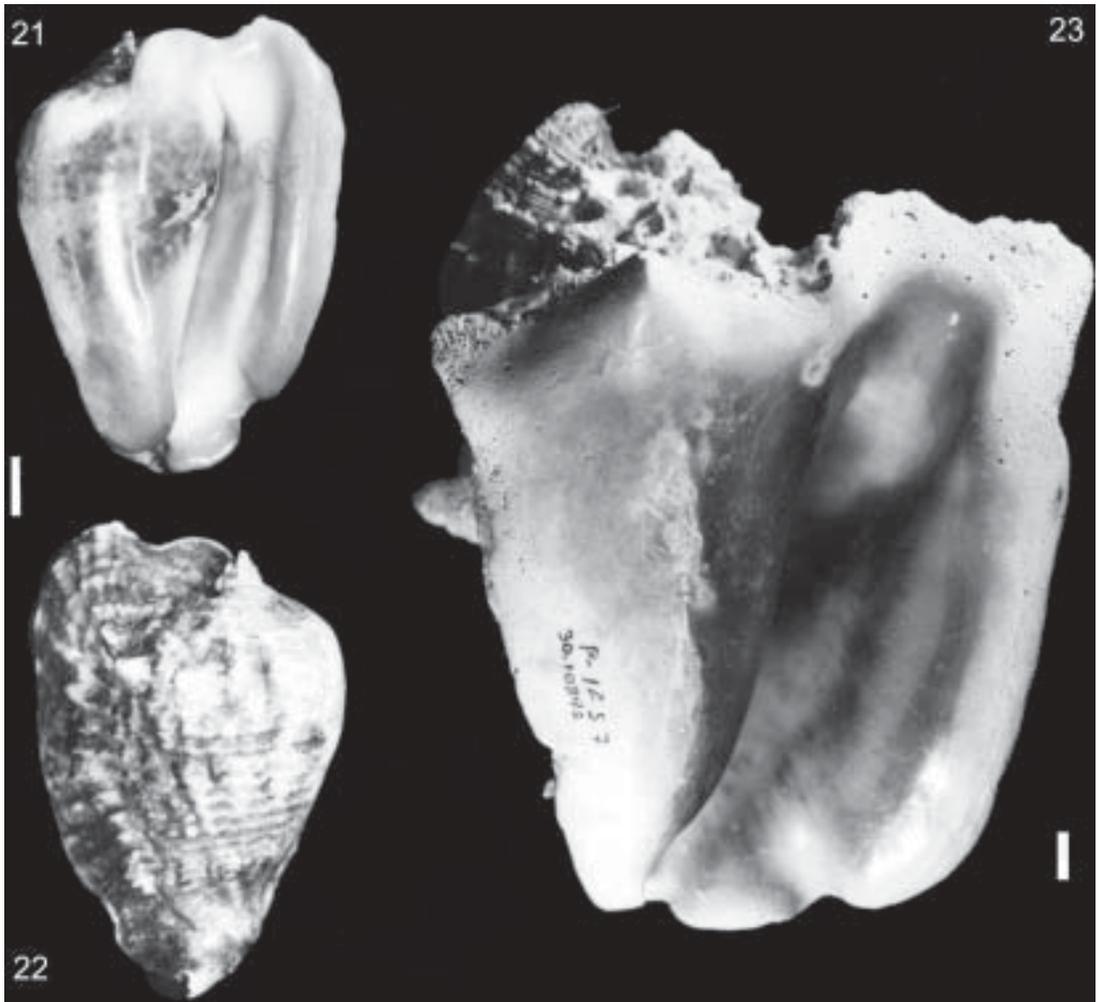


Figures 15-20. "Aporrhaid" shells. 15-16. *Cuphosolenus serresianus*, dorsal and ventral views (MNHN, CH128); 17-18. *Aporrhais pespelicani*, dorsal and ventral views (MZSP 28809, Scotland); 19-20. *A. occidentalis*, dorsal and ventral views (MNHN, Canada). Scales = 10 mm.

is immersed in water (even in long-fixed specimens), the mucus of the hypobranchial gland quickly expands and becomes a dense jelly mass, precluding the dissection. Some structures such as the anterior region of the digestive system and snout were processed by standard histological techniques; serial sections of 10 μm were produced, and stained with Mallory's triple strain. Radulae, jaws and opercula were also examined under Scanning Electron Microscopy (SEM) at the Laboratório de Microscopia Eletrônica do Instituto de Biociências da Universidade de São Paulo and in Museu de Zoologia da Universidade de São Paulo. All drawings were produced with the aid of a camera lucida.

The computer program "Tree Gardner 2.2" (Ramos, 1997), which basically works upon the

program "Hennig86" (Farris, 1988), was used for the final stage of the cladistic analysis. The outgroup method was used for the polarization of the character states. The outgroup choice is explained under discussion of the characters. Although most of the autapomorphies have been deleted from this analysis, those concerned to the ingroup are maintained, because the main concern of this paper is to establish the ground plan of the stromboideans, i.e., the set of synapomorphies, and consequently symplesiomorphies, which defines it (node #1). Some papers have following this approach (e.g., Pinna, 1996) and the retention of the ingroup autapomorphies has been proposed (Yeates, 1992). Some multistate characters are considered in an ordered (additive) optimization, this approach is



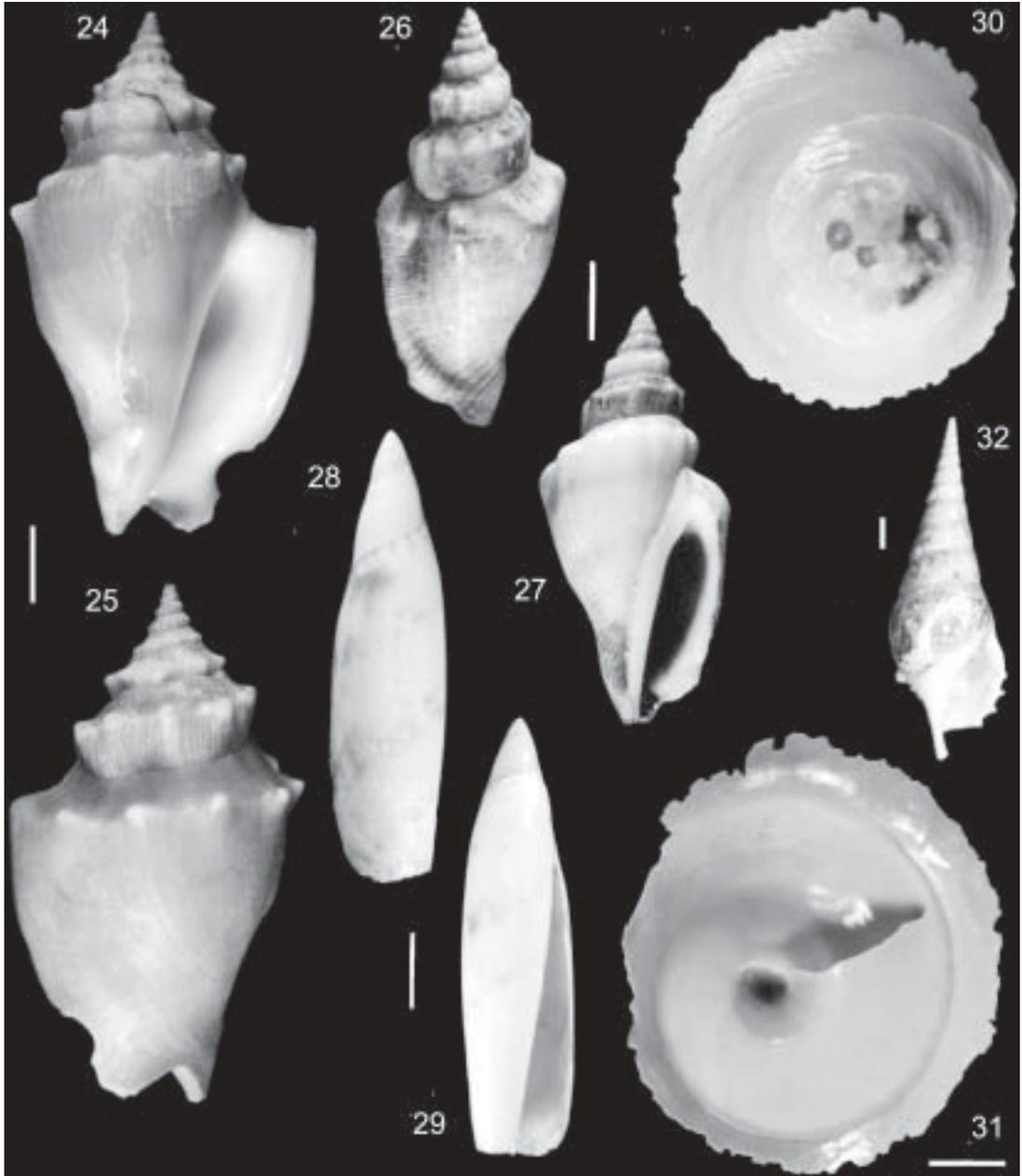
Figures 21-23 Shells. 21-22. *Tricornis raninus*, ventral and dorsal views (AMNH, Tahiti); 23. *Eustrombus gigas*, ventral view (UMML 30.10892, Jamaica). Scales = 10 mm.

mostly based on the ontogeny or in comparative method (Lipscomb, 1992; Wilkinson, 1992).

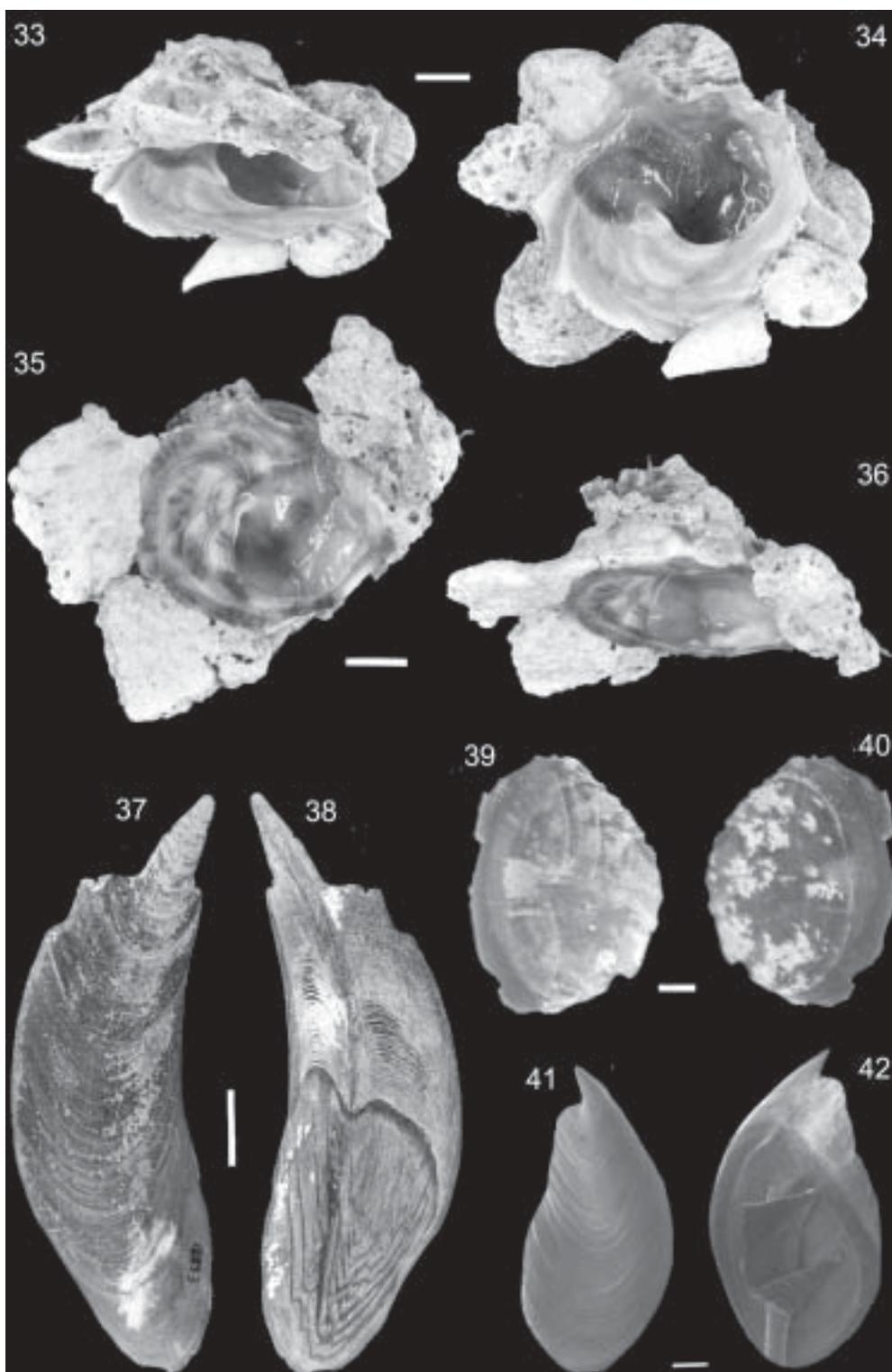
The selection of the outgroups was based on the traditional taxonomy, searching species of supposedly basal position among the Caenogastropoda.

Abbreviations in the figures: **aa**, anterior aorta; **ab**, anterior chamber of pallial oviduct; **ac**,

anterior extremity of ctenidial vein; **af**, afferent gill vessel; **ag**, albumen gland; **an**, anus; **ap**, aperture of pallial gonoducts; **at**, anterior projection of head-foot; **au**, auricle; **ba**, bursa copulatrix aperture; **bc**, bursa copulatrix; **bb**, bulged region of subradular membrane; **bg**, buccal ganglion; **bm**, buccal mass; **bo**, buccal ganglion connective; **bp**, brood pouch;



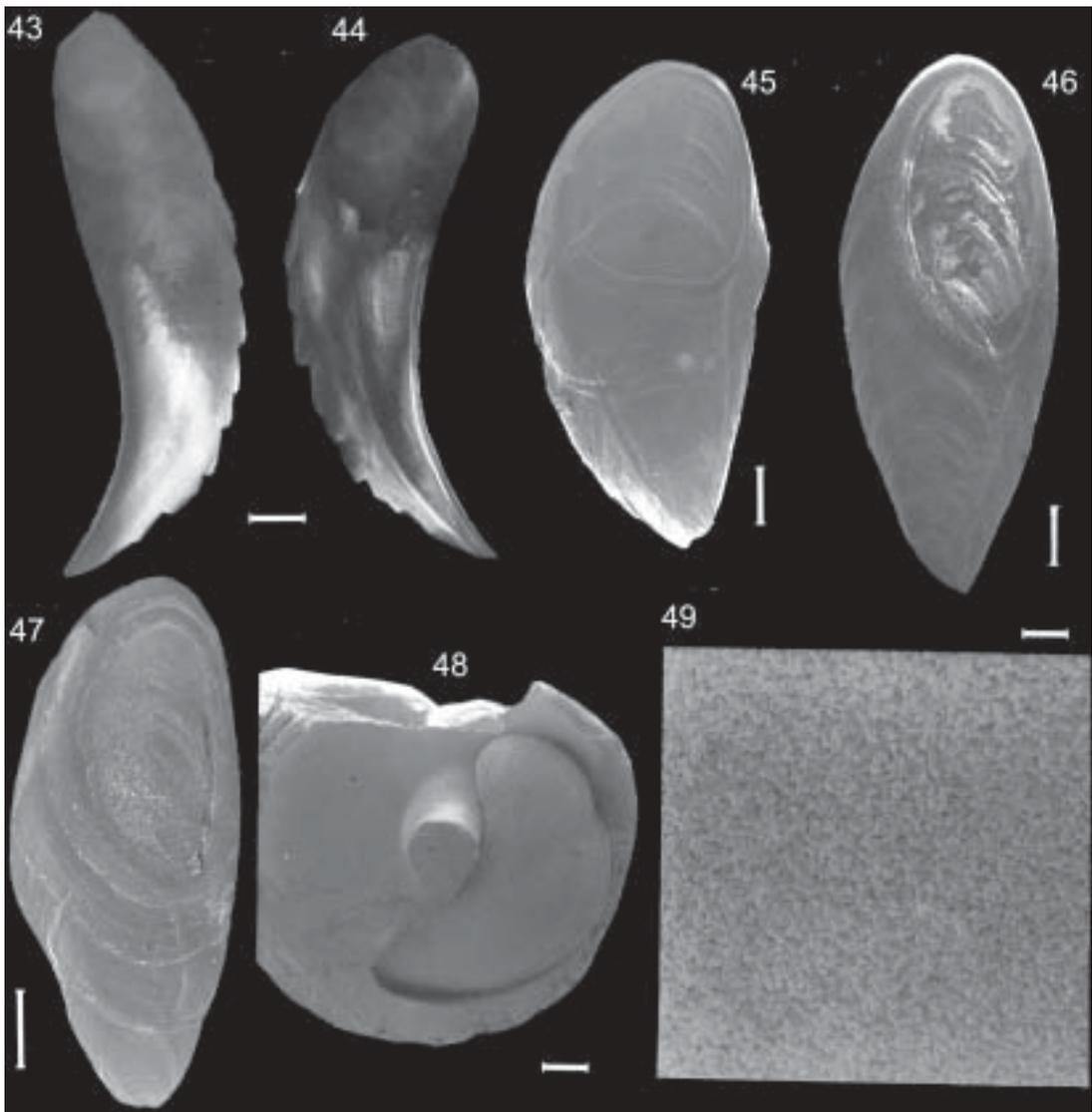
Figures 24-32 Shells. 24-25. *Strombus gracilior*, ventral and dorsal views (AMNH, Panama); 26-27. *Canarium urceus*, dorsal and ventral views (AMS, Australia); 28-29. *Terebellum terebellum*, dorsal and ventral views (AMS, Australia); 30-31. *Onustus indicus*, dorsal and ventral views (AMS, Australia); 32. *Tibia insulaechorab*, ventral view (AMNH, Pakistan). Scales = 10 mm.



Figures 33-42. Shells and opercula. 33-34. *Xenophora conchyliophora*, lateral and ventral views (UFRJ 7768, Espirito Santo, Brazil), scale = 10 mm; 35-36. Same species, ventral and frontal views (USNM 857859, Belize), scale = 10 mm; 37-38. *Strombus goliath*, operculum, outer and inner views, scale = 10 mm; 39-40. *X. conchyliophora*, operculum, inner and outer views, scale = 2 mm; 41-42. *Tylospira scutulata*, operculum (SEM), external and internal views, scale = 1 mm.

br, subradular membrane; **bs**, blood sinus; **bt**, buccal (oral) tube; **ca**, capsule gland aperture; **ce**, cerebral ganglion; **cf**, circular muscle fibers; **cg**, capsule gland; **ci**, circular muscle fibers; **cm**, columellar muscle; **cv**, ctenidial vein; **dc**, dorsal chamber of buccal mass; **dd**, duct to digestive gland; **df**, dorsal fold of buccal mass; **dg**, digestive gland; **ef**, esophageal folds; **eg**, sub-esophageal ganglion; **en**, endostyle; **es**, esophagus; **et**, esophageal typhlosole; **ff**, foot lateral furrow; **fg**, food groove; **fo**, female right furrow in head-foot; **fp**, female pore; **fs**, region ho-

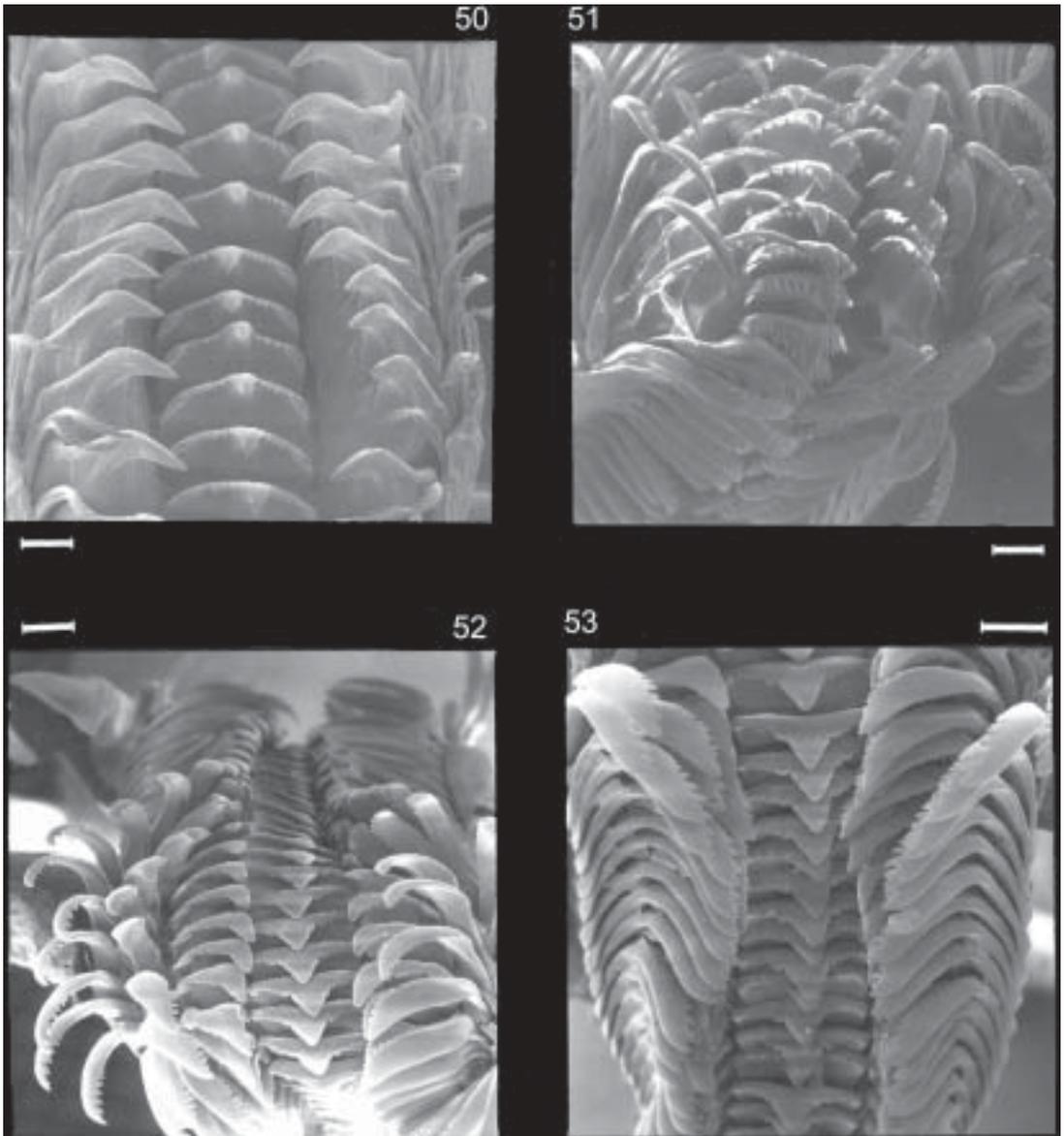
mologous to foot sole; **ft**, foot; **gf**, gastric fold; **gi**, gill; **gp**, gono-pericardial duct; **gs**, gastric shield; **hg**, hypobranchial gland; **i3**, insertion of m3 in radular nucleus; **if**, inner fold of ctenidial vein; **ih**, inner ligament of radular sac in ventral surface of horizontal muscle; **il**, inner lamina of pallial gonoduct; **im**, insertion of mantle in head-foot; **in**, intestine; **io**, intestine origin; **ir**, insertion of m4 in tissue on radula ("to"); **is**, insertion of m5 in radular sac; **jw**, jaw; **kc**, kidney chamber; **kd**, dorsal lobe of kidney; **kl**; kidney intestinal loop; **km**, membrane be-



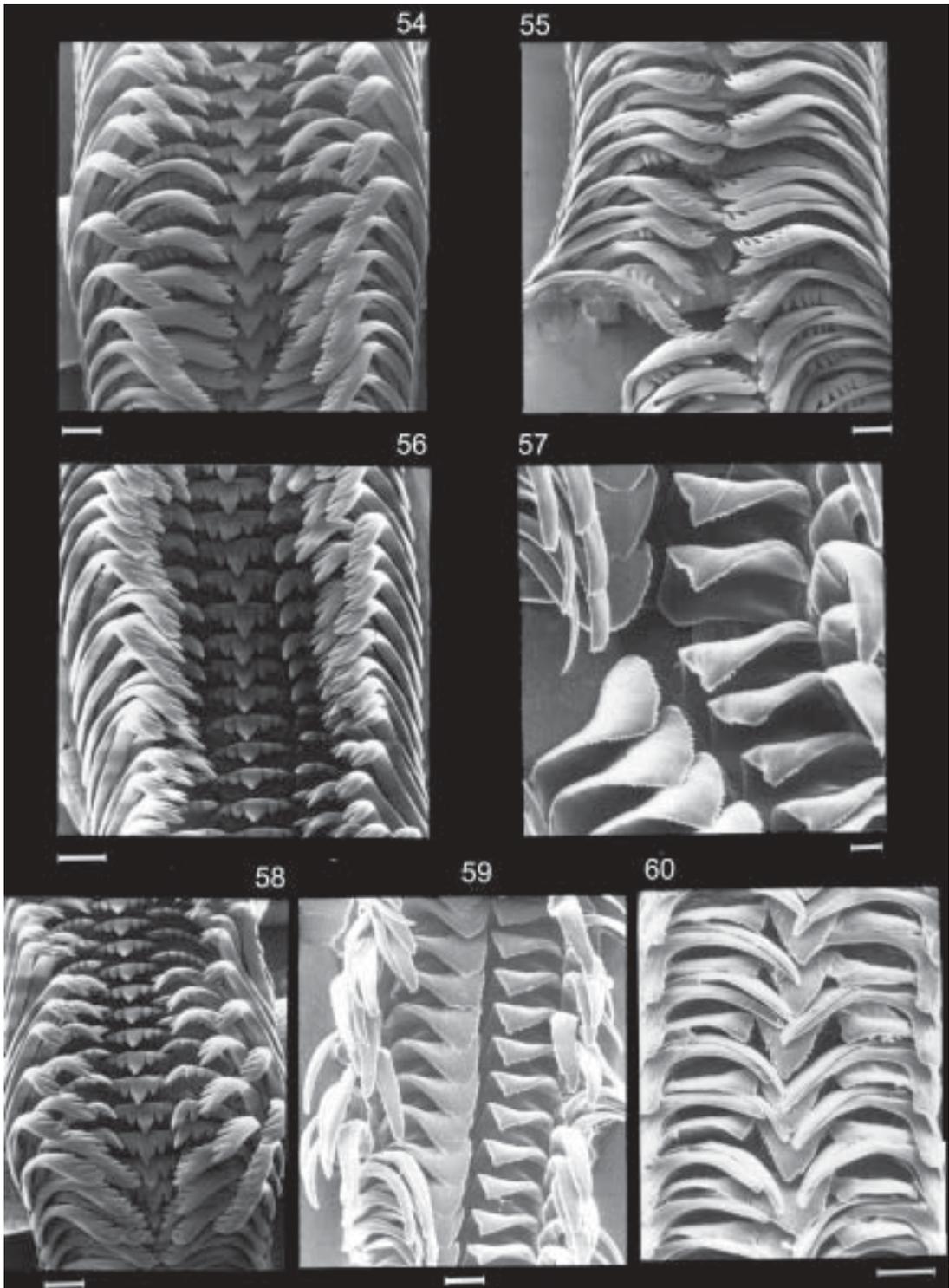
Figures 43-49. Opercula and shell (SEM). 43-44. *Strombus pugilis* operculum, outer and inner views, scale = 2 mm; 45. *Cuphosolenus serresianus* operculum, inner views, Scale = 0.5 mm; 46. *Aporrhais occidentalis* operculum, inner view, scale = 1 mm; 47. *A. pespelicani* operculum, inner view, scale = 1 mm; 48. *A. pespelicani*, fragment of middle level of spire, apical view shown calcareous septum separating empty region of spire, scale = 0.5 mm; 49. Detail of fig. 48, showing texture of septum surface, scale = 10 μ m.

tween kidney and pallial cavity; **ks**, ventral folded lobe of kidney attached to intestine; **lf**, longitudinal muscle fibers; **m1** to **m13**, extrinsic and intrinsic odontophoric muscles; **ma**, mouth abductor muscle; **mb**, mantle border; **mc**, buccal sphincter; **me**, mesentery; **mf**, middle fold of pallial oviduct; **mj**, jaw muscles; **mo**, mouth; **nc**, nephridial gland central vessel; **ne**, nephrostome; **ng**, nephridial gland; **nr**, nerve ring; **nv** nerve; **oc**, odontophore cartilage; **od**, odontophore; **of**, oblique muscle fibers; **og**, osphradial ganglion; **ol**, outer lamina of pallial gonoduct; **om**, ommatophore; **op**, operculum; **os**,

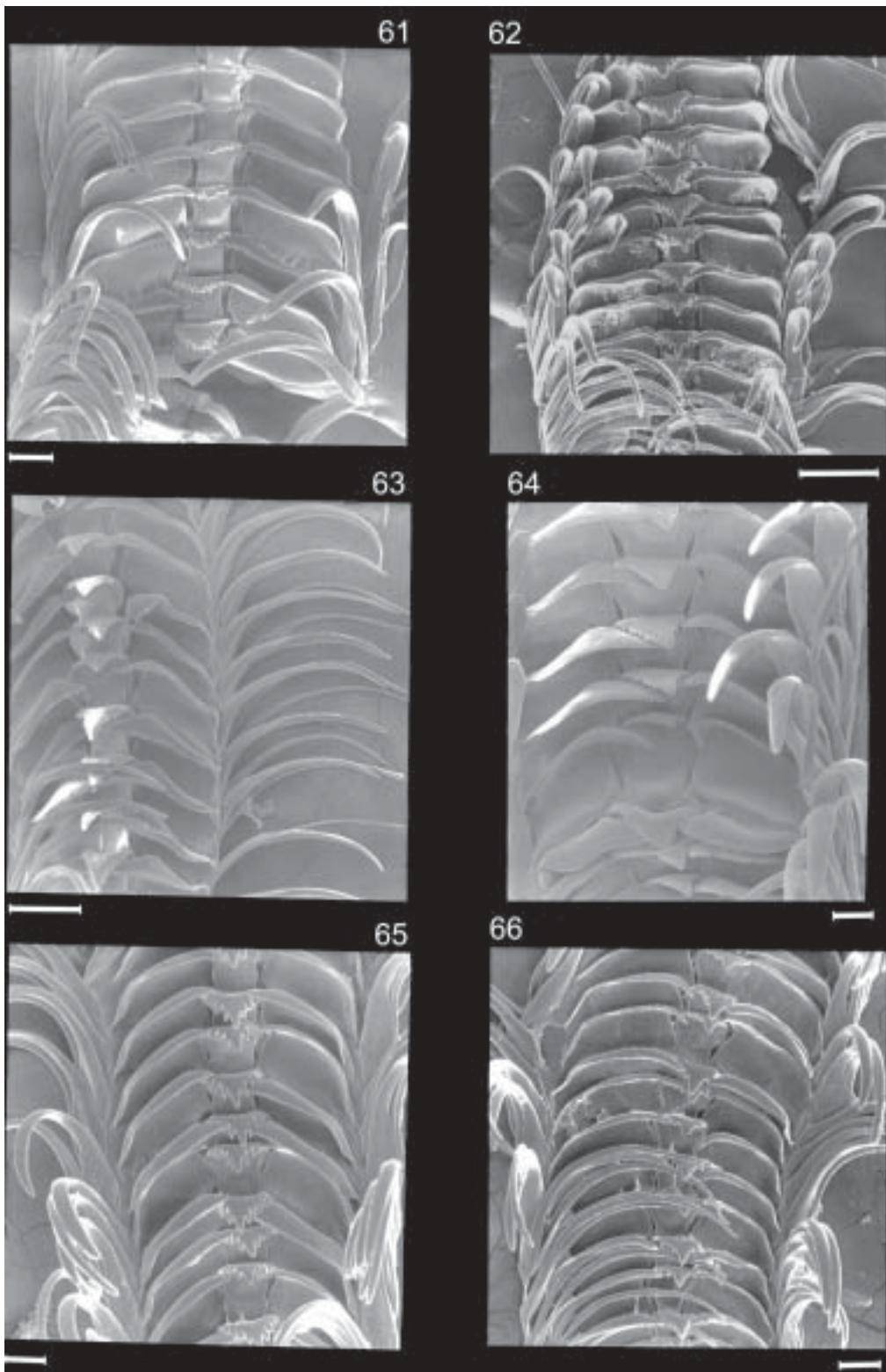
osphradium; **ot**, osphradium satellite fold; **ov**, oviduct; **oy**, ovary; **pa**, posterior aorta; **pc**, pericardium; **pd**, penis groove; **pe**, penis; **pg**, furrow of pedal glands in anterior foot projection; **ph**, penis distal folds; **pi**, penis outer folds; **pj**, penis projection; **pl**, penis longitudinal fold; **pn** pedal ganglion; **pp**, penis papilla; **ps**, pallial sperm groove; **pt**, prostate tissue; **pu**, pleural ganglion; **py**, pallial cavity; **ra**, radula; **rc**, seminal receptacle; **rm**, retractor muscle; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **sa**, style sac aperture; **sc**, subradular cartilage; **sd**, salivary duct; **se**, septum between esophagus and



Figures 50-53. Radulae (SEM). 50. *Strombus pugilis*, scale = 0.2 mm; 51. *S. alatus*, scale = 0.1 mm; 52-53. *E. goliath*, scales = 0.5 mm.



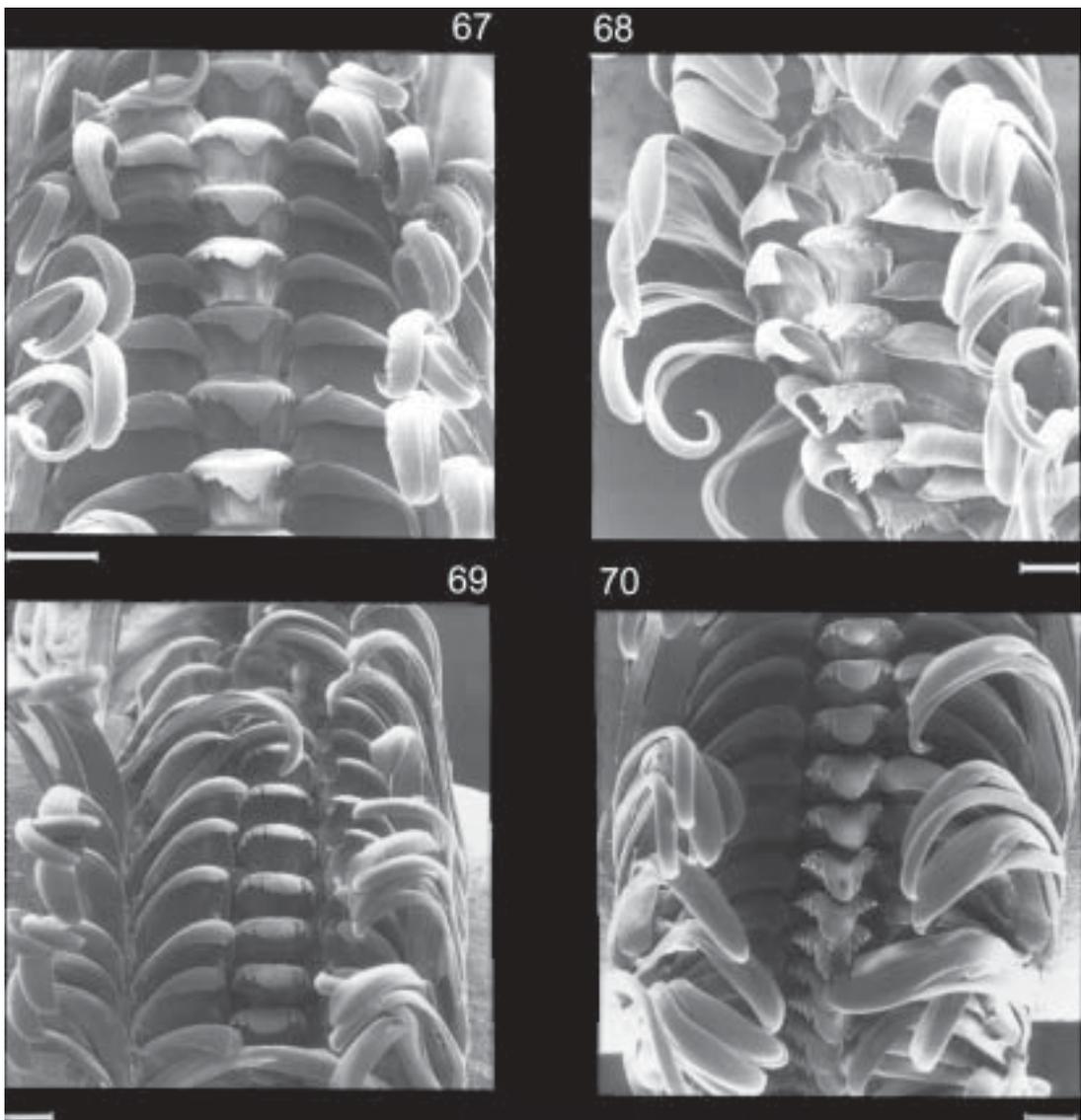
Figures 54-60. Radulae (SEM). 54-55. *Aliger costatus*, scales = 0.2 mm; 56. *A. gallus*, scale = 0.2 mm; 57. *Tylospira scutulata*, scale = 20 μ m; 58. *A. gallus*, scale = 0.2 mm; 59-60. *T. scutulata*, scales = 50 μ m.



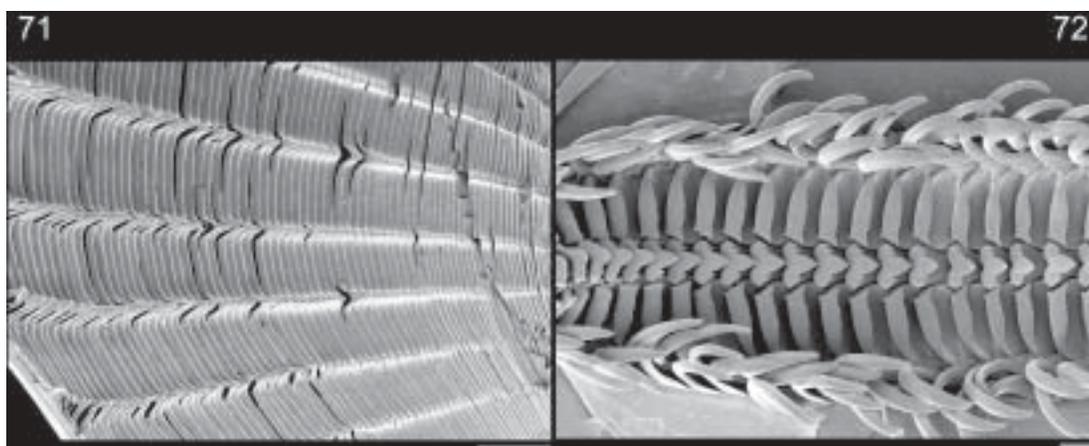
Figures 61-66. Radulae of *Aporrhais* spp (SEM). 61-62. *C. serresianus*, scales (61)= 50 μ m, (62)= 100 μ m; 63-64. *A. occidentalis*, scales (63)= 100 μ m, (64)= 50 μ m; 65-66. *A. pespelicani*, scales = 50 μ m.

odontophore in buccal mass; **sg**, salivary gland; **sh**, septum in posterior region of haemocoel; **sn**, snout; **so**, salivary orifice; **sp**, septum-like anterior region of gill; **ss**, style sac; **st**, stomach; **sv**, seminal vesicle; **sy**, statocyst; **te**, cephalic tentacle; **tg**, integument; **tm**, transversal muscles; **tn**, tentacular nerve; **to**, tissue on middle region of radula; **tp**, pallial tentacle; **ts**, testis; **va**, vaginal tube; **vd**, vas deferens; **ve**, ventricle; **vg**, vessel parallel to right margin of pallial cavity and generally within out lamina of pallial gonoduct; **vn**, secondary vessel of nephridial gland; **vs**, vesicles of pallial oviduct; **wo**, parasitic worm.

Abbreviations of institutions: **AMS**, Australian Museum, Sydney; **BMNH**, The Natural History Museum, London; **BMSM**, The Bailey-Matthews Shell Museum, Sanibel Island, Florida; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **MZSP**, Museu de Zoologia da Universidade de São Paulo, Brazil; **UMML**, Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C.



Figures 67-70. Radulae of xenophorids (SEM). 67-68. *Onustus caribaeus*, scales (67)= 200 μm , (68)= 100 μm ; 69-70. *Xenophora conchyliophora*, (69) UFRJ specimen, (70)= USNM specimen, scales = 100 μm .



Figures 71-72. *Onustus indicus* (SEM). 71. Operculum, detail of outer surface, middle region, scale = 1 mm; 72. Radular teeth, scale = 0.2 mm.

Systematics

Family STROMBIDAE

Genus *Strombus* Linné, 1758

(type species: *S. pugilis* Linné, 1758)

Strombus pugilis Linné, 1758

(Figs. 1-4, 43, 44, 50, 73-96)

Synonymy see Matthews, 1980:56-58. Complement:

Strombus pugilis: Melo, 1964:152; Dodge, 1956:258-262; Brownell, 1977:668-679 (figs. 3, 4-1,4); Walls, 1980:76 (figs.); Abbott & Dance, 1982:77 (fig.) Oliveira *et al.*, 1981:114; Alcolado, 1983:9; Rios, 1985:61 (pl. 22, fig. 272); Suttly, 1986:121 (fig. 135); Jong & Coomans, 1988:63; Sanders, 1990:63-65; Moraes *et al.*, 1992:779-784; Geary *et al.*, 1992:77-84; Reed, 1992a:227; 1992b:228; 1992c:229; 1993a:71-75 (figs. 3-4); 1993b:77-79; Petuch, 1993:53-54 (fig. 4); Rios, 1994:68 (pl. 23, fig. 260); Merlano & Hegedus, 1994:158 (pl. 49, fig. 575); Reed, 1995a:117-121; Abbott & Morris, 1995:185 (pl. 50).

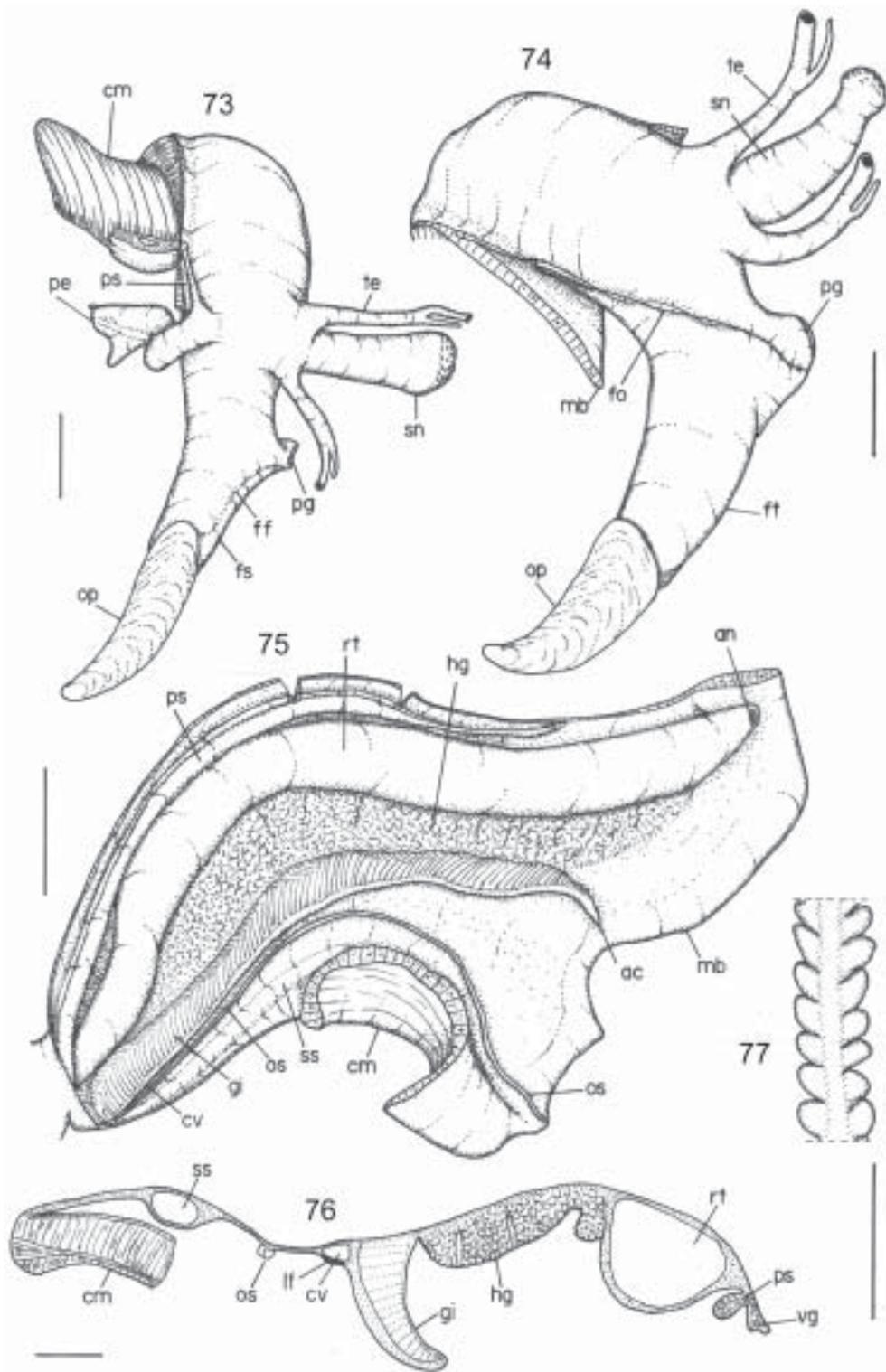
Strombus pugilis worki Petuch, 1993:51-53 (figs. 1-3).

Description

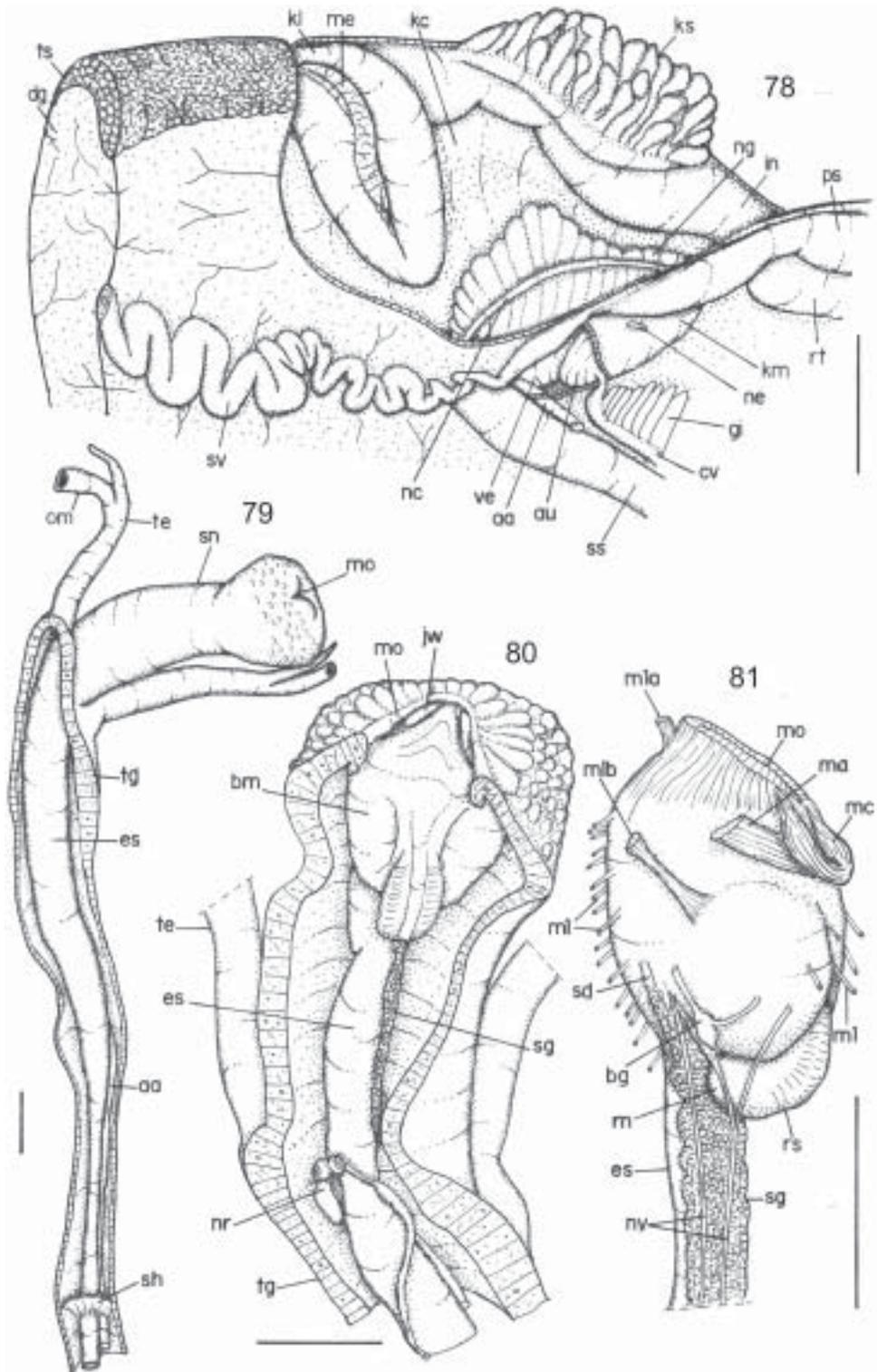
Shell (Figs. 1-4). Usual shell form with regular and robust subsutural spines (Figs. 1, 2), as described by Matthews (1980:58-62, figs. 1a-g).

Some variation occurs, inclusive in degree of spination, spines are lacking in some populations (Figs. 3, 4).

Head-foot (Figs. 73, 74, 79, 80). Color (life and preserved) homogeneously clear beige with some dark brown spots in exposed areas, with variable concentration among specimens. Head clearly demarked. Snout very long – about same length as foot, cylindrical, walls thick, muscular (Fig. 80), with bulging anterior extremity at tip of which mouth opens (Figs. 79, 80). Snout walls with outer thin layer of oblique muscular fibers; intermediate very thick layer of longitudinal fibers; inner thick layer of circular fibers, with only narrow space for esophagus (Fig. 80). Snout anterior region with broader cavity filled by odontophore. Snout capable of contract and shortening, but not to invaginate as a proboscis. Peri-oral region of snout with several, broad, low papillae. Tentacles very long – little longer than snout, stubby, walls thickly and muscular; base somewhat flattened, covering lateral and part of ventral and dorsal regions of base of snout; cylindrical more distally; bifurcate near tip, ommatophore as broader, cylindrical and dorsal branch; remaining tentacle as shorter, narrower, tapered, ventral branch. Ommatophore tip flattened. Eye dark, very complex, lens and retina separated by fluid; iris colorful. Foot slightly narrowed, cylindrical, without crawling sole; transverse flattened projection in antero-ventral foot region (propodium) at some distance from base of snout, in its distal margin central furrow of pedal glands; from this projection run pair of shallow, longitudinal furrows, one on each side to opercular pad.



Figures 73-77. *Strombus pugilis* anatomy. 73. head-foot of male, dorsal view, mantle and visceral mass removed; 74. Same for female, columellar muscle not shown; 75. pallial cavity, ventral-inner view; 76. pallial cavity roof, transversal section in its middle region; 77. Osphradium, detail of its middle region, ventral view. Scales: 73-75 = 10 mm, 76 = 2 mm, 77 = 0.5 mm.



Figures 78-81. *Strombus pugilis* anatomy. 78. part of anterior region of visceral mass and posterior region of pallial cavity, ventral view, kidney opened longitudinally and its ventral lobe (ks) deflected, pericardium also partially opened; 79. head and haemocoel, ventral view, foot and columellar muscle removed; 80. snout opened longitudinally in its ventral median line, ventral view; 81. buccal mass, lateral-right view. Scales: 5 mm.

Males with penis inserted in lateral-right region (Fig. 73), near right insertion of mantle border. Females with furrow running from right side of aperture of pallial oviduct to near right margin of propodium (Fig. 74) (male and female structures described below). Columellar muscle greatly developed, very thickly and muscular, very broad, of about 1.5 whorls; haemocoel narrow, running along columellar muscle center. Thin muscular septum, diaphragm-like, located in posterior third part of haemocoel, separating it into two cavities.

Operculum (Figs. 43, 44, 73, 74). Corneus, long, unguiculate, nucleus terminal, occupying small part of aperture, inserting terminally in foot. Outer surface concentrically undulated. Inner scar terminal, from which two inner folds, as reinforcements, running longitudinally to nucleus. About 2/3 of operculum projected beyond opercular pad. Outer margin with about 9 small, spine-like, uniform projections. Foot opercular pad attaching very firmly to operculum contouring folds.

Mantle organs (Figs. 75-78). Mantle border wide, thickly muscular (mainly in siphonal region), color pale cream. Mantle cavity large and somewhat deep – about equal to total body whorl. Osphradium narrow, long, bipectinate (Fig. 77); anterior extremity closing to mantle border in middle-left region of siphon; after running obliquely towards posterior-right, approaching from middle of gill (Fig. 75); posterior third of osphradium very narrow, but still bipectinate. Osphradium leaflets very small (only seen at higher magnifications), slightly thick, alternate (Fig. 77). Osphradium posterior end at about same level as that of gill. Gill narrow, very long – about same length as pallial cavity (Fig. 75). Gill anterior extremity near mantle border, with short, broad, septum-like anterior region with leaflets lacking (Fig. 75:ac); leaflets beginning gradually at some distance from anterior extremity; gill leaflets triangular, tall, curved to right, base somewhat narrow, tapering gradually to rounded tip (Fig. 76). Ctenidial vein narrow, with somewhat uniform width along its length, connecting with auricle just posterior to gill. Conspicuous muscle fibers running longitudinally on ventral surface of ctenidial vein all along its length (Fig. 76:lf); anterior extremity of those muscle fibers spreading in septum-like, anterior region of gill (ac). A proportional broad space (about three times width of gill base) between gill and rectum. Hypobranchial gland well developed, occupying almost en-

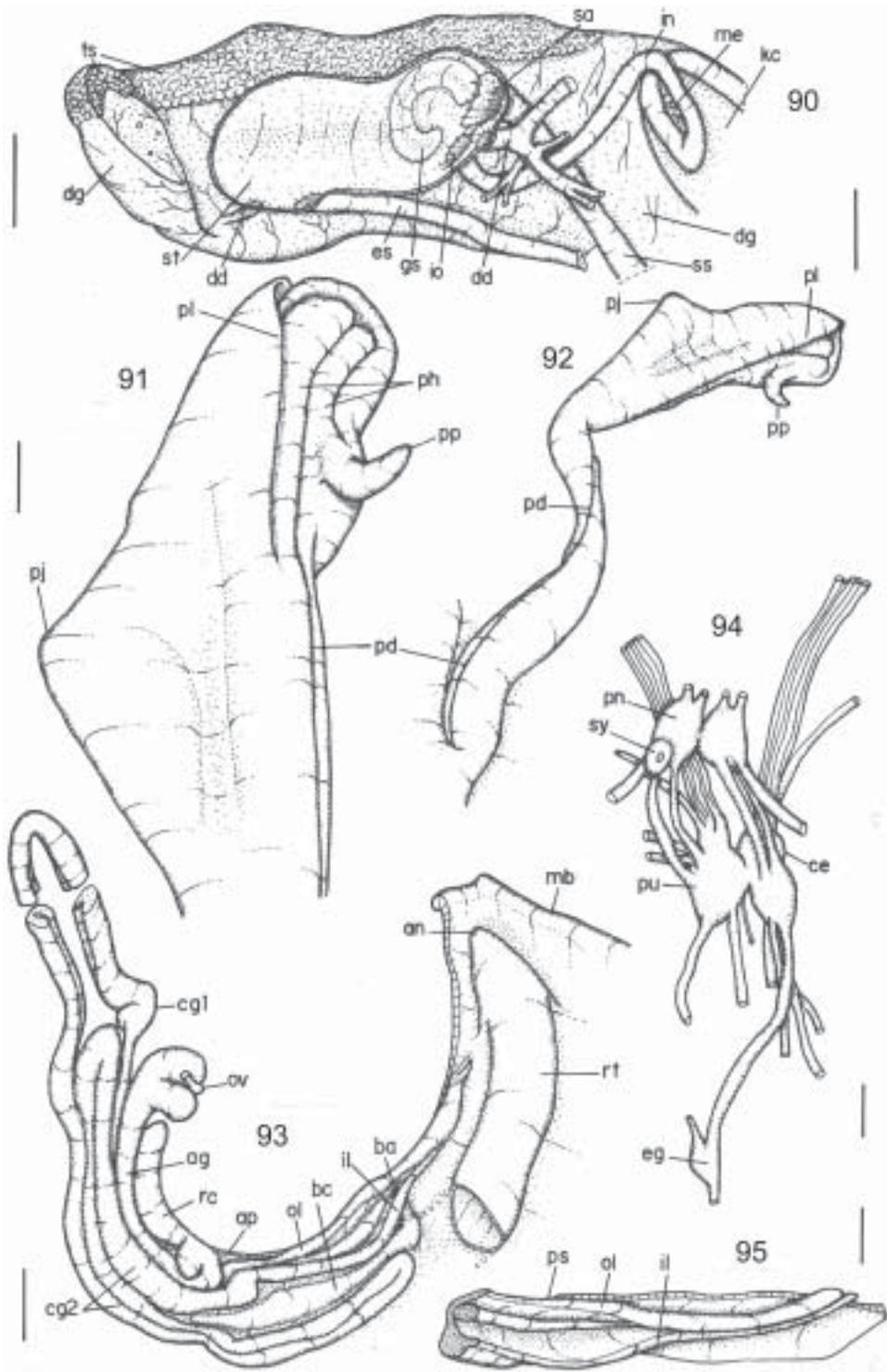
tire space between gill and rectum, with thick glandular tissue, sometimes folded on surface, with small mucus chambers (Fig. 76). Rectum long and broad, normally filled with elliptical fecal pellets made up largely of gravelly sediment. Anus siphoned, simple, close to right extremity of mantle border (Figs. 75, 93), with several inner terminal papillae. Pallial gonoducts running in posterior 2/3 of pallial cavity, between rectum and right margin of pallial cavity, as described below. Part of style sac running in pallial cavity, between osphradium and its left margin, finishing at some distance from siphon region (Figs. 75, 76).

Circulatory and excretory systems (Fig. 78). Heart of medium size, located just behind posterior end of gill, slightly dislocated anterior, with short portion of gill ventral to pericardium. Anterior surface of pericardium partially exposed in pallial cavity; part of dorsal surface connected to style sac; left surface attached to digestive gland and right surface to kidney. Auricle connection with ctenidial vein not terminal, but slightly anterior to ctenidial vein posterior end. Kidney occupying most of posterior limit of pallial cavity and about half a whorl posterior to it, slightly triangular, amply hollow. Intestine crossing renal right-dorsal margin, also presenting ample loop in region of entrance to kidney chamber; this loop remaining free within kidney chamber, but connected at its inner surface by mesentery. Dorsal surface of kidney chamber uniform, velvet-like, apparently without glandular tissue. Right-ventral lobe of kidney somewhat large, its right margin smooth, attached to rectum and covering part of it; other regions of this lobe with mosaic of tall, irregular, broad folds, close to one another. Nephridial gland large, broad, thickly glandular; covering left-dorsal margin of kidney chamber along its limit with pericardium; presenting longitudinal, central vessel, and successive transversal, pinned lobes connected to this vessel; this longitudinal vessel inserting like a septum in wall between kidney and pallial cavity, dorsal and to right of nephrostome. Nephrostome a slit in middle region of membrane between kidney and pallial cavity; its immediately posterior region a chamber part delimited by septum-like region of nephridial gland vessel.

