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PHYLOGENETIC ANALYSES OF CERITHIOIDEA (MOLLUSCA, CAENOGASTROPODA) BASED ON COMPARATIVE MORPHOLOGY

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ABSTRACT

A detailed morphological study is performed on the following cerithioidean species: 1) family Thiaridae, Aylacostoma exoplicata *n.sp., from Pará, Brazil;* Aylacostoma ci *n. sp., from Roraima, Brazil;* Aylacostoma tenuilabris *(Reeve), from São Paulo, Brazil;* Melanoides tuberculatus *(Müller), Eurasian species introduced in Brazil; 2) family Planaxidae,* Supplanaxis nucleus *(Bruguière), from Venezuela; 3) family Pleuroceridae,* Doryssa ipupiara *n. sp., from Roraima, Brazil;* Doryssa atra *(Bruguière), from French Guyana;* Doryssa macapa *(Moricand), from Amapá, Brazil;* Pachychilus *sp., from Chiapas, Mexico; 4) family Turritellidae,* Turritella hookeri *Reeve, from Rio de Janeiro, Brazil; 5) family Modulidae,* Modulus modulus *(L.), from Venezuela and Brazilian coasts; 6) family Cerithiidae,* Cerithium atratum *(Born) from Brazilian coast;* Bittium varium *(Pfeiffer) from S.E. Brazil; 7) family Diastomatidae,* Finella dubia *(Orbigny) from São Paulo, Brazil; 8) family Litiopidae,* Alaba incerta *(Orbigny) from Rio de Janeiro, Brazil; 9) family Batillariidae,* Batillaria minima *(Gmelin) from Venezuela; 10) family Cerithideidae,* Cerithidea costata *from Venezuela; 11) family Campanilidae,* Campanile symbolicum *Iredale, from Western Australia; and 12) family Vermetidae,* Serpulorbis decussatus *(Gmelin), from Espirito Santo, Brazil. (The Thiaridae and Pleuroceridae are freshwater groups, the remainder marine.)*

A cladistic analysis is undertaken using standard techniques, 122 characters (181 states) (included some autapomorphies) and polarization by outgroup method: archaeogastropod (Patellogastropoda, Vetigastropoda, Cocculiniformia and Nerithimorpha) and sometimes other caenogastropod outgroups. The consensus tree has the following topology: (Modulus modulus ((Campanile symbolicum (Serpulorbis decussatus - Turritella hookeri)) (Batillaria minima ((Pachychilus sp (Doryssa ipupiara (Doryssa atra - Doryssa macapa))) ((Cerithidea costata (Cerithium atratum (Alaba incerta (Bittium varium - Finella dubia)))) (Supplanaxis nucleus (Melanoides tuberculatus (Aylacostoma tenuilabris (Aylacostoma exoplicata - Aylacostoma ci)))))))))*, length = 331, CI= 55, RI= 73. The Cerithioidea is a monophyletic taxon, supported by 23 synapomorphies and includes* Campanile *and* Serpulorbis.

KEYWORDS: Cerithioidea, phylogeny, morphology, new species.

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INTRODUCTION

The Cerithioidea is an enigmatic group abundant in species, with representatives in almost all aquatic habitats. This taxon had been regarded as the stem group of the order Caenogastropoda (Haszprunar, 1988). The comprehension of this group is, then, extremely important for understanding the order.

Being such an important group, some studies on the entire superfamily, or part of it, are found in the literature (e.g., Morrison, 1954), introducing an systematic order and looking for its relationship among the Prosobranchia. Although, a mark of the cerithioidean knowledge is the paper of Houbrick (1988). In that paper, the author undertaken a full historic; analysis on each character interesting for systematics of 14 of the 17 families considered within the superfamily; summarized the data from his own papers and of other authors; finalizing with cladistic and phenetic analyses of the group. Ponder (1991) made a reanalysis of the Houbrick's results, and inserted some new data and other outgroups. Haszprunar (1988: 416), on the other hand, noted that no synapomorphic character unites the Cerithioidea, remaining grouping taxons by shared plesiomorphies, such as lack of penis, opened pallial oviduct, spiral operculum, etc. This point was also noted by Ponder & Lindberg (1997: 226), in a recent phylogenetic analysis of the Gastropoda. The cerithiids, in particular, occupies a position in the consensus tree (fig. 2, p. 182 of that paper) among the caenogastropods, just between the architaenioglossans and the remainder caenogastropods.

The human interest by Cerithioidea is not only for systematics, it contains some species of medical importance, being hosts of some human disease etiologic agents, such as *Paragonimus westemani* and *Clonorchis sinensis* (Abbott, 1948; 1952; Davis, 1971; Brandt, 1974). Some thiarids are used as probable competitors of Planorbidae (Pulmonata), host of schistossomiasis (Pointier, Toffart et al., 1991; Pointier, Fredich et al., 1991; Freitas & Santos, 1995). By detrivory, they are important agents in drainage and marine ecosystems.

As part of a larger project on comparative morphology of Caenogastropoda, 19 species belonging to 12 cerithioidean families were selected for analysis.

Most of the analyzed species come from Western Atlantic (when marine) and Neotropical (when freshwater) regions. In Neotropical region two families of Cerithioidea are represented, the Thiaridae (genus *Aylacostoma*) and the Pleuroceridae (genus *Doryssa*). In the area west of the Andes, 83 nominal species of these families occur, although the systematic organization is too obscure which rendering any study impractical. The present paper is a step in direction of a better systematic organization of the Neotropical cerithioideans. It provides anatomical comparative descriptions and systematic analysis of 7 species, which may be the base for future revisions. Practically all systematic papers on Neotropical cerithioideans only include species descriptions (e.g., Scott, 1954). From those, only Ihering (1902; 1909) and Morrison (1954) have some comprehensive revision aspects, the last concerned about worldwide melanians. Except for some brief data found in Scott (1953), Morrison (1954) and Martinez-Escarbassiere & Royero (1995), and with some detail in Abbott (1955), no other anatomical data on Neotropical cerithioidean has been published.

The main objective of this paper is to provide a new phylogenetic analysis based on comparative morphology, of the 19 species of 12 cerithioidean families. The analysis involves characters never before examined, such as the heart site, mantle border, intrinsic odontophore muscles, etc. Also a comparison with non-caenogastropod outgroups, i.e., species of the archaeogastropod grade, is provided and commented (see outgroup choice section for specific groups utilized). The concern is to test the cerithioidean monophyly, and if other groups such as Campaniloidea and Vermetoidea are actually separated taxa.

MATERIAL AND METHODS

A detailed list of the specimens examined follows each species description. Institutional abbreviations are: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; MZSP, Museu de Zoologia da Universidade de São Paulo; USNM, National Museum of Natural History, Smithsonian Institution.

All dissected specimens were preserved in

70% ethanol, and were extracted from the shells by decalcification in Railliet-Henry fluid, or the shells were broken. Dissections were made by standard techniques under a stereomicroscope with the specimen immerse in water. Some structures of the largest specimens, such as the buccal mass and genital ducts, and entire small specimens were dehydrated in ethanol series, stained in carmine, cleared and fixed in creosote; or embedded in paraffin, sectioned at 7 μm and stained with Mallory triple strain. Protoconchs, opercula, radulae and jaws were also examined under SEM at the "Laboratório de Microscopia Eletrônica do Instituto de Biociências da Universidade de São Paulo". All drawings were made with the aid of a camera lucida. Anatomical terminology in general follows Houbrick (1988).

Some species studied herein were also studied previously by other authors; in these cases, the description is restricted to additional or interesting aspects. Respective references are evoked for complement the descriptions.

All measurements are in mm. The length of shells was obtained directly from the shell even in species with the apex lost. The width of shells was obtained with the shell in frontal view. In the more abundant lots only three to six specimens were measured. All measured specimens are separated in the collection within the respective lot, for this reason in some species there is no precise indication provided as to which specimens were measured.

The final stage of the cladistic analysis was performed by the computer package Hennig86 (Farris, 1988) and Tree Gardner 2.1 (Ramos, 1997). The character polarization was determined by outgroup method.

Morphological analysis is based mainly on data searched directly on the examined specimens, but previous anatomical or biological studies are also used, complementing and basing each family character. The papers are the following: 1) Pleuroceridae: Magruder, 1935; Binder, 1959; Dazo, 1965; Davis, 1969, 1971; Brandt, 1974; Chambers, 1980; Dillon & Davis, 1980; Dillon, 1991; 2) Modulidae: Risbec, 1927; Abbott, 1944; Houbrick, 1980a; 3) Campanilidae: Houbrick, 1981a, 1989; 4) Potamididae: Johansson, 1956; Houbrick, 1991a; 5) Turritellidae: Randles, 1900; Graham, 1939; Johansson, 1946; Flores & Macsotay, 1977; Bieler & Hadfield, 1990; 6) Thiaridae: Raymond, 1852; Graham, 1939; Abbott, 1948, 1952; Binder, 1959; Berry & Kadri, 1974; Brandt, 1974; Chaniotis et.al., 1980; 7) Cerithideidae: Bequaert, 1942; Bright, 1958, 1960; Driscoll, 1972; Houbrick, 1986a; 8) Cerithiidae: Marcus & Marcus, 1963; Houbrick, 1973, 1977, 1980, 1980a, 1981a, 1985, 1986a, 1992; 9) Batillariidae: Bequaert, 1942; Driscoll, 1972; Houbrick, 1978; 10) Diastomatidae: Houbrick, 1981b; 11) Vermetidae: Morton, 1951a, b, c; 12) Litiopidae: Houbrick, 1987b; 13) Planaxidae: Barkati & Ahmed, 1982; Houbrick, 1987a, inclusive with cladistic analysis in genus level, 1990, 1991b.

In figures, the following abbreviations are used: **aa**, anterior aorta; **ac**, anterior gastric chamber; **af**, gill afferent vessel; **ag**, albumen gland; **ak**, anterior kidney lobe; **an**, anus; **ap**, aperture of pallial gonoduct; **au**, auricle; **ba**, brood pouch aperture; **bb**, bursa aperture; **bc**, bursa colupatrix; **bg**, buccal ganglion; **bm**, buccal mass; **bp**, brood pouch; **br**, subradular membrane; **ca**, capsules; **ce**, cerebral ganglion; **cg**, capsule gland; **cm**, columellar muscle; **cp**, central pad; **cr**, crescentic ridge; **cv**, ctenidial vein; **dd**, duct to digestive gland; **df**, inner folds of dorsal wall of buccal mass; **dg**, digestive gland; **di**, diverticle of m7; **dp**, duct of pedal gland; **dw**, dorsal wall of buccal mass; **ds**, dark spot; **ea**, esophageal aperture; **es**, esophagus; **ef**, esophageal fold; **eg**, esophageal pouch; **ep**, epipodium; **fn**, flap covering nephrostome; **ft**, foot; **fs**, foot sole; **ga**, gastric arched dorsal fold; **gd**, pallial gonoduct; **gf**, gastric folds; **gi**, gill; **go**, gonad; **gp**, gonopericardial duct or ligament; **gs**, gastric shield; **hg**, hypobranchial gland; **hm**, horizontal muscle; **ic**, inner chitinous layer of shell; **ih**, inner connection of radular sac with horizontal muscle; **il**, inner lamina of pallial gonoduct; **in**, intestine; **ir**, insertion of m4 in tissue on radular ribbon; **is**, insertion of m5 in radular ribbon; **it**, intestinal typhlosole; **ji**, insertion of jaw and peribuccal muscles in odontophore; **jm**, jaw and peribuccal muscles; **jw**, jaws; **ki**, kidney; **km**, membrane between kidney and pallial cavity; **ks**, kidney septum; **m1** to **m16**, odontophore muscles; **mb**, mantle border; **me**, mesopodium; **mo**, mouth; **mt**, mantle; **ne**, nephrostome; **nr**, nerve ring; **nv**, nerve; **oc**, odontophoric cartilage; **od**, odontophore; **ol**, outer lamina of pallial oviduct; **om**, ovarium;

op, operculum; **or**, ovopositor; **os**, osphradium; **ov**, oviduct; **pa**, posterior aorta; **pc**, pericardial chamber; **pd**, pedal gland; **pe**, pallial spermoduct; **pg**, pedal gland anterior furrow; **pi**, pre-intestinal gastric fold; **pk**, posterior kidney lobe; **pl**, pallial cavity; **po**, pedal ganglion; **pr**, pleural ganglion; **ps**, pedal sole; **pt**, pedal tentacle; **pu**, posterior furrow of pedal sole; **ra**, radular ribbon; **re**, receptaculum seminis; **rf**, right furrow of head-foot; **rn**, radular nucleus; **rp**, receptaculum aperture; **rs**, radular sac; **rt**, rectum; **sa**, dorsal sorting area; **sc**, subradular cartilage; **sd**, salivary gland duct; **se**, salivary gland aperture; **sf**, satellite osphradian fold; **sg**, salivary gland; **si**, siphonal inflexure; **sn**, snout; **so**, statocyst; **sp**, style sac aperture; **sr**, adrectal sinus; **ss**, style sac; **st**, stomach; **sv**, seminal vesicle ♂; **te**, cephalic tentacle; **to**, tissue of esophagus on odontophore; **tr**, tissue on middle region of radula; **tv**, transversal vessels between gill and adrectal sinus; **up**, union of m5 with its pair; **va**, seminal vesicle aperture; **vd**, vas deferens; **ve**, ventricle; **vw**, ventral wall of buccal mass.

SYSTEMATICS

Family Thiaridae
Genus *Aylacostoma* Spix, 1827

(Type species: *A. glabrum* Spix, 1827 = *Melania scalaris* Wagner, 1827)

Aylacostoma exoplicata new species
(Figs 1-3,51, 72, 82, 83, 114-135)

Types: Holotype MZSP 28694. Paratypes: MZSP 28695, 1 specimen; MZSP 29697, 1 specimen; MZSP 28346, 63 specimens; USNM 890885, AMNH 292172, ANSP A18961, 2 specimens each. All from type locality.

Type locality: Brazil; Pará; Tucuruí, Caraîpé River (xi/1982, Motta, C.S. col., sta. INPA mol-100)

Diagnosis: osphradium about 1/9 of gill length, satellite fold at left of osphradium; gill with broad, sharp pointed filaments; vessels in area between gill and rectum present; anus posterior to pallial oviduct anterior end; stomach central pad with broad posterior and narrow anterior regions, two gastric dorsal rounded folds.

Description:

Shell (figs 1-3). Medium size (up to 25 mm), turriform, apex eroded, clear brown with some sparse, spiral, reddish dark brown, minute spots. Protoconch only present in young specimens (from brood pouch), with two whorls almost smooth, convex, rounded; gradually spiral ribs begins, becoming strong on next whorls. Junction of protoconch and teleoconch difficult to determine. Teleoconch with about five whorls; sculpture of broad spiral cords, uniform in size, about eight in penultimate whorl; with a narrow and shallow furrow between. Aperture elliptical, angled posteriorly, with shallow anterior canal. Peristome glossy, cream in color. Umbilicus absent.

Head-foot. Pigmented by dark transverse bands around snout, tentacles (figs 122-123) and dorsal region of foot. Head protruding. Snout large, dorso-ventrally flattened (figs 114-116), anterior margin somewhat bilobed. Tentacles long, stubby, eyes dark on a small elevation near outer base. Foot of medium size, without divisions; a furrow present in front margin of anterior pedal gland (figs 114-116). Several specimens with posterior region of head bulging by developed embryos into brood pouch (fig. 116), its aperture a small slit situated ventrally close to right fusion of mantle (figs 115-116). Columellar muscle of about one and half whorls.

Operculum (fig. 51). Ovate, corneous, nucleus sub-terminal, externally lamellate, occupies partially aperture. Muscle scar elliptic, near inner margin.

Mantle organs (figs 117, 118, 120, 121). Entire mantle border with small lobed tentacles, more developed in both extremities. Mantle cavity rather deep, about two whorls. Osphradium very-long, ridge-like, lies on left margin of pallial cavity at about 9/10 of gill length. Anterior extremity of osphradium posterior to that of gill. Satellite fold at left side of osphradium, with about its same length (figs 118, 121: sf). Gill very long, about same length as pallial cavity; filaments triangular, low, tip sharp pointed turned to right; ctenidial vein well developed. Between gill and rectum a proportionally broad area with well spaced vessels connected with a large ad-rectal sinus (figs 118, 121); hypobranchial gland thin, between gill and ad-rectal sinus. Ad-rectal sinus broad, rectum running free within it. Anus siphoned, in right extremity of mantle border, posterior to end of pallial oviduct. Pallial oviduct runs along right side of pallial cavity.

Circulatory and excretory systems (figs 117, 119, 120). Heart large, situated posteriorly in pallial cavity behind gill, auricle large and anterior, ventricle spherical, small and posterior. Aorta runs attached to style sac, large anterior aorta on left; very thin and narrow posterior aorta on right. Kidney pale cream, proportionally large, occupying about half a whorl, situated at posterior-right limit of pallial cavity. Kidney composed of two lobes: posterior lobe larger, attached to right surface of intestine, solid, glandular, with several small vessels connected to a larger central and longitudinal vessel, bulges on right into pericardium chamber and anteriorly into pallial cavity; anterior lobe smaller, attached to left surface of rectum, hollow, with successive transverse folds inserted in a central, longitudinal, larger vessel (fig. 120). Nephrostome a slit in right extremity of membrane between kidney and pallial cavity, close rectum.

Digestive system (figs 117, 119, 122-135). Mouth lies at anterior extremity of snout, longitudinal, ventral, thickly muscular. Buccal mass lies within snout just behind mouth (figs 122, 123); esophagus dorsal, odontophore ventral. Jaws consists of two plates, anterior and median borders with irregular cut-edges (figs 72, 128), lateral edges rounded. Two longitudinal folds begin from jaws and run towards posterior. Salivary ducts open near two small protuberances in middle region of longitudinal folds in inner-dorsal region of buccal cavity (fig. 128). Odontophore with an atypical muscle arrangement (fig. 125-132): **m1)** jugal muscles, several differentiated muscles around buccal mass anterior region, with their origin in inner face of buccal wall and snout; **m2)** pair of large retractor muscle of buccal mass (pharynx), origin in inner surface of lateral haemocoel wall, at side of esophagus, insertion in lateral surface of buccal mass, mainly on its dorsal wall, only some fibers inserted in odontophore; **m3)** pair of small ventral retractor muscle of odontophore, origin in dorsal region of foot ventral to esophagus, insertion in middle-ventral region of odontophore surface; **m4)** pair of lateral compressor tensor of radula, origin attached to anterior and lateral regions of cartilages, surrounding ventrally each cartilage, keep free only median surface of cartilages, insertions of jaws and peri-buccal muscles (ji); in dorsal surface of each m4 a thin, but strong subradular membrane inserts, which subradular cartilage attaches; this membrane bears a region sharply bulged, anterior to subradular cartilage; m4 also inserts in a tissue covering middle and dorsal region of radular ribbon (tr); **m5)** pair of middle ventral tensor of radula, origin in anterior outer surface of m4, surround inner ventral and median faces of m4, insertion in middle region of subradular cartilage, in level and below of m4 insertion in tissue on radula (tr); **m6)** horizontal muscle, short and broad, insertion in lateral-dorsal region of each cartilage; **m7)** anterior-ventral tensor muscle of radula, small and thin, origin part in m11 muscle, and part in adjacent region of subradular membrane, insertion in ventral-middle region of radular sac; with m7 also runs a hollow diverticle from radular sac (di), probably a sinus of anterior aorta; **m10)** pair of odontophore protractor, origin in ventral-median region of peribuccal wall, insertion in ventral-anterior region of odontophore, in m5 surface; **m11)** pair of dorsal middle tensor muscle, very thin, origin in middle inner region of subradular membrane, insertion in ventral region of peribuccal wall; **m12)** pair of dorsal compressor of cartilages, thin and narrow, origin in anterior extremity of cartilages, insertion in dorsal margin of cartilages near horizontal muscle origin. Radula short, forming a "S". Radular nucleus flattened and thick. Radula (figs 82-83): rachidian teeth with seven cusp upper and none down. Lateral teeth long, with seven cusp being third larger. Both marginal teeth similar one another, long, curved, spoon-like, with seven broad cusps; inner marginal teeth discretely broader than the outer marginal teeth. Organization of digestive tube between odontophore and esophagus similar to a valve, bearing attached a tall fold (fig. 128: to). Esophagus simple, long, narrow. Anterior esophagus with two low longitudinal folds in its inner dorsal side (fig. 128). Posterior esophagus very narrow, without inner folds. Pair of buccal ganglion in posterior region of buccal mass, close to insertion of m2 muscle, large, white, connected one another by a median connective (fig. 127).

Stomach large and complex (figs 134, 135), separates almost completely digestive-gonad glands from pericardial and pallial structures, occupies about half whorl. Stomach internally with a large, elliptic, flattened fold in ventral side (central pad) with anterior half narrow and posterior half broad with a median compression; another smaller fold surround posterior half of central pad (crescentic ridge). Duct to digestive gland single, situated ventrally in middle-right region of central pad, partially surrounded also by anterior-left region of crescentic ridge. Esophageal aperture at left of duct to digestive gland; near this another longitudinal, low, narrow fold in left margin of stomach wall (fig. 135: gf). Gastric shield small and thin, between right anterior region of central pad and right margin of gastric wall. Dorsal gastric wall with differentiated, somewhat elliptic sorting area in left side, bearing sigmoid, low, successive folds; in right-posterior region two broad folds, each one with posterior region rounded and broad, and anterior region narrowing gradually; left anterior region of dorsal wall smooth. Stomach still having anteriorly a small smooth chamber bearing two anterior apertures, at left intestine origin, at right origin of style sac. Style sac large, about half of stomach size. Intestine origin preceded by two tall folds (fig. 135), posterior fold triangular and short, anterior fold rounded, tapers gradually in ventral surface of intestine becoming an intestinal typhlosole; between both folds a furrow which communicates intestine with style sac. Stomach and style sac inner surfaces almost entire covered by thin, yellowish iridescent chitin. A broad furrow in ventral region of style sac inner surface. Style elliptic, yellowish-transparent. Digestive gland surrounds posterior half of ventral surface of stomach and two whorls posterior to it (fig. 119). Intestine long, narrow, surrounds style sac ventrally (figs 117, 119, 135), other loop in dorsal-anterior region of this, after towards anteriorly edging right margin of pallial cavity; after kidney suddenly becoming broad. Rectum with successive oblique, broad, somewhat uniform inner folds in its dorsal surface (fig. 117). Several fecal pellets inside rectum, aligned and compacted parallel to folds. Near anus, inner folds thinner and more numerous. Anus siphoned, posterior from mantle edge.

Genital system. Only females found. Ovary developed in largest specimens; occupies superior regions of each whorl on digestive gland (fig. 119). Oviduct yellowish, thick walled, somewhat broad, lies on columella; in pallial cavity suddenly expands. Pallial oviduct posteriorly closed at about 1/6 of its length (fig. 133). Inner lamina thin and broad, keeping a furrow close to columellar muscle. Outer lamina very thick mainly in its posterior half. Bursa, a small long and sub-elliptical furrow in middle region of pallial oviduct, bordered at left by a small fold. Anterior extremity of pallial oviduct, anterior to anus and near columella, close to small, sphincter-like aperture of brood pouch. Two folds penetrate in brood pouch aperture, one of them from inner lamina and other attached to thick outer lamina (fig. 115). Brood pouch a sac with thin walls (figs 122-124), situated behind head at right and dorsal to esophagus, free in haemocoel except for its thick walled anterior extremity. Internally several low radial folds around its aperture, one of them very large, with irregular surface (fig. 124); this fold may be protracted (fig. 115); remainder inner surface smooth; sometimes brood pouch compress m2 muscle of buccal mass (fig. 123). Up to five young specimens can occur within brood pouch in different growth stages, from one to five whorls. Young specimens imbibed in yellow mucus.

Measurements (figured specimens, in mm). Holotype: 21.8 by 9.0; MZSP 28695: 22.9 by 9.9; MZSP 28696: 16.1 by 7.0.

Distribution. Only known from type locality.

Etymology: the specific name refers on protractible fold of brood pouch aperture.

Aylacostoma ci new species

(Figs 4-6, 44, 52, 73, 84, 85, 136-149)

Types: Holotype MZSP 28691. Paratypes: MZSP 28392, 1 specimen; MZSP 28693, 1 specimen; MZSP 28345, 65 specimens; USNM 890886, 2 specimens. All from type locality.

Type locality: Brazil; Rondônia; U.H.E. Samuel, Jamari River, (20/viii/1987, Motta, C.S. col., sta. INPA mol-118).

Diagnosis. Pigment of head-foot scantier. Tentacles of mantle border more developed. Osphradium broad and short, less than half of gill length. Gill narrower with filaments tall. Broad space between gill and osphradium. Absence of well-developed vessels between gill and rectum except ad-rectal sinus. Stomach with a distinctive sorting area edged by a fold "Y" in shape. Rectum inner surface smooth. Pallial oviduct with a developed closed chamber. Pallial oviduct with about half closed. Brood pouch without large fold.

Description.

Shell (figs 4-6, 44). Medium size (up to 22 mm), turriform, apex eroded, dark brown with some sparse, spiral, reddish, minute spots. Protoconch (fig. 44) only present in young specimens (from brood pouch), two whorls almost smooth, convex, rounded; spiral ribs begin gradually, becoming strong on next whorls. Junction of protoconch and teleoconch difficult to determine. Teleoconch with about five whorls; sculpture only spiral, broad cords, uniform in size, about 10 in penultimate whorl; between spiral cords a narrow and shallow furrow. Aperture elliptical, angled posteriorly, shallow anterior canal. Peristome glossy, color cream. Umbilicus absent.

Head-foot (fig. 136). Pigmented by dark successive transversal striae around snout. Other structures pale-brown in color. Other characters similar to those of preceding species.

Operculum (fig. 52). Similar to that of preceding species.

Mantle organs (figs 139, 141). Entire mantle border with well developed tentacles, more concentrated at left extremity. Mantle cavity of almost two whorls. Pallial oviduct, rectum and anus situated as in those of previous species. Osphradium long, ridge like, thick, lying on left margin of pallial cavity, less than half of gill length, anterior extremity curved, posterior to that of gill; satellite fold absent. Between osphradium and gill a considerable space mainly in posterior region. Gill very long, about same length than pallial cavity, bearing many triangular, somewhat tall filaments, tip central, rounded. Between gill and rectum a proportionally broad, smooth area without developed vessels. Hypobranchial gland very thin. Ad-rectal sinus proportionally large, surrounding rectum.

Circulatory and excretory systems (fig. 142). Heart and kidney characters and situation similar to those of preceding species.