Digestive system. Mouth in central region of snout tip (Fig. 79). Buccal mass spherical, large, just posterior to mouth (Fig. 80); occupying 1/4-1/3

of snout length. Dorsal wall of buccal mass thickly muscular, its inner surface with pair of well-developed jaws (Figs. 82, 83); each jaw plate elliptical, with rounded median and anterior cutting edge, color orange. From jaws, pair of broad, thick, longitudinal folds begins; each fold running medially covering shallow, dorsal chamber with inner surface covered by several low, longitudinal folds. A septum or valve-like flap separating esophagus and odontophore. Buccal or peri-oral muscles (Figs. 80-89) mostly very strong: **m1**) jugal muscles, several small muscles spread by buccal mass outer surface, connecting it to adjacent inner surface of snout, more concentrated near median line, ventral and dorsally; **mj**) protractor muscle of buccal mass and jaw muscles, originating in lateral and dorsal surface of mouth, inserting in lateral and dorsal regions of buccal mass, mainly in odontophore; **m1a**) concentration of jugal muscles in middle-anterior region of protractor muscle, connecting it to dorsal-anterior extremity of snout inner surface; **m1b**) pair of lateral-dorsal dilator jugal muscles, long, flattened, originating in anterior, dorsal, inner surface of snout, inserting in lateral, slightly dorsal surface of buccal mass; **mc**) mouth sphincter, circular fibers of ventral-anterior surface of buccal mass, internal to mj, except in its ventral region; **ma**) pair of mouth abductors, short, thick, broad, originating near median line in ventral region of mouth, inserting in lateral-inner surface of snout anterior extremity. Odontophore muscles and structures: **m3**) thin layer of muscular fibers, originating in each side of odontophore near mj inserting, covering most of odontophore lateral surface (on m4), both sides of this muscle connect with each other between radular nucleus and odontophore, producing muscular "bridge" covering middle region of radular ribbon; thin membrane attached to m3 also connecting to radular sac and nucleus; **to**) tissue covering middle region of radular ribbon preceding radular region exposed for use; **m4**) large and broad pair of dorsal tensors of radula, originating in posterior region of cartilages, surrounding ventral, lateral and dorsal surfaces of each cartilage (only free median cartilage surface and inserting of mj), inserting in subradular membrane and in lateral edge of "to"; **br**) subradular membrane, connecting to median edge of each m4 in its ventral, anterior and dorsal region, covering entire ventral surface of subradular cartilage and part of radular sac (in region crossing odontophore), bulg-

ing anteriorly as bulbous, hollow projection just anterior to radular end (**bb**); **m5**) pair of ventral tensor muscles of radula, short, broad, somewhat thick, originating in posterior surface of cartilages on m4 originating, covering median surface of cartilages and part of m4, inserting in ventral surface of radular ribbon approximately near level of m4 inserting; **m6**) horizontal muscle, very thick and broad, inserting in dorsal surface of both cartilages, with insertion fibers inter-digitating with fibers of mj inserting; **ih**) inner ligaments connecting inner-ventral-anterior surface of horizontal muscle (m6) with radular sac; **m7**) pair of narrow and long muscles, originating in median-dorsal margin of m4, running on subradular membrane towards anterior, penetrating among "ih" within radular sac; inserting like fan in posterior region of radular ribbon close to radular nucleus; **m10**) pair of ventral protractor muscles of odontophore, short and somewhat thin, originating in ventral-anterior region of snout inner surface, inserting in median-anterior region of m4; **m10a**) small pair similar to m10 but of more median originating; **m11**) pair of narrow and long median tensor muscles, originating in inner, bulged region of subradular membrane (**bb**), running anteriorly attached to it, contouring anterior surface of odontophore, inserting in inner surface of ventral snout wall near median line; **m12**) small pair of anterior tensor muscles, originating in odontophore cartilages, just anterior to "mj" insertion, running short distance towards external, inserting in subradular membrane just in its inserting on m4. Radula very short, little longer than odontophore length. Radula (Fig. 50): rachidian broad, central cusp large, sharp and tall, with about 1/5 of rachidian width, secondary cusps very small, vary from four to five pairs, lateral pair in apex of broad marginal thickness; lateral tooth tall, base broad, gradually and irregularly narrows until sharp tip curved medially; inner and outer marginal teeth similar with each other, tall, very slender, long, near tip from five to six pairs of long, pined cusps. Pair of buccal ganglion sited in esophagus originating, between it and posterior-dorsal region of odontophore and radular sac (Fig. 81), somewhat small but with proportional large branches; large connective unites both, crossing between radular nucleus and odontophore. Salivary glands cluster around esophagus as thin glandular layer (Figs. 80, 81), between layer of nerves (more external) and outer esophageal surface (more internal), more con-



Figures 90-95. *Strombus pugilis* anatomy. 90. visceral mass, anterior region, ventral view, ventral wall of stomach removed, anterior gastric structures seen if digestive gland was transparent; 91. penis, detail of apical region; 92. penis, whole view, base in right view; 93. pallial oviduct, kidney and adjacent rectum removed, part of anterior structures also shown; 94. central nervous system (nerve ring), ventral view; 95. detail of anterior extremity of pallial sperm groove, just before its passage to pallial floor, inner lamina (il) artificially deflected. Scales: 90-93 = 5 mm; 91, 95 = 2 mm; 94 = 1 mm.

centrated anteriorly near buccal mass; salivary glands anterior to nerve ring; their ducts visible only in anterior limit of salivary glands, in short distance penetrate in dorsal wall of buccal mass, running in base of local inner folds, open in middle surface of their anterior region.

Esophagus very long, broad, thin walled. Anterior esophagus with pair of typhlosoles, between then a smooth surface (Fig. 82). In remainder esophageal inner surface several low, longitudinal folds. In middle esophagus both typhlosoles gradually faint; posterior esophagus only with low, longitudinal, narrow folds. Stomach large, spacious, with about 3/4 whorl in length (Fig. 90), immerse in digestive gland except in some exposed areas of its dorsal and ventral surfaces. Esophagus inserts in stomach in middle-posterior region of its left

margin. Posterior duct to digestive gland narrow, located in esophageal insertion turned towards ventral and posterior. Stomach anterior margin with three apertures: right and broader aperture of style sac; middle-ventral, narrower aperture of anterior duct to digestive gland, which in short distance bifurcates successively and irregularly; right-dorsal aperture of intestine. Stomach inner surface with only ventral, elliptical fold in middle level of ventral-right gastric surface; remainder surface only uniform, smooth surface; gastric shield chitinous, transparent, surrounding dorsally, at some distance anterior gastric apertures. Style sac enormously long, running initially immerse in digestive gland dorsal to intestine (Fig. 90), crossing dorsal-left region of pericardium, at left of kidney chamber (Fig. 78) and lies by pallial cavity wall between

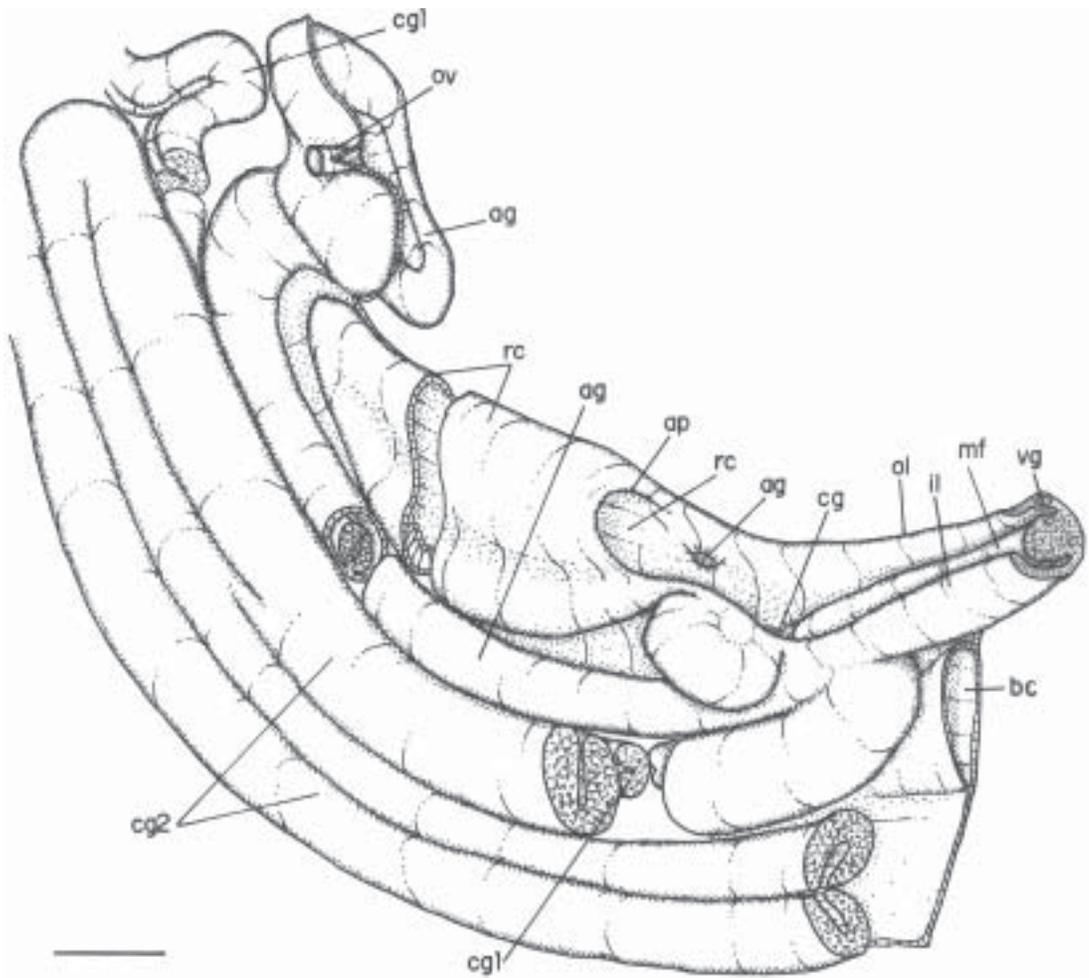


Figure 96. *Strombus pugilis* pallial oviduct, ventral view, anterior and posterior extremities not shown, some transverse sections artificially produced to show inner surfaces. Scale: 2 mm.

osphradium and left margin of this cavity until near siphon border (Figs. 75, 76). Intestine running initially immerse in digestive gland, crossing from left to right side between style sac and duct to digestive gland until posterior-right border of kidney (Fig. 90), free loop present within kidney chamber, connected internally by mesentery membrane (Figs. 78, 90), after running at right marginal to kidney and pallial cavity as above described.

Genital system. Male. Testis lies right surface of digestive gland from almost its posterior region to region close to kidney (Figs. 78, 90). Visceral vas deferens running close to columella, in middle-ventral surface of visceral mass; half whorl before pericardium become very thick walled and convolute, as differentiable seminal vesicle (Fig. 78); near pericardium gradually narrows and becomes almost straight, crossing from middle to right region where exits to pallial cavity. Pallial vas deferens – or prostate – long and narrow (Fig. 75), an opened spermatic groove. Outer lamina of spermatic groove thin, glandular, attached to inner surface of mantle, followed by well-developed mantle vessel (Fig. 76). Inner lamina of sperm groove as tall fold, thick glandular, rounded free margin. In middle region of pallial sperm groove a median, longitudinal fold appears. In about middle region of anterior third part of pallial cavity left margin, pallial sperm groove narrows, middle fold finishes, its laminae become somewhat symmetric (Fig. 95), and crosses to pallial floor, running slight short distance until penis base (Figs. 73, 92). Penis long and with somewhat complex tip (Figs. 91, 92). Sperm groove running in deep and narrow furrow until tip median border, where bifurcates in “Y” shape, its left branch joints with shallow cavity let by longitudinal flap which covers partially penis tip; right branch of sperm groove returns in proximal direction, finishes in base of somewhat long, cylindrical papilla. In approximately opposite side of papilla, but weakly more proximal, triangular, flattened expansion (pj).

Female (Figs. 93, 96). Ovary and visceral oviduct similar in site to equivalent structures of male. Visceral oviduct thin walled and narrow, inserts in very complex pallial oviduct in right-posterior limit of pallial cavity. In this region, narrow gonopericardial duct also present. Albumen gland, as continuation of oviduct, beige, long, with length about half of total pallial oviduct length; its initial region presents two loops of glandular tissue, run-

ning as duct attached to mantle, section circular, thick walled; pair of large, central folds, thick glandular, running close to one another connected to narrow base; aperture of albumen gland simple, in front of that of seminal receptacle. Albumen gland still has loop immerse in inner lamina close to its aperture. Seminal receptacle as large and flattened sac, smooth internally, walls glandular, somewhat thin, length about 1/4 of total pallial oviduct length; limited at right by pallial cavity and at left by albumen gland; aperture anterior, slight ample. Capsule gland very long and complex, beginning just anterior to albumen gland aperture, after runs dorsal and posteriorly until dorsal surface of kidney, returns anteriorly running dorsal to rectum, before anterior third of pallial cavity suddenly returns towards posterior in dorsal-right margin of rectum; in end of pallial cavity newly towards anterior, running between its preceding loop and albumen gland, and ventral to its first loop; near middle region of pallial oviduct suddenly towards right and open just anterior to its origin; capsule gland most “U” in section, thick walled, clear cream to white in color; its duct generally turned in direction to its neighbor loop. Pallial oviduct, after capsule gland, becomes thick walled groove, with inner and outer laminae covering partially median, broad, glandular fold (mf). Well-developed vessel running between outer lamina of pallial oviduct and mantle all along its length. Bursa copulatrix large and broad, between final branch of pallial oviduct and anterior loop of albumen gland; bursa aperture just anterior to end of median fold (fig. 93:ba). Before anterior third of pallial cavity, pallial oviduct (groove) narrows, crossing to floor of pallial cavity, in short distance becomes single, shallow furrow protected by thin flap. This groove running towards anterior and ventral at right of head (Fig. 74); becomes deep and suddenly finished near foot anterior expansion in aperture of pedal glands. In lot MZSP 28477 all examined females present vestigial penis in middle region of head groove, phenomenon very rare in other samples. On development see Brownell (1977).

Nervous system (Fig. 94). Circum-esophageal ganglia as typical for caenogastropods, of epiathroid type, located posteriorly on esophagus, far from buccal mass, just posterior to snout base. Short sub-esophageal connective. About seven parallel pairs of nerves emerging from cerebral-pleural ganglia and running anteriorly, initially close to

each other in about same plane, enervating snout and buccal mass structures. Statocyst with single statolith. Pair of ophthalmic nerves very large, running from cerebral ganglia to tentacles.

Measurements of shells (in mm). MZSP 28477: 75.8 by 47.0; MZSP 16040, ♂ 1, 78.7 by 51.7; ♀ 2, 81.6 by 58.0.

Distribution. From Florida, USA, to Santa Catarina, Brazil.

Habitat. In muddy or sandy-mud substrata, from intertidal zone to about 5 m depth.

Material examined. BRAZIL. **Bahia;** Salvador; Ribeira beach, 3-5 m depth, 5♂, 5♀, MZSP 28477 (fishermen & Simone col., 24-27/ii/1977); Itaparica, Frade Island, MZSP 30138, 1♂ (P.S. Souza Jr. Col., 10/iv/1999). **São Paulo;** Ubatuba; off Ubatuba, 55 specimens, MZSP 28718 (IOUSP, otter trawl); Enseada das Palmas, 1♀, MZSP 25046 (IOUSP, 3/vii/1962); Flamengo beach, 1♀, MZSP 25045 (IOUSP, 23/x/1961); São Sebastião, Capim Gordo de Dentro beach, 1♀, MZSP 16040 (Pe. C. Valle col., ii/1965); Barequeçaba, 1♀ observed alive, MZSP 28716 (Simone col., 17/vii/1996); Bertioga, 2♂, 6♀, MZSP 28669 (Simone col., vii/1977); Ilha Bela; Perequê beach, 1♀, MZSP 28719 (Simone col., 5/vi/1993). **Santa Catarina;** Porto Belo, 20 specimens, MZSP 28717 (Matthews col., iv/1976).

Strombus alatus Gmelin, 1790
(Figs. 5-7, 51, 97-106)

Synonymy see Clench & Abbott (1941). Complement:

Strombus alatus: Walls, 1980:73 (Figs); Abbott & Dance, 1982:77 (fig.); Oliveira *et al.*, 1981:115; Alcolado: 1983:9; Moscatelli, 1987:42 (Figs. 15-16); Hargreave, 1995:48 (pl.4, Figs. 1-3); Merlano & Hegedus, 1994:158; Abbott & Morris, 1995:183: (pls. 8, 50).

Strombus pugilis alatus: Olsson & Harbison, 1953:273 (pl. 34, Figs. 7, 7a); Rios, 1985:61; 1994:68.

Description

Shell (Figs. 5-7). Very similar to that of preceding species, except for less developed subsutural spines and darker colored inner surface of aperture. Some specimens hardly separated from some forms of *S. pugilis* (Fig. 7). See more comments in the discussion after this Description

Head-foot and operculum (Fig. 97). Very similar to those of preceding species, included papillate anterior region of snout around mouth. Only two differences observed: darker color of exposed areas (some regions even black) and male with shorter penis.

Mantle organs (Figs. 98, 99). Very similar to those described for *S. pugilis*. With following distinctive features: 1) osphradium weakly narrower, but also bipectinate; 2) osphradium posterior end more anterior than that of gill; 3) anterior, septum-like region of gill (ac) longer and strongly curved to left.

Circulatory and excretory systems. Heart (Fig. 101) and kidney characters similar to those described for *S. pugilis*.

Digestive system. Buccal mass, odontophore muscles and esophagus characters similar to those of preceding species, except for absence of m10a muscle. Stomach also similar but with inner surface weakly more complex (Fig. 100); tall dorsal fold running longitudinally along posterior half of style sac and short distance of anterior region of stomach; immediately posterior to end of this fold other transversal fold present, disposed somewhat perpendicular to that, edges anterior margin of gastric shield; pair of outstanding folds running in ventral surface of stomach, unites both ducts to digestive glands; another elliptical, tall, longitudinal fold in middle level of ventral-right gastric region (this fold single similar to *S. pugilis*). Disposition of structures annexed to stomach and intestine loops also as described for *S. pugilis*. Fecal pellets see Robertson (1961:7, fig. 1).

Genital system. Male. Visceral tubes and glands similar to those of preceding species. Pallial sperm groove (prostate) (Fig. 101) with asymmetrical laminae; inner lamina very thicker and beige in color; outer lamina thin and white in color, attached to mantle, no median fold. Penis characters similar to those of *S. pugilis*, inclusive location of penis groove and tip structures and projections, only following distinctive features (Figs. 102, 103): 1) penis slightly shorter and more robust; 2) apical left branch of sperm groove finished in base of triangular, flattened projection, and **not** cylindrical, tall, strong papilla as in *S. pugilis*.

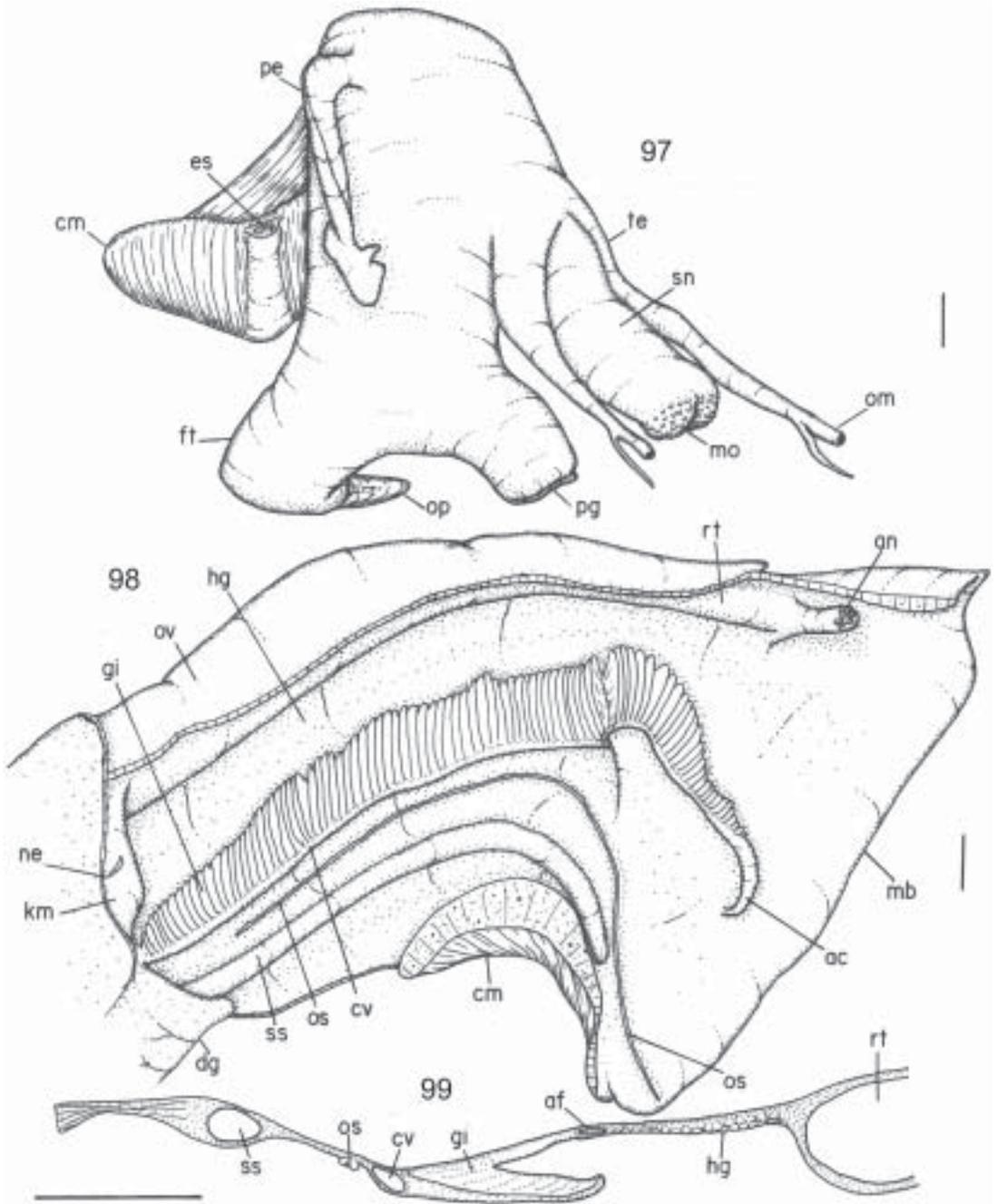
Female. Visceral and pallial oviducts very similar in situation and characters to those of anterior species; with following distinctive features (Figs. 104-106): 1) posterior region of pallial ovi-

duct, just where visceral oviduct inserts, very convolute, bearing four or five strong, irregular whorls; 2) albumen gland broader and amply opened in its anterior end; 3) capsule gland with only one insertion anterior to that of albumen gland (Fig. 105)

(while *S. pugilis* this insertion is double, with dorsal branch narrower).

Measurements of shells (in mm).
 MZSP 28808, ♀ 1:87.4 by 58.0; ♀ 2:85.8 by 49.6.

Distribution. Florida, USA.



Figures 97-99. *Strombus alatus* anatomy. 97. head-foot, male, frontal view; 98. pallial cavity, female, inner-ventral view; 99. pallial cavity, transversal section in middle region of its roof. Scales = 5 mm.

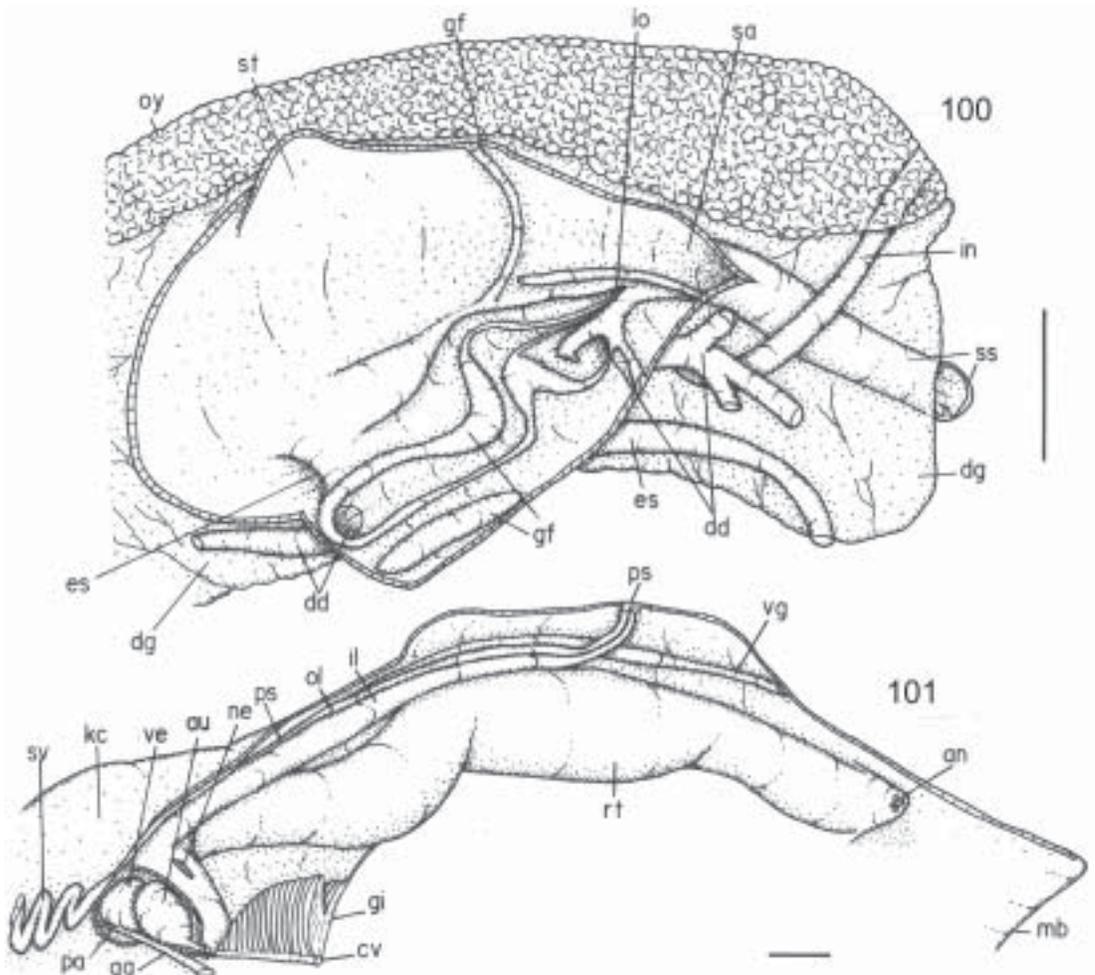
Habitat. Same than that of *S. pugilis*, intertidal sandy substrates.

Material examined. UNITED STATES OF AMERICA. **Florida;** Sanibel Island; AMNH 163722, 1♂ (P. Raeihle leg. xi/1975); Lighthouse point, 2♂, 8♀, MZSP 28808 (ex-BMSM) (J.H. Leal col., 6/x/1997).

Discussion. The conchological differences and similarities between *S. pugilis* and *S. alatus* were well commented and explored by Dodge (1956). That paper dispenses any complementation, except that *S. pugilis* has comparable degree of shell variation than *S. alatus*. There are, inclusive, specimens with subsutural spines missing (Figs. 3, 4). The typical form of *S. alatus* shell, shown in most of the books, is slender, thin walled, almost with-

out spines (only subsutural nodes) and richly colored (zigzag dorsal dark spots, dark brown outer lip) (Clench & Abbott, 1941; Walls, 1980). However this shell form is not the commonest. Most of the specimens present greatly similarity with *S. pugilis*, only differing by less developed subsutural spines (but still well delimited) and outer lip weakly more projected, internally dark colored. All *S. alatus* shell characters have superposition with some variants of *S. pugilis* and vice-versa, becoming hard to define true separation.

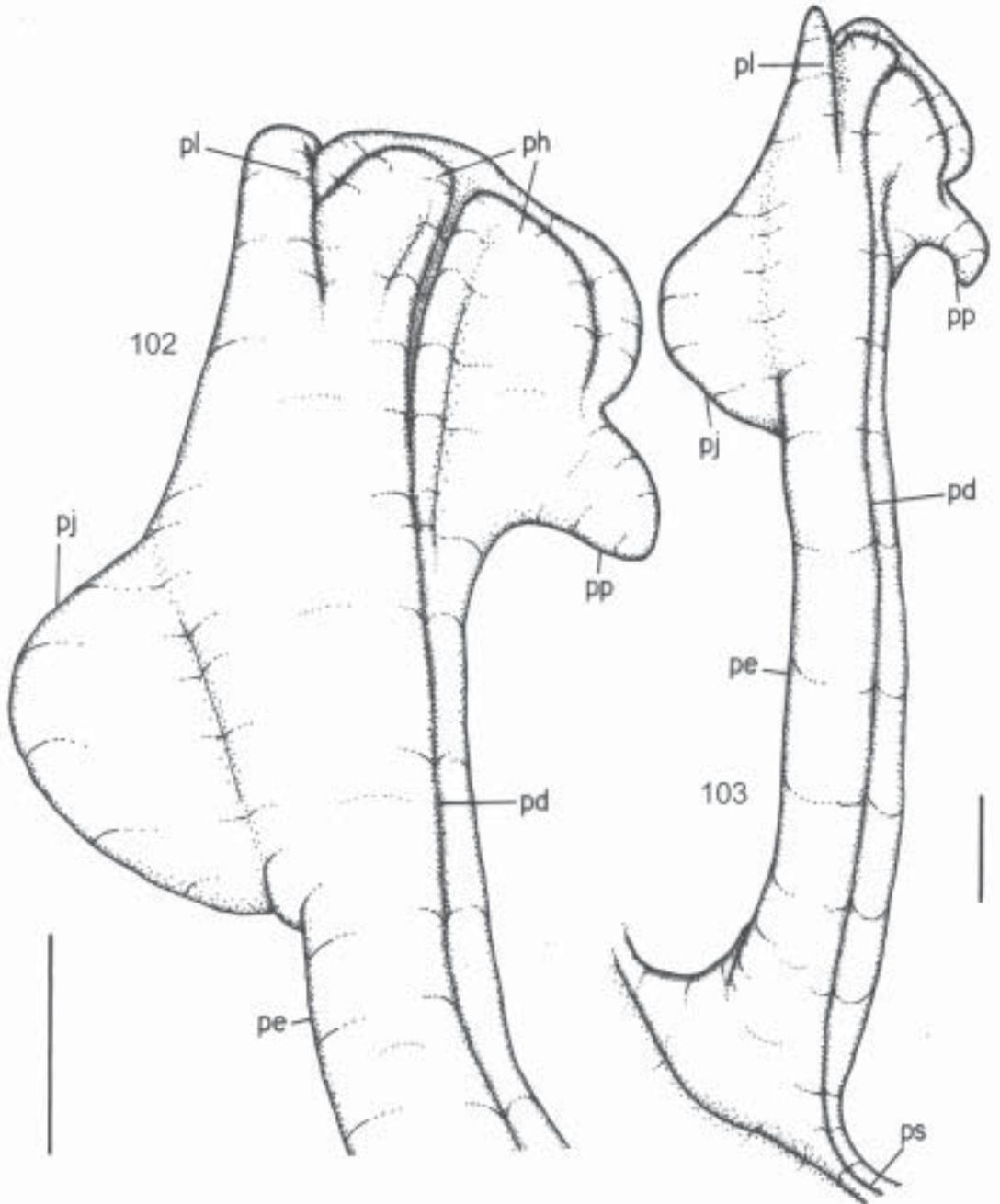
The soft parts characters, on the other hand, helped little, because the differences degree between both samples is equivalent to those of the shells. Most of the differences of morphological characters were explored above. The considered most important dif-



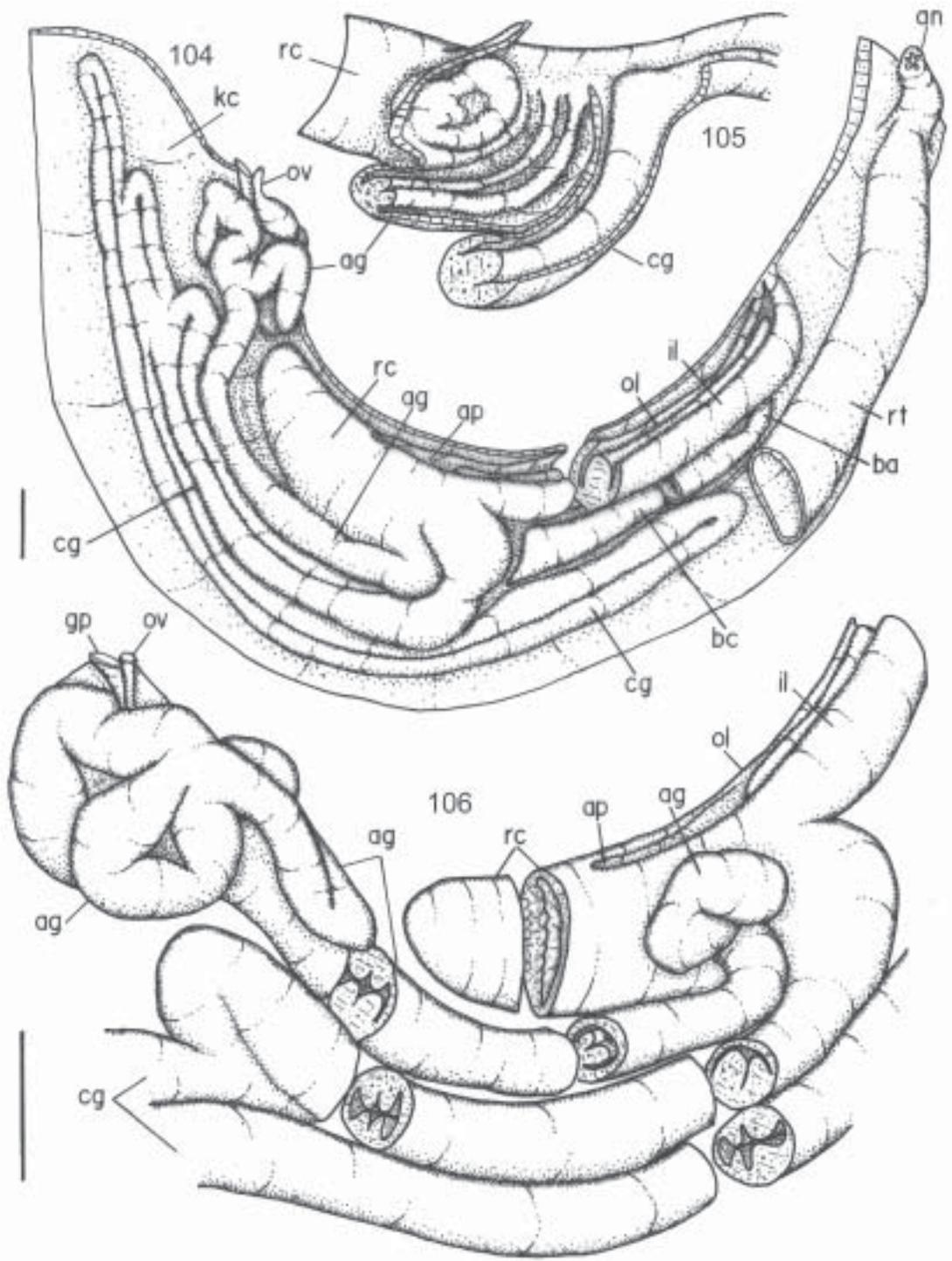
Figures 100-101. *Strombus alatus* anatomy. 100. anterior region of visceral mass, ventral view, stomach opened by a incision in its right margin, its ventral wall deflected to left, adjacent tubes seen if the digestive gland was transparent; 101. right region of pallial cavity and adjacent anterior extremity of visceral sac, male, ventral view, ventral wall of pericardium removed. Scales = 5 mm.

ferences are in anterior region of genital system: 1) the lateral projection of the penis tip (a developed cylindrical papilla in *S. pugilis* and flattened, triangular projection in *S. alatus*); 2) the middle fold of pallial sperm groove (present in *S. pugilis* and absent in *S. alatus*) and 3) middle region of pallial oviduct, just where albumen and capsule glands insert (*S. pugilis* have three branches inserted in the main

axis of the pallial oviduct, and each one is narrower, while *S. alatus* have only two branches and each one is broader). However, no spectacular morphological difference was found; all related differences, even those of the genital system, can be regarded as extreme of variation of a single, wide distributed, variable species. Whichever the taxonomic level that the above differences indicate, if variation of a single



Figures 102-103. *Strombus alatus* penis (two specimens). 102. detail of apex; 103. whole view. Scales = 2 mm.



Figures 104-106. *Strombus alatus* pallial oviduct, ventral view. 104. whole view, some transversal sections artificially done, renal tissue and part of rectum removed to show portions dorsal to them; 105. detail of region of albumen and capsule glands insertions, both opened longitudinally, ventral wall of albumen gland deflected to right; 106. detail of posterior region, mantle totally removed, some transversal sections artificially done. Scales: 5 mm.

species, if belong to separated subspecies or species, will be only confirmed after further studies, mainly of comparison of specimens from several points of Western Atlantic coast. For moment, but with these informations in mind, above cited differences were regarded as indicative of specific separation.

The population of *S. pugilis* from Salvador Bay, Bahia, is distinct in lacking so developed subsutural spines. However, the soft parts have the same characters than the specimens from other regions, with well-developed spines, indicating the degree of shell variation rather than some taxonomic separation. However other singularity was found in all examined females of the Salvador population, they have a small penis in the same local where the males have the (large) penis. This phenomenon, called "masculinized females" or "imposex", had been observed also in some Caribbean populations of *S. pugilis* (Reed, 1993a, b).

Strombus gracilior Sowerby, 1825
(Figs. 24, 25, 107-111, 372)

Strombus gracilior: Keen, 1971:420 (fig. 607); Walls, 1980:73 (fig.); Abbott & Dance, 1982:77 (fig.); Jimenez-Arce, 1993:345-349.

Description

Shell (Figs. 24, 25). Somewhat similar to both preceding species, but with longer spire (about same length than aperture). Subsutural spines or pointed nodes also present, color reddish. Other details of shell characters see Keen (1971:420, fig. 607), Walls (1980:73).

Head-foot and operculum (Fig. 107). Characters very similar to those of preceding species, inclusive broad papillae in anterior snout surface. Genital female furrow present. Penis very long, described below.

Mantle organs (Fig. 108). Very similar characters to those of both preceding species. Gill anterior small septum (ac) present; gill filaments with narrow and long tip. Osphradium anterior end very close to mantle border; its posterior region running close to gill.

Circulatory and excretory systems. Characters similar to those of *S. pugilis*.

Digestive system. Buccal mass and odontophore characters similar to those of *S. pugilis*, inclusive presence of ma, mc, m10a and m7 of multiple origin. Radula (Fig. 372) very simi-

lar to those of preceding species; rachidian with 5 cusps, being central cusp about double in length than neighbors; lateral tooth with about 5 cusps being median terminal, longer and about 3 times larger than neighbor; inner and outer marginal teeth similar with each other, with about 8 cusps in inner, sub-terminal margin. Esophagus also similar to that of *S. pugilis* but generally with broader, thin walled region posterior to nerve ring. Salivary glands apertures weakly more posterior as those of *S. pugilis*, but also in middle region of dorsal folds of buccal mass. Stomach, intestine and digestive gland as described for *S. pugilis*.

Genital system. Male. Visceral and pallial organs characters very similar to those of preceding species. Penis very long and narrow in basal region, in distal 2/3 becomes broad (Fig. 107). Penis distal region slight similar to those of both preceding species (Figs. 109, 110), with following differences: 1) penis longitudinal fold poorly developed, only visible in dorsal surface close to penis distal end; 2) distal end margin thinner and undulating; 3) lateral papilla larger and longer; 4) lateral branch of penis groove running along entire lateral papilla, almost up to its tip.

Female. No examined female presented well-preserved posterior regions, neither that of pallial oviduct, but, what was possible to exam, they are similar to those of *S. pugilis*. Pallial oviduct (Fig 111) basically similar in fashion to that of *S. pugilis*. Albumen gland differs in running dorsal to receptacle and capsule gland (not visible in ventral view). Seminal receptacle almost all closed (tubular).

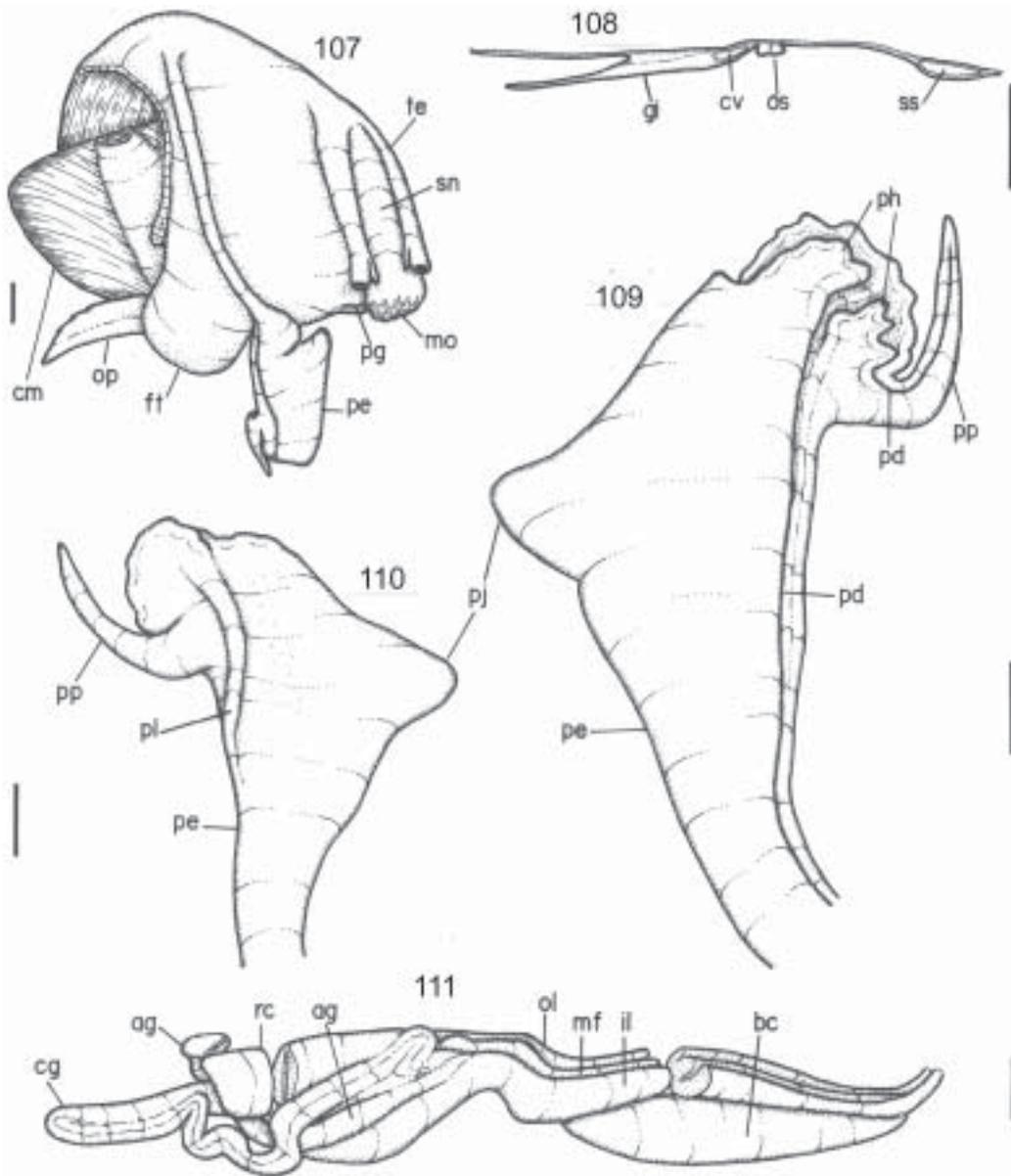
Measurements of shells (in mm). AMNH 278381, ♂ 1:63.5 by 37.3; ♂ 3:65.2 by 36.6.

Distribution. From Gulf of California to Peru.

Habitat. Intertidal to 45 m depth.

Material examined. PANAMA; Pacific coast; Gobernadora Island, North shore, AMNH 278381, 6 specimens (Walter Sage col., 31/i/1991).

Discussion. Like the shell, *S. gracilior* is very similar in inner morphological characters to *S. pugilis* and *S. alatus*, being a close Pacific relative of both Atlantic species. The main differences are explored above. Apparently the analysis of the penis and of the pallial oviduct characters are of particular importance for specific separation of these species.



Figures 107-111. *Strombus gracilior* anatomy. 107. head-foot, male, frontal view, mantle and visceral mass extracted; 108. Pallial cavity, transversal section in its middle region; 109. Penis, ventral view, detail of apical region; 110. Same, dorsal view; 111. Pallial oviduct, ventral view (more details not possible because of preservation problems). Scales = 2 mm.

Genus *Eustrombus* Wenz, 1940
(revalidated; type species *S. gigas* Linné, 1758)

et al., 1981:120 Alcolado, 1983:1-9; Rios, 1985:62 (pl. 22, fig. 275); 1990:7-10; 1994:69 (pl. 23, fig. 263).

Eustrombus goliath (Schröter, 1805) new comb.
(Figs. 8, 9, 37, 38, 52, 53, 112-139)

Synonymy see Matthews (1980:91). Complement: *Strombus goliath*: Melo, 1964:151; Walls, 1980:81 (Figs); Abbott & Dance, 1982:76 (fig.); Oliveira

Description

Shell (Figs. 8, 9). Well characteristic shell with ample outer lip. One of the largest Atlantic gastropods. Other details in Matthews (1980:92-97, Figs. 5a-f).

Head-foot (Figs. 112, 114-116, 118). All head-foot structures similar to those described by preceding species, with following distinctive features: color homogeneous clear beige with several dark brown spots in exposed areas, sometimes coalescent. Peri-oral region of snout smooth, without papillae. Foot posterior surface with mosaic of folds forming somewhat uniform net; several large vessels running longitudinally within muscles near this folded surface. Columellar muscle very thick, in section (Fig. 115) ventral layer of oblique fibers just on columella; second layer extremely thick of transversal (dorso-ventral) fibers, in right side several lateral fibers running within transversal fibers; around haemocoel thin layer of circular fibers from which lateral fibers originating immerse in transversal fibers. Between this circular fibers and integument, dorsal wall of haemocoel still presents four thin layers of muscles in following order from internal to external (Fig. 114): 1) oblique, 2) longitudinal, 3) other oblique perpendicular to inner layer, 4) other circular preceding integument. Diaphragm-like muscular septum of haemocoel very developed (Figs. 118, 119).

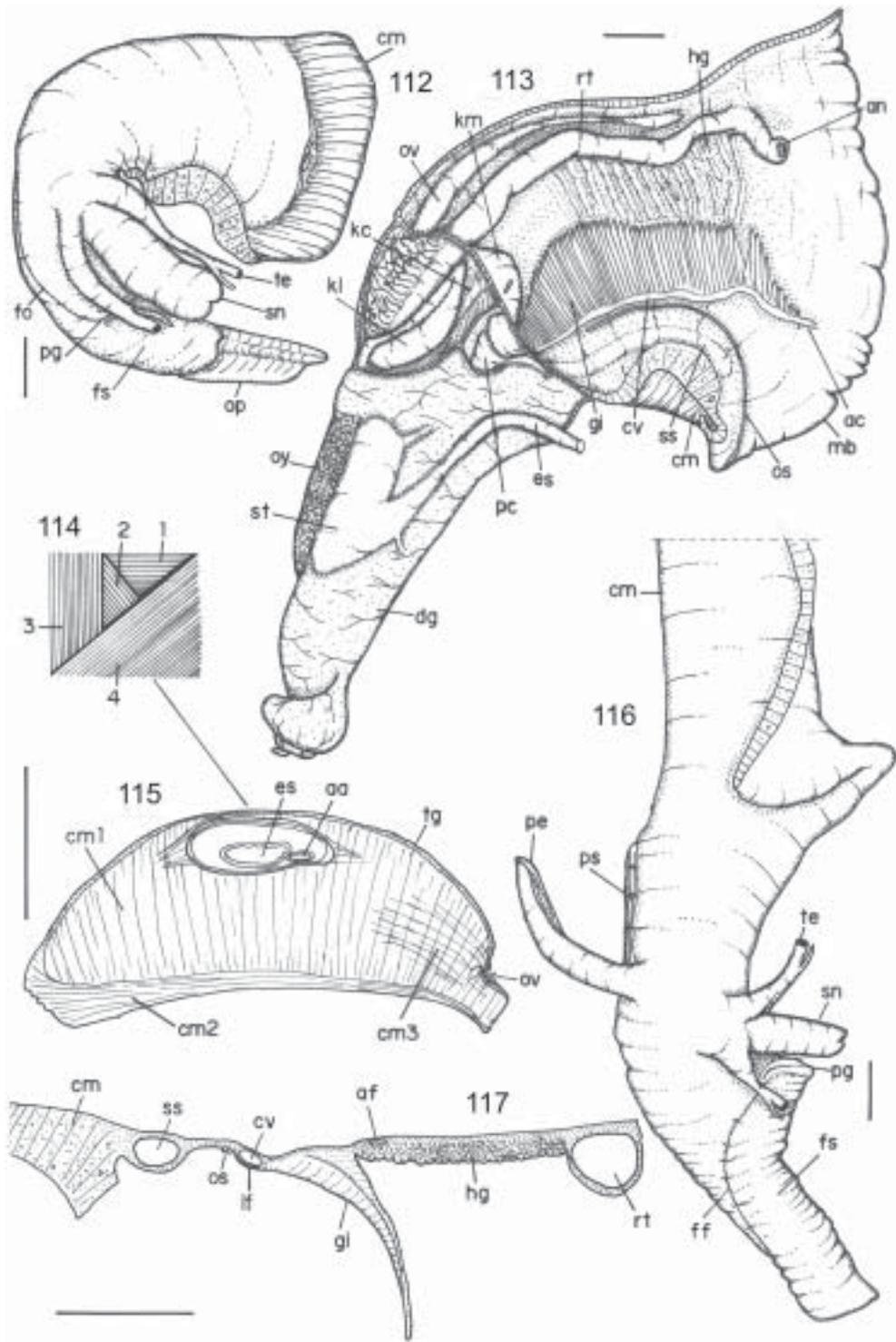
Operculum (Figs. 37, 38). Similar to that described for preceding species, but much more robust, with central, longitudinal fold taller and broader. No spines on outer margin.

Mantle organs (Figs. 112, 117, 134). Organization and components also similar to those described for preceding species, with following distinctive features: mantle border very ample, thick muscular (mainly in siphon region) pale cream in color, with some dark-brown spots. Osphradium narrow, long, also bipectinate; anterior extremity close to mantle border in left region of siphon; running obliquely to posterior and right region, approaches from gill in its middle level; posterior third of osphradium very narrow. Osphradium posterior end at some distance from that of gill. Gill very long – about same length than pallial cavity, narrow; anterior extremity near mantle border, also with short, broad, septum-like region with leaflets missing (ac); gill leaflets triangular, very tall, curved to right, somewhat broad base, taper suddenly, tip sharp and long. Between gill and rectum a space about twice that of gill base. Hypobranchial gland with transversal folded surface, with small mucous chambers, reddish stained in anterior regions. Rectum long and broad, normally replete of graveled sediment in elliptical fecal pellets. Anus siphoned,

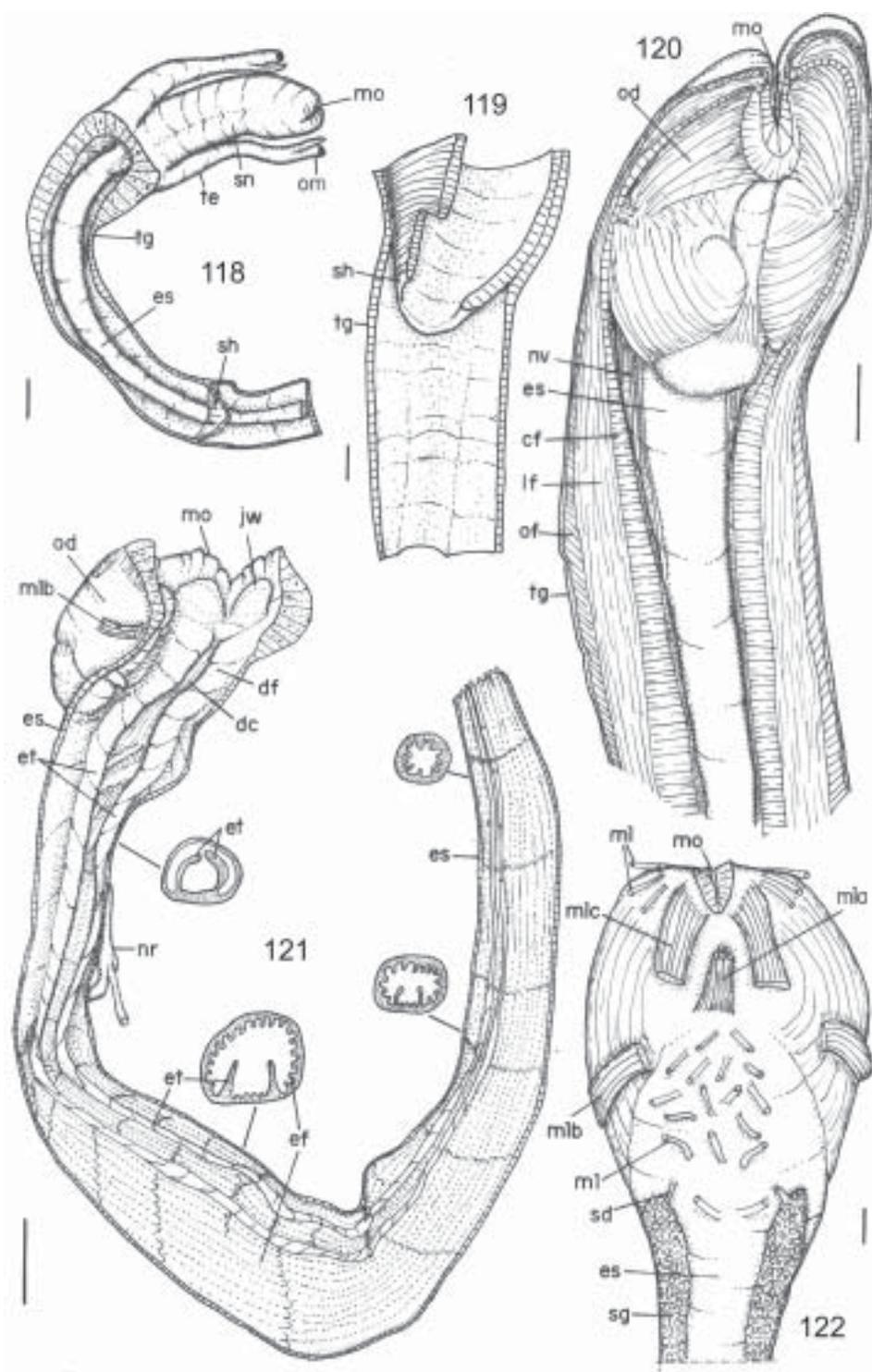
presenting several small papillae in its margin, sited at some distance of right extremity of mantle border. Pallial gonoducts running in posterior 3/4, between rectum and right margin of pallial cavity, both described below.

Circulatory and excretory systems (Figs. 113, 134). Organization and site similar to those of preceding species, with following distinctive features: dorsal surface of kidney chamber with glandular tissue well-developed (dorsal lobe), thin, covered by uniform transversal, low folds. Ventral lobe of kidney very large, its right margin attached to rectum, presenting several transversal folds, remainder with mosaic of tall, irregular, broad folds, close to one another, with several secondary pores. Nephridial gland large, broad, triangular in section (Fig. 134). Nephridial gland main vessel as described for *S. pugilis*.

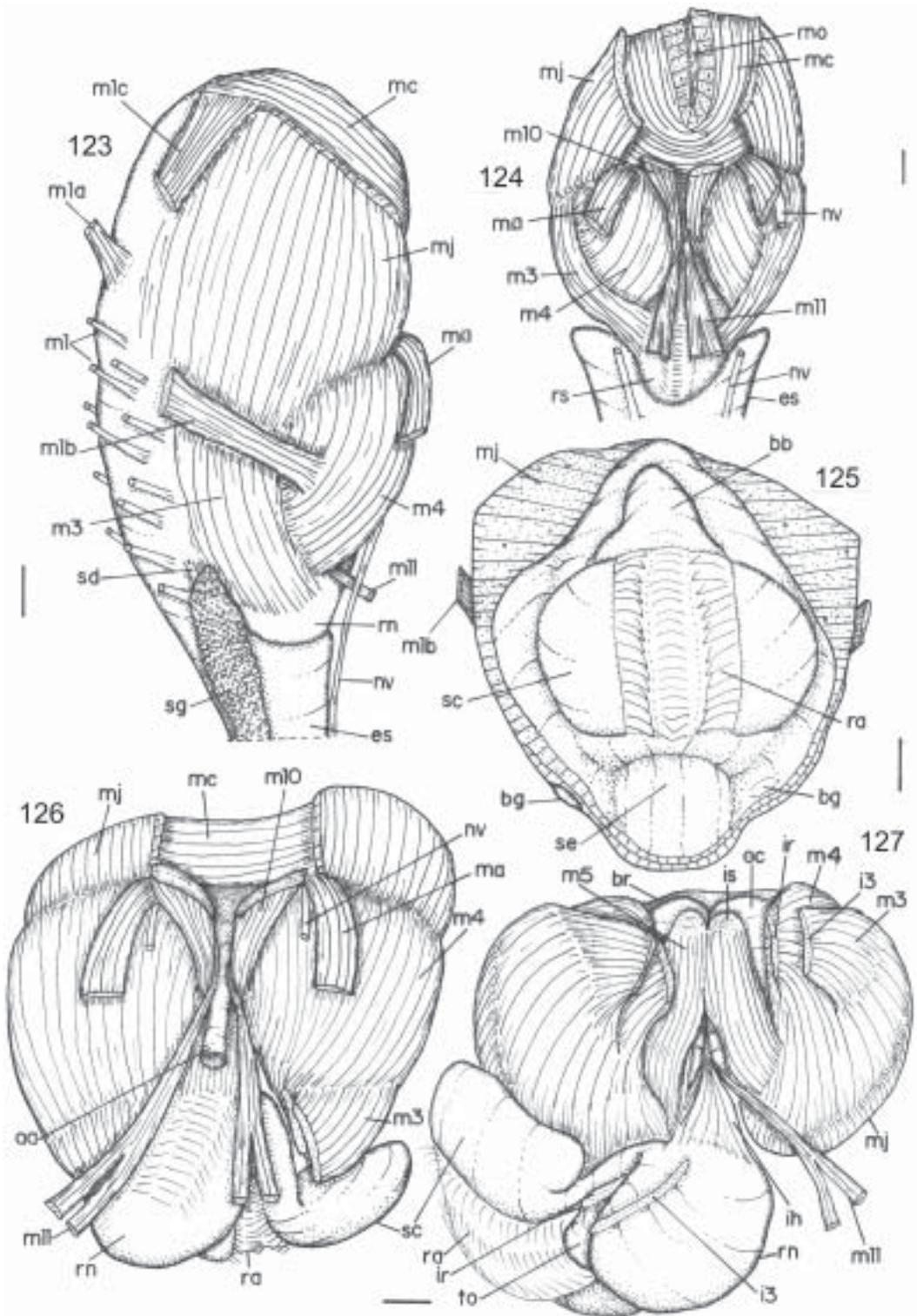
Digestive system. Similar components and characters to those of preceding species, with following distinctive characters (Figs. 120-130): **m1c** pair of anterior dilator of mouth, originating in lateral-dorsal-anterior inner surface of snout, inserting in lateral-dorsal region of mouth on “mc”; **m3** thin layer of muscular fibers, originating in both sides of odontophore near mj insertion, cover most of odontophore lateral surface (on m4), inserting somewhat thick, in each side of radular nucleus; m3 covers m4, but one is partially separated from another by membrane, transversally inserted in dorsal margin of m3 and in ventral margin of m4 (Figs. 128, 129); **m5** connected one to its pair; **ih** very thick; **m10** thicker; **m10a** absent. Radula (Figs. 52, 53): rachidian broad, central cusp large and broad, with about 1/3 of rachidian width, secondary cusps very small, vary from four to five pairs, lateral pair in apex of broad marginal thickness; lateral tooth tall, somewhat triangular and curved, base broad, apex sharp and large, preceded by about five small secondary cusps only in lateral edge; inner and outer marginal teeth similar with each other, tall, slender (but broader as those of *S. pugilis*), with slightly pointed tip preceded in inner margin by about ten small cusps. Salivary glands also anterior to nerve ring (Figs. 122, 123); their ducts visible only in anterior limit of salivary glands, in short distance penetrate in dorsal wall of buccal mass and run in base of local inner folds, open in their anterior region. Esophagus very long, broad, thin walled (Figs. 118, 120, 121). Anterior esophagus with pair of typhlosoles, between then



Figures 112-117. *Eustrombus goliath* anatomy. 112. head-foot of female, frontal view, mantle and visceral mass extracted; 113. pallial cavity and visceral mass of female, ventral view, kidney and pericardium opened to show inner structures; 114. dorsal haemocoel wall, detail of a dissected region showing different muscular layers, ventral view (4 as inner layer); 115. columellar muscle, transversal section of its posterior region, female; 116. head-foot of male, dorsal view, mantle and visceral mass extracted, columellar muscle only partially shown; 117. pallial cavity roof, transversal section in its middle region. Scales: 20 mm.



Figures 118-122. *Eustrombus goliath* anatomy. **118.** head and haemocoel, ventral view, foot and columellar muscle removed; **119.** same, detail of muscular septum (sh) region, esophagus and aorta removed; **120.** snout, ventral view, ventral half of integument and muscular wall removed; **121.** buccal mass and esophagus, both opened longitudinally with inner surface exposed, buccal mass sectioned at left and esophagus ventrally, some transversal sections of indicated levels (of a non-cut piece) also shown; **122.** buccal mass, dorsal view. Scales 118, 121 = 10 mm; 119, 122 = 2 mm; 120 = 5 mm.



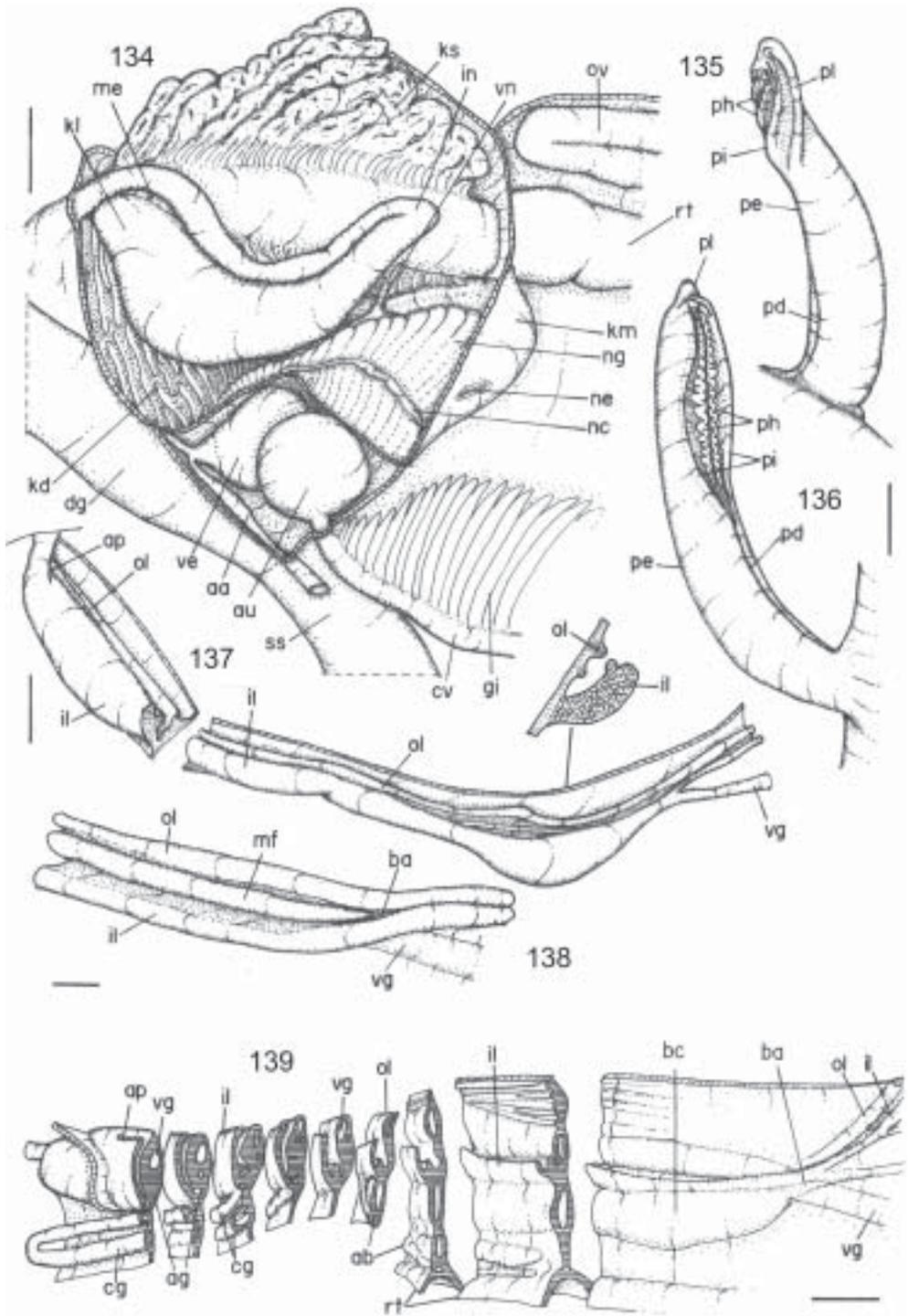
Figures 123-127. *Eustombus goliath* anatomy. 123. buccal mass, lateral-right view; 124. same, ventral view; 125. odontophore isolated, dorsal view; 126. same, ventral view; 127. same, ventral view, radula and adjacent structures extracted and deflected. Scales = 2 mm.

some oblique, low, glandular folds. In remainder esophageal inner surface several low, longitudinal folds. In middle esophagus both typhlosoles gradually faint; posterior esophagus only with low, longitudinal, narrow folds (Fig. 121). Stomach (Figs. 131-133) large, spacious, with about 3/4 whorl in length, immerse in digestive gland except in some exposed areas of its dorsal and ventral surfaces. Esophagus inserts in stomach in middle region of its left margin. Stomach anterior margin with three apertures: right and broader aperture of style sac; very narrow right-ventral aperture of duct to digestive gland; right-dorsal aperture of intestine. Stomach inner surface with two posterior folds in dorsal surface; a larger, oblique and slight straight; a smaller and "U"-shaped. Ventral fold elliptical. Other fold surrounding posterior margin of gastric shield (Fig. 132). Second duct to digestive gland broad, long, bifurcates successively, just posterior to esophagus insertion. Style sac enormously long (Figs. 113, 131, 133), running, as preceding species, initially immerse in digestive gland dorsal to intestine, crossing dorsal-left region between pericardium and kidney; after lies on pallial cavity wall between osphradium and left margin of this cavity until near siphon border. Intestine running immerse in digestive gland, surrounding style sac insertion, crossing from left to right side between style sac and duct to digestive gland until posterior-right border of kidney (Fig. 131), free loop present within kidney chamber, connected internally by mesentery membrane (Figs. 113, 131, 134), running at right marginal to kidney and pallial cavity as above described.