Digestive system (figs 137, 142, 144-149). Buccal mass, jaws (fig. 73) and salivary glands characters similar to those of preceding species. Odontophore muscles cite and characters also similar to those of anterior species (figs 145, 146, 148, 149) except subradular membrane which is opened posteriorly. Radula (figs 84, 85): rachidian tooth with 7 apical and no basal cusp; lateral tooth with 6 cusps, being second larger; marginal teeth spoon-like, with 8 cusps each, outer marginal with terminal region discretely narrower than inner one. Stomach size and situation similar to that of preceding species. Stomach (fig. 147) internally with a large, long, flattened central pad with a deep, medial, longitudinal furrow, curves at right in posterior region; crescentic ridge narrow, surround posterior half of central pad. Dorsal sorting area well differentiable (sa) at left, edged internally by a fold "Y"-shaped, one of its branch begins anterior to esophageal opening. Two tall folds begin between intestine and style sac origins. Site of esophageal entrance and origin of digestive gland duct, intestine and style sac similar to those of previous species. Digestive gland of about three whorls posterior to stomach. Intestine characters similar to that of preceding species except in rectum that lacks transversal inner folds (fig. 143).

Genital system (figs 137, 138, 140, 142). Only females found. Characters of ovary and oviduct similar to those of preceding species. Pallial oviduct posteriorly closed at about half of its length (figs 140, 142). A chamber in posterior half of pallial oviduct in its ventral surface, opens anteriorly near posterior limit of pallial oviduct aperture, maybe a bursa copulatrix. Except this chamber no other differentiable structures. Brood pouch (figs 137, 138) well-developed, situation and aperture similar to those of preceding species. Inner surface of brood pouch smooth with some folds radially disposed around its aperture, no large folds. Up to eight specimens can occur within brood pouch in different growth stages, from one to three whorls. Young specimens imbibed in yellow mucus.

Measurements (figured specimens, in mm). Holotype: 18.8 by 8.6; MZSP 28692: 20.4 by 8.9; MZSP 28693: 17.7 by 7.2.

Distribution. Only known from type locality.

Etymology. The specific epithet "ci", from Amazonian Tupy language, means "mother" (Cascudo, 1962), an allusion to parthenogenesis.

Aylacostoma tenuilabris (Reeve, 1860)

(Figs 7, 8, 31, 45, 53, 86, 150-168)

Hemisinus tenuilabris Reeve, 1860 (pl. 5, fig. 22); Ihering, 1902: 668 (fig. 4); 1909: 307; Oliveira et al., 1981: 98.

Hemisinus (Verena) tenuilabris tenuilabris: Morretes, 1949: 78.

?*Aylacostoma behni:* Henry & Simão, 1986: 507-516 (non Reeve, 1860).

Aylacostoma glabrum: Nuttall, 1990: 259-261 (figs 290, 291) (part, not Spix, 1827).

Aylacostoma tenuilabris tenuilabris: Vaz et al., 1987: 373.

Types: The Natural History Museum, London, Zoology Department, BMZD 1984222, sintypes with lectotype designed by Nuttall (1990). (Not seen.)

Description.

Shell (figs 7, 8, 31, 45). Large size (up to 40 mm), turriform, apex eroded, brown in color with several sparse reddish spots. Protoconch (fig. 45) present only in young specimens (from brood pouch), similar to those of preceding species except in being taller. Protoconch with two first whorls smooth and almost in same plane, next whorls gradually becoming larger and turned down. After third whorl thin and low spiral sculpture appears, bearing dark spiral spots regularly spaced (fig. 31). Teleoconch with up to six whorls, last whorl outstandingly large in relation to spire. Sculpture narrow spiral cords, uniform in size, about five in penultimate whorl; a somewhat broad, shallow furrow between. Some specimens present low, axial ribs in two or three first whorls. Aperture long, elliptical, angled posteriorly, shallow anterior canal. Umbilicus absent.

Head-foot (figs 150, 163). Head-foot structures very similar to those of preceding species, including pigment, low ommatophore and brood pouch aperture small, close to right fusion of mantle.

Operculum (fig. 53). Differs from preceding species only by somewhat long outline, nucleus also sub-terminal.

Mantle organs (figs 151, 152, 155, 156). Mantle border with small, lobed, well-spaced tentacles, more developed in both extremities. Osphradium very long, ridge-like, with about 7/10 of gill length; anterior extremity somewhat bulged, posterior to gill beginning; posterior extremity sharp, anterior to gill end. Gill very long, about same length than pallial cavity, filaments triangular and low; tip of each filament sharp, turned to left; gill anterior extremity sharp and near mantle border. Ctenidial vein narrow anteriorly, gradually becoming broader in posterior gill half, almost same width than gill; broad insertion in auricle. Between gill and rectum a very broad space in anterior half of cavity, and narrow in posterior half; entirely covered by visible vessels; in anterior region longitudinal vessels, posteriorly they curve to left; in posterior region only transversal, sometimes dichotomic vessels. Hypobranchial gland yellowish-transparent, very thin, situated in area between gill and rectum; in posterior region discretely thicker. Ad-rectal sinus extremely broad, rectum running free within its space, gradually adrectal sinus narrows anteriorly. Anus siphoned, near mantle border. Pallial oviduct narrow, white, running between adrectal sinus and right margin of pallial cavity, finishes posterior to anus, more details below.

Circulatory and excretory systems (figs 152, 156). Heart similar to those of preceding species, with aortas attached to style sac. Circulatory distinctive characters are broad adrectal sinus and broad posterior region of ctenidial vein. Kidney very large and complex, almost a half whorl in length. Kidney composed by two lobes separated with each other by a thin irregular septum (fig. 152: ks). Left lobe lying pericardium, bearing several hollow chambers not uniform in size, disposed somewhat transversal to pericardium wall; a small portion bulges into pallial cavity. Right lobe broad, triangular, lying at right of intestine; has two regions, a ventral with hollow chambers similar to those of left lobe, and a dorsal solid-glandular. Nephrostome small, slit-like, in right extremity of membrane between kidney and pallial cavity, close ad-rectal sinus. Blood in fixed specimens white, jelly-like.

Digestive system (figs 151, 156-168). In general similar to those of preceding species. Distinctive features follow. Jaws with elevated, cuspided anterior margin. Inner dorsal wall of buccal mass (fig. 162) with two broad and low longitudinal folds running to esophagus. Odontophore (figs 164-168) with well developed muscle fibers in its ventral surface, provided by ventral wall of buccal mass, they contours radular ribbon and inserts part with m7 and part in ventral region of mouth (fig. 165: m13). Pair of m5 and horizontal muscle proportionally short. Pair of m11 originating in inner middle region of subradular membrane inserting in m7 and in anterior extremity of cartilages. Mass of tissue in region between odontophore and esophagus very tall (fig. 164: to). Radula (fig. 86): similar to those of preceding species, with following number of cusps: rachidian tooth with 7 upper cusps being central larger; lateral tooth with 5 cusps being second larger; marginal teeth with 5 terminal cusps. Buccal ganglia large, with minute dark spots (fig. 165). Anterior extremity of anterior esophagus with a pair of vestigial pouches, with minute oblique folds in lateral regions of large folds; these folds continuation from those of dorsal buccal mass wall. Esophagus narrow, without glands; inner, narrow, longitudinal folds. Stomach large and very complex (figs 157-160); central pad very large, occupying most gastric length, with two longitudinal furrows (being one of them posterior-left) and a narrow anterior region; gastric shield differentiable; crescentic ridge large, surrounding posterior half of central pad, but not inserting in it; esophageal opening in a deep furrow, from which two folds begins and run to intestine origin (gf) where unite one with other; two or three ducts to digestive gland close one another, opening in esophageal deep furrow, near central pad left margin; dorsal sorting area well developed having one narrow fold and a furrow lying its posterior margin, and a short rounded fold at left; style sac long, with style (fig. 161); intestine originating from two tall folds situated in anterior-left region of anterior gastric chamber, one of them lies in intestine as a typhlosole (fig. 160). Digestive gland lies from antero-ventral region of stomach and also 1.5 whorls posterior to it. Intestine separated from style sac, with two loops close to it (fig.159). Rectum broad, flattened, running in a broad ad-rectal sinus; internally smooth surface, without folds. Anus siphoned near mantle border.

Genital system (figs 153-155, 163). Only females found. Ovary very small, immersed in posterior region of digestive gland near columella, color white. Oviduct white, narrow, lies columella. Before pallial cavity a narrow pericardial duct. Pallial oviduct very complex, with posterior half closed; posterior extremity a single tube; afterwards two folds begin and gradually becoming larger in a posterior deep flattened chamber (fig. 153: b1); a ventral channel begins ventral to left fold (fig. 153: b2), runs ventrally to anterior opened half of oviduct, and finishes in left furrow; upper cited posterior deep chamber runs dorsally attached to ventral channel, larger and more complex: in its middle region two small folds (fig. 154) well spaced with each other in right side, and two longitudinal broad glandular folds in its left side; these four folds finish gradually in level of oviduct aperture (figs 153, 155: ap), ventral and at right of ventral channel; anterior third of oviduct with a central, U-shaped in section, channeled fold, covered by two laminae, one in each side. Oviduct finishes posterior to anus close aperture of brood pouch. Aperture of brood pouch small (fig. 150), sphincter-like, without inner structures except small radial folds. Brood pouch a large sac (figs 150, 163), bulging behind head and internally compressing esophagus to left. Internally some sparse septa, and about 30 young specimens from one to five whorls, being younger more abundant (about 20). No visible mucus around young in brood pouch, however a transparent membrane surrounds specimens from one to two whorls.

Measurements (in mm). 34.0 by 14.7 (figured specimen); 35.3 by 15.1; 36.2 by 14.7; 36.2 by 16.0; 34.0 by 14.3.

Distribution. Upper Paraná Basin, São Paulo State.

Habitat. The specimens were found crawling on sand in shallow water (0.5 to 1 m), in river and lakes with some flow.

Material examined. Brazil; São Paulo; Avaré city, Jurumin Dam, near Paranapanema, MZSP 28309, 70 specimens (J. Colfat col, 16/i/96); Jurumim Dam, Ribeirão das Posses River, MZSP 28288, 6 specimens (A.A.O. Afonso & R. Henry col., 21/ix/1996).

Observations: *A. tenuilabris* was included in synonymy list of *A. glabrum* Spix, 1827 (from Prov. St. Sebastiani = Rio de Janeiro) by Nuttall (1990: 259), which also included *A. behni* (Reeve, 1860) (from Pernambuco), based on shell similarities. The identification of the specimens studied herein is maintained as *A. tenuilabris* until a deeper knowledge on specimens from the other two type localities, this question is then considered opened. The identification of the material used here is mainly based on comparison with lots studied by Ihering (1902, 1909), of MZSP, which restricted the locality from "Brazil" to practically only São Paulo drainages. The two specimens figured by

Nuttal (1990: 260), including the lectopype, are apparently of young specimens, which explains the specific name.

Genus *Melanoides* Oliver, 1804
(Type species: *M. fasciolata* Oliver, 1804 = *Thiara tuberculata* Müller, 1774)

Melanoides tuberculatus (Müller, 1774)
(Figs 9, 10, 46, 47, 54, 55, 87, 169-188)

Synonymyc list see Starmühler (1969: 224) and Brandt (1974: 164-165). Complement:

Thiara (Melanoides) tuberculata: Abbott, 1948: 289-290 + pl. 3, fig. 13.

Melanoides tuberculatus: Starobogatov & Izzatullaev, 1980: 31, figs 5, 11.

Melanoides tuberculata: Houbrick, 1987a: 44; Oliveira et al., 1981:97.

NB.: according to Stone *et al.* (1965) the genera with the suffix -oides are masculine in gender, thus *"tuberculatus"* is more appropriate than *"tuberculata"*.

Description.

Shell (figs 9, 10, 46, 47). Medium sized (up to 30 mm), turriform, narrow, apex generally present. Protoconch of two smooth whorls; junction of protoconch and teleoconch not clear; gradually several spiral and axial ribs appear, both predominating, giving a reticulate effect (fig. 46), spiral ribs somewhat tall. Periostracum heavy, brown. Sculpture spiral ridges of somewhat uniform width, about 10 in penultimate whorl; a somewhat broad, shallow furrow between; axial ribs close with each other (about 18 in penultimate whorl), spiral ridges runs on axial ribs (fig. 47). Ostracum pale beige with sparse axial dark brown bands. Aperture elliptical without clear canal. Other details in Brandt (1974: 165-166, pl. 12, figs. 9-12).

Head-foot (figs 169-171, 173). Color dark brown, coalescent spots in anterior region of head and dorsal regions of foot. Snout broad, dorso-ventrally flattened, anterior margin bilobed. Tentacles with about same length than snout. Eyes dark, near tentacle's base, without ommatophore. Brood pouch described below. Other head-foot structures similar to those of preceding species.

Operculum (figs 54, 55). Dark, elliptical, nucleus sub-terminal; occupies entire aperture. Inner scar elliptical, near inner margin.

Mantle organs (figs 172, 174-176). Mantle border with some lobed tentacles, different in size and well spaced one another. One or two tentacles in right extremity and three or four in left extremity more developed. Osphradium ridge-like, with about half of gill length, situated posterior to gill beginning. Space between gill and rectum proportionally narrow. Rectum large, broad, with fecal pellets oblique, compacted. Anus siphoned. Pallial oviduct described below.

Excretory and circulatory systems (figs 174, 176). Heart as described for preceding species. Kidney proportionally large, about a third whorl in length, with two lobes. Both lobes hollow, with a series of transversal septa, inserted in a longitudinal vessel. A thin transversal membrane between both lobes; other membrane between posterior (visceral) lobe and pericardial cavity. Anterior (pallial) lobe with radial septa and glandular tissue more developed. Nephrostome in right-posterior extremity of membrane between kidney and pallial cavity, close to rectum.

Digestive system (figs 177-181, 183-188). Very similar to those described for preceding species. Distinctive and interesting features follow. Two pair of folds in inner surface of dorsal wall of buccal mass, posterior to jaws, with two pairs of dark spots laterally (fig. 179); m4 and m5 insertion connected one with other; m5 connected with its pair in distal region near they insertion (figs 184-188); pair of m11 with insertion in anterior region of cartilages, in ventral region of peri-buccal muscles and in m7. Radula short, "S"-shaped. (figs 187, 188). Radula (fig. 87): similar to *Aylacostoma* preceding species, rachidian tooth with 7 cusps; lateral tooth with 5 cusps, second cusp larger; marginal teeth with 5 cusps. Esophagus without crops nor glands, internally three narrow folds. Stomach (figs 177, 178) with relatively large dorsal-left sorting area divided into 2 regions: anterior and lateral-left (this larger); lateral-left region lied at right by two folds, that anterior broader and shorter than that posterior (fig. 178: gf). Central pad long, with central, longitudinal, shallow furrow, curved to right posteriorly. Crescentic ridge absent or fused with posterior region of central pad (fig. 177: cr). Intestine aperture preceded by only one fold, rounded and tall, situated between it and style sac aperture, lies within intestine as a typhlosole (fig. 177: it). Style sac free from intestine, with length shorter than half of remainder gastric length; style present.

Genital system (figs 171, 173, 174, 182). Only females found. Pallial oviduct distinct in being entirely closed, a narrow tube with thick walls. Other accessory tube origins in outer-right-posterior region of rectum, just in a chamber replete of ova, covering externally rectum (figs 174, 182); inserts in pallial oviduct anterior half (exact insertion variable in each specimen). Aperture of brood pouch a small pore, sometimes papilla-like, in right region of head-foot, close columellar muscle. Brood pouch an enormous sac, dorsal to esophagus, with thin walls, free in haemocoel except for its aperture. Brood pouch posteriorly bilobed, left lobe larger and longer; esophagus runs between both lobes (fig. 173), inner surface smooth except by some sparse small transversal septa. Brood pouch bearing more than hundred young specimens from one to six whorls, about 80% with one whorl. Other details of genital system and number of young specimens in brood pouch see Starmühlner (1969), Berry & Kadri (1974).

Measurements (in mm). 21.4 by 6.6; 22.2 by 7.0; 21.8 by 6.2 (figured specimen).

Distribution. Eurasia. In Brazil apparently introduced in all main macrobasins, particularly confirmed in Paraná and Amazon macrobasins, and in the Pantanal.

Habitat. Rivers or lakes in regions with some current.

Material Examined. Brazil. Tocantins; Araguaçu, Agua Fria river, 27 km north of Araguaçu, MZSP 28725, 11 specimens (Lima, Rocha & Furlin col., 6-12/vii/1997). Mato Grosso do Sul; Salobrinho river, MZSP 28348, 31 specimens (T. Lipparelli col. 5/95).

Remarks on thiarids. The scope of the present study is not to propose the philosophical bases for establish species in parthenogenetic animals. A pragmatic approach is taken here accepting as representative of species each lot with specimens bearing a own group of morphological characters. However, it is recognized that the aim is matter for long debates.

Aylacostoma exoplicata differs from *A. ci* mainly in having a larger osphradium, an osphradium satellite fold present, broader and shorter gill filaments, more developed folds in rectum, simpler pallial oviduct, a large protractible fold in the brood pouch aperture and the odontophore muscle m11 connected to the peri-buccal region. Despite these anatomical differences and the large geographical distance between both species, they have great conchological similarity; the shell of *A. ci* is has about 10 spiral cords on the penultimate whorl, in contrast to about 8 in *A. exoplicata.*

Both species differ from *A. jaryensis* (Pilsbry in Baker, 1913) in having a broader shell and the sculpture not so developed. They differ from *A. sulcata* (Baker, 1913) in having a narrower shell and deeper suture. They differ from *A. elongata* (Baker, 1913) in having a broader shell and more sculptured surface. There is no other *Aylacostoma* with which both species can be confused.

A. exoplicata and *A. ci* differ anatomically from *A. tenuilabris* in having fewer young specimens in the brood pouch, the pallial oviduct simpler, the stomach lacking a deep furrow in the esophagus and in the duct to digestive gland apertures, posterior lobe of kidney with a pinnate glandular organization, anterior lobe of kidney not so glandular and odontophore muscle m11 connected to cartilages.

The three *Aylacostoma* species differ from *A. guaratinica* (Scott, 1953) in lacking so outstanding spiral sculpture and suture, and in having more young specimens in brood pouch.

Melanoides tuberculatus differs from the three *Aylacostoma* species studied here mainly in having axial shell sculpture developed, much more young specimens in brood pouch, brood pouch larger and bilobed posteriorly, dark spots in head organized in mosaic (not in transversal bands), single fold in proximal extremity of intestinal typhlosole (in stomach), anterior lobe of kidney in mantle roof (not attached to rectum), gastric crescentic ridge attached to central pad and pallial oviduct altogether closed bearing two tubes. On the other hand, the four studied thiarids have similar organization to that given by Abbott (1952) for *Thiara granifera* (Lamarck) from Guam.

The significance of the above cited differences, if specific, generic or familiar levels, only will be more secure with further morphological analysis of more species of each group.

Melanoides tuberculatus is an alien species in South America, coming from Eurasia, introduced in Brazilian basins maybe by aquarists or studies for competition with planorbids. This species is spreading by several macrobasins competing directly with native cerithioideans. They live probably in the same niche of native cerithioideans - water with some energy degree - rather than planorbids, which are animals of water with lower energy. In locals where *M. tuberculatus* occurs, the native cerithioideans are found in a despicable number (person. obs.), showing direct competition and danger of extinction.

Family Planaxidae

Genus *Supplanaxis* Thiele, 1929

(Type species: *Purpura nucleus* Bruguière, 1789)

Supplanaxis nucleus (Bruguère, 1789)

(Figs 17-19, 56, 74, 88, 189-206)

Synonymy: see Houbrick, 1987a: 25. Complement: *Planaxis nucleus:* Warmke & Abbott, 1961: 70 (pl. 13 fig. a); Abbott, 1974: 102 (fig. 975); Abbott & Dance, 1983: 62 (fig.); Jong & Coomans, 1988: 43.

Description.

Shell (figs 17-19). Elliptical outline, spire sharp. Periostracum velvet-like, whitish. Ostracum black. Aperture opisthocline, peristome ample, dark purple, complex scultured, with several inner ribs and strong canal. Other details described by Houbrick (1987a: 25-27, fig. 17).

Head-Foot (figs 189-192). White with gray spots in dorsal region of foot, dorsal and lateral regions of head, snout and tentacles. Tentacles gray spots disposed in longitudinal bands in lateral regions of foot spots disposed in oblique bands (fig. 190). Ommatophore small, eye dark, relatively small. Snout sub-cylindrical, with plane, white anterior extremity, mouth approximately in center. Male with a clear groove in outer region of right tentacle, running ventrally near foot, white internally, dark gray in margins. Female with pore of brood pouch in middle region between right tentacle and columellar muscle; a clear furrow runs from aperture of pallial oviduct to brood pouch aperture. Brood pouch described below. Other details see Houbrick (1987a: 27, figs. 19-21).

Operculum (fig. 56). Yellowish-brown, semi-transparent, nucleus sub-terminal, outline elliptical, occupies entire aperture.

Mantle organs (figs 193-195). Mantle border simple, without tentacles, gray with a mosaic of clear spots; right side thickened and notched. Mantle cavity of about 1.5 whorl. Osphradium long, ridge-like, with about same gill length; anterior extremity of osphradium more anterior than that of gill and disposed parallel to mantle border. Gill elliptic, leaflets many, triangular, tip long, somewhat sharp. Between gill and rectum a proportionally broad area. Hypobranchial gland thin, only visible in posterior region of cavity. Rectum, anus and pallial gonoducts described below. Other details of mantle organs in Houbrick (1987a: 27, fig. 22).

Circulatory and excretory systems (figs 194, 200). Heart similar to those described for preceding species. Aortas attached to style sac and intestine. Kidney proportionally short, about 1/6 whorl, internally a solid white tissue. Nephrostome a slit in middle region of wall between kidney and pallial cavity.

Digestive system (figs 192-194, 196-198, 201-206). Buccal mass similar to preceding species, distinctive features follow. Jaws almost vestigial, a pair of small triangular plates not fixed directly in dorsal peri-buccal wall, but in a thin, transparent membrane (figs 74, 201). Four narrow longitudinal folds in inner dorsal surface of buccal cavity, two broader, close odontophore, and two median (fig. 201). Dark spots in lateral-anterior region of buccal cavity (fig. 201: ds). Aperture of salivary glands in middle-inner margin of broader folds (fig. 201: se). Odontophore (figs 202-206) also similar to those of preceding species, but with radula very long, sometimes coiled. A dark spot always present in dorsal region of radular sac just anterior to radular nucleus (figs 201, 202). Radular sac slack, keeping radular ribbon free within it. Odontophore distinctive features: 1) **m11** pair narrow, originating in middle region of inner surface of subradular membrane, inserting in ventral region of radular sac, in its outer surface; 2) **m11a**, other accessory pair of muscles origin lateral to m11, runs anteriorly, presenting a small connection with anterior extremity of cartilages, afterwards unite with its pair inserting in radular ribbon internally to radular sac (fig. 206); 3) some small connection of anterior extremity of radular sac with inner-ventral surface of horizontal muscle (fig. 205: ih). Radula (fig. 88): rachidian tooth with 9 cusps, being central cups very broad and arched, and lateral cusps small and uniformly sized; lateral tooth very broad and flattened, with 6 cusps, being fourth cusp larger and broad; inner marginal tooth spoon-like, broad terminal margin with 7 cusps; outer marginal tooth spoon-like, with terminal margin "V" shaped, with about 18 cusps of small, uniform size. Salivary glands as described by Houbrick (1987: 27, fig. 19b), having glandular tissue also anterior to nerve ring (fig. 197). Anterior esophagus with two folds in ventral region and two pouches in dorsal region with successive oblique septa (fig. 196). Middle esophagus with dorsal pouches. Posterior esophagus single, without inner folds. Stomach (fig. 198) very large; inner surface almost entire smooth; central pad small septum-like, in middle-ventral region, not covering duct to digestive gland. No differentiable folds or sorting areas. Digestive gland begins ventrally in stomach near style sac and runs two whorls posterior to it (fig. 194). Style sac simple, cylindrical, with a left small fold, intestine origin in left region of style sac tip. Intestine narrow, contours dorsally style sac, in its right ventral region, runs anteriorly; in pallial cavity suddenly expands. Rectum very large, with fecal pellets compacted obliquely as in preceding species (fig. 193). Anus siphoned posterior situated from mantle border. Other details of digestive system in Houbrick (1987a: 27).

Genital system. Male: pallial spermoduct simple, almost all opened, thick glandular walled (fig. 193). Female: gonopericardial duct visible; pallial oviduct with bursa opening anterior to aperture of seminal receptacle; bursa contours left region of receptacle and stays posterior to it (fig. 199), other details see Houbrick (1987a: 29, fig. 19a). Brood pouch aperture a small pore situated in middle region between right tentacle and right insertion of mantle (fig. 190), preceded by a posterior furrow. Brood pouch two large chambers in dorsal region of foot, one in each side (fig. 191); each chamber U-shaped, with outer branch connected with brood pouch aperture (described above and by Houbrick 1987a: 29-33, fig. 21b). Within brood pouch about a thousand small embryos, apparently in same development level (less than one whorl).

Measurements (MZSP 28255, in mm). 15.9 by 11.1; 13.1 by 8.5; 13.7 by 9.3.

Distribution. Gulf of Mexico and Caribbean Sea.

Habitat. Under rocks, medium to supra tidal, near estuaries.

Material examined. Venezuela; **Nova Esparta**; Margarita Island (Simone col.); Pedro Gonzales, Puerto Cruz, MZSP 28256, 31 specimens; La Isleta, El Yaque beach, MZSP 28344, 12 specimens (7/ii/1995); Porlamar, Caracola beach, MZSP 28255, 46 specimens.

Remarks. Houbrick (1987a: 27) describes the color of head-foot as black but the specimens here studied are gray. The characters of female pallial gonoducts of the specimens examined are similar to description of Houbrick (1987a:29) but the distribution of bursa and seminal receptacle are little different if compared with that shown in fig. 19a of that paper, which shows the bursa almost entirely anterior to receptacle. In the specimens examined, the bursa contours the receptacle and stays posterior to it. It is important to establish, however, that specimens from Florida, studied by Houbrick, was not examined herein, and these differences show that further investigations are necessary.

Family Pleuroceridae

Genus *Doryssa* H. & A. Adams, 1854

(Type species: *Bulimus atrus* Bruguière, 1792)

Doryssa ipupiara new species

(Figs 12, 57, 58, 75, 76, 89, 90, 207-224)

Types: Holotype MZSP 28687. Paratypes: MZSP 28688, 1 specimen; MZSP 28689, 1 specimen; MZSP 28690, 1 specimen; MZSP 28265, 14 specimens; USNM 890884, 2 specimens. All from type locality.

Type locality: Brazil; Roraima; Apui lake, Maracá Island (sta. INPA-mol 101, Motta, C.S. col.).

Diagnosis. Shell with shallow suture, acuminate, sculptured by strong spiral cords and axial threads. Eyes not visible externally. Ctenidial vein very broad in its posterior half. Gill filaments long and sharp. Stomach without complex folds. Pallial gonoducts with massive laminas, without chambers.

Description.