Genital system. Male organs similar to those of preceding species. Vas deferens long and narrow in pallial cavity (Fig. 137), an opened spermatid groove (prostate). Outer lamina of spermatid groove thin, glandular, attached to inner surface of mantle, low longitudinal fold near its base, followed by well-developed mantle vessel. Inner lamina of sperm groove a tall fold, thick glandular, rounded free margin, other longitudinal low fold running near margin all along its length. In about middle region of anterior third part of left margin of pallial cavity prostate finishes, pallial sperm groove narrows, secondary folds finish, its laminae become somewhat symmetric, and crosses to pallial floor, running slightly short distance until penis base (Fig. 116). Penis long and cylindrical (Figs. 116, 135, 136). Proximal half of penis groove deep and

narrow. Distal half of penis groove opened, two pairs of folds appear; those external folds become borders of lateral concavity; those internal folds become glandular, with uniform sinuous margin as zigzag; between these inner folds slight deep furrow; this furrow bifurcates near tip (where both inner folds finish) in "T"-fashion. In opposite side of this concavity oblique, tall fold (pl) beginning gradually in distal region of penis and finishes connecting with concavity distal margin (Figs. 136, 136). In specimen MZSP 31413 some small and sparse papillae occur in apical penis folds.

Female organs also similar as those of preceding species. Pallial oviduct most than half opened, complex, occupying about 2/3 of pallial cavity length (Fig. 113). Visceral oviduct connects subterminally in ventral surface of broad albumen gland; this gland opens in short distance and becoming groove, but closed duct running in left margin and opening within this groove in level between posterior and middle third parts of pallial oviduct (Fig. 139). Capsule gland beginning just anterior to albumen gland aperture, running posteriorly at left of albumen gland; in region dorsal to kidney returns anteriorly parallel and at left of this first loop; finishes just anterior to its beginning. Capsule gland a simple glandular tube except in its final region, where there is fold. At short distance of capsule gland aperture other branch of capsule gland begins, running anteriorly close to right margin of rectum, finishes suddenly as blind sac. Inner pallial oviduct lamina thin and tall in posterior half; gradually becomes low. Middle fold beginning anterior to capsule gland aperture, running longitudinally. Outer lamina thick, glandular in its posterior half, gradually faint. Some longitudinal folds appear in mantle at right of pallial oviduct in its anterior third part. A blood vessel running all along outer lamina and continues parallel to right pallial cavity margin where oviduct crosses to pallial floor (vg). Bursa copulatrix similar to that of *S. pugilis*, long, broad, flattened, with simple inner surface; opens in pallial oviduct at short posterior distance from where it crosses to pallial floor (Fig. 138). Pallial oviduct in anterior third part of right margin of pallial cavity becomes single groove, with similar sized walls (Fig. 138), crossing to pallial floor and running obliquely posterior to head until anterior projection of foot; finishes close to aperture of pedal gland right extremity. The state of capsule gland probably indicates that no examined females were fully mature.



Figures 134-139. *Eustrombus goliath* anatomy. **134.** Anterior region of visceral mass, ventral view, pericardium and kidney opened longitudinally, ventral renal wall deflected upwards to show inner renal structures. **135.** penis, ventral view; **136.** same, dorsal view; **137.** male pallial sperm groove, ventral view, with a detail of a transversal section in indicated region; **138.** female pallial oviduct, detail of its anterior region before crossing to pallial floor; **139.** entire pallial oviduct, ventral view, several transversal sections artificially done to shown its inner structures, probably not fully mature. Scales: 134 = 1 mm; 135-137, 139 = 10 mm; 138 = 2 mm.

Measurements of shells (in mm).

MZSP 31413, 311.8 by 221.0.

Distribution. Brazil, from Ceará to Espírito Santo.

Habitat. In muddy or sandy-mud substrates, from intertidal zone to about 50 m depth.

Material examined. BRAZIL. Ceará; Paracuru, 1♂, MZSP 18893, 2♀, MZSP 28443 (H.R. Matthews col., 7/xi/1972). Rio Grande do Norte; Rio do Fogo, MZSP 31413, 1♀ (fishermen col., viii/1999). Pernambuco; 2♀, MZSP 28597, 1 shell, 25012. Bahia; Salvador; Itapuã beach, 0.5 m depth, 1♀, MZSP 28596 (S.G. Paes col., vii/1977); 1-5 m depth, 2♂, 2♀ observed alive, MZSP 28443 (Simone col., 23-27/ii/1997).

Eustrombus gigas (Linné, 1758)

(Figs. 23, 140-146, 374)

Synonymy see Clench & Abbott, 1941:12. Complement: (N.B. the following complement is limited mostly to systematic papers, since the bibliography on *E. gigas* is very massive.)

Strombus gigas: Bergh, 1895:346-359 (Pl. 22, figs. 26-30; pl. 23, figs. 54-59); Parker, 1922:205-209; Little, 1965:338-357 (Figs. 1-12); Brownell, 1977:668-679 (figs. 2, 3, 4-3, 6); Walls, 1980:80 (fig.); Abbott & Dance, 1982:75 (fig.); Suttly, 1986:12, 113, 124 (Figs. 6, 124, 138); Muñoz *et al.*, 1987:353-361; Ogawa & Corral, 1987:362-369; Jong & Coomans, 1988:62-63; Haywood & Wells, 1989:156-157 (fig.); Berg *et al.*, 1992:433-438; Stoner & Ray, 1993:571-582; Davis *et al.*, 1993:236-243 (figs. 3-4); Merlano & Hegedus, 1994:157-158 (pl. 49, fig. 574); Stoner, 1994:155-165; Stoner & Lally, 1994:73-84; Davis, 1994:101-108; Stoner & Davis, 1994:390-411; Ray & Stoner, 1994:47-59; 1995a:83-94; 1995b:207-222; Abbott & Morris, 1995:184-185 (pl. 50); Stoner *et al.*, 1995:125-137; Berg & Glazer, 1995:247-258; Martin-Mora *et al.*, 1995:981-994; Mulliken, 1996:17-28; Stoner & Ray, 1996:101-108; Stager & Chen, 1996:14-20; Grana-Raffucci & Appeldoorn, 1997:857-861 (fig. 1); Stoner & Smith, 1998:1-15 (figs. 2, 4, 6).

Description

N.B.: extensive anatomical description is given by Little (1965).

Shell (Fig. 23). Very large, similar to that of *E. goliath*, differing mainly in lacking so expanded outer lip and in having more developed nodes in spire. Other details in Clench & Abbott (1941:12-13), protoconch see Davis *et al.* (1993).

Head-foot and operculum. Same characters to that of *E. goliath*, except narrower operculum (other details in Little, 1965:348-353, Figs. 8-10).

Pallial cavity. Very similar characters to those of *E. goliath*, but weakly longer and narrower. Osphradium very narrow, its posterior limit in adjacent level between posterior and middle thirds of gill.

Circulatory and excretory systems. Both with characters very similar to those of *E. goliath*.

Digestive system. Characters of all organs very similar to that of *E. goliath*, inclusive odontophore (Fig. 144) and stomach (for stomach description see Little, 1965:346-348, fig. 6). Radular teeth (Fig. 374): similar attributes as those of *E. goliath*, distinctive features following: 1) rachidian tooth with 3-4 pairs of secondary cusps; 2) marginal teeth with about 6 secondary cusps.

Genital system. Male. Visceral and pallial organs very similar to those of preceding species. Pallial sperm groove with inner lamina thick due long prostate gland; low fold along its face with mantle (Fig. 143). Outer lamina very thin, indistinguishable from mantle. Penis (Figs. 141, 142) similar to that of *E. goliath*, with following differences: 1) weakly longer; 2) pair of undulated folds gradually presenting series of small papillae only in its distal half (or third part) of expanded region of penis; due undulation, this single series of papillae of each fold looks as several series of papillae; 3) row of papillae (similar to those of folds) at distal margin of penis tip. Other details of penis in Bergh (1895).

Female (Figs. 140, 145, 146). Visceral organs similar to those equivalent to males and to preceding species. Pallial oviduct of immature female (Fig. 140) slightly narrow, running at right and dorsal to rectum. Albumen gland narrow and long, part located in dorsal-anterior region of kidney, contours at left seminal receptacle and inserts just anterior to it. Receptacle large and elliptical, its aperture long, along its anterior 2/3, turned to right. Capsule gland a long tube running towards posterior, edging left region of albumen gland; its distal half running dorsal to kidney, bearing four successively shorter, right projections. Capsule gland in-

serting just anterior to that of capsule gland. Remainder pallial oviduct a long and narrow furrow with large, middle fold in its posterior half. Bursa copulatrix long, flattened, located between rectum and oviduct with about half of its length; bursa aperture at short distance from region where it crosses to pallial floor, slightly far from anus. Mature female (Figs. 145, 146) presenting similar fashion of immature female and slightly similar to *S. pugilis*; albumen gland remains connected to receptacle, contouring its left surface; capsule gland becomes more convolute but still presenting 4 expansions at right in its region dorsal to kidney, about 2 loops in inner lamina in region of its aperture; middle fold of anterior 2/3 of pallial oviduct present. Oviduct in pallial floor similar to those of preceding species. On development see Brownell (1977), Martin-Mora *et al.* (1995).

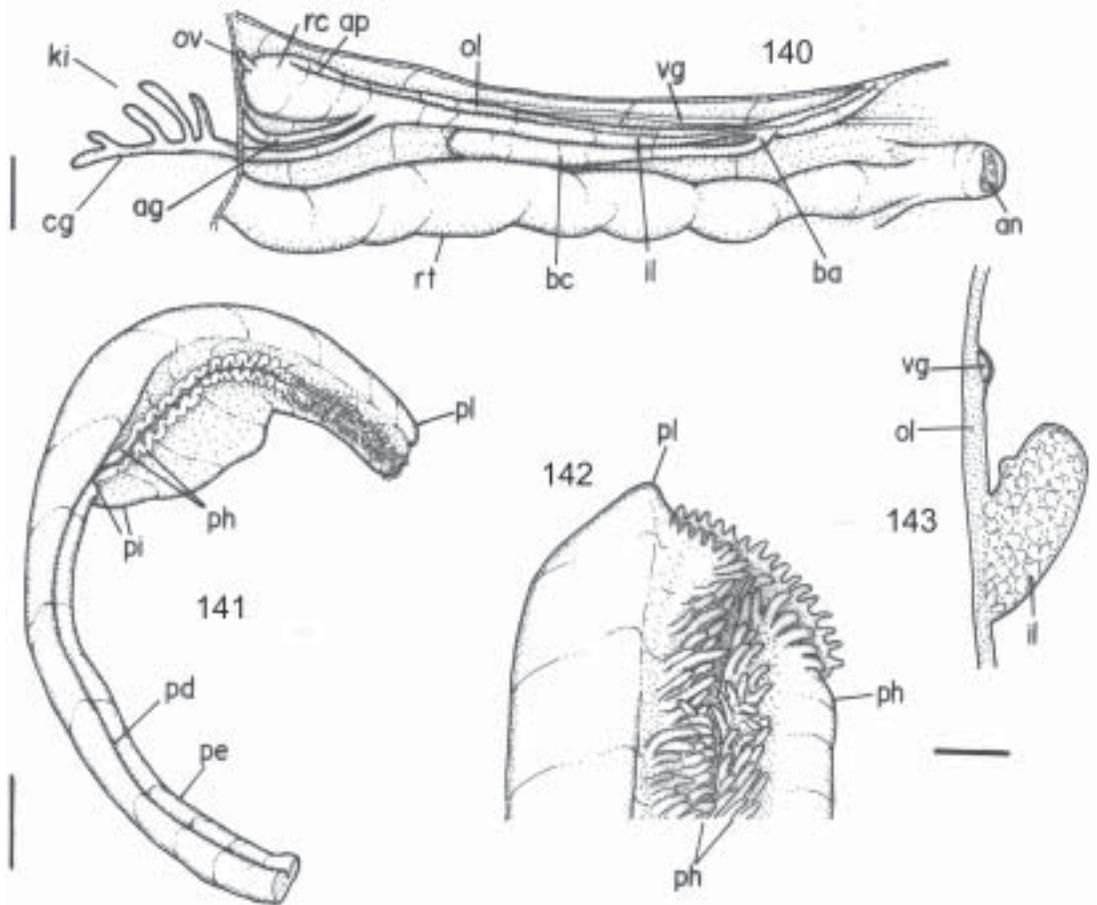
Nervous system. See Little (1965:355, Figs. 11, 12).

Measurements of shells (in mm). UMML (30.10892), 179.6 by 142.3.

Distribution. Gulf of Mexico and Caribbean.

Habitat. Same of preceding species, see also Stoner (1994), Ray & Stoner (1995a).

Material examined. UNITED STATES OF AMERICA; **Florida**; Florida Keys, 7 mile bridge, AMNH 267252, 1♀ (25/x/1975). BAHAMAS; **Binimi** Island; east side of Turtle Rock, AMNH 93325, 3♂, 1♀ (W.K. Emerson leg; 14/vi/1956), AMNH 164013, 1♂; AMNH 93326, 1♂ (W.K. Emerson leg, 14/vi/1956) AMNH 16013, 1♂; Nassau, AMNH 1827, 1♂ (R.P. Whitfield leg, 1899). JAMAICA; 70°07'N

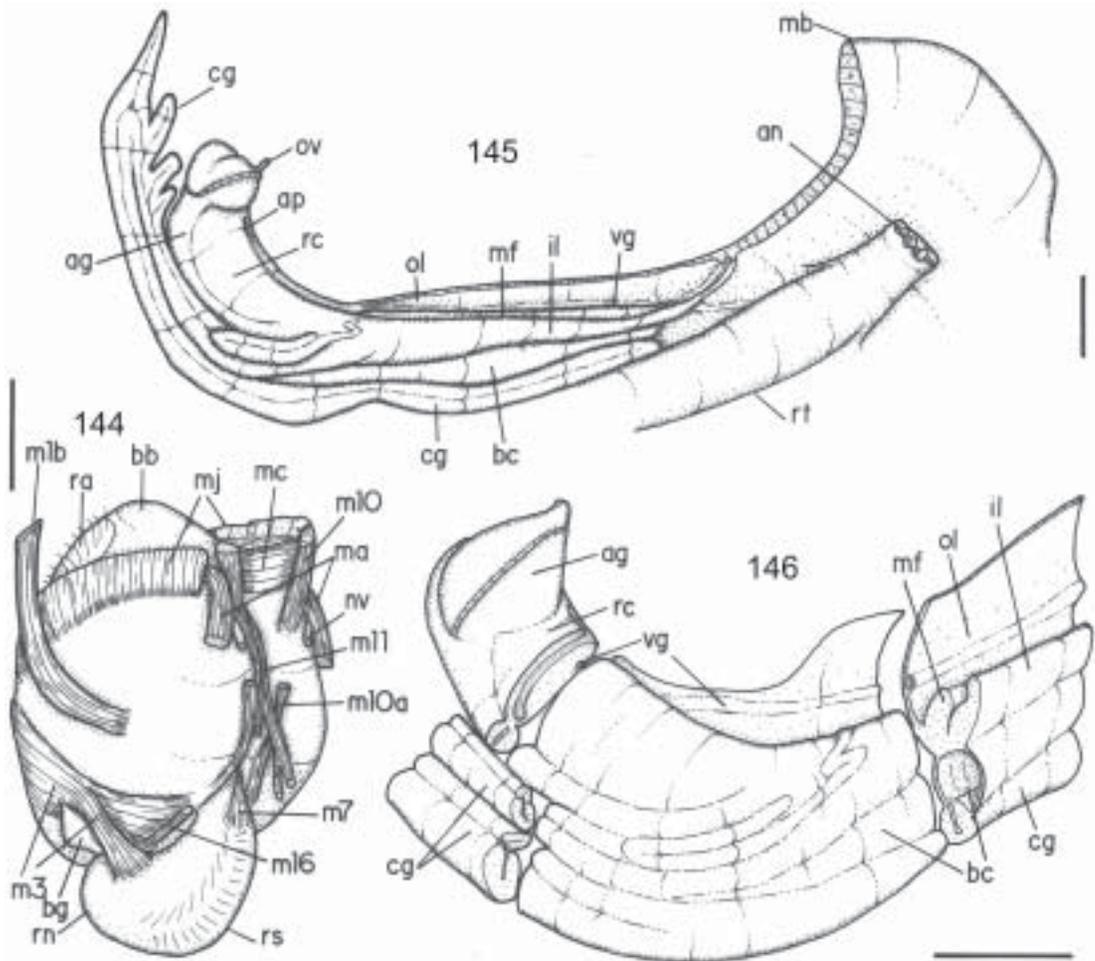


Figures 140-143. *Eustrombus gigas* anatomy. 140. pallial oviduct of immature female, ventral view, rectum, anus and adjacent mantle also shown; 141. penis, extracted, ventral view; 142. same, detail of apical region; 143. prostate, transversal section in its middle region. Scales: 140-141 = 10 mm; 142-143 = 1 mm.

78°20'W, 18 m depth, UMML 30.10892, 1♀ , (Sta. P-1257, otter trawl, 15/vii/1970).

Discussion. The close relationship between *E. goliath* and *E. gigas* is demonstrated not only by the shell characters, but also by the similarity of the inner anatomy. However, there are differences enough for specific separation of these allopatric populations. The stronger anatomical differences between both species are in the genital system. In the penis, *E. gigas* presents several papillae in the undulating folds of its distal, expanded region, while *E. goliath* lacks papillae, only presents the undulating folds. The distal border of penis of *E. gigas* also presents series of papillae, absent in *E. goliath*. However, in the *E. goliath* specimen MZSP 31413, some papillae in same

localization as those of *E. gigas* are present, but weakly developed. The pallial oviduct of *E. gigas* presents several differences from that of *E. goliath*, being more similar to those of previous described *Strombus* spp. However, no fully mature female of *E. goliath* was examined, which precludes any detailed comparison. Trying to help the interpretation of the comparative morphology between both species, the immature pallial oviduct of *E. gigas* was also examined and is described herein. It was possible to note that the both species present connection between the albumen gland and the adjacent left margin of the receptacle, which differs them from the other examined strombids. Except this, the fashion is similar of that of the family.



Figures 144-146. *Eustrombus gigas* anatomy. 144. odontophore, extracted, lateral-right view; 145. pallial oviduct of mature female, ventral view, part of rectum, anus and adjacent mantle also shown; 146. same, detail of its posterior region, some transversal sections artificially done showing inner organization. Scales: 144 = 2 mm; 145-146 = 10 mm.

Genus *Aliger* Thiele, 1929(Revalidated, type species: *S. gallus* Linné, 1758)***Aliger costatus*** (Gmelin, 1791) new comb.

(Figs. 10, 11, 54, 55, 147-163)

Synonymy see Matthews, 1980:76-77. Complement:

Strombus costatus: Melo, 1964:152; Brownell, 1977:668-679 (figs. 3, 4-2, 5); Walls, 1980:77 (figs); Abbott & Dance, 1982:76 (fig.); Oliveira *et al.*, 1981:120; Alcolado, 1983:9; Rios, 1985:61 (pl. 22, fig. 273); Domaneschi, 1986:311-316 (fig.); Jong & Coomans, 1988:63; Berg *et al.*, 1992:433-438; Davis *et al.*, 1993:236-243 (figs. 3-4); Rios, 1994:68 (pl. 23, fig. 261), Merlano & Hegedus, 1994:157 (pl. 49, fig. 571); Abbott & Morris, 1995:184 (pls. 8, 50); Grana-Raffucci & Appeldoorn, 1997:857-861 (fig. 1); Morton, 1997b (fig. 8:3); Stoner & Smith, 1998:1-15 (figs. 3, 5, 7).

Description

Shell (Figs. 10, 11). For shell description see Matthews (1980:77-82, Figs. 3a-g). Shell very heavy, thick walled, thickness more than 10 mm in some shell areas such as nodes and outer lip. Protoconch see Davis *et al.* (1993).

Head-foot (Fig. 147). All head-foot structures similar to those described in *E. goliath*, except in being weakly more slender, columellar muscle slight thinner and males with longer and slender penis.

Operculum. Also similar to those described for preceding species, but with intermediary degree of robustness.

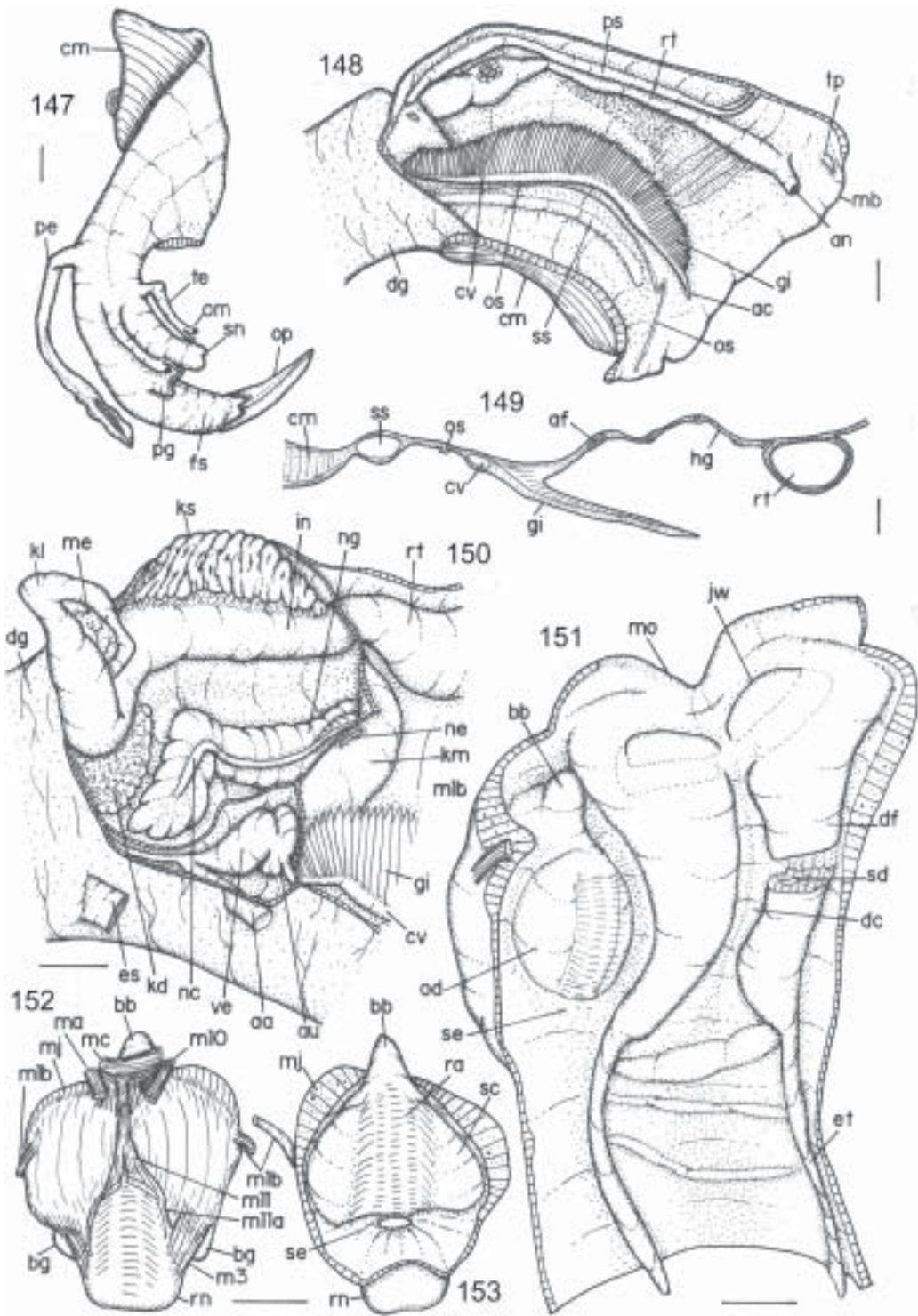
Mantle organs (Figs. 148-150). Organization and components also similar to those described for *E. goliath*, distinctive features following. Mantle border not so ample. Osphradium with sigmoid region in level where it approaches from anterior extremity of gill (Fig. 148). Osphradium posterior end anterior from that of gill. Gill long (weakly shorter than pallial cavity), base narrow; gill leaflets very tall, curved to right, somewhat broad base, taper suddenly, tip sharp and long. Between gill and rectum proportional broad space (about twice that of gill base), with some differentiable transversal vessels. Hypobranchial gland developed only anteriorly, with transversal folded surface, small mu-

cous chambers, color reddish. Rectum long and broad, normally replete of graveled sediment in fecal pellets. Pallial tentacle long and narrow, located anterior to anus at some distance from mantle border. Anus siphoned, sited at some distance of right extremity of mantle border (Figs. 148, 162), presenting some small papillae in its margin. Pallial gonoducts running in posterior 3/4, between rectum and right margin of pallial cavity (Fig. 163).

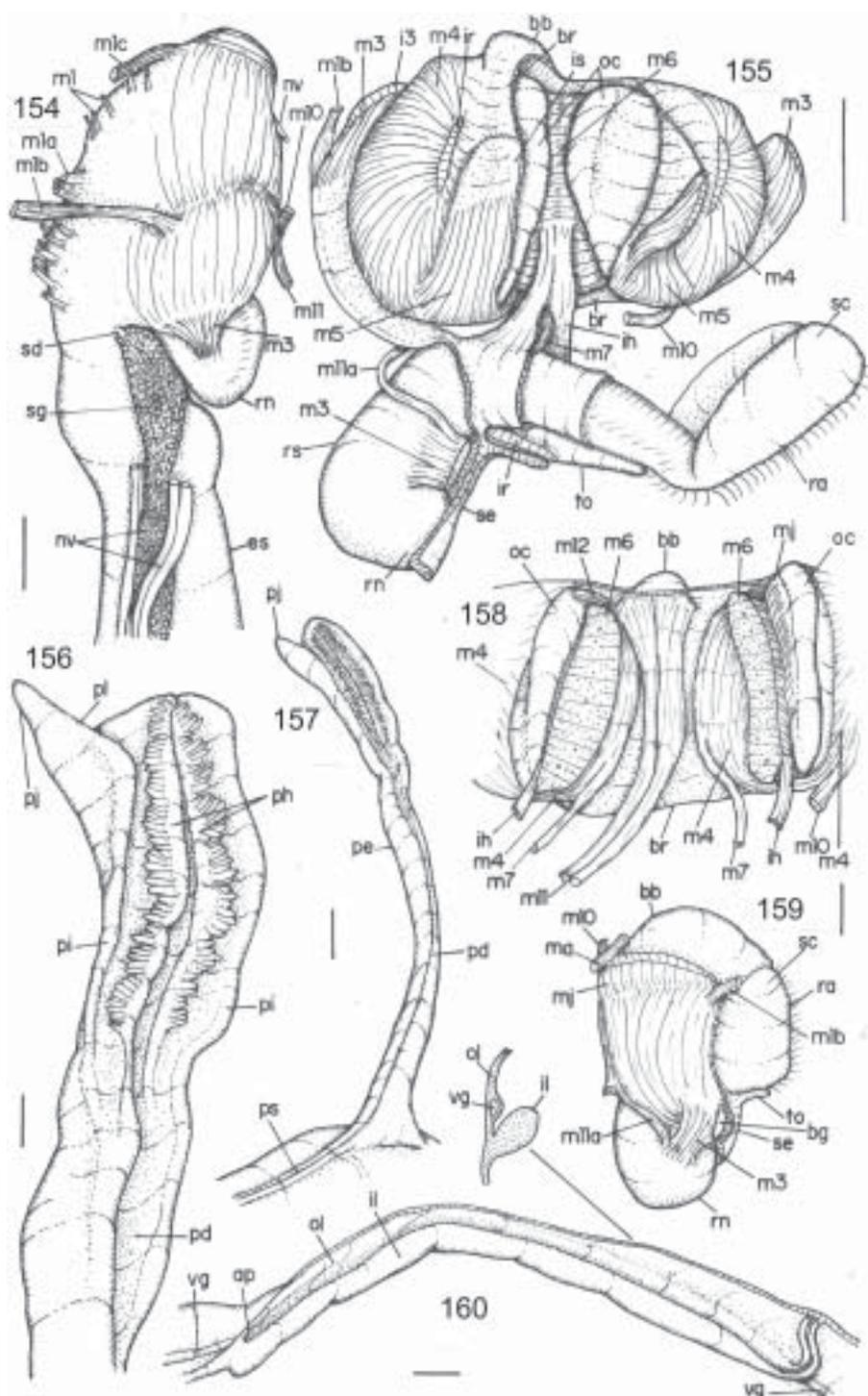
Circulatory and excretory systems (Fig. 150). Organization and site similar to those of *E. goliath*, inclusive with thin dorsal renal lobe and mesentery in intestinal loop. Differs in having taller nephridial gland and dorsal lobe simpler, without transversal folds.

Digestive system. Similar components and characters to those of *E. goliath*. In buccal mass (Figs. 151-155, 158, 159) differs in having m11a pair, branch of each m11 inserted in radular nucleus, close to ventral limit of m3 insertion; **m5** more ample connected to subradular membrane (br); **m11** insertion in br broader. Radula (Figs. 54, 55): rachidian broad, central cusp large, with about 1/3 of rachidian width, secondary cusps of considerable size (about half of central cusp size), vary from two to three pairs; lateral tooth somewhat triangular, curved, base broad, apex sharp and large, preceded by from four to five smaller cusps in lateral edge; marginal teeth similar to those of *E. goliath* but with about seven cusps. Salivary glands (Fig. 154) also anterior to nerve ring; their ducts visible only in anterior limit of salivary glands, in short distance penetrate in dorsal wall of buccal mass and run in base of local inner folds, open in their anterior region. Pair of dorsal buccal mass folds broad, narrowing suddenly posterior to buccal mass (Fig. 151). Esophagus very long, broad, thin walled, with morphological regions as in preceding species. Stomach similar to that of *E. goliath* but with more developed select area in dorsal surface, bearing several, longitudinal, uniform folds. Intestine similar to that of *E. goliath* inclusive loop in kidney chamber attached by mesentery (Fig. 150) and by papillate anus (Fig. 163).

Genital system. **Male** organs similar to those of preceding species. Pallial sperm groove practically entire opened (Fig. 160). Outer lamina thin, followed by well-developed pallial vessel. Inner lamina thick, elliptical in section, thinner in base. No median folds. Both laminae suddenly become similar sized, low, sigmoid in region where



Figures 147-153. *Aliger costatus* anatomy. 147. head-foot, male, frontal view; 148. pallial cavity and part of visceral sac, ventral view; 149. pallial cavity, transversal section in middle level of its roof; 150. anterior extremity of visceral sac and adjacent region of pallial cavity, ventral view, kidney and pericardium opened longitudinally, ventral kidney wall deflected to right (upwards in fig.); 151. buccal mass, opened by a longitudinal section in its left side, inner view; 152. odontophore isolated, ventral view; 153. same, dorsal view. Scales: 147-148 = 10 mm; 150 = 5 mm; 149, 151-153 = 2 mm.

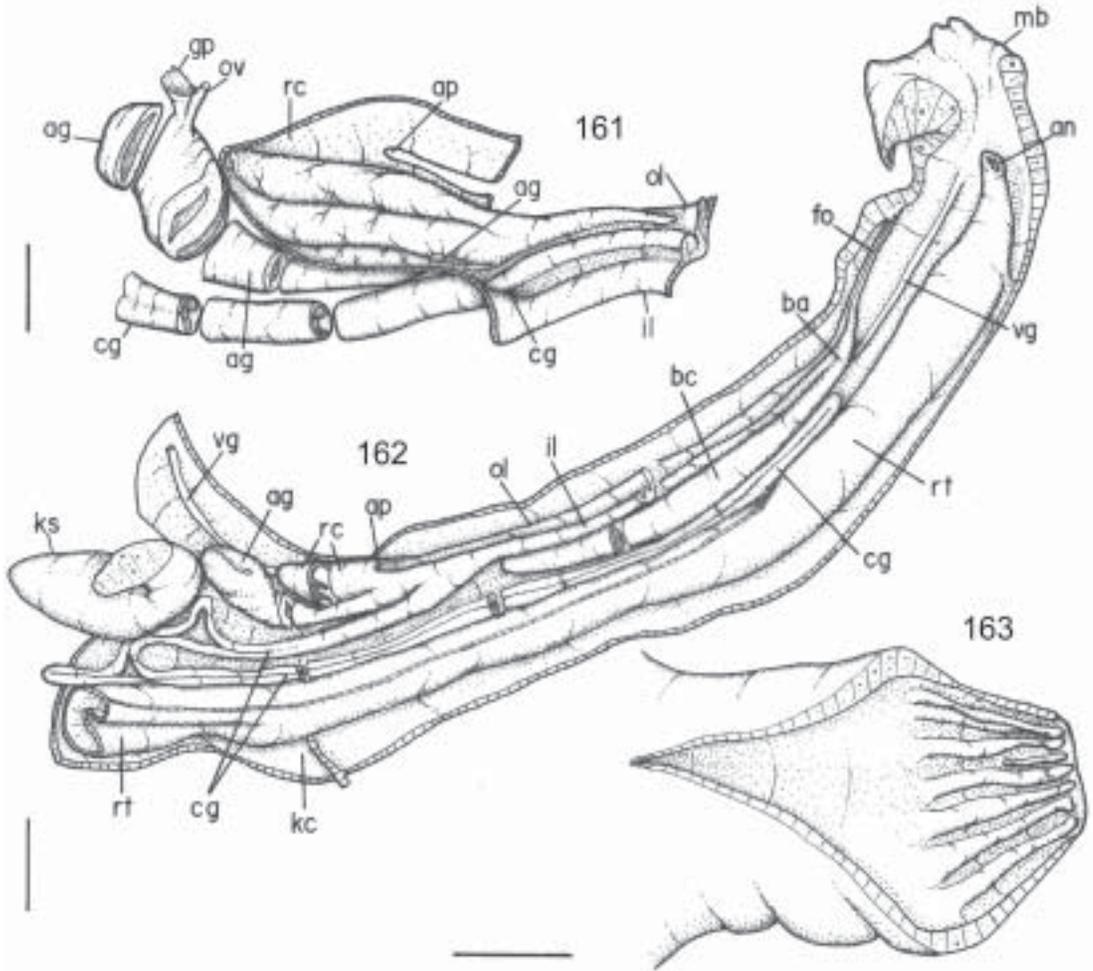


Figures 154-160. *Aliger costatus* anatomy. 154. buccal mass and anterior extremity of esophagus, lateral-right view; 155. odontophore, ventral view, several muscles deflected, exposing inner structures, m5 separated from its pair, right pair deflected, radula, radular sac and subradular membrane partially extracted and deflected downwards; 156. penis, detail of its apex; 157. penis, whole view; 158. detail of fig. 155 with m6 sectioned longitudinally, showing ventral surface of dorsal structures; 159. whole odontophore, lateral-left view; 160. pallial sperm groove, ventral view, with a detail of a transversal section in indicated region. Scales: 157, 160 = 5 mm; 154-156, 157-159 = 2 mm.

crosses to pallial floor. Penis similar to that of *E. goliath* but longer and slender (Figs. 147, 156, 157). Sperm groove opened in distal third part of penis, two pairs of folds appear; those external folds become borders of lateral concavity; those internal folds become glandular, with sinuous margin bearing several papillae in edge; between these inner folds slight deep furrow which ends near tip (Fig. 156). In opposite side of this concavity an oblique, tall fold, which begins gradually in distal 1/4 of penis and finishes connecting with concavity distal margin; in taller region bears outstanding projection (pj).

Female. Ovary and visceral oviduct similar to those of preceding species. Visceral oviduct

edges left margin of kidney on columellar muscle, inserts sub-terminally in ventral side of pallial oviduct, gonopericardial duct narrow just posterior to it. Pallial oviduct (Figs. 161, 162) similar to those of preceding species, with following distinctive characters: albumen gland beige in color, with two flattened inner ducts connected to each other in posterior region; seminal receptacle with very broad dorsal wall bearing three tall folds; capsule gland narrow but more sinuous, mainly in its region dorsal to kidney which bears several loops; insertion of capsule gland in pallial oviduct broader but simpler, without any chamber or additional loop; bursa copulatrix very long. Accessory mantle vessel parallel to pallial oviduct also present. Furrow at right



Figures 161-163. *Aliger costatus* anatomy. 161. pallial oviduct, posterior half, ventral view, some transversal sections artificially done, receptaculum opened longitudinally and its ventral wall deflected upwards, scale = 5 mm; 162. pallial oviduct, whole ventral view, kidney tissue removed and rectum posterior region deflected to show structures dorsal to them, scale = 10 mm; 163. anus, ventral view, partially opened longitudinally, scale = 2 mm.

of head-foot integument similar to those of preceding species. On development see Brownell (1977).

Measurements of shells (in mm). MZSP 28502, ♂ 1:124.5 by 102.5.

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

Habitat. In muddy or sandy-mud substrates, from 5 to about 50 m depth.

Material examined. BRAZIL. **Bahia;** Salvador; Banco da Panela, 16-20 m depth, 1♂, 1♀, MZSP 28462 (Simone col., 26/ii/1997); Ribeira beach, 5 m depth, 1♂, 1♀, observed alive, MZSP 28502 (Simone & fishermen col., 27/ii/1997); off Alcobaça, MZSP 31550, 1♂ (Coltro leg., viii/1999). **Rio de Janeiro;** Arraial do Cabo; Prainha, 1♀, MNRJ HSL 7416, 1♀, MNRJ 5943 (H.S. Lopes col., iii/1951); Forno beach, 1♀, MNRJ 5944, 1♀, MNRJ 5945 (Sá & Nunan col., 18/xii/1983).

Aliger gallus (Linné, 1758)
(Figs. 12, 56, 58, 164-177)

Synonymy see Matthews, 1980:68-69. Complement:

Strombus gallus: Melo, 1964:152; Walls, 1980:80 (Figs); Abbott & Dance, 1982:76 (fig.); Oliveira *et al.*, 1981:119; Alcolado, 1983:9; Rios, 1985:61 (pl. 22, fig. 274); Suty, 1986:13, 44 (Figs. 7, 45); Jong & Coomans, 1988:63; Ubaldi, 1990:73-80 (Figs. 70-79); Rios, 1994:68 (pl. 23, fig. 262); Merlano & Hegedus, 1994:157, (pl. 49, fig. 572); Abbott & Morris, 1995:184 (pl. 50).

Description

Shell (Fig. 12). Well characteristic shell with long and tubular anal siphon, described in Matthews (1980:70-74, Figs. 2a-f).

Head-foot (Figs. 164, 167). All head-foot structures similar to those described by preceding species, differs in having darker color in exposed areas and male with long and slender penis.

Operculum. Similar to that described for *A. costatus*.

Mantle organs (Figs. 165, 166, 168). Organization and components also similar to those described for preceding species, distinctive features following. Mantle border with siphon and anal projections long, slightly thick muscular, pale cream in color. Osphradium narrow, long, anterior half

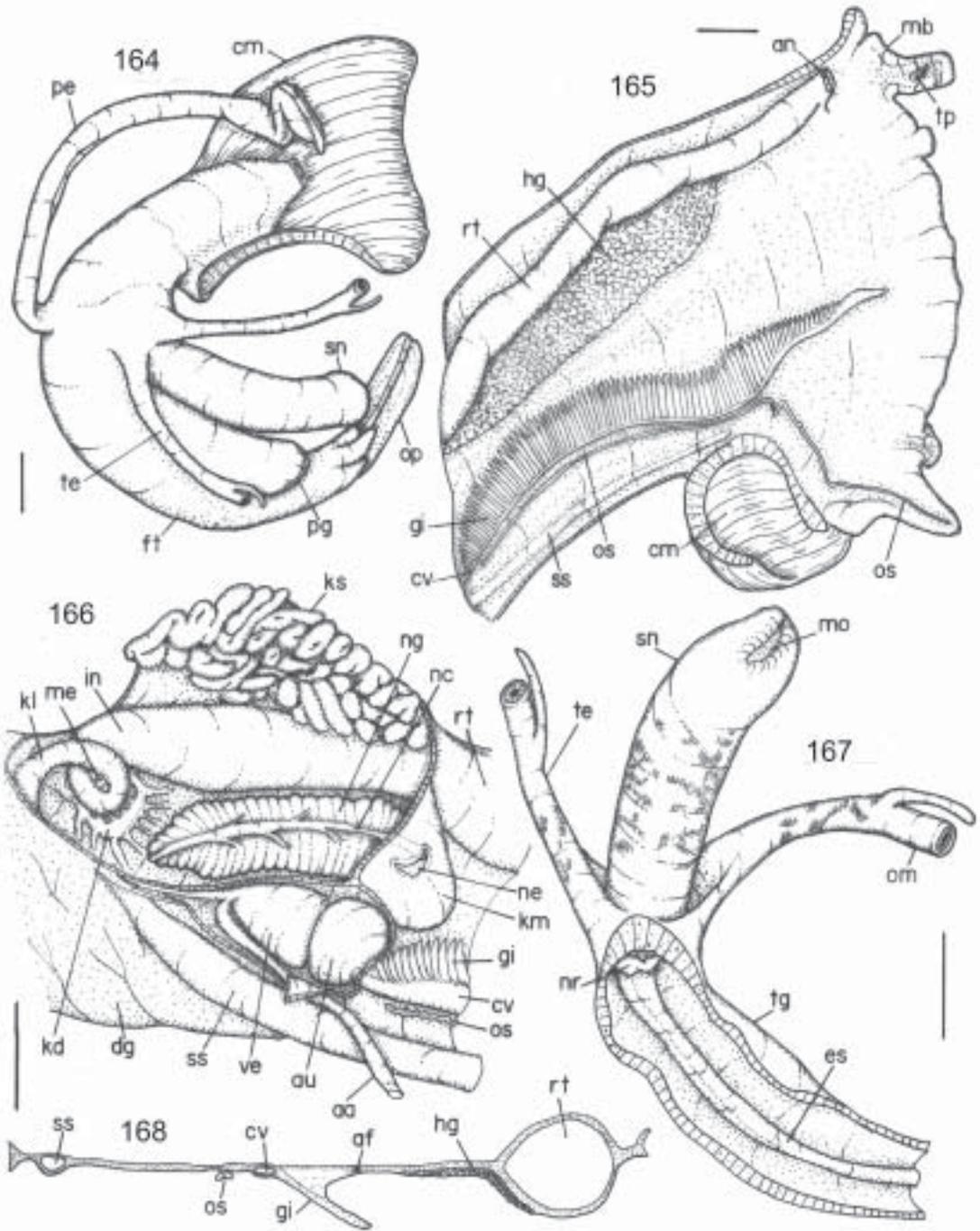
gradually deflecting from gill somewhat sinuously, running in center of siphon until near its distal border; posterior half of osphradium close to gill, finished in about same level than posterior gill limit. Gill long – about 7/8 of pallial cavity; near mantle border also short, broad, septum-like anterior extremity with leaflets missing; leaflets beginning gradually at some distance from anterior extremity; gill leaflets triangular, not so tall, curved to right, somewhat broad base, taper suddenly, tip sharp and long. Between gill and rectum proportional broad space (about twice gill base). Hypobranchial gland occupying posterior-right region of space between gill and rectum and part of left rectum surface, glandular tissue thin, surface uniform. Pallial tentacle anterior to anus present. Rectum long and broad. Anus siphoned, presenting some small papillae in its margin, sited in base of anal siphon. Pallial gonoducts running in posterior 3/4, between rectum and right margin of pallial cavity, both described below.

Circulatory and excretory systems (Fig. 166). Organization and site similar to those of *A. costatus*, but with dorsal renal lobe thinner and with marginal expansions.

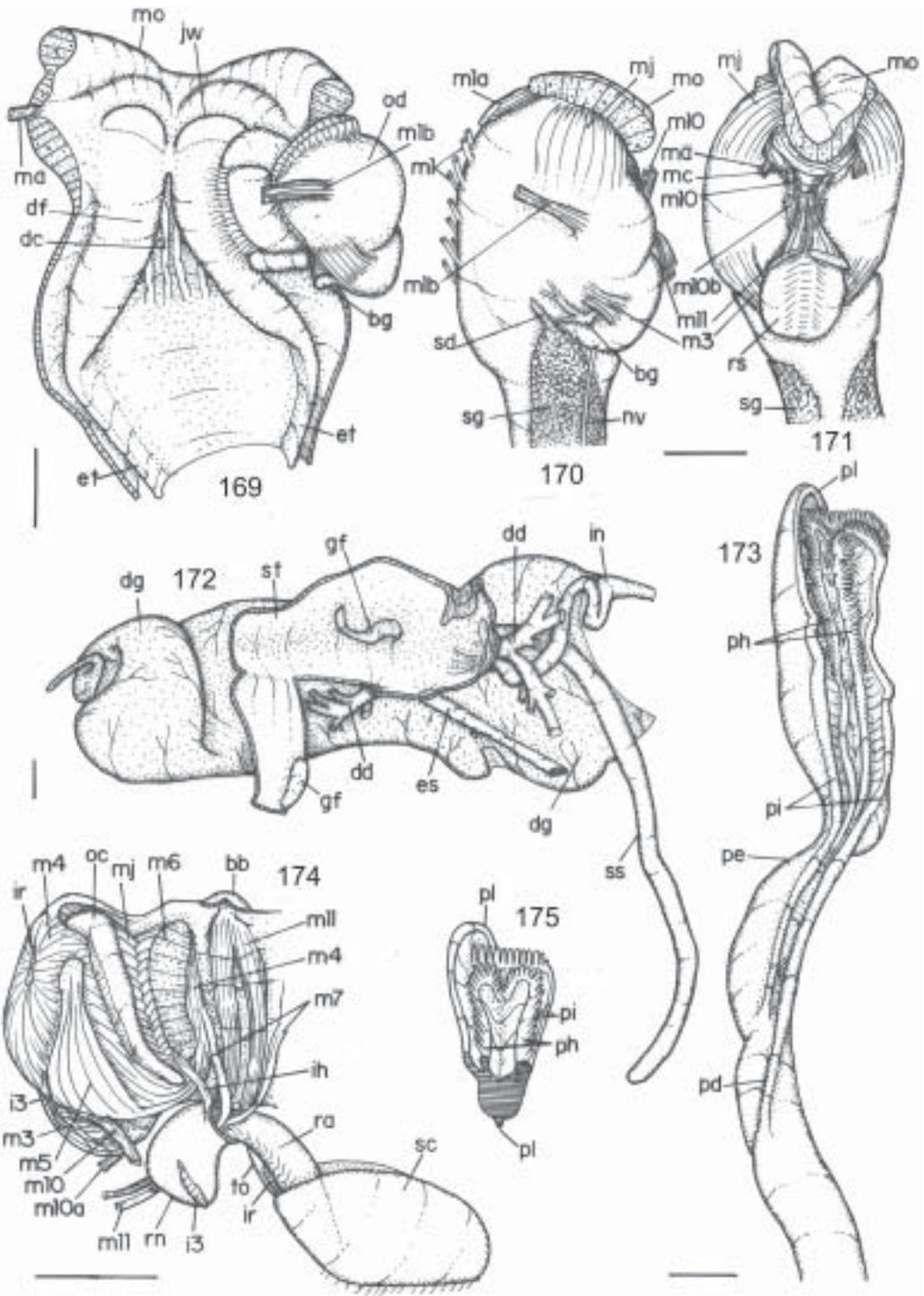
Digestive system. Similar components and characters to those of preceding species. Odontophore (Figs. 169-171, 174) as described for *E. goliath* and *A. costatus*, except in lacking m11a and in having m10b pair, small and thin, originating in ventral snout inner surface near median line, inserting, in short distance from their origin, in median region of membrane covering odontophore (which origins m3), just anterior to m10. Radula (Figs. 56, 58): very similar to that of *A. costatus*, only differing in marginal teeth, which present about five cusps. Dorsal wall of buccal mass (Fig. 169) with pair of folds very broad, each one originating near each jaw plate; between both folds a chamber with longitudinal, uniform, low folds; these folds faint before anterior esophagus. Salivary glands also anterior to nerve ring; their ducts visible only in anterior limit of salivary glands, in short distance penetrate in dorsal wall of buccal mass (Figs. 170, 171) and run in base of local inner folds, open in their middle-anterior region. Esophagus very long (Fig. 167), broad, thin walled. Esophagus inner surface with pair of typhlosoles in anterior half as in preceding species. Stomach (Fig. 172) similar to that of *E. goliath*, but with single arched fold in middle region of its dorsal wall and other elliptical

fold in approximately opposite (ventral) side; anterior duct to digestive gland broad and more left sited, in intermediary level between style sac and

intestine origin; series of radial, low folds in region near intestine origin. Intestine (Fig. 172) running immerse in digestive gland, surrounding style



Figures 164-168. *Aliger gallus* anatomy. 164. head-foot, male, frontal view; 165. pallial cavity, ventral-inner view, gonoducts not shown; 166. anterior extremity of visceral sac, ventral view, pericardium and kidney opened longitudinally, ventral kidney wall deflected to right (upwards in fig.), in this specimens the intestinal loop within kidney is small, but generally it is large; 167. head and part of haemocoel, ventral view, foot and columellar muscle removed; 168. pallial cavity, transversal section of middle level of its roof. Scales = 5 mm.



Figures 169-175. *Aliger gallus* anatomy. 169. buccal mass opened longitudinally in its right side, inner-ventral view of its dorsal wall and lateral view of odontophore; 170. buccal mass, lateral-right view; 171. same, ventral view; 172. whole visceral mass, anterior region in ventral view, ventral wall of stomach partially removed and deflected downwards, adjacent gastric tubes shown if the digestive gland was transparent, style sac whole shown, even its pallial region; 173. penis, middle and apical regions; 174. left half of odontophore, left view, m6 sectioned longitudinally, radula and adjacent structures extracted and deflected downwards; 175. penis, semi-diagrammatic representation of its apical region. Scales = 2 mm.

sac insertion, crossing from left to right side between style sac and duct to digestive gland until posterior-right border of kidney, free loop within kidney chamber, connected internally by mesentery (Fig. 166); running at right marginal to kidney and pallial cavity as above described.

Genital system. Male organs similar to that of *A. costatus*, but with penis longer (Fig. 164). Internal folds of penis distal region also papillate, but with papillae slender; papillate (Figs. 173, 175) folds contour distal penis margin and approach with each other in middle region. In this distal margin outer fold also bears several papillae similar to those of inner folds. In opposite side of these folds an oblique, tall fold (pl), beginning gradually in distal 1/4 of penis, finishing connecting with concavity distal margin, no projections present.

Female. Female genital organs and glands very similar to those described for *A. costatus*, with following distinctive or notable features (Figs. 176, 177): 1) albumen gland broader since its beginning, with ampler duct; 2) albumen gland beginning with two or three irregular whorls; 3) seminal receptacle

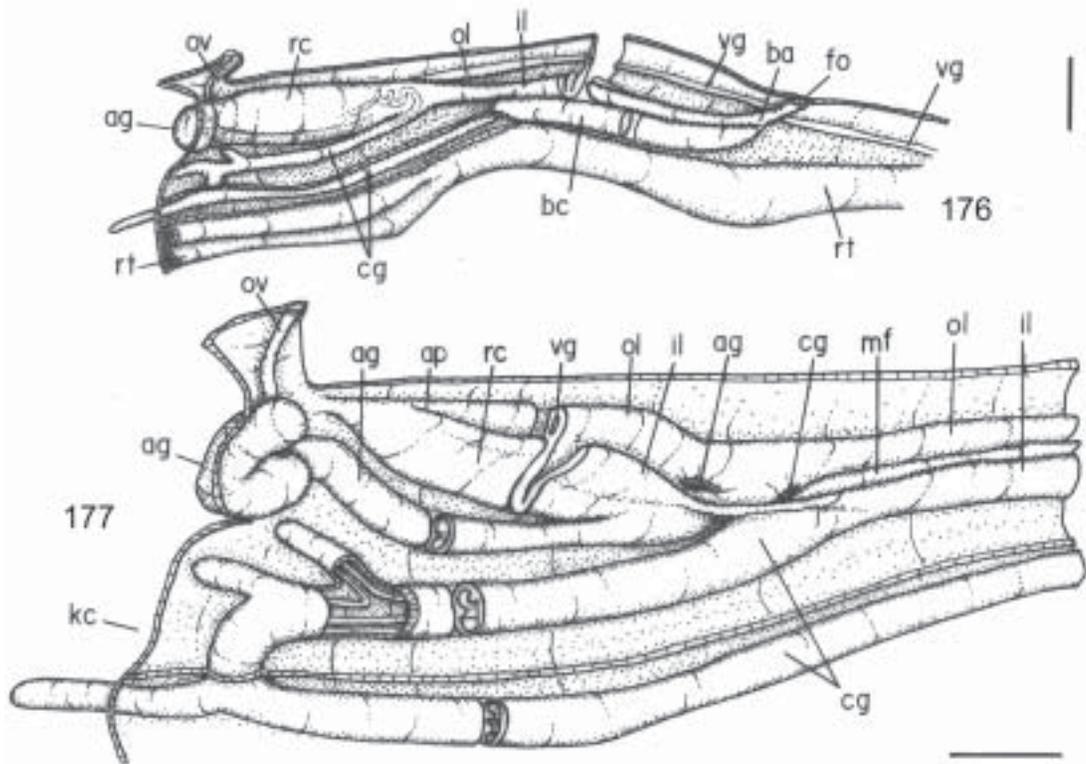
opened by ventral long aperture; outer lamina not folded, thick-glandular; inner lamina thin; 4) capsule gland "U"-shaped, curve posterior close to kidney, left branch running dorsal to rectum; 5) three blind-sac posterior projections in capsule gland, left projection longer, part running dorsal to kidney; 6) dorsal inner surface of capsule gland with pair of parallel, longitudinal folds, only outer fold entrances in projections; 7) pallial oviduct attached direct in mantle somewhat short, about half of pallial cavity length crosses to pallial floor; 8) aperture degree of pallial oviduct larger, being opened since posterior region of receptacle.

Measurements of shells (in mm). MZSP 28560♀ : 116.5 by 57.8; 28779♂ , 128.0 by 59.3.

Habitat. In muddy or sandy-mud substrates, from intertidal zone to about 50 m depth.

Distribution. Florida, USA, to Espirito Santo, Brazil.

Material examined. BRAZIL. Bahia; Salvador; Baia de Todos os Santos, 1♂ observed alive, MZSP 28560 (B.L. Albuquerque col., ii/1997);



Figures 176-177. *Aliger gallus* pallial oviduct. 176. whole ventral view, posterior region of rectum deflected to show parts dorsal to it, scale = 5 mm; 177. enlarged magnification, posterior region, some transversal sections artificially done, scale = 2 mm.

1♀, MZSP 28712 (L. Trinchão col.); 2♂, 1♀, MZSP 28779 (M. & J. Coltro leg); off Alcobaça, MZSP 31556, 1♂, 1♀ (Coltro leg., viii/1999).

Genus *Tricornis* Jousseau, 1886

(New stratum; type species *S. tricornis* Lightfoot, 1786)

Tricornis raninus (Gmelin, 1791)
(Figs. 21-22, 178-189, 377, 378)

Synonymy see Matthews, 1980:84-85. Complement:

Strombus (Tricornis) raninus: Matthews, 1980:84-90 (Figs. 4a-g); Walls, 1980:85 (Figs); Abbott & Dance, 1982:76 (fig.); Rios, 1985:62 (pl. 22, fig. 276); Jong & Coomans, 1988:63; Davis *et al.*, 1993:236-243 (figs. 3-4); Rios, 1994:69 (pl. 23, fig. 264); Merlano & Hegedus, 1994:157 (pl. 49, fig. 573); Seyer, 1994:200-207; Abbott & Morris, 1995:185-186 (pl. 50).

Description

Shell (Figs. 21-22). Somewhat similar to that of *A. gallus*, differing mainly in lacking long anal projection of outer lip and by thicker walls. Other details see Matthews (1980:85-89), protoconch see Davis *et al.* (1993).

Head-foot (Fig. 178). Very similar to those of preceding species. Especial reticulation of integument, present in *Eustrombus* and *Aliger* spp, of dorsal foot surface absent. Snout narrow and very long, smooth anterior margin. Penis and female genital furrow described below.

Operculum (Fig. 180). Somewhat similar to those of *S. pugilis*, except for absence of well-developed marginal spines. However, localization of correspondent spines still visible between small concavities (in inner surface) along outer operculum margin.

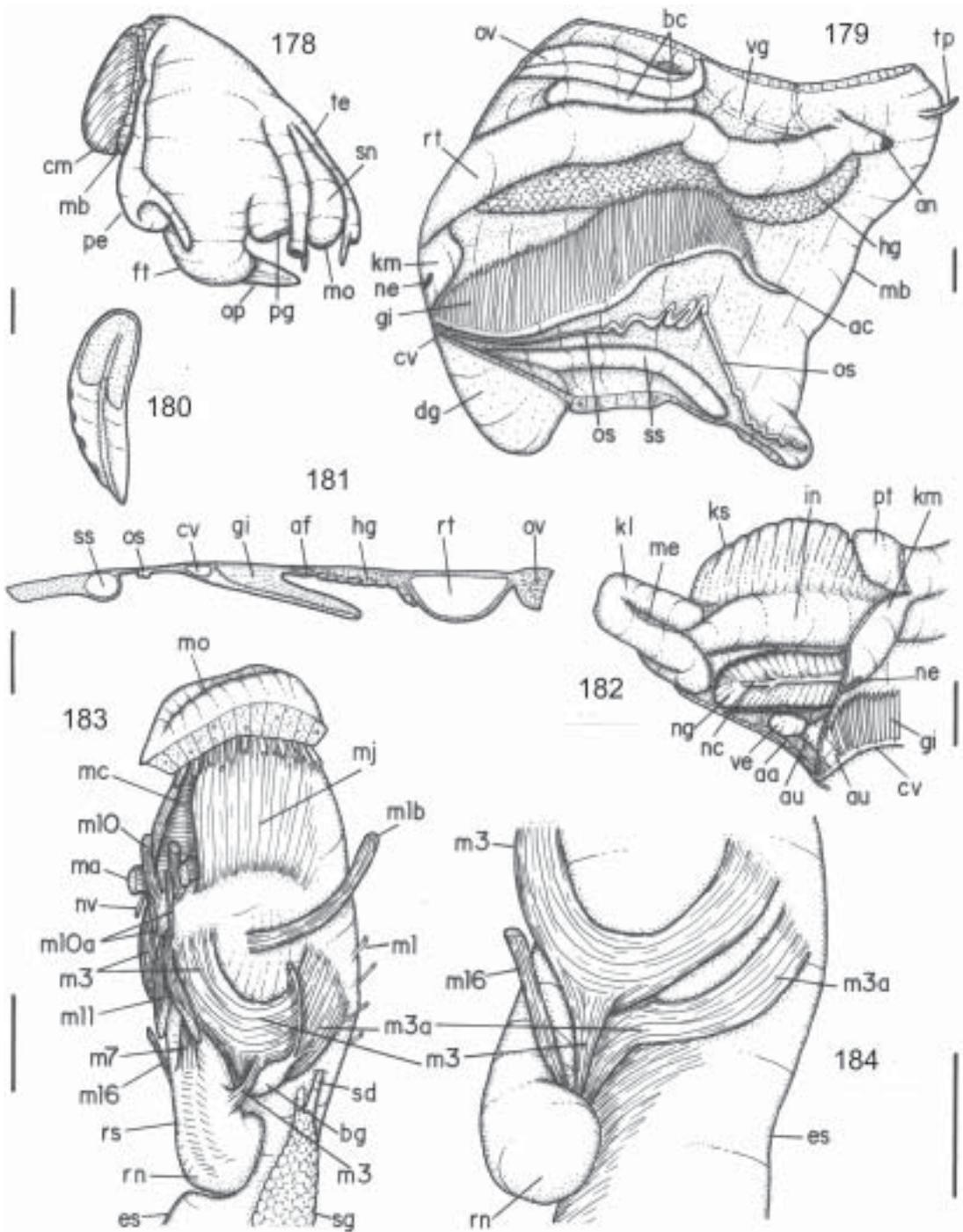
Mantle organs (Figs. 179, 181, 189). Slightly similar characters to those of *A. costatus*, with following distinctive features. Osphradium very sinuous, mainly in anterior region and in middle region, where it approaches from gill; in this region very strong sinuosity. Posterior third part of osphradium very narrow, compressed between ctenidial vein and style sac; osphradium leaflets of this region difficult to be seen in some specimens. Gill filaments long, with rounded tip. Pallial tentacle present, located in right region of mantle bor-

der just anterior to anus, somewhat long (Figs. 179, 189).