Shell (fig. 12). Of medium size (up to 30 mm), turriform, apex eroded, color black or dark brown in. Protoconch not seen. Teleoconch acuminate, of about seven whorls, suture shallow, out surface almost straight. Sculpture strong spiral cords, about seven in penultimate whorl, between spiral cords a narrow and shallow furrow. Spiral cords with uniform undulations giving an effect of axial orthocline threads, about 15 in penultimate whorl. Periumbilical area without axial sculpture. Aperture elliptical, angled posteriorly, shallow anterior canal. Peristome clear beige with some sparse dark brown spots, very thick in some specimens. Umbilicus lacking.

Head-Foot (figs 207, 208). Color homogeneous dark brown with some sparse clearest areas. Fixed specimens with uniform cover of clear mucus. Head protruding. Snout large, acuminate, base broad, anterior margin flattened, somewhat bilobed. Mouth longitudinal, antero-ventral and thickly muscular. Tentacles long, stubby, with a basal outer ommatophore. Eyes present but only visible by dissection of ommatophore. Foot of medium size, without divisions, a furrow in anterior margin of pedal glands. Columellar muscle of about 1.5 whorls.

Operculum (figs 57, 58). Somewhat circular, corneous, nucleus sub-central, externally spiral, occupies partially aperture, varies from multispiral (fig. 58) to slightly palcispiral (fig. 57). Muscle scar large, rounded, near inner margin.

Mantle organs (figs 210, 211). Mantle border simple, without neither tentacles nor papillae. Mantle cavity of about two whorls. Siphon a small area in left extremity with thickened muscular tissue. Osphradium very long, ridge-like, lying left margin of pallial cavity at about a half of gill length; anterior extremity posterior than that of gill. Gill very long, about same length than pallial cavity, filaments triangular, tall; tip with sharp turned to right. Ctenidial vein normal sized anteriorly, becomes larger forming a large sinus posteriorly; its posterior extremity suddenly narrows in insertion in auricle. Between gill and rectum a proportionally narrow area. Pallial genital ducts runs at right margin, edged at left by large rectum. Anus siphoned, near right extremity of mantle border.

Circulatory and excretory systems (figs 209, 210, 217). Heart characters and situation similar to those described for preceding species. Kidney proportionally large, about half whorl, situated in posterior-right limit of pallial cavity, about half in pallial roof and half in visceral mass. Kidney with only one lobe close to intestine; this lobe solid, richly vascularized, bordered by two flattened chambers. At left a chamber with smooth walls covered by two thin transparent membranes: posteriorly that of pericardium, anteriorly that of pallial cavity roof. At right a chamber with transversal folds in both sides, one of them attached to left surface of intestine. Nephrostome close to rectum, long, covered ventrally by a solid flap, flattened, with five to six transversal folds (fig. 210: fn); inserted at left in right border of kidney and at right in posterior extremity of outer lamina of pallial gonoduct; posteriorly inserts in posterior wall of pallial cavity, anteriorly free.

Digestive system (figs 212, 215-224). Buccal mass just behind mouth (fig. 212). Jaws plates in anterior and middle borders, cut edge rounded, regular (figs 75, 76), a pair of small projections in region between both jaws, each one with a radiate arrangement (fig. 75). Salivary ducts aperture near anterior region of two longitudinal folds of inner dorsal wall of buccal cavity. Odontophore muscles distinctive features (figs 218-224): 1) **m10** inserted posteriorly, in m4, and not in m5; 2) **m15**, differentiated muscle fibers of ventral wall of buccal mass surrounding antero-ventral region of radular sac, inserting in m10 in each side; 3) **m7** absent; 4) **m11** originating in inner surface of subradular membrane and inserting in peribuccal wall, without connections with radula nor cartilages; 5) **m11a**, a pair of small muscles, origin in anterior extremity of cartilages, insertion in median region of inner surface of subradular membrane between m11 origins; 6) **m8** very long and narrow, origin in ventral wall of buccal mass (vw), insertion in radular nucleus. Radula very long, coiled in its posterior region. Radular teeth (figs 89, 90): rachidian teeth with 5 cusps, central cusp very larger (about double), no basal cusps; lateral tooth with 5 cusps, first cusp broad and undulated; second cusp broad, straight, tip rounded; inner marginal tooth spoon-like, with 3 broad terminal cusps; generally central cusp larger but some variation occurs in same ribbon; outer marginal tooth similar to inner one but narrower and with 3 cusps generally same sized. Salivary glands cluster around esophagus just posterior to nerve ring, have two lateral expansions being left one longer. Esophagus narrow (fig. 212), ventral region with two parallel typhlosoles. Esophageal pouch single, large, with inner surface replete of many tall papillae; occupies anterior and middle esophagus (fig. 215). Posterior esophagus with 5 to 6 longitudinal, similar sized folds. Stomach large, about half whorl (fig. 216). Central pad relatively small, duct to digestive gland in middle region of its left margin. Crescentic ridge small, surrounding at some distance posterior region of central pad. Gastric shield small, in anterior-right side of central pad; dorsal sorting area elliptical, surrounded by smooth areas. Intestine and style sac united one another in almost they entire left region, separated only by a constriction. Intestine narrow, with single loop in right side of style sac. Rectum broad, with several fecal pellets obliquely compacted. Anus described above.

Genital system (figs 213, 214). Male and female genital organs similar. Gonad in superior region of first whorls, on digestive gland. Visceral gonoduct close columella. Pallial gonoduct almost entire opened, simple, without chambers or annex structures except a expansion covering nephrostome, connected to posterior extremity of outer lamina (fn). Pallial gonoduct finishes posterior to anus. No ovopositor differentiable.

Measurements (in mm). Holotype: 24.4 by 11.2 (figured specimen); MZSP 28688: 26.0 by 12.3; MZSP 28690: 23.8 by 11.9.

Distribution. Only known from type locality.

Etymology. The specific epithet "ipupiara", from Amazonian Tupy language, means a entity who lives under water (Cascudo, 1962).

Doryssa atra (Bruguière, 1792)

(Figs 14, 59, 77, 91, 92, 225-544)

Synonymy see Tillier, 1980: 14.
Complement: *Doryssa atra:* Morretes, 1949: 75.

Description.

Shell (fig. 14). Large, very long, dark brown; whorls discretely convex. Axial sculpture present in first whorls, gradually disappear, last whorls only with spiral sculpture (about 10 in penultimate whorl). Peristome cream in color, with some sparse dark brown spots. Other details in Tillier (1980: 14, pl. 1, fig. 1).

Head-foot (figs 225, 236). Color dark brown with some clearer spots, of imprecise borders, sparse in integument; this color gradually becomes paler up to posterior regions of head. Head protruding. Snout large, broad, somewhat short, dorso-ventrally flattened; anterior margin multilobed. Mouth longitudinal, antero-ventral and thickly muscular; most of ventral-anterior snout folds converge to mouth. Tentacles stubby, ommatophore in they basal outer region sessile in head. Eyes dark, proportionally small, in anterior-dorsal region of ommatophores. Foot of medium size, without divisions; anterior furrow of pedal glands; a small mesopodial tentacle in posterior extreme of foot. Columellar muscle of about 1.5 whorls.

Operculum (fig. 59). Similar to that of preceding species.

Mantle organs (figs 226-228, 232). Mantle border simple, without neither tentacles nor papillae. Mantle cavity of about two whorls. Siphon inconspicuous. Osphradium long, ridge-like, with about half of gill length; anterior and posterior than that of gill, and preceded by a zigzag. Gill narrow and long, about same length than pallial cavity, filaments triangular, low; tip rounded, almost central. Ctenidial vein well developed, without large dilatation. Between gill and rectum a relatively broad area with some transversal, sparse vessels. Hypobranchial gland inconspicuous. Adrectal sinus around entire rectum, but little evident. Rectum broad, with fecal pellets obliquely disposed. Anus siphoned near mantle border. Genital ducts in right margin described below.

Circulatory and excretory systems (figs 226, 231, 232). Heart characters similar to those of preceding species, with aortas attached to anterior region of style sac and adjacent intestine. Kidney short, about 1/6 whorl; almost entire solid, except a chamber surrounding its connection with rectum; inner surface of this chambers as follows (fig. 226): at left covered by several tall septa; these septa thin, somewhat uniform, smooth, dark brown except they free vertex which are clear beige and thicker; these septa gradually fuse one another in left kidney region in a massive, radial furrowed tissue, mainly situated in pallial cavity; at right two regions: posterior region free from rectum bearing tall, transversal folds with irregular surface; anterior region with area about twice longer than posterior one, bearing several transversal folds attached to rectum surface, somewhat low and well spaced one another, these folds are present even outside nephrostome. Nephrostome a broad aperture between rectum and anterior kidney region, protected at left by a solid flap, with 4-5 folds, similar to that of preceding species, inclusive insertion in outer lamina of pallial gonoduct (figs 226, 232).

Digestive system (figs 229-231, 236-243). Buccal mass of medium size, situated almost entire within snout. Jugal muscles similar to those of preceding species except by a large development of a pair (figs 237, 239, 240: **m16**), denominated lateral dilator of mouth, origin in lateral-anterior inner surface of snout, insert in anterior-lateral region of peri-buccal muscular mass, being some fibers inserted directly in pad where jaws connect. Jaws (figs 77, 239) somewhat large and broad, cut edge rounded. Inner surface of dorsal wall of buccal mass with 4 folds in anterior extremity, two of them larger, connected in jaws, and two narrow running laterally; after some distance lateral and jaw fold fuses one another, originating a pair of broad dorsal folds which run to esophagus; between both folds a broad, thin walled furrow. Aperture of duct of salivary glands in middle and outer margin of dorsal folds. Pair of **m2** distinct in having origin anterior in haemocoel lateral inner surface, being turned anteriorly in retracted condition. Odontophore distinctive features (figs 241-243): 1) **m15** developed; 2) **m11** pair originated in inner-anterior surface of subradular membrane, near its detachment of subradular membrane (anterioly) bear two pairs of small muscles, dorsal pair very narrow, connected with anterior extremity of cartilages, ventral pair narrow, connected with radular ribbon, internally to radular sac; afterwards, m11 turn anterior-ventrally and inserts in dorsal region of transition snout-foot, close to radular sac; in this site bear a pair of small and short muscles connected to external side of radular sac; 3) **m8** very long and narrow; 4) **m10** posterior inserted, close m4. Asymmetry of odontophore (figs 241, 242) shown in all examined specimens (right side more anterior than left side). Radular ribbon very long, coiled in its posterior region. Radula (figs 91, 92) similar to that of preceding species, rachidian tooth with 7 cusps, being central cusp larger (about double); lateral tooth with 5 cups, third cusp larger; inner marginal tooth long and broad, with 3 broad terminal cusps; outer marginal tooth rook-like, rounded apex. Salivary glands large, run dorsally from region near m2 to anterior esophagus, where twist ventrally and run to region of nerve ring, not passing through it. Anterior esophagus (figs 236-239) with about five folds in dorsal side, being both marginal folds tall and flat. Middle esophagus with single pouch, large, with inner surface completely covered by somewhat tall papillae; tall folds of anterior esophagus become low in middle esophagus, but taller than 3 or 4 small folds which run between them; this group of folds runs parallel one another in ventral side of pouch. Posterior esophagus narrower, with 5 to 6 low, slightly uniform, longitudinal folds. Stomach (figs 229, 230) with little less than a half whorl, internally very complex. Dorsal wall with 3 differentiated sorting areas, two small anterior and a larger in posterior-right side; among these sorting areas 2 semicircular, thick folds with lobed edge, concavity anterior-right; other fold, narrow, edging at right posterior sorting area and contours right extremity of thick folds. Gastric shield well developed. Central pad with about a third of ventral gastric area and divided in three lobes by transversal furrows, anterior lobe close shield, middle lobe with duct to digestive gland in its left margin, and posterior lobe bulged and covered by a mosaic of "U" shaped acina. Crescentic ridge edging at some distance posterior lobe of central pad, connected with it at right. Esophageal aperture simple, near duct to digestive gland. Anterior gastric chamber short; a large but short fold in intestine origin present, with transversal successive furrows in its edge. Digestive gland begins in middle-ventral region of stomach and has 1.5 whorls posterior to it. Intestine opened to style sac in almost its entire left side (fig. 231), but separated from it by a constriction. Intestine, after separation with style sac, contours it and arrives in its posterior right region; after a loop return to anterior where exits to pallial cavity. Rectum and anus above described.

Genital system (figs 233-235). Both, masculine and feminine genital systems similar with each other. Gonad in superior region of digestive gland. Visceral gonoduct run close columella, a thick walled narrow duct. In right-posterior region of pallial cavity emerges and expands as an opened groove. Outer lamina simple, with flap protecting nephrostome inserted in its posterior extremity. Inner lamina thicker, with a very long chamber running within its border, from region close rectum to its anterior third part, where opens in a long furrow. Male pallial sperm groove with inner surface more complex than that of female, presenting some longitudinal folds posteriorly and oblique folds anteriorly. Pallial gonoduct finishes close, but posterior to anus. No ovopositor differentiable.

Nervous system. Nerve ring (fig. 244) as normal cerithioideans and very similar to that described by Marcus & Marcus (1964) for *Cerithium atratum*. Connective between pedal ganglia short. Connective between cerebral ganglia relatively long. Statocysts with several statolyths (statoconia).

Measurements (in mm). 42.4 by 15.2; 51.0 by 18.4; 36.7 by 13.8.

Distribution. French Guyana, Surinam, North Brazil (Amazon region).

Material examined. French Guyana; St. Takari Tante, Sinnamery River, 6 specimens, MZSP 28286 (INPA, 20/xi/1989).

Remarks. Doryssa atra resembles the shell characters of *D. transversa* (Lea, 1850) (fig. 13, a specimen from MZSP number 28726, from Boa Vista, Roraima) from which differs in having broader shell and shorter spire, but, from the Brazilian *Doryssa*, that is which *D. atra* have more affinity.

Doryssa macapa (Moricand, 1856)

(Figs 11, 60, 93, 94, 254-264)

Melania macapa Moricand, 1856: 176 (pl. 6, fig. 7); Reeve, 1860 (pl. 29, fig. 194).
Doryssa macapa: Morretes, 1949: 75.
Complement in Ihering, 1902: 663.

Description.

Shell (fig. 11). Of medium size, turriform, very eroded apex, only 4-5 last whorls present. Walls heavy, thick. Whorls outline almost straight, suture little evident. Sculpture strong axial threads (about 22 in penultimate whorl), each thread uniformly lobed by transversal furrows, giving an effect of spiral sculpture (about 6 in penultimate whorl). Between axial threads smooth surface. Last whorl with 6 or 7 spiral broad threads in peri-umbilical and siphonal regions (inferior) and axial threads with about 6 lobes (as above described) in superior region. Aperture simple, without canal, somewhat elliptical, posterior region strongly angular. Lips glossy, thick, simple. Periostracum dark brown, almost black, opaque.

Head-foot (figs 245-248). Color dark brown, almost black, posterior regions and foot sole beige. Head protruding, broad. Snout broad, short, dorso-ventrally flattened, anterior margin bilobed. Mouth longitudinal, antero-ventral, thick muscular. Tentacles stubby, base broad. Ommatophore sessile in head, situated in outer, ventral region of tentacles base. Eyes dark, somewhat small, in anterior extremity of ommatophore. Foot of medium size, without divisions; anterior furrow of pedal glands. Columellar muscle of about 1.5 whorls. Female with ovopositor described below.

Operculum (fig. 60). Similar to that of preceding *Doryssa* species.

Mantle organs (figs 257-259). Mantle border simple, without neither tentacles nor papillae; edge dark brown, gradually becoming clear with dark minute spots posteriorly. Mantle cavity of almost two whorls. Siphon inconspicuous. Osphradium long, ridge-like, with about 1/3 of gill length; anterior extremity posterior than that of gill and preceded by a zigzag. Gill narrow and very long, about same length than pallial cavity; filaments triangular, low; tip rounded, almost central. Ctenidial vein gradually becomes broad, in posterior region about same width than gill. Between gill and rectum a somewhat narrow area with some transversal, sparse vessels. Hypobranchial gland inconspicuous. Adrectal sinus very broad, rectum running free within it. Rectum broad, with several fecal pellets obliquely disposed. Anus siphoned, posterior from mantle border. Genital duct in right margin described below.

Circulatory and excretory systems (figs 256, 258). Heart characters similar to those of preceding *Doryssa* species, aortas attached to style sac antero-dorsal region. Kidney short, about 1/4 whorl, almost entire solid, except a flattened chamber surrounding rectum; left surface of this chamber covered by uniform transversal folds without development of septa; right surface of this chamber with several transversal, not uniform folds (fig. 258), with irregular surface, attached to outer surface of rectum; these folds also present in anterior region of nephrostome. About half of kidney in pallial cavity and half in visceral mass between pericardium and rectum. Nephrostome a broad aperture between rectum and kidney (as in preceding *Doryssa* spp), protected at left by a massive flap of smooth surface, inserted in outer lamina of pallial gonoduct (fig. 257).

Digestive system (figs 248-251, 253-256, 262-264). Buccal mass similar to that of *D. atra*, inclusive presence of **m16**; distinctive features are (figs 248-250): 1) dorsal pair of dark spots longer; 2) a pair of broad folds at side of jaws, inserting in dorsal folds in posterior region of jaws, part of m16 inserts in these folds. Odontophore distinctive features are (figs 262-264): 1) region of insertion of pair of **m5** very long and large, united in borders with subradular membrane; 2) **m11** pair somewhat thick, each with single connection in radular sac, insert posteriorly in snout and foot transition; 3) **m12** developed; 4) **m10** pair posteriorly inserted, in m4; 5) **m7** pair originating from small, differentiated fibers of both m4 dorsal-anterior region, unite one with other in region anterior to subradular membrane, inserts in radular sac anterior than connection of m11; 6) a pair of long, dark spots, in dorsal region of cartilages, seen by transparency though subradular membrane and cartilage (ds); 7) subradular cartilage with a projection in each side of its ventral-posterior extremity; 8) **m8** very long and narrow. Radular ribbon long. Radula (figs 93, 94) similar to those of preceding *Doryssa* species; rachidian tooth with 5 cusps, being central cusp very larger (more than double); lateral tooth with 5 or 6 cusps, third cusp very larger and broader; marginal teeth with rounded cut edge and 3 small cusps in inner region of this edge; outer marginal tooth with cusps discretely smaller than inner one. Salivary glands similar to those of *D. atra*, except right gland, which has a narrow branch through nerve ring, after become thick and contours anterior esophagus (fig. 249); left salivary gland only anterior to nerve ring. Anterior and middle esophagus (fig. 251) with single, large pouch covered by many tall papillae, in right side a pair of parallel folds (continuation from those of dorsal wall of buccal mass) tall anteriorly, gradually decrease in posterior region; between both folds a relatively broad space, smooth, with flaccid wall. In anterior region of posterior esophagus gradually folds faint and papillae become sparse, after esophagus becomes a broad tube with smooth, flaccid walls; this flaccid posterior region of esophagus pleats. Stomach (figs 254-256) long, little more than half whorl. Stomach dorsal wall without clear sorting areas, most smooth; anteriorly 3 folds, those two right folds arched, that left fold almost straight, oblique; in middle-left region a broad chamber of esophageal aperture; in right posterior region of this aperture 2 transversal folds, that anterior narrow, that posterior somewhat broad. Central pad narrow and with about half of gastric length; divided by a constriction into 2 lobes, anterior lobe with smooth surface and connected anteriorly with gastric shield, posterior lobe covered by a mosaic if irregular sized acina, some of them U-shaped. Crescentic ridge narrow, surrounding at some distance, posterior extremity of central pad. Duct to digestive gland broad, situated between posterior lobe of central pad and left gastric wall. Anterior chamber of stomach greatly compressed at left by esophagus, separated from posterior chamber by a narrow fold. Apertures of intestine and style sac united with each other; a small, short fold in intestine origin. Style long, about half of remainder stomach length. Digestive gland begins in middle ventral region of stomach and runs two whorls posterior to it. Intestine opened into style sac at almost its entire left side, but separated from it by a constriction. Intestinal loops similar to other *Doryssa* species. Rectum and anus above described.

Genital system (figs 246, 247, 252, 257-261). Gonad in superior region of digestive gland, distinct in having long, transversal, spaced acina. Visceral gonoduct narrow and thick walled, running close to columella. Pallial spermoduct (fig. 260) almost entire open (sperm groove) with a flap inserted in outer lamina, covering nephrostome; inner lamina with a long and narrow seminal vesicle within its border, opened anterioly in a narrow and long aperture in middle region; anterior region of sperm groove with several glandular folds and channels, irregular, finishing posterior to anus. Pallial oviduct (figs 257, 261) similar to sperm groove but simpler, with smooth inner surface; presents bursa very long (almost since from its posterior limit) and with aperture anteriorized; pallial oviduct finishes in a level discretely anterior to anus. Ovopositor in right-dorsal region of foot (figs 246, 247, 252), with two elevated, beige thickness, posterior larger and V-shaped, anterior small and somewhat triangular. A furrow runs from oviduct aperture to dorsal-anterior margin of ovopositor. In ovopositor of immature females (figs 247, 252) only that small thickness present, but narrower.

Distribution. Lower Amazon Basin.

Measurements (in mm). 50.8 by 19.0; 40.4 by 18.5; 46.3 by 18.7.

Material examined. Brazil; **Amapá**; north of Porto Grande, Araguari River, 10 specimens, MZSP 28290 (INPA; Magalhães, C. col.; 18/viii/1992).

Genus *Pachychilus* I. & H. Lea, 1850
(Type species: *Melania graphium* Morelet)

Pachychilus sp.
(Figs 15, 16, 61, 95, 96, 265-281)

Description.

Shell (figs 15, 16). Long, turriform, up to nine whorls. Color clear beige with broad axial bands dark brown, irregular, of imprecise borders; apex clear; other clear narrow band in suture. Each whorl little convex, almost straight outline; suture inconspicuous. Surface almost smooth, five last whorls sculptured by narrow and low spiral lines, discretely irregular. Aperture simple, canal weak. Protoconch present, of two convex glossy whorls.

Head-Foot (figs 265-267). Color consisting by transversal bands intercalated brown and beige, of imprecise limits; posterior regions and foot sole beige. Head protruding, relatively large. Snout large, broad, bilobed anterior margin with several oblique furrows. Mouth longitudinal, in anterior snout extremity. Tentacles stubby, long. Ommatophore sessile in head, situated in ventral-outer region of tentacles base. Eyes dark, situated in a small depression of central-dorsal region of each ommatophore. Foot of medium size, without divisions; anterior furrow of pedal glands. Ovopositor in right-dorsal region of foot, described below. Columellar muscle of about one whorl.

Operculum (fig. 61). Palcispiral, circular, nucleus discretely excentric, occupies entire aperture. Scar very long, elliptical, near inner margin.

Mantle organs (figs 268, 270, 271). Mantle border simple, thick, without pigment except very small, circular, brown, sparse spots. Two flaps well differentiable in right extremity, anterior to anus and genital ducts. Siphon inconspicuous. Osphradium long, ridge-like, with about half of gill length; anterior end posterior to that of gill. Gill narrow and long, about same length than pallial cavity; filaments triangular, low; tip rounded, almost central. Ctenidial vein narrow. Between gill and rectum a relatively narrow area. Hypobranchial gland inconspicuous. Adrectal sinus broad, rectum running free within it. Rectum broad, with several fecal pellets obliquely disposed. Anus siphoned, posterior from mantle border. Genital ducts in right margin described below.

Circulatory and excretory systems (figs 270, 272, 273). Heart characters similar to those of preceding species, with aortas attached to anterior region of style sac. Kidney of about 1/4 whorl, almost entirely solid; about half exposed in pallial cavity and half in visceral mass between pericardium and rectum. A chamber preceding nephrostome with left surface smooth and right surface attached to rectum, with two longitudinal and broad folds, between both folds a relatively deep furrow. Nephrostome, as in *Doryssa* preceding species, broad, between rectum and kidney, and protected at left by a flap inserted in outer lamina of pallial gonoduct. Some low and well spaced transversal folds in region of nephrostome, and anterior to it, in face with rectum.

Digestive system (figs 267-270, 272-280). Buccal mass of medium size, situated almost entire within snout. Jugal muscles mainly distributed in dorsal region. Pair of **m16** present but narrow. Jaws of medium size and dark brown in color. Outer surface of dorsal buccal mass wall with a pair of semi-circular, dark brown spots (fig. 274: ds). Inner surface of this wall with a pair of longitudinal, broad folds, beginning in jaws; each fold presents a central, longitudinal furrow in they broadest region; both folds continue in esophagus. Duct of salivary glands in outer and posterior margin of these folds. Odontophore distinctive features (figs 275-278): 1) **m2** narrow; 2) **m15** absent or inconspicuous; 3) **m7** originated from anterior-median-dorsal region of m4 and not from subradular membrane; 4) **m11** pair similar to that of *Doryssa atra*, but with only a pair of connections with outer side of radular sac near its insertion; 5) a fusion of m5 borders with subradular membrane; 6) **m5** inserted in radular ribbon by large and long area; 7) **m8** very long and narrow. Radula very long and intensely coiled. Subradular cartilage with a long ventral projection in each side, parallel to tissue on radula (to). Radular teeth (figs 95, 96):

rachidian tooth with 7 cusps, being central cusp larger (about double), basal region with a low projection having a broad central elevation and a narrow elevation in each side; lateral tooth with 6 not aligned, robust cusps, being third cusp larger; marginal teeth with 3 terminal pointed cusps, being these cusps closer in outer marginal tooth. Pair of salivary glands fused with each other and anterior to nerve ring. A narrow branch of salivary gland pass through nerve ring and newly become thick, contours esophagus to left (fig. 274). Both regions of salivary glands differ in color, anterior to nerve ring white, posterior to it beige. Anterior and middle esophagus (figs 269, 274) with a pair of longitudinal folds in a side of a single and large pouch; this pouch beige colored with several white papillae; papillae somewhat tall and well spaced with each other. Posterior esophagus with 4-5 longitudinal folds. Stomach (figs 279, 280) with little less than half whorl. Dorsal inner surface with a sorting area differentiable in anterior-right region; two arched folds in center (concavity anterior-right); two longitudinal folds in right side, a sorting area of low folds around arched folds; and a small chamber, with radial folds, of aperture of esophagus, edged at right by a narrow fold. Gastric shield somewhat large. Central pad with about a third of ventral gastric area, bears a broad furrow in its posterior region. Crescentic ridge surrounds, at some distance, posterior region of central pad, united with this in right side. Duct to digestive gland between left extremity of crescentic ridge and central pad. Anterior gastric chamber short, with a broad, low fold in intestine origin. Digestive gland begins in middle-ventral region of stomach and runs 3 whorls posterior to it. Style sac of about half of remainder gastric length (fig. 272). Intestine united with style sac at almost its entire left region, separated one another by a constriction. Intestine, after style sac, contours its right side and, close to stomach, has other loop turned towards anterior (fig. 272). Rectum and anus described above.

Genital system (figs 268, 273, 281). Male and female organs similar with each other. Gonad in superior region of digestive gland. Visceral gonoducts run close columella. Pallial gonoducts almost entire opened (grooves). Outer lamina simple, thick walled, with a flap protecting nephrostome inserting in its posterior limit. Inner lamina similar to outer lamina, but with its posterior region thicker, having also in this region a sac-like chamber, somewhat short (about 1/4 of total length of pallial gonoduct), opens in a small orifice. Pallial gonoduct finishes posterior to anus. Female with a long, somewhat rectangular ovopositor in right-dorsal region of foot (fig. 265), with imprecise anterior margin; a furrow from aperture of pallial oviduct, and runs ventrally to antero-dorsal region of ovopositor. Ovopositor with a distinctive white color.

Measurements (in mm). 23.0 by 11.7; 21.5 by 10.7.

Habitat. In river under rocks, shallow water.

Material examined. Mexico; Chiapas; near Palenque ruins, 3 specimens, MZSP 28285; 1 shell, MZSP 28282 (R. Pinto da Rocha & S.A. Casari col; 28/ix/1996).

Remarks on pleurocerids. The interesting, almost smooth shell lets little doubts on the generic attribution of these last specimens, if the diagnosis of Morrison (1954) and Burch & Cruz-Reyes (1987) were used. Due lack of comparative material and the large quantity of species in the local, the specific identification is not given, to avoid worse error.

The thiarids and pleurocerids have few anatomical characters in common in a detailed comparison. On the other hand, conchological characters are similar and a sure separation of both groups in conchological base is very hard to be defined, at least in South American species (as also noted Morrison, 1954: 367). The strong sculpture of examined *Doryssa* and the poor sculpture of the examined thiarids are not constant in each taxon, and exceptions, in both groups, are common.

The broad nephrostome of pleurocerids covered by a flap of pallial gonoducts is a distinctive character. Also, other interesting data is the chamber of inner lamina of pallial gonoducts (called seminal vesicle in male or bursa copulatrix in female), this character surely merits further investigation. This structure maybe is not a functional part of genital system, but so from excretory system, working as an ureter. In discordance with the use of this chamber as an ureter are: 1) its site (outer lamina of pallial gonoduct); 2) lack of direct connection between this chamber with kidney chamber, separated by a thin membrane (however, a similar thin membrane separates kidney chamber from ad-rectal sinus) and

3) presence of the nephrostome. On the other hand, what allow a function as an ureter of this chamber are the following data: 1) the presence, almost indistinguishable, in both sexes; 2) its development even in young specimens with remainder genital system until incipient; and 3) its anatomical disposition, connecting kidney chamber with region closer to mantle border (more developed in *Doryssa* than *Pachychilus*). Anyway, a similar structure is not found in any other studied gastropod beyond pleurocerids. This character was probably lost in *D. ipupiara*.

Woodart (1934) described the genital system of the pleurocerid *Goniobasis laqueata* (Say). The pallial oviduct of this species has a short and broad seminal receptacle, apparently in the same localization of the bursa of the examined species. The seminal receptacle nature of the structure of *G. laqueata* was confirmed histologically by that author, presenting sperms.

Family Turritellidae
Genus *Turritella* Lamarck, 1799
(Type species: *Turbo terebra* Linné, 1758)

Turritella hookeri Reeve, 1849
(Figs 20, 62, 97, 287-298)

Turritella hookeri Reeve, 1849 (pl. 11, fig. 61); Kobelt, 1897: 29 (pl. 6, fig. 11); Rios, 1970: 37 (pl. 9); Abbott, 1974: 95; Rios, 1975: 44 (pl. 12, f. 159); 1985: 46 (pl. 18, f. 206); 1994: 65 (pl. 22, f.248).

Description.

Shell (fig. 20). Of medium size (up to 40 mm), white, turriform. Protoconch of one whorl, smooth, glossy, carinate in periphery. Teleoconch up to 12 whorls, opaque, sculptured by two strong spiral threads and growth lines. Aperture simple, circular, without canal or projections. Other details in Reeve (1849).

Head-foot (figs 282, 283, 287, 298). Homogeneous pale beige in color. Head protruding, relatively small. Snout proportionally small, cylindrical, strongly bilobed in antero-ventral margin. Tentacles stubby, somewhat long. Eyes dark in outer region of tentacles' base, without ommatophore. Foot proportionally large, without divisions. Anterior furrow of pedal glands deep. Columellar muscle long, from 3 to 4 whorls. Food groove well developed, with thick walls, in median posterior region of floor of pallial cavity since its beginning, contours right side of head and finishes in median-ventral region of snout's base. Wall behind head very thick muscular.

Operculum (fig. 62). Circular, multispiral, corneous, nucleus central, occupies entire aperture, fimbriated edge. Muscle scar elliptic near inner margin.

Mantle organs (figs 285, 286, 294, 298). Mantle border of homogeneous pale beige color, entirely with small, uniform, relatively long papillae. Right insertion of mantle border very posterior, just in a richly muscular elevation behind head. Mantle cavity of almost three whorls. Osphradium difficulty visible, immerse in endostyle. Endostyle (figs 285, 286: f2) lies almost entire left margin of pallial cavity on ctenidial vein, anatomically leaned in food groove. Gill with about same length than cavity; filaments very tall, triangular, except in both extremities, where gradually become low; tip pointed. Relatively long posterior region of ctenidial vein free from gill. Between gill and rectum a relatively broad space. Hypobranchial gland white, thin, mainly developed in posterior 2/3 of cavity. Rectum broad and long. Anus siphoned, tall, posterior situated. A large fold from anus to near mantle border, perpendicular to this (fig. 286: f1). Pallial gonoducts long and narrow, compressed between rectum and right margin of mantle cavity, described below.

Circulatory and excretory systems (figs 284, 286, 294). Pericardial cavity posterior to kidney, connected to anterior region of style sac. Anterior and posterior aortas run attached to style sac. Anterior aorta very broad, runs parallel to esophagus up to buccal mass. Kidney short, situated in posterior-right limit of pallial cavity. Kidney with single lobe, color white, internally solid (without hollow chambers); bulges anteriorly to pallial cavity in a form of a tall elevation. Nephrostome a slit in median region of membrane between kidney and pallial cavity.

Digestive system (figs 284, 287-294). Mouth longitudinal and ventral, deeply introduced in snout antero-ventral furrow. Buccal mass very narrow, part within snout and part in head. Dorsal buccal mass wall with two inner longitudinal folds. Jaw plates very thin and transparent, situated in anterior region of dorsal folds. Odontophore small, with following distinctive features: 1) **m1** (jugal muscles) and **m10** pairs very developed in ventral margin, with broad fibers turned anteriorly and other narrower turned posteriorly (**m3d**); 2) **m2** absent; 3) **m4** with fibers no only connected to tissue on middle region of radular ribbon, but also with its posterior region and even with radular nucleus; 4) **m5** short, 5) **m8** and **m9** absent. Radula very short and narrow. Radular teeth (fig. 97): narrow, long, similar sized cusps in free margins of all teeth; rachidian tooth with 21 cusps in pointed cut edge; lateral tooth with about 16 cusp in each side of its pointed edge; marginal teeth rook-like, with about 20 cusps in each side of they free region; outer marginal tooth discretely more curved than inner one. Salivary glands small, posterior to nerve ring, ducts through it. Esophagus very long, narrow, thin walled. Esophageal inner surface with 2 almost vestigial crops, with oblique small folds (fig. 291). Right crop only visible in lateral region of a large fold. Left crop larger. Other posterior regions of esophagus only with low, well spaced, longitudinal folds.

Stomach (figs 284, 288) occupying about half a whorl, separates almost completely digestive-gonad glands from pericardial-pallial structures. Internally divided, by a constriction, into 2 chambers. Posterior chamber larger, bearing esophageal aperture at left and a large fold at right, this a central-pad-like structure which covers single duct to digestive gland; other regions smooth. Anterior chamber with smooth surface, two apertures as anterior limit connected with each other; larger that of style sac; smaller, at left, that of intestine. Style sac relatively large, about half of remainder stomach length, cylindrical, covered internally by yellowish iridescent chitin. Style present. Intestine (fig. 284) beginning opened to style sac, afterwards becoming a tube, contours to right side of style sac, crosses ventrally kidney and emerges in right side of pallial cavity. Rectum broad, bearing several fecal pellets obliquely disposed. Anus upper described. Digestive gland green, occupying about two whorls (keeps empty first shell whorls).

Genital system. Male (figs 285, 286). Testis small, in peri-columellar region of digestive gland. Vas deferens runs close to columella, white and narrow. In right side of posterior limit of pallial cavity, spermoduct suddenly expands, after short distance opens and becomes a groove with thick glandular walls (prostate); no differentiable inner structures. Sperm groove long, lies almost entire pallial cavity right margin, finishes posterior to anus.

Female (figs 283, 294, 295, 298). Ovary small, pale gray, in peri-columellar region of digestive gland. Oviduct white and narrow, runs close to columella. In right side of posterior limit of pallial cavity, oviduct suddenly expands and becomes a wide, thin walled tube (fig. 294). Bursa copulatrix a sac attached to inner ventral surface of posterior region of pallial oviduct, with narrow anterior aperture. Seminal receptacle similar to bursa, attached to inner dorsal surface, in opposite side of bursa. Capsule-albumen glands difficult in being separated one another, a small glandular mass covering receptacle and part of adjacent inner dorsal surface of oviduct. After a short distance, pallial oviduct opens, becoming a groove with very thin transparent walls, lies to region posterior to anus. Ovopositor in right region of head-foot, a transversal elevation of clearer colored muscles close to columellar muscle, and a nodular projection in same level, but near food groove (fig. 283).

Where pallial oviduct opens (fig. 294: ap), capsules exit and stay in pallial cavity. From 10 to 12 large capsules aligned along pallial cavity in mature females (fig. 298). Capsules compress greatly pallial structures, mainly gill, such filaments fit between capsules.

Capsules (figs 296-298). Proportionally large, diameter almost 1 mm, rounded, somewhat flattened. Covered by hard, yellow, glossy membrane (fig. 296). From 2 to 5 young specimens in each capsule having one whorl each (fig. 297). Some undeveloped eggs also commonly occur. Young specimens immersed in yellow jelly-like mucus.

Measurements (in mm). 19.5 by 5.1 (figured specimen); 24.0 by 6.6.

Distribution. From Rio de Janeiro to São Paulo continental slope.

Habitat. Sandy bottoms, from 10 to 156 m depth (MZSP 19417, only shells).

Material examined. Brazil; Rio de Janeiro; off Campos Bay (R. V. Astrogaroupa, sandy bottom); 22°35'47"S 41°55'01"W, 20 m, MZSP 28387, 1♂; 22°05'15"S 40°45"05"W, 35 m, MZSP 28388, 1♂ (23/vii/1991); 22°47'01"S 41°30'21"W, 57 m, MZSP 28389, 1♀ (iii/1992).

Remarks. The anatomy of *T. hookeri* differs from that of *T. communis* (cf. Randles, 1900; Johansson, 1946 and Fretter & Graham, 1962: 366, fig. 189) by having the bursa and receptacle closed; capsule gland thin; developed pallial food groove covering osphradium region; and ovopositor less developed. The brood strategy of *T. hookeri* - some large capsules aligned in pallial cavity, appears to be different from that of the Caribbean *T. variegata* L. (Flores & Macsotay, 1972). This species has external posture with almost one thousand small capsules. However, according to data by Houbrick (1988), the strategy of *T. hookeri* is the normal of the family.

Family Modulidae
Genus *Modulus* Potiez & Michaud, 1838
(Type species: *Trochus modulus* Linné, 1758)

Modulus modulus (Linné, 1758)
(Figs 21-24, 63, 98, 99, 299-313)

For synonymic list see Abbott (1944): 2. Complement:

Modulus modulus: Warmke & Abbott, 1961: 70 (pl. 11, fig. j); Rios, 1970: 41; Flores & Macsotay, 1972: 49; Abbott, 1974: 102 (fig. 976); Rios, 1975: 44 (pl. 12, f. 163); Houbrick, 1980a: 117-142; Oliveira et al., 1981: 98; Abbott & Dance, 1983: 63 (fig.); Rios, 1985: 48 (pl. 18, f. 217); Jong & Coomans, 1988: 43 (pl. 34, fig. 202); Leal, 1991: 361; Rios 1994: 61 (pl.21, f. 233);

Aplodon modulus: Morretes, 1949: 78.

Description.

Shell (figs 21-24). Turbinoid, heavy, umbilicated, described several times in literature (e.g., Abbott 1944: 2; Houbrick 1980a: 118-120 + figs 1 a-h). A considerable shell variation occurs, specimens from São Paulo coast (figs 21, 23) have nodes taller, more spaced, and external keel less developed than those of northern waters (figs 22, 24) (op. cit. and person. obs.). When broken, shell wall considerably thick, columella without folds, inner surface white in color with violet spot in upper regions of each whorl. Protoconch and other details in Houbrick (1980a: 119, figs 1d-h).

Head-foot (figs 299-301). Color pink in all anterior structures. Head protruding. Snout large, cylindrical, strongly bilobed anterior-ventral margin. Mouth longitudinal, cited deeply in snout furrow. Tentacles long, eyes dark, situated about in its middle region on small ommatophores. Foot relatively large, without divisions, with deep anterior furrow of pedal glands. Musculature around haemocoel dorsally thick (fig. 300), outer layer of oblique muscle fibers, two very thick middle layers of radial muscle fibers, and an inner layer of circular fibers around haemocoel; another thin layer of circular fibers between outer and middle muscular layers in region of columellar muscle. Columellar muscle of about half whorl; anterior-right third with a thickness of fibers obliquely disposed; in posterior third suddenly become thin. Female ovopositor described below. Other details in Houbrick (1980a: 120-121, fig.2).

Operculum (fig. 63). Circular, corneus, palcispiral to multispiral, occupies almost entire aperture, nucleus central.

Mantle organs (figs 302, 303, 306). Mantle border pink in color, entirely papillated, papillae not uniform in size; left border thick muscular. Mantle cavity of almost one whorl. Osphradium ridge-like, in situ with about same length than gill, but longer than gill if straightened; anterior osphradium region with a zigzag. Gill very long, almost same length than pallial cavity, filaments triangular, narrow, very tall. Between gill and rectum a proportionally broad area with hypobranchial gland well-developed, color pink, bearing several transversal chambers and several apertures in surface, finishes near anus. Rectum and genital ducts described below. Anus siphoned, posterior in cavity. Other details of mantle organs in Houbrick (1980a: 121-124, figs. 1 a-d).

Circulatory and excretory systems (figs 305, 306). Heart large, similar to those described for preceding species. Aorta runs attached to style sac. All examined specimens with pericardium filled by a hard greenish transparent substance resembling a cartilage consistence, its dissection is necessary for heart exposure. Kidney short, about 1/10 whorl, with single lobe, white in color, solid, without chambers. Nephrostome slit-like in middle region of wall between kidney and pallial cavity. Other details in Houbrick (1980a: 132).

Digestive system (figs 302-313). Buccal

mass posteriorly situated, almost outside of snout; around mouth aperture a very strong, thick layered circular muscle. Jaws in two tapered plates in dorsal wall of buccal mass, just where 2 strong, broad, tall parallel and longitudinal folds begin, run in dorsal inner surface posteriorly; in anterior esophagus right fold gradually faints, left fold continues in middle esophagus (fig. 307). Odontophore similar to those of preceding species, with following distinctive characters (figs 310-313): 1) radular ribbon short; 2) **m8** very short, broad, with almost same width than radula; 3) **m11** pair originating in posterior region of inner surface of subradular membrane (near radula), runs anteriorly with small connection in m7 and large connection in peribuccal wall; 4) a pair of small and narrow muscles originating in median-dorsal region of m4 and running ventrally as part of m7; 5) **m7** with four components in origin (two from m11 and two from m4), and 3 connected diverticles from radular sac; 6) **m10** posteriorly inserted, near m4; 7) ligament of radular sac with inner-anterior surface of horizontal muscle; 8) horizontal muscle (**m6**) long, almost same length than cartilages. Radular teeth (figs 98, 99): rachidian with somewhat rounded outline, with 5 cusps being central cusp larger (about double); lateral tooth with 4 or 5 cusps, second cup larger; marginal teeth spoon-like, with rounded terminal cusps, inner and outer marginal teeth very similar with each other. Both salivary glands extend through nerve ring, bearing glandular tissue anterior and posterior to it (fig. 308). Esophagus broad and complex (figs 307-309). A tall fold initiated in inner dorsal wall of buccal mass, divides dorsally anterior and middle esophagus in two broad pouches, right pouch longer; both generally with several oblique, uniform folds, but some variation occurs, these folds can be, in some specimens, longitudinal or concentric; separating ventrally each pouch a space with none, or up to three marrow and low longitudinal folds. Tall dorsal fold, in some specimens, with a deep median furrow in its middle region, being practically a third short pouch, internally some longitudinal low folds. Posterior esophagus a simple tube with smooth inner surface. Stomach (figs 304, 305) large; well developed folded dorsal sorting area; central pad-like fold small, flattened and thin; aperture of esophagus and digestive gland as showing in fig. 304, at left of this fold; short smooth chamber preceding aperture of style sac and intestine. Style sac long, with style, separated from intestine. Intestine origin close to style sac aperture, dorsal to it, contours left-ventral side of style sac, with single loop return to anterior; in right posterior limit of pallial cavity suddenly expands becoming very wide rectum with compacted fecal pellets obliquely disposed. Anus siphoned, posterior situated in cavity (fig. 302). Digestive gland begins in middle-ventral region of stomach and runs posteriorly two whorls more. Other details of digestive system in Houbrick (1980a: 124-127).

Genital system. Male (figs 302, 305, 306). Testis in several lobes dispersed in ventral and outer regions of digestive gland and stomach, touching kidney when developed. Vas deferens white, broad, with thick walls, running close columella; several consecutive secondary branches, each one coming from a lobe; between rectum and right posterior limit of pallial cavity, vas deferens opens, becoming a simple groove with thick glandular walls.

Female. Pallial oviduct very similar to that figured by Houbrick (1980a:130, fig. 8b), a small posterior region closed occurs in examined specimens; bursa and receptacle have a larger closure degree. Other details of genital system in Houbrick (1980a: 127-131). Ovopositor (fig. 299) a bulbous, swollen flap with thick glandular walls and a central longitudinal furrow (see Houbrick, 1980a: 121, fig. 2b). Female MZSP 24995 presents two spermatophores within pallial oviduct, very similar to that described by Houbrick (1980a: 128, figs. a-b).

Measurements (in mm). MZSP 28258: 12.0 by 13.1; 10.1 by 13.0; 8.9 by 10.8; MZSP 28257: 8.3 by 11.2 (figured specimen); 14.7 by 13.7).

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

Habitat. Intertidal or upper infratidal rocks, moving on algae, in regions with waves of low energy.

Material examined. Venezuela; Nova Esparta; Margarita Island, Porlamar, Guaraguao Bay, Vella Vista beach, 6 specimens, MZSP 28257 (Simone col. 6/ii/1995). Brazil; Alagoas; Maceió, Sete Coqueiros Beach, 1 specimen, MZSP 24992 (Montouchet col., 19/ix/1970); Rio de Janeiro; Cabo Frio, Conchas Beach, 1 specimen, MZSP 24995 (Marini col., 6/i/1973); São Paulo; Ilha Bela, Central beach, 48 specimens, MZSP 28258 (Simone col., v/1994); Barra Velha, 1 specimen observed alive, MZSP 28698 (Simone col., 27/x/1996).

Remarks. Although the specimens from Caribbean present in the shell some differences with those from Brazil (figs 21-24), they have uniformity of the inner anatomical characters. A separation in specific level is then poorly recommended. *M. modulus* differs anatomically from *M. candidus* Petit (cf. Risbec, 1927, figs 26, 27) in having esophagus not so broad and its insertion not near from intestine origin.

Family Cerithiidae
Genus *Cerithium* Bruguière, 1789
(Type species: *C. nodulosum* Bruguière, 1789)

Cerithium atratum (Born, 1778)
(Figs 25, 26, 67, 100, 101, 314-328)

Synonymy see Marcus & Marcus (1964: 497), Houbrick (1974: 54). Complement:

Cerithium atratum: Morretes, 1949: 79; Rios, 1970: 42 (pl. 9); Abbott, 1974: 104 (fig. 992); Rios 1975: 47 (pl. 13, f. 172); Oliveira et al., 1981: 101; Abbott & Dance, 1983: 66 (fig.); Leal, 1991: 360.

Cerithium (Thericium) atratum: Rios, 1985: 49 (pl. 19, f. 220); 1994: 62 (pl. 21, f. 235)

Description.

Shell (figs 25, 26). Described by Kobelt (1898: 192), Marcus & Marcus (1964: 497-498), Houbrick (1974: 54) and others.

Head-foot (figs 314, 315, 319, 320). Color dark brown spots sparse in integument, sometimes very intense, inclusive pedal sole. Snout relatively very large, dorso-ventrally flattened, bilobed anterior margin. Tentacles relatively short (about half of snout length), each with a small ommatophore in outer region of its base. Eyes dark, small. Female with ovopositor in right region of foot described below. Operculum (fig. 67) with sub-terminal nucleus. Other characters see Marcus & Marcus (1964: 498-500). Several specimens with a broad furrow in middle region of columellar muscle (fig 315: hl)

Pallial cavity (figs 317, 318, 321). Mantle border entirely with single lined, similar sized small papillae. Osphradium bipectinate, very long, with about same gill length, two regions differentiable: anterior half broader and somewhat sinuous, posterior half narrower. Osphradium in transversal cut with a longitudinal narrow axis and several very small rounded leaflets, disposed intercalated (fig. 318). Mantle, in siphonal region, with thicker walls. Fold anterior to gill, perpendicular to border, forming a septum (h2). Gill very long, narrow, filaments tall, triangular, tip pointed, finishes before posterior limit of cavity. Other characters in Marcus & Marcus (1964: 500-501).

Circulatory and excretory systems (fig. 321). Heart as described for preceding species, anterior and posterior aortas attached to style sac and intestine. Kidney with single lobe. A well developed posterior renal vessel from which several transversal secondary vessels begin within glandular white tissue. A thickness of glandular tissue around its wall with pericardium. Pallial region of kidney solid, with radial furrows. Nephrostome a single slit in middle region of wall between kidney and pallial cavity.

Digestive system (figs 319-328). Buccal mass in anterior half of snout. Jaws of considerable size, from which two dorsal folds begin, run longitudinally in dorsal inner surface of buccal mass; aperture of salivary glands in they middle region. Odontophore (figs 326-328) similar to described for preceding species, distinctive features: 1) **m8** absent; 2) **m2** narrow and with some anterior fibers inserted in m4; 3) **m11** not inserted in cartilages, and neither in anterior region of peribuccal wall; 4) **m7** with origin part in m11 and part in adjacent region of subradular membrane; 5) **m5** somewhat narrow and anteriorized. A pair of dark spots in dorsal region of cartilages (figs 322, 325: ds), remainder of cartilages white. Radular teeth (figs 100, 101): rachidian tooth short and broad, with 5 cusps, central cusp very larger (about three times the neighbors) and a low, triangular, central, basal projection; lateral tooth with 5 cusps being second cusp very larger, more than 3 times the neighbors; marginal teeth spoon-like, with a rounded cut-edge and two small cusps in inner region of this edge; inner and outer marginal teeth very similar with each other. Left salivary gland small, attached to posterior region of nerve ring, right salivary gland long, large, begins in right-posterior side of nerve ring, towards left and runs in left side of middle esophagus (figs 319, 320).

Ducts of salivary glands large, run through nerve ring, attached to dorsal wall of anterior esophagus until above cited aperture in buccal mass. Esophagus complex shaped (figs 322, 323), with two longitudinal lateral pouches bearing several transversal, somewhat uniform folds. In anterior esophagus these pouches are ventral, after nerve ring they twist and become dorsal. In opposite side of these pouches two low longitudinal folds. No visible glands in inner esophageal surface. Posterior esophagus simple, without folds. Stomach (fig. 324) very large and complex (Marcus & Marcus: 504-505, fig. 6; Houbrick, 1974: 44, fig, 15); esophagus opens near intestine-style sac origin; central pad very large, almost touching posterior limit of stomach, somewhat free, only attached in ventral gastric surface by a longitudinal thin lamina; gastric shield and dorsal sorting area well developed; a small ring-like fold, continuous with anterior region of central pad, separate two gastric chambers, a larger and posterior, which bears most gastric structures, and other small and anterior, with smooth surface, preceding style sac-intestine apertures; crescentic ridge absent or only visible in left-posterior region of central pad as an annex fold (fig. 324: cr). Intestine and style sac united by a longitudinal aperture of almost their entire dorsal region; but this connection is maintained closed. Style sac long, style present. Intestine, after separated from style sac, contours its posterior region, runs newly anteriorly in dorsal region of style sac where presents two loops in M-shape (figs 321, 324), maintained in this position by small muscle fibers between intestine and style sac. Rectum very broad, with successive oblique folds (fig. 317). Fecal pellets oblique, compacted. Anus siphoned. Other details of digestive system in Marcus & Marcus (1964: 502-505).

Genital system. Male organs described by Marcus & Marcus (1964: 505-506, fig. 8). Open pallial spermoduct very long (fig. 317).

Female organs also described by Marcus & Marcus (1964: 506-507, figs 9-11). It is interesting to note presence of seminal receptacle and a bursa copulatrix; albumen gland introduced in ventral wall of kidney chamber, in some specimens this gland compress greatly kidney tissue. Ovopositor (figs 315, 316) in right-dorsal side of foot, bearing two parallel folds; posterior fold narrow and long; anterior fold shorter and broader in its distal end; between both folds a deep furrow.

Nervous system. Nerve ring as described by Marcus & Marcus (1964:501-502, fig.3), situated posteriorly in esophagus, removed from buccal mass (fig. 320).

Measurements (in mm). MZSP 28259: 35.3 by 14.7 (figured specimen); 35.8 by 15.3; 38.0 by 15.0.

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

Habitat. Intertidal or low infratidal, moving on mud or muddy sand bottoms, generally among rocks.

Material examined. Brazil; Pernambuco; Ponta das Pedras, 14 specimens, MZSP 28261 (Montouchet col, 30/viii/1970). Bahia; Salvador, Ribeira beach, 12 specimens, MZSP 28472 (Simone col., 27/ii/1997). São Paulo; Ubatuba, Enseada das Palmas, 51 specimens, MZSP 28259 (28/ii/1962); Base Norte IOUSP, 14 km SW downtown, 23°57'S 45°06'W, 43 specimens, MZSP 28260 (Marcus & Marcus col., ii/1964) (lot studied by Marcus & Marcus, 1964); São Sebastião, São Francisco beach, 1 specimen observed alive, MZSP 28349 (25/x/1996, Simone col.); Alcatrazes Island, Porto dos Faroleiros, 1 specimen observed alive, MZSP 28324 (01/xii/1996, Simone col., Projeto Alcatrazes).

Genus *Bittium* Leach in Gray, 1847
(Type species: *Strombiformis reticulatum*
daCosta, 1778)

Bittium varium (Pfeiffer, 1840)
(Figs 27, 28, 48, 64, 78, 102, 103, 329-344)

Cerithium varium Pfeiffer, 1840: 256-257.