Circulatory and excretory systems

(Fig. 182). Both similar to those of preceding species, distinctive or notable features following. Pericardium part located dorsal to posterior region of gill. Auricle triangular, connected to ctenidial vein before its posterior end, i.e., small portion of ctenidial vein as bind-sac present. Ventral kidney lobe, connected to intestine, large, comparable to those of *Eustrombus* and *Aliger* spp. Dorsal kidney lobe thin, occupying almost entire dorsal surface between intestine and nephridial gland. Intestinal loop with mesentery present. Nephridial gland large, its location and central vessel as described for preceding species.

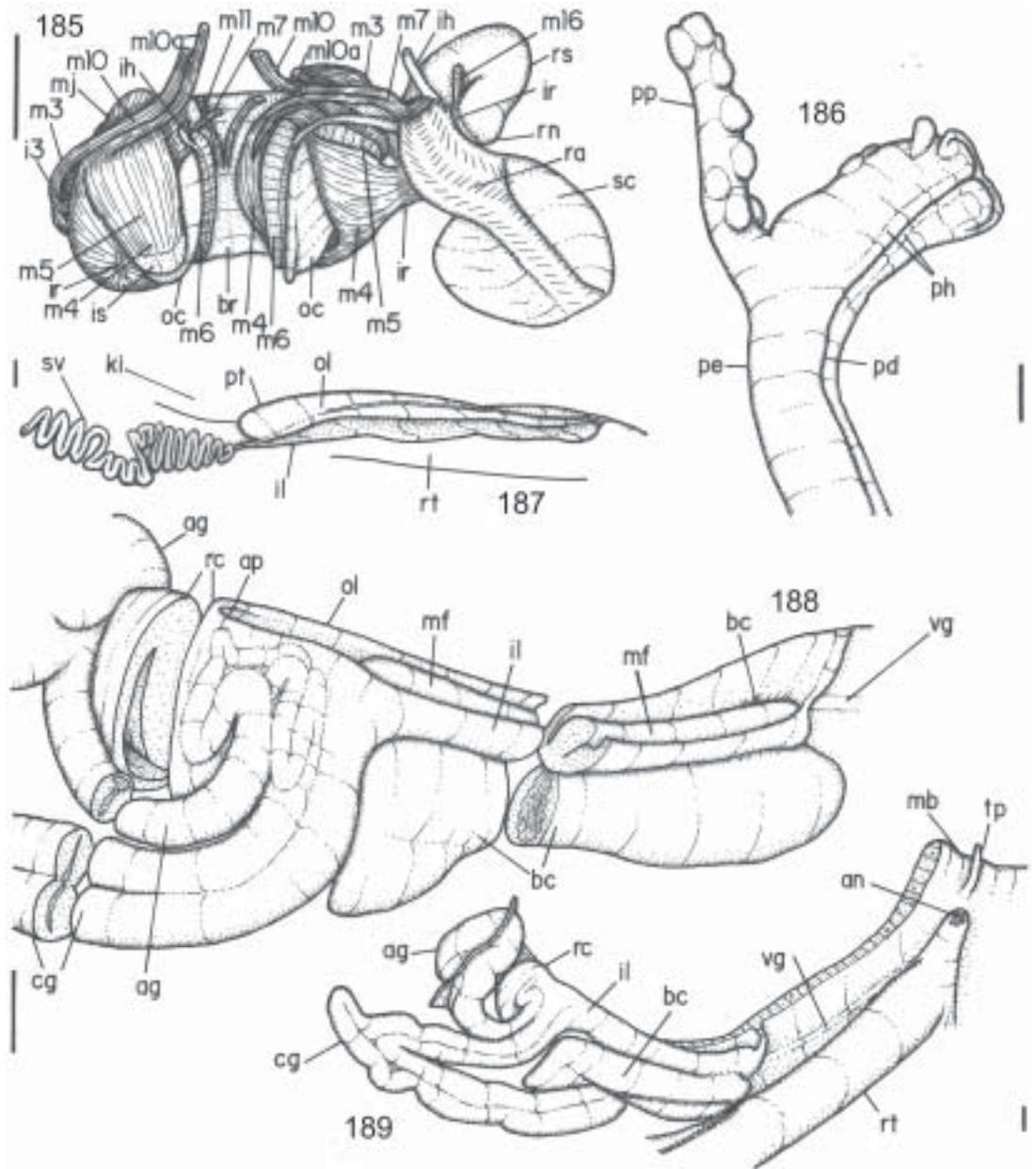
Digestive system. Buccal mass characters similar to those of *A. costatus*, notable or distinctive features following (Figs. 183-185): **m1b** and **ma** present; **m3** double pair, pair more anterior, in form of lateral-posterior arches surrounding posterior region of odontophore, from ventral to dorsal surfaces; muscular branch connects both m3 crossing just dorsal to radular nucleus; other pair more posterior, beginning in dorsal surface surrounding posterior border of anterior pair, connect with each other just dorsal to radular nucleus attached to esophageal wall; some transversal muscular fibers spray by ventral wall of esophagus beyond m3, up to level posterior to radular nucleus; **m10a** present, insertion covered by m3; **m11** originating very broad, inserting in posterior region of br (and not in anterior region); **m11a** small and narrow pair, originating in snout ventral inner surface adjacent to radular nucleus, running dorsal and posterior, insert close to median line in dorsal surface of radular nucleus. Radular teeth (Figs. 377, 378): similar to those of *Eustrombus* and *Aliger* species, cusp formula: 5, 4, 6. Esophagus characters similar to those of *E. goliath*, but generally presenting very tall pair of folds in anterior esophagus and secondary folds (beyond that pair normally large) taller in middle esophagus. Salivary glands small, anterior to nerve ring; their aperture in middle region of dorsal folds of buccal mass. Stomach similar to that of *A. costatus*, but shorter in antero-posterior direction and broader laterally; posterior duct to digestive gland broader and bifurcated in short distance, almost double; ventral gastric folds present; dorsal gastric fold narrower and double, beginning just posterior to



Figures 178-184. *Tricornis raninus* anatomy. 178. Head-foot, male, frontal view, mantle and visceral mass extracted; 179. Pallial cavity, ventral-inner view; 180. Operculum, inner view; 181. Pallial cavity, transversal section in its middle region; 182. Kidney, pericardium and adjacent region of pallial cavity, ventral view, kidney and pericardium opened by a longitudinal section in each, intestinal loop inside kidney and ventral renal lobe deflected; 183. Buccal mass, extracted, lateral-right view; 184. Same, detail of region between buccal mass and esophagus. Scales: 183-184 = 2 mm, others = 5 mm.

stomach posterior limit, running as typhlosole along dorsal gastric inner surface and along adjacent intestinal loop. Intestinal loops (included that of kidney connected by mesentery), rectum and anus characters very similar to those of preceding species.

Genital system. Male (Figs. 178, 186, 187). Testis similar to those of preceding species. Seminal vesicle convolute, running approximately in middle ventral region of visceral mass, at left from kidney. Prostate gland well-developed, long, broad in its posterior end close to anterior-ventral sur-



Figures 185-189. *Tricornis raninus* anatomy. 185. Odontophore, ventral view, both cartilages deflected, horizontal muscle (m6) sectioned, right muscles (left in fig.) extracted from radular sac; 186. Penis, ventral view, detail of apical region; 187. Middle male genital organs, ventral view (shown half whorl after and half before posterior end of pallial cavity); 188. Pallial oviduct, ventral view, 2 transversal sections artificially done showing inner organization; 189. Pallial oviduct in situ, and part of pallial cavity anterior to it. Scales = 2 mm.

face of kidney; gradually narrows along distance equivalent to half of pallial cavity length; almost entirely opened as furrow, only tubular in its posterior end. Penis long, basal 2/3 narrow and cylindrical. Penis distal region broader and slightly flattened; long, large and cylindrical papilla in lateral margin, inserted approximately in opposite side of penis furrow and removed from penis distal end. Penis furrow running up to penis distal end and bifurcates in "T" shape edging distal margin. Some slightly spherical small glands distributed along papilla and lateral region of penis distal end.

Female (Figs. 188, 189). Visceral and pallial organs similar to those of preceding species. Distinctive or notable features of pallial oviduct following. Albumen gland very convolute in its posterior region, producing bulged volume of about half of its length. Seminal receptacle very short, broad, glandular walls, outer wall thicker and convex, entirely closed (tubular), aperture anterior-right. Capsule gland "U"-shaped, about half running dorsal to kidney, projection single, posterior. In inner lamina of pallial oviduct, just in insertion of albumen and capsule gland, several glandular coils. Median fold of pallial oviduct present. Bursa copulatrix long, corrugate inner surface, walls relatively thick-glandular, aperture sub-terminal, at right. Remainder of oviduct (running in pallial floor and head-foot) similar to those of preceding species, anterior end of this in continuation to furrow of pedal glands.

Measurements of shells (in mm). AMNH 91203♀ (5): 90.0 by 63.4.

Distribution. New Carolina, USA to Rio Grande do Norte, Brazil.

Habitat. Subtidal muddy and sandy bottoms.

Material examined. TAHITI; **Port-au-Prince**, AMNH 91203, 2 males, 6 females (A. Curtiss leg. i/1950).

Discussion. Although there are clear conchological similarity between *T. raninus* and *A. gallus*, the characters of inner anatomy allow a closer relationship of *A. gallus* with *A. costatus* rather than with *T. raninus*. For example, *T. raninus* presents the following main characters differing from those 2 species: 1) absence of reticulate integument in dorsal foot surface; 2) osphradium more sinuous; 3) pericardium more anteriorly removed; 4) odontophore muscle m11 inserted more posteriorly, removed from bulged

part of subradular membrane (bb); 5) distal region of penis with a lateral papilla far from penis groove; 6) absence of penis small papillae along penis furrow margins; 7) shorter pallial oviduct with a shorter receptacle and aperture of the bursa more posterior. On the other hand no observed characters approach *T. raninus* from the 2 *Aliger* species, neither from the 2 *Eustrombus* species. All these 5 Western Atlantic species were up to now included within the genus *Tricornis* (Rios, 1994). For this reason, *T. raninus* is maintained as *Tricornis* until a better knowledge of supra-specific taxa, while the other species were removed to other genera.

Genus *Conomurex* P. Fisher, 1884

(New stratum, type species *S. luhuanus* Linné, 1758)

Conomurex luhuanus Linné, 1758

(Figs. 190-202, 376, 383)

Synonymy see Abbott, 1960:136. Complement: *Strombus (Conomurex) luhuanus*: Wilson & Gillett, 1972:38 (pl. 17, fig. 5); Walls, 1980:144 (Figs); Abbott & Dance, 1982:80 (fig.); Yamaguchi, 1994:107-111; Reed, 1995b:159-160; Watters & Valentine, 1994:8-9; Ishii, 1997:646-647; Morton, 1997b (fig. 5:2; fig. 7:2); Wiedemeyer, 1998:1-7 (figs. 1-5).

Description

Shell (Fig. 383). Very small spire, aperture long and narrow, somewhat similar to shell of conids (Conoidea). Strombid notch of outer lip well-developed. Other details see Abbott, 1960:135-136.

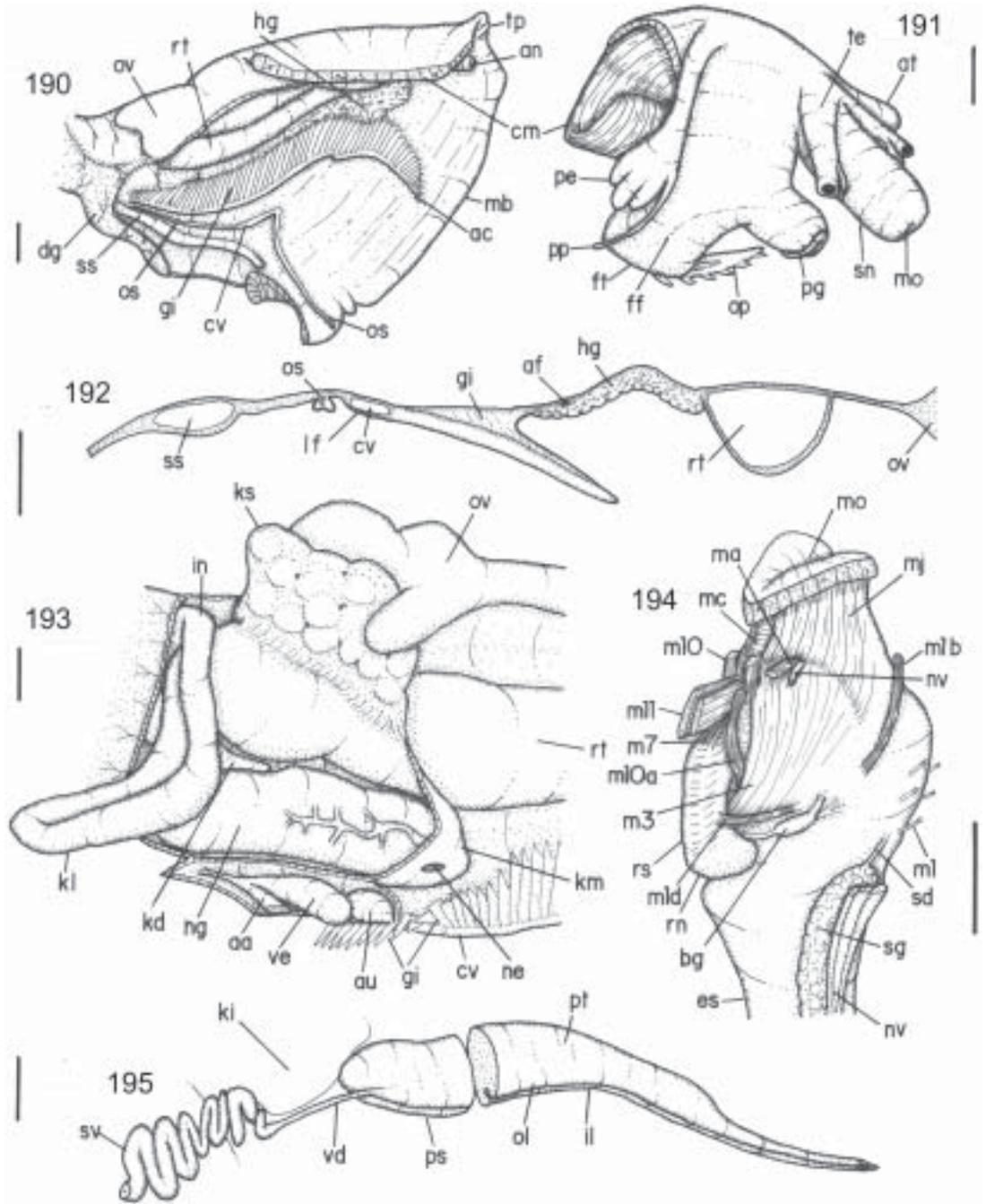
Head-foot (Fig. 191). Very similar characters to those of preceding strombids. Dorsal integument of foot smooth (not reticulate). Anterior surface of snout smooth (not papillate). Anterior muscular projection at left from head present, turned forwards. Other details in Abbott (1960, pl. 110).

Operculum (Fig. 191). Similar features than that of *S. pugilis*, with spines in outer surface (See also Abbott, 1960, pl. 112-6).

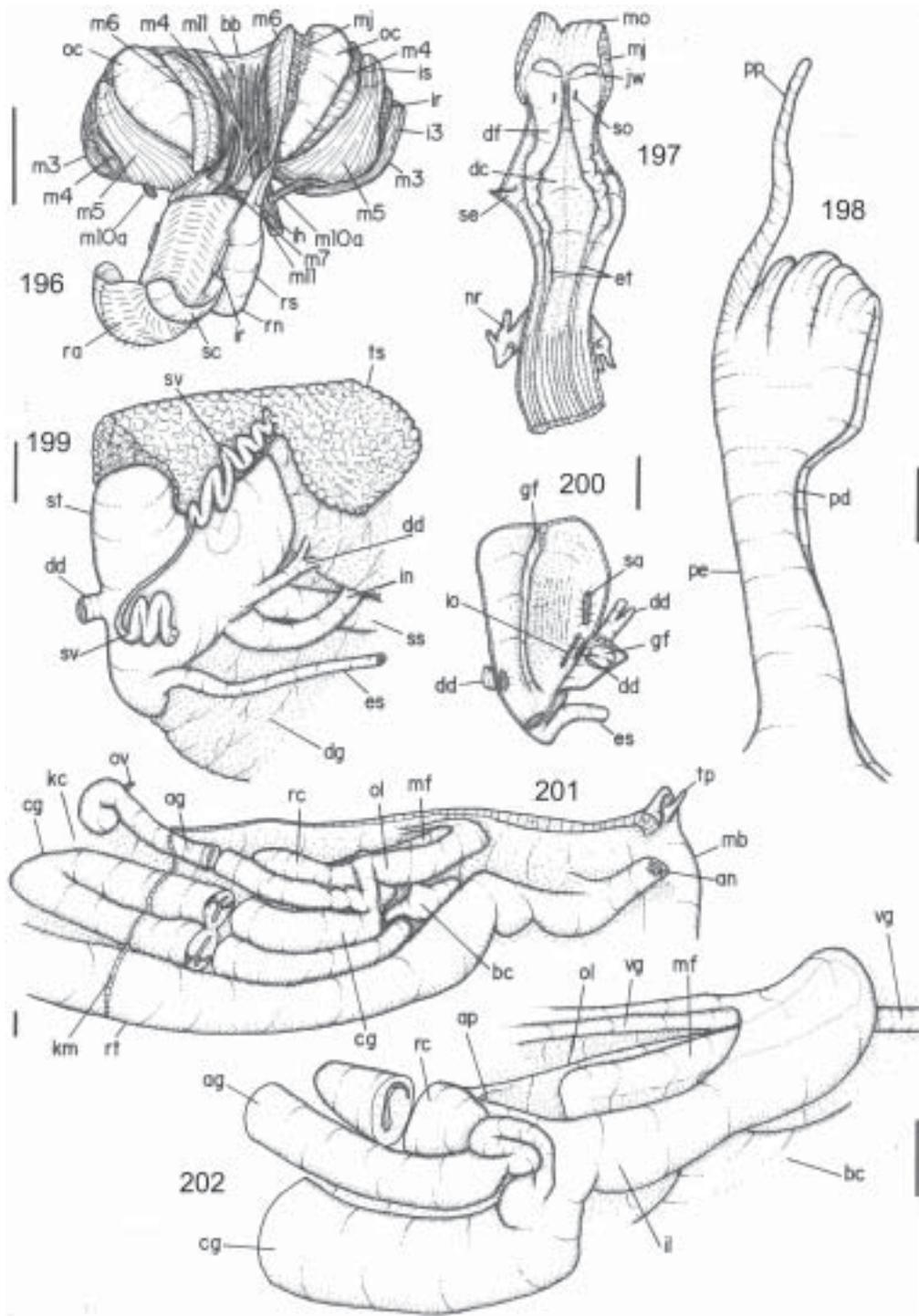
Mantle organs (Figs. 190, 192, 193, 201). General characters similar to those of *S. pugilis*, differences and notable characters following. Pallial tentacle in front of anus present. Osphradium with strong angle in its middle region. Osphradium

posterior region very narrow, its posterior end almost in same level than that of gill. Gill filaments with broad base; suddenly narrow after base, distal

2/3 region narrowing gradually. A considerable part of visceral mass encroaches to right-posterior region of pallial cavity.



Figures 190-195. *Conomurex luhuanus* anatomy. 190. Pallial cavity, ventral-inner view; 191. Head-foot, frontal view, mantle and visceral mass extracted; 192. Same, transversal section in its middle region; 193. Kidney, pericardium and posterior region of pallial cavity, ventral view, kidney and pericardium opened by longitudinal section in each, intestinal loop inside kidney and ventral renal lobe deflected; 194. Buccal mass, extracted, lateral-right view; 195. Middle male genital organs, ventral view (shown half whorl after and half before posterior end of pallial cavity). Scales: 190-191 = 5 mm, others = 2 mm.



Figures 196-202. *Conomurex luhuanus* anatomy. 196. Odontophore, ventral view, both cartilages deflected, horizontal muscle (m6) sectioned, radular sac extracted from m4 and m5 insertions and deflected downwards; 197. Dorsal wall of buccal mass and anterior esophagus, ventral view, esophagus opened longitudinally; 198. Penis, dorsal view; 199. Stomach and adjacent region of visceral mass anterior to it, ventral view, part of digestive gland removed; 200. Stomach opened longitudinally, ventral view; 201. Pallial oviduct and adjacent structures, ventral view, a transversal section artificially done showing inner organization; 202. Same, detail of its middle and anterior regions, a transversal section done in seminal receptacle. Scales = 2 mm.

Circulatory and excretory systems

(Fig. 193). Pericardium and heart with similar characters to those of preceding species, except in being more removed to anterior, part located dorsal to posterior end of gill. Auricle connection with ctenidial vein subterminal, i.e., with short posterior portion of ctenidial vein, as blind sac, present. Kidney also similar to those of preceding species, distinctive and notable features following. Intestinal free loop, connected by mesentery, present. Ventral lobe large, surface irregular, connected to adjacent intestine by slightly thin and tall fold. Dorsal lobe small and thin. Nephridial gland large (comparable in size with ventral lobe), long, somewhat smooth surface, central longitudinal vessel, inserted ventral and at right to nephrostome, present.

Digestive system. Buccal mass and odontophore characters similar to those of *S. pugilis*, with following distinctive and notable features (Figs. 194, 196, 197). Jaws relatively large. Dorsal folds of buccal mass broad, with aperture of salivary glands slightly long, located in anterior region, closer to median margin Dorsal chamber shallow. Odontophore muscles: **m1b**) present; **m1d**) narrow and small pair, originating in posterior-lateral surface of m3, inserting in lateral surface of radular sac just anterior to radular nucleus; **ma**) present; **m3**) united with its pair anterior to radular nucleus, without connection with this; **m10** and **m10a**) present, being m10a covered by m3; **m11**) broad in origin. Radula also similar to those of preceding species (Fig. 376); rachidian tooth with 5 cusps, central cusp triangular, about 3 times large than neighbors, lateral reinforcements as additional pair of cusps present in most of teeth; lateral tooth with about same width than rachidian, generally with 5 cusps, median cusp larger (several times larger than neighbors), terminal, triangular, long; inner and outer marginal teeth similar with each other, slightly broad, long, curved, tip sharp and triangular, 3 subterminal, small cusps in inner margin (other details in Abbott, 1960, pl. 112, Figs. 1-4). Salivary gland small, anterior to nerve ring. Esophagus characters similar to that of *S. pugilis*, anterior esophagus smooth except for pair of (main) folds (continuation from those of dorsal wall of buccal mass); in level of nerve ring and middle esophagus several additional, longitudinal, narrow folds appear, between both main folds smooth surface; posterior esophagus with about 8

similar sized, longitudinal folds (being a pair continuation of main folds).

Stomach large, somewhat triangular, irregular outer surface (Figs. 199, 200); esophagus inserts in left-posterior region; anterior duct to digestive gland slightly narrow, located about in middle region of posterior surface; about in middle region of left-anterior surface 3 connections: 1) posterior duct to digestive gland ventral and slightly narrow, 2) intestine in middle and slightly at left and 3) style sac dorsal and broad. Portion of stomach located anterior and at right from these 3 connections. Stomach inner surface (Fig. 200) most smooth except for 1) ventral fold (similar to those of preceding species) in "U" shape, 2) gastric shield in dorsal-anterior surface, elliptical, with some low transversal folds and 3) slightly tall transversal fold which edges posterior surface of gastric shield. Intestinal loops, style sac situation, digestive gland, rectum and anus characters very similar to those of preceding species.

Genital system. Male. Testis, as in preceding species, located in right region of visceral mass (Fig. 199), color clear beige, anterior limit about 1/4 whorl anterior to that of stomach. Seminal vesicle beginning in right-anterior region of ventral surface of visceral mass, running with some coils towards posterior and left, crossing posterior region of gastric ventral surface as narrow, not-convoluted tube, after newly becomes convolute, running in median region towards anterior, edges left limit of kidney (Figs. 195, 199). Vas deferens becomes narrow, slightly straight tube before its aperture in pallial cavity posterior-right region. Prostate gland (Fig. 195) broad, long, with shallow furrow in its left margin, narrows gradually. Pallial sperm furrow crossing to pallial floor approximately between anterior and middle third parts of cavity length. Penis stubby, slightly broad (Figs. 191, 198). Basal 2/3 region narrower, almost cylindrical. Distal 1/3 region broad, slightly flattened; penis groove finishes in outer margin of penis tip; in opposite side very long and narrow papilla, section almost circular, tip rounded, covered by superficial, oblique, narrow furrows; between papilla and penis groove end a broad, flattened region, with some transversal, superficial furrows in both sides (ventral and dorsal), 2 of these furrows generally deeper, producing 3 folds in this region. (Other details of penis in Abbott, 1960, pl. 112-5).

Female (Figs. 201, 202). Visceral organs similar in characters to those of preceding species. Pallial oviduct with fashion also similar to those of preceding species, distinctive and notable features following. Albumen gland very long, coiled posterior part relatively short. Seminal receptacle elliptical, entirely tubular (closed), broad inner glandular fold in outer surface. Capsule gland "U"-shaped, without projections. Few glandular coils in inner lamina of pallial oviduct in region of insertion of albumen and capsule glands. Portion of pallial oviduct between these insertions and its cross to pallial floor very short (about half of albumen gland length); its anterior end as blind-sac and after as furrow turned posteriorly. Median fold present, but also short. Bursa copulatrix short, slightly elliptical; its aperture in middle region of its right margin; it opens in middle level of opened part of pallial oviduct. Female furrow of head-foot similar to those of preceding species.

Measurements of shells (in mm). AMS 339176, ♂ 6:50.2 by 31.2; ♂ 4:52.6 by 31.0.

Distribution. Central and West Pacific, from Japan to Indonesia and Australia.

Habitat. On muddy flats, intertidal and subtidal.

Material examined. AUSTRALIA; Queensland, Moreton Bay (between Donwiche & Myora) Stradbroke Island, 27°29'S 153°25'E, AMS 339176, 4 males, 9 females (W.F. Ponder & P.H. Colman col., 13/iii/1969).

Genus *Canarium* Schumacher, 1817

(Type: *Strombus urceum* Linné)

Canarium urceus Linné, 1758

(Figs. 26, 27, 203-215, 371, 379)

Synonymy see Abbott, 1960:65. Complement:

Strombus (Canarium) urceus: Bergh, 1895:362-368 (pl. 22, figs. 19-25; pl. 23, figs. 31-36); Wilson & Gillett, 1972:40 (pl. 18, fig. 2); Walls, 1980:108 (Figs); Abbott & Dance, 1982:77 (fig.); Watters & Valentine, 1994:8-9.

Description

Shell (Figs. 26, 27). Of small size, characters see Abbott (1960:63-65, pl. 41).

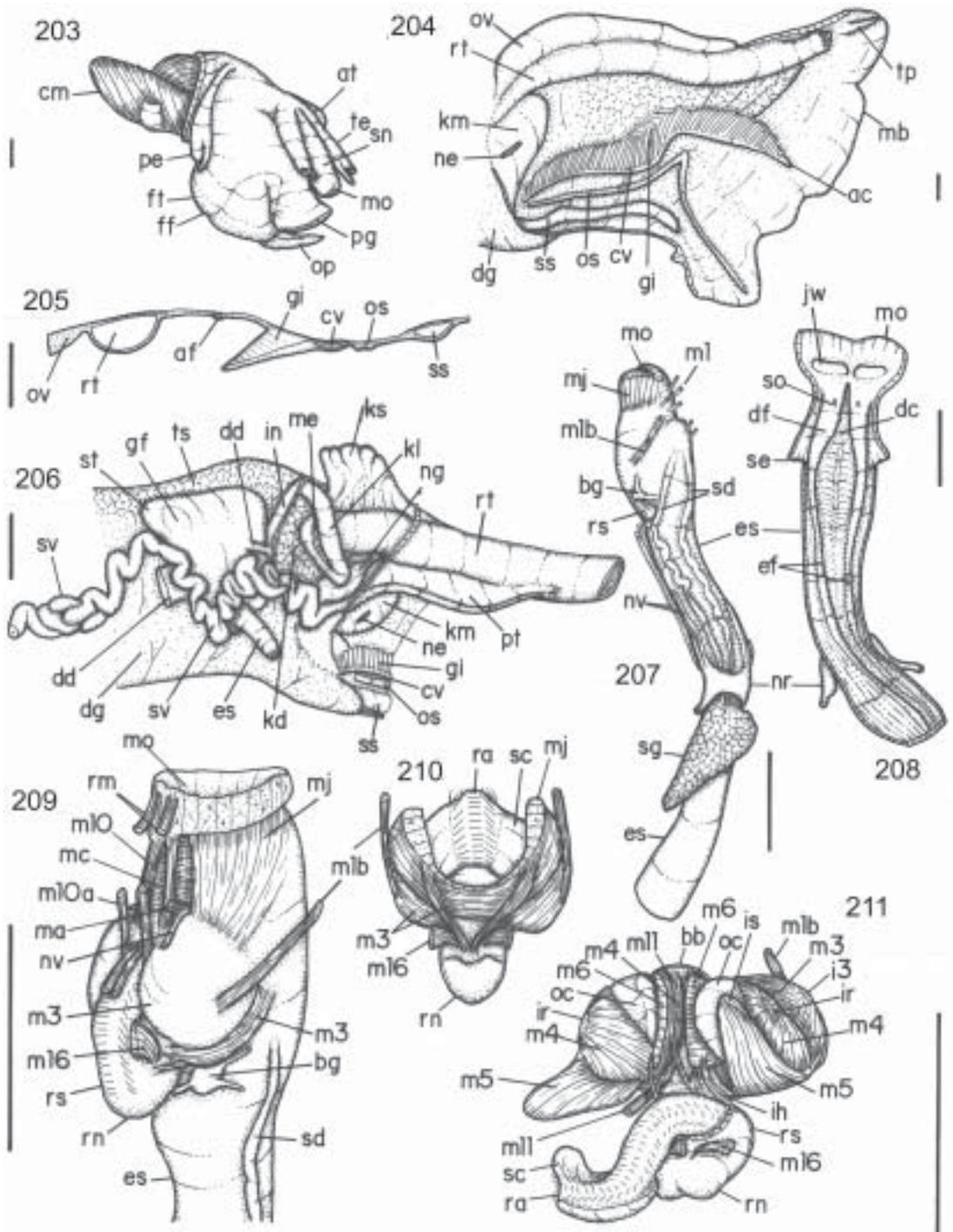
Head-foot (Fig. 203). Very similar characters to those of preceding species.

Operculum (Fig. 379). Similar features to that of *S. pugilis*, inclusive small spines in outer margin.

Mantle organs (Figs. 204-206). General features similar to those of preceding species. Distinctive or notable characters following. Pallial tentacle, anterior to anus, present. Osphradium slightly broad, with strong curve in its middle region; posterior end almost in same level from that of gill. Gill filaments triangular, almost straight borders, turned to right. Afferent vessel slightly far away from gill right margin.

Circulatory and excretory systems (Fig. 206). Both similar to those described for preceding species. Interesting features following. Pericardium part located dorsal to gill, auricle connection with ctenidial vein sub-terminal. Intestinal free loop in kidney present. Two renal lobes, ventral lobe large, irregular surface, dorsal lobe low, but more developed as those of preceding species. Nephridial gland characters very similar to those of *C. luhuanus*.

Digestive system. Buccal mass and odontophore characters similar to those of preceding species. Following distinctive or notable features (Figs. 207-211). Pair of small retractor muscle of snout (**mr**) in ventral region of snout close to median line. Dorsal chamber slightly deep. Aperture of salivary glands in middle of anterior region of dorsal folds. Odontophore muscles: **m1d** just like that of *C. luhuanus*; **ma** present; **m3** narrow, beginning in each side of dorsal wall of buccal mass, running in surface edging posterior-lateral odontophore region, connect with each other just anterior to radular nucleus; **m10** and **m10a** present, **m10a** covered by **m3**; **m16** strong pair, originating in ventral inner surface of snout, in region adjacent to posterior region of odontophore, running towards dorsal in short distance, inserting in dorsal surface of radular nucleus in its face turned to odontophore. Radular teeth (Fig. 371): similar to those of *C. luhuanus*, but with slightly shorter marginal teeth; cusp formula: 7, 5, 4, 6 (Other details in Bergh, 1895 and Abbott, 1960). Salivary glands different from all other examined strombids (but similar to normal fashion of lower caenogastropods) posterior to nerve ring; their ducts pass through nerve ring running in dorsal surface of esophagus up to dorsal wall of buccal mass (Figs. 207-209), open as above described. Esophagus characters similar to those described for *C. luhuanus*. Stom-



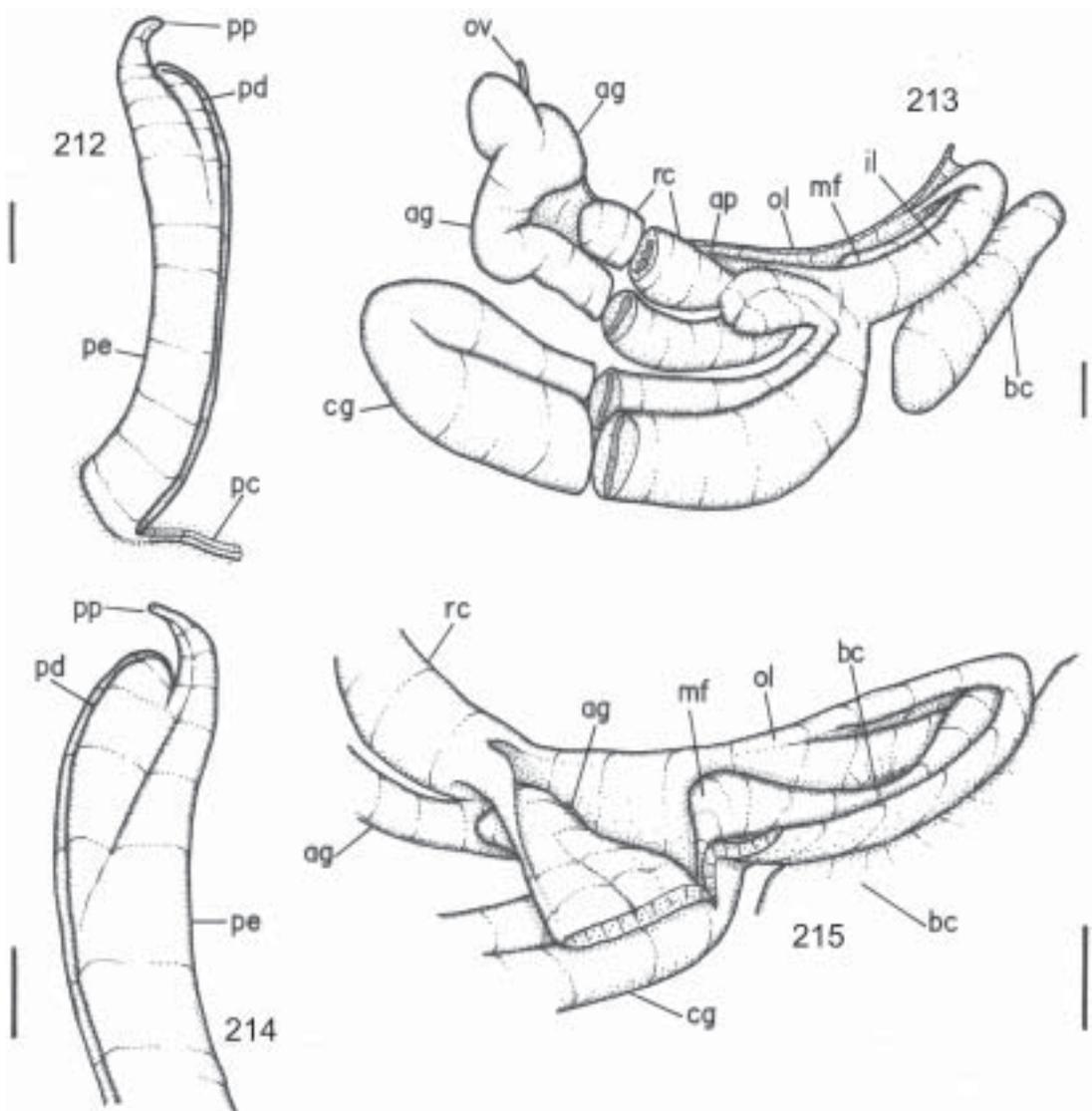
Figures 203-211. *Canarium urceus* anatomy. **203.** Head-foot, male, frontal view, mantle and visceral mass extracted; **204.** Pallial cavity, ventral-inner view; **205.** Same, transversal section in its middle region; **206.** Last whorl of visceral mass and posterior region of pallial cavity, ventral view, part of digestive gland close to stomach removed, kidney opened by longitudinal section, intestinal loop inside kidney and ventral renal lobe deflected; **207.** Buccal mass, esophagus and adjacent structures, dorsal, slightly lateral-left view; **208.** Dorsal wall of buccal mass and anterior esophagus, ventral view, esophagus opened longitudinally; **209.** Buccal mass, extracted, lateral-right view; **210.** odontophore, extracted, dorsal view; **211.** Same, ventral view, both cartilages deflected, horizontal muscle (m6) sectioned, radular sac extracted from m4 and m5 insertions and deflected downwards, right m5 (left in fig.) deflected. Scales = 2 mm.

ach features similar to those of *C. luhuanus*, except for broader outline, broader anterior duct to digestive gland and transversal tall inner ford absent (Fig. 206). Digestive gland, intestinal loops, rectum and anus characters similar to those of preceding species.

Genital system. Male. Testis with normal fashion of preceding species. Seminal vesicle very convolute, sigmoid in outline, edges left border of stomach and kidney (Fig. 206). Prostate slightly broad, with about half of pallial cavity length, some-

what uniform width along its length. Penis slightly short (Fig. 203), dorso-ventrally flattened, uniform width along its length except for slightly broader apical region (Figs. 212, 214). Penis groove running along outer margin and also edges rounded region of penis apex. A broad, triangular papilla by side of rounded region. Bilateral shallow furrow running obliquely in distal 1/3 of penis, inclusive in both sides of terminal papilla.

Female. Visceral structures similar to those of preceding species. Pallial oviduct (Figs. 213,



Figures 212-215. *Canarium urceus* anatomy. 212. Penis, dorsal view; 213. Pallial oviduct, ventral view, a transversal section artificially done showing inner organization; 214. Penis, ventral view, detail of its apical region; 215. Pallial oviduct, ventral view, detail of its middle and anterior regions, inner lamina sectioned at level of insertion of capsule gland and deflected downwards. Scales = 1 mm.

215) slightly short – about half of pallial cavity length. Albumen gland long, its coiled region occupying about 1/4 of its length. Seminal receptacle long, elliptical, entirely tubular (closed). Capsule gland broad, short, presenting single loop. Few coils in inner lamina in region adjacent to albumen and capsule glands insertion. Albumen gland insertion slight far removed (posterior) from that of capsule gland. Opened part of pallial oviduct (groove) relatively short (about half of total length of pallial oviduct), slightly broad, median fold present. Bursa copulatrix short, elliptical, its aperture about in middle region of its right margin, which locates in middle region of opened part of pallial oviduct. Anterior extremity of pallial oviduct, before it cross to pallial floor, preceded by blind-sac region and narrow fold turned posteriorly. Female furrow of pallial floor and head-foot similar to those of preceding species.

Nervous system. Described and figured by Bergh (1895).

Measurements of shells (in mm). AMS 095713:52.5 by 24.1; ♀ 1:49.2 by 24.0.

Distribution. W. Pacific, from Japan to Australia.

Material examined. AUSTRALIA; **Queensland;** Dampier, Causeway beach, 20°40.5'S 116°41.5'E, AMS C095713, 1 female, 2 shells (N. Coleman col., 23/ix/1972, sta. #21350B, WA); Port Darwin, west side, Swires Bluff, 12°30.5'S 130°46.5'E, AMS C342926, 1 male, 5 females (O.J. & J. Cameron col., 18/ix/1970, sta. #35268NT).

Genus *Lambis* Röding, 1798

(Type species *S. lambis* Linné, 1758)

Lambis lambis (Linné, 1758)

(Figs. 216-230, 375, 381, 382)

Synonymy see Abbott, 1961:153. Complement: *Strombus lambis* Linné, 1758:3508.

Lambis (Lambis) lambis: Wilson & Gillett, 1972:36 (pl. 14, fig. 1, pl. 15); Walls, 1980:61 (Figs); Boneka et al., 1993:159-161.

Lambis lambis: Abbott & Dance, 1982:81 (fig.); Gibbins, 1995:10 (fig.); Ueno, 1997:11-15; Morton, 1997b (fig. 4:1-5).

Description

Shell (Figs. 381, 382). Very characteristic, with 6 long spines in outer lip projected outside

and upside. In female spines turned more dorsally than males. Outer lip thick, tentacular notch conspicuous. More details in Abbott (1961:151-153).

Head-foot (Figs. 216, 217). Characters very similar to those of preceding species, inclusive tentacles, snout, foot, female genital furrow and male penis origin. No dorsal reticulate tissue of foot.

Operculum (Fig. 216). Very similar to that of *S. pugilis*.

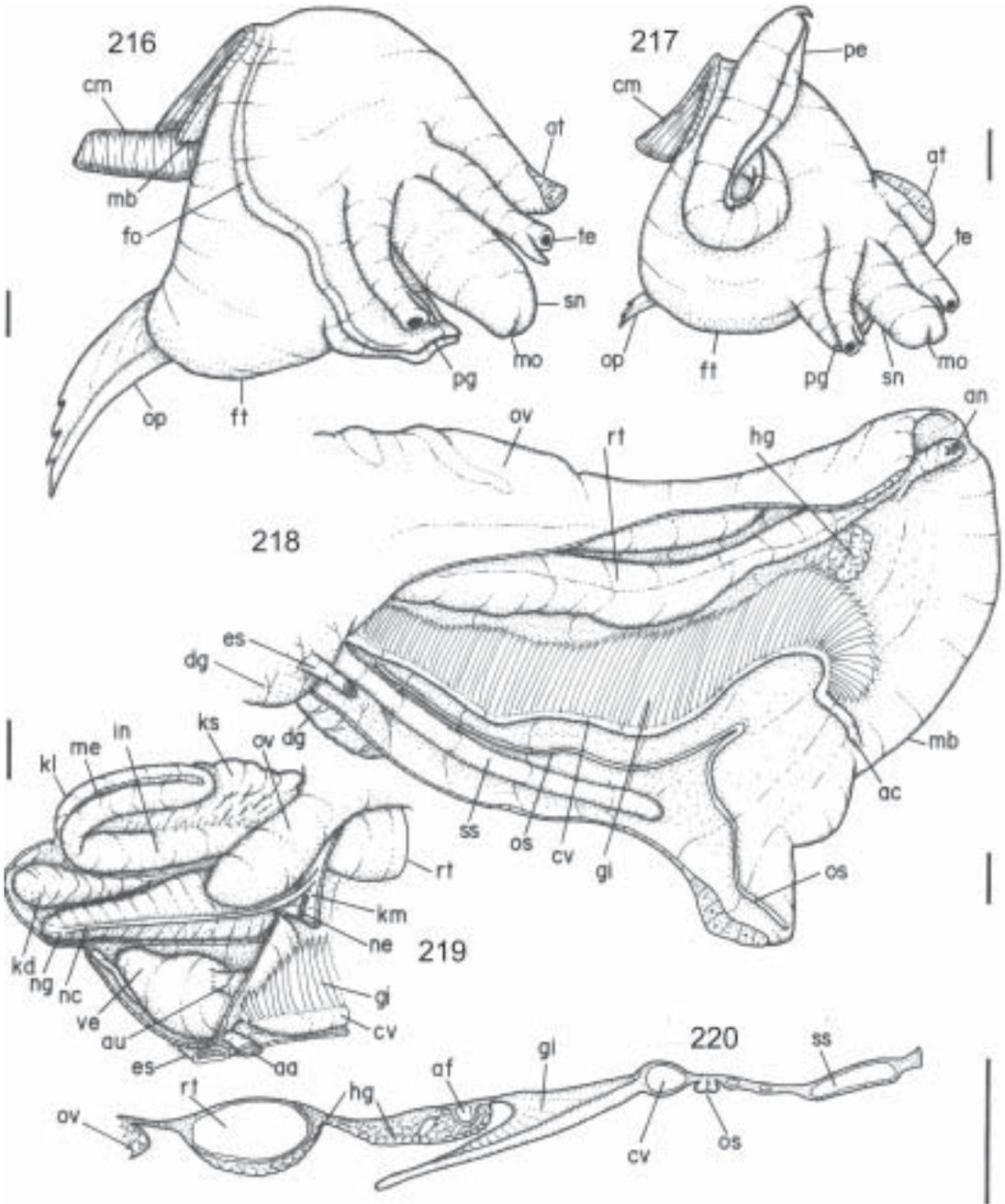
Pallial cavity (Figs. 218-220). Despite projections (spines) of shell outer lip, there is no detectable adjacent projection in mantle border, which is simple and slightly thick. Style sac anterior extremity at some distance from mantle border. Osphradium bipectinate, similar in situation and characters to those of preceding species, anterior extremity on mantle border, posterior extremity slightly anterior to that of gill; a conspicuous angle (pointed to right) between its middle and anterior third parts. Ctenidial vein slightly broad, with ventral wall presenting several longitudinal muscle fibers. Gill large, similar in size and situation to those of preceding species. Anterior projection of ctenidial vein (ac) present. Gill filaments triangular and tall, long tip. Between gill and rectum space approximately similar to that of gill area. Hypobranchial gland large, thick between gill and rectum, thin in ventral surface of rectum, orange in color. Several transversal mantle septa crossing within hypobranchial gland.

Circulatory and excretory systems (Fig. 219). Heart characters similar to those of preceding species. Located slightly dorsal to gill posterior end, auricle connection in ctenidial vein not terminal. Posterior extremity of ctenidial vein a blind-sac form. Kidney dorsal lobe small, brown, with several transversal furrows. Kidney ventral lobe large, attached to rectum by narrow fold; several, deep furrowed surface; color beige. Intestinal loop with mesentery similar to those of preceding species.

Digestive system. General aspect similar to that of preceding strombids. Buccal mass large. Odontophore with following distinctive features (Figs. 221-225): 1) **m3** pair well-developed, connected posteriorly to radular nucleus lateral surface; 2) **m10a** pair narrow and long, originating close to m10, running towards posterior, inserting in middle-ventral region of m5, part covered by m3; 3) **m16**, pair small and short, originating in ventral region of snout adjacent to odontophore, penetrate just

anterior to m3 inserting in anterior region of radular nucleus, where insert in it; 4) **m17**, pair slightly long and narrow, originating in subradular membrane just in its bulged region (bb) between m11 and m4, running parallel to m11, crossing ventral

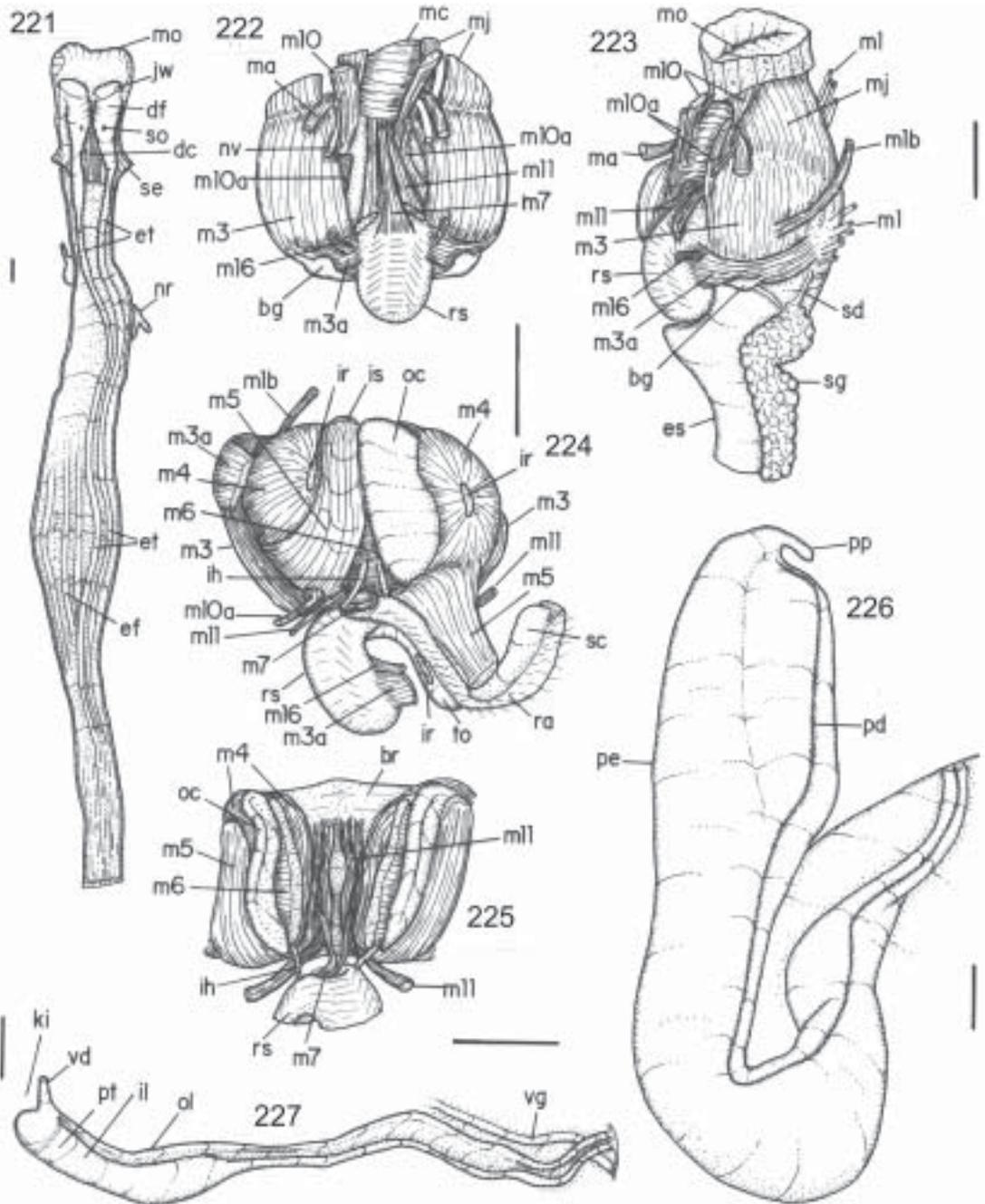
to m7, inserting in median-dorsal region of m4. Radular teeth (Fig. 375) similar to preceding species, cusp formula: 5, 4, 5, 5. Salivary gland thin, anterior to nerve ring, more concentrated just posterior to buccal mass. Ducts of salivary gland vis-



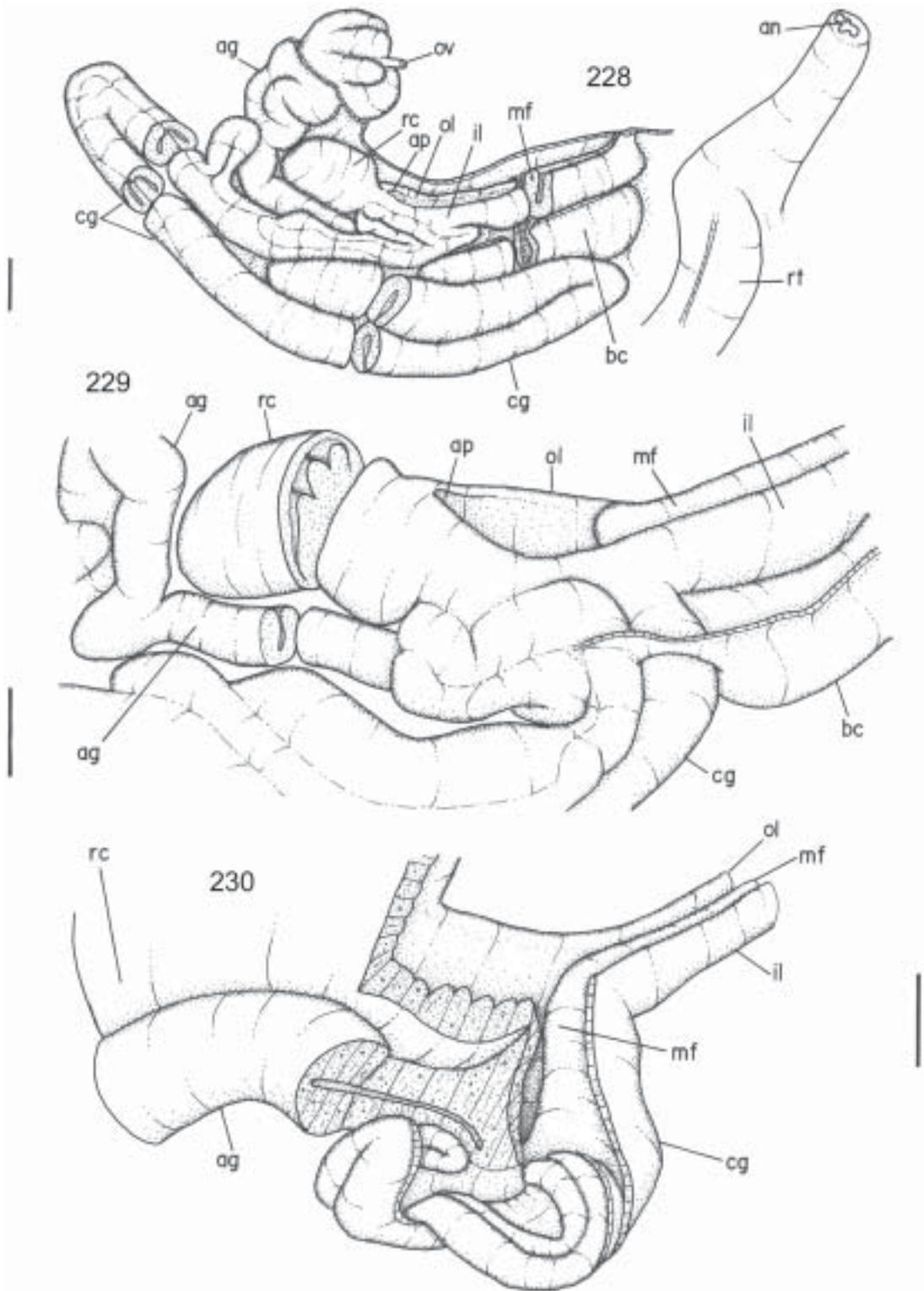
Figures 216-220. *Lambis lambis* anatomy. 216. Head-foot, female, frontal view, mantle and visceral mass extracted; 217. Same, male; 218. Pallial cavity, ventral-inner view; 219. Kidney, pericardium and posterior region of pallial cavity, ventral view, kidney and pericardium opened by longitudinal section in each, intestinal loop inside kidney and ventral renal lobe deflected; 220. Pallial cavity, transversal section in its middle region. Scales = 5 mm.

ible at short distance in lateral-dorsal region on buccal mass, after run immerse in dorsal folds, open in middle region of dorsal folds. Dorsal folds of

buccal mass also running along entire esophagus; secondary longitudinal, narrow folds gradually appear in middle esophagus and become larger but



Figures 221-227. *Lambis lambis* anatomy. 221. Dorsal wall of buccal mass and anterior esophagus, ventral view, esophagus opened longitudinally; 222. Odontophore, extracted, ventral view; 223. Buccal mass, lateral-left view; 224. Odontophore, ventral view, both cartilages deflected, radular sac extracted from m4 and m5 insertions and deflected downwards, left m5 (right in fig.) also deflected; 225. Same, horizontal muscle (m6) sectioned and deflected showing inner surface of subradular membrane (br), radular sac partially shown; 226. Penis, dorsal view; 227. Prostate and pallial sperm groove, ventral view, anterior adjacent region of mantle also shown. Scales = 2 mm.



Figures 228-230. *Lambis lambis* anatomy. 228. Pallial oviduct, ventral view, transversal sections artificially done showing inner organization, adjacent anterior region of pallial cavity also shown; 229. Same, detail of its middle and posterior regions, a transversal section also artificially done; 230. Same, middle region, inner lamina sectioned at level of insertion of capsule gland and deflected downwards. Scales: 228 = 5 mm; others = 2 mm.

fewer in posterior esophagus. Other details in Woodward (1894).

Genital system. Male. Visceral structures similar to those of preceding species. Prostate slightly large, posterior region bulging in dorsal surface of kidney; bear shallow furrow turned to right (Fig. 227). Prostate suddenly finishes at about 1/3 of pallial part of sperm groove, remainder sperm groove narrow and simple. In approximate level of anterior third of pallial cavity gradually crosses to pallial floor. Penis slight short (Fig. 217), basal half thick and cylindrical, distal half broader and slightly flattened (Fig. 226). Distal half with pair of low folds running in ventral and dorsal sides. Penis groove running in margin of distal half, finishes in base of apical, short papilla. Apical papilla is continuation of pair of longitudinal folds.

Female (Figs. 228-230). Visceral and pallial organs characters similar to those of preceding species. Albumen gland highly convolute in its posterior half, somewhat straight in its anterior half; very thick glandular walls. Albumen gland inserting in capsule gland in region close to its insertion, preceded by coiled region immersed in inner lamina. Capsule gland long and thick, running towards posterior initially parallel to albumen gland, after encroaches in dorsal and anterior region of kidney; a secondary projection present just between kidney and pallial cavity, towards right. Capsule gland suddenly curves and runs towards anterior up to anterior extremity of pallial oviduct, where newly presents sudden curve to right, running between its preceding loop and remainder pallial oviduct. Capsule gland loops located dorsal to rectum. Seminal receptacle elliptical, slightly flattened, its aperture only anterior. Dorsal surface of receptacle with three large, longitudinal folds. Remainder pallial oviduct thick furrow, with median large fold. Bursa copulatrix long, dorso-ventrally flattened, located between anterior region of capsule gland and pallial oviduct; open in pallial oviduct just posterior to its crossing to pallial floor. Pallial floor part of oviduct similar to those of preceding species (Fig. 216).

Measurements of shells (in mm). AMS 339175, ♀ 1:136.0 by 73.4; ♂ 2:12.0 by 51.0.

Distribution. Indo-Pacific.

Habitat. Coral and mud rubble, subtidal.

Material examined. AUSTRALIA. Queensland; Lizard Island, SE side of Casuarina Beach 14°41'S 145°27'E, 3 m depth, AMS 339175,

3♂, 1♀, (Ponder, Coleman & Loch col., 01-12/xii/1974).

Genus *Terebellum* Röding, 1798

(Type species: *T. subulatum* Lamarck, 1799 = *Bulla terebella* Linné)

Terebellum terebellum (Linné, 1758)

(Figs. 28, 29, 231-248, 373, 380)

Synonymy see Jung & Abbott, 1967:452-453.

Complement:

Terebellum terebellum: Wilson & Gillett, 1972:40 (pl. 18, fig. 11); Walls, 1980:56 (Figs) Abbott & Dance, 1982:83 (fig.); Morton, 1997b (pl. 2; fig. 2:7-9).

Description

Shell (Figs. 28, 29). Very atypical for strombid, fusiform outline; outer lip thin, with cut-edge. Periostracum glossy. Canal wide, turned anteriorly. Other details in Jung & Abbott (1967:449-452).

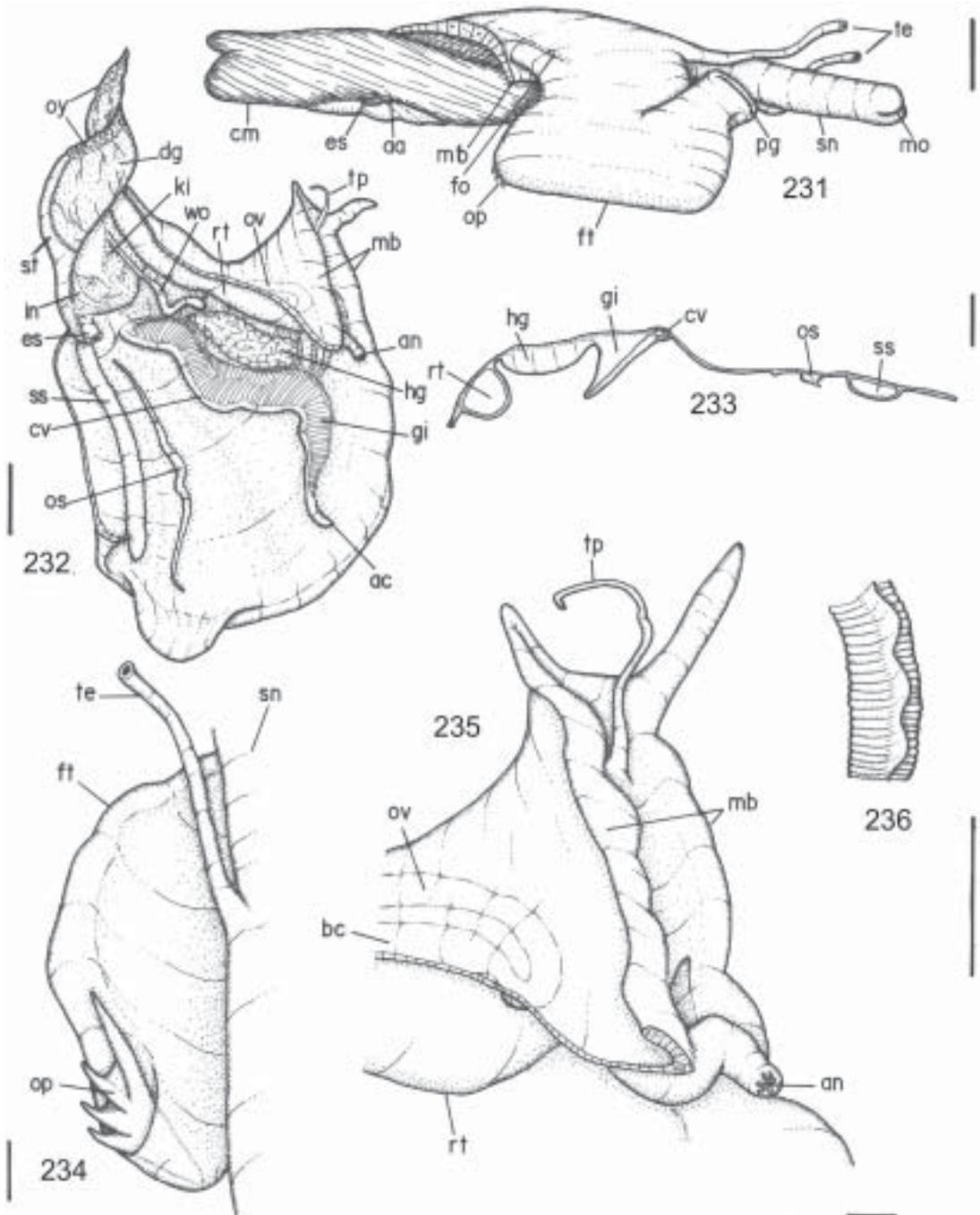
Head-foot (Figs. 231, 234, 238). Slender, long antero-posteriorly. Head outstanding. Snout long and cylindrical, anterior end slightly rounded. Tentacles very long, presenting only ommatophores, without pointed projections (although Jung & Abbott, 1967, described a very small ventral papilla). Foot similar to those of anterior species, inclusive anterior projected propodium with transversal furrow of pedal glands, but broader, slightly flattened towards antero-posterior. Posterior-ventral region of foot with deep concavity surrounding operculum pad. Columellar muscle long, about 1.5 whorls, broad and thick; its posterior region thinner and bifid.

Operculum (Figs. 234, 380). Similar to those of preceding species, but shorter, slightly broader, with 4-5 lateral, successive larger, pointed projections. Located deeply introduced in concavity of posterior-ventral region of foot, about half of its dorsal region covered by semi-transparent membrane. Scar relatively small, close to inner and posterior margins.

Pallial cavity (Figs. 232, 233, 235). Mantle border slightly thick, ample, simple, double folded. Siphon developed from inner fold, broad and somewhat short. Upper-right region part fused in both sides of rectum, producing supra-rectal chamber. Between this chamber and right extremity of bor-

der slight broad solid region. In exposed surface of this right extremity two long, pointed projections (Fig. 235); ventral projection shorter and with cen-

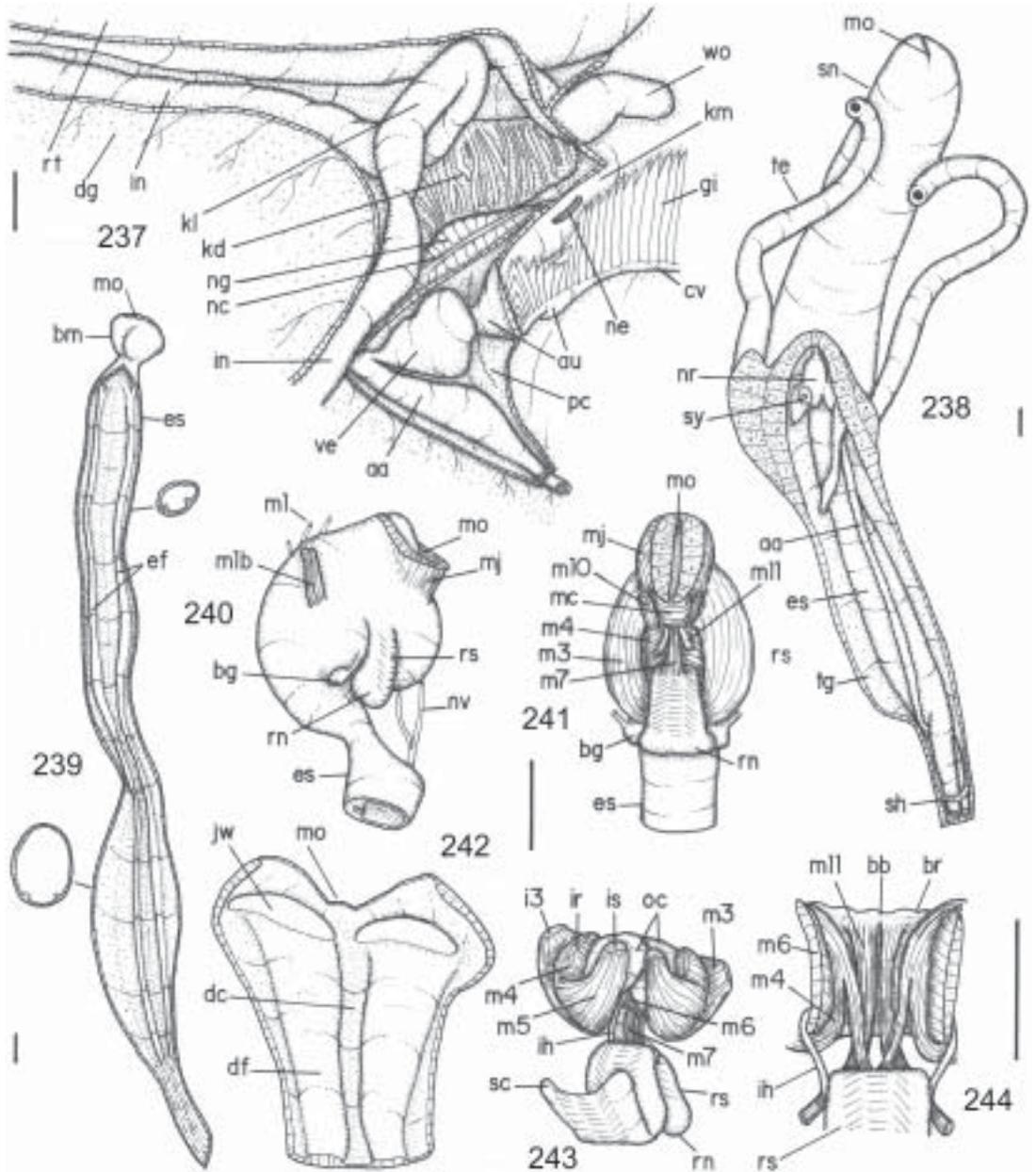
tral, longitudinal furrow; dorsal projection longer and slightly cylindrical. Pallial tentacle slender and very long, originating at left from origin of both



Figures 231-236. *Terebellum terebellum* anatomy. 231. Head-foot, female, lateral-right view, mantle and visceral mass extracted; 232. Pallial cavity (ventral-inner view) and visceral mass; 233. Pallial cavity, transversal section in its middle region; 234. Foot and adjacent region of head, ventral view; 235. Mantle border, detail of superior (right) extremity, ventral-slightly frontal view, mantle region inferior to rectum extracted; 236. Osphradium, detail of its middle region showing middle fold, ventral view. Scales: 231-232 = 5 mm; 233-234 = 2 mm; 235-236 = 1 mm.

mantle projections. Style sac running, similar to those of preceding species, parallel to left margin of pallial cavity. Osphradium long (about same length of pallial cavity), central region broader, both extremities gradually narrow and become pointed.

Most of osphradium bipectinate (about 3/4 of its length), ridge-like in extremities. Osphradium leaflets with rounded profile, connected to central axis that extends beyond leaflets border as a slightly tall, undulated, thin fold (Fig. 236). Between

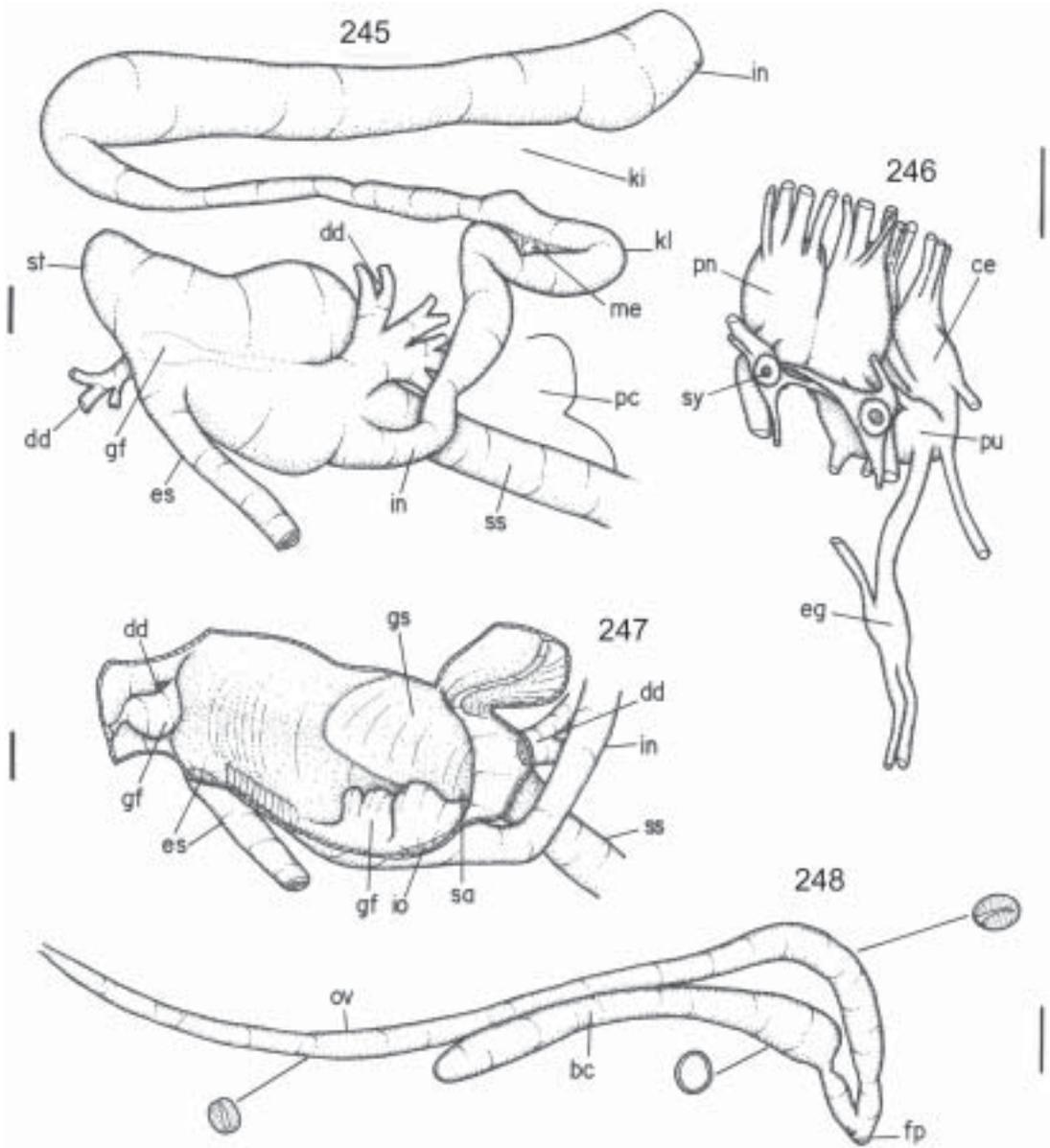


Figures 237-244. *Terebellum terebellum* anatomy. 237. Region between visceral mass and pallial cavity, ventral view, kidney and pericardium opened by longitudinal section in each, intestinal loop inside kidney deflected; 238. Head and haemocoel, ventral view, foot and columellar muscle extracted; 239. Buccal mass and esophagus, this opened longitudinally with inner surface exposed, 2 details of transversal sections in indicated levels also shown; 240. Buccal mass, lateral-right view; 241. Same, ventral view; 242. Same, dorsal wall, ventral-inner view; 243. Odontophore, ventral view, both cartilages deflected, radular sac extracted from m4 and m5 insertions and deflected downwards; 244. Same, detail of central region, horizontal muscle (m6) sectioned and deflected showing inner surface of subradular membrane (br), radular sac partially shown. Scales = 1 mm.

osphradium and gill a somewhat broad area, mainly in anterior region. Gill long and narrow, situated longitudinally in right half of cavity. Gill filaments slightly tall, triangular, apex pointed. Ctenidial vein broad, of uniform width along its length. Anterior projection of ctenidial vein (ac) present. Between gill and rectum a narrow area (less than half than area between osphradium and gill). Hypobranchial

gland thick, massive, white, covering most of space between gill and rectum except anterior quarter; transversal mantle septa running through hypobranchial gland. Rectum slight narrow, most immerse in mantle except left surface. Anus siphoned, projected beyond mantle border.

Visceral mass (Figs. 232, 237). With about 3 whorls dorso-ventrally compressed. Gonad occu-



Figures 245-248. *Terebellum terebellum* anatomy. 245. Stomach and adjacent digestive tubes shown in situ if remainder structures were transparent, ventral view; 246. Central nervous system, isolated, ventral view; 247. Stomach, ventral view, ventral gastric wall sectioned and deflected showing inner surfaces; 248. Pallial oviduct, ventral view, with 3 details of transversal sections in indicated levels. Scales = 1 mm.

pies superior, narrow band, stomach and digestive gland occupy remainder space. Pericardium, kidney and intestinal loops similar to those of preceding species. (A long and somewhat large worm present in all specimens, located between kidney and intestinal loop adjacent to it, encroaches short part within pallial cavity, immerse in integument, between kidney and rectum. From this point up to mantle border several worm capsules attached by pallial cavity.)

Circulatory and excretory systems (Figs. 232, 237). Heart similar to those of preceding species; auricle located posterior and dorsal to gill posterior extremity. Short posterior portion of ctenidial vein as blind sac. Kidney with single, dorsal lobe, low, with several transversal furrows. Very long, hollow region of kidney between visceral mass and intestine preceding rectum. Nephridial gland slightly large, localization and central vessel characters as in preceding species. Intestinal loop with mesentery and nephrostome similar to those described for anterior species.

Digestive system. Buccal mass relatively small (Fig. 239), characters similar to those of preceding species, with following distinctive or notable features (Figs. 239-244): 1) pair of jaw plates broad; 2) **m1b** pair present; 3) **m3** pair thin, inserted with each other just anterior to radular nucleus and part to it; 4) ligament of radular sac with ventral surface of horizontal muscle (**m6**) (ih) present; 5) **m10a** absent, 6) **m7** and **m11** relatively short. Radular teeth (Fig. 373) similar to preceding species, except for narrower inner and outer marginal teeth, cusp formula: 7, 6, 7, 7. Salivary gland absent. Esophagus broad, long, thin walled. Single pair of longitudinal folds all along esophagus. Low, secondary longitudinal folds only present posteriorly, close to stomach. Stomach large and broad, slightly irregular (Figs. 245, 247). Esophagus inserting in left-posterior side. Anterior duct to digestive gland close to esophagus insertion, slightly more dorsal, separated by semi-circular, large fold. Intestine originating in anterior-left region; between esophagus insertion and intestine origin several low, longitudinal folds as sorting area. Posterior duct to digestive gland large, located close to and at right form intestine origin. Style sac originating dorsal to that of posterior duct to digestive gland, tall septum separates both. Pair of tall folds extends at left from this septum by short distance, edging dorsally intestine origin. Gastric shield large. Remainder areas of stomach inner sur-

face smooth (Fig. 247). Style sac very long, similar to those of preceding species (Fig. 232). Intestine surrounding ventrally style sac origin, running towards right just posterior to adjacent duct to digestive gland (Figs. 237, 245); by relatively short portion becomes exposed in kidney chamber, where possesses free loop, connected to its base by mesentery; after this free loop runs posteriorly immersed in digestive gland; close to posterior level of stomach suddenly curves towards anterior and becomes exposed all along kidney chamber; after runs by pallial cavity as above described.

Genital system. Only females examined. Ovary narrow, occupying superior (right) region of visceral mass (Fig. 232), color dark beige. Pallial oviduct entirely closed (tubular), narrow, long, slender (Figs. 235, 248); running immerse in mantle tissue ventral to rectum, close to pallial floor; in anterior region curves to left, running short distance. Oviduct walls thick. Female pore very small, turned posteriorly. Bursa copulatrix long (about half of pallial oviduct length), situated parallel and at left from pallial oviduct, slightly thin walls, circular in section; in region preceding female pore suddenly narrows and by short distance becomes narrow tube. A shallow furrow running in pallial floor from genital pore to anterior, gradually disappear in half way between female pore and pedal glands furrow (some specimen present no furrow at all). Some male characters in Bergh (1895)

Measurements of shells (in mm). AMS 122659, ♀ 2: 54.1 by 13.7; ♀ 3: 44.0 by 11.0.

Distribution. Indo-Pacific.

Nervous system (Fig. 246). Described and figured by Bergh (1895).

Habitat. Intertidal sandy flats.

Material examined. AUSTRALIA; Queensland; Cairns Reef, S.E. of Cooktown, 15°42'W 145°30'E, AMS 122659, 3 females (I.W. Loch col., 20/vii/1974).

Genus *Tibia* Röding, 1798

(Type species: *Murex fusus* Linné, 1758)

Tibia insulaechorab Röding, 1798

(Figs. 32, 249-252)

Tibia (Tibia) insulaechorab insulaechorab: Walls, 1980:49 (figs).

Tibia insulaechorab: Abbott & Dance, 1982:82 (fig.); Kronenberg & Burger, 2002:39-46.

Description

The following description is based on a single female not well preserved, then is very incomplete.

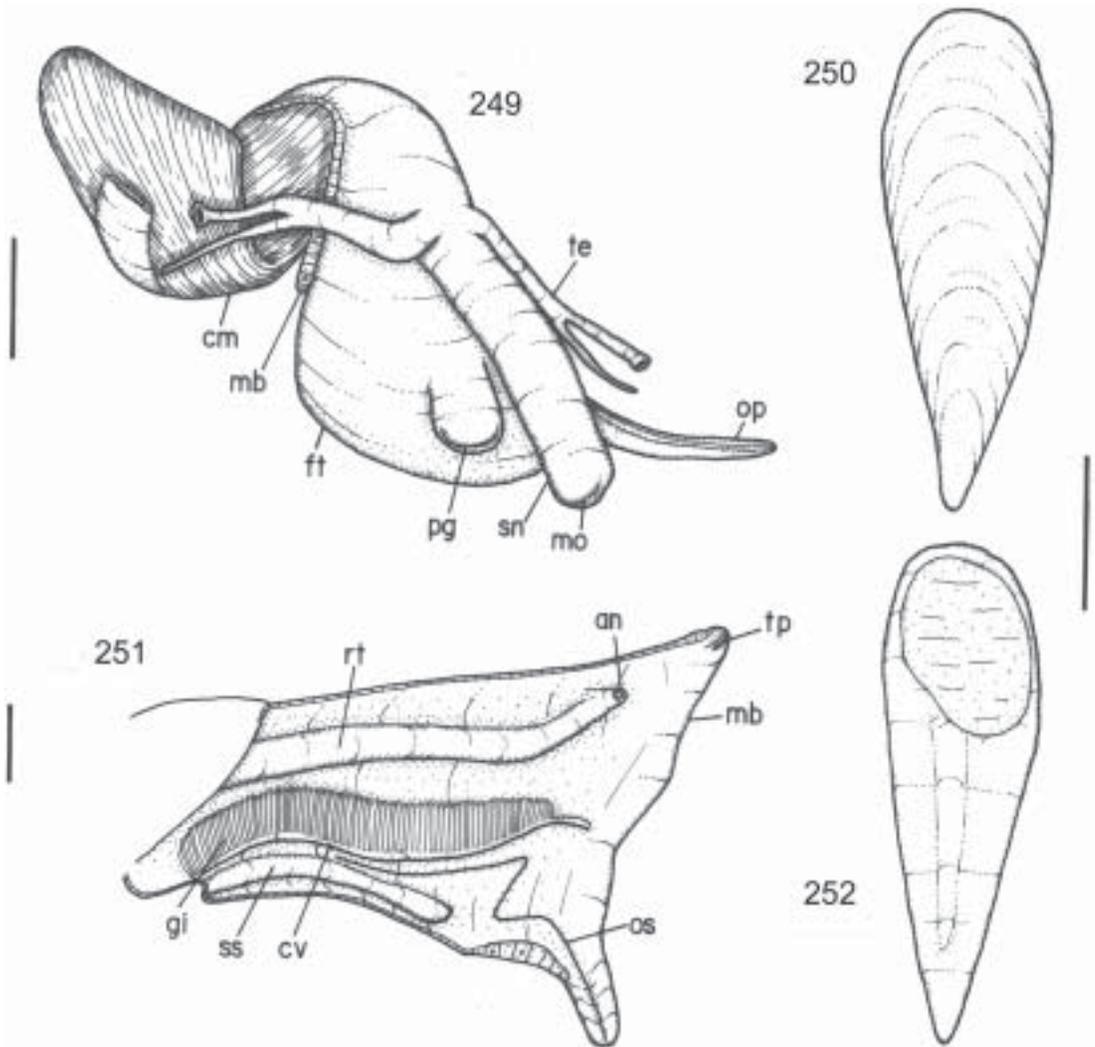
Shell (Fig. 32). Very typical *Tibia* species, with spire very long, conic; aperture relatively small; out lip with 4 short spines and very long spine forwards.

Head-foot (Fig. 249). Characters slightly similar to preceding strombid species. Snout very long and slender, anterior region rounded, with smooth surface. Tentacles with very long ommatophore, eye bulged in tip. Ommatophore base in approximately middle level of tentacle, remainder distal region of tentacle slightly longer than

ommatophore. Foot slightly broad and thick (not cylindrical). Propodium similar to those of preceding species, far removed from snout base. Opercular pad terminal and dorsal.

Operculum (Figs. 250, 252). Long, relatively large, occupies most of aperture area. About 2/3 projected beyond foot. Operculum base slightly rounded, gradually narrows up to somewhat sharp extremity where nucleus locates. No spines. Inner scar almost rounded.

Pallial organs (Fig. 251). Mantle border broad and ample. A single projection in siphon region. Pallial tentacle anterior to anus present. Style sac running in pallial cavity left border at about 2/3 of cavity length. Osphradium very narrow,



Figures 249-252. *Tibia insulaechorab* anatomy. 249. Head-foot, female, frontal view; 250. Operculum, outer view; 251. Pallial cavity, ventral-inner view; 252. Operculum, inner view. Scales = 10 mm.

bipectinate; anterior region running along middle surface of siphon projection; middle region strongly sigmoid; posterior end approximately in middle level of gill. Osphradium posterior half close to gill, its anterior half gradually removed from gill. Gill large, long, with about 3/4 of cavity length, anterior projection of ctenidial vein (ac) present. Gill filaments relatively tall, sharp apical region. Between gill and rectum an area equivalent to that of gill. Rectum broad, anus siphoned, with several papillae, not close to mantle border.

Measurements of shells (in mm). 113.4 by 40.7.

Distribution. Red Sea and North Indic Ocean.

Material examined. PAKISTAN; Karachi, AMNH 162366, 1 female, (M.A. El-Husseini leg.)

Family STRUTHIOLARIIDAE

Genus *Tylospira* Harris, 1897

(Type species *Buccinum scutulatum* Gmelin, 1791)

Tylospira scutulata (Gmelin, 1791)
(Figs. 13, 14, 41, 42, 57, 59, 60, 253-273)

Synonymy see Darragh (1991:167). Complement:
Tylospira scutulata: Morton, 1950:461.
Struthiolaria scutulata: Walls, 1980:34 (fig.).

Description

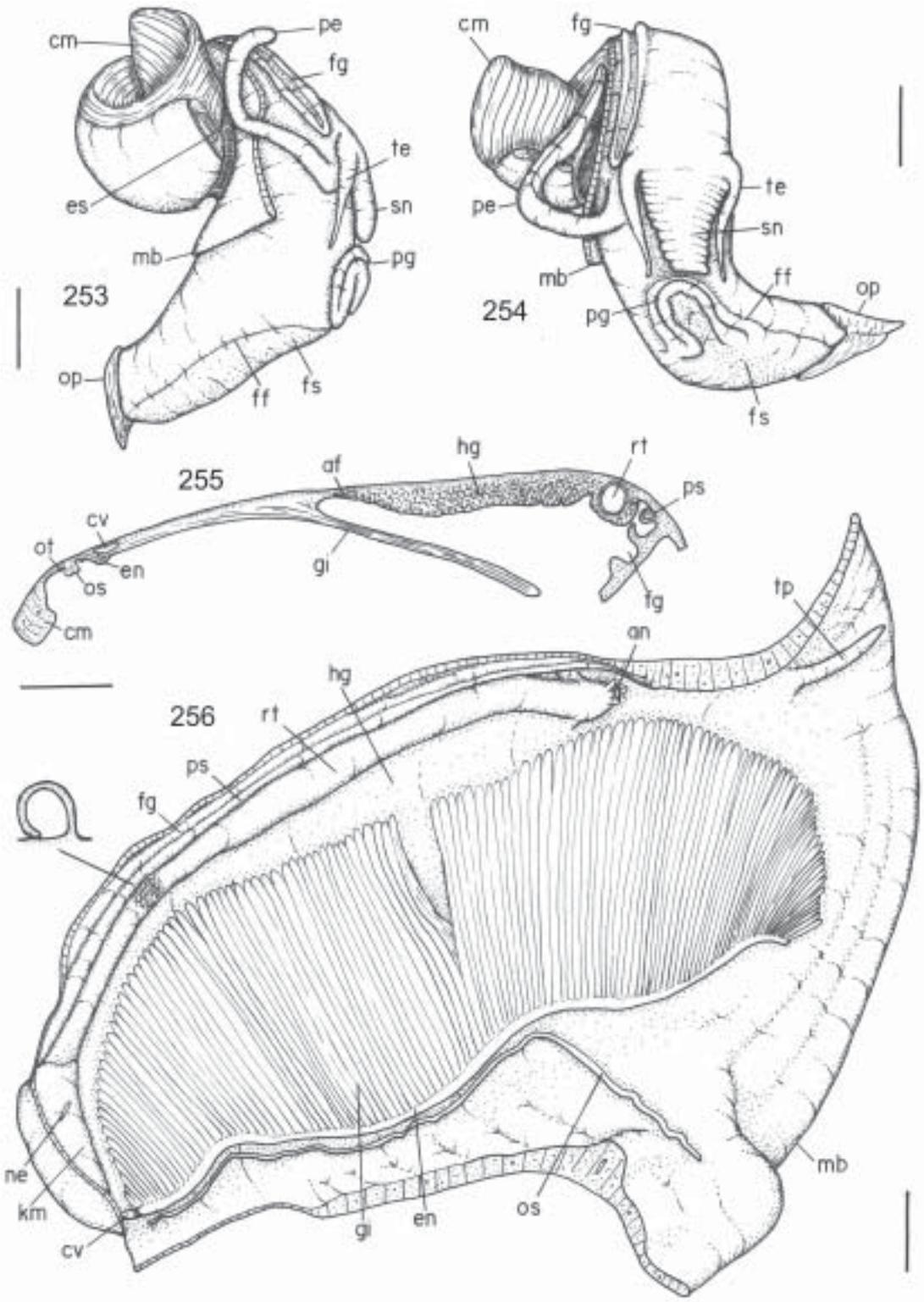
Shell (Figs. 13-14). See description and discussion of Darragh (1991:167-170, Figs. 8A-D, 9A-D).

Head-foot (Figs. 253, 254, 259, 261, 272). Color homogeneous clear beige to clear brown. Head outstanding. Snout broad, conical, somewhat flattened dorso-ventrally, with strong transversal folds slight uniformly distributed, deep furrow between each fold and its neighbor. Mouth ample, terminal, slight ventral; smooth borders. Snout walls very thick in base, narrows gradually. Tentacles long, about same length than snout, slender, base broader, taper gradually; ommatophore small, in ventral tentacles surface, slight over tentacles base. Several strong longitudinal muscle fibers internally visible, originate from snout base. Eye dark, very small, not visible in frontal view. Foot large, stubby, cylindrical, with crawling sole; anterior aperture of pedal glands on low elevation (anterior sole edge), edged by thick borders; shallow furrow edges both

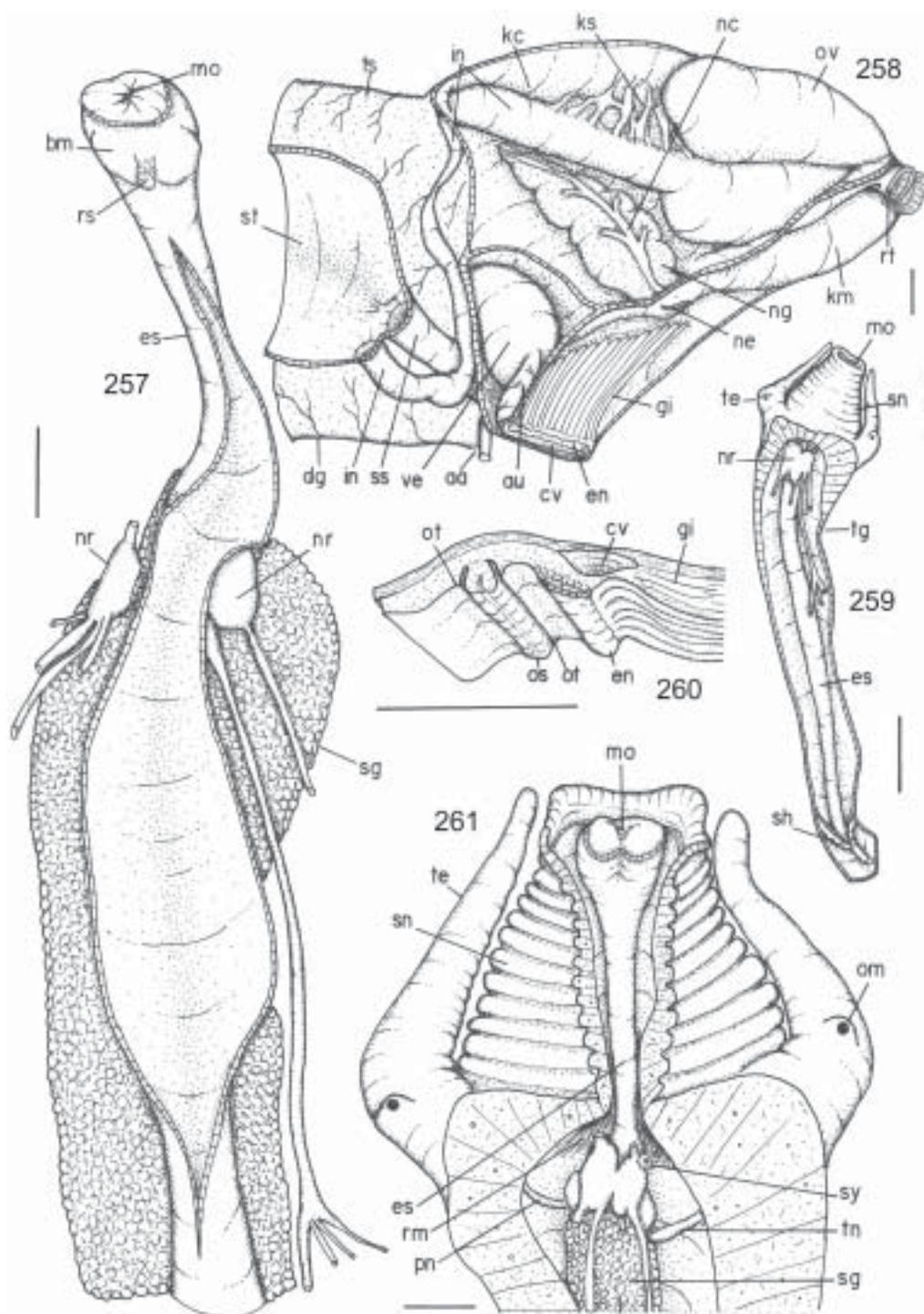
sides of foot sole. Opercular pad sub-terminal, dorsal. Food groove well-developed, beginning gradually in right-posterior side of pallial floor, become pair of tall folds, being right fold taller and narrower, turned to right covering anterior half of gonoducts. Food groove run in pallial floor parallel to its right margin until posterior-right region of head, where both folds unite with each other close to base of right tentacle (Fig. 272). No detectable groove uniting food groove anterior extremity and mouth. Snout inner haemocoelic cavity very narrow, edged by strong pair of retractor muscles entirely attached to inner surface (Fig. 261:rm)

Operculum (Figs. 41, 42). Horny, oval, superior margin rounded, inferior margin sharp pointed bearing spine. Nucleus terminal. Inner scar very broad, edged by thick lateral borders. Inner border thicker, as base of spine. Occupies small part of shell aperture.

Mantle organs (Figs. 255, 256, 258, 260, 271, 273). Mantle border very ample, undulated, without pigments. Pallial tentacle in its right region, inserted about in middle level between anus and mantle border. Osphradium very long, ridge-like, entirely edged in both sides by very narrow satellite fold (Figs. 260, 273:ot); anterior extremity far from gill and at some distance from siphon region of mantle border; gradually approaches from gill and run close to gill left margin since its middle third part; osphradium posterior extremity slightly anterior to that of gill. Endostyle well-developed (Figs. 255, 260), glandular ridge somewhat broad and low; running along, ventral and slightly at left ctenidial vein, in almost total its length; only very short posterior portion free from endostyle. Ctenidial vein narrow and slight uniform along its length. Gill very large, bears several broad, triangular, low filaments; each filament with very long (about same length than their base) projection at right covering right half of pallial cavity; apex of gill filaments rounded, close to head-foot food groove. Between gill and rectum a tall hypobranchial gland bearing some small glandular chambers, covers also ventral rectum surface. Rectum somewhat narrow, replete of several elliptical fecal pellets (without apparent organization). Anus siphoned, located between middle and anterior side of pallial cavity; bears three equidistant papillae (Figs. 256, 272). Pallial gonoducts running between rectum and right margin of pallial cavity, crossing to pallial floor just anterior to anus. Female with



Figures 253-256. *Tylospira scutulata* anatomy. 253. head-foot, male, lateral-right view; 254. same, frontal view; 255. pallial cavity, transversal section in middle region of its roof and right part of its floor; 256. pallial cavity, inner-ventral view, with a detail of a transversal section in indicated region of sperm groove. Scales: 253-254 = 5 mm; 255-256 = 2 mm.



Figures 257-261. *Tylospira scutulata* anatomy. 257. buccal mass, anterior and middle esophagus and adjacent structures, ventral view, esophagus opened longitudinally with inner surface exposed; 258. anterior region of visceral sac, ventral view, ventral wall of stomach and pericardium removed, kidney opened longitudinally with ventral wall deflected upwards, part of pallial cavity also shown; 259. head and part of haemocoel, ventral view, foot and columellar muscle removed; 260. portion of pallial roof middle region showing endostyle, osphradium and adjacent structures; 261. head extracted, ventral view, snout opened longitudinally in median line, inner structures exposed. Scales: 260 = 5 mm, others = 1 mm.

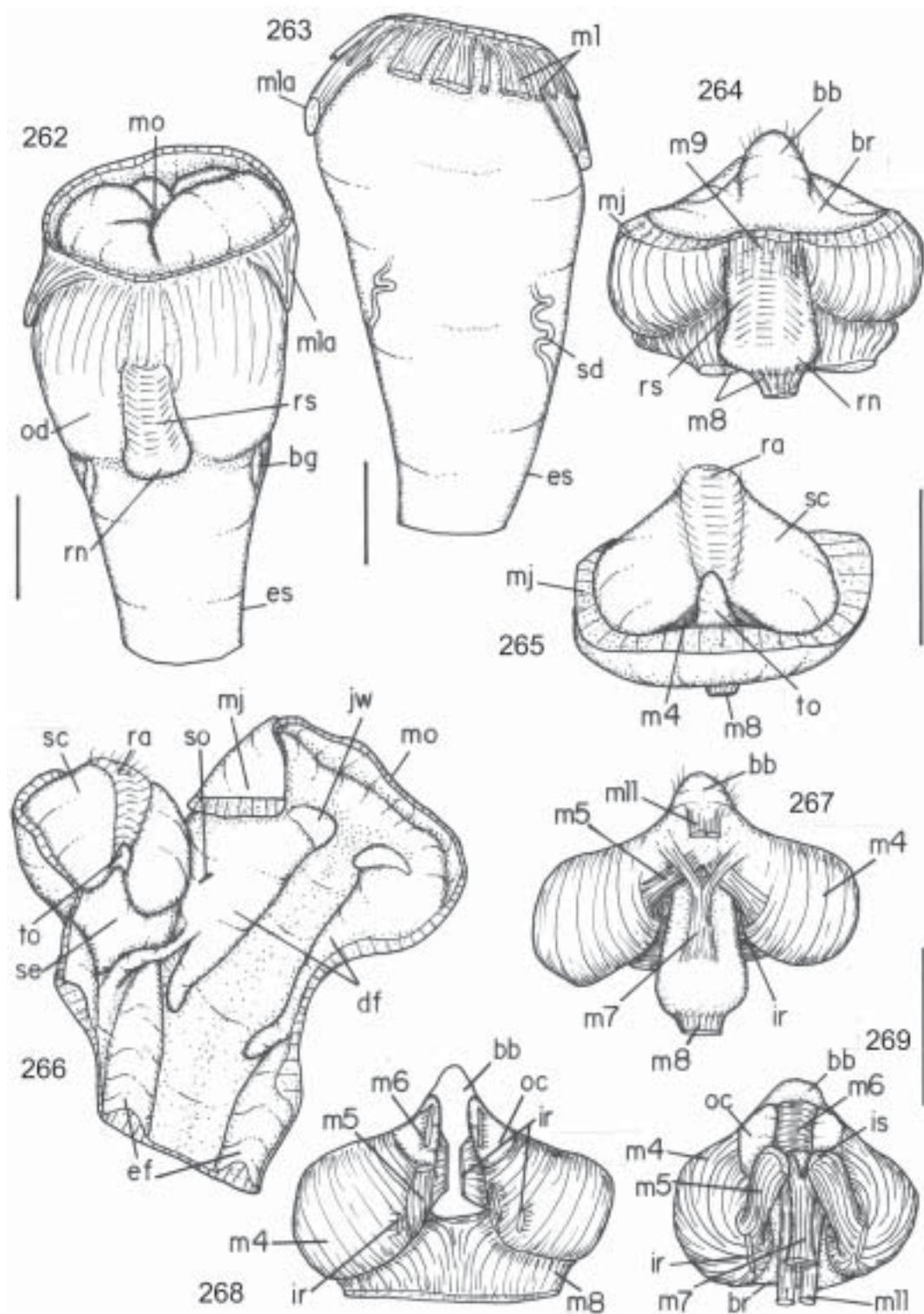
large isolated bursa copulatrix anterior to anus described below.

Circulatory and excretory systems (Fig. 258). Heart somewhat large, located behind left third of pallial cavity posterior extremity; auricle in left side just posterior to gill; ventricle very large. Kidney broad, slight triangular, occupying middle and right third parts of pallial cavity posterior extremity and about a third of whorl posterior to this. Kidney most hollow, ventral lobe part attached to rectum, comprising mosaic of several low glandular folds, greatly compressed by pallial oviduct in females. Nephridial gland larger than glandular tissue of kidney, located in dorsal region of membrane between kidney and pericardium cavities; bears large, longitudinal, ventral vessel with anterior insertion septum-like, at right of nephrostome, similar to preceding species. Neither other glandular tissue nor intestinal loop in kidney chamber. Nephrostome a slit about in middle region of membrane between kidney and pallial cavities. (Other details of struthiolariids in Morton, 1956).

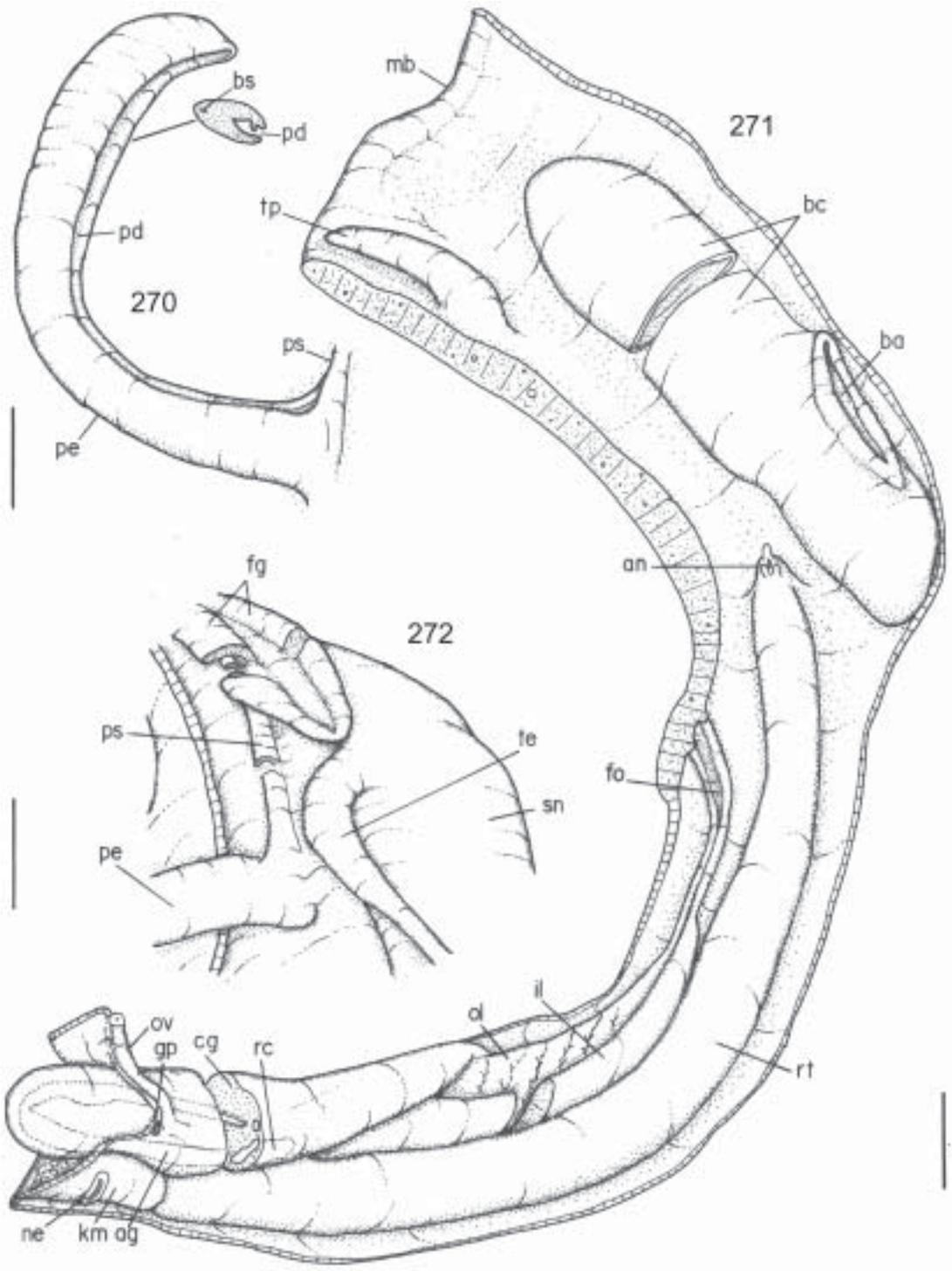
Digestive system. Buccal mass with reduced odontophore (Figs. 257, 261), anterior esophagus narrow, all these structures compressed by narrow space let by snout thick walls. Buccal mass just posterior to mouth, with about 1/5 of snout length; several thin muscle fibers unite radially mouth with adjacent lateral snout walls; pair larger (**m1a**) sited one in each side. Odontophore (Figs. 262-269) very small and short, muscles connecting odontophore with mouth and jaws proportionally thick (**mj**); **m9** thick muscle, originating in ventral region of mouth, inserting in anterior region of ventral surface of radular sac; **m8** broad but thin impair muscle originated in ventral snout surface just posterior to odontophore and inserted in ventral-posterior margin of odontophore, inclusive in radular nucleus, this muscle also have transversal fibers connecting both cartilages (Fig. 268); **m3** absent; **m4** pair as in preceding species, but shorter; **m5** pair also as in preceding species but shorter, narrower and separated with each other; **m6**, horizontal muscle, very short and thin, located close to bulged part of subradular membrane (bb); **m7** very short, originating in anterior-ventral extremity of m4, in its middle level both m7 branches fuses, inserting in ventral surface of radular nucleus; **m11** pair short but strong, originating in inner surface of bulged region of subradular membrane, running attached to this membrane dorsal to m7, after

odontophore running united with m8. Subradular membrane and odontophore cartilages similar to those of preceding species, but shorter. Radula (Figs. 57, 59, 60): rachidian broad, cut-edge somewhat triangular, curved; lateral tooth similar to rachidian but shorter and turned medially; inner and outer marginal teeth similar with each other, flattened, tall, slight slender, tip somewhat rounded, all teeth with series of several very small cusps in cut-edges; high degree of radular deformation, some specimens present rachidian missing or fused with lateral tooth (Fig. 59). Dorsal wall of buccal mass with differentiated inner lip (Fig. 266). Jaws pair small, located in anterior extremity of pair of broad dorsal folds. Salivary gland ducts very narrow (Fig. 263), open in middle region of dorsal folds (Fig. 266). Dorsal folds finish just posterior to odontophore, bifid posterior extremities, inner branch short and tall, outer branch low and longer, approaching from their pair, covering septum between esophagus and odontophore. In bifurcation of each branch, other pair of folds appears, somewhat tall, running short distance and faint. Posterior to these anterior folds, all esophageal inner surface smooth, without folds, glands or crops (Fig. 257). Anterior esophagus narrow, become broader posterior to nerve ring, narrows gradually in its posterior extremity. Salivary glands a large mass surrounding esophagus posterior to nerve ring (Figs. 257, 261); ducts very narrow, sinuous, running attached to esophageal and buccal mass lateral surfaces. Stomach (Fig. 258) broad, with about half whorl in length, without detectable inner folds, very thin walls. Intestine and style sac originating in left-anterior gastric extremity (Fig. 258). Remainder gastric structures similar to description by Morton (1951) for *Struthiolaria papulosa*. Style sac separated from intestine since its beginning, cylindrical, immerse in digestive gland, somewhat short, anterior extremity close to pericardium (Fig. 258). Digestive gland surrounding most of stomach, inclusive between it and kidney. Intestine narrow, originating at left from style sac, surrounding ventrally style sac, crossing to right side immerse in digestive gland, running in right margin of kidney, without renal free loop, exits in pallial cavity. Rectum and anus above described.

Genital system. Male. Testis yellowish, located in right surface of digestive gland and stomach (Fig. 258). Visceral sperm duct narrow, running in middle region of columellar muscle and in



Figures 262-269. *Tylospira scutulata* anatomy. 262. buccal mass and adjacent esophagus, ventral view; 263. same, dorsal view; 264. odontophore extracted, ventral view; 265. same, dorsal view; 266. buccal mass opened longitudinally in its left side; 267. odontophore, ventral view, first layer of muscles removed; 268. same, dorsal view, radula and adjacent structures removed, m6 sectioned to show ventral structures; 269. same, ventral view, m6 not cut. Scales = 0.5 mm.



Figures 270-272. *Tylospira scutulata* anatomy. 270. penis, whole view, with a transversal section in indicated level also shown; 271. right margin of pallial cavity roof, female, showing pallial oviduct, rectum and structures anterior to them, some transversal sections artificially done; 272. head-foot, male, lateral-right view, detail of region of penis base. Scales = 2 mm.

left margin of kidney, presenting seminal vesicle. Pallial sperm duct opened, posterior third part thick glandular (prostate), most part has only tall fold coiled to right forming a tube (Figs. 255, 256), this structure also covered by right fold of food groove (Fig. 272). Penis somewhat long (Figs. 253, 254), cylindrical, with deep sperm groove; penis apex somewhat broad, rounded with small lateral projection corresponding to distal end of sperm groove (Fig. 270). Left flap of penis with secondary, inner, low fold in its distal half (Fig. 270).

Female (Fig. 271). Visceral organs similar in site to those of male. Pallial oviduct posterior extremity in right-dorsal region of kidney, compressing its tissue. Visceral oviduct inserts in left and middle region of glandular mass of pallial oviduct just posterior to narrow gonopericardial duct. Large glandular mass occupies about a third of pallial oviduct length and may correspond to capsule and albumen gland united; presents thick glandular, beige walls with duct "U"-shaped, broad and flattened (Fig. 271); left branch of this duct finishes anteriorly as blind sac and may be connected to visceral oviduct; right branch of this duct slightly broader, running anteriorly towards groove part of oviduct. Pallial oviduct gradually becomes an opened groove in its middle third part, with thick glandular walls and transversal-oblique folded inner surface; inner lamina of this groove broader. Pallial oviduct anterior third part gradually become single groove, comprised by two parallel, low folds; in region posterior to anus crosses to pallial floor and runs at right of head and finishes in right margin of anterior foot projection, similar to preceding species. A probable bursa copulatrix long antero-posteriorly, with thin, transparent ventral wall, located anterior and at left of anus, anterior extremity near mantle border; aperture slit-like, surrounded by muscle fibers, located in its left-posterior margin. Several examined females present

vestigial penis in same site, but very smaller than that of males.

Nervous system (Fig. 261). Similar to that of preceding species, somewhat concentrated, sub-esophageal ganglion located far from nerve ring. Statocysts with single statoliths. Other details in Morton (1956).

Measurements of shells (in mm). AMS 325325, ♀ 2:46.4 by 27.0; ♂ 3:45.0 by 26.7.

Distribution. Australian region.

Material Examined. AUSTRALIA. **New South Wales**, Sydney, 800-1000 m off Port Botany (**type locality**), 33°58'75"S 151°11'03"E, 7 m depth, 1♂, AMS 28625 (1-6/iv/1992); 33°58'13"S 151°11'16"E, 5 m depth, 2♀, AMS 28627 (7/iv/1992); 33°59'S 151°12'E (vii/1992); AMS 350261, 1♂; AMS 350265, 1♀, AMS 350266, 2♂; AMS 350267, 1 specimen; AMS 350269, 1♂; off Foster, 32°11'S 152°33'E, 18 m depth, AMS 350278, 1♀, (ii/1971, trawled); 3 km of little Bay, 33°59'S 151°16.78'E, 59 m depth, AMS 350292, 1 specimen; 2 km E of Long Bay, 33°58.83'S 151°17'E, 66 m depth, AMS 350288, 1 specimen (22/viii/1973, dredged); AMS 350289, 1 specimen (30/vii/1973, dredged); 2.3 km E of Malabar, 33°59.45'S 151°16.27'E, 66 m depth, AMS 350287, 1 specimen (26/ix/1973, dredged); 33°59.45'S 151°16.9'E, 66 m depth, AMS 350286, 2 specimens (25/x/1973, dredged); 1.6 km E of Malabar, 33°58.25'S 151°17'E, 66 m depth, AMS 350291, 1 specimen (31/vii/1973, dredged); off Balmoral, 33°49.5'S 151°15.3'E, 6 m depth, AMS 350294, 3 specimens (vi/1970, Coleman col.).

Genus *Struthiolaria* Lamarck, 1816

(Type: *Murex pesstruthiocameli* Chemnitz = *Buccinum papulosum* Martyn)

Struthiolaria papulosa (Martyn, 1784)

(Figs. 274-278)

Synonymy see Suter (1913). Complement:

Struthiolaria papulosa: Walls, 1980:34; Abbott & Dance, 1982:75 (fig.); Morton, 1997a:7 (pl. 1, fig. 10; pls. 2-4).

Description

Shell. Somewhat similar to that of preceding species, except in being larger and in having subsutural nodes. Other details in Suter (1913).

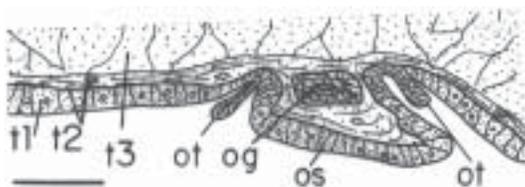
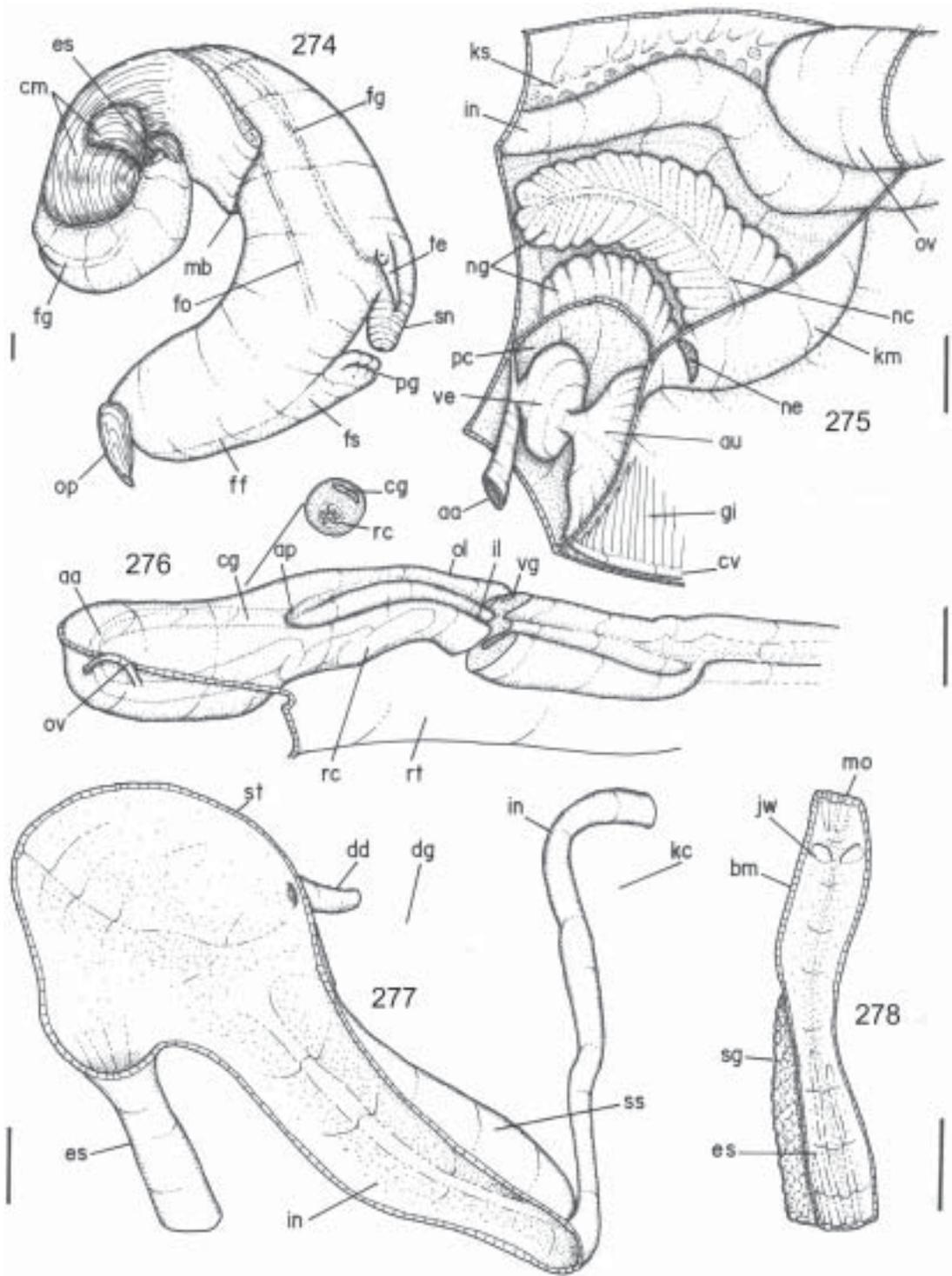


Figure 273. *Tylospira scutulata* serial section in osphradium, Mallory, 7 μ m. Scale = 0.1 mm. Lettering: t1, ciliated columnar epithelium; t2, dense conjunctive tissue; t3, greasy conjunctive tissue.



Figures 274-278. *Struthiolaria papulosa* anatomy. 274. Head-foot, female, lateral-right view, mantle and visceral mass extracted; 275. Kidney and pericardium, ventral view, ventral walls of both removed, renal wall part deflected upwards; 276. Pallial oviduct, ventral view, a transversal section artificially done; 277. Stomach and adjacent digestive tubes, ventral view, shown in situ if remainder structures were transparent, stomach opened longitudinally with inner surface exposed; 278. Buccal mass and anterior esophagus, both opened longitudinally, ventral view, note absence of odontophore. Scales = 2 mm.

Head-foot and operculum (Fig. 274). General characters very similar to those of *T. scutulata*. Differs by simpler anterior region of food groove (with single low fold). Retractor muscles of snout covering haemocoel surface, protruding inside this cavity mainly in snout base.

Pallial organs (Fig. 275). Characters similar to those of *T. scutulata*, including tall gill filaments, endostyle and satellite fold of osphradium. Hypobranchial gland thick, color cream.

Circulatory and excretory systems (Fig. 275). Heart and kidney features similar to those of *T. scutulata*. Distinctive of notable attributions following. Auricle amply connected to anterior wall of pericardium, at right of its connection with ctenidial vein. Nephridial gland slightly more developed, with thin portion covering entire membrane between kidney and heart and its lobed part with oblique furrows converging to central, longitudinal vessel; this vessel inserts at right from nephrostome.

Digestive system. Characters close to those of *T. scutulata*. Distinctive or notable features following. Buccal mass of examined specimen with odontophore altogether reduced (Fig. 278), only a narrow tube [however Morton (1951, fig 15) referred radula for this species]. Pair of jaws thin. Esophagus slender, inner surface with 3-4 longitudinal, low folds. Salivary gland white, soft, filling most of haemocoel, sectioned by several transversal muscles. Their aperture not seen. Stomach large, somewhat spherical (Fig. 277), esophageal insertion in middle of right region, duct to digestive gland single, in ventral-anterior surface, intestine-style sac aperture anterior. Style sac long, open to adjacent intestine, only separated by pair of longitudinal folds. Style sac and adjacent attached intestine entirely immerse in digestive gland. Intestine, after detached from style sac, running towards posterior and right lying on posterior renal wall. No intestinal free loop in renal chamber. Anus also with 3 papillae.

Genital system. No male examined (see Morton, 1950; 1997a).

Female. Visceral organs as described for *T. scutulata*. Pallial oviduct characters (Fig. 276) also similar to those of *T. scutulata*, differing by longer and more convolute duct of albumen gland, with some inner longitudinal folds and by presence of middle fold in open portion of oviduct. Bursa copulatrix similar to that of preceding species, sepa-

rated from oviduct and with posterior-right aperture. Shallow furrow of pallial floor beginning just anterior to pallial oviduct, running in right surface of foot in direction to propodium, but faint before it. Other details in Morton (1997a, pl. 3, figs 1, 2).

Central nervous system. Figured by Morton (1997a, pl. 4 below).

Distribution. New Zealand.

Habitat. Sandy, shallow waters.

Material examined. NEW ZEALAND. North Island, Tokerau, Doubtless Bay, MAS C353040, 1♀ (D.F. McMichael col., ii/1964).

Family APORRHAIIDAE

Genus *Cuphosolenus* Piette, 1876

(Type: *Pterocera tetracer* Orbigny, Jurassic of Europe)

Cuphosolenus (?) *serresianus* (Michaud, 1828)
new comb.

(Figs. 15, 16, 45, 61, 62, 279-296)

Synonymy see Renard (1997). Complement:
Aporrhais serresianus: Poppe & Goto, 1991:116
(pl. 16, Figs. 12-13).
Aporrhais serresiana: Walls, 1980:34 (fig.); Forli,
1989:50-54.

Description

Shell (Figs. 15, 16). Very characteristic, with fusiform outline and projected outer lip bearing four or five long and slender spines. More details in Poppe & Goto (1991:116).

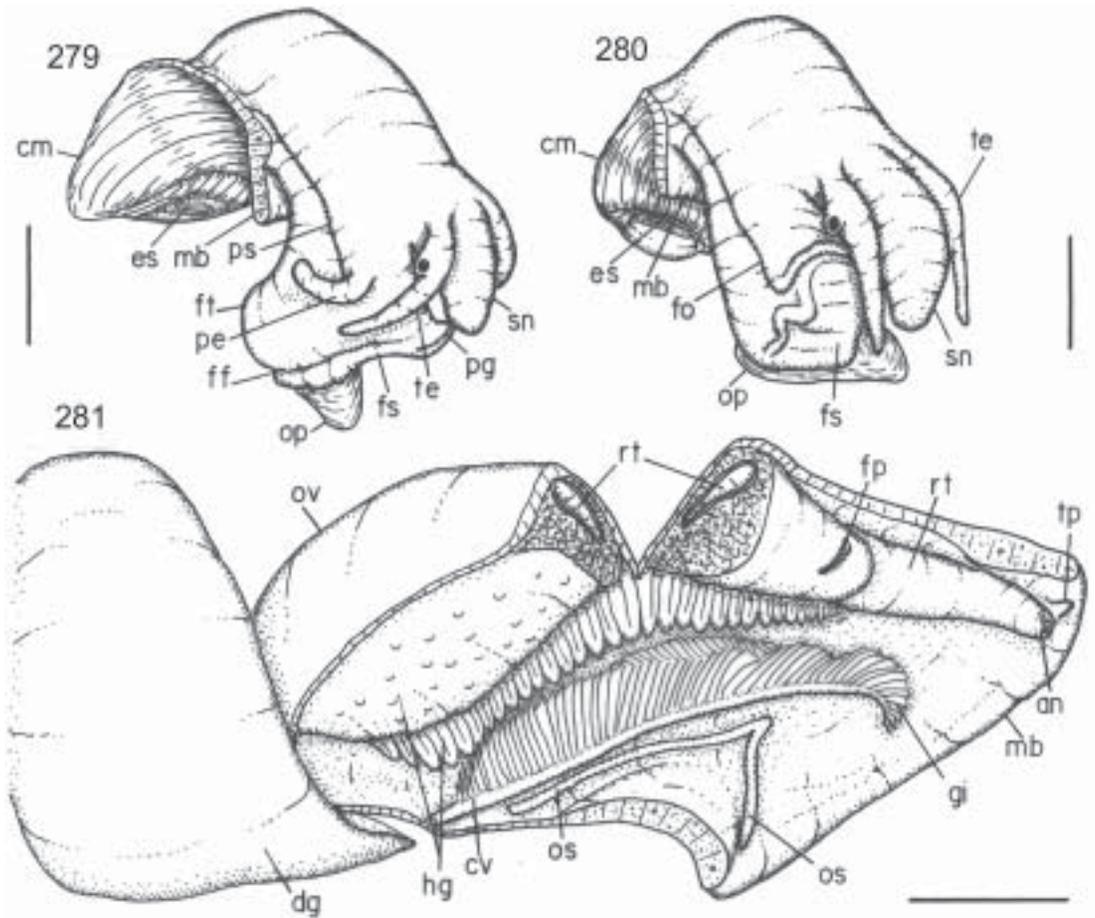
Head-foot (Figs. 279, 280, 283). Color homogeneous clear beige. Head outstanding. Snout broad, long, dorso-ventrally flattened, anterior extremity slightly bilobed. Snout inner layer of circular muscular fibers. Pair of well-developed snout retractor muscles, located in its ventral inner surface, close to median line; originating in anterior-dorsal surface of foot, run longitudinally in haemocoel towards anterior, gradually insert in region immediately posterior to ventral surface of mouth (Fig. 283). Mouth a longitudinal slit, terminal. Tentacles long, stubby, little longer than snout; ommatophores small, slight over their bases. Eyes dark, on ommatophores tip. Foot somewhat small, about double of snout size and with about 1/3 whorl in length; anterior transversal furrow of pedal glands on small elevation, slight away from snout base; crawling sole developed, edged in each side and

dorsally by shallow furrows. Opercular pad sub-terminal, small, and dorsal. Genital furrows and structures described below. No food groove.