Cerithium gibberulum C. B. Adams, 1845: 5; Reeve, 1865 (pl. 18, fig. 123).

Cerithium (Bittium) gibberulum: Smith, 1890a: 291; Kobelt, 1898: 245 (pl. 43, fig. 1).

Bittium varium: Dall, 1889a: 258; 1889b: 140; Morretes, 1949: 79; Warmke & Abbott, 1961: 73 (pl. 13, fig. h); Marcus & Marcus, 1963: 74-91 (f. 77-95); Rios, 1970: 43; Houbrick, 1977: 104 (f. 4-5); Rios, 1985: 51 (pl. 19, f. 229); Jong & Coomans, 1988: 44 (pl. 15, fig. 212); Rios, 1994: 63 (pl. 21, f. 238).

Diastoma varium: Abbott, 1974: 107 (fig. 1037); Rios, 1975: 49 (pl. 13, f. 179).

Description.

Shell (figs 27, 28, 48). Small (up to 10 mm) slender, turriform, up to nine whorls. Periostracum opaque, yellowish, transparent. Two first whorls smooth (fig. 48), gradually axial and spiral threads appear, both predominating; in they intersection small nodes; these nodes generally paler than remainder shell and variable in size according to specimen, in some specimen very small nodes, in other very large nodes, long in spiral axis and sometimes coalescent. Spiral threads varying from 4 to 4 in penultimate whorl. A large axial thread generally present in dorsal region of last whorl. Outer lip deflected, canal small. Color clear beige with brown spots scarce and sparse; in some specimens these spots greater; sometimes entire shell dark brown. Other details see Marcus & Marcus (1963: 74-76). When decalcified, inner chitinous layer visible, pale brown, transparent (fig. 335: ic).

Head-foot (figs 329, 330, 332, 333). Pigmented by a mosaic of dark spots, sometimes coalescent, inclusive in pedal sole. Head protruding. Snout sub-cylindrical, relatively small (about 2/3 of tentacles length), bilobed anterior margin. Tentacles long, with dark eyes in they base without ommatophore. Foot very large, about 1/3 whorl, two parallel low furrows run between mesopodium and metapodium. A deep longitudinal furrow in posterior half of mesopodian sole. Female with a well developed ovopositor in right side of foot described below. Columellar muscle of about one whorl. Other details see Marcus & Marcus (1963: 76-78, fig. 80).

Operculum (fig. 64). Yellowish, semi-transparent, circular, palcispiral, sub-central nucleus, occupies almost entire aperture. Scar broad, circular, near inner margin.

Pallial organs (figs 331, 334, 335). Mantle border flanged by short, broad, flattened papillae. Pallial cavity of about 1.5 whorls. Osphradium of about same length than gill, pectinate, brown pigmented. Satellite osphradium fold thin, white, surrounds anterior limit and both sides of it; about same length than osphradium in each side. Gill long, begins at some distance from mantle border, filaments triangular, somewhat tall. Between gill and rectum a relatively narrow space. Hypobranchial gland thin, in posterior half of this space. Rectum and genital ducts in right margin, described below. Anus siphoned relatively posterior of mantle edge. Other details in Marcus & Marcus (1963: 78-80, fig. 88).

Circulatory and excretory systems (fig. 334). Heart large, with characters similar to those of preceding species. Kidney white in color, short (about 1/12 whorl), with single lobe. Lobe solid, flattened between style sac and pallial cavity. Nephrostome small, near right region of membrane between kidney and pallial cavity.

Digestive system (figs 78, 332, 334, 337-344). Mouth longitudinal, situated within snout anterior furrow. Jaws (fig. 78) two proportionally large and broad plates. Buccal mass relatively posterior in snout. Inner surface of dorsal wall of buccal mass with two longitudinal folds (fig. 339), beginning in jaws; very broad in middle region presenting each one a median longitudinal furrow. Odontophore (figs 342-344) similar to those of preceding species but short, with horizontal muscle very broad and short; radular sac short ventrally attached to dorsal wall of esophagus; m11 connected with anterior region of cartilages and running only to m7, without connection with peribuccal region. Radular teeth (figs 102, 103): rachidian tooth with 7 and sometimes 9 cusps being central cusp larger, a small long projection in each side of its base; lateral tooth with 5 cusps being second cusp larger; inner marginal tooth rook-like, with 5 cusp in each side of its free region; outer marginal tooth similar to inner marginal but narrower. Salivary glands posterior-dorsal to nerve ring, with ducts running through nerve ring and inserting in dorsal wall of buccal mass. Anterior esophagus with 4 folds, ventral folds larger, originate from folds of dorsal wall of buccal mass; pigmented by brown, easily seen by transparency (fig. 338). Middle esophagus with 4 similar sized folds, twisted in relation to anterior esophagus. No apparent glands in esophagus. Stomach (figs 340, 341) as described by Marcus & Marcus (1963: 81, fig. 83) with well developed dorsal sorting area; gastric shield protruding; central pad small; crescentic ridge similar to central pad, subcircular and posterior to it; style sac short (about 1/4 of stomach length), connected with intestine by a furrow; style present. Rectum relatively short and narrow, with several fecal pellets obliquely disposed. Other details of digestive system in Marcus & Marcus (1963: 82-87).

Genital system. Male (figs 334, 336).

Spermoduct relatively broad, color white, walls thick, running close to columella. In right region of pallial cavity, beside rectum, becomes an open groove with thick glandular walls (prostate).

Female. Pallial oviduct very large (when developed), described by Marcus & Marcus (1963: 89, fig 87), with 2 receptacles in inner lamina and one bursa in outer lamina. Ovopositor (fig. 333) a large flap in dorsal right region of foot, with a longitudinal middle furrow originated from pallial cavity right floor, and becoming deeper anteriorly. Other details of genital system in Marcus & Marcus (1963: 87-91).

Measurements (in mm). 5.2 by 2.1; 4.3 by 1.8 (figured specimens).

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

Habitat: Generally moving on algae, intertidal and infratidal levels. Sometimes are found crawling on rocks and corals.

Material examined. Brazil; Rio de Janeiro; Angra dos Reis, Leste Beach, 60 specimens, MZSP 25146 (18/vii/1966); São Paulo; Ubatuba, Andorinhas Beach, 6 specimens, MZSP 28251 (22/i/1963); São Sebastião, Barequeçaba beach, 6 specimens observed alive, MZSP 28613 (16/v/1997, Simone col.); Guaecá beach, 4 specimens observed alive, MZSP 28635 (17/v/1997, Simone col.).

Family Diastomatidae

Genus *Finella* A. Adams, 1869

(Type species: *C. pupoides* A. Adams, 1860)

Finella dubia (Orbigny, 1842)

(Figs 29, 30, 49, 65, 66, 104, 105, 345-361)

Chemnitzia dubia Orbigny (in Sagra), 1842: 226 (pl. 17, figs 4-6); 1846: 398.

Bittium (?) yucatecanum Dall, 1881: 90.

Alaba cerithiidioides Dall, 1889a: 258.

Bittium (Alabina) cerithioides: Morretes, 1949: 79.

Alabina cerithiideoides: Warmke & Abbott, 1961: 73 (pl. 13, fig. b).

Finella dubia: Abbott, 1974: 108 (fig. 1039); Rios, 1975: 49 (pl. 13, f. 182); 1985: 52 (pl. 19, f. 230); Jong & Coomans, 1988: 45 (pl. 15, fig. 213); Rios, 1994: 63 (pl. 21, f. 241).

Description.

Shell (figs 29, 30, 49). Small (up to 10 mm), slender, turriform, up to 9 whorls. Color generally pale beige with brown apex; sometimes entirely brown. Sculpture thin axial regular ridges; in first whorls spiral sculpture also present, but more insipid than axial ones, gradually faint; some specimens with a stronger spiral ridge in periphery of first whorls, almost a carina, with nodes in intersection with axial ridges. Strong and broad axial thread sometimes present, rarely up to three per specimen. Periostracum opaque, yellowish, transparent. When decalcified, inner chitinous layer present, pale brown, transparent (fig. 348: ic). Aperture simple, elliptical, canal weak.

Head-foot (figs 345, 346, 350). Pigmented by dark brown spots in head, tentacles and lateral region of foot; most part pale beige. Head protruding. Snout sub-cylindrical, relatively small (about half of tentacles length), bilobed anterior margin. Tentacles long, with dark eyes near they base without ommatophore. Foot large, without visible divisions except a shallow furrow between sole and dorsal regions; an evident anterior flap (j1), in its border a furrow of pedal glands. A deep longitudinal furrow in posterior half of sole. No ovopositor developed. Columellar muscle of about 1.5 whorls.

Operculum (figs 65, 66). Similar to that of *B. varium*.

Pallial organs (figs 347, 348, 351). Mantle border flanged by short, broad, flattened papillae, narrower in siphon region. Pallial cavity of about 1.5 whorls. Osphradium long, discretely shorter than gill; ridge-like, with some sparse constrictions; brown pigmented. Satellite fold around osphradium, broad in its anterior half, gradually narrows in both sides in posterior half, which have about same osphradium length; color white. Gill somewhat long, begins at some distance from mantle border, filaments rectangular and low. Between gill and rectum a relatively broad space when genital ducts run. Rectum narrow, near right margin of cavity (but not in extremity), dorsal to genital ducts, bears fecal pellets somewhat spherical, not obliquely compacted. Anus siphoned, posterior from mantle border.

Circulatory and excretory systems (figs 350, 351). Very similar to those described by *B. varium*.

Digestive system (figs 348-358). Mouth and buccal mass similar to those of *B. varium*. Two broad dorsal inner folds of buccal mass (fig. 349), each one with a middle longitudinal furrow in their posterior region; these folds continue in anterior esophagus by a short distance; they suddenly finish broad and flattened. Odontophore (figs 353-355) also similar to that of *B. varium*, but shorter, with odontophoral cartilages somewhat circular and m11 not connected to cartilages. Radular teeth (figs 104, 105): rachidian tooth narrow and tall, with 9 cusps being central cusp larger, no basal projections or cusps; lateral tooth with 9 cusps being second larger and terminal; marginal teeth rook-like, inner marginal tooth with 6 small cusps in each side and a sharp terminal larger cusp; outer marginal tooth without distinguishable cusp. Salivary glands small, posterior to nerve ring. Middle and posterior esophagus without inner glands or folds. Stomach (figs 356, 357) also similar to that of *B. varium*, with short style sac and crescentic ridge subcylindrical; but with dorsal sorting area having fewer folds, and proximal intestinal region dark colored (fig. 358: ds). Intestine with single loop in right side of style sac. Rectum somewhat narrow (described above). Digestive gland with more than four whorls posterior to stomach (fig. 348).

Genital system. Gonad in both sexes occupying superior region of digestive gland (fig. 348). Male (fig. 359): pallial spermoduct broad, white in color, thick glandular, opened at almost all its length. Female (figs 348, 351, 360, 361): pallial oviduct very broad, almost all opened; outer lamina simple, thick glandular; inner lamina also thick; bursa copulatrix of considerable size in middle region of outer lamina, immerse in its wall, with a narrow anterior aperture. No other structures. No ovopositor.

Measurements (in mm). 3.7 by 1.4; 4.5 by 1.6 (figured specimens).

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

Habitat. similar to that of *B. varium*, but appears to occur deeper.

Material Examined. Brazil; São Paulo; Ubatuba, Andorinhas Beach, 40 specimens, MZSP 25111 (IOUSP, 22/i/1963).

Remarks on B. varium and F. dubia. Finella dubia differs anatomically from *Bittium varium* in having 1) foot smaller and simpler (without furrows); 2) osphradium not clearly pectinate; 3) gill smaller; 4) fecal pellets longitudinal (not obliquely compacted) in rectum; 5) dorsal sorting area in stomach less developed; 6) ovopositor absent. Although, both species have the following similarities if compared with other studied cerithioideans: 1) small size; 2) inner chitinous layer of shell; 3) relatively small snout; 4) intestine with similar loops and rectum narrow; 5) crescentic ridge of stomach short and rounded; 6) posterior-median furrow of foot sole; 7) style sac short; 8) anterior-dorsal region of stomach and proximal intestine dark pigmented; 9) satellite fold around osphradium. These characters, some of them clearly synapomorphies, indicate a close relationship between both species. *B. varium* appears to be better regarded as Diastomatidae, rather than Cerithiidae. However, further studies, mainly on type species of each taxon, are necessary for a definitive systematic placements.

F. dubia differs anatomically from *Diastoma melanoides* (Reeve) (cf. Houbrick, 1981c) in having less mantle border papillae, snout smaller, operculum with nucleus more central, radular lateral tooth with more and smaller cusps, radular marginal teeth rook-like and salivary glands short. On the other hand, the pallial oviduct and stomach are similar. Houbrick (1981c) brings interesting discussion on systematic relationship of the diastomatids, referring a close placement to the Cerithiidae, Potamididae and Melanopsidae.

F. dubia differs considerably in anatomical characters from *F. pupoides* Adams, 1860 and from *F. purpureoaplicata* Preston, 1905 (Ponder, 1994). *F. dubia* lacks so developed pallial tentacles, so extensible snout and accessory structures of posterior region of pallial oviduct. These data show that a new revaluation of the generic attributions must be taken into consideration. However, *F. dubia* is maintained in *Finella* until a revision study of these taxa.

On the other hand, *B. varium* and *F. dubia* have similarity with *Diala* sp (Ponder, 1991), in shell shape, operculum, radular features, presence of large osphradium satellite fold, and central pad and crescentic ridge similar sized ("gastric folds" in fig. 8). Ponder (1991) pointed out a close relationship of *Diala* with the litiopids, and suggested a possible family rank, Dialidae.

Family Litiopidae

Genus *Alaba* H. & A. Adams, 1853

(Type species: *Rissoa melanura* C.B. Adams)

Alaba incerta (Orbigny, 1842)

(Figs 68, 80, 106, 107, 362-376)

Eulima incerta Orbigny (in Sagra), 1842: 218 (pl. 26, figs 7-9).

Rissoa tervaricosa C. B. Adams, 1845: 6.

Cerithium melanura C. B. Adams, 1850: 116.

Alaba tervaricosa: Smith, 1890b: 320; Dall, 1889a: 258; 1889b: 146: Morretes, 1949: 78.

Alaba incerta: Warmke & Abbott, 1961: 74 (pl. 13, fig. r); Rios, 1970: 44; Robertson, 1971: 51 (pls. 2-3); Abbott, 1974: 110 (fig. 1121); Rios, 1975: 49 (pl. 13, f. 181); 1985: 51 (pl. 19, f. 227); Houbrick, 1987b: 9-17 (figs. 1-3, 5, 7, 10-12, 15-20); Jong & Coomans, 1988: 45; Leal, 1991: 360; Rios, 1994: 63 (pl. 21, f. 240).

Description.

Shell. Small (up to 15 mm), turriform, thin, white, up to 12 whorls. Protoconch of four whorls, first whorl smooth, others with numerous axial riblets; anal slit present (see also Robertson, 1971: 51, pls. 2-3; Houbrick, 1987b: 12, fig.10). Periostracum transparent, thin. Teleoconch with convex whorls, deep suture. Sculpture six to seven spiral, low and broad furrows. Last whorl with none or up to 4 strong axial threads. Aperture ample, elliptical, simple, canal weak; outer lip generally thick. No inner chitinous layer detectable. Other details in Houbrick (1987b: 10, figs 10-11); Rios (1994).

Head-foot (figs 362-366). Homogeneous pale cream in color, without spots. Head protruding, somewhat broad. Snout short but broad, dorso-ventrally flattened, bilobed anterior margin. Tentacles very long (more than double of snout length), slender. Eyes dark, proportionally small, near tentacles base, without ommatophore. Foot somewhat large; a furrow of pedal glands in anterior margin; its superior margin extends beyond foot limit in both sides as a pair of propodial tentacles. Other furrow of pedal gland in median-posterior region of foot sole, longitudinal, finishes before posterior foot margin. Epipodium present, lying lateral-dorsal region of foot and inner opercular surface (fig. 365); epipodial edge entire with tentacles; those of lateral region longer and larger, three or four in each side; those tentacles around operculum shorter, lobed, being two posterior discretely larger. Female with ovopositor described below. Columellar muscle of about one whorl. Other details in Houbrick (1987b: 10-11, figs 2-3).

Operculum (figs 68, 364). Elliptical, corneus, yellowish, semi-transparent; nucleus excentric, near inferior margin. Muscle scar proportionally small, sub-elliptical, close inner margin; surrounded externally by a well-developed ridge (fig. 364: k3). Most part of operculum free, only leaned on epipodium dorsal surface. Other details see Robertson (1971, pl. 4, f. 16) and Houbrick (1987b: 10-11, fig. 1).

Mantle organs (figs 369, 370, 376). Mantle border smooth, somewhat thick, white. Mantle cavity of about 1.5 whorls. Osphradium long, about 2/3 of gill length, pectinate, low; anterior extremity more anterior than that of gill; posterior region clearly narrower. Satellite fold of osphradium present, low, running left, anterior and right sides of osphradium; finishes posteriorly more or less where osphradium also finishes. Anterior half of osphradium and satellite fold somewhat parallel to mantle border, at some distance of this (except anterior extremity, which arrives close to mantle border). Gill very long, about same length than pallial cavity, narrow; bears several long, tall, triangular filaments; tip of each filament sharp, somewhat central. Ctenidial vein narrow, slight uniform width. Between gill and rectum a relatively narrow area. Hypobranchial gland thin. Rectum narrow, edging left margin of pallial gonoducts; internally some fecal pellets obliquely disposed. Anus siphoned, near mantle border. Gonoducts running in right margin commented below. Other details in Houbrick (1987b: 13).

Circulatory and excretory systems (figs 370, 376). Heart characters and site similar to those of preceding species, aortas attached to style sac. Kidney short, about 1/6 whorl; internally a solid, white tissue compressed between rectum and pericardium in anterior half, and between rectum and stomach in posterior half. Nephrostome a small slit in middle region of membrane between kidney and pallial cavity.

Digestive system (figs 366-368, 371-376). Mouth in anterior and ventral region of snout furrow, longitudinal, thickly muscular. Buccal mass posterior to snout. Jaws (figs 80, 367) two somewhat large plates, yellowish, with medial cut edge. From jaws two broad folds begin (fig. 367). Both folds of inner surface of dorsal wall of buccal mass run longitudinally to esophagus; both folds broader in middle region, just where present a longitudinal, central furrow each, in such anterior extremity duct of salivary glands opens. Odontophore (figs 371-373) broad and short, with following distinctive features: 1) **m2** pair very thin and narrow; 2) a flap of solid tissue on middle region of radula (to); 3) **m4** and **m5** short and anteriorly inserted in radular ribbon; 4) pair of m5 united one with other in a larger degree; 5) **m11** pair somewhat broad, without connections in cartilages, continues in m7; 6) **m7**, beyond its origin in m11 pair, also part originated in subradular membrane; 7) some ligament of radular sac anterior extremity in inner surface of horizontal muscle. Radula short, with radular sac dorsal surface connected with ventral surface of membrane that covers buccal mass, but without development of muscle m8. Radular teeth (figs 106-107): rachidian tooth broad, with 5 cusps being central cusp larger, and 2 basal, lateral, low projections; lateral tooth with 4 or 5 cusps being second cusp larger; inner marginal tooth rook-like with 2 or 3 small cusps in each side of a larger terminal cusp; outer marginal tooth similar to inner one but narrower. Esophagus somewhat short and broad. Anterior esophagus with a pair of broad folds in a side, continuation from those of buccal mass (fig. 367). Middle esophagus with a pair of narrow longitudinal folds, close one another (both continuations from those of anterior esophagus), and several transversal, narrow folds, differentiating an esophageal pouch. Posterior esophagus narrow, marked by a sudden change of pouch folds from transversal to longitudinal; becomes a simple tube with 6 to 7 longitudinal, similar sized folds. Stomach (figs 370, 374-376) somewhat short, about 1/3 whorl, but broad. Central pad short, rounded, situated in middle-right region of stomach ventral surface; covers ventrally a well-developed gastric shield. Crescentic ridge broad, arched, situated in posterior region of central pad, from which has a similar size. Duct to digestive gland situated in left insertion of crescentic ridge in central pad, just where begins a fold which divides transversally inner space of stomach. Esophagus aperture anteriorized, at left of anterior gastric chamber and near intestine origin; from esophageal aperture two ventral parallel folds begin, both run posteriorly and finish in transversal fold; from esophageal aperture other fold begins and runs dorsally parallel to transversal fold. Dorsal sorting area only differentiable by two or three transversal narrow folds in anterior region. Intestine and style sac apertures connected one with other. Style sac broad, short (less than half of remainder stomach), with style. Intestine connected to style sac in almost its entire left side, but separated by a constriction (fig. 376). Intestine contours style sac from left to right side, after another loop turned anteriorly. Rectum and anus described above. Other details of alimentary tract in Houbrick (1987b: 13, fig. 12).

Genital system. Both, male and female, described by Houbrick (1987b: 13, fig. 5). Male with open pallial spermoduct. Female (fig. 370) with open, thick pallial oviduct; lateral lamina with seminal receptacle in its posterior border; inner lamina with bursa copulatrix in its posterior border and a sperm groove in remainder border. Ovopositor (fig. 363) a small lobe near central region of right foot margin, edged posteriorly by a furrow, this furrow runs dorsally since pallial oviduct aperture (see also Houbrick, 1987b, fig.3).

Measurements. MZSP 28386 length 6.8 mm; width 2.6 mm.

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

Habitat. On algae and gravel, infratidal level.

Material examined. Brazil; Rio de Janeiro; off Campos bay, 21°40'12"S 40°37'30"W, 16 m, sandy bottom, 1♀, MZSP 28386 (R.V. Astrogaroupa).

Remarks. Interesting and useful comparison of litiopids, among cerithioideans, is found in Houbrick (1987b: 16-17). Although presenting several differences proper of the family, that author pointed out some similarity of litiopids with cerithiids.

Family Batillariidae

Genus *Batillaria* Benson, 1842

(Type species: *Cerithium zonalis* Bruguière, 1792)

Batillaria minima (Gmelin, 1791)

(Figs 32-39, 69, 108, 377-389)

Synonymy see Bequaert, 1942: 7-8. Complement: *Batillaria minima:* Warmke & Abbott, 1961:72 (pl.

13, fig. v); Rios, 1970: 42; Abbott, 1974: 103 (fig. 990); Rios, 1975: 52 (pl. 14, f. 195); Abbott & Dance, 1983: 63 (fig.); Rios, 1985: 49 (pl. 19, f. 219); Jong & Coomans, 1988: 44 (pl. 33, fig. 206); Rios, 1994: 64 (pl. 21, f. 244).

Description.

Shell. The high degree of shell variation and anomalies is a character of this species, as also noted Abbott (1974: 103). Some samples are found in figs 32-39. Color varies from pale cream to dark brown; can be homogeneous (fig. 34), in strong spiral bands (figs 32, 35), pale spiral bands (fig. 33) or axial bands (figs 38, 39). The outline varies from broad (fig. 32) to slender (fig. 38); from almost straight (fig. 35) to convex (figs 32-34); or deformed (figs 36, 37). The spiral ribs vary from outstanding (figs 33, 34) to weak (figs 38, 39). Among several other parameters. More details in Bequaert (1942: 8, pl. 1 figs 2-3; pl. 5, figs 1-6).

Head-foot (figs 377, 385). Pigmented by dark brown spots sparse in head and dorsal region of foot, other regions greenish beige. Head protruding. Snout dorso-ventrally flattened, broad, somewhat bilobed anterior margin. Tentacles long, stubby. Eyes dark, on small ommatophores in middle-outer region of tentacles. Foot of medium size, without divisions; a furrow of pedal glands in anterior margin. Left insertion of mantle more posterior than right one. Columellar muscle of about 1.5 whorls.

Operculum (fig. 69). Circular, brown, multispiral, nucleus central, fimbriated edge. Muscle scar elliptic near inner margin. Occupies entire aperture.

Mantle organs (figs 380, 381, 386). Mantle border entirely flanged by small, somewhat uniform papillae; not pigmented or sometimes with brown filiform spots, perpendicular disposed. Mantle cavity of about 1.5 whorls. Osphradium long, ridge-like, with little more than half of gill length; its anterior end about in same level than that of gill. Gill very long, discretely shorter than cavity and somewhat broad; filaments triangular, tip sharp, almost central; ctenidial vein broader than osphradium in its posterior half. Between gill and rectum a proportionally narrow space. Hypobranchial gland thin, inconspicuous. Adrectal sinus not visible. Rectum very broad, bearing elliptical, long fecal pellets compacted obliquely. Anus siphoned posterior from mantle border. Pallial gonoducts run at right margin, described below.

Circulatoty and excretory systems (figs 380, 386). Heart similar to those of preceding species, aortas attached to gastric style sac and adjacent intestine loops. Kidney short, about 1/4 whorl, solid, white, with single lobe. Nephrostome slit-like, in middle region of wall between kidney and pallial cavity.

Digestive system (figs 378, 379, 382, 385-389). Mouth in anterior extremity of snout, longitudinal, ventral, thick muscular. Buccal mass of medium size, almost all within snout. Jaws two very small triangular plates; pale beige; attached to a flaccid, transparent membrane inserted in dorsal wall, posterior to mouth. Pair of dorsal inner folds very broad (fig. 382), a small median angle of each in they middle region, which marks aperture of salivary gland ducts; folds gradually narrow in direction to esophagus; posterior regions of these folds with dark brown spots. Odontophore (figs 387-389) similar to those of preceding species. Distinctive features are: 1) radula very long, coiled in its posterior region; 2) **m2** narrow; 3) **m11** with a branch inserted in anterior extremities of odontophore cartilages, without connection with peribuccal muscles; 4) **m7** part originating in adjacent region of subradular membrane (beyond from m11); 5) **m8** very long and narrow. Radular teeth (fig. 108): rachidian tooth with 5 cusp, central cusp several times larger than lateral cusps, a pair of basal cusp; lateral tooth with 4 cusps being second very larger and triangular; inner marginal tooth spoon-like, with 4-5 cusps, being lateral cusp larger; outer marginal tooth similar to inner one but with 6-7 smaller cusps. Salivary glands large, long, posterior to nerve ring; right salivary gland with glandular tissue also anterior to nerve ring. Esophagus with two very long, narrow and shallow pouches, each one with several oblique glandular folds; folds of dorsal wall of buccal mass stay in base of each pouch, in transition, dark pigment present (fig. 382: ds). Stomach (figs 378, 379) large, more than half whorl. Central pad very large and long, occupying almost entire ventral surface of stomach. Anterior chamber short. Duct to digestive gland in anterior region of left border of central pad. Gastric shield broad. Crescentic ridge absent. Intestine and style sac fused in a long distance (entire left region). Style sac with about half of remainder stomach length. Intestine, after free from style sac, bears two loops in right side of this, in this region, intestine with dark spots. Intestine free from kidney tissue. Rectum and anus see pallial cavity. Digestive gland restricts to posterior region of stomach, and with about three whorls posterior to it.

Genital system. Gonad occupies superior regions of each whorl, on digestive gland. Male (fig. 384). Spermoduct a narrow duct close to columella; in right posterior region of pallial cavity expands, becomes a long, thick glandular furrow, without special inner structures except a fold in inner lamina; finishes posterior to anus. Female (fig. 383). Oviduct also close to columella, in right posterior region of pallial cavity expands but maintains closed at about 1/8 of its length in pallial cavity; afterwards opens, becoming a thick glandular groove. Both laminae present a posterior chamber each, blind sacs opened anteriorly in furrows which runs just in lamina borders; in inner lamina a bursa copulatrix, and in outer lamina a seminal receptacle, this smaller than bursa. Pallial oviduct finishes posterior to anus. Gonopericardial duct or ligament present in both sexes, small. No ovopositor differentiable.

Measurements (in mm). 13.4 by 5.0; 13.1 by 5.0; 12.5 by 4.3; 13.2 by 5.6 (figured specimens).

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

Habitat. Estuarine environment, moving on mud or on root trees.

Material examined. Venezuela; Nova Esparta; Margarita Island, Porlamar city, Caracola estuary, 150 specimens, MZSP 28262 (30/i/1996, Simone col.).

Remarks. *B. minima* differs in its digestive system from Californian *B. zonalis* (Brug.) (cf. Driscoll, 1972) in having longer stomach and central pad more developed.

Family Cerithideidae

Genus *Cerithidea* Swainson, 1840
(Type species: *Murex decollata* Linné, 1758)

Cerithidea costata (da Costa, 1778)

(Figs 40, 41, 50, 70, 71, 109, 110, 390-405)

Synonymy: see Bequaert, 1942: 2. Complement: *Cerithidea costata:* Warmke & Abbott, 1961: 71 (pl. 13, fig. s); Abbott, 1974: 102 (fig. 980); Jong & Coomans, 1988: 43 (pl. 33, fig. 203).

Description.

Shell (figs 40, 41, 50). Most specimens covered by a brown mass of vegetal fibers, with about double of width and length than shell, only aperture free (fig. 40). Protoconch of two whorls smooth, convex, generally eroded (fig. 50). Other details in Bequaert (1942: 2-3, pl. 1, fig. 1; pl. 2, figs 1-7).

Head-Foot (figs 390-392). Pigmented by uniform bluish gray in dorsal region of foot and head, and transversal violet-brown bands in snout and sometimes in tentacles; foot sole white; sometimes tentacles entirely violet-brown; posterior regions pale beige. Head protruding. Snout large, dorsoventrally flattened, bilobed anterior margin. Tentacles long, stubby, with dark eyes approximately in its middle region; region from tentacles base to eye clearly broader than distal region. No ommatophore. Foot of medium size, without divisions; a furrow in anterior margin of pedal glands. Columellar muscle of about 1.5 whorls.

Operculum (figs 70, 71). Circular, corneus, nucleus central, multispiral. Edge fimbriated. Occupies entire aperture. Muscle scar elliptic, near inner margin.

Mantle organs (figs 393-396). Mantle border almost smooth, some specimens with 5 to 7 small papillae sparsely disposed. Pallial eye well-developed, dark, with lens, situated in a small elevation in left region, just in incurrent canal. Mantle cavity rather deep, about two whorls. Osphradium very long, ridge-like, lying left margin of pallial cavity, close gill, little less than half of gill length; osphradium anterior extremity posterior than that of gill. Gill long, about same length than pallial cavity; filaments triangular, tall, tip almost central; sharp anterior extremity near mantle border. Ctenidial vein of medium size. Between gill and rectum a proportionally narrow area. Hypobranchial gland inconspicuous. Rectum broad, covered by ad-rectal sinus, internally several elliptical fecal pellets compacted obliquely. Anus siphoned, posterior to right extremity of mantle border. Pallial gonoducts run between rectum and right margin of cavity, narrow, long, finish posterior to anus.

Circulatory and excretory systems (figs 395, 396). Heart large, pericardium also large, exposed in end of pallial cavity; left limit the style sac (dorsally) and kidney (ventrally), right limit the anterior extremity of gonad and columellar muscle, from which anterior aorta attaches. Kidney long (about half whorl) but narrow, runs at right of style sac; with single lobe, solid, yellow. Membrane between kidney and pallial cavity small, with nephrostome at right close rectum.

Digestive system (figs 392, 395-403). Mouth in anterior extremity of snout, longitudinal, ventral, thickly muscular. Buccal mass part within snout. Jaws two thin triangular plates, cut edge in anterior and median borders. Inner surface of buccal mass dorsal wall (fig. 397) with two longitudinal broad and low folds, beginning from each jaw; aperture of salivary ducts in middle region of inner margin of each fold. Odontophore muscles (figs 400-403) similar to those of preceding species, with following distinctive features: 1) **m4** and **m5** connected with each other in a higher degree, almost all outer border of m5 attached to ventral region of m4; 2) m4 posteriorly inserted in tissue covering middle region of radula; 3) **m11** pair originating in middle-inner region of subradular membrane, with 3 anterior insertions: a narrow connections to anterior extremity of cartilages, other originating m7 and other running anteriorly to peribuccal muscles (fig. 403); 4) **m8** absent. Radula short, forming a "S". Radular nucleus flattened and thick. Radular teeth (figs 109-110): rachidian tooth of somewhat rounded outline, with nine cusps, being central cusp larger, no basal cusp; lateral tooth with 5 cusp being second lager and terminal; inner marginal tooth spoon-like, with 3 terminal cusps being lateral cusp larger; outer marginal tooth similar to inner one, but with 5-6 smaller cusps. Esophagus single, long and narrow, with 2-3 low longitudinal folds, no visible glands. Stomach large, occupies half whorl excluding style sac. Stomach (figs 395, 396, 398, 399) with 2 inner chambers separated with each other by a constriction. Posterior chamber longer, central pad long, duct to digestive gland in middle region of left border of central pad; crescentic ridge surrounds this duct and contours posterior half of central pad; esophageal aperture simple, in middle of left side of stomach. Apertures of intestine and style sac as anterior limit of stomach, united one another by a very short distance. Style sac cylindrical, very long - about half whorl, arriving in level of posterior region of pallial cavity (figs 395, 396). Intestine narrow, almost entirely free from style sac; contours ventrally style sac from left to right side, where there is other loop to right; in pallial cavity suddenly expands. Rectum and anus described above.

Genital system. Gonad, in both male and female, occupying superior and external surface of each whorl, on digestive gland; when mature, runs ventrally and at right stomach and style sac, arriving in level of posterior region of pallial cavity, at left of posterior half of style sac (figs 395, 396). Visceral gonoduct runs close columella, a thick walled duct; in pallial cavity expands. Male pallial sperm groove (fig. 405) almost entire opened and thick glandular, no special inner structures except a longitudinal, medial fold in its posterior extremity (fig. 405: n2). Female pallial oviduct (fig. 404) also almost entirely opened and thick glandular; bursa copulatrix sac-like, situated in posterior region of inner lamina border, opens anteriorly in a groove, which runs in remainder length of inner lamina border; no other differentiable structure. Pallial oviduct finishes in a right furrow of head; this furrow runs ventrally until near sole, and surrounds posterior-ventrally ovopositor. Ovopositor (fig. 391) a somewhat triangular thickness of right-dorsal region of foot, with dorsal limit imprecise.

Measurements (in mm). 18.8 by 5.4; 15.1 by 4.7 (figured specimens); 12.8 by 4.8; MZSP 28264: 9.6 by 4.0.

Distribution. Florida to South Caribbean.

Habitat. Estuarine environment, moving on mud or on root of trees. in general with a cover of cellulose, brown, around entire shell, only aperture was free (fig. 40).

Material examined. Venezuela; Nova Esparta; Margarita Island; Porlamar city, Caracola estuary, MZSP 28263, 36 specimens (30/i/1996, Simone col.); La Restinga, Central beach, MZSP 28264, 19 specimens.

Remarks. In early papers, species of the genera *Cerithidea* and *Batillaria*, were grouped within the family Potamididae. More recently, Houbrick (1988: 89), based on anatomical differences, separated each genus in a family proper: Cerithideidae and Batillariidae respectively, both separated from Potamididae. In that paper, the author referred, however, that maybe Cerithideidae could be considered as a subfamily of Potamididae.

In comparison with the data on *Cerithidea californica* given by Bright (1958; 1960), *C. costata* differs in having esophageal crop absent, duct to digestive gland inserting in stomach (and not in distal extremity of esophagus), opened pallial oviduct and bursa copulatrix present. Driscoll (1972) presents a detailed study on digestive system of *C. californica*, in which the stomach of *C. costata*, in particular, is very similar, differs in lacking the ridges near intestine origin.

Family Campanilidae

Genus *Campanile* Fischer, 1884

(Type species: *Cerithium giganteum* Lamarck, 1804 [Eocene])

Campanile symbolicum Iredale, 1917

(Figs 42, 81, 111, 406-422)

Synonymy see Houbrick (1981a: 282). Complement:

Campanile symbolicum: Abbott & Dance, 1983: 68 (fig.).

Description.

Shell (fig. 42). Relatively large (more than 240 mm), turriform, heavy, thick walled. Whorls with almost straight outer surface, suture almost invisible, Periostracum white, calcified. Other details in Houbrick (1981a: 266-268, figs. 1-2).

Head-foot (figs 406, 408, 411). Homogeneous beige in color. Head protruding. Snout relatively small, cylindrical, with a deep anterior, ventral, longitudinal, furrow. Tentacles somewhat long, broad, dorso-ventrally flattened. Eyes dark, on small ommatophores situated approximately in middle-outer region of tentacles. Foot large (about 1/3 whorl); furrow of pedal glands deep, with thick borders in anterior margin, gradually becomes narrow in lateral region, surrounds entire foot sole. Columellar muscle long, about 2.5 whorls, flattened and thick. Other details in Houbrick (1981a: 268-271, figs. 3a, b, 4a). Dorsal wall of haemocoel thick muscular in anterior half; posterior half thinner; separating both regions a diaphragm-like septum surrounding esophagus (fig. 411: o1).

Operculum. Sub-circular, corneus, sub-central nucleus, palcispiral; occupies partially aperture (fig.408) (see also Houbrick, 1981a: 268, figs 1e-f).

Mantle organs (figs 407, 410, 412, 422). Mantle border entirely with small papillae, somewhat uniform in size; in region of siphonal canal a deep concavity. Mantle cavity very deep, more than 2 whorls. Osphradium long, bipectinate, somewhat elliptical outline; length little more than 1/3 of gill length; filaments very thin and close with each other, right filaments larger and discretely more numerous than left filaments; right filaments attached to ctenidial vein and probably irrigating to it; left margin free; dorsal surface of osphradium altogether attached to mantle (fig. 422). Gill long, little more than half of cavity, narrow, filaments triangular tall, tip pointed, almost central; gill begins relatively posterior from mantle border. Ctenidial vein broad since anterior gill margin, about 1/3 of its length (posterior) free from gill, running at left in floor of pallial cavity, close kidney. Between gill and rectum a relatively broad space; in posterior 2/3 of this space several transverse vessels, sometimes dichotomic, inserted in an inconspicuous ad-rectal sinus. Hypobranchial glands a lamina covering vessels between gill and rectum; some specimens bearing a tall fold lying anterior half of rectum. Rectum described below. Anus siphoned, very posterior from mantle border. Other details in Houbrick (1981a: 271-274, figs 3c, 4a, b).

Circulatory and excretory systems (figs 407, 409, 410). Heart similar to those of preceding species, proportionally small, anterior and posterior aortas not attached directly in stomach, but in a lobe of digestive gland. Kidney very long, more than half whorl, somewhat flattened, brown in color. Anterior-pallial half of kidney almost solid, bearing several glandular septa radially disposed; nephrostome a slit near posterior limit of pallial cavity. Posterior-visceral half of kidney with two regions, that at left lying pericardium, almost solid, bearing several transversal glandular septa; that at right replete of several vessels close with each other, connected in a main vessel which runs in median region (fig. 409).

Digestive system (figs 407, 411-421). Mouth deeply situated in median-ventral furrow of snout, bordered by several inner folds. Buccal mass proportionally very large, situated almost entire posterior to snout. About half of buccal mass constituting by greatly developed jaws and peribuccal muscles. Jaws (figs 81, 416) two very large plates, somewhat thick; anterior cut edge smooth and dark brown; other regions pale brown. Inner surface of dorsal wall of buccal mass with 2 broad longitudinal folds as ventral limit of a dorsal chamber; dorsal inner surface of this dorsal chamber with several narrow longitudinal folds (figs 413-416: o2). Pair of narrow furrows in lateral region, longitudinal, finishes posteriorly in each esophageal pouch. Esophageal pouch a pair of semi-spherical, hollow structures, well delimited between buccal mass and esophagus limit, lateral situated (fig. 415). Odontophore (figs 417-421) similar to those of preceding species; distinctive features are: 1) **m1**, jugal muscles very developed, mainly near median line in dorsal and ventral regions, connecting strongly odontophore and buccal mass in adjacent inner wall of snout; 2) **m2** absent; 3) broad insertion of jaws and peribuccal muscles (ji); 4) very short radula (less than 30 rows of teeth); 5) **m6**, horizontal muscle very thick (fig. 419); 6) a pair of probable **m8** in inner region of odontophore; 7) **m11** not connected with cartilages, inserted in radular nucleus; 8) **m13**, a strong muscle originated in ventral peribuccal region, inserted in radular nucleus. Radula (fig. 111) see Houbrick (1981a: 274, fig. 6; 1989: 2, figs. 1-2) description. Esophagus single, without visible glands; folds of dorsal chamber of buccal mass gradually faint in anterior half of esophagus inner surface; posterior esophagus with a single longitudinal fold developed. Salivary glands broad in anterior and posterior regions of nerve ring, passing through it; gradually narrow until middle region of esophagus. Salivary glands aperture in dorsal posterior region of buccal mass. Stomach and posterior digestive gland not seen, but well described by Houbrick (1981a: 275-276, fig. 5b; 1989: 3, figs. 3-5); style sac rudimentary, central pad-like structure, two openings to digestive gland. Intestine sinuous within anterior digestive gland. Rectum somewhat broad, with fecal pellets almost spherical, not compacted obliquely; anus siphoned, very posterior from mantle border. Other details of digestive system in Houbrick (1981a: 274-276, figs 4-5; 1989: 3).

Genital system. Male and female organs not seen completely, they are well described by Houbrick (1981a: 277-278, fig.4). Note the probable protandry, seminal receptacle within pericardium, and a thick opened pallial oviduct without chambers.

Nervous system (figs 411, 413). Pair of buccal ganglion small, anterior to esophageal pouches. Other details in Houbrick (1981a: 276-277, fig. 5a).

Measurements (in mm). USNM 867174: 55.0 by 20.0; USNM 691560: 78.2 by 28.0.

Distribution. SW Australia coast.

Habitat. See Houbrick (1981a: 279).

Material examined. Australia; Western Australia; Cape Naturaliste, Bunker Bay, 7 specimens, USNM 691560 (Rosewater & Wilson col. 13/viii/1966); Denmark, Wilson Inlet, Ocean Beach, 1 specimen, USNM 867174 (27/i/1988, Houbrick, R.S. col.).

Remarks. *C. symbolicum* was included in the genus *Cerithium* in early papers (see Houbrick, 1981a: 280-282 for a full historic) among others, and finally transferred to fossil genus *Campanile* by Iredale (1917), becoming the single survivor of a large, diverse, complex taxon, that attained its apogee during the early Tertiary. Specimens of Campanilidae generally had large size, sometimes greater than a meter in length (Jung, 1987; Houbrick, 1989).

The anatomy of *C. symbolicum* was extensely studied by Houbrick (1981a) and the aberrant characters of this species let some doubts on its systematic placement. Based on new studies including aspects of *Campanile* (Haszprunar, 1985, 1988; Salwini-Plawen & Haszprunar, 1987; Healy, 1983; 1986a, b), Houbrick made a reevaluation of his previous paper in 1989, raising to it a superfamilial rank: Campaniloidea.

In present study the above cited controversy was considered, *C. symbolicum* was included in phylogenetic analysis with hope if it belongs to another, i.e., non-cerithioidean group, this would appear. Comments on each character are found in Discussion. Although having a large size for a cerithioidean, *C. symbolicum* probably evolved from giant forms, being result of a miniaturization process. If so, several adaptations to large size, as bipectinate osphradium, large jaws, complex stomach, etc., are still present and may be regarded as autapomorphies. The *Campanile* diaphragm-like septum of haemocoel is similar to those that occur in Strombidae (person. obs.), and appears to be other adaptation to large size.

Family Vermetidae

Genus *Serpulorbis* Sasso, 1827

(Type species: *V. arenaria* Linné, 1758)

Serpulorbis decussatus (Gmelin, 1791)

(Figs 43, 79, 112, 113, 423-439)

Synonymy see Clessin, 1904: 99. Complement:

Serpulorbis decussata: Warmke & Abbott, 1961: 66 (pl. 12, fig. d).

Serpulorbis decussatus: Rios, 1970: 40 (pl.8); Abbott, 1974: 101 (fig.); Rios, 1975: 45 (pl.12, f. 164); 1985: 47 (pl. 18, f. 214); Jong & Coomans, 1988: 43; Rios, 1994: 67 (pl. 22, f. 259).

Description.

Shell (fig. 43). Irregularly uncoiled as normal vermetid, relatively large, about 100 mm. Sculptured by irregular longitudinal and transversal low ridges, both predominating, producing a reticulation. Aperture simple, not notched. More details in Clessin (1904: 99-100).

Head-Foot (figs 423-427). Scarcely pigmented by brown spots, most pale cream. Head greatly protruding and clearly broader than other regions. Snout large, as an extension of head, without clear limit, cylindrical. Mouth ample, longitudinal, in anterior-ventral snout region. Tentacles shorter than snout and situated ventrally near foot. Eyes small, dark, on small ommatophores situated in ventral-basal region of tentacles. Foot very small and complex. Pedal sole a deep concavity. Anterior region of foot thick and probably main extensible structure; ventral surface smooth; dorsal region with following structures: laterally insertion in ventral base of head by a pair of flaps (figs 424-427: p1); in median-anterior region a glandular pad (p2) with 7-8 longitudinal, low folds and a concavity in posterior region, covering these folds; between flaps and posterior to glandular pad a pair of well developed foot tentacles (figs 423, 424, 427: pt), each one based broad and tip sharp; a longitudinal, opened furrow in almost they entire length, except near median line (just where duct of pedal gland opens). Pedal glands enormous (fig. 425), elliptical, long, situated in ventral region of haemocoel, internally two bands of glandular, oblique folds, separated by a narrow space which runs longitudinally in middle region; duct of pedal gland broad, penetrates in median region of foot muscle jointed with a pair of nerve, opens between both pedal tentacles (fig. 427). Ventral insertion of mantle very posterior. Food groove runs in left region of head-foot complex, posterior and anterior extremities only shallow furrows, its middle region with tall, thick borders; near head towards right and contours its right region, finishes ventrally near mouth. Columellar muscle very long, more than half of total shell length, anterior 2/3 thick and broad, suddenly becomes narrow and thin in its posterior 1/3. Operculum absent.

Mantle organs (figs 428, 430, 431). Mantle border thin, with minute, sparse papillae, somewhat regularly disposed; color pale brown, white near papillae. Mantle cavity deep, about half of soft parts length. Osphradium very long and narrow, slightly far from gill and from left extremity of mantle cavity; anterior extremity curved and anterior to that of gill; total length about 8/10 of that of gill. Gill very long, little shorter than pallial cavity length, filaments triangular, narrow; tip very long and pointed; anterior gill end very posterior from mantle border. Ctenidial vein of somewhat uniform width; relatively long posterior region free from gill. Between gill and rectum a broad anterior and narrow posterior area. Rectum extremely broad, thin walled. Anus siphoned, posterior from mantle border. Gonoduct running in right margin described below. From both insertions of mantle in head, several nerves radially disposed clearly visible; some of them (from left side) insert in osphradium, while others run medially and anteriorly near mantle border (fig. 430: nv).

Circulatory and excretory systems (fig. 428). Heart proportionally small, situated in left-dorsal region of pallial cavity posterior extremity; pericardium connected to anterior region of stomach. Kidney very simple and small, somewhat elliptical, situated between pericardium and rectum in posterior region of pallial cavity. Internally a solid and flattened renal tissue. Nephrostome a slit situated in middle region of membrane between kidney and pallial cavity.

Digestive system (figs 425, 426, 428-432, 435-439). Mouth in ventral-anterior region of snout, ample. Buccal mass large, slightly spherical, occupying almost entire space of head and snout. Peribuccal and jaws muscles well developed, almost same size of odontophore. Jaws (figs 79,

439) pair large, situated in base of thick muscles. Dorsal region of buccal mass simple, without inner folds. Odontophore (figs 435-438) with following distinctive features: 1) a rotation of odontophore, being some internal structures up side down in relation to those of preceding species; 2) insertion of jaws and peribuccal muscles somewhat horizontal and in posterior region of m4; 3) **m5** short, inserting in middle region of radular ribbon, situated in posterior extremity of odontophore; 4) **m4** dorsal and posterior, part situated down of subradular cartilage; another annex muscular bridge present beyond that normal connection with tissue on radula, dorsal to it and fused with outer tissue of buccal mass; 5) **m2** absent; 6) **m10** very thick and broad, inserted close to m5; 7) **m11** running posteriorly, without connection with cartilages nor with peribuccal wall; 8) **m7** originating part from m11 and part from adjacent region of subradular membrane; 9) **m8** very broad but short. Radular teeth (figs 112, 113): rachidian tooth with 7 cusps being central cups very larger, a pair of basal, lateral projections; lateral tooth with 3 cusps being first cusp larger and terminal; marginal teeth rook-like, without cusps, apex sharp; inner marginal tooth broader than outer one. Pair of buccal ganglion close to with each other, near median line (fig. 439). Esophagus broad, thin walled, without inner folds or glands, begins in dorsal and not in posterior side of buccal mass. Stomach (fig. 432) very large and long, about 1/5 of total soft parts length. Esophageal insertion in left side and very posterior, from it a broad furrow begins and contours posterior gastric extremity, edged by two narrow folds. Two ducts to digestive glands; that anterior ample, situated in middle-ventral region of stomach, edged anteriorly by a Y-shaped fold; that posterior also ample, situated in posterior gastric wall, attached to posterior digestive gland. A dorsal fold, longitudinal, median, with posterior extremity in level of anterior duct to digestive gland, gradually narrows into near intestine origin, Other small and short fold ventral to posterior duct to digestive gland. Style sac unclear, but probably situated in right side of dorsal fold (fig. 428). Intestine origin in anterior extremity of stomach. Intestine somewhat broad and of uniform weight; after stomach towards right and posteriorly, immerse in anterior digestive gland; runs obliquely some distance and afterwards towards anteriorly; near posterior limit of pallial cavity bears a loop and newly towards posterior lying right region of visceral mass; finally towards anterior abruptly, runs ventrally to kidney and emerges in pallial cavity. Rectum and anus described above. Digestive gland distinct in being two separated lobes (figs 430, 432); that anterior very short, at left and posterior to kidney (dd1); that posterior very longer, with length about 1/3 of that of soft parts (dd2); between both glands no connection, only gastric wall visible. Both digestive glands with apparently similar tissue.

Genital system (figs 433, 434). Only female examined. Oviduct restrict to a side of visceral mass, from posterior extremity to stomach, on posterior digestive gland. Oviduct cross ventrally stomach and anterior digestive gland; in left-posterior region of pallial cavity inserts in left extremity of pallial oviduct; before its aperture, inserts a small, sac-like seminal receptacle, immerse in outer lamina. Albumen and capsule glands small, situated at left and anterior to oviduct aperture. After some distance, pallial oviduct suddenly expands, after gradually narrows. Pallial oviduct closed at about 1/10 of its posterior length, remainder an opened groove with thick-glandular walls; finishes posterior to anus.

Measurements (in mm). 41.0 by 9.7 (figured specimen).

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

Habitat. Sessile, attached to corals and rocks, sometimes on gorgonians. Infratidal level.

Material examined. Brazil; Espirito Santo; Guarapari, 2 specimens MZSP 28347 (Coltro leg.).

Remarks. *S. decussatus* differs anatomically from *S. zelandicus* (Quoy & Gaimard, 1834) (cf. Morton, 1951a) in having poor pigmented head-foot, gill filaments narrower, and apparently other organization of pedal mucous gland and oviduct. The anatomical data of *S. decussatus*, however, indicates a double mode of feeding: ciliary feeding by food grove, and by mucus string with the presence of pedal tentacles and great development of pedal gland. This double mode of feeding is found in *S. zelandicus* (cf. Morton, 1951a) and *Vermetus novaehollandiae* (Yonge, 1932). Several organs of *S. decussatus*, in addition, appear to work up side down in relation to those of other cerithioideans. This is more evident by position of cephalic tentacles (ventral in head) and by odontophore, in which several muscles have inverted arrangement. This fact is shown, for example, by site of m11-m7 complex, turned towards posterior, while normally they are turned towards anterior.

Characters Description and Discussion

The organization of the following section is based on papers of other recent phylogenetic analyses (e.g., Pinna, 1996). The account on each character begins with an abbreviated descriptive sentence followed by plesiomorphic and derived condition (s); also followed by CI and RI (consistency and retention indices, respectively), values for the character under the most parsimonious hypothesis. The indices are shared with the outgroups. A list of terminal taxa exhibiting the apomorphic condition is presented after each derived state, following the order presented in the descriptions.

The outgroup choice was done in following terms: hypothesizing the Cerithioidea as the "stem group" of the Caenogastropoda (Haszprunar, 1988), the choice of a non-caenogastropod prosobranch group was regarded as better for present analysis, rather than other caenogastropod taxon. Other caenogastropods, however, were used in the cases in which homologies of structures in archaeogastropods were uncertain or not possible.

The following non-caenogastropods are included in present analysis as outgroups: 1) Patellogastropoda: *Propilidium curumim* Leal & Simone (1998); 2) Cocculiniformia: *Addisonia enodis* Simone, 1996a, *Copulabyssia* sp. (person. obs.); 3) Vetigastropoda: *Haliotis aurantium* Simone, 1997, *H. poutalesii* Dall, 1881, *H. tuberculata* Linné, 1758, *H. lamellosa* Lamarck, 1822 (Simone, 1997); *Pleurotrochus atlanticus* Rios & Matthews, 1968 (MZSP 23824, 18387); *Calliostoma depictum* Dall, 1927 (MZSP 28322); 4) Neritimorpha: *Helicina* sp (MZSP 28673), *Neritina zebra* (Bruguière, 1792) (MZSP 28204). However, it is impracticable to include all these species in the table, being reunited in the single collective term "archaeogastopods". However, the term "Archaeogastropoda" denotes a paraphyletic taxon, only utilized in present discussion without taxonomic sense. A similar approach is provided by Sasaki (1998) in a phylogenetic analysis of the basal gastropods, in such some data are also extracted.