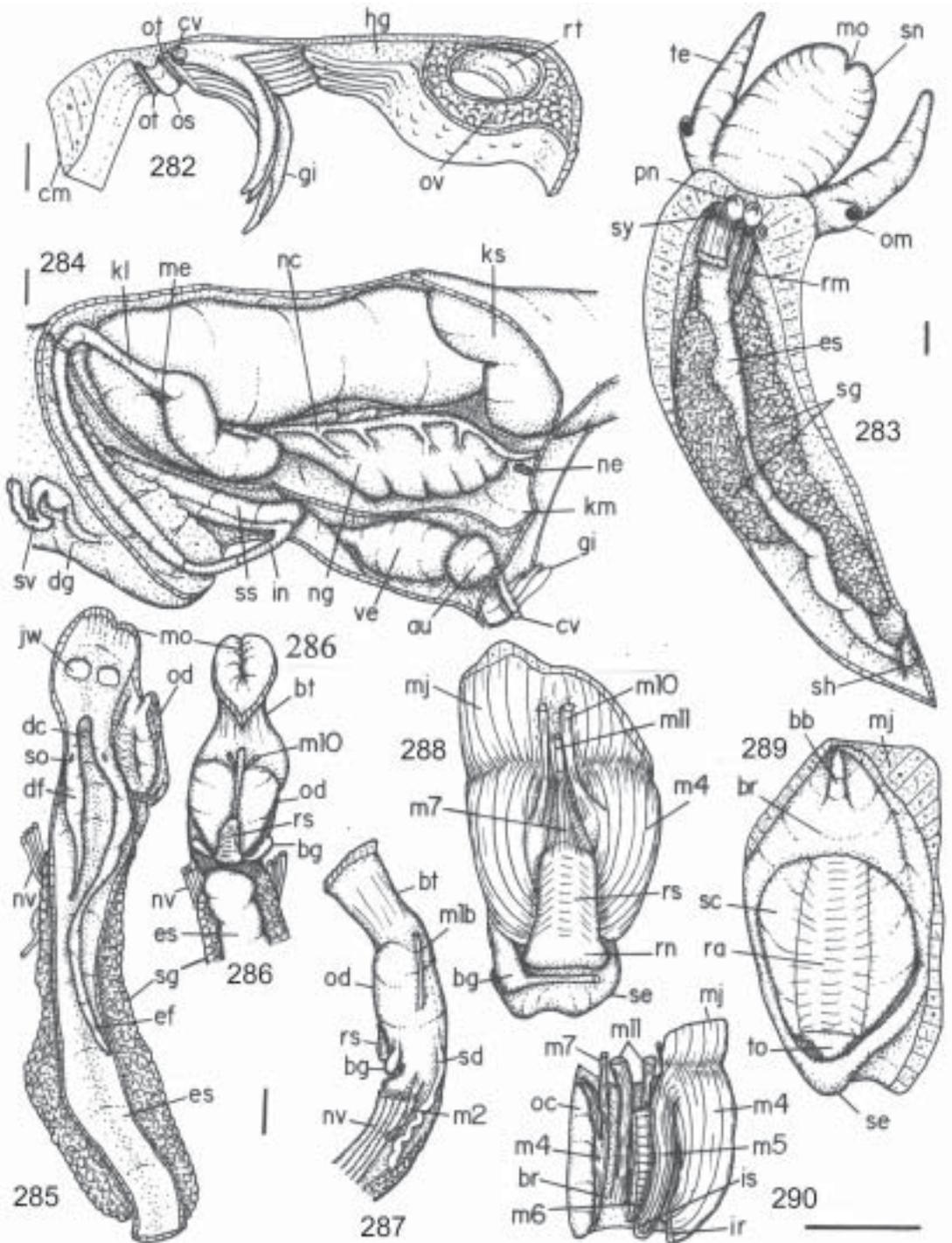
Operculum (Fig. 45). Horny, elliptical, borders uniformly thin, about half projected to left, beyond foot limits (Figs. 279, 280). Nucleus terminal. Outer concentric undulations. Inner scar ample and sub-central. Occupies part of aperture.

Mantle organs (Figs. 281, 282, 296). Mantle border ample, thick, undulated, pale beige in color. Pallial tentacle very small, located in right extremity, anterior to anus; missing in some specimens. Osphradium very long, ridge-like, slight broad, yellow, entirely edged by very narrow satellite yellow fold; anterior extremity far from that of gill and at some distance from mantle border; gradually approaches from gill, running close to gill left margin since its middle third part; osphradium pos-

terior extremity slightly anterior from that of gill. Gill long, narrow (about 1/5 of pallial cavity width), anterior region curved to left; gill filaments with low base and tall, slender and sharp projection located about in its center. Between gill and rectum a slight narrow space (about same width than that of gill). Hypobranchial gland tall and complex, occupies most of area between gill and rectum except anterior and posterior extremities of this area; bears several glandular transversal folds, narrow and wide folds intercalated; left part of rectum and oviduct surfaces also covered by this gland, but thinner. Rectum somewhat narrow, running right margin of pallial cavity, immerse in pallial oviduct (in females). Anus siphoned, near right extremity of mantle border, some inner papillae present. Male sperm groove narrow and pallial oviduct broad, both described below.



Figures 279-281. *Aporrhais serresianus* anatomy. 279. Head-foot, male, lateral-right view; 280. same for female; 281. Pallial cavity, ventral-inner view, and anterior region of visceral mass, female, pallial oviduct and rectum with an artificial transversal section. Scales = 2 mm.



Figures 282-290. *Cuphosolenus serresianus* anatomy. 282. pallial cavity, transversal portion of its middle region; 283. head and haemocoel, ventral view, foot and columellar muscle extracted; 284. anterior extremity of visceral mass, ventral view, ventral wall of pericardium and kidney removed, digestive gland covering style sac removed and deflected downwards and to left; 285. buccal mass, anterior and middle esophagus, ventral view, buccal mass opened in its lateral-right side and esophagus opened longitudinally in its middle region, odontophore in lateral view; 286. buccal mass, ventral view; 287. same, lateral-left view; 288. odontophore extracted from buccal mass, ventral view; 289. same, dorsal view; 290. same, ventral view, mainly left structures shown, m6 sectioned longitudinally to show ventral surface of dorsal structures. Scales = 0.5 mm.

Circulatory and excretory systems

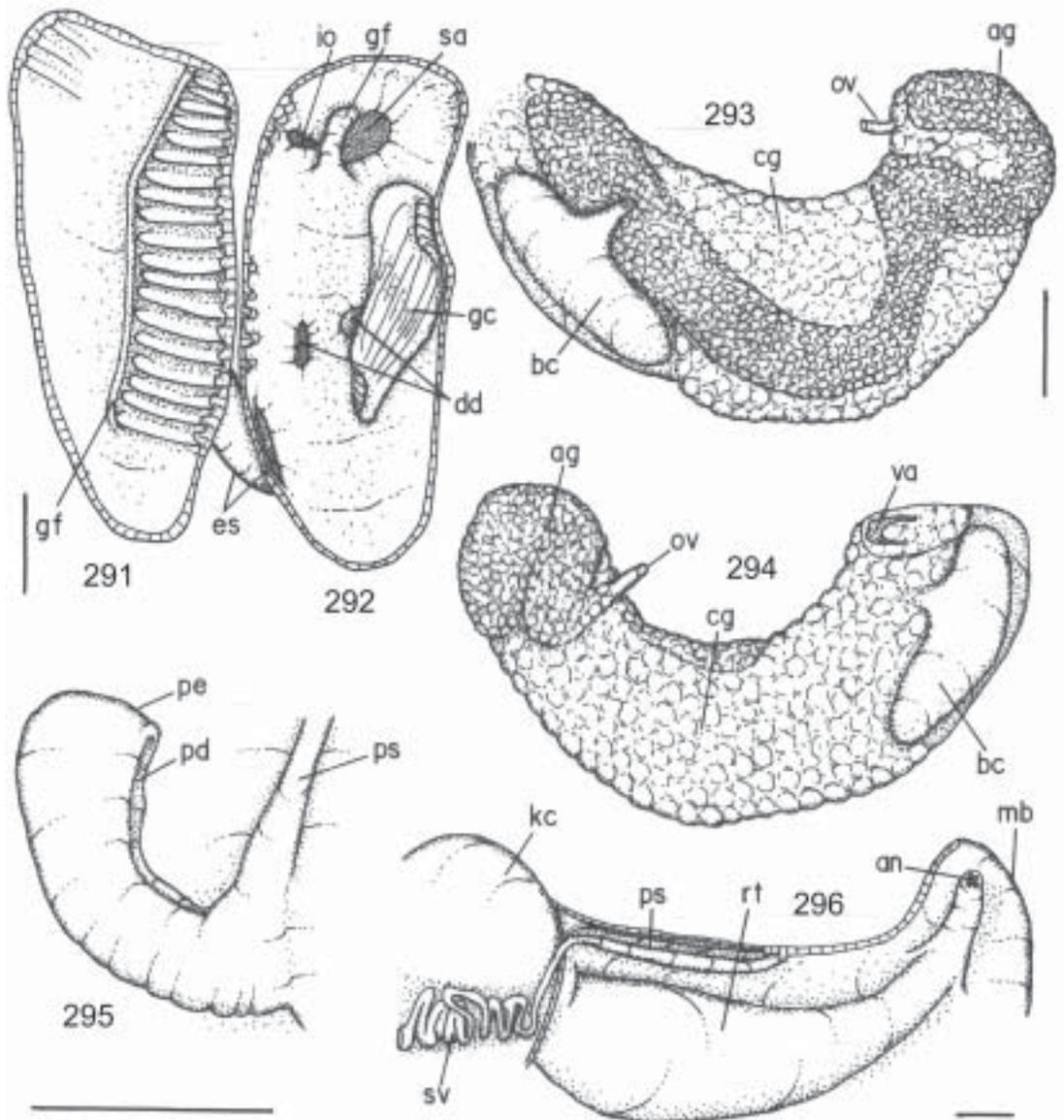
(Fig. 284). Heart somewhat large, located behind left third of posterior end of pallial cavity; auricle anterior to ventricle; ventricle very large. Kidney large and broad, occupying middle and right third parts of posterior margin of pallial cavity and about half whorl behind it. Kidney mostly hollow; kidney tissue greatly compressed by intestinal loop (see below). Only ventral lobe present, located in anterior region, partly attached to rectum, dorsal to posterior extremity of pallial oviduct in females. Nephridial gland greenish, very large and tall, occupies most of surface of membrane between kidney and pericardium; bears central, longitudinal, ventral vessel (nc) with anterior extremity septum-like, connected at right from nephrostome, as in preceding species. Style sac not exposed within renal chamber. Nephrostome small slit located in middle region of membrane between kidney and pallial cavity.

Digestive system. Buccal mass reduced, with small odontophore. Anterior esophagus narrow, somewhat free in lumen of snout. Buccal mass of about 1/4 of snout length, separated from mouth by rather long, broad, muscular oral tube. No outstanding jugal muscle (**m1**), except **m1b**, similar to those of *Strombus* spp. Odontophore (Figs. 285-290) similar to those described for *S. pugilis*, inclusive **m1b** (very narrow), with following distinctive features: 1) proportionally very smaller; 2) jaws and buccal muscles (**mj**) very developed, suddenly narrow before their insertion in odontophore anterior-ventral-lateral margins; 3) **m2**, pair of odontophore retractor muscles (retractor of pharynx), narrow and long, originating in lateral-ventral region of haemocoel just posterior to snout, running anteriorly parallel to esophagus, inserting in lateral-posterior surface of odontophore, almost in transition with dorsal wall of buccal mass; 4) **ma** absent or mixed in oral tube; 5) **m3** absent, however, thin but strong transparent membrane covers ventral and lateral surfaces of odontophore, contours radular sac inclusive covers region between radular nucleus and odontophore, this membrane may be homologue to **m3**; 6) most of other muscles, from **m4** to **m11**, similar situated but narrow and shorter; 7) **m5** narrow, not united one with its pair; 8) ligament between inner surface of **m6** and radular sac (**ih**) absent. Pair of buccal ganglia large, each one lateral located, connective broad, located just anterior to radular nucleus (Figs. 286-288). Radular ribbon

short, little more than odontophore length if straightened. Radula (Figs. 61, 62): rachidian slight narrow, central cusp large, about five pairs of small secondary cusps; lateral tooth very broad, more than twice rachidian width, with single sharp cusp in median region, towards medially; inner and outer marginal teeth similar with each other, very tall, slender, sharp pointed, curved, without cusps. Jaws somewhat large (Fig. 285) but very thin and flexible, anterior cut-edge rounded yellowish; jaws located in posterior region of oral tube. Dorsal wall of buccal mass (Fig. 285) with pair of broad folds, each one beginning gradually from each jaw plate; aperture of salivary glands longitudinal slits located about in middle of each fold in level of odontophore. Ventral septum between odontophore and esophagus present. Esophagus narrow in region of nerve ring, its inner surface both folds of dorsal wall of buccal mass run; right fold suddenly finishes in level of nerve ring; left fold running more posterior but also suddenly finishes. Salivary glands a large glandular mass surrounding nerve ring and esophagus posterior to it (Fig. 283); salivary ducts narrow, pass through nerve ring and open in folds of dorsal buccal mass wall as above described. Stomach (Figs. 291, 292) somewhat narrow (about half of local visceral width) and with about 1/3 whorl in length; in its dorsal inner surface a well-developed sorting area with several transversal folds; esophagus opens amply in left and middle-posterior lateral surfaces; two ducts to digestive gland, both originating about in middle region of ventral gastric surface, anterior duct at right; gastric shield well-developed, long, located at right of anterior duct to digestive gland aperture. Anterior gastric surface with two apertures: at left intestine origin, at right aperture of style sac; both apertures close to one another but separated by short, slender fold inserted in adjacent ventral surface. Intestine and style sac altogether fused with each other, but separated by pair of longitudinal folds, being dorsal fold taller. Style sac slight narrow, long, running immerse in dorsal margin of digestive gland, until its middle level of kidney, not exposed within renal chamber (Fig. 284). Intestine ventral to style sac immerse in digestive gland, after detach it, entrances in middle-left region of kidney chamber and runs attached to digestive gland until right-posterior extremity of this chamber (Fig. 284); after towards anteriorly as free and narrow loop connected to dorsal wall of this chamber by me-

sentery; return to right-posterior extremity of renal chamber and gradually becomes broad, running in right margin of renal chamber until exits to pallial cavity. This broad region of intestine and rectum replete of several small, elliptical fecal pellets. Digestive gland with 3.5 whorls; its anterior extremity ventral and at left to kidney, surrounding stomach and more two whorls posterior to it. Rectum and anus above described.

Genital system. Male. Testis in right side of visceral mass by side of digestive gland, orange in color. Seminal vesicle brown, somewhat flattened, convolute, running on columellar muscle edging left margin of kidney (Fig. 296); in posterior limit of pallial cavity narrows, crossing from middle to right region and exits to pallial cavity. Prostate an opened groove, inner lamina very thick, outer lamina thin, attached to mantle (Fig. 296).



Figures 291-296. *Cuphosolenus serresianus* anatomy. 291. stomach, dorsal wall, ventral-inner view; 292. same, ventral surface, dorsal-inner view, dorsal wall extracted; 293. pallial oviduct, dorsal view, mantle removed; 294. same, ventral view, anterior extremity removed (see fig. 281); 295. penis, whole view; 296. right region of anterior extremity of visceral mass and pallial cavity, male, ventral view. Scales = 1 mm.

Prostate running attached to mantle at right and ventral to rectum at about half of pallial cavity length; gradually crossing to pallial floor as narrow furrow until base of penis. Penis small (Fig. 279), its base at some distance from right tentacle; short, curved, penis furrow opened and deep in its posterior surface. Penis tip broad, light rounded, with penis furrow finishing laterally (Fig. 295).

Female. Visceral structures similar in location to those equivalent of male. Pallial oviduct (Figs. 293, 294) broad, slight flattened, located ventral to rectum and with about 3/4 of its length (Fig. 281). Anterior end of visceral oviduct narrow, inserts in middle-posterior region of apparent uniform glandular mass. Albumen gland long, narrow, in continuation from visceral oviduct, "U" in section, color white, slight sinuous, immerse in capsule gland. Capsule gland broad, yellow. Vaginal tube single, running longitudinally between and along albumen and capsule glands. Bursa copulatrix elliptical, small, located in lateral-left region of anterior extremity of pallial oviduct; connects with albumen gland duct by narrow and slight long duct. Female pore a sub-terminal, ventral, transversal slit far from mantle border (Fig. 281). Just ventral to female pore, but not connected to it, a furrow begins, running anteriorly in pallial floor and in right region of head-foot mass; finishes, as in preceding species, in anterior furrow of pedal glands right extremity (Fig. 280).

Central nervous system. Very similar to those of strombids, inclusive with five pairs of parallel nerves running anteriorly from cerebral ganglia.

Measurements of shells (in mm). MNHN: 28.0 by 26.0; 27.6 by 23.0; 48.2 by 32.2.

Distribution. Iceland to south Mediterranean Sea.

Habitat. Muddy bottoms, from subtidal to 1000 m depth.

Material examined. FRANCE, Gulf of Lion 42°15.6'N 03°42.9'E, 1153-1275 m depth, 25 specimens, MNHN (N/O "Europe", sta. 14, IFREMER/DEPRO96, F. Galgani col. 26/vi/1996); 42°27'20"N 03°27'40"E, 350-450 m depth, MNHN, 3 specimens (Campagne Banyuls – ECOMARGE Rech Lacaze-Duthiers CH 128, R.v. Cosel & C. Vandon col., 03/viii/1985).

Discussion. *C. serresianus* differs conchologically from the type species of the ge-

nus, the Jurassic *C. tetracer* (Wenz, 1938), in being shorter and in having a spine more in the outer lip. However both species have similarity in the aperture fashion and in the sculpture, rather than any other species. Further information on the generic attribution of the species is given in section on discussion of the cladogram.

Genus *Aporrhais* DaCosta, 1778

(Type species *A. quadrifidus* daCosta, 1778 = *Strombus pespelicani* Linné)

Aporrhais occidentalis Beck, 1836
(Figs. 19, 20, 46, 63, 64, 297-314)

Aporrhais occidentalis: Abbott, 1974:143 (fig. 1576); Walls, 1980:34; Abbott & Dance, 1982:75 (fig.); Abbott & Morris, 1995:183: (pl. 47).

Aporrhais occidentalis: Poppe & Goto, 1991:115.
Drepanochilus occidentalis: Morton, 1997a (pl. 3, fig. 4); 1997b (fig. 8:4-5).

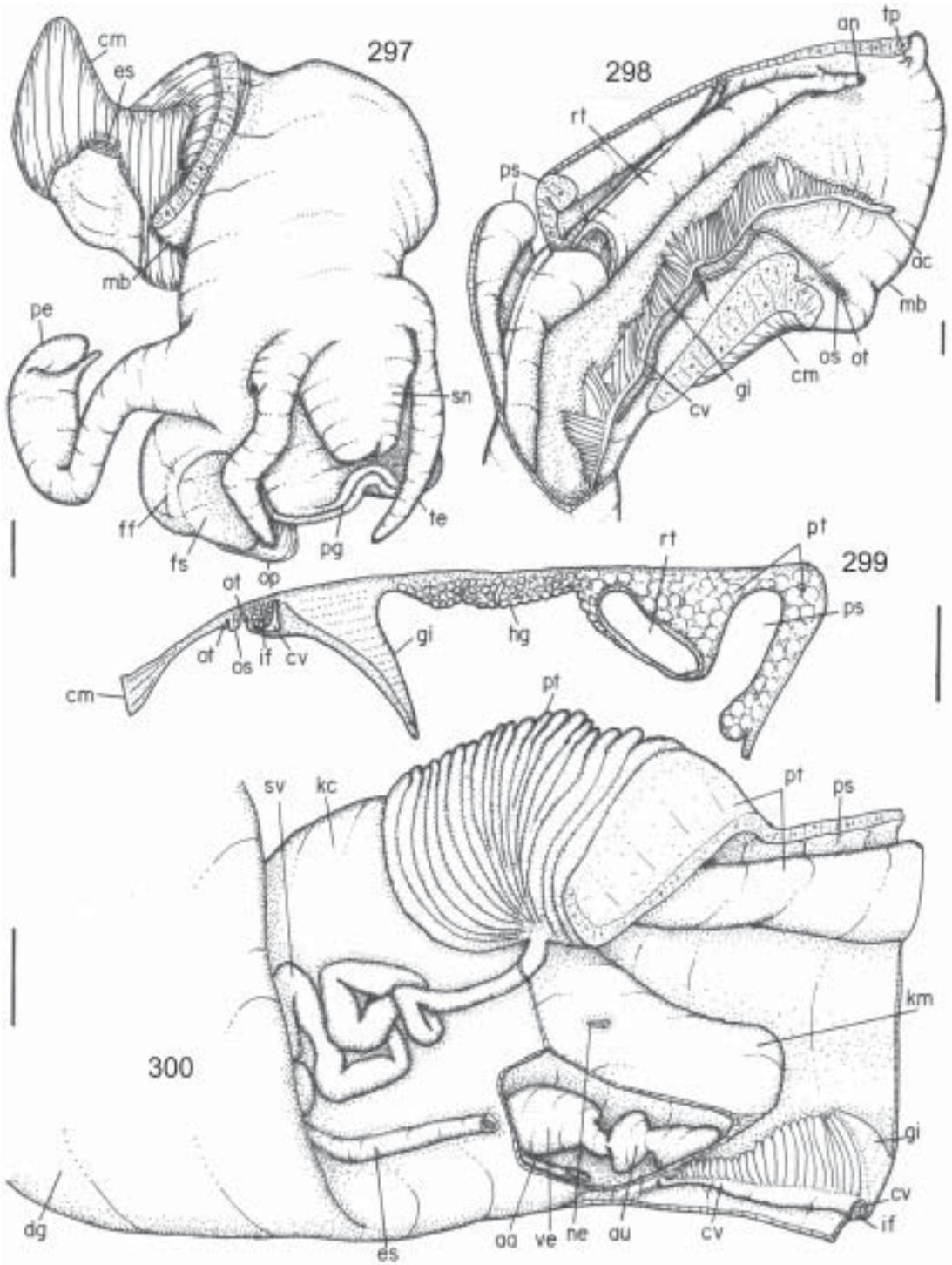
Description

Shell (Figs. 19, 20). Characterized by lacking spines in projected, thick outer lip. Other details in Abbott (1974:143).

Head-foot (Figs. 297, 304). Similar to that of preceding species, but more robust, longer foot tentacles and penis.

Operculum (Figs. 46, 297). Similar to that of preceding species.

Mantle organs (Figs. 298-300, 314). Mantle border similar to that of preceding species, inclusive very small tentacle anterior to anus. Pallial cavity organs with following notable features in relation of those of *C. serresianus*: 1) osphradium with about same proportions, with narrow satellite fold, with posterior half clearly narrower than anterior half; 2) ctenidial vein large, with somewhat uniform width along its length; tall fold in left side of inner surface of ctenidial vein, bulging within its lumen, running all along its length (Fig. 299:if); 3) gill filaments broader and proportionally shorter; 4) anterior extremity of gill with short narrow area, as small septum, without filaments (ac); 5) hypobranchial gland also very developed, with small chambers and transversal folds, but all folds similar sized; small and thinner region covering left margin of rectum and pallial oviduct; 6) rectum broad, initially running immerse in inner lamina of



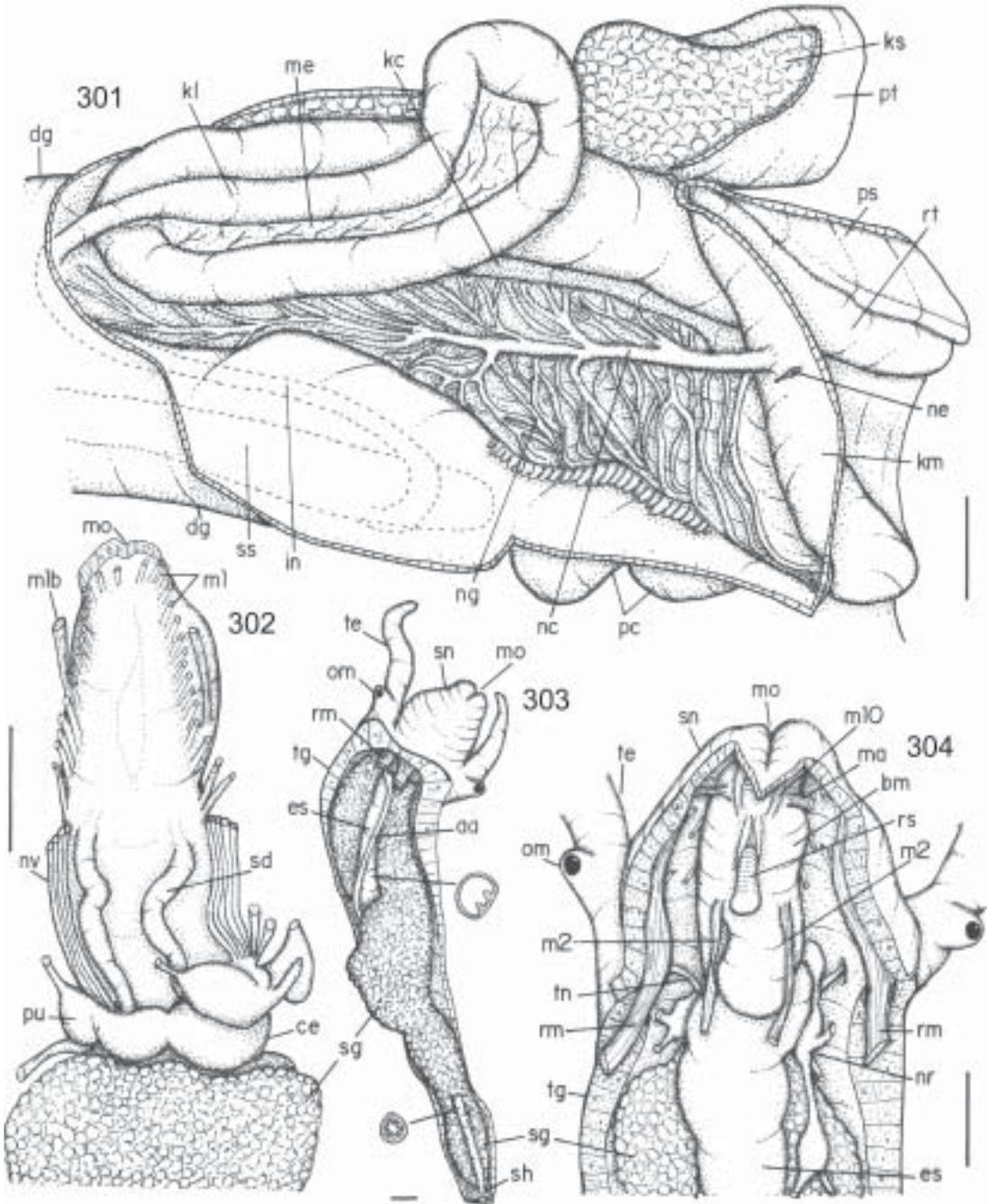
Figures 297-300. *Aporrhais occidentalis* anatomy. 297. head-foot, male, frontal view; 298. pallial cavity, male, ventral-inner view, sperm groove and rectum with an artificial transversal section; 299. pallial cavity roof, transversal section in its middle region; 300. anterior extremity of visceral mass and posterior of pallial cavity, male, ventral view, ventral wall of pericardium removed, anterior part of outer lamina of prostate also removed. Scales = 2 mm.

prostate groove in males or in pallial oviduct of females.

Circulatory and excretory systems

(Figs. 300, 301). Heart somewhat similar to that of

anterior species, but slightly dislocated anteriorly, auricle sited anterior and at right to posterior end of gill; auricle anterior surface attached to pericardium, with ctenidial vein inserted approximately



Figures 301-304. *Aporrhais occidentalis* anatomy. 301. anterior region of visceral mass, ventral view, kidney opened longitudinally and its ventral wall deflected to left, to right and anteriorly; 302. buccal mass and adjacent esophagus, dorsal view; 303. head and haemocoel, ventral view, foot and columellar muscle removed, two transversal sections in indicated regions of esophagus also shown; 304. head, ventral view, snout opened longitudinally in median line, inner structures exposed. Scales = 2 mm.

in its middle region and small portion anterior to this insertion. Kidney also similar to that of *C. serresianus*, but with following distinctive features: 1) renal tissue beige in color, somewhat homogeneous, flattened, attached to rectum and ventral surface of kidney chamber, or to dorsal surface of prostate or pallial oviduct posterior extremities; 2) nephridial gland enormous and very complex (Fig. 301), attached most to dorsal surface of renal chamber; a central, longitudinal vessel running to anterior, inserts as small septum at right to nephrostome as in preceding species; from this longitudinal vessel several tall and irregularly dichotomic folds insert, these folds very tall near vessel and gradually decrease in regions far from it, some folds running also close to posterior-dorsal extremity of kidney chamber as uniform series of small folds.

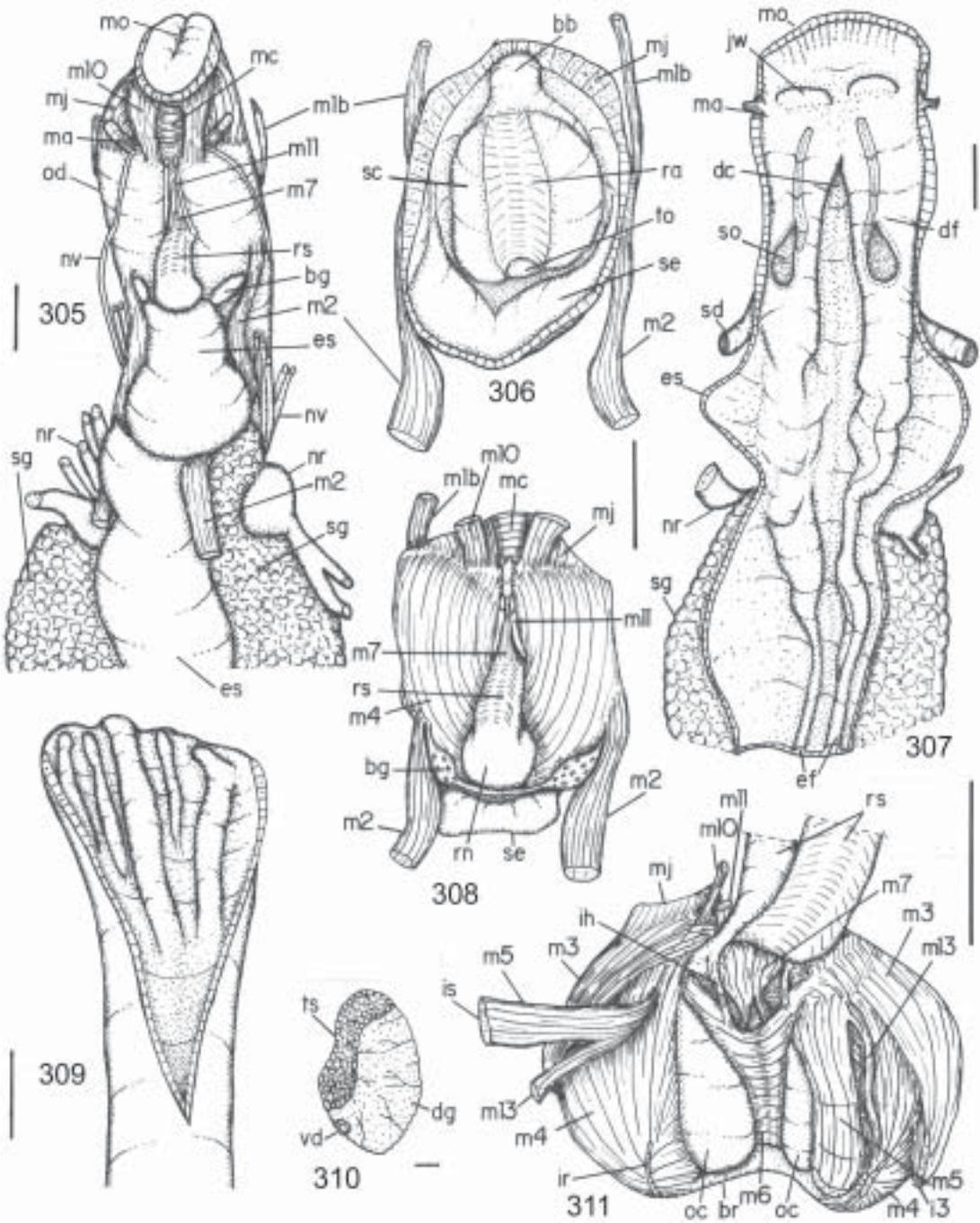
Digestive system. Buccal mass large, about half of snout length, located just posterior to mouth (Fig. 304). Dorsal wall of buccal mass with dorso-lateral series of jugal muscles in both sides (Fig. 302:m1) among others of smaller size. Dorsal wall inner surface with pair of broad and thin jaw plates from which pair of broad dorsal folds begins (Fig. 307). Aperture of salivary glands very large, located about in middle region of dorsal folds, posteriorly rounded, anteriorly sharp. From each salivary gland aperture a median, shallow furrow begins, surrounding median-anterior margin of each aperture and running towards anterior approximately along middle surface of each dorsal fold; near jaws faint (Fig. 307). Odontophore muscles very similar to those of *Strombus* spp, with following distinctive or notable features (Figs. 302, 304-308, 311): 1) **m1b** and **m2** present; 2) **m3** thin, but entirely muscular, insert one with its pair just anterior to radular nucleus; 3) **m4**, **m5**, **m6**, **m7**, **m10**, **m11**, **ih**, **to** and **se** as in strombids; 4) **m13** pair, narrow branch of m5 inserting with m4. Pair of buccal ganglia very large (Fig. 308), laterally situated (just anterior to m2 insertion), pigmented with several brown spots in their surface; connective anterior and ventral to radular nucleus. Salivary glands a homogeneous mass filling region posterior to nerve ring of haemocoel, surrounding esophagus (Fig. 303). Salivary ducts broad, dorsal, pass through nerve ring (Fig. 302), running distance equivalent to half of buccal mass length, penetrate in dorsal wall of buccal mass and open in short distance as above described. Radular ribbon short, about same length than odontophore. Radula

(Figs. 63, 64): rachidian broad, central cusp large (about 1/3 of tooth width), secondary cusps very small, vary from four to six pairs (variable even in both sides of a single tooth); lateral tooth very similar to those of preceding species, pointed tip, turned inwards, no cusps; inner marginal tooth broader than outer marginal tooth and with flattened tip, both marginal teeth without cusps, with weak serrate. Anterior esophagus with pair of inner longitudinal folds as continuation of folds of dorsal wall of buccal mass, running until posterior esophagus (Fig. 307). Stomach large, with about half whorl in length and about 2/3 of local visceral mass width (Fig. 312); general characters similar to those of *C. serresianus*, inclusive tall and short fold between intestine and style sac apertures, differs in having: 1) a broad, rounded fold in ventral posterior region; 2) both ducts to digestive gland not in same level, anterior duct close to aperture of style sac and posterior duct close to esophageal aperture; 3) two differentiated transversal folded sorting areas in each side of anterior-dorsal gastric wall. Style sac and adjacent intestine (Fig. 301) connected to each other and entirely immerse in digestive gland as in *C. serresianus*. Intestinal loops also similar to those of preceding species, inclusive free loop connected by mesentery within kidney chamber (Fig. 301); differ only by initial loop (after style sac) not so exposed within renal chamber (Fig. 301). Digestive gland clear beige, with 2.5 whorls posterior to stomach. Rectum somewhat broad, generally running immerse in inner lamina of pallial gonoducts (Figs. 298, 193, 208). Anus siphoned, slight posterior to mantle border (Figs. 298, 314), with several inner, not uniform sized papillae (Fig. 309).

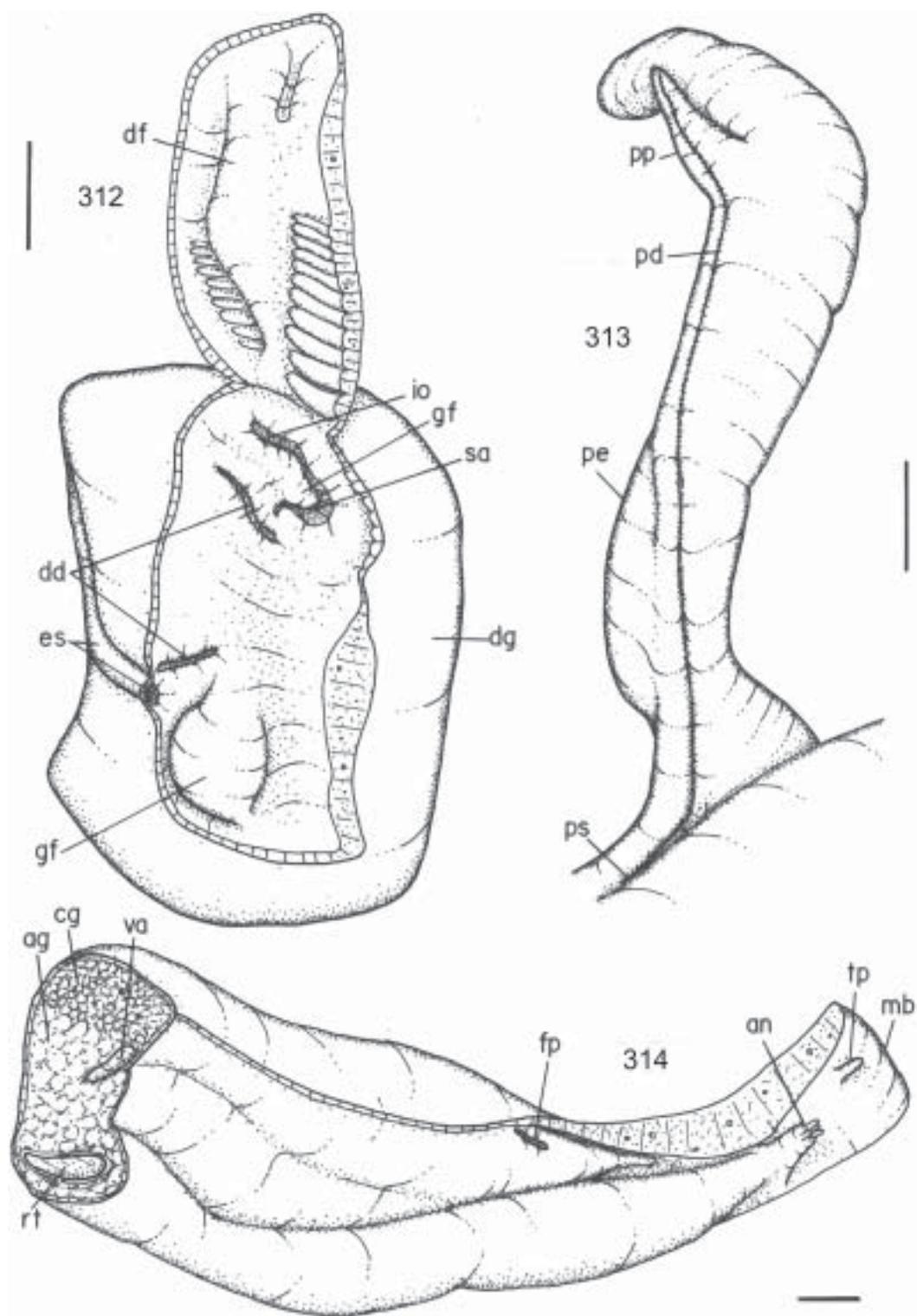
Genital system. Male. Testis in peri-columellar and dorsal regions of digestive gland (Fig. 310), as in *C. serresianus*, orange in color. Vas deferens running on columellar surface, beige in color. Seminal vesicle located about half whorl before pallial cavity (Fig. 300), broad, coiled and brown pigmented, running at left from kidney; close to pallial cavity posterior limit towards right and inserts in left region of prostate. Prostate very broad, bulging in ventral surface of kidney (Fig. 300). Prostate posterior region larger, with several, parallel, glandular leaflets, united with each other in their dorsal and left margins. In pallial cavity these leaflets gradually fuse and became smaller, originating thick outer lamina of pallial

sperm groove, attached to mantle (Fig. 298-300). Inner lamina covers right and dorsal surfaces of rectum. Between middle and anterior third parts

of pallial cavity prostate narrows, becoming similar bordered furrow, crossing to pallial floor; running until penis base. Penis long and complex



Figures 305-311. *Aporrhais occidentalis* anatomy. 305. buccal mass and adjacent esophagus, ventral view; 306. odontophore extracted from buccal mass, dorsal view; 307. same than fig. 305 but with odontophore removed and esophagus opened longitudinally; 308. odontophore extracted, ventral view; 309. anus, ventral view, partially opened longitudinally; 310. visceral mass, transversal section in its middle region, columellar side at left; 311. odontophore, ventral view, most of muscles deflected at left, a little deflected at right, radula and adjacent structures removed upwards. Scales = 1 mm.



Figures 312-314. *Aporrhais occidentalis* anatomy. **312.** visceral mass just in region of stomach, dorsal view, dorsal gastric wall partially removed and deflected upwards, inner surfaces exposed; **313.** penis, whole view; **314.** right region of pallial cavity, ventral view, posterior region of pallial oviduct and rectum removed. Scales = 2 mm.

(Fig. 297); penis groove deep, narrow, running along penis until tip of lateral, sub-terminal papilla (Fig. 313). Papilla stubby, circular in section and slightly long. Penis tip broad, rounded and very thick (penis tip and papilla remember right hand of a boxing glove).

Female (Fig. 314). Visceral organs similar in location to those of males. Pallial oviduct bulges ventral anterior region of kidney chamber and about 2/3 of pallial cavity length anterior to it. No visible chambers or clear divisions of glands. Albumen gland lies at left, whitish, broader posteriorly. Capsule gland lies at right, yellowish, broader anteriorly. Vaginal tube narrow, running between both glands. Female pore sub-terminal, ventral, close to columellar muscle, short portion of glandular tissue stay anterior to female pore as ridge. Pallial vessel running parallel to pallial oviduct narrow but present. Female furrow of head foot similar to those of preceding species, beginning just ventral to female pore; in middle region anterior lamella of this furrow taller, covering it; anterior region of this furrow deep, finishes in anterior furrow of pedal glands.

Measurements of shells (in mm). MNHN: (fig. 19) 52.0 by 34.7; ♀ 3:51.6 by 35.8.

Distribution. From Canada to North Carolina, USA.

Habitat. Sandy bottoms, from 12 to 108 m depth.

Material Examined. CANADA; **Sud Terre-Neuve**, 45°52'N 55°13'W, 165-170 m depth, 2♂, 2♀, MNHN (R.V. Cryos, sta. L111, Casel col., 12/ii/1985).

N.B.: *Chenopus occidentale* is type species of the genus *Arrhoge* Gabb, 1868.

Aporrhais pespelicani (Linné, 1758)
(Figs. 17, 18, 47-49, 65, 66, 315-323)

Synonymy see Renard (1997). Complement:

Aporrhais pespelicani: Morton, 1950:457-461 (Figs. 4, 5); Walls, 1980:34 (fig.); Abbott & Dance, 1982:75 (fig.); Oliveira *et al.*, 1981:114; Forli, 1989:51-54; Taylor & Miller, 1989:228-230 (Figs. 2, 22a); Poppe & Goto, 1991:115 (pl. 16, Figs. 8-11); Fechter & Falkmer, 1993:44-45 (fig.); Blumer, 1996:123-131 (err. *A. pespelecani*).

Aporrhais pes-pelicani: Morton, 1997a:3-7 (pls. 1, 2 – part; pl. 3, figs. 9, 10); 1997b (fig. 7:1).

Description

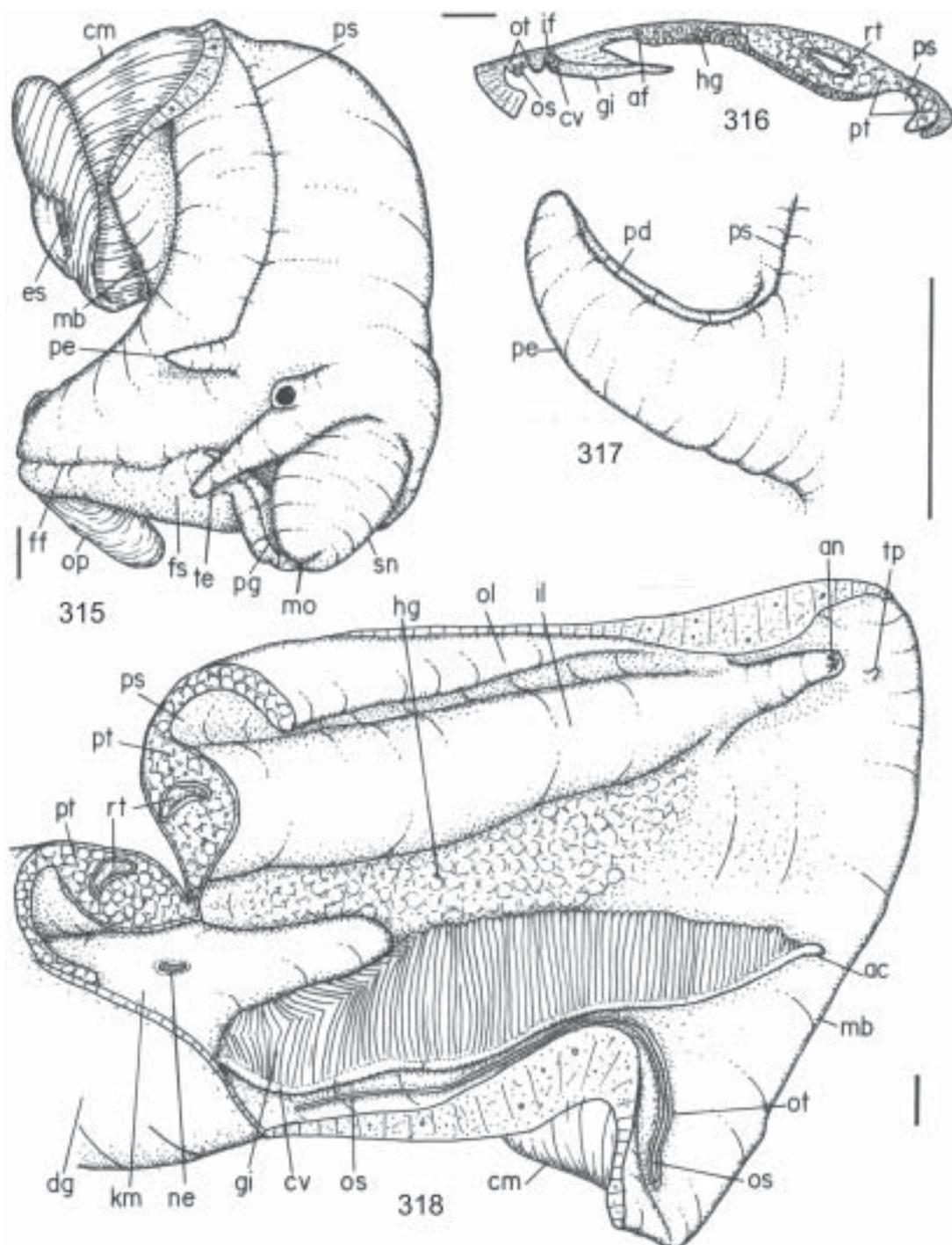
Shell (Figs. 17, 18). In general similar to that of *A. occidentalis*, differs mainly in outer lip, which has three to four stubby, flattened, pointed, short projections. Other details in Poppe & Goto (1991:115-116). First shell whorls empty in mature specimens, visceral mass beginning after several whorls, stays separated from filled whorls by calcified septum (Fig. 48), about three whorls posterior from body whorl. Outer surface of this septum microscopically rough (Fig. 49).

Head-foot (Fig. 315) and **operculum** (Fig. 47). Very similar to those of *A. occidentalis*, only differing in smaller size of penis in males and anterior extremity of female furrow, both described below.

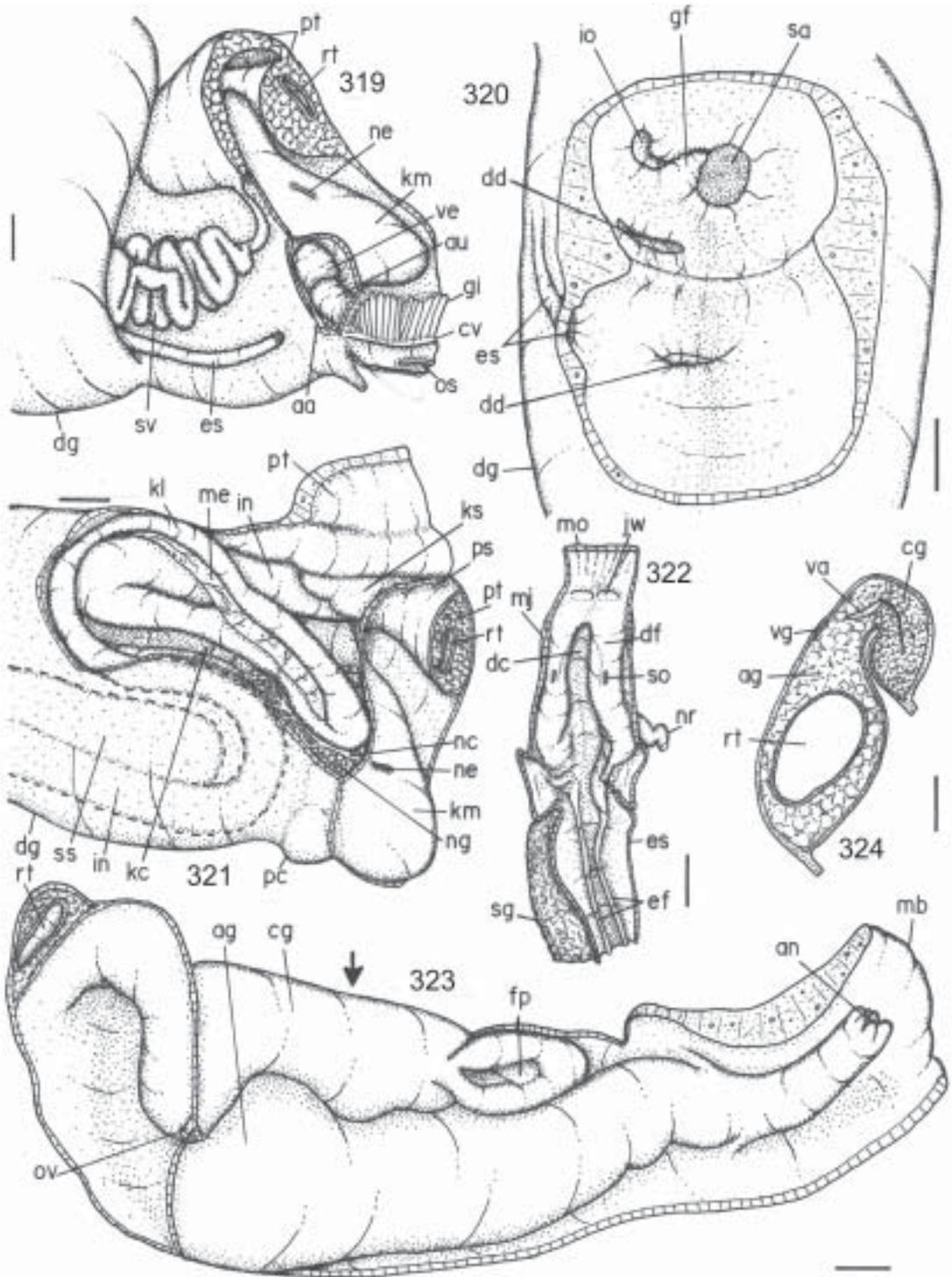
Pallial organs (Figs. 316, 318, 323). Very similar to those of preceding species, inclusive with very small tentacle anterior to anus (tp) (missing in some specimens); satellite fold around osphradium (ot); longitudinal fold within left region of ctenidial vein (if); anterior, septum-like extremity of gill (ac); and hypobranchial gland slight tall, without transversal folds. Only differs in having shorter gill filaments (Fig. 316). Other details in Morton (1997a, pl. 2 top).

Circulatory and excretory systems (Figs. 319, 321). Heart similar to that of preceding species but not so anteriorized, however, pericardium and auricle stay slightly anterior to posterior end of gill, auricle anterior margin attached to anterior margin of pericardial chamber, with insertion of ctenidial vein in its left extremity. Kidney also very similar to that of *A. occidentalis*, including large size of nephridial gland and relations with digestive tubes; differs in having nephridial gland smoother surface (not septate) and its central vessel not so straight, running irregularly.

Digestive system. Buccal mass, odontophore muscles and esophagus very similar to those of *A. occidentalis*, inclusive lateral series of **m1**, presence of **m1b**, **m13** and size of salivary ducts. Differs by slightly longer oral tube and smaller aperture of salivary glands ducts (Fig. 322) (but each one also has median furrow running anteriorly). Radula very similar to preceding *Aporrhais* species, mainly to *C. serresianus*, in having secondary cusps of rachidian of larger size, and number of secondary cusps in average four pairs (Figs. 65, 54). Esophagus and salivary glands (Fig. 322) also similar to those of *A. occidentalis*,



Figures 315-318. *Aporrhais pospelicani* anatomy. 315. head-foot, male, frontal-lateral-right view; 316. pallial cavity roof, male, transversal section in its middle region; 317. penis, whole view; 318. pallial cavity, male, ventral-inner view, a transversal section artificially done in prostate and rectum. Scales = 1 mm.



Figures 319-324. *Aporrhais pespelicani* anatomy. 319. anterior extremity of visceral mass and adjacent region of pallial cavity, ventral view, ventral wall of pericardium removed; 320. visceral mass just in region of stomach, dorsal view, dorsal gastric wall removed, inner surface exposed; 321. same than fig 319, ventral wall of kidney sectioned and deflected upwards, anterior region of style sac and adjacent intestine shown through digestive gland; 322. dorsal wall of buccal mass and adjacent esophagus, ventral view, esophagus opened longitudinally; 323. right region of pallial cavity, ventral view, anterior surface of kidney chamber also shown at left of fig.; 324. same, transversal section in region indicated by an arrow in fig. 323. Scales = 1 mm.

but middle esophagus lacks inner folds; posterior esophagus with four-five longitudinal, similar sized folds. Stomach shorter and simpler than that of *A. occidentalis*, without detectable sorting areas and broad posterior fold (Fig. 320), still differs by low, transversal constriction in middle region of stomach, by more posterior location of anterior duct to digestive gland and posterior duct more distant from esophageal aperture; fold between style sac and intestine also present. Style sac length, limits and degree of fusion with intestine, as well as intestinal loops, rectum and anus similar to those of preceding species, inclusive mesentery in renal intestinal loop (Fig. 321), rectum passing through inner lamina of pallial gonoducts (Figs. 316, 321, 324) and anus papillated, siphoned (Figs. 318, 323).

Genital system. Male. Visceral and pallial organs very similar to those of *A. occidentalis*. Seminal vesicle (Fig. 319) dark brown in color. Prostate gland, as in *A. occidentalis*, presents broad posterior region bulging in ventral surface of kidney and, in pallial cavity, thick walled, with inner lamella surrounding rectum (Fig. 319); differs in lacking several leaflets in its posterior-ventral region, only uniform glandular mass present (Figs. 316, 318, 319, 321). Penis very small (about half of tentacle length) (Fig. 315), flattened, curved, narrowing gradually, tip rounded (Fig. 317). Penis groove running in its posterior surface, finishes almost in penis tip.

Female (Figs. 323, 324). Visceral and pallial organs similar to those of preceding species. Pallial oviduct bulges in ventral surface of kidney and runs at about half of pallial cavity length; differs from that of *A. occidentalis* in having ventral furrow separating partially capsule and albumen glands and female pore terminal and broader (Fig. 323:fp). Furrow of pallial floor similar to those of preceding species, differs only in its anterior extremity, which presents short portion dorsal to pedal gland furrow (and not fuses with it), i.e., both furrows present short portion parallel with each other. Other details of pallial oviduct in Johansson (1948).

Measurements of shells (in mm). MZSP 28809, (fig. 17): 46.0 by 30.7; 41.8 by 27.7.

Distribution. From Iceland, Mediterranean Sea to Morocco.

Habitat. Muddy bottoms, from 10 to 180 m depth.

Material Examined. SCOTLAND; **West Coast**, Loch Spelve, Mull, dredged, MZSP 28809 (ex-BMNH), 7 specimens (R.V. Calanus, IDT & SW col., 29/viii/1975).

Family XENOPHORIDAE

Genus *Onustus* Swainson, 1840

(Type species *Trochus indicus* Gmelin, 1791)

Onustus caribaeus (Petit de la Saussaye, 1856)
(Figs. 67, 68, 325-344, 384-386)

For synonymy see Lambiotte (1979:75) and Ponder (1983:64). Complement:

Xenophora caribaea: Rios, 1985:60 (pl. 22, fig. 270); 1994:73 (pl. 25; fig. 281).

Tugurium caribaeum: Abbott & Dance, 1982:73 (fig.).

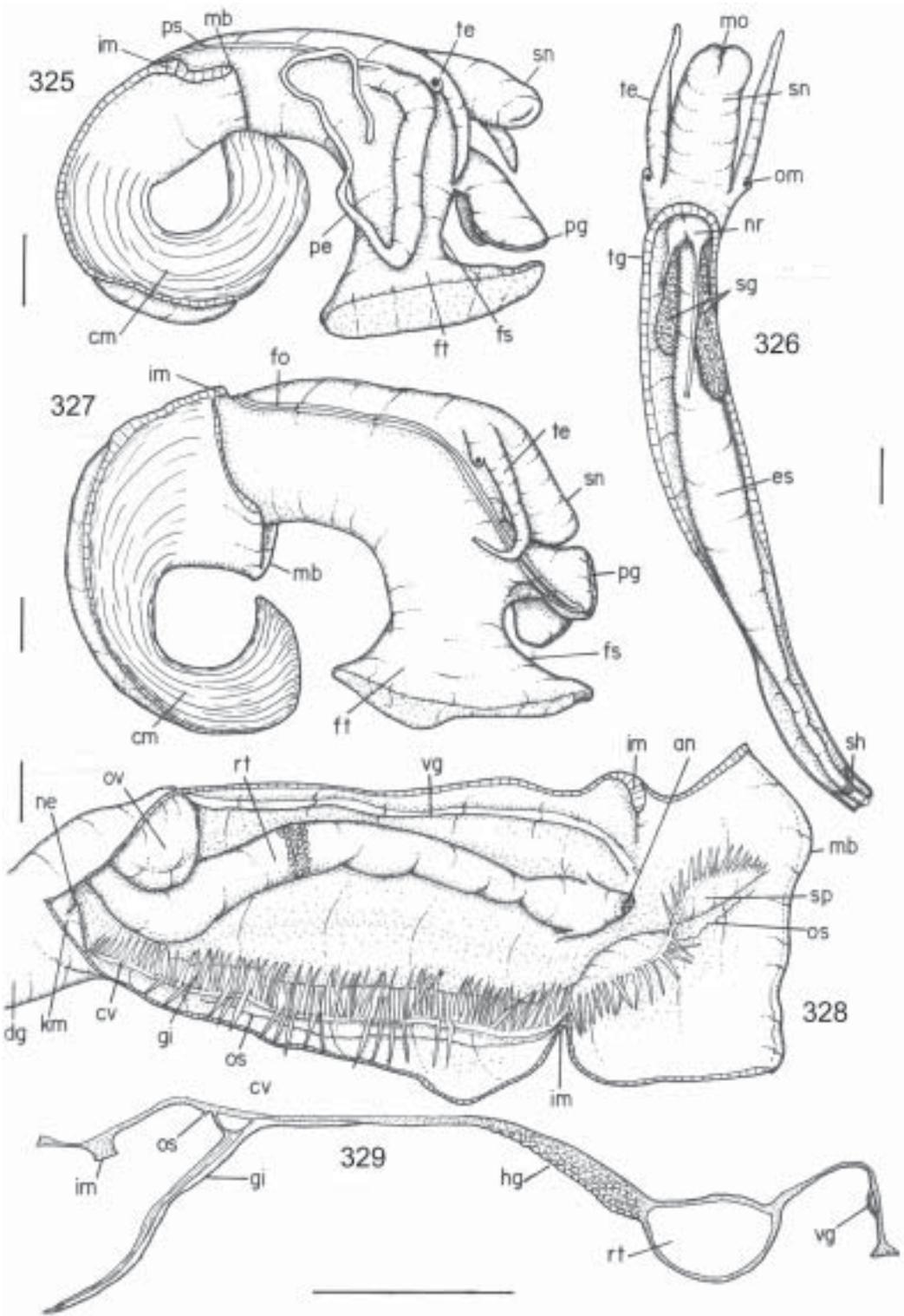
Tugurium caribaeus: Merlano & Hegedus, 1994:162.

Description

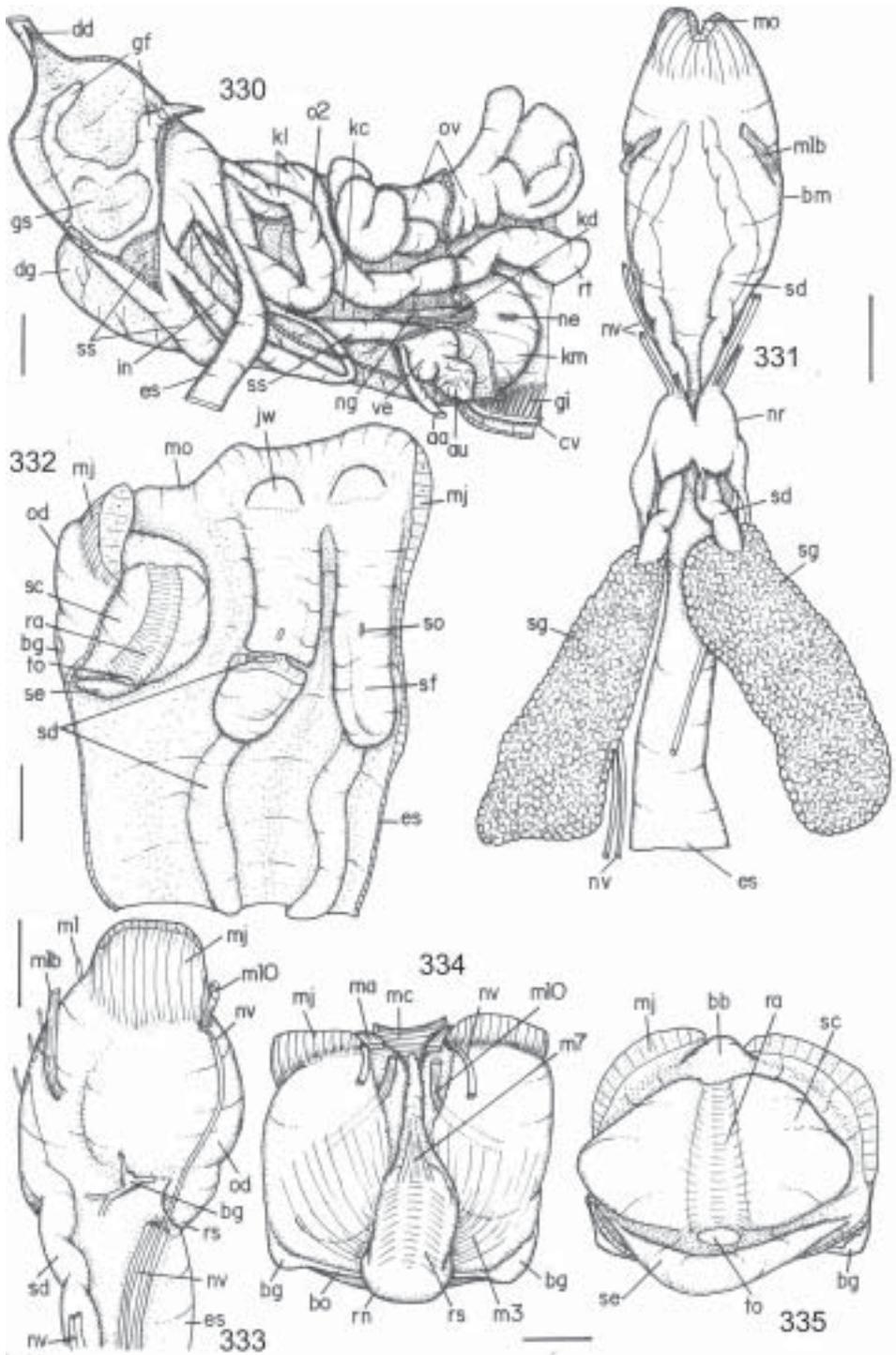
Shell (Figs. 384-386). Lateral projections very broad. Umbilicus opened. Outer lip concave and arched. Other details in Ponder (1983:64, Figs. 31a, b).

Head-foot (Figs. 325-327). Color homogeneous pale beige. Head outstanding. Snout broad, slight dorso-ventrally flattened, anterior margin somewhat bilobed; mouth longitudinal, slightly ventral. Longitudinal muscle fibers present in inner surface of snout. Tentacles long, stubby, generally longer than snout. Eyes dark, located on small ommatophores slight over tentacles base. Foot well-developed, with clear crawling sole; anterior extremity projected, with transversal furrow of pedal glands; opercular pad very large – about same size than remainder foot regions, somewhat plane, located in dorsal and posterior limit of foot. Genital grooves and structures at right of head, described below. Columellar muscle flattened, with almost one whorl. Ventral insertion of mantle in head-foot mass very posterior; lateral mantle regions not connected to head-foot surface until near median line (im), resulting in narrow entrance to pallial cavity.

Operculum. Corneous, outline roughly triangular, nucleus terminal, located about middle region of inferior margin. Outer surface with concentric undulations. Inner surface with large scar restricted to superior half of opercular surface; in-



Figures 325-329. *Onustus caribaeus* anatomy. 325. head-foot, male, lateral-right view, operculum removed; 326. head and haemocoel, ventral view, foot and columellar muscle removed; 327. same than fig. 325, female; 328. pallial cavity, female, ventral-inner view; 329. same, transversal section in its middle region. Scales = 5 mm.



Figures 330-335. *Onustus caribaeus* anatomy. **330.** anterior whorl of visceral mass and adjacent region of pallial cavity, ventral view, stomach opened longitudinally and its ventral wall deflected to show its inner surface, ventral wall of kidney and pericardium removed, inner structures exposed; **331.** buccal mass, anterior esophagus and adjacent structures, dorsal view; **332.** Buccal mass, opened in its left side, ventral view, inner surfaces exposed, odontophore in lateral view, a transversal section of right dorsal fold artificially done; **333.** buccal mass, lateral-right view; **334.** odontophore extracted from buccal mass, ventral view; **335.** same, dorsal view. Scales; 330 = 5 mm; 331-333 = 2 mm; 334-335 = 1 mm. Lettering: o2, intestinal region where the homogeneous fecal mass become elliptical fecal pellets.

ferior half with several radial striae originating from nucleus. Occupies entire shell aperture.

Mantle organs (Figs. 328-330, 341). Mantle border narrow, smooth, without pigment. Mantle cavity deep (about 1.5 whorls), narrow, with constriction between its middle and anterior third parts, produced by insertion in head-foot (im). Osphradium long, extremely narrow, tenuous line edging left gill border; anterior extremity slightly posterior to that of gill; posterior extremity markedly anterior to that of gill. Gill very long – about same length than pallial cavity; has two regions: 1) posterior, with about 2/3 of its length, edging left margin of cavity, bearing several slightly narrow filaments; each filament with low base and very long and narrow projection in left side on ctenidial vein, this projection tapering gradually to sharp pointed tip; 2) anterior, about 1/3 of this length, situated obliquely, somewhat parallel to mantle border, with very narrow, filiform filaments on septum, these filaments similar to projection part of filaments of posterior region. Ctenidial vein narrow, only visible in posterior 2/3 of gill. Between gill and rectum a broad space. Hypobranchial gland moderately developed, mainly near rectum. Rectum broad, running near median line of pallial cavity roof; broad space between rectum and right extremity of pallial cavity in which longitudinal vessel runs approximately along its middle level. Anus siphoned, located about in same level of pallial cavity constriction and posterior to septum part of gill, with several papillae in its margin.

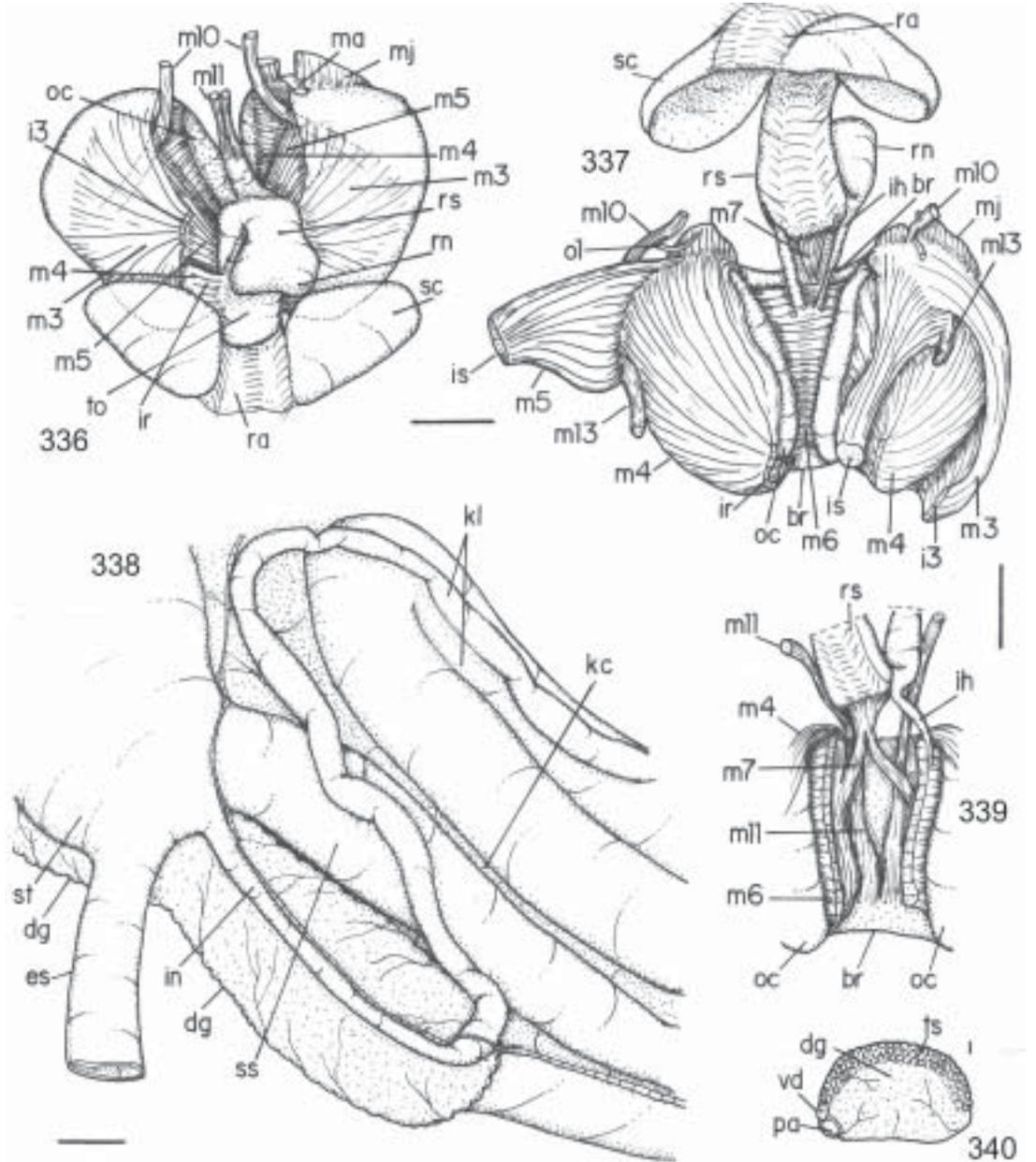
Circulatory and excretory systems (Figs. 330, 338, 341). Heart of slightly small size, located just behind posterior end of gill, in left-anterior extremity of visceral mass. Auricle anterior to ventricle. Kidney chamber very ample, with little more than half whorl in length and occupying most of anterior visceral mass width. Kidney tissue very scanty, restricted to low and thin lobe near membrane between kidney chamber and pallial cavity, strongly compressed by intestinal loops, style sac and pallial oviduct (described below). Nephridial gland very small, located in dorsal region of membrane between kidney and pericardial chambers. Nephrostome a transversal slit about in middle region of membrane between kidney and pallial cavity.

Digestive system. Buccal mass large, just posterior to mouth, occupies about 1/2 of snout length (Fig. 326). Dorsal wall of buccal mass thick

muscular, mainly anterior to jaws. Jaws in two plates, of medium size (Fig. 332). Powerful muscles unite dorsal wall of mouth, jaws and odontophore (mj). Odontophore well-developed, with muscles very similar to those of *Strombus* species, with following distinctive features (Figs. 331-337, 339): **m1b** present but narrow; **m3** thin, covers both sides of ventral surface of odontophore except region close to median line, inserts one with its pair just anterior to radular nucleus, with also small connection to this; **m13** pair of somewhat narrow muscles, originating just between m4 and m5, in their ventral region adjacent to odontophore, near median line, insertion close to that of m4; **m10** narrow but very long, inserted almost in lateral surface of odontophore, covered by m3, running anterior and medially, exiting from m3 near median line, in this region a small muscular connection with adjacent region of mj (o1); **m2** and **m10a** absent. Remainder characters of odontophoric structures as described for, e.g., *S. pugilis*, inclusive septum between odontophore and esophagus (se), tissue on middle region of radula (to), insertions of m7 and m11, and inner ligaments between horizontal muscle (m6) and radular sac (ih). Radula short, little more than odontophore length (Fig. 334). Radula (Figs. 67, 68): rachidian broad, central cusp large, occupying about 1/2 of its cut-edge, secondary cusps smaller, vary from two to four pairs; lateral tooth very broad (almost twice rachidian width), curved, apex sharp turned medially, without secondary cusps; inner and outer marginal teeth similar with each other, tall, slender, somewhat flattened, curved, with sub-terminal series of about 15 small cusps in inner margin. Pair of buccal ganglion well developed (Fig. 334), located laterally, connected to each other by long connective which cross between m3 and radular nucleus. Inner surface of dorsal wall of buccal mass with pair of broad folds (Fig. 332), each one beginning gradually posterior to each jaw, becomes outstanding, connected by narrower base, both suddenly finish, just posterior to level of septum, in tall and rounded fashion. Pair of salivary glands very large (Figs. 326, 331), separated with each other; left salivary gland generally longer, more posterior and ventral; both salivary glands with broad ducts (Figs. 331-333), running anteriorly through nerve ring, near posterior limit of buccal mass penetrating in its dorsal wall, running immerse in each local fold, open somewhat broadly in middle region of these folds.

Esophagus long, thin walled, without inner glands, folds or crops (Fig. 326); posterior to nerve ring becomes broad, narrows gradually in its posterior region. Stomach large and spacious (Figs. 330, 338), about 1/3 whorl in length; single and broad duct to digestive gland located in poste-

rior-right gastric region; inner surface with fold surrounding gastric shield, bears narrow sessile projection in direction to duct to digestive gland; esophagus inserts in stomach in its ventral-anterior region; in dorsal-anterior region intestine and style sac origin. Style sac narrow and very long



Figures 336-340. *Onustus caribaeus* anatomy. 336. odontophore, posterior view, radula and adjacent structure partially removed; 337. same, ventral view, m5 of left side deflected, radula and adjacent structures removed upwards, right m3 (at left of fig.) removed; 338. detail of visceral mass, ventral view, just anterior to stomach, digestive gland and ventral wall of kidney partially removed; 339. odontophore, ventral view, only its median region shown, m6 sectioned longitudinally to show ventral surfaces of dorsal structures; 340. visceral mass, transversal section in its middle region, columellar side at left. Scales: 336-337, 339 = 1 mm; 338, 340 = 2 mm.

(Figs. 330, 338); its posterior region running dorsally through anterior extremity of digestive gland, and entire dorsal surface of kidney chamber (about 2/3 of its length); anterior extremity rounded, anterior and at right to pericardium, almost in limit between kidney and pallial cavity. Style sac and intestine altogether separated with each other. Intestine first loops narrow, at beginning running parallel and at left to style sac (Figs. 330, 338), part immerse in digestive gland, suddenly towards ventrally and become exposed in kidney chamber, crossing posterior and at right up to posterior limit of kidney, turn anteriorly and gradually become broader, in this local its contents changes from homogeneous broad mass to several, elliptical, small fecal pellets; in middle-left region of kidney returns to posterior-right extremity of kidney running, very broad, dorsally to its narrow precedent loop; in this local newly returns anteriorly lying dorsal surface of kidney, somewhat sinuous, exiting to pallial cavity (Fig. 330). All intestinal loops within kidney chamber connected to its dorsal surface by short mesentery. Rectum and anus above described.

Genital system. Male. Testis covers dorsal and right regions of digestive gland (Fig. 340) and stomach. Vas deferens very narrow, running in dorsal surface of columellar muscle near median line; near kidney gradually become sinuous. Seminal vesicle broad and intensely coiled (Figs. 341), bulging ventral-anterior surface of kidney chamber. Suddenly vas deferens narrows and exits to pallial cavity in its posterior-right extremity. In pallial cavity vas deferens opens, becoming a groove (Fig. 341); its posterior half running in pallial roof right margin; gradually crossing to pallial floor, running at right of head until penis base (Fig. 325). Penis very long (about same length than pallial cavity) (Fig. 325); basal region broad and flattened, gradually narrows in middle region, becoming slender; basal and middle region with deep sperm groove (Fig. 344); apical third part also flattened, with sperm groove shallow and with lamina becoming median fold; penis apex tapered.

Female. Visceral genital organs location similar to those of male. Oviduct in ventral region of kidney, very narrow, edging its left mar-

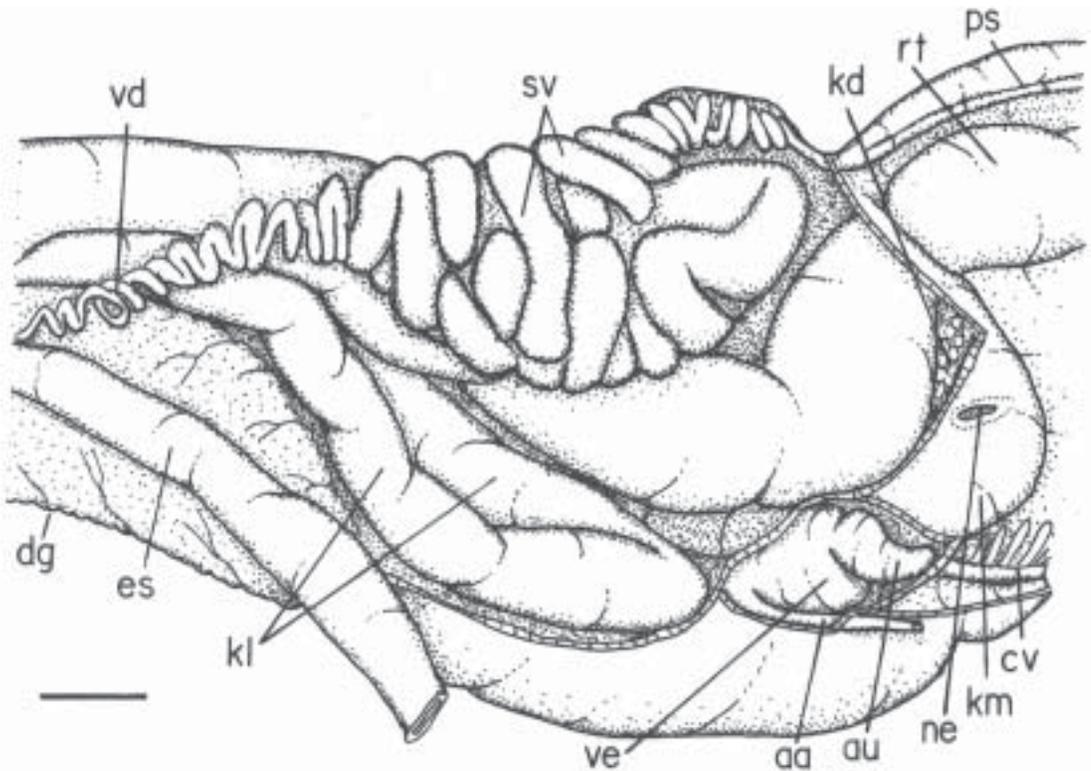
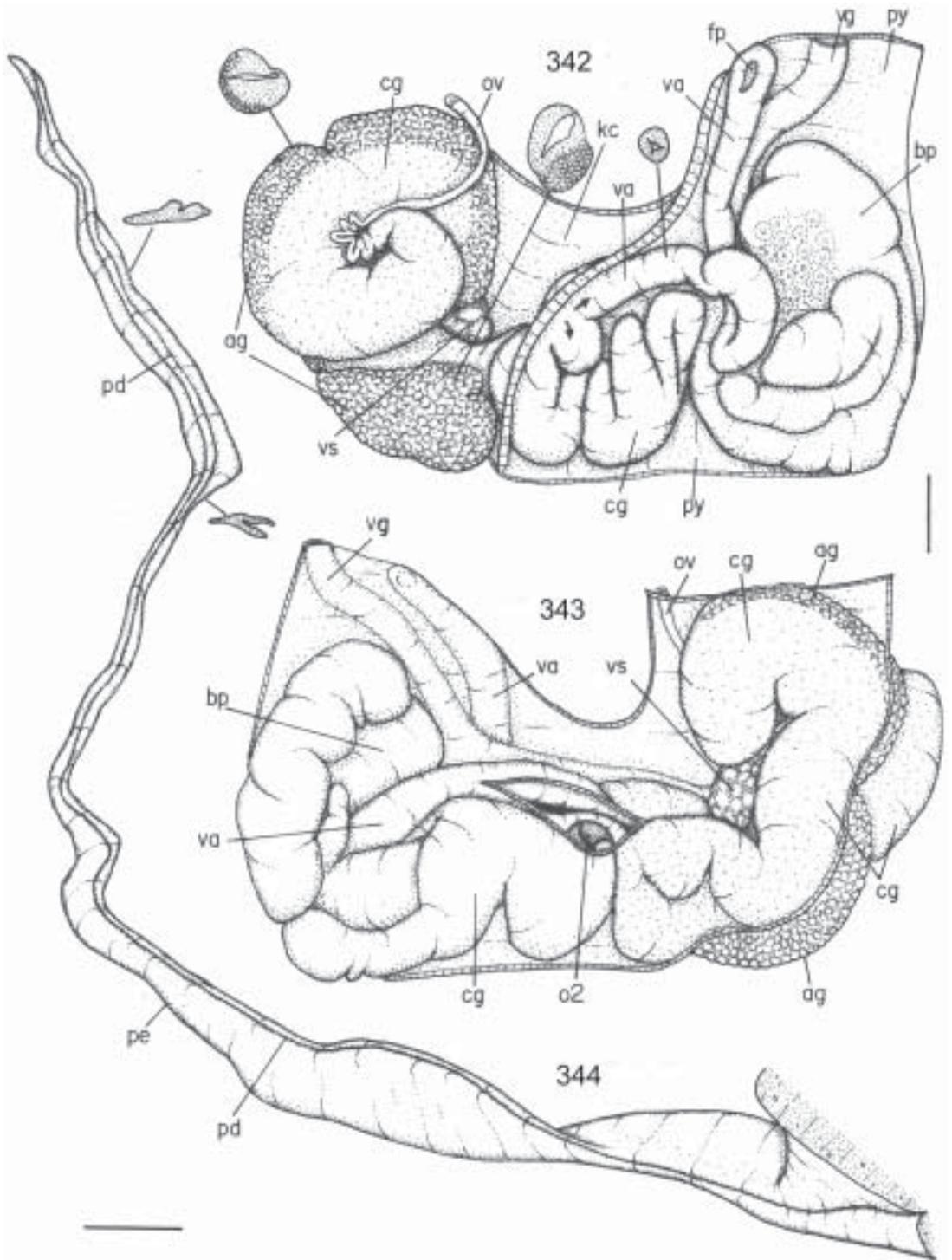


Figure 341. *Onustus caribaeus* anterior extremity of visceral mass, male, ventral view, ventral wall of pericardium removed, ventral wall of kidney sectioned in its left region (down in fig.) and deflected upwards, the large seminal vesicle attached to it still shown. Scale = 2 mm.



Figures 342-344. *Onustus caribaeus* anatomy. 342. pallial oviduct, which locates half within kidney chamber (at left in fig.), ventral view, representations of three transversal section in indicated levels also shown (not in same scale); 343. same, dorsal view, shown if the mantle was transparent, in middle region a longitudinal section shown inner structures just where the oviduct bifurcates; 344. penis, whole view, representations of two transversal sections in indicated levels also shown. Scales = 2 mm. Lettering: o2, small chamber uniting anterior and posterior halves of capsule gland with vaginal tube.

gin; near anterior-right renal extremity bulges within kidney chamber, after some distance gradually become sinuous, very broader and with thick glandular walls; this broader region of oviduct bulges in dorsal surface of kidney chamber (Figs. 328, 330), in form of irregular spire, broad and flattened inner duct edged by two glandular masses (Figs. 342, 343): 1) albumen gland external, white, with large acina; 2) capsule gland inner, yellow, of uniform aspect. A sac with several solid vesicles inserts in anterior portion of this renal region of oviduct. In transition to pallial cavity this broader region suddenly narrows, becomes hollow and bifurcated. Right branch with very thick, glandular walls, yellow, very sinuous and irregular; finish in short distance from posterior limit of pallial cavity in brood pouch, a sac replete of mature ova. Left branch narrow, muscular and glandular walls, lies left surface of right branch with loop posterior to brood pouch; afterwards, attached to mantle, running short distance in pallial roof and finish in somewhat broad vaginal pore. A shallow furrow running in right limit of pallial floor, right region of head and finishes as deep furrow in right side of anterior foot projection, close to pedal glands furrow (Figs. 327).

Nervous system (Figs. 326, 331). Similar to those of preceding species but with sub-esophageal ganglion close to nerve ring. About five parallel pair of nerves inserted in cerebral and pleural ganglia anterior margin, running anteriorly.

Measurements of shells (in mm). MZSP 28811: 116.4 by 75.0; 94.3 by 57.5.

Distribution. From North Carolina, USA, to Rio Grande do Sul, Brazil.

Habitat. Broken shell bottoms, from 35 to 450 m depth.

Material Examined. BRAZIL, **Rio de Janeiro**, off Cabo Frio, about 20 m depth, MZSP 28810, 2♀, 1♂ (P.M. Costa col., otter trawl, 1996). **São Paulo**; off São Sebastião, 24°30.3'S 44°13'W, 455 m depth, MZSP 28811, 2♀, (proj. PADCT, sta. 6628, 7/xii/1997).

Onustus indicus (Gmelin, 1971)

(Figs. 30, 31, 71, 72, 345-353)

Synonymy see Lambiotte (1979:70) and Ponder (1983:59-60). Complement:

Tugurium indicum: Abbott & Dance, 1982:74 (fig.).

Description

Shell (Figs. 30, 31). Attached small objects only present close to apex. Outer surface glossy, oblique striate. Umbilicus large, also striate. Other details in Ponder (1983:60).

Head-foot (Figs. 346, 349). Characters very similar to those of *O. caribaeus*. Distinctive or notable features following. Snout broader, with pair of flat lateral, longitudinal expansions. Anterior surface of snout, surrounding mouth, covered by broad and low papillae. Female furrow finishes in right end of pedal gland furrow. Opercular pad with projection attached to operculum projected forwards in retracted condition.

Operculum (Fig. 71). Similar features as those of preceding species, except for outer surface sculptured by net of radial and concentric folds.

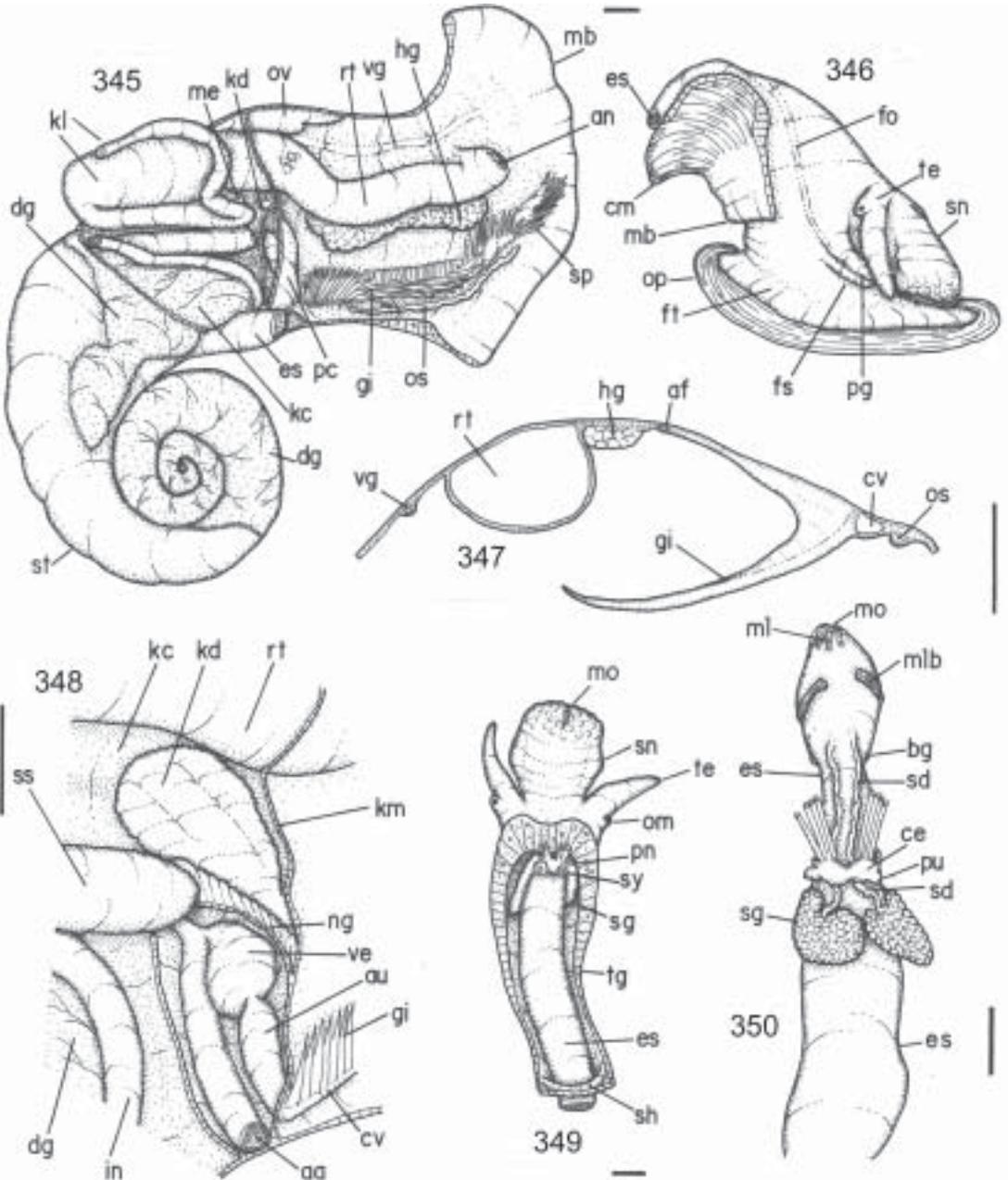
Pallial organs (Figs. 345, 247, 248). Characters very similar to those of *O. caribaeus*. Distinctive or interesting features following. Osphradium shorter and very broader. Hypobranchial gland thicker, white, lies close to rectum left margin. Gill filaments slightly broader, curved to right.

Circulatory and excretory systems (Figs. 345, 348). Characters close to those of *O. caribaeus*. Distinct or notable features following. Pericardium and heart slender and located slightly perpendicular to left pallial cavity margin. Renal dorsal lobe or nephridial gland a thin and small layer restrict to anterior region close to nephrostome. Intestinal loops inside renal chamber with same fashion as those of *O. caribaeus*, but distal portion broader, with mesentery more evident.

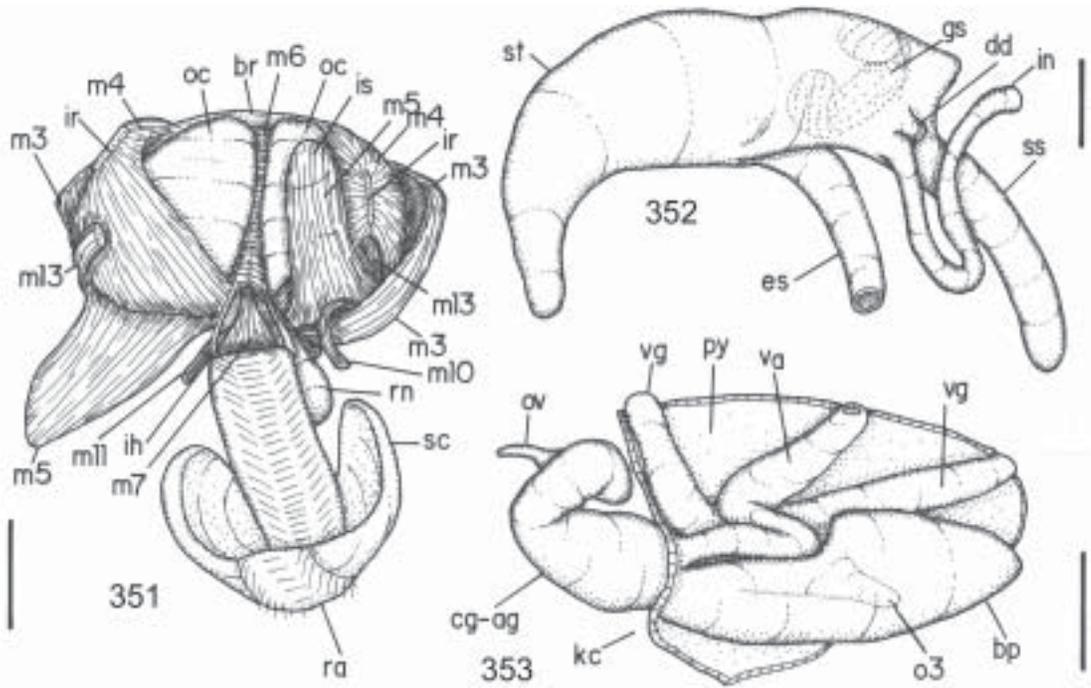
Digestive system. Buccal mass characters (Figs. 349-351) similar to those of *O. caribaeus*, except for presence of **m1a**, **m10** slightly broader and **m11** turned towards anterior. **M13** also present, originated from m4. Dorsal chamber deeper, with some longitudinal, low folds. Pair of salivary gland smaller, flattened, reniform (Fig. 350). Aperture of salivary glands more anterior situated (close to jaws) slit-like, longitudinal. Dorsal folds fashion and inner surface of esophagus as those described for *O. caribaeus*. Radular teeth (Fig. 72): characters closely similar to those of *O. caribaeus*, except for longer central cusp of rachidian and by absence of cusps in marginal teeth. Stomach (Figs. 345, 352) longer than that of *O. caribaeus*, inner surface smooth, gastric connections concentrated in anterior-right region, esophageal insertion

broad, more posterior and left. Intestinal origin and duct to digestive gland narrow, close to each other, just ventral to style sac origin. Style sac as long as kidney chamber, similarly to preceding species most exposed in this chamber and separated from intes-

tine. Gastric shield in anterior-dorsal gastric region (Fig. 352). Intestine initially narrow, with loop ventral and at left from style sac, part lying posterior wall of renal chamber. Rectum and anus as in preceding species.



Figures 345-350. *Onustus indicus* anatomy. 345. Pallial cavity and visceral mass, ventral view, kidney opened longitudinally with inner intestinal loops deflected upwards; 346. Head-foot, female, lateral-right view; 347. Pallial cavity roof, transversal section in its middle region; 348. Detail of fig. 345 with anterior region of kidney and pericardium opened by longitudinal sections, inner structures exposed; 349. Head and haemocoel, ventral view, foot and columellar muscle extracted; 350. Buccal mass, anterior esophagus and adjacent structures, dorsal view. Scales = 2 mm.



Figures 351-353. *Onustus indicus* anatomy. 351. Odontophore, ventral view, both cartilages deflected, radular sac extracted from m4 and m5 insertions and deflected downwards, right m5 (left in fig.) also deflected, scale = 1 mm; 352. Stomach and adjacent digestive tubes, ventral view, seen in situ if remainder structures were transparent, gastric shield (gs) seen by transparency, scale = 5 mm; 353. Pallial oviduct, ventral view, adjacent mantle region also shown, connection of brood pouch (bp) with remainder oviduct as a tall papilla (o3) seen by transparency, scale = 2 mm.

Genital system. Male. Visceral and pallial structures with characters similar to those of *O. caribaeus*. Penis as shown by Ponder (1983, fig. 14s) with flattened, paler distal region with penis furrow running in margin.

Female. No fully mature female examined. Characters of visceral and pallial genital organs close to those of *O. caribaeus*. Pallial oviduct clearly not mature, but with fashion similar to that of preceding species (Fig. 353). Visceral oviduct suddenly increases in region dorsal to kidney preceding pallial cavity, in a coiled albumen-capsule gland. Just after pallial cavity posterior limit, this gland connects to 2 branches. Right-ventral branch a long vaginal tube, sigmoid, thick walled. Left-dorsal branch a broad brood pouch in such aperture forms inner tall papilla located approximately in its central region. Genital pore papilla-like, located in middle-ventral region of pallial oviduct. Female genital furrow in pallial floor and at right of head-foot similar to that of *O. caribaeus*.

Central nervous system. Very similar to that of *O. caribaeus*.

Measurements of shells (in mm). Specimen #1: 69.5 by 35.0; #2: 52.0 by 18.0.

Distribution. Tropical Indian and Pacific Oceans.

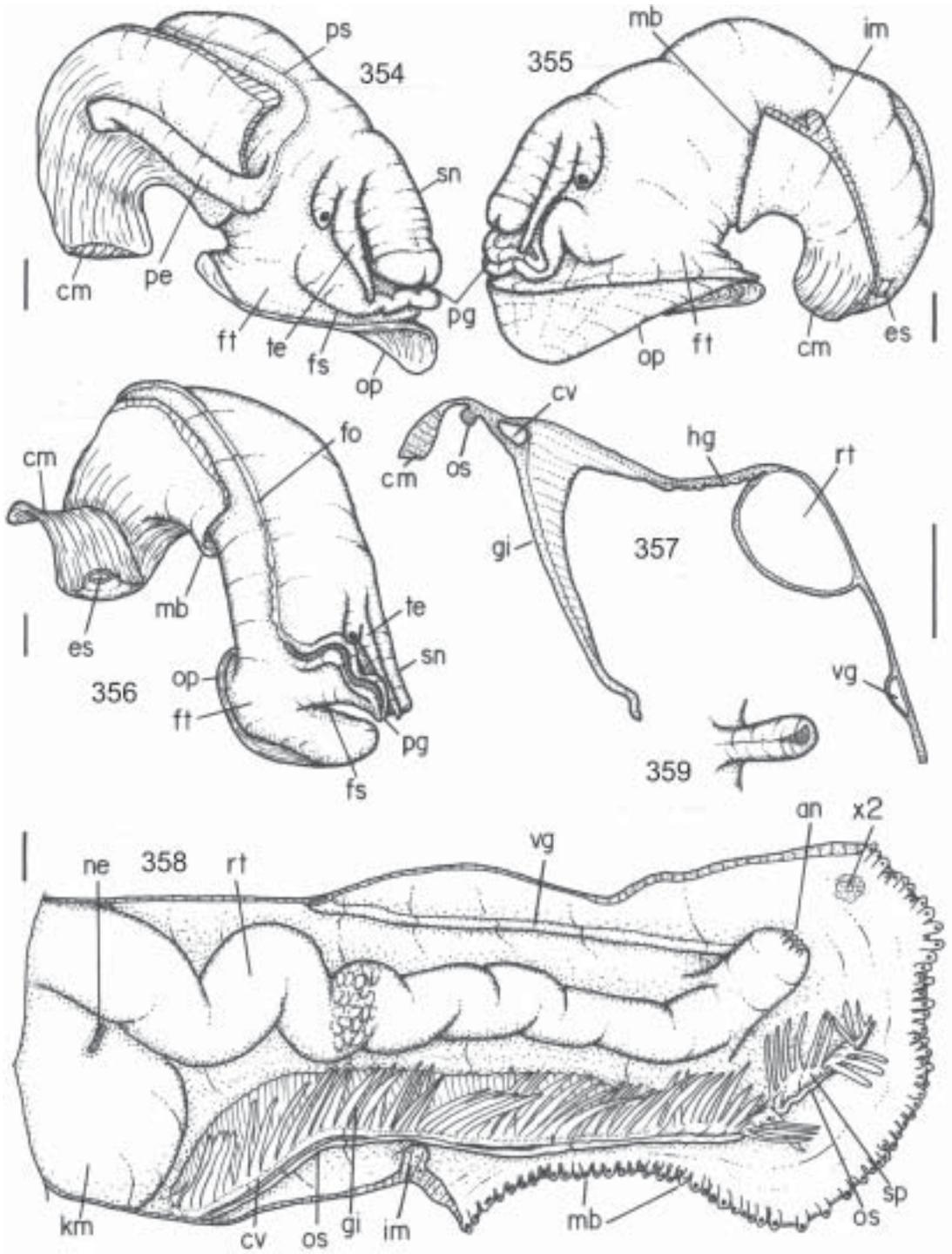
Material examined. AUSTRALIA. Queensland. Off North Keppel Island, off Yeppon, 23°02'S 151°10'E, AMS 353279, 1♀, 1♂, 1 shell (T. Nielsen & P.T. Nielsen col., viii/1979, sta. 555B).

Genus *Xenophora* Waldeheim, 1807
(Type species *Trochus conchyliophorus* Born, 1780)

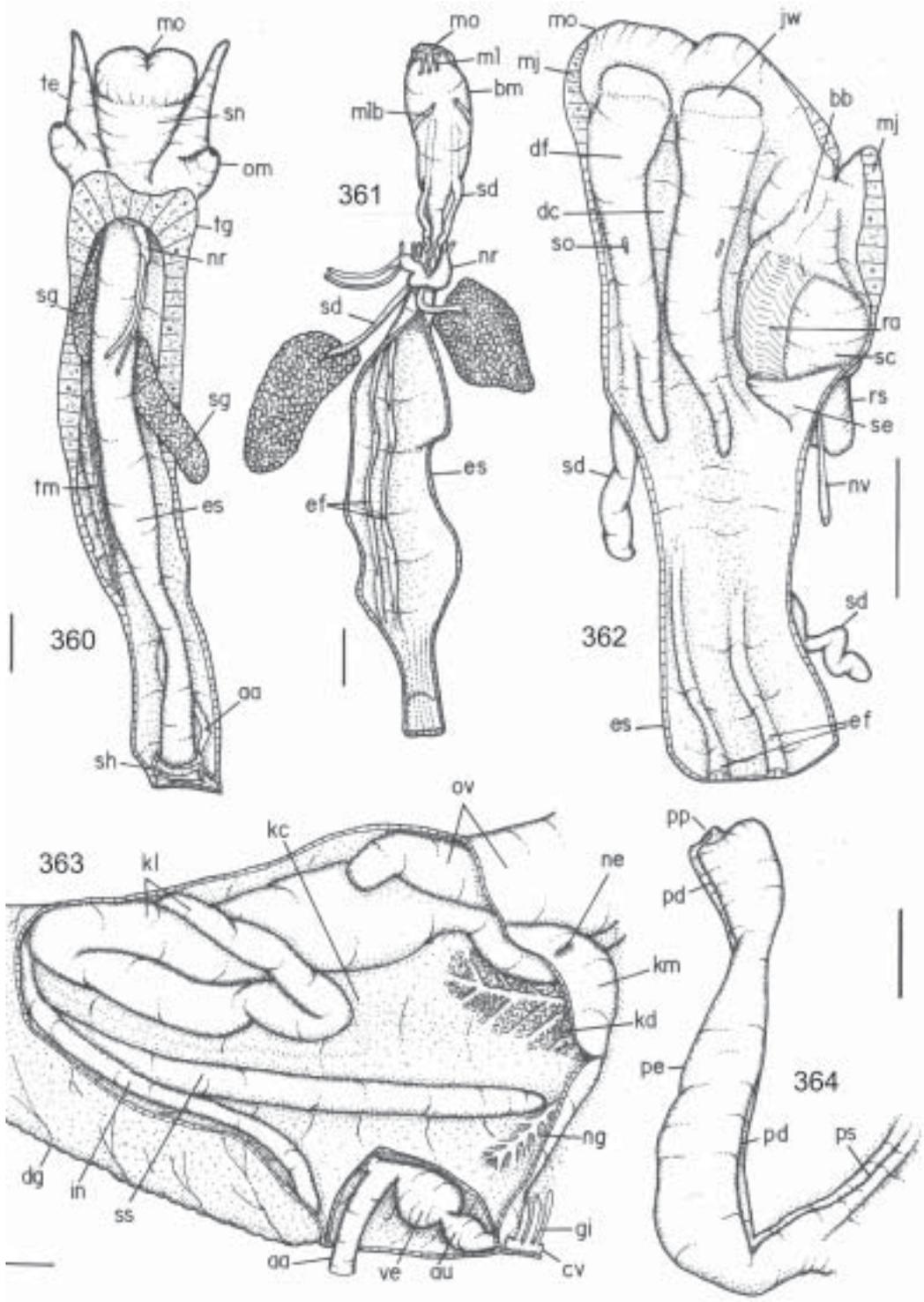
Xenophora conchyliophora (Born, 1780)
(Figs. 33-36, 39, 40, 69, 70, 354-370)

Synonymy see Lambiotte (1979:82) and Ponder (1983:19-20). Complement:

Xenophora conchyliophora: Olsson & Harbison, 1953:274; Walls, 1980:34 (fig.); Abbott & Dance, 1982:73 (fig.); Rios, 1985:60 (pl. 21, fig. 269); Suty, 1986:23-24 (fig. 16); Jong & Coomans, 1988:62; Rios, 1994:73 (pl. 25,



Figures 354-359. *Xenophora conchyliophora* anatomy. 354. head-foot, male, lateral-right view; 355. same, lateral-left view; 356. head-foot, female, lateral-right view; 357. pallial cavity roof, transversal section in its middle region; 358. same, ventral-inner view; 359. detail of an isolated papilla of mantle border. Scales = 2 mm. Lettering: x2, pallial gland.



Figures 360-364. *Xenophora conchyliphora* anatomy. 360. head and haemocoel, ventral view, foot and columellar muscle removed; 361. buccal mass, anterior-middle esophagus and adjacent structures, dorsal view, esophagus partially sectioned longitudinally in median line with inner surface exposed; 362. buccal mass and anterior esophagus, ventral view, both sectioned in their right side, odontophore slightly in lateral view; 363. anterior extremity of visceral mass, ventral view, ventral wall of pericardium and kidney removed, inner structures slightly deflected; 364. penis, whole view. Scales = 2 mm.

fig. 280); Merlano & Hegedus, 1994:162 (pl. 50, fig. 592); Abbott & Morris, 1995:182 (pl. 51).

Description

Shell (Figs. 33-36). Adequate description in Ponder (1983:20, Figs. 17a-h).

Head-Foot (Figs. 354-356, 360). Very similar to preceding *Onustus* species, with following distinctive features: 1) snout with differentiated anterior area around mouth, broader and with glossy surface; 2) ommatophore very longer and broader, inserting practically directly in head just posterior to tentacles; 3) foot more robust, larger and with anterior projection broader.

Operculum (Figs. 39, 40). Very similar to that of preceding species.

Mantle organs (Figs. 357-359, 363). Composition and situation of structures similar to those of preceding species, with following differences: 1) mantle border entirely with series of small papillae, somewhat irregularly distributed; each papillae presents inner pigmented structure near its tip; this structure has rounded distal surface and tapered proximal surface, a nerve running from this structure into papilla base (Fig. 359); these papillae simpler in specimens from Caribbean and more developed in Brazilian specimens; 2) osphradium of similar position but very broader, in strong ridge form; 3) posterior extremity of osphradium almost in same level than that of gill, its anterior region running close to septum-like part of gill; 4) gill with similar regions, inclusive that septum-like anterior; gill filaments broader, with more cylindrical and robust rods and very undulated remainder region. A small, circular and flat gland located anterior to anus, at some distance from mantle border (Fig. 358:x2).

Circulatory and excretory systems (Figs. 358, 363). Heart similar to that of preceding species. Kidney also similar to that of *Onustus*, with tissue also greatly compressed by intestinal loops, style sac and genital ducts; kidney chamber practically only thin walled sac containing these structures. Moreover, bears renal tissue in anterior extremity of renal chamber and nephridial gland, but both even thinner as those of preceding species.

Digestive system. Very similar to that of preceding species, with following notable features: 1) odontophore with about same muscles (Figs. 365-368), inclusive m1a and m13, m3 pair

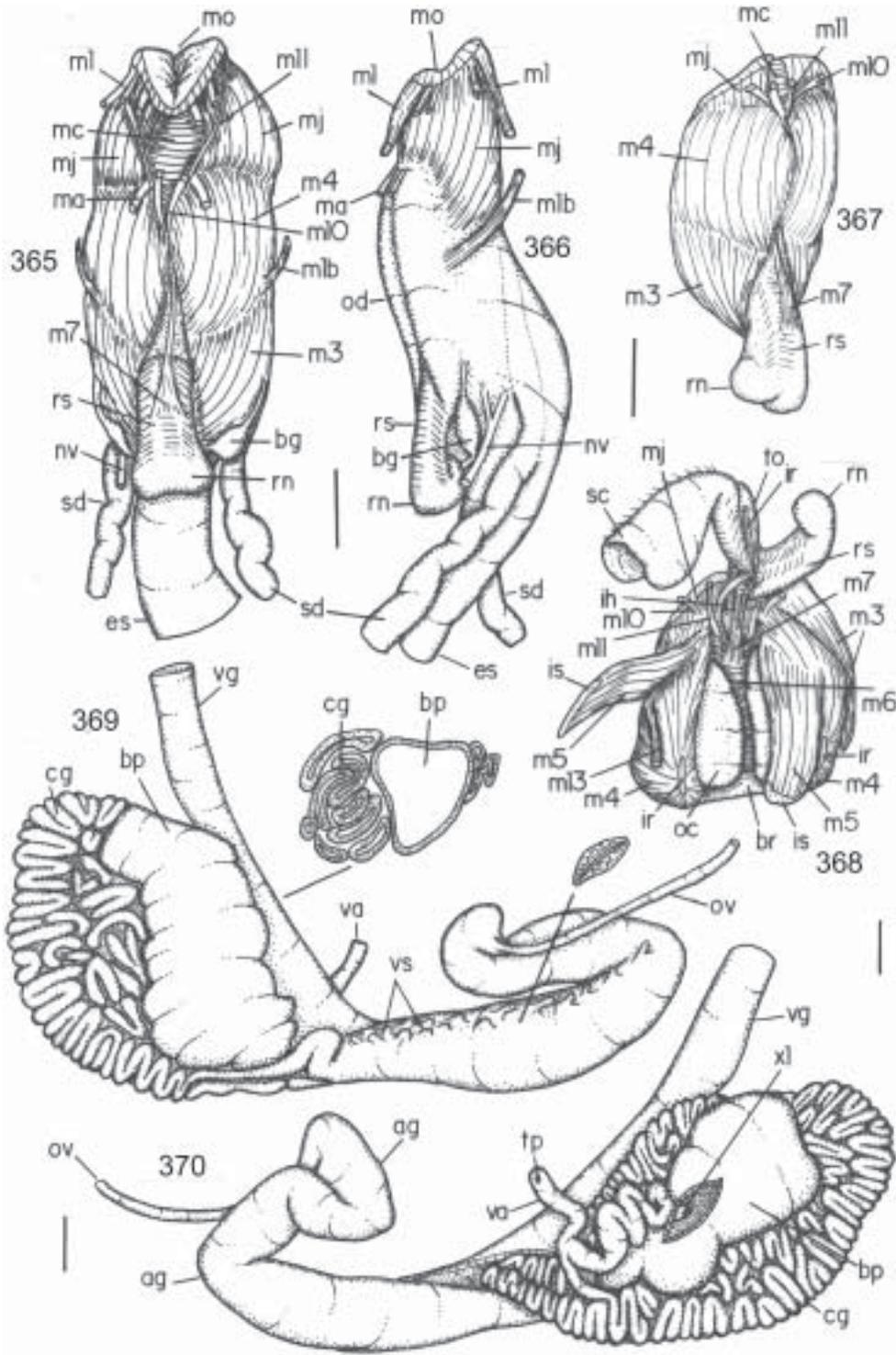
connected to each other also anterior to radular nucleus, but united to it in larger degree; 2) radula (Figs. 69, 70): rachidian tooth with broader central cusp, marginal teeth with slightly broader tip without cusps, and small depression near their middle level of outer margin; 3) pair of inner folds of dorsal wall of buccal mass (Fig. 362) with about same size, but their posterior limit presents form of narrow fold; 4) esophagus with pair of longitudinal, low folds in its inner surface (Fig. 361); in posterior extremity of esophagus these folds faint and its inner surface presents several lower longitudinal folds; 5) stomach, intestinal loops (inclusive those within renal chamber) and style sac size and location (Fig. 363) similar to those of preceding species.

Genital system. Male. Visceral and pallial sperm ducts very similar to those of *O. caribaeus*. Penis shorter (Fig. 354), somewhat flattened, with deep sperm groove; weak constriction before its tip; penis tip broad, blunt, with small central papilla where sperm groove finishes (Fig. 364).

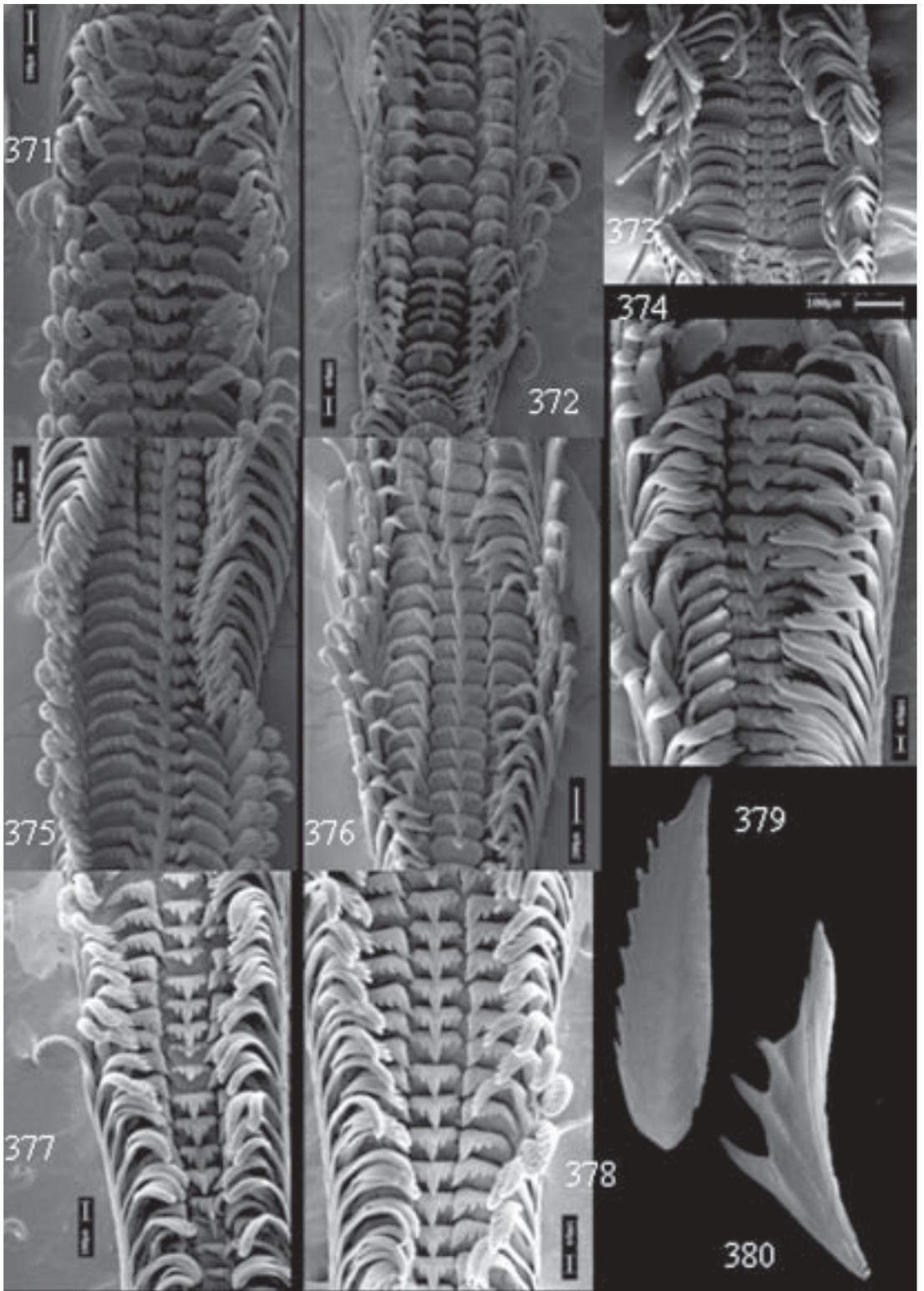
Female. Visceral oviduct similar to that of preceding species. Pallial oviduct similar in location – about half of its length located within renal chamber (Fig. 363), but differently constituted. Visceral oviduct (Figs. 369, 370), in dorsal region of kidney, suddenly expanding and becoming “U”-shaped, large, thick-walled albumen gland. Dorsal surface of albumen gland series of small vesicles (vs), more anterior vesicles lower and closer to each other. Oviduct becoming narrow where it exits to pallial cavity, but short distance behind tubular capsule gland becomes intensely coiled, these coils covering most of pallial oviduct surface. After several coils in ventral-posterior region of pallial oviduct inserts in vaginal tube. Coils of capsule gland surrounding brood pouch (Figs. 369, 370); aperture of this pouch narrow papilla located approximately in middle region of its dorsal surface. From this papillate aperture coiled tube running with iridescent, thick walls; after about five whorls this tube also inserts in vaginal tube. Vaginal tube somewhat short, thick walled, attached to pallial roof posterior-right region. A furrow in right side of pallial floor, similar to that of preceding species, also present (Fig. 355), but before its anterior end presents deeper and opened region.

Nervous system. Similar to that of preceding species.

Measurements of shells (in mm). MZSP 31569: 31.5 by 40.5; 26.0 by 33.8.



Figures 365-370. *Xenophora conchyliophora* anatomy. 365. Buccal mass, ventral view; 366. Same, lateral-left view; 367. Odontophore extracted from buccal mass, ventral view; 368. Same, ventral view, both cartilages deflected laterally, right muscles (left in fig.) partially deflected to left, radula and adjacent structures deflected upwards; 369. Pallial oviduct, dorsal view, mantle and other adjacent structures removed, transversal sections in the two indicated levels also shown; 370. Same, ventral view, a small longitudinal section done in middle region of brood pouch (bp) ventral surface to show the papillate origin of its duct (x1).



Figures 371-380. Radulae and opercula in SEM. 371. *Canarius urceus*; 372. *Strombus gracilior*; 373. *Terebellum terebellum*; 374. *Eustrombus gigas*; 375. *Lambis lambis*; 376. *Conomurex luhuanus*; 377-378. *Tricornis raninus*; 379. *Canarius urceus*; 380. *Terebellum terebellum*. Scales (379-380)= 1 mm.

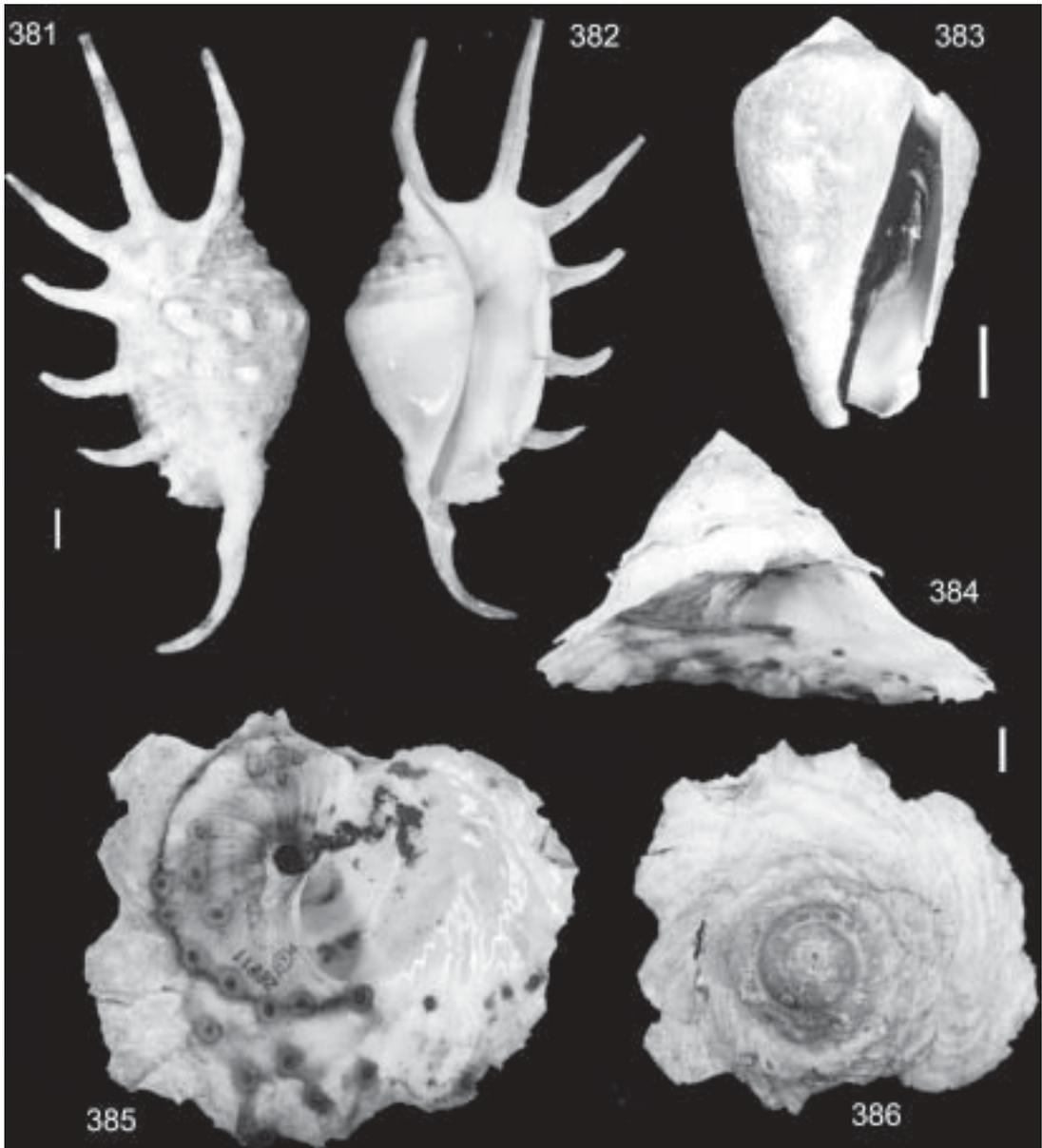
Distribution. In Atlantic, from North Carolina, USA, to Bahia, Brazil. It is also reported to Pacific.

Habitat. Broken shells bottoms, subtidal to 85 m depth.

Material examined. BELIZE; **Carrie Bow Cay**, Twin Cay, lagoon between cays, USNM 857859, 1♀, (Kool, S. col., 6/vi/1985). BRAZIL; **Bahia**; Salvador, MZSP 28557, 1♂ (B.L. Albu-

querque col., 1997); off Alcobaça, MZSP 31569, 2♂ (Coltro leg., viii/1999). **Espirito Santo**; 19°28'S 38°22'W, 74 m depth, UFRJ 7768, 3♂, 1♀ (Revissee D39)

Discussion. The examined Caribbean specimen (Figs. 35, 36) has a darker color of ventral surface of the shell, while the Brazilian species the same region of the shell is pale cream (Figs. 33, 34). The papillae of the mantle border is less developed in



Figures 381-386. Shells. 381-382. *Lambis lambis*, Australia (AMS 339175), dorsal and ventral views; 383. *Conomurex luhuanus*, Australia (AMS 339176), ventral view; 384-386. *Onustus caribaeus*, São Paulo, Brazil (MZSP 28811), ventral, lateral and dorsal views. Scales = 10 mm.

the Caribbean specimen as those of the Brazilian specimens (Figs. 358, 359), but also present a small pigmented structure in the tip (photoreceptor?). Despite these two differences, both samples are interpreted as variation of a same species.