Several species belonging to other caenogastropod taxa were also examined (e.g., Simone, 1995a, 1995b, 1995c, 1996b), and sometimes are included in discussion. However, in the table only the following species are mentioned: 1) Viviparidae: *Viviparus acerosus* (Bourguignat, 1862) (person. obs.) 2) Littorinidae: *Littorina flava* (King & Broderip) (Simone, 1998) and 3) Hydrobiidae: *Pothamolithus ribeirensis* (Pilsbry) (Simone & Moracchioli, 1994).

The term "basal" caenogastropods means those groups which lack canal in shell aperture and generally precede the Cerithioidea in most catalogues, e.g. Abbott (1974), Rios (1994). In particular those examined species of Littorinidae and Hydrobiidae.

Shell

1. Form: 0= globose; 1= turriform (all taxa **except** *M. modulus* and vermetids); 2= uncoiled (*Serpulorbis decussatus*) (CI= 66, RI= 75, not additive).

The globose shell shape appears to be the rule among the vetigastropods and nerithimorphs, as well as in basal caenogastropods (littorinids, hydrobioids). This type of shell shape is found in the cerithioideans only in Modulidae, and thus regarded as plesiomorphic. Other cerithioideans present an elongated-turriform shell shape, some of them very long, as *Turritella*, while others not so long, as Planaxidae. The elongated shell shape is almost absent in archaeogastropods, and present in few other caenogastropod taxa (some ctenoglossans and terebrids), thus, it is here considered apomorphic.

2. Differentiated siphonal canal: 0= absent; 1= present (*Supplanaxis nucleus, Doryssa macapa, M. modulus, Batillaria minima, Campanile symbolicum*) (CI= 20, RI= 0).

3. Anterior notch in aperture: 0= absent; 1= present (All taxa except *Turritella hookeri* and *Serpulorbis decussatus*) (CI= 50, RI= 83).

Most of cerithioideans present, in different degrees of development, siphonal canal in the shell aperture. This character is absent in archaeogastropods and basal caenogastropods. The canal of the cerithioideans does not correspond with a great development of a muscular siphon of the mantle edge, like those of the higher caenogastropods (see discussion on mantle), and so appears to have been acquired independently. Among the cerithioideans the canal is absent only in turritellids and vermetids. In the present analysis the canal was separated into two characters, its presence (#3) and if greatly differentiated in the shell aperture (#2). This last state revealed to be developed in several taxa independently.

4. Determinate growth: 0= absent; 1= present (All taxa except *Turritella hookeri, Campanile symbolicum, Serpulorbis decussatus*); 2= periodical determinate growth (*Cerithidea costata, Bittium varium, Finella dubia, Alaba incerta* (CI= 50, RI= 80).

Determinate growth, i.e., development of a differentiated aperture in the adult form, appears to be the rule among the cerithioideans (see also Vermeij & Signor, 1992), and is practically absent among archaeogastropods and basal caenogastropods. This character may be convergent with determinate growth of higher caenogastropods, and other gastropods (e.g., Pulmonata). This character, among cerithioideans, is absent only in turritellids, vermetids and *Campanile*, appeared in the tree as a reversion. Periodical determinate growth, i.e., presence of several differentiable lips, marked in the shell by axial varices, is found in cerithideids and also in the miniaturized forms examined, such as *Bittium, Finella* and *Alaba*.

5. Periostracum: 0= chitinous; 1= calcified (*Campanile symbolicum*) (CI= 100, RI= 100).

This character is a *Campanile symbolicum* autapomorphy, also pointed out by Houbrick (1981a).

6. Inner chitinous layer: 0= absent; 1= present (*Bittium varium, Finella dubia*) (CI= 100, RI= 100).

A developed inner chitinous layer, resembling those of hydrobioid Barleeidae (Simone, 1995a), is easily found in both taxa when the shell is decalcified or broken.

7. Size: 0= medium/large; 1= miniaturized (adult form smaller than 8 mm) (*Bittium varium, Finella dubia, Alaba incerta*) (CI= 50, RI= 66).

8. Autotomy of protoconch: 0= absent; 1= present (*Aylacostoma* spp, *Doryssa* spp.) (CI= 50; RI= 80).

Snout

9. Type: 0= cylindrical, deep ventral-anterior furrow; 1= flattened, bilobed anterior mouth (Thiarids, *Supplanaxis nucleus*, pleurocerids, cerithids, *Finella dubia, Alaba incerta, Batillaria minima, Cerithidea costata*) (CI= 100, RI= 100).

Two types of snout occur in the cerithioideans, most of them present a dorso-ventrally flattened snout, with the buccal mass partly or even completely within it. In this type, the mouth is almost terminal and is approximately in the same plane of the integument. In contrast, the other type is cylindrical, the buccal mass is only partly or completely outside, posterior to it, and the mouth is in the posterior region of a longitudinal, ventral-anterior furrow. This last type is also found in archaeogastropods and basal caenogastropods, and is regarded as plesiomorphic. Species of some genera such as *Supplanaxis, Bittium, Finella* and *Alaba*, the snout is not clearly dorso-ventrally flattened, but the inner organization is more similar to that of flattened type and is regarded as this type in present analysis. The explanation of the flattened type of snout is the apomorphic lack of peri-buccal muscular rod. Some cerithioidean species have very extensible snout, as scaliolids (Ponder, 1994).

10. Size: 0= normal (about 1/4 whorl); 1= large and flattened (*Cerithium atratum*); 2= small and flattened (*Bittium varium, Finella dubia, Alaba incerta*); 3= large and cylindrical (*Serpulorbis decussatus*) (CI= 100, RI= 100, not additive).

Foot

11. Size: 0= normal (about 1/3 whorl); 1= very large (*Turritella hookeri, Bittium varium,*

Campanile symbolicum); 2= small (*Serpulorbis decussatus*) (CI= 66, RI= 0, not additive).

12. Pedal gland furrow: 0= anterior only; 1= edge of entire sole (*Campanile symbolicum*) (CI= 100, RI= 100).

13. Tentacles: 0= absent; 1= a pair anterior (*Serpulorbis decussatus*); 2= single posterior (*Doryssa atra*); 3= several (*Alaba incerta*) (CI= 75, RI= 0, not additive).

The normal cerithioidean lacks any special pedal structure, such as tentacles. This lack is shared with basal caenogastropods. Although the 3 species cited above have foot tentacles. The position of these taxa in the obtained tree suggested independent origin of those foot accessory structures.

14. Posterior furrow of pedal gland: 0= absent; 1= present (*Bittium varium, Finella dubia, Alaba incerta*) (CI= 50, RI= 66).

Operculum

15. Nucleus situation: 0= central; 1= eccentric (cerithids, *Finella dubia, Alaba incerta*); 2= subterminal (thiarids, *Supplanaxis nucleus*) (CI= 66, RI= 92, additive).

16. Type of coiling: 0= multispiral; 1= paucispiral (cerithids, *Finella dubia, Alaba incerta*); 2= concentric (unguiculate) (thiarids, *Supplanaxis nucleus*); 3= absent (*Serpulorbis decussatus*) (CI= 75, RI= 87, not addictive).

17. Outline: 0= circular; 1= sub-elliptical (cerithids, *Finella dubia, Alaba incerta*); 2= elliptical (thiarids, *Supplanaxis nucleus*) (CI=100, RI= 100, additive).

The multispiral operculum with central a nucleus, the standard in vetigastropods and found in some cerithioideans (Modulidae, Campanilidae, Turritellidae, Vermetidae, Batillariidae, Pleuroceridae and Cerithideidae), is regarded as plesiomorphic. The concentric sculptures (unguiculate) operculum, with almost terminal nucleus, resembling those of most neogastropods, is also found in some cerithioideans (Planaxidae and Thiaridae). Observing the tree, it is possible to note that this subterminal nucleate, unguiculate type is the last step of an evolutionary lineage, leaving from multispiral central-nucleate type, having the paucispiral, eccentric nucleate operculum as intermediary (present in Cerithidae, Diastomatidae and Litiopidae).

The sampled vermetid, *S. decussatus*, lacks operculum, as well as all members of the genus *Serpulorbis* (see Morton, 1951a; Hughes, 1983). However, most vermetids possess multispiral, circular opercula (Morton, 1951b, c; Hughes, 1983).

Cephalic tentacles

18. Eye site: 0= basal; 1= sub-basal (all cerithioideans except the listed following); 2= middle (*M. modulus, Batillaria minima, Campanile symbolicum*) (CI= 40, RI= 25, additive).

In archaeogastropods, the normal site of the eyes is the external base of the tentacles. This character is not found in the cerithioideans examined, all of which have the eyes located slightly over the tentacle base outer surface. In this way, the proximal region of the tentacle works as a small stalk for the eyes. This is clear observing living, crawling animals. In some cerithioideans, such as *Modulus, Batillaria* and *Campanile*, the eyes are located in the middle level of tentacles length, character regarded as extreme link. The eyes not just in the tentacles base appears to be the rule among the caenogastropods, as this is found in littorinids and most of higher groups.

19. Transverse section and site: 0= cylindrical and dorsal; 1= flattened and dorsal (*Campanile symbolicum*); 2= cylindrical and ventral (*Serpulorbis decussatus*) (CI= 100, RI= 100, not additive).

20. Ommatophore: 0= absent; 1= peduncle (*Supplanaxis nucleus, M. modulus, Cerithium atratum, Batillaria minima, Campanile symbolicum*); 2= sessile (pleurocerids) (CI= 28, RI= 58, additive).

The ommatophore is defined herein as a small secondary stalk in the base of eyes, away from the tentacle axis but originated from it. The eyes to be located away from the tentacles. In the case of pleurocerids, the ommatophore has a very broad sessile base. Ommatophores are present in some outgroups such as vetigastropods and heterobranchs, however of different localization and of apparent independent origin from cephalic tentacles base.

21. Length: 0= medium (equivalent to snout); 1= short (about half of snout length) (*Cerithium atratum, Serpulorbis decussatus*); 2= long (about 1.5 times the shout length) (*Bittium varium, Finella dubia, Alaba incerta*) (CI= 66, RI= 66, not additive).

Columellar muscle

22. Length: 0= 1-2 whorls; 1= more than 3 whorls (*Turritella hookeri, Campanile symbolicum, Serpulorbis decussatus*) (CI= 100, RI= 100).

Mantle edge

23. Appendices: 0= none; 1= several papillae (*Turritella hookeri, M. modulus*, cerithids, *Finella dubia, Batillaria minima, Cerithidea costata, Campanile symbolicum, Serpulorbis decussatus*); 2= tentacles (thiarids) (CI= 40, RI= 72, not additive).

Most cerithioideans have the mantle edge entirely covered by small papillae. There are not similar found among the examined archaeogastropods nor basal caenogastropods, and their presence is regarded as apomorphic. However, some vetigastropods (e.g., Fissurellidae) and patellogastropods (e.g., Patellidae) present papillae in mantle edge, but normally longer and with complex receptors. A smooth mantle border, although, also occurs among cerithioideans (Pleuroceridae, *Alaba*, Planaxidae), could be a secondary loss. Strongly lobed tentacles on the mantle border are found in the examined thiarids, appearing to be a synapomorphy of the family. However, slender pallial tentacles occur in scaliolids (Ponder, 1994). The uniformity or not of the mantle edge papillae appears to be of secondary importance, once both conditions can occur in single species (e.g., *Modulus modulus).*

No cerithioideans have a differentiated siphon, the anterior-right region of mantle edge is, at most, thick muscular and undulating, edging the shell canal.

24. Anal flap: 0= absent; 1= present (*Pachychilus* sp.) (CI= 100, RI= 100).

25. Mantle ventral insertion in head foot: 0= close to mantle border; 1= far from mantle border (*Turritella hookeri, Cerithidea costata, Campanile symbolicum, Serpulorbis decussatus*) (CI= 50, RI= 66).

The insertion of the mantle in the head-foot in the columellar muscle ventral surface, is very posterior in some species and appears to be associated with taxa that need to protrude greatly from the shell, without moving it, such as vermetids and turritellids. However this character was also found in *Campanile* and *Cerithidea.*

26. Mantle eye: 0= absent; 1= present (*Cerithidea costata*) (CI= 100, RI= 100).

In the case of cerithideids, in the region of the siphon there is a well-developed, apomorphic eye, which includes a lens (Houbrick, 1986a, 1988). The cerithid *Gourmia gourmyi* (Crosse) has about 7 pallial eyes in the incurrent siphon, but these are simpler (Houbrick, 1981b).

Osphradium

27. Type: 0= ridge-like and smooth; 1= ridge-like and pectinate (cerithids, *Finella dubia, Alaba incerta*); 2= elliptical and pectinate (*Campanile symbolicum*) (CI= 100, RI= 100, not additive).

28. When ridge-like: 0= smooth; 1= bipectinate (*Cerithium atratum*); 2= monopectinate (*Bittium varium, Finella dubia, Alaba incerta*); ?= inapplicable (elliptical osphradium) (*C. symbolicum*) (CI= 100, RI= 100, additive).

The typical cerithioidean osphradium is the ridge-like type with a smooth, homogeneous surface; this is shared also with other caenogastropods such as littorinids and hydrobioids (Taylor & Miller, 1989; person. obs.). But the osphradium is pectinate in two cerithioidean groups. In the first group the osphradium has small bipectinate leaflets, but has maintained its long, ridge-like shape, e.g., *Cerithium atratum* (this paper); *C. nodulosum* Bruguière (cf. Houbrick, 1992a: 127, figs 92B-C), *Rhinoclavis aspera*

(Linné) (Taylor & Miller, 1989: 230, figs 4-6, 22b) and other cerithids (Risbec, 1943). The long, monopectinate osphradia of *Bittium, Finella* and *Alaba* were here included in the same group as the *Cerithium* osphradia; the unipectinate condition is regarded as a result of miniaturization, similar to what has occurred in Columbellidae among Muricoidea (person. obs.) and Pisanianurinae among Ranellidae (Warén & Bouchet, 1990). The second type of pectinate osphradium is that of *Campanile.* This is similar to those of higher caenogastropods, and has caused some confusion in the systematic allocation of this species. In fact, the *Campanile* osphradium superficially resembles those of neogastropods in having an elliptical outline, but careful analysis shows that it differs greatly. Contrary to those of higher caenogastropods, the osphradium of *Campanile* has (fig. 422): 1) the leaflets inserted in the mantle in the entire superior region (while in the higher caenogastropods the leaflets are free, mainly inserted near osphradial ganglion and adjacent area); 2) a proportionally greater number of leaflets, being apparently thinner and more densely packed; and 3) the insertion of the right leaflets in ctenidial vein which, observed internally, apparently presents effective action in blood osphradium drainage. The former character is shared with the pectinate osphradium of the Architaenioglossa (person. obs. on *Pomacea* spp.). In the present analysis, both the pectinate cerithioidean osphradium groups, with clear differences, are allocated in different points in the tree, suggesting independent origin. An almost certain independent origin of the pectinate condition of the osphradium is also found in higher caenogastropods and ampullariids. Bipectinate osphradium is also known in other cerithioidean taxon, *Plesiotrochus* (Houbrick, 1990b). However, the affinity of this taxon with those above mentioned is matter still unclear.

29. Anterior extremity: 0= posterior to gill; 1= anterior to gill (*Supplanaxis nucleus, Alaba incerta, Serpulorbis decussatus*) (CI= 33, RI= 0).

30. Length: 0= about 2/3 of gill; 1= less than 1/2 gill (*Aylacostoma ci, Melanoides tuberculatus,* pleurocerids, *Cerithidea costata, Campanile symbolicum*); 2= equivalent to gill (*Aylacostoma exoplicata, Supplanaxis nucleus, Turritella hookeri, M. modulus,* cerithids, *Finella dubia*) (CI= 22, RI= 46, not additive).

The length of the osphradium relative to that of gill, appears to be an important character at the specific level, but poor for analysis at higher ranks, because it may vary within a single genus (e.g., *Aylacostoma*) and appears in several points in the tree (see low indices). Another character of poor value for higher systematics, for the same reasons, is the position of the anterior osphradium end in relation to that of the gill (if anterior or posterior to it).

31. Anterior extremity shape: 0= simple; 1= strong zigzag (*M. modulus*); 2= delicate zigzag (*Doryssa atra, D. macapa*) (CI= 100, RI= 100, not additive).

The osphradium with a zigzag in its anterior region appears to be another adaptation for increasing the surface of this sensory organ as an alternative to the pectinate condition. This is more developed in *Modulus.*

32. Distance from the left margin of the pallial cavity: 0= close; 1= far (*Cerithium atratum, Alaba incerta, Serpulorbis decussatus*) (CI= 33, RI= 0).

33. Satellite fold: 0= absent; 1= at left (*Aylacostoma exoplicata*); 2= both sides (*Bittium varium, Finella dubia, Alaba incerta*) (CI= 100, RI= 100, not additive).

Two types of satellite osphradial folds, apparently of independent origin, were found, a type in *Aylacostoma exoplicata,* restrict to the left side of osphradium, located between it and left margin of the pallial cavity. Other type occurs in miniaturized forms (*Bittium, Finella* and *Alaba*) surrounding almost entire the osphradium length (except for the posterior region) and appeared as a shared synapomorphy. A similar fold was also described for *Faunus ater* (Linné) (cf. Houbrick, 1991b) but sited at right of osphradium, between the later and the ctenidial vein (Houbrick, 1991b, fig. 23B: glandular ridge). The satellite fold resembles a little the endostyle present in filter feeding gastropods such as Crepidulidae and Struthiolariidae (person. obs.)

Ctenidial vein

34. Width: 0= normal (discretely broader than osphradium); 1= very broad (*Doryssa* spp.) (CI= 100, RI= 100).

The ctenidial vein may be a contractile organ, even so, the degree of dilatation appears to be a distinctive feature of examined *Doryssa* species. For instance, in *D. ipupiara*, the posterior region of this vessel is broader than the gill.

35. Posterior region free from gill: 0= long; 1= short (thiarids, *Supplanaxis nucleus*, pleurocerids, cerithids, *Finella dubia, Alaba incerta, Cerithidea costata*) (CI= 50, RI= 87).

Most cerithioideans have the posterior end of the gill close to the pericardium and the ctenidial vein penetrates the pericardium immediately posterior to the gill. Some other cerithioideans, such as *Modulus, Turritella, Batillaria, Campanile* and *Serpulorbis*, have a long section of the ctenidial vein between the gill and the pericardium, comparable to vetigastropods (e.g., *Haliotis, Calliostoma*, person. obs.) outgroups, is regarded as plesiomorphic.

36. Attachment in osphradium: 0= absent; 1= present (*Campanile symbolicum*) (CI= 100, RI= 100).

It is possible that the ctenidial vein not only is attached, but also collects the blood coming from the osphradium leaflets as well usually from the gill leaflets. This matter merits further research.

Head and floor of pallial cavity

37. Head size: 0= normal (about 1/2 of foot width); 1= narrow (about 1/4 of foot width) (*Turritella hookeri*); 2= broad (about same width as foot) (*Doryssa atra, D. macapa, Cerithium atratum, Campanile symbolicum*) (CI= 50, RI= 33, not additive).

38. Food groove in dorsal region of head-foot complex: 0= absent; 1= present (*Turritella hookeri, Serpulorbis decussatus*) (CI= 50, RI= 50).

39. Food groove in right and ventral region of head: 0= absent; 1= present (*Turritella hookeri, Serpulorbis decussatus*) (CI= 100, RI= 100).

The character food groove is separated in the present analysis in two regions: that of dorsal region of head-foot (#38), which are also found in other filter-feeding gastropods, such as Viviparidae, Crepidulidae and Struthiolariidae (person. obs.) (probably not homologous); and that part of the groove surrounding the right and ventral region of the head (#39), this part is absent in other groups.

Gill

40. Base of filaments: 0= broad; 1= narrow (pleurocerids, *Turritella hookeri, M. modulus, Serpulorbis decussatus*) (CI= 25, RI= 57).

41. Tip position in filaments: 0= central; 1= right (*Aylacostoma exoplicata; Supplanaxis nucleus, Turritella hookeri*) (CI= 33, RI= 0).

42. Tip form: 0= sharp; 1= rounded (pleurocerids); 2= flat (*Finella dubia*) (CI= 100, RI= 100, not additive).

43. Filament height and thickness: 0= short and thin; 1= tall and thin (*Turritella hookeri, Serpulorbis decussatus*); 2= tall and thick (*M. modulus*) (CI= 66, RI= 50, not additive).

44. Area between gill and rectum: 0= broad; 1= narrow (*Bittium varium, Finella dubia, Alaba incerta, Batillaria minima, Cerithidea costata, Serpulorbis decussatus*) (CI= 20, RI= 33).

45. Visible vessels between gill and rectum: 0= absent; 1= present (*Aylacostoma exoplicata, A. tenuilabris, Doryssa atra, D. macapa, Campanile symbolicum*) (CI= 25, RI= 25).

The gill of caenogastropods is greatly modified in relation to those of most examined archaeogastropod outgroups, making comparison difficult. Comparison with the Neritimorpha (*Neritina, Nerita*, person. obs.), and *Addisonia enodis* Simone, 1996a (Cocculiniformia) were performed. The distance between the gill and rectum appears to increase in some cerithioidean groups, especially those groups with some environmental adversity, such as estuarine and fresh-water species. In some species, inclusive, transverse vessels are clearly present in this area. The transverse vessels the in roof of the pallial cavity resemble the adaptation in air-breading prosobranchs as, e.g., *Helicina* (Neritimorpha) and Cyclophoridae (Architaenioglossa) (person. obs.). Transverse vessels between the gill and the rectum are also clear in *Campanile.*

Hypobranchial gland

46. Aspect: 0= thick, with chambers; 1= thin, smooth, solid (all taxa except *M. modulus*) (CI= 100, RI= 100).

The hypobranchial gland with several inner chambers and folds is the normal condition in vetigastropods and littorinids, this condition occurs among cerithioideans only in *Modulus*. It is regarded here as the plesiomorphic state. In the remainder of the examined species the hypobranchial gland is a thin, homogeneous glandular layer, even in *Campanile*. In this species, however, some specimens (but not all) develop a tall glandular fold of homogeneous glandular tissue (fig. 412).

Adrectal sinus

47. Type: 0= inconspicuous; 1= very broad, associated with the kidney lobe (thiarids); 2= very broad, associated with large nephrostome (pleurocerids) (CI= 100, RI= 100, not additive).

The adrectal sinus is generally inconspicuous, but in some cerithioideans it is well developed, becoming a large chamber where the rectum runs free. This condition, regarded as apomorphic, occurs in the freshwater thiarids and pleurocerids and is absent in remainder ingroup species and also in all outgroups. The relationship between the adrectal sinus and the kidney, however, differs in both families as above explained.

Rectum

48. Width: 0= medium (about 1/8 of pallial cavity width); 1= wide (about 1/4 of pallial width) (all cerithioideans **except** the following); 2= narrow (*Bittium varium, Finella dubia, Alaba incerta*) (about 1/16 of pallial width) (CI= 100, RI= 100, additive).

49. Fecal pellets: 0= aligned; 1= oblique/compacted (all cerithioideans except *Finella dubia* and *Campanile symbolicum*) (CI= 33, RI= 66).

50. Inner surface: 0= smooth; 1= oblique folds (*Aylacostoma exoplicata*) (CI= 100, RI= 100).

51. Anus site: 0= near mantle border; 1= far from mantle border (all cerithioideans **except** thiarids and pleurocerids) (CI= 25, RI= 72).

The rectum of the cerithioideans is characteristically very wide, this state is different from those of the examined outgroups, it is regarded as apomorphic. The miniaturized forms (*Bittium, Finella* and *Alaba*), however, present a narrow rectum, apparently due to reversal. The wide rectum generally contains great quantities of fecal pellets obliquely compacted, a condition not observed in the examined outgroups and regarded also as apomorphic (see Bandel, 1974 for more comments). There are two exceptions, in *Campanile* and *Finella* the fecal pellets are aligned longitudinally. The anus of all examined cerithioideans is siphoned, i.e., preceded by a part of the rectum detached from the mantle. Observation of live specimens shows that the siphoned anus appears to be an adaptation for approaching it to mantle border during evacuation, with subsequent retraction. Siphoned anus is also found in vetigastropods (e.g., *Haliotis*) and littorinids, and could be plesiomorphic.

Kidney

52. Lobes: 0= single; 1= two, anterior lobe in mantle roof (*Melanoides tuberculatus*); 2= two, anterior lobe attached to rectum, anterior lobe mostly solid (*Aylacostoma tenuilabris*); 3= same, with anterior lobe mostly hollow (*Aylacostoma exoplicata, A. ci*) (CI= 100, RI= 100, additive).

53. Tissue arrangement: 0= solid; 1= hollow, with two chambers (thiarids); 2= hollow, with single chamber (pleurocerids); 3= very large and complex (*Campanile symbolicum*) (CI= 100, RI= 100, not additive).

54. Length: 0= less than 1/4 whorl; 1= more than 1/4 whorl, double lobed (thiarids); 2= more than 1/4 whorl, single lobed (pleurocerids); 3= more than 1/2 whorl (*Campanile symbolicum*) (CI= 100, RI= 100, not additive).

The kidney is obviously more complex in freshwater groups. In pleurocerids several complex folds appeared, representing a large increase of renal surface. In thiarids, beyond folded chambers, the kidney is divided into 2 lobes; in *Melanoides* the anterior lobe of the kidney stays within the membrane between the kidney and the pallial cavity, while in *Aylacostoma* spp the anterior lobe runs anterior-right, attached to the rectum. Apparently the thiarid bilobed kidney is not equivalent to the bilobed kidney of other gastropods (e.g., tonnids, see Simone, 1995b), because the rectum does not cross between both lobes. The disposition and type of the renal inner folds, in both families, are of great value for species comparison, but of little value in higher systematics. Observing the details of the pleurocerid and thiarid kidneys, it is difficult infer any close relation between them.

The kidneys of marine forms are generally very simple and short, appearing as a undifferentiated solid tissue. *Campanile*, however, is an exception in having a very large, complex kidney.

55. Nephrostome: 0= slit-like, situated about in center of membrane; 1= slit-like, situated close to rectum (thiarids); 2= wide opened, protected by a flap of gonoduct (pleurocerids) (CI= 100, RI= 100, not additive).

In most cerithioideans, like other caenogastropods, the nephrostome is a slit, surrounded by thin muscular fibers, and is located approximately in the center of the membrane that separates the kidney from the pallial cavity. This condition is considered plesiomorphic. However, in the two freshwater groups, this condition is modified. In the thiarids the nephrostome is located to the right, very close to the rectum and partially closed by it. The pleurocerids have also the nephrostome close to the rectum, but it is very wide, apparently without muscular fibers, and protected on the left and ventrally by a flap inserted in the outer lamina of the pallial gonoduct. This flap may be the homologue of the cyrtophore organ or seminal receptacle of *Pleurocera acuta* and *Goniobasis livescens* (see Dazo, 1965, fig. 9 and pl. 4). The kidney of the ingroup animals could an interesting structure for histological and ultrastructural comparative study, and it is possible that several other characters could appear, including the possibility that pleurocerids have an ureter.