Discussion of Characters

The account on each character begins with abbreviated descriptive sentence followed by plesiomorphic and derived condition(s); also included the CI and the 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, in the same general order as presented in the descriptions.

The following species were used as direct outgroups, and basing the character states polarization: 1) *Aylacostoma tenuilabris* (Reeve, 1860), Thiaridae; 2) *Modulus modulus* (Linné, 1758), Modulidae, both Cerithioidea, such anatomical study is published in Simone (2001); 3) *Pomacea canaliculata* Lamarck, 1801, Ampullarioidea, Ampullariidae; 4) *Neocyclotus prominulus* (Orbigny, 1840), Cyclophoroidea, Cyclophoridae, both with anatomical study in press (Simone, in press). The analysis has additional base of comparison, a pool of other Caenogastropoda [*Littorina flava* (King & Brooder) (Simone, 1998), Hydrobioidea (Simone & Moracchioli, 1994; Simone 1995a), Tonnoidea (Simone, 1995b), several muricoideans such as *Buccinanops* spp (Simone, 1996), *Thala crassa* Simone, 1995(c), some conoideans such as Terebridae (Simone 1999)] and several archaeogastropod representatives. In the discussion, the term “archaeogastropod” is used in traditional sense, however is recognized as a paraphyletic taxon; the phrase “basal caenogastropods” refers to those taxa which generally precede the stromboideans in most catalogues as, e.g., Abbott (1974), Rios (1994), in particular the architaenioglossans, Cerithioidea, Littorinoidea and Hydrobioidea. The phrase “higher caenogastropods” in general refers to Tonnoidea and Neogastropoda. When mentioned “examined species” only the ingroup species are included.

Due to incompleteness of data, *Tibia insulaechorab* is not included in the present analysis except in some points of the discussion and com-

parative morphology. The same approach is done in species not included herein but with some anatomical data known.

Although the tree is presented only in the end of this section, the approach of the characters, including their discussion, takes into account their position along it. Additionally, some multistate characters are considered ordered (additive). In those cases, analysis considering them as unordered was also performed. Any fortuitous change in the result with the unordered approach is also reported.

Shell

1. Form: 0 = trochiform; 1 = fusiform (Strombidae, Struthiolariidae and Aporrhaidae) (CI = 0.50; RI = 0.66).

In the archaeogastropod grade the normal feature is the trochiform or globose shell, considered then as plesiomorphic state (although several groups derived to modified forms such as limpet or ear-like fashions). The so-called “fusiform” shell is that with a bi-conic outline and a somewhat long spire, the aperture generally is lateral rather than anterior-terminal as those shells of basal caenogastropods. The shell of the xenophorids is arbitrarily called trochiform, based only on superficial similarities. However it is recognized that some differences with the typical trochiform, i.e., of the trochids, shell exist. Thus, the present conchological classification, as plesiomorphic state, revealed a xenophorid reversion.

2. Outer lip: 0 = thin and simple; 1 = thick and expanded (Strombidae, Struthiolariidae, *Aporrhais occidentalis*); 2 = with spines (*C. serresianus*, *A. pospelicani*, *L. lambis*) (CI = 0.33; RI = 0.33; ordered).

The outer lip characters are distinctive features of the stromboideans, being in generally expanded and complex (sometimes with special sculptures, projections, spines, etc.), adapted for anchoring the animal in the substratum; this is not found in the outgroups, and is regarded as apomorphic. In addition to the expansion of the outer lip, some Aporrhaidae and *Lambis* also developed spines. Xenophorids also present ample outer lip, mainly in superior surface, but thin, not considered an apomorphic state. The ordered optimization of the character states is based on the ontogeny, because in the specimens' development, the outer lip be-

comes thick and only after the spines appear. Observing the tree, the presence of spines (state 2) appeared 3 times independently, and the xenophorids (node 7) reverted to state zero. Some other characters related to the outer lip are discussed by Kronenberg & Vermeij (2002), mainly concerned to the glazed condition of its edge and to the presence of denticles along its edge. The glazed outer lip edge apparently is another synapomorphy of the node 14, with a probably convergence with *T. raninus*.

3. Tentacular notch in outer lip: 0 = absent; 1 = present (Strombids, **except** *E. goliath* and *T. terebellum*) (CI = 0.50; RI = 0.88).

This notch is located at the right of the siphonal notch of the shell aperture, a long recognized character of strombids (Woodward, 1894). This notch is used by the animal for extending the right cephalic tentacle under the protection of the shell; the left tentacle is in general protected by the siphonal canal. This character is not developed in *E. goliath*, and may be a reversion. In some specimens of *E. goliath*, however, a shallow groove is distinguishable (e.g., MZSP 31413).

4. Siphonal canal in shell aperture: 0 = absent; 1 = present (Strombidae, Struthiolariidae and Aporrhaidae) (CI = 0.50; RI = 0.66).

A canal in the shell aperture is present in almost all higher caenogastropods and even in some basal ones (e.g., Cerithioidea). Because several other examined outgroups, such as archaeogastropods and other basal caenogastropods, lack this character, the presence of a developed canal is regarded as apomorphic. However, the canals are different from those of the higher caenogastropods (but similar to that of the cerithioideans), not being accompanied by a clear differentiation of the mantle. The region of the mantle adjacent to the canal is only indented, without the development of a muscular siphon.

5. Subsutural sculpture: 0 = absent; 1 = irregular nodes (*A. costatus*, *A. gallus*, *T. raninus*, *L. lambis*); 2 = somewhat regular nodes (*S. pugilis*, *S. alatus*, *S. gracilior*, struthiolariids) (CI = 0.40; RI = 0.76; unordered).

The subsutural sculpture is another source of data of the stromboideans, in general this region

has irregular sized, stubby, flattened nodes, which in general increase in direction to the dorsal surface of the body whorl. However, *S. pugilis*, *S. alatus* and *S. gracilior* have regular, slender and somewhat tall nodes. In the case of *S. pugilis*, these nodes can be even called spines.

6. Relative height of spire: 0 = about similar length to aperture or aperture shorter than spire; 1 = spire shorter than half aperture length (*S. pugilis*, *S. alatus*, *E. goliath*, *E. gigas*, *A. costatus*, *A. gallus*, *T. raninus*, *L. lambis*); 2 = spire less than 1/10 of spire length (*C. luhuanus*) (CI = 0.66; RI = 0.87; ordered).

This character appeared as a synapomorphy of a subgroup within Strombidae, uniting all species but *T. terebellum* and *C. urceus*. On the other hand, a reversion is found in *S. gracilior*. The proportion spire-aperture is not an isolated character, it is accompanied by several inner organs changes or adaptations discussed below. All the modifications are consequence of the lateralization of aperture, which migrates to right (some discussed in following sections). As the state 2 is clearly an extreme trend of the state 1, they were considered ordered, however, the state 2 is a *C. luhuanus* autapomorphy.

Head-foot

7. Snout form: 0 = conical, flattened; 1 = conical, oval in section, with transverse furrows in retracted condition, capacity of great distention (struthiolariids); 2 = long, circular in section, thickly muscular, distal tip broader (Strombidae) (CI = 1; RI = 1; unordered).

The strombids are regarded as possessing an acrembolic proboscis (e.g., Walls, 1980; Ball et al, 1997). In the Gastropoda there are two types of structures which can be (and are) called as "proboscis": 1) an elongation ventral to cephalic tentacles with some obvious degree of retraction and expansion, but without capacity of invagination within haemocoel; 2) the same but with capacity of total (sometimes partial) invagination within haemocoel. The second type, is regarded as "true" proboscis herein; the former appears to be better regarded as a "snout". The difference between a proboscis and a snout is not only the invagination capacity, they can be differentiated also in morphol-

ogy. The proboscis possesses a pair (in general) of retractor muscles and a space for its invagination within the haemocoel, called rhynchodeal cavity, structures absent in the strombids. With these data in mind, the strombid structure is better regarded as a snout, despite its elongation. This agrees with the term “non-retractile muzzle” that was used by Woodward (1894) for *Lambis lambis*. There are even gastropods with both, a snout and a proboscis, as the tonnoideans (Simone, 1995b). The snout of the Xenophoridae and Aporrhaidae is similar to that of outgroups, regarded as plesiomorphic state. The snout of the struthiolariids is very thick walled, a very narrow inner haemocoelic space is present, and also presents several transversal, somewhat regular folds in outer surface (state 1); according to Morton (1951), the Struthiolariidae have great capacity of elongation of the snout, sometimes longer than the shell length; this capacity is perhaps indicated by the above cited morphological characters. Morton (1951) also called “proboscis” the snout of the Struthiolariidae, but the above discussion is also applicable in this taxon. The snout of the strombids is long (state 2), presents thick muscular walls in layers (Fig. 120), and also has a narrow inner space; but observing several living and fixed specimens it is possible to note that the elongation capacity of the strombid snout is very poor if compared to that of the struthiolariids.

This character is apparently a junction of some separated characters (e.g., shape, sculpture, and length). An analysis with all features separated (as mono-state characters) was made and nothing changed in the result, thus the character was maintained as presented (non-ordered multistate character). In the case of the struthiolariids, no living specimens were observed, but the literature data (Morton, 1950, 1951) and the upper described different fashion (which revealed different musculature arrangement) allowed the different state.

8. Snout anterior margin around mouth: 0 = similar to surface of other snout regions; 1 = smooth, glossy (*X. cochyliophora*); 2 = papillate (*S. pugilis*, *S. alatus*, *S. gracilior*, *O. indicus*) (CI = 0.66; RI = 0.66, unordered).

In general, nothing beyond concentric and/or radial furrows are present in anterior surface of snout in examined specimens (surrounding mouth). This snout region may be that which explores the environment and indubitably has a concentration

of receptors. However, the upper cited species also present clear anatomical specialization of this snout region as described above.

9. Retractor muscle of snout: 0 = absent; 1 = in two separated muscles in ventral inner region (aporrhoids); 2 = immersed in the inner muscular layer of snout (struthiolariids, xenophorids) (CI = 0.50; RI = 0.66; unordered).

A pair of strong and well-delimited muscles is found in ventral-inner surface of the snout of aporrhoids. This pair originates in the dorsal-anterior surface of the foot and inserts gradually close to mouth. Something similar is also found in the struthiolariid and xenophorids, but the muscles are not exposed in the haemocoelic chamber like those of the aporrhoids, they are immersed in the snout base wall as an inner layer of muscles. These muscles of the struthiolariid and xenophorids are still visible in dissection when the inner snout surface is exposed, however these are not found in the strombids, and may be a reversion, as a consequence of the great development of snout muscular tissue.

10. Foot anterior margin: 0 = low, close to snout base; 1 = protruded, slight far from snout base (“propodium”) (all examined species) (CI = 1; RI = 1).

The term “propodium” has been used for any anterior structure of foot, although not all gastropod “propodia” are homologous, and a better definition of the terminology is necessary. The conceptual propodial region of foot can be considered as the dorsal region between the anterior pedal glands furrow and the snout base (or the rhynchostome). Then a “true” highly modified propodium is that of burrowing snails such as Olividae, Naticidae, etc. The stromboidean “propodium” is only a stalk for the anterior pedal glands furrow, projected anteriorly. This state differs from any other foot adaptations of examined outgroups, regarded as apomorphic.

11. Foot sole: 0 = conspicuous; 1 = inconspicuous in a flattened foot (*T. terebellum*); 2 = inconspicuous in a cylindrical foot (remaining strombids) (CI = 1; RI = 1, unordered).

The foot of the strombids has been long recognized to be highly modified (e.g., Woodward,

1894), without a distinct crawling sole. Practically it is only a cylindrical muscular stalk for the operculum, used by the animal to make its famous leaping movements. In all strombids examined, the region homologous to the sole is notable, in general delimited laterally by shallow furrows and anteriorly by the “propodium” where there is the transverse furrow of the pedal glands. The propodium is homologous to the anterior margin of other crawling prosobranchs, but it is localized somewhat far from the snout base; differing from same region of the outgroups. A very similar foot is also present in the species of the other families (struthiolariids, aporrhoids and xenophorids), although these still possess a clear crawling sole, which is also delimited by shallow lateral furrows. The anterior extremity of the sole in those families is a projected flattened projection, sometimes even peduncled, far from the base of the snout as in strombids. The feet of *T. terebellum* and *Tibia insulaechorab* appear to be somewhat intermediary between those species of other families and the remainder of the strombids, and this supposition was confirmed in the tree, however, the character states were a priori considered as non-ordered.

12. Opercular pad: 0 = in middle-dorsal region of foot posterior slope; 1 = sub-terminal (all examined species) (CI = 1; RI = 1).

The location of opercular pad in examined species is also dorsal, like other gastropods, but differs in being sub-terminal, i.e., the posterior border of opercular pad is the same of that of the foot. This state is regarded as apomorphic.

13. Food groove: 0 = absent; 1 = present (*T. scutulata*, *S. papulosa*) (CI = 1; RI = 1).

The food groove running longitudinally the right surface of pallial floor is a synapomorphy of the struthiolariids (Morton, 1951; Boss, 1982). This structure is used for carrying the particles collected by the gill. A surprisingly similar food groove is found in cerithioideans Turritellidae and Vermetidae (Simone, 2001) and in several calyptraeideans and viviparids (Fretter & Graham, 1994; Simone, in press). These food grooves are certainly homoplastic. The struthiolariid food groove differs from that of the cerithioideans and viviparids by finishing before the head, and does not arrive close to the mouth, and from that of the calyptraeideans in being double folded.

14. Columellar muscle: 0: slightly narrow, haemocoel dorsal to it; 1: very broad with a narrow haemocoel almost within it (all examined species) (CI = 1; RI = 1).

The columellar muscle is not only very broad in all examined species, but also restricts the haemocoelic space to a narrow tube. This state is more developed in the strombids, maybe working as a base for the peculiar leaping foot movement (see also Parker, 1922; Little, 1965).

15. Visceral mass at left of pallial cavity: 0 = absent; 1 = present (strombids, struthiolariid, aporrhoids) (CI = 0.50; RI = 0.66).

The visceral mass, including anterior limit of digestive gland and reno-pericardial organs, is in general restricted to the posterior end of the pallial cavity in prosobranchs. However, in above referred taxa there is a part of the visceral mass, mainly of the digestive gland, at the left, and slightly ventral to the posterior end of the pallial cavity, i.e., there is a region of the visceral mass anterior to the posterior end of pallial cavity. This condition may be because of the lateral placement of the shell aperture and is found in other groups with lateral apertures also, like, e.g., the neogastropods Conidae, Olividae and Marginellidae (person. obs.).

16. Ommatophores in tentacles: 0 = absent; 1 = present (all examined species) (CI = 1; RI = 1).

Ommatophore is defined herein as a small secondary stalk for the eyes, letting them slight away from the tentacle axis. The absence of an ommatophore, as in several basal caenogastropods, is regarded as plesiomorphic. The very long ommatophore of *Tibia* species (Walls, 1980, this study) represents maybe a synapomorphy of the genus.

17. Eye location: 0 = slightly over tentacles base; 1 = almost at mid level of tentacle length (aporrhoids, xenophorids); 2 = almost at tentacle tip (strombids); 3 = at tentacle tip (*T. terebellum*) (CI = 100; RI = 100; ordered).

In the caenogastropods, the normal fashion is the eye located not just in the tentacles base, but slightly over it, with the basal region of the tentacles working as a small stalk for the eyes. All examined species but struthiolariid present the eye

at least in middle level of tentacles length. In strombids, in particular, the eyes are very complex, present a large muscular ommatophore and is almost terminal, only a small and narrow part of the tentacles stay ventrally to it, working as an ommatophore appendix. This is clearer in *Terebellum*, in which only the ommatophores are present. The ordered optimization of this character is based on the comparative method, suggested by a single tendency for the tip positioned ommatophore.

18. Insertion of the mantle: 0 = in head level; 1 = more posterior (all examined species) (CI = 1; RI = 1).

In caenogastropods, the mantle attaches to the head-foot in its ventral surface (columellar region), and this attachment is in general close to mantle border. However, in the examined species the insertion (attachment) of the mantle is more posterior and far from mantle border, regarded as apomorphic. This condition appears to be associated with animals which need to protrude the head-foot from the shell without move it, as is the case of the species here studied and others, as cerithioideans Turritellidae, Vermetidae and Campanilidae (Simone, 2001).

19. Mantle cavity aperture: 0 = wide; 1 = narrow (xenophorids) (CI = 1; RI = 1).

The upper mentioned ventral attachment of the mantle in head-foot is more developed in the xenophorids, which includes the lateral regions. This morphological state keeps a narrow entrance to the pallial cavity in these animals; however, some pallial organs such as gill and osphradium also lie beyond the level of mantle insertion, in a secondary anterior pallial chamber.

20. Dorsal surface of foot: 0 = smooth; 1 = reticulate (*E. goliath*, *E. gigas*, *A. costatus*, *A. gallus*) (CI = 0.50; RI = 0.75).

The dorsal surface of foot, in living and in fixed specimens of above species, presents an enigmatic reticulation of the integument, formed by tall and pigmented folds. The immediate inner tissue of this area is a region with great quantity of blood sinuses. In the homologous region of the other species, including *S. pugilis*, *S. alatus* and *T. raninus*, this reticulation is absent, only transverse folds due the contraction are visible.

21. Diaphragm-like septal muscle in posterior region of the haemocoel: 0 = absent; 1 = present (all species); 2 = very developed, double layered (*E. goliath*, *E. gigas*) (CI = 1; RI = 1; ordered).

This structure is a muscular septum in posterior extremity of the haemocoel, almost in transition with the visceral mass. It closes almost completely the haemocoel, only the esophagus and anterior aorta cross it about in its center. This structure is regarded as apomorphic, because is not found in outgroups except in cerithioidean *Campanile* (which presents this structure slightly more anterior) (Houbrick, 1981; Simone, 2001); this muscular septum may be an adaptation to the large size, helping the hydrostatic pressure during the protraction of foot; maybe this explains the great development of this structure in the giant *E. goliath* and *E. gigas*, for this reason, the states are considered ordered.

Operculum

22. Nucleus: 0 = central or sub-central; 1 = terminal (all examined species) (CI = 1; RI = 1).

The terminal opercular nucleus is regarded as apomorphic because of the more central condition of the nucleus found in most archaeogastropods and basal caenogastropods, but terminal nucleus is also (homoplastically?) found in some cerithioideans and higher caenogastropods. Apparently, the strombids only move by means of leaping movement, helped by the operculum, however, both leaping and crawling progression had been described by aporrhoids and struthiolariids (Woodward, 1894; Morton, 1951; Boss, 1982).

23. Projection beyond foot: 0 = absent; 1 = present (all examined species) (CI = 1; RI = 1).

The opercula of the strombids, struthiolariids, aporrhoids and xenophorids present a projection beyond foot posterior extremity, maybe for anchoring it in the substrate. This excess of operculum, beyond opercular pad, is not found in outgroups and is regarded as apomorphic.

24. Form: 0 = rounded; 1 = very long, pointed (strombids); 2 = somewhat triangular (xenophorids); 3 = with spine near nucleus

(struthiolariids); 4: elliptical (aporrhoids) (CI = 1; RI = 1; unordered).

25. Occupies entire shell aperture: 0 = yes; 1 = no (all examined species **except** xenophorids) (CI = 0.50; RI = 0.66).

The operculum is other structure that had been analyzed in the stromboidean systematics. Its form is characteristic of each family. Only in xenophorids, however, the operculum occupies entire shell aperture, which appeared, according to the tree, as a reversion.

26. Spines: 0 = absent; 1 = several along outer edge (strombids **except** *E. goliath* and *E. gigas*); 2 = single, close to nucleus (struthiolariids) (CI = 0.66; RI = 0.88; unordered).

Mantle organs

27. Mantle border: 0 = narrow; 1 = ample (all examined species) (CI = 1; RI = 1).

This condition is associated with ample outer lip of the shell. Species with lip projections in shell such as *Lambis* species (Woodward, 1894, this study) and *A. gallus*, generally present weak projections of mantle border correspondent to them.

28. Mantle margin: 0 = smooth; 1 = papillate (*X. cochyliophora*); 2 = with a tentacle at right (anterior to anus) (*A. costatus*, *A. gallus*, *T. raninus*, *C. luhuanus*, *C. urceus*, *T. terebellum*, struthiolariid, aporrhoids) (CI = 0.55; RI = 0.75; unordered).

The almost entirely papillate mantle border of the *X. cochyliophora* easily differs it from *O. caribaeus* and *O. indicus*, and may be a generic character. This difference was noted by Ponder (1983). The tentacle anterior to anus is very long in the struthiolariids [*T. scutulata* and others (Morton, 1951)], very short, but still differentiable in the aporrhoids. Although, in some specimens of aporrhoids this tentacle is missing. A considered homologue tentacle is present in above listed strombids, as well as in *Tibia insulaechorab*. The pallial tentacle anterior to anus resulted in one of the stromboidean synapomorphy, although lost in xenophorids and in some strombids such as those of nodes 15 and 17 (fig. 387). Some xenophorids possess a glandular mass in same region of mantle

in which the other species bring the tentacle (e.g., *X. cochyliophora*).

29. Osphradium length: 0 = about half of the gill; 1 = very long (about same length than gill) (all examined species) (CI = 1; RI = 1).

30. Osphradium type: 0 = ridge-like; 1 = bipectinate (strombids); 2 = with a satellite fold (struthiolariid, aporrhoids) (CI = 0.66; RI = 0.85; unordered).

Although very long, the osphradium of the strombids is entirely bipectinate, with small and thin leaflets, regarded as apomorphic. The bipectinate condition of the strombids was noted also by Woodward (1894) for *Lambis lambis* and Matthews (1980) for *S. pugilis* and *E. goliath*. This condition, however, resembles the bipectinate osphradium found in some cerithioideans, such as the Cerithiidae (Houbrick, 1992; Simone, 2001).

The satellite fold is maybe glandular, and surrounds entirely the osphradium of the struthiolariids and aporrhoids, regarded as apomorphic and may be an enlargement of normal fold of caenogastropod osphradia. Osphradium satellite folds enlargement are, however, found also in some cerithioideans (Simone, 2001), but they do not surround entire osphradium.

31. Osphradium anterior region: 0 = close to gill; 1 = far from gill (all examined species **except** xenophorids) (CI = 0.50; RI = 0.66).

The osphradium of caenogastropods in general runs close to left margin of gill, but in strombids, struthiolariids and aporrhoids the anterior region of the osphradium gradually becomes away from the same region of the gill.

32. Osphradium anterior extremity: 0 = far from mantle edge; 1 = near to mantle edge (strombids **except** *T. terebellum*) (CI = 1; RI = 1).

The proximity of the anterior end of the osphradium is clear in which some contracted specimens even exteriorize it, just in the region of the siphon.

33. Osphradium posterior extremity: 0 = anterior to that of gill; 1 = in same level to that of gill (*S. pugilis*, *T. scutulata*, *X. cochyliophora*) (CI = 0.20; RI = 0.20).

This character resulted little informative, because its state 1 appeared as 3 independent parallel acquisitions of the above species.

34. Middle region of osphradium, where it gradually becomes far from gill: 0 = simple, only weakly curved; 1 = with a strong, sigmoid region (*A. costatus*, *A. gallus*, *T. raninus*); 2 = with a sudden, angled curve pointing to right (*C. luhuanus*, *C. urceus*, *L. lambis*) (CI = 0.50; RI = 0.50, unordered).

35. Endostyle: 0 = absent; 1 = present (*T. scutulata*, *S. papulosa*) (CI = 1; RI = 1).

The so-called "endostyle" (analogy with that of the Cephalochordata) is an apomorphic glandular ridge running at left from gill, on ctenidial vein. This structure is also present in other struthiolariids (Morton, 1951) and surprisingly similar to other filter-feeding caenogastropods such as Crepidulidae and Turritellidae, regarded as probable homoplasy.

36. Longitudinal muscles in ventral wall of ctenidial vein: 0 = absent; 1 = present (strombids) (CI = 1; RI = 1).

Well-developed longitudinal muscle fibers immerse wholly along ventral wall of ctenidial vein is present in all examined strombids. These muscle fibers arrive until the septum-like anterior gill end (ac), and is absent in the other ingroup species.

37. Ctenidial vein lumen: 0 = cylindrical; 1 = compressed due a tall inner fold (*A. occidentalis*, *A. pespelicani*) (CI = 1; RI = 1).

The well-developed inner fold of above species is probably glandular and runs all along left side of ctenidial vein, compressing its lumen. Nothing similar was found in the other species, which have a cylindrical (somewhat circular in section) lumen.

38. Gill anterior septum-like region: 0 = absent; 1 = small, without filaments (strombids, *A. occidentalis*, *A. pespelicani*); 2 = a tall septum with filaments in its free border (xenophorids) (CI = 1; RI = 1, unordered).

A short region in a form of a septum is the anterior limit of the strombid and some aporrhaid gill. This region appears to be a specialized area of the ctenidial vein, however, further studies may

bring new revelations on the structure and function of this gill region. A similar region, but shorter, was also found in conoidean Terebridae (Simone, 1999). The gill of the xenophorids passes from longitudinal to oblique in region anterior to mantle insertion in head-foot, and from sessile based filaments to a form of a tall septum in which the filaments are slender and located in its free margin. A homology with the small septum of the strombids and some aporrhoids with the septum-like region of xenophorid gill was not performed a priori, but it was suggested and confirmed in the tree.

39. Gill length: 0 = about 2/3 of the pallial cavity; 1 = almost same length than pallial cavity (all examined species) (CI = 1; RI = 1).

40. Form of the gill filaments: 0 = low, triangular; 1 = tall, triangular (strombids, *A. occidentalis*, *A. pespelicani*); 2 = low, with a very long projection at right (*T. scutulata*, *C. serresianus*); 3 = low, with a very long projection at left or on ctenidial vein (xenophorids) (CI = 1; RI = 1, unordered).

41. Base of the gill filaments: 0 = broad (about same as or broader than the width between gill and rectum); 1 = narrow (about half of that area) (strombids, *O. caribaeus*, *O. indicus*) (CI = 0.50; RI = 0.83).

In some females with greatly developed pallial oviduct, the interpretation of this character can be precluded, because it pushes the rectum towards left.

42. Gill posterior extremity: 0 = far from posterior extremity of the pallial cavity; 1 = close to (almost touching) posterior extremity of the pallial cavity (all examined species) (CI = 1; RI = 1).

The characters 39 to 42 are polarized according to comparisons with basal caenogastropods.

43. Hypobranchial gland: 0 = large, thick, with chambers; 1 = large, thick, with intercalated broad and narrow glandular folds (*C. serresianus*); 2 = inconspicuous and thin (xenophorids) (CI = 1; RI = 1, unordered).

The hypobranchial gland is normally thick in stromboideans, with mucus chambers. If the ani-

mal is dissected under water, even in long-fixed specimens, the hypobranchial gland quickly increases and becomes a massive jelly mass covering most of pallial cavity.

44. Rectum position in pallial cavity: 0 = running in its right margin; 1 = running almost in its center (xenophorids) (CI = 1; RI = 1).

Beyond the narrow aperture of the pallial cavity, the xenophorids also have the pallial organs with a rotation to left. The rectum runs almost in center of this cavity and a broad area between it and the right margin of the cavity appears, without any apparent structure.

45. Rectum: 0 = narrow; 1 = wide (strombids, *A. occidentalis*, *A. pespelicani*, xenophorids) (CI = 1; RI = 1).

Most of examined archaeogastropods and basal caenogastropods present narrow rectum, regarded as plesiomorphic. However, wide rectum is also found in the cerithioideans and other caenogastropods.

46. Anus position: 0 = approached to mantle border; 1 = posterior removed from mantle border (*T. scutulata*, *A. occidentalis*, *A. pespelicani*, xenophorids) (CI = 0.33; RI = 0.66).

47. Anus papillae: 0 = absent; 1 = only three (struthiolariids); 2 = several (all remainder examined specimens) (CI = 1; RI = 1; ordered).

The anus, as most of caenogastropods and some archaeogastropods, is siphoned in ingroup taxa, i.e., preceded by a rectal region not attached to adjacent mantle. Moreover, the anus of these species has three or several well-developed papillae, regarded as apomorphic. The ordered optimization is based on the comparative method, because the state 2 appears to be a modification of the state 1.

48. Pallial genital ducts: 0 = running only in pallial roof; 1 = anterior region running in pallial floor (all examined species) (CI = 1; RI = 1).

Some basal caenogastropods present an anterior part of the genital ducts running at right of head-foot mass as, e. g., some cerithioideans, but in general differs in having a discontinuous duct, strongly interrupted where crossing from roof to

floor of the cavity (more clear in female). On the other hand, in the stromboideans this passage is gradual, continuous, regarded as apomorphic.

49. Differentiated vessel running near right margin of the pallial cavity: 0 = absent or inconspicuous; 1 = present (strombids, xenophorids, *A. occidentalis*, *A. pespelicani*) (CI = 1; RI = 1).

This upper cited vessel runs from anterior region of visceral mass, cross almost entire length of the pallial cavity right margin and faints where approaches from mantle border. In some strombids, this vessel runs in outer lamina of pallial oviduct. Apparently, this vessel is not homologue to the ad-rectal sinus of several caenogastropods, because it runs at right and far from rectum, in contrast to normal ad-rectal sinus, which runs at left from rectum and in general attached to it.

Kidney

50. Tissue constitution: 0 = most solid; 1 = most hollow (all examined species) (CI = 1; RI = 1).

51. Lobes: 0 = two similar sized lobes; 1 = two lobes, dorsal lobe very smaller (*E. goliath*, *E. gigas*, *A. costatus*, *A. gallus*, *T. raninus*, *C. luhuanus*, *C. urceus*, *L. lambis*); 2 = single ventral lobe (*S. pugilis*, *S. alatus*, *S. gracilior*, *T. scutulata*, aporrhoids); 3 = single anterior lobe (xenophorids, *Terebellum*) (CI = 0.75; RI = 0.90; unordered).

Two lobed kidney was also described for *Lambis lambis* (cf. Woodward, 1894; Risbec, 1927), but the left lobe has been demonstrated to be the nephridial gland, normally massive in stromboideans.

52. Kidney chamber size: 0 = small (about 1/4 whorl); 1 = large (1/2 whorl or more) (all examined species) (CI = 1; RI = 1).

53. Loops of intestine within renal chamber, connected by a mesentery: 0 = none; 1 = one (strombids, aporrhoids); 2 = two or more (xenophorids) (CI = 1; RI = 1; ordered).

The regarded ordered condition is based on the comparative method, in which the state 2 appears to be a modification of the state 1.

54. Nephridial gland: 0 = absent; 1 = present (all examined species) (CI = 1; RI = 1).
55. Nephridial gland type: 0 = absent; 1 = of medium size (about 1/2 of the membrane between the kidney and pericardium chambers) (strombids, struthiolariid); 2 = very large (aporrhoids); 3 = very small (xenophorids) (CI = 0.75; RI = 0.75; unordered).
56. Nephridial gland vessel: 0 = inconspicuous; 1 = large, anterior region septum-like, inserted at right of nephrostome (all examined species) (CI = 1; RI = 1).

The kidney of the ingroup species (characters 50-56) is very modified if compared with that of other caenogastropods. It is almost a large hollow chamber for intestinal passage, in the case of the xenophorids, for example, the intestinal loops occupy most of inner available space of renal chamber. The renal tissue is small, sometimes greatly compressed by intestine. The aporrhoids the renal tissue is very reduced, with an enlargement of the nephridial gland. The stromboidean kidney merits further study, mainly on the intestinal function within it. The presence of a mesentery, also pointed out by Little (1965), is of great value, mainly in analysis of the celomatic condition of the molluscs.

Digestive system

Buccal mass and odontophore

57. Buccal mass size: 0 = normal (about 1/2 of snout); 1 = reduced (about 1/4 of snout) (struthiolariid, *C. serresianus*) (CI = 0.33; RI = 0.33).
58. Mj (jaws and buccal muscles) pair insertion mixed with those of m6 (horizontal muscle): 0 = absent (both muscles separated); 1 = present (strombids, xenophorids) (CI = 1; RI = 1).
59. M1a: 0 = absent; 1 = present (strombids, *X. conchyliophora*, *O. indicus*) (CI = 0.50; RI = 0.83).
60. M1b pair: 0 = absent; 1 = present (strombids, aporrhoids, xenophorids) (CI = 1; RI = 1).
61. Ma pair: 0 = absent; 1 = present (strombids, *A. occidentalis*, *A. pespelicani*, xenophorids) (CI = 1; RI = 1).
62. Pair of retractor of buccal mass muscles (m2): 0 = present; 1 = absent (all examined species **except** aporrhoids) (CI = 0.50; RI = 0.66).
This pair of muscles is calling "m2" in other papers (e.g., Simone, 2001). The retractor of buccal mass (pharynx) pair is in general strong, origins in middle-lateral region of the haemocoel or dorsal to foot and inserts in lateral-posterior surface of odontophore in most of basal caenogastropods. Its absence in the most ingroup species is notable and considered apomorphic loss. Some cerithioideans (Simone, 2001) and littorinoideans (Simone, 1998) also lost this muscle pair.
63. M3 pair: 0 = absent; 1 = thin, united with each other anterior to radular nucleus (xenophorids, *A. occidentalis*, *A. pespelicani*, *T. terebellum*); 2 = thick, united with each other anterior to radular nucleus (*S. pugilis*, *S. alatus*, *S. gracilior*, *C. luhuanus*, *C. urceus*); 3 = thick, inserted in radular nucleus (*E. goliath*, *E. gigas*, *A. costatus*, *A. gallus*, *T. raninus*, *L. lambis*) (CI = 0.75; RI = 0.93; ordered).
The additive optimization of this character is based on the comparative method, since each state appears to be a specialized modification of the preceding state. However a unordered approach was also performed and nothing changed in the result, except the RI (changed to 0.90). In both cases (ordered or not), the states are successively distributed each one along the tree, with a notable reversion (3 to 2) in node 15.
64. Ligament between ventral surface of m6 (horizontal muscle) and radular sac (ih): 0 = absent; 1 = present (strombids, xenophorids, *A. occidentalis*, *A. pespelicani*) (CI = 1; RI = 1).
65. M5 pair: 0 = separated with each other; 1 = united with each other in median line (strombids, xenophorids) (CI = 1; RI = 1).
66. M7 pair insertion: 0 = in two bands; 1 = single, fan-like (all examined species) (CI = 1; RI = 1).

67. M12 pair: 0 = absent; 1 = present (strombids **except** *C. luhuanus*, *C. urceus*, *T. terebellum*) (CI = 1; RI = 1).
68. M13: 0 = absent; 1 = present, separated from m5 (xenophorids); 2 = present, as part of m5 (*A. occidentalis*, *A. pespelicani*) (CI = 1; RI = 1; unordered).

The odontophore intrinsic and extrinsic muscles (characters 57-68) are very valuable for comparative morphology. Although with the upper cited particularities, the stromboidean odontophore is very similar to those of basal caenogastropods in several aspects, included the lack of muscles in dorsal extremity of the radular ribbon. Then, the basal caenogastropod-stromboid type of odontophore does not move the radula in a coming and going movement, but so the muscles stretch and stick firmly the radula and the subradular cartilage and the entire odontophore works as an eraser. The definitive name of each muscle or pair of muscles depends of further functional, physiological and phylogenetic studies of each one, for this reason, after first mentioned suggestive name (when firstly described), each muscle (or pair of muscles) is only referred by its number (e.g., "m4"). In general, but not all, the number of each muscle (or pair of muscles) is designated obeying intention of homologies with previous analyzed taxa (Simone, 2001, in presses). The m3 pair, in particular, is a well characteristic muscle of some ingroup species, which may be developed from the membrane involving the lateral and ventral surface of the odontophore.

Although several characters were obtained from the odontophore, some care needs to be taken in their analysis, because the odontophore of the *C. serresianus* and mainly of the struthiolariids apparently are in reduction process. This fact indicates that simplification, reduction or reversion of characters can occur.

69. Buccal ganglia pair location: 0 = almost central; 1 = lateral (all examined species); 2 = large, pigmented with brown spots (*A. occidentalis*, *A. pespelicani*) (CI = 1; RI = 1; ordered).

The buccal ganglia pair is easily visible in buccal mass posterior-ventral region and have a large connective uniting both, crossing anterior to radular nucleus. In most of outgroups, they are al-

most central, i.e., close to median line. Beyond the stromboideans, also several cerithioideans developed lateral located buccal ganglia (Simone, 2001). In both upper cited aporrhoids the buccal ganglia are enormous, and pigmented with brown spots, resembling the homologue structures of the cerithioidean Thiaridae. *C. serresianus* also have a large pair of buccal ganglia, but smaller as those of other two species, and spots are not visible. Due to the state 2 feature appears to be a specialization of the state 1, they are considered ordered.

70. Dorsal folds of buccal mass inner surface: 0 = continuous in esophagus; 1 = finish after odontophore level (*T. scutulata*, xenophorids) (CI = 0.50; RI = 0.75).

Radula

71. Radular length: 0 = very long (about double of odontophore); 1 = short (about same length than odontophore) (all examined species) (CI = 1; RI = 1).
72. Radular marginal teeth: 0 = spoon-like; 1 = slender, long, with a sharp tip (all examined species) (CI = 1; RI = 1).
73. Rachidian secondary cusps: 0 = very smaller than central cusp; 1 = large (about half than central cusp) (*A. costatus*, *A. gallus*, xenophorids) (CI = 0.50; RI = 0.75)

Several radular characters were searched, but, except the above ones (characters 71-73), they are inconclusive or autapomorphic (at species level). The ingroup radula is difficult comparable with those of the archaeogastropods, then more detailed comparison was done with those of the basal caenogastropods. The basal caenogastropods in general present spoon-like marginal teeth, i.e., with the tip broader than the basal and central regions and generally with several small cusps in cut edge. Different from examined species, several basal caenogastropods also present basal cusps in rachidian tooth, this data was not considered herein, being probable outgroup apomorphies.

Salivary glands

74. Location: 0 = cluster around and posterior to nerve ring; 1 = cluster anterior to nerve ring

(strombids **except** *C. urceus*); 2 = two separated masses of elliptical outline posterior to nerve ring (xenophorids); 3 = absent (*T. terebellum*) (CI = 1; RI = 1; unordered).

75. Ducts: 0 = narrow, passing through nerve ring; 1 = narrow, anterior to nerve ring (strombids **except** *C. urceus*); 2 = wide, passing through nerve ring (xenophorids, *A. occidentalis*, *A. pespelicani*) (CI = 0.66; RI = 0.87; unordered).
76. Ducts anterior region: 0 = free from dorsal folds of buccal mass; 1 = passing through in these folds (strombids, xenophorids) (CI = 1; RI = 1).

The salivary glands of most strombids are peculiar in being anterior to nerve ring, with ducts not passing through it, resembling what occurs in the neogastropods. The strombid salivary glands are, on the other hand, somewhat reduced, their anterior border stay in transition buccal mass-esophagus, gradually faint and disappear in level anterior to nerve ring. This fact is not only due the elongation of the anterior esophagus, because the other ingroup taxa and *C. urceus* have a comparable elongation and the salivary ducts stay posterior to nerve ring with ducts passing through it. *C. urceus* has remarkable reversions in the characters 74 and 75 according to the tree.

Esophagus

77. Inner surface: 0 = with glands; 1 = without detectable glands (all examined species) (CI = 1; RI = 1).

Differentiable glands, crops and chambers are the rule among most archaeogastropods and basal caenogastropods, however, these are apomorphically absent in stromboideans.

78. Inner folds: 0 = a pair; 1 = none (struthiolariid, *C. serresianus*, *O. caribaeus*, *O. indicus*); 2 = central canal and other secondary folds (strombids) (CI = 0.40; RI = 0.66; unordered).
79. Insertion in stomach: 0 = middle level of its left surface; 1 = anterior level (struthiolariid; xenophorids); 2 = posterior level (*C. luhuanus*, *C. urceus*, aporrhoids,

C. serresianus) (CI = 0.40; RI = 0.50; unordered).

Although very long and broad, the esophagus of the ingroup taxa tends to be a simple, thin walled tube.

Stomach

80. Ducts to digestive gland: 0 = two; 1 = one (xenophorids) (CI = 1; RI = 1).

81. Style sac and intestine: 0 = united with each other; 1 = separated (strombids, xenophorids, *T. scutulata*) (CI = 0.50; RI = 0.75).

Although several examined species present total separation of the intestine from style sac, they are plesiomorphically united in some struthiolariids (Morton, 1951) and in the aporrhoids. A full discussion on gastropods style sac occurrence and function is found in Yonge (1932).

82. Style sac length: 0 = up to posterior margin of kidney; 1 = up to half level of kidney (aporrhoids); 2 = up to anterior extremity of kidney (xenophorids); 3 = up to anterior region of pallial cavity (strombids) (CI = 1; RI = 1; ordered).
83. Style sac position in anterior region of visceral mass: 0 = ventral; 1 = dorsal (all examined species) (CI = 1; RI = 1).

84. Style sac runs: 0 = entirely immerse in the digestive gland; 1 = part exposed within kidney chamber (strombids, xenophorids) (CI = 1; RI = 1).

The stomach (characters 80-84) of the stromboideans is ample and complex, generally replete of food. A structure in particular, the style sac, is always present containing the crystalline style and is notable by great elongation in several species of the ingroup. As also noted by Woodward (1894), Risbec (1927), Yonge (1931) and Matthews (1980), the strombids present maybe the longer style sac among the gastropods, running almost entire last whorl, in pallial cavity roof between osphradium and left margin of this cavity, ending close to mantle border. Although different in length, the other families' species style sacs run in same direction and present about the same limits, only varying the elongation and exposure within kidney

chamber. This is the reason for regarding the character 82 states as ordered, because they only vary in degree. The style sac running dorsally, also differs from most of examined style bearing outgroups.

For stomach function and enzymes of *Lambis crocata* (Link) see Yonge (1932).

Intestine

85. Loops: 0 = most immerse in digestive gland; 1 = most in renal chamber (all examined species **except** struthiolariids) (CI = 1; RI = 1).

Almost all examined species presents most of intestine within renal chamber, only a short portion is immerse in digestive gland, running ventral to style sac. This character differs from that of the outgroups, which present the intestinal loops immerse in digestive gland, with a single passage to kidney. The presence of a mesentery on renal intestinal loops is briefly commented above (kidney section). An intestinal loop within kidney chamber is shown by Woodward (1894) for *Lambis lambis* (confirmed herein), but not by Risbec (1927, fig. 12) for *S. epidromus* Linné, 1958.

86. Fecal pellets: 0 = absent; 1 = several pellets, with elliptical outline, chaotically compacted (all examined species) (CI = 1; RI = 1).

Bandel (1974) did an ample study on fecal pellets in prosobranchs. The absence of pellets is regarded as plesimorphic based which happen in archaeogastropods. However, several types of fecal pellets are found in caenogastropods and further study is necessary to be sure on their homologies. The fecal pellets of the examined species at least differ from those of the cerithioideans, which present longer pellets in general compacted in an oblique organization.

An interesting discussion on alimentary habits of strombids was presented by Robertson (1961).

Male genital system

87. Testis site: 0 = dorsal to digestive gland; 1 = at right to digestive gland (strombids) (CI = 1; RI = 1).

The testis and also the ovary of the strombids are dislocated to right region of the visceral mass, inclusive of the stomach. This differs from the normal fashion found in gastropods, which present dorsal or peri-columellar gonads.

88. Seminal vesicle location: 0 = ventral to digestive gland, edging the kidney; 1 = bulging into ventral surface of kidney chamber (xenophorids) (CI = 1; RI = 1).

The seminal vesicle is an intensely coiled tube running on columellar muscle in region just posterior to pallial cavity, present in all examined species. However in the xenophorids it is slight dislocated to right and bulges into kidney chamber as a large compacted mass.

89. Prostate tissue: 0 = not detectable; 1 = reunited in posterior region of pallial sperm groove (all examined species except struthiolariids); 2 = along entire pallial sperm groove (*S. pugilis*, *S. alatus*, *S. gracilior*, *E. goliath*, *E. gigas*, *A. costatus*, *A. gallus*, *T. raninus*) (CI = 0.66; RI = 0.88, unordered).

The pallial sperm groove above mentioned excludes the part running in the floor of the pallial cavity up to penis base, which normally is only a shallow and simple furrow.

90. Penis kind of appendages in distal region: 0 = lacking appendages; 1 = an ample, flat, longitudinal projection in a side, and a lateral papilla in other side (*S. pugilis*, *S. alatus*, *S. gracilior*); 2 = semi-circular in section, with a pair of longitudinal undulating folds along middle region (*E. goliath*, *E. gigas*); 3 = a pair of whole papillated folds (*A. costatus*, *A. gallus*); 4 = lateral papilla in base of a broad and thick tip (*A. occidentalis*); 5 = median papilla in tip (*L. lambis*); 6 = papilla long in opposite side of penis groove (*C. luhuanus*, *C. urceus*); 7 = long and massive papilla located at some distance from tip, in same side of penis groove (*T. raninus*); 8 = bifid tip with penis groove running in outer surface of basal branch (*T. terebellum*); 9 = pair of opposed lateral flaps, with penis groove running in a side (*O. indicus*) (CI = 1; RI = 1; unordered).

91. Dorsal longitudinal flap of penis tip: 0 = absent; 1 = only a low, bilateral fold (*L. lambis*); 2 = a tall fold, covering part of penis tip, presenting a apical projection (*S. pugilis*, *S. alatus*, *S. gracilior*; *E. goliath*, *E. gigas*, *A. costatus*, *A. gallus*) (CI = 1; RI = 1, ordered).

It is notable the complexity of the strombid penis tips (characters 90-91), without comparison even with other ingroup taxa (except *A. occidentalis*). The function of those penis structures needs further studies.

Even though no all states of the character 90 are clearly homologous, they are maintained assured by the not-ordered optimization of the different states. Anyway, all them resulted in non-homoplastic synapomorphies.

The character 91 states are presently regarded as ordered, based on the comparative method, which state 2 appears to be a greater development of the condition in the state 1. However, if the character 91 was considered as unordered, the branches after the node 12 (of the presented tree) collapse, becoming a polytomy in a consensus of 7 trees, only *Strombus* (node 15) and *Eustrombus* (node 17) remain.

Female genital system

92. Pallial oviduct position: 0 = anterior to kidney; 1 = bulging in anterior-dorsal region of kidney (all examined species) (CI = 1; RI = 1).

93. Pallial oviduct closure degree: 0 = entire opened; 1 = partially opened (*S. pugilis*, *S. alatus*, *S. gracilior*, *E. goliath*, *A. costatus*, *T. raninus*, *C. luhuanus*, *C. urceus*, *T. scutulata*, *L. lambis*); 2 = entire closed (tubular) (aporrhoids, xenophorids, *T. terebellum*) (CI = 0.50; RI = 0.71; ordered).

This item excludes the part running in right region of head-foot of females which is an opened furrow in all species.

This character is considered ordered because all states apparently vary only in degree. However, if the states are performed under a unordered optimization, nothing changes, neither the indices.

94. Capsule gland: 0 = in continuation from oviduct; 1 = separated from oviduct, as a sinuous duct most dorsal to rectum (strombids **except** *T. terebellum*); 2 = presenting secondary expansions (*S. pugilis*, *S. alatus*, *E. gigas*, *A. costatus*, *A. gallus*, *L. lambis*) (CI = 0.50; RI = 0.85; ordered).

This character is considered ordered because the state 2 appears to be a modification of the state 1. When it was considered unordered, the result did not change, but the RI changed to 0.77. Observing the distribution of these character states along the three it is interesting to note that the state 1 appeared in the node 10, and the state 2 in the node 13. However 2 reversions (2 to 1) occurred (*S. gracilior* and *E. goliath*).

95. Vesicles in middle region of pallial oviduct: 0 = absent; 1 = along a side (*X. conchyliophora*); 2 = united in a sac (*O. caribaeus*) (CI = 1; RI = 1; unordered).

Although both states appeared in present study merely as species autapomorphies, it is possible that they represents a synapomorphy of some xenophorid taxon, even of the entire family.

96. Seminal receptacle: 0 = absent; 1 = a closed sac posterior to aperture of pallial oviduct (*S. pugilis*, *S. alatus*, *S. gracilior*, *E. goliath*, *E. gigas*, *A. gallus*, *T. raninus*, *C. urceus*); 2 = same, with folded dorsal wall (*A. costatus*, *C. luhuanus*, *L. lambis*) (CI = 0.50; RI = 0.81; ordered).

This character is regarded as ordered because the state 2 is apparently a specialization of the character 1. The change to a unordered condition did not change the result, but the RI became 0.77. Anyway, the state 2 appeared as an independent acquisition (convergence) of the 3 species.

97. Glandular brood pouch in a sac-like form: 0 = absent; 1 = terminal (*Onustus* spp.); 2 = immerse in capsule gland (*X. conchyliophora*) (CI = 1; RI = 1).

98. Bursa copulatrix: 0 = absent; 1 = as separated structure anterior to anus, with an own aperture (struthiolariids); 2 = a sac connected to anterior extremity of pallial oviduct (before it crosses to pallial floor) (strombids) (CI = 1; RI = 1; unordered).

Probably, the struthiolariid structure named here as bursa, is the same that Morton (1997a, pl. 3, fig. 1) called brood pouch.

99. Intermediary middle fold in anterior region of pallial oviduct before it crosses to pallial

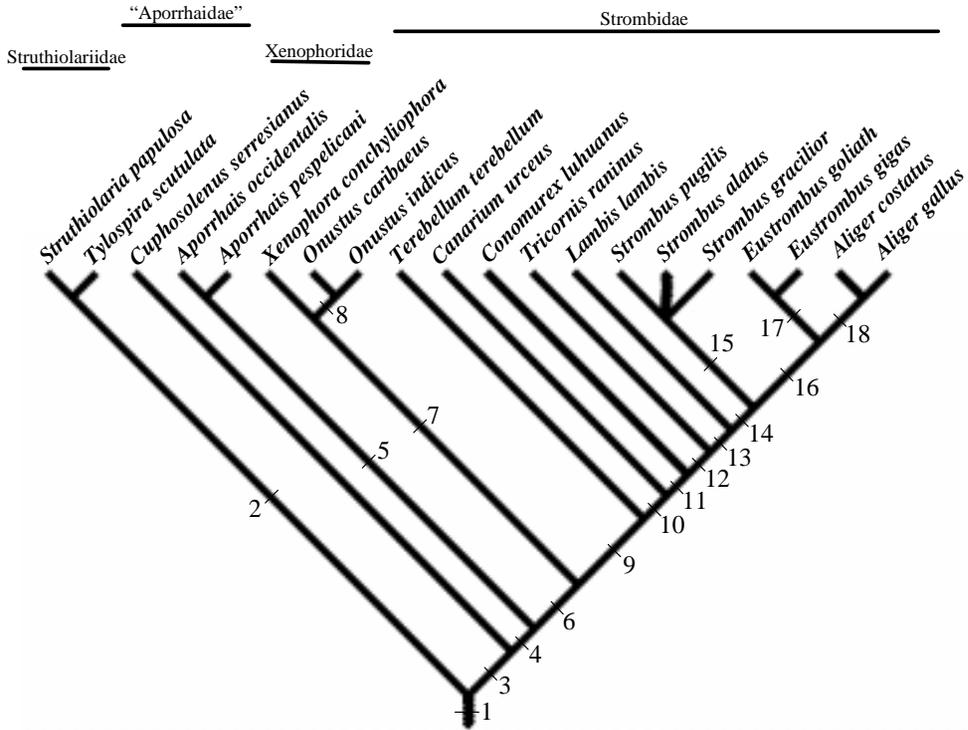


Figure 387: single most parsimonious tree, length: 209, CI 74, RI 86, with numbered nodes.

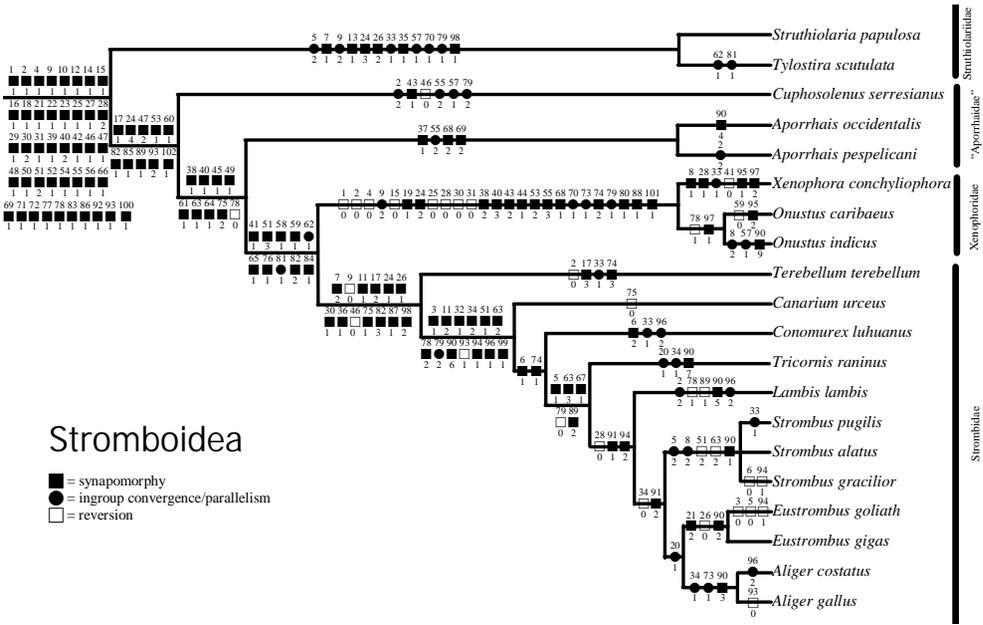


Figure 388: single most parsimonious tree, length: 209, CI: 74, RI: 86, 102 characters, 153 states, showing nodes synapomorphies (superior number the character, inferior number its state; solid square = exclusive synapomorphy, circle = ingroup convergence; white square = reversion).

Discussion of the cladogram (Figs. 387, 388)

Analysis of nodes and taxonomy

The superfamily Stromboidea is well established morphologically and is supported by 42 synapomorphies (node 1). The family Xenophoridae is undoubtedly a stromboidean taxon, closer to the strombids than to the other families traditionally considered stromboidean, such as the aporrhais and the struthiolariids. The family Struthiolariidae, by present analysis, is the most basal clade of the superfamily, while the family Aporrhaidae appeared is paraphyletic.

The family Struthiolariidae is supported by 12 synapomorphies, while another 10 synapomorphies support the remaining stromboideans (node 3) as a separated unnamed taxon.

Cuphosolenus serresianus is represented in a branch separated from remainder stromboideans by 9 synapomorphies (node 4). This species was considered up to now as *Aporrhais*, a hypothesis not consistent with the present results. The approach of this paper is not to create new genera for this species. The genus *Cuphosolenus* proposed herein was searched from the relatively rich fossil record of the aporrhais, and *C. serresianus* shares shell characters with the type species *C. tetracer* from Europe, although of the Jurassic age. However, the generic attribution of *C. serresianus* is still considered an open question. The division of the traditional sense of the family Aporrhaidae into several families has been the rule among the paleontologists which recently studied the group (e.g., Korotkov, 1992; Kiel & Bandel, 1999).

Four synapomorphies unite *A. occidentalis* and *A. pespelicani* (node 5) in a branch. As *A. pespelicani* is the type species of the genus, *Aporrhais* is maintained for this 2 species.

The families Xenophoridae (node 7) and Strombidae (node 9) are both well supported, by 25 and 13 synapomorphies respectively. The xenophorids, however, presented 8 reversals; this fact can indicate a probable paedomorphous origin for the clade. The genus *Onustus* is supported by 2 synapomorphies (node 8), the branch includes the type species of the genus (*O. indicus*). The analysis also includes the type species of the genus *Xenophora* (*X. conchyliophora*), the type genus of the family. This result shows a closer relationship

of the xenophorids with strombids rather reminder previously considered stromboideans. The stromboidean condition of the xenophorids have been also suggested by other studies, such as on locomotion and shell-righting behavior (Berg, 1974), and on protoconch (Kiel & Perrilliat, 2001).

Within Strombidae (node 9), *T. terebellum* is most basal, separated from the remaining strombids by 13 synapomorphies (node 10). This node encompasses the strombids with cylindrical foot, which suggests that *Tibia* would be close to *Terebellum* in the tree if included in the analysis. The further allocation of *Tibia* on the cladogram is important for the analysis of the validity of the family Rostellariidae, as advocated by Kronenberg & Burger (2002).

The remaining strombids, from node 10 to 14, with 2, 5, 3 and 2 synapomorphies respectively, represent the species currently included in the genus *Strombus* (except *Lambis*). However, with *Lambis* in the middle of the *Strombus* taxa, a division of the genus is necessary, or it is required to consider *Lambis* as subgenus or synonym of *Strombus*. An apparently good taxonomical resolution appears if the respective subgenera are transformed in genera. They are the case of *C. urceus* (node 10), type species of the *Canarium*; of *C. luhuanus* (node 11), type species of *Conomurex*; of *T. raninus* (node 12), considered as *Tricornis* (type species *T. tricornis*) because of previous attributions (e.g., Walls, 1980, Rios, 1994). *Lambis lambis*, the type species of *Lambis*, is represented in the node 13.

Node 14, supported by 2 synapomorphies, groups most of western Atlantic American strombids (except for *S. gracilior*, from neighboring Pacific waters). Node 15, supported by 5 synapomorphies, encompasses the similar species *S. pugilis*, *S. alatus* and *S. gracilior*. As *S. pugilis* is the type species of the genus *Strombus* (the type genus of the family and of the superfamily), the 3 species are maintained in this genus.

Node 16, supported by a single synapomorphy, groups the Western Atlantic large sized species until now considered as *Tricornis*. Although they could be considered as *Strombus* in sharing synapomorphies with the type species of the genus, it was preferred to revalidate available *Strombus* synonyms, producing a more informative taxonomy. Node 17, including the type species of the genus *Eustrombus*, *E. gigas*, is supported by 3

synapomorphies and represents the larger American gastropods (*E. gigas* and *E. goliath*). Node 18, supported also by 3 synapomorphies, groups *A. costatus* and *A. gallus*, the latter being the type species of the genus *Aliger*.

The present sample is appropriate in having several type species of most genera, including that of the superfamily (*Strombus pugilis*). However it is necessary to emphasize that the present work is not regarded to be the “phylogenetic study of the Stromboidea”. The main concern, as said in the introduction, is to test the monophyly of this taxon and to search their ground plan (node #1) based on samples of species, as a basis for future phylogenetic analysis of all Caenogastropoda. Thus the taxonomy presented here is undoubtedly a step in a more natural sense of taxa, but obviously is not the definitive.

Some multistate characters were considered ordered, mainly based on ontogeny. All them were, as reported above, additionally considered unordered and the result (and any fortuitous chance of result or indices) is exposed in the discussion that follows the character presentation. Another analysis considering all characters as unordered was also performed, the result is 7 equally parsimonious cladograms, with length of 210, CI of 0.74 and RI of 0.85. The following nodes collapse (of the cladogram of the Fig. 387) in the strict consensus cladogram of these 7 trees: 12, 13, 14, 16 and 18. A successive weighting of these unordered matrix result in 5 equally parsimonious cladograms of length 1384, CI of 87 and RI of 93. A strict consensus of these 5 trees shows the collapse of the following nodes (of the cladogram of the Fig. 287): 12, 14, 16 and 18. Another analysis was performed excluding all autapomorphies. The cladogram has the same topology, but the indices change to length = 190; CI = 71 and RI = 86.

Evolution of the main characters

A character noted in the stromboideans is the small size of the animal in relation to the size of the shell. This character was not used in the analysis because of the difficulty in establishing standards for the scoring.

It was possible to note a trend to increase the body size and towards a heavy shell along the tree. Apparently the stromboidean strategy of de-

fense is to anchor the shell in the soft substratum, for which an increase in size and weight is an obvious advantage.

The stromboidean foot presents another clear evolutionary trend. Firstly in having the operculum located in the distal end of the foot, and partly expanded beyond it. These characters allow the animals to relocate themselves in the soft substratum with the aid of the operculum. This evolutionary trend has the apogee in the strombids (node 10), which no more have clearly crawling sole, moving exclusively by leaping movements.

The snout of the basal taxa has a pair of ventral retractor muscles. These muscles become part of the snout wall in the more advanced taxa, being imperceptible in the strombids, maybe due to the enormous development of the snout wall musculature. Something similar is found in the struthiolariids. However, as discussed above, no stromboidean has a true proboscis.

The pallial cavity of the stromboideans is notable in having a large ctenidium and a very long osphradium. The osphradium becomes bipectinate in the strombids, an independent acquisition from the bipectinate condition seen in some other caenogastropods such as Ampullariidae, Campanilidae, Cerithiidae and “higher” caenogastropods. The gill generally presents long filaments, a trend that reaches its apogee in the filter-feeding struthiolariids. The long filaments of the gill and a superficial similarity of shell led some authors to consider that the xenophorids were related to the Calyptraeidea.

A rather notable trend of the stromboideans is the elongation of the gastric crystalline style sac and its separation from the intestine. A long style sac is already present in the basal members of the group, but connected to the intestine and immerse in digestive gland. It becomes still longer in the xenophorids, partly exposed in the renal cavity, however it does not extend to the pallial cavity. In the strombids the style sac becomes still longer, lying along the pallial cavity roof, ending close to the mantle border. Despite the degree of elongation, all stromboidean species have the style sac running approximately in the same region of the body (as discussed above), encroaching through anterior structures. The second trend, the separation of the style sac-intestine, starts with a partial separation (by folds) in basal stromboidean species, and ends as total anatomical separation at node 6.

Another distinct feature of the stromboideans is the complexity of the pallial oviduct and its degree of closure. The complexity of glands, tubes and associated structures is clear in the xenophorids and strombids. Further studies are necessary to clarify the function and even the names of all the structures detected in the present study. The basic plan of the stromboidean pallial oviduct is at least a half closed (tubular) duct, while in the aporrhoids, xenophorids, and *Terebellum* it is entirely closed. A notable feature of the all stromboidean females is the presence of a furrow in right side of head-foot, connecting the pallial oviduct to anterior furrow of pedal glands.

Due to the focus on characters suitable for resolving higher relationships in the present study, several characters, mainly those associated with genitalia, such as the pallial oviduct and the penis, were not considered. surely they would be very important in a more restricted analysis dealing with species level differences.

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