Heart

56. Aortas attachment: 0= free from stomach; 1= in style sac and adjacent intestine (all cerithioideans except *Campanile symbolicum*) (CI= 50, RI= 80).

The heart of the cerithioideans, although of normal monotocardian type, present a great value for the identity of the superfamily, in having the aortas attached directly to the style sac (only separated by pericardium membrane), and sometimes in adjacent intestinal loops. This condition was not found in any other examined gastropod, which have, in general, a portion of gonad and digestive gland, or even kidney tissue, between stomach and pericardium. The cerithioidean condition may be due the great development of stomach, but is not explained by this phenomenon alone. The examined hydrobioids, which present also a proportionally large stomach, there is some separation (even small) between style sac and pericardium (see, e.g., Simone & Moracchioli, 1994, on *Pothamolithus* spp.). Among the cerithioideans, the attachment of the aortas to the style sac is less evident in those species with reduction of style sac, such as *Serpulorbis* and *Campanile*.

57. Site: 0= anterior-left from kidney; 1= posterior to kidney (all cerithioideans) (CI= 100, RI= 100).

The position of the pericardium posterior to the kidney is a character shared with some other caenogastropods such as littorinids.

Digestive system
Buccal mass

58. Site: 0= posterior to snout; 1= part within snout (thiarids, *Supplanaxis nucleus*, pleurocerids, cerithids, *Finella dubia, Alaba incerta, Batillaria minima, Cerithidea costata*) (CI= 100, RI= 100).

This character has relation to the length of the oral tube, which connects the mouth with the buccal mass. The oral tube is very short and wide in above listed species.

59. Jaw size: 0= normal; 1= very large (*Campanile symbolicum*); 2= small, inserted in a membrane (*Supplanaxis nucleus, Batillaria minima*) (CI= 66, RI= 0, not additive).

The jaws consisting of two plates are found in all examined species of cerithioideans, and are like those seen in several outgroups of vetigastropods (e.g., *Haliotis* spp.; Simone, 1997). The size of the jaws, however, presents valuable comparative data. Although apparently subjective, careful examination leaves little doubt as to in which category the jaws belong. Most cerithioideans have jaws of medium size, but in *Campanile* the jaws are exceptionally large (fig. 416) (Houbrick, 1981a). In *Supplanaxis* and *Cerithidea* the jaws are very small, almost vestigial, as two small triangular plates attached to a flaccid transparent membrane (fig. 74). The functional utility of each jaw type is an interesting topic for future research.

Odontophore

The cerithioidean odontophore is different of any other known among the prosobranchs, both archaeogastropods and higher caenogastropods, in lacking muscles in both extremities of the radular ribbon. This character could be extremely valuable if the odontophore of littorinids and hydrobioids were not surprisingly similar. Although the names for each muscle are given in the descriptions, obviously these can be changed with further functional or phylogenetic analysis. For this reason, each muscle (or pair of muscles) is referred to by its number (e.g., m4). Although functional experiments have not been performed, muscle function can be suggested based on the anatomical disposition. The radula in the cerithioidean odontophore does not appear to work in a back-and-forth movement of the radular ribbon, gliding on cartilages, as in most other gastropods. The muscles of the cerithioidean odontophore apparently work firmly holding the radula and the subradular cartilage to the odontophore, and the whole odontophore works as a grazer. Apparently the glide between radula and cartilages is absent.

The configuration of the musculature of the cerithioideans odontophore provides valuable systematic and phylogenetic data, but has been poorly examined. Some data is given by Starmühler (1969, on *Melanatria, Cleopatra* and *Melanoides*) which, together with the data given herein, may be the basis of further systematic and functional studies.

60. M2: 0= present; 1= absent (*Turritella hookeri, Campanile symbolicum, Serpulorbis decussatus*); 2= narrow and long, inserting posteriorly (cerithids, *Finella dubia, Alaba incerta*) (CI= 66, RI= 83, not additive).

The pair of retractor of buccal mass (m2) and the horizontal muscle (m6) are the only muscles with more obvious correlation with odontophore muscles of the other gastropods. The pair m2 is, however, absent in *Campanile, Turritella* and *Serpulorbis*, the loose condition is regarded as apomorphic.

61. M3: 0= absent; 1= present (*Aylacostoma exoplicata, A. ci*) (CI= 100, RI= 100).

62. M4: 0= turned posterior; 1= turned anterior (*Serpulorbis decussatus*) (CI= 50, RI= 0).

The m4 (and other muscles) are inverted in *S. decussatus* when compared with those of other cerithioideans, a condition shared with *Littorina flava* (Simone, 1998), and probably is an outgroup convergence.

63. M5 origin in m4: 0= median; 1= lateral (all cerithioideans) (CI= 100, RI= 100).

64. Union m5-m5: 0= absent; 1= present (all cerithioideans except *M. modulus*) (CI= 100, RI= 100).

65. Horizontal muscle (m6): 0= normal (somewhat thin); 1= very thick (*Campanile symbolicum*) (CI= 100, RI= 100).

66. Site of m6: 0= dorsal; 1= anterior-ventral (*Serpulorbis decussatus*) (CI= 50, RI= 0).

Other character shared with *Littorina flava* and also probably due to inversion of odontophore.

67. Anterior thickness of m6: 0= absent; 1= present (pleurocerids) (CI= 100, RI= 100).

68. Connection of m7 with m4: 0= present; 1= absent (thiarids, *Doryssa* spp., cerithids, *Finella dubia, Alaba incerta, Campanile symbolicum*) (CI= 25, RI= 70).

69. Connection m7-m11 with snout: 0= absent; 1= present and anterior (*Aylacostoma exoplicata,*

Melanoides tuberculatus, M. modulus, Cerithidea costata); 2= present and posterior (pleurocerids) (CI= 33, RI= 42, not additive).

70. Connection of m7 with cartilages: 0= absent; 1= present (*Aylacostoma tenuilabris, Melanoides tuberculatus, Bittium varium, Batillaria minima, Cerithidea costata*) (CI= 20, RI= 0).

71. M8: 0= absent; 1= short and broad (*Turritella hookeri, M. modulus, Campanile symbolicum, Serpulorbis decussatus*); 2= narrow and long (pleurocerids, *Batillaria minima*) (CI= 50, RI= 83, additive).

72. M8: 0= absent; 1= connected to outer membrane around odontophore (*Turritella hookeri, M. modulus, Campanile symbolicum, Serpulorbis decussatus*); 2= free from any membrane (pleurocerids, *Batillaria minima*) (CI= 50; RI= 83, additive).

The m8 is a single muscle that connects the radular nucleus with the odontophore in some cerithioideans. When present, it may have two forms: short and broad or long and narrow. Nothing similar to m8 was found in the outgroups.

73. M10: 0= origin in m4; 1= origin in m5 (all cerithioideans except pleurocerids and *M. modulus*) (CI= 50, RI= 88).

74. M10 very thick, forming a single block: 0= absent; 1= present (*Turritella hookeri, Serpulorbis decussatus*) (CI= 100, RI= 100).

75. M11: 0= origin in m4; 1= free from m4 (all cerithioideans) (CI= 100, RI= 100).

76. M11a: 0= absent, 1= present (*Doryssa ipupiara, D. atra, Supplanaxis nucleus*) (CI= 33, RI= 0).

77. M11: 0= part of m4; 1= attached to subradular membrane (all cerithioideans) (CI= 100, RI= 100).

The complex m7-m11 is another peculiarity of the cerithioidean odontophore. Typically, the m11 is that pair of small muscles inserted in the inner surface of the subradular membrane and originating in the buccal region. The pair m7 originates from m11 and the adjacent region of the subradular membrane and inserts in the radular sac. However, there is great variation among the species examined. Sometimes differentiation of m7 and m11 is difficult, mainly in those cases where no insertion in the buccal region exists. Examination of the outgroups show the m7-m11 complex originated from the median-dorsal margin of m4, inserting directly in the radular sac. Apparently, in cerithioideans, the m7-m11 complex separated from m4, situating nearer median line, attached only in subradular membrane (and not in m4). In several cerithioideans, the m7-m11 complex developed muscular connections with the buccal muscles, the anterior region of the cartilages, and other adjacent areas. Variation occurs within species of single genera (e.g., *Aylacostoma*), and while this character may be of great value for species comparisons, it is of less value in analyzing higher level relationship. In the examined pleurocerids, the connection with the mouth is posterior, almost in the transition of the snout with foot. Several annex muscles of the m7-m11 complex were detected, but they are also of poor value at higher systematic levels.

78. Length of m12: 0= small; 1= long (*Aylacostoma exoplicata, A. ci*) (CI= 100, RI= 100).

79. M12: 0= absent; 1= present (all cerithioideans) (CI= 50, RI= 66).

A distinctive character of cerithioideans is the presence of the pair of muscles m12, which apparently may have the function of complementing the action of the horizontal muscle. The m12 pair is present in all examined cerithioideans, including *Campanile symbolicum*, and absent in other examined groups. A somewhat similar pair of muscle are found in viviparids and ampullariids, but disposed more longitudinal.

80. M15 (annex of m10): 0= absent; 1= as part of buccal walls (*Doryssa* spp); 2= free from buccal walls (*Melanoides tuberculatus*) (CI= 100, RI= 100, not additive).

81. M16: 0= absent; 1= present (pleurocerids) (CI= 100, RI= 100).

Radula

82. Radula length: 0= long (about double than odontophore length); 1= short (about same length as the odontophore) (thiarids, *Turritella hookeri, M. modulus,* cerithids, *Finella dubia, Alaba incerta, Cerithidea costata, Campanile symbolicum, Serpulorbis decussatus*) (CI= 20, RI= 50).

83. Radular marginal teeth: 0= spoon shaped; 1= hooked (*Turritella hookeri, Bittium varium, Finella dubia, Alaba incerta, Campanile symbolicum, Serpulorbis decussatus*) (CI= 50, RI= 80).

Several radular characters were analyzed, but they were almost all inconclusive or autapomorphic. Except the length, the single other radular character of interest in the studied species is the form of the marginal teeth. Most cerithioideans have the spoon-like marginal teeth, with the distal end broad and generally with cusps in its distal edge. Due to similarity with the marginal teeth of the examined outgroups (e.g., basal caenogastropods), the spoon-like form is regarded as plesiomorphic. On the other hand, some species have marginal teeth that are rook-like, i.e., sharp pointed distal end, with or without secondary small cusps edging it. This type occurs in *Campanile, Turritella, Serpulorbis* and in the miniaturized forms *Bittium, Finella* and *Alaba.* Other comments on radula characters see Bandel (1984).

Salivary glands

84. Site of glandular tissue: 0= only posterior to nerve ring; 1= anterior and posterior to nerve ring (*Supplanaxis nucleus, Doryssa ipupiara, D. macapa, Pachychilus sp., M. modulus, Campanile symbolicum*); 2= only anterior to nerve ring (*Doryssa atra*) (CI= 40, RI= 50, additive).

The salivary glands of cerithioideans are generally typical of the basal gastropodan grade. The glandular part stay posterior the to nerve ring, edging the esophagus. The ducts, attached to the esophagus, pass through the nerve ring and open in the dorsal wall of the buccal mass. Some species have a glandular tissue also anterior to the nerve ring, as *Supplanaxis, Modulus* and *Campanile.* But this phenomenon is very unusual among the pleurocerids, where most of glandular tissue is anterior to the nerve ring and, at least in *Doryssa atra,* the salivary glands are only anterior to the nerve ring (there is no branch through it) resembling slightly what happen in neogastropods. Something similar occurs in *Faunus ater* (cf. Houbrick, 1991b: 47). The location of the salivary ducts opening is given in the description of each species, however, this character is very difficult to observe, generally the observation being based on external view by transparency. Maybe detailed histological examination may change the detail.

85. Site in haemocoel: 0= around esophagus; 1= extending posterior by haemocoel (*Doryssa ipupiara, D. atra, Batillaria minima*) (CI= 33, RI= 0).

Buccal mass

86. Folds in dorsal wall of buccal mass: 0= a pair; 1= two pairs (*Melanoides tuberculatus, Supplanaxis nucleus, Doryssa atra*) (CI= 33, RI= 0).

87. Buccal ganglia site: 0= near median line; 1= lateral (thiarids, *Supplanaxis nucleus,* pleurocerids, cerithids, *Finella dubia, Alaba incerta, Batillaria minima, Cerithidea costata*) (CI= 100, RI= 100).

The site of the pair of buccal ganglia in outgroups and in some cerithioideans, is on the dorsal wall of the buccal mass, near the median line. Although, in most examined cerithioideans, the buccal ganglia have lateral, sometimes very close to insertion of m2; with a long connective uniting both. This condition is regarded as apomorphic based on comparisons with state of the outgroups. In thiarids, the buccal ganglia are pigmented and very large.

Esophagus

88. Inner surface: 0= two pouches; 1= one pouch (pleurocerids); 2= several narrow longitudinal folds (thiarids); 3= few (2-4) broad longitudinal folds (*Bittium varium, Finella dubia, Cerithidea costata*); 4= transversal folds (*Alaba incerta*); 5= smooth (*Serpulorbis decussatus*) (CI= 71, RI= 77, not additive).

89. Middle esophagus inner surface: 0= transversal folds; 1= papillate (pleurocerids); 2= longitudinal folds (thiarids, *Bittium varium, Finella dubia, Cerithidea costata, Campanile symbolicum*); 3= smooth (*Serpulorbis decussatus*) (CI= 37, RI= 54, not additive).

90. Pouch form: 0= open; 1= small lobes (*Campanile symbolicum*) (CI= 100, RI= 100).

91. Glandular tissue: 0= present; 1= absent (all cerithioideans **except** *M. modulus*) (CI= 50, RI= 75).

The esophagus with a pair of glandular pouches is found among vetigastropods (e.g., *Haliotis, Pleurotomaria*, person. obs.) and in some cerithioideans. This condition is regarded as plesiomorphic. However, clear glandular pouches are only found in *Modulus*; the other cerithioideans having a pair of pouches, there are only oblique folds, without clear glandular tissue (the walls are thin). Two other esophageal conditions occur among cerithioideans. The first is that of pleurocerids (Abbott, 1955; this study), which have only one large pouch lined internally by tall papillae (similar to those which occur in inner surface of pouches of the vetigastropods). The other derived condition is the esophagus being a single tube, presenting, at most, longitudinal folds. This is found in thiarids, *Bittium, Finella, Cerithidea* and *Serpulorbis*. In *Campanile*, the pouches are reduced and differentiated, becoming two semispherical chambers situated laterally anterior to the nerve ring; apparently the *Campanile* pouches are homologous to pouches of other cerithioideans as well as of the littorinids (Simone, 1998) and architaenioglossans (Ponder & Lindberg, 1997).

Stomach

92. Width: 0= narrow; 1= broad (all cerithioideans) (CI= 100, RI= 100).

The stomachs of cerithioideans are characteristically very large - almost completely separating the anterior from the posterior regions of the body, and occupies about a half whorl. This condition is not found in the archaeogastropods and is regarded as apomorphic.

93. Central pad: 0= absent; 1= flap-like (*Turritella hookeri, M. modulus, Campanile symbolicum, Serpulorbis decussatus*); 2= broad fold (remaining cerithioideans); 3= with acinous lobe (*Doryssa atra, D. macapa*) (CI= 100, RI= 100, additive).

94. Central pad a broad fold: 0= long; 1= short (*Bittium varium, Finella dubia, Alaba incerta*) (CI= 100, RI= 100).

In the ventral gastric surface of cerithioideans there is a central pad. This structure surrounds the duct to the digestive gland and it is situated between this duct and the gastric shield. The central pad is found in 2 main forms: 1) flap-like, relatively thin and free (*Modulus, Turritella, Serpulorbis* and *Campanile*), and 2) a broad large fold, greatly attached to gastric surface (other species). In this last case, the central pad may become very complex, with several folds, some of them with differentiated acina, as in some pleurocerids (Binder, 1959, fig. 8 of *Potadoma*; Starmühlner, 1969; this study) and in *Faunus* (Houbrick, 1991b, fig. 24).

95. Crescentic ridge: 0= absent; 1= part of central pad (*Aylacostoma* spp., pleurocerids, *Bittium varium, Finella dubia, Alaba incerta, Cerithidea costata*); 2= isolated from central pad (*Melanoides tuberculatus, Cerithium atratum*) (CI= 50, RI= 81, additive).

96. Crescentic ridge form: 0= ridge-like; 1= broad (*Bittium varium, Finella dubia, Alaba incerta*) (CI= 100, RI= 100).

The crescentic ridge is another structure found on the ventral inner surface of the stomach; this ridge generally surrounds the posterior region of the central pad and may, or may not, fuse with it some point. The crescentic ridge is broad and almost of the same size than central pad in miniaturized forms (*Bittium, Finella* and *Alaba*) and in *Diastoma melanoides* (Houbrick, 1981c, fig. 5G).

97. Ducts to digestive gland: 0= two; 1= single (all taxa except *Campanile symbolicum* and *Serpulorbis decussatus*) (CI= 33, RI= 66).

Most cerithioideans have a single duct to the digestive gland, in contrast with double ducts of some other caenogastropods [e.g., littorinids (Simone, 1998), tonnids (Simone, 1995b), nassarids (Simone, 1996b)]. In some in hydrobioids, both conditions can occur, showing that this character (single or double duct to digestive gland) can change. Two examined species (*Campanile symbolicum* and *Serpulorbis decussatus*) have 2 ducts to the digestive gland. In *S. decussatus*, these ducts are widely separated with each other and even the digestive gland is divided in two separated lobes. The condition of a double duct is regarded as plesiomorphic, but the analysis of the tree revealed the possibility of reversion. If so, these two species (and maybe the members of each family) developed from species with single duct. This has been observed in examined *Aylacostoma* spp.; *A. exoplicata and A. ci* have single duct, while *A. tenuilabris* has 2 and even, in some specimens, 3 ducts to digestive gland (inserted directly in stomach). These data, in congener species, demonstrates that reversion to a double duct in the stomach is possible. Due to the proximity of *A. tenuilabris* digestive gland ducts in stomach, this species state has been scored in same state of other *Aylacostoma* spp.

98. Style sac and intestine: 0= entirely fused; 1= separated by a constriction (pleurocerids, *Turritella hookeri,* cerithids, *Finella dubia, Alaba incerta, Batillaria minima*); 2= entirely separated with each other (thiarids, *M. modulus, Cerithidea costata*) (CI= 22, RI= 41, additive).

The assumed plesiomorphic condition of the separation of the style sac from the intestine is found in littorinids, with almost no separation between the intestine and style sac (present in *Supplanaxis, Campanile* and *Serpulorbis.* Separation of the intestine and style sac by a constriction, but united anatomically by a narrow aperture; is seen in pleurocerids, *Cerithium, Bittium, Finella, Alaba, Batillaria* and *Turritella.* A third condition has the intestine altogether separated from the style sac since their origin; this condition having found in thiarids, *Modulus* and cerithideids. The intestine separated from style sac is regarded as the apomorphic end of a transformation series, and is homoplastic with hydrobioids. (An interesting additional discussion on alimentary canal of some cerithioideans is found also in Graham, 1939.)

99. Pre-intestinal fold: 0= absent; 1= double (thiarids, *Campanile symbolicum*); 2= single (*Doryssa atra, D. macapa, Pachychilus sp*) (CI= 50, RI= 66, not additive).

100. Intestinal typhlosole: 0= absent; 1= present (thiarids, *Campanile symbolicum*) (CI= 50, RI= 75).

101. Fold at left, posterior to those folds which precede the intestine: 0= absent; 1= present (*Aylacostoma* spp) (CI= 100, RI= 100).

The ventral inner surface of the stomach of some cerithioidean species is very complex, with folds and sorting areas. Most of the searched characters are autapomorphic, except those above listed. The nomenclature follows in general that of Houbrick papers.

102. Anterior chamber of stomach: 0= absent; 1= present (all cerithioideans) (CI= 100, RI= 100).

The anterior chamber, delimited posteriorly by a constriction, generally shows a smooth surface and precedes the intestine-style sac apertures. Presence of this anterior chamber, absent in all examined outgroups, is regarded as apomorphic.

103. Style sac length: 0= about 1/2 stomach length (or 1/4 whorl); 1= very long (about than 1 whorl) (*Cerithidea costata*); 2= inconspicuous (*Campanile symbolicum, Serpulorbis decussatus*) (CI= 40, RI= 0, not additive).

The style sac of *Campanile* and *Serpulorbis* is hard to delineate. In the former species it maybe reduced or only a small part of the intestine, and in *Serpulorbis* it may be very widely open to the stomach (see also Morton, 1951a, fig. 9). In contrast *Cerithidea* has a very long of style sac, its length more than half a whorl, and it invades the pallial cavity (see also Driscoll, 1972).

104. Esophagus aperture: 0= anterior; 1= middle (all cerithioideans except *Alaba incerta, Batillaria minima* and *S. decussatus*); 2= posterior (*Serpulorbis decussatus*) (CI= 40, RI= 57, not additive).

The entrance of esophagus in the stomach is generally situated in its middle-right region, in contrast with stomach of basal caenogastropods (littorinids, hydrobioids) in which the esophagus aperture is almost at the same level as the style sac. The anterior migration of the esophageal aperture is only found in *Alaba* and *Batillaria* among the examined cerithioideans. *Serpulorbis*, in contrast, has a posterior esophageal aperture.

105. Digestive gland: 0= single; 1= double (*Serpulorbis decussatus*) (CI= 100, RI= 100). See comments in character 92.

106. Digestive gland anterior limit: 0= anterior to stomach; 1= middle (thiarids, pleurocerids, *Turritella hookeri*, cerithids, *Finella dubia, Alaba incerta, Batillaria minima, Cerithidea costata*); 2= posterior (*Supplanaxis nucleus*) (CI= 50, RI= 71, not additive).

107. Intestinal loops: 0= several; 1= up to two (thiarids, *Supplanaxis nucleus*, pleurocerids, cerithids, *Finella dubia, Alaba incerta, Cerithidea costata*) (CI= 100, RI= 100).

Genital system

108. Gonad site: 0= around digestive gland; 1= superior region of digestive gland only (all cerithioideans) (not examined in *Campanile symbolicum*) (CI= 100, RI= 100).

109. Pallial oviduct: 0= simple groove; 1= glandular groove (probably with a chamber in each lamina) (all cerithioideans) (CI= 100, RI= 100).

110. Chamber in outer lamina of pallial oviduct: 0= single; 1= none (pleurocerids, *Cerithium atratum, Cerithidea costata, Campanile symbolicum*) (CI= 25, RI= 50).

111. Chamber in inner lamina of pallial oviduct: 0= single, 1= none (*Aylacostoma exoplicata, A. ci, Melanoides tuberculatus, Finella dubia, Campanile symbolicum, Serpulorbis decussatus*); 2= double (*Supplanaxis nucleus*, cerithids) (CI= 28, RI= 28, not additive).

112. Some genital chamber outside of oviduct: 0= absent; 1= in kidney (*Cerithium atratum*); 2= in pericardium (*Campanile symbolicum*) (CI= 100, RI= 100, not additive).

These states are not homologous, as confirmed by the tree, and are regarded as not additive.

113. Degree of closure of pallial oviduct: 0: almost entirely open (a furrow); 1= posterior half closed (a half tube) (*Aylacostoma* spp); 2= entirely closed (a tube) (*Melanoides tuberculatus*) (CI= 33, RI= 55, additive).

The open condition of cerithioidean pallial gonoducts has been regarded as secondary by some authors, i.e., derived from closed ducts (Fretter 1951: 583; Johansson 1956; Houbrick 1988). This possibility obviously exists, but cannot be advocated "a priori". Within and outside cerithioideans both conditions occur. Within cerithioideans most taxa have both spermduct and oviduct almost entirely open (a short region in posterior extremity is closed), but closure in different degrees, from half- to entirely closed, occur in Thiaridae and Cerithideidae. In other Caenogastropoda, open pallial oviducts are uncommon, occurring in some Littorinoidea and Rissoidae (Johansson 1956; Ponder 1976) and strombids (person. obs.). On the other hand, open pallial spermducts are common, Tonnidae and Olividae, for example, have it entirely open (Marcus & Marcus 1959; Simone 1995b; person. obs.). Costellariidae have it partially opened (Ponder 1972; Simone 1995c). Pallial gonoducts also occur in other groups beyond caenogastropods, such as Cocculiniformia, Neritimorpha and Architaenioglossa and basal Heterobranchia. Comparison is difficult as homology of these structures is uncertain, and both conditions, open and closed, occur. In the present analysis the open condition is regarded as plesiomorphic, in agreement with Haszprunar (1988: 388).

The pallial oviduct, in cerithioideans, is more than a single groove. All examined species have a very glandular pallial oviduct and sometimes it has other glands and chambers (receptacle, bursa and others). The presence and the number of accessory structures in the inner and outer lamina of pallial oviduct appears to be of great value in species comparison, but of little value at higher levels. Several conditions can be found in species of the same group (see, e.g., Houbrick, 1992a). The polarization of pallial oviduct structures is difficult, as there is no clear homology of these structures with those of the examined outgroups.

Observing the disposition of the species in the tree, and their pallial oviducts, it was possible to note that the basic plan of this organ is the following. A deep open glandular furrow with a small chamber in each lamina (bursa and receptacle) as in *M. modulus* and other species. Although each small chamber disappeared or duplicated in species of different groups. In general, however, the pallial oviduct variation turns around that basal standard.

Johansson (1953) provides additional discussion of pallial oviduct possible evolution.

114. Ovopositor: 0= absent; 1= present (*Doryssa macapa, Pachychilus* sp, *Turritella hookeri, M. modulus,* cerithids, *Alaba incerta, Cerithidea costata*) (CI= 14, RI= 14).

Several female cerithioideans present an obvious ovopositor in the right side of the head-foot, at the anterior extremity of a ciliated furrow that originates in the anterior extremity of the pallial oviduct. Other cerithioideans have the furrow but no clear ovopositor; this condition indicating an absence of this structure, or that this structure is present but not anatomically defined. In these cases the taxon is considered having the plesiomorphic state. In single genera (e.g., *Doryssa*) some species have an ovopositor while others do not. The ovopositor is regarded as apomorphic due its absence in all examined outgroups, including higher caenogastropods. However, at least in *Littorina ziczac* (Gmelin, 1791) an ovopositor is apparently present (Marcus & Marcus, 1963). Observing the tree, the ovopositor is one of the cerithioidean synapomorphy, however, it disappeared or becoming anatomically undefined in some taxa.

115. Ciliated furrow in right side of head: 0= absent; 1= present (all cerithioideans) (CI= 100, RI= 100).

116. Aperture on right side for a inner brood pouch: 0= absent; 1= present (thiarids, *Supplanaxis nucleus*) (CI= 100, RI= 100).

117. Development of an epithelial chamber within haemocoel-foot muscles: 0= absent; 1= present (thiarids, *Supplanaxis nucleus*) (CI= 100, RI= 100).

118. Brood pouch: 0= absent; 1= dorsal and single (thiarids); 2= ventral and double (*Supplanaxis nucleus*) (CI= 100, RI= 100, not additive).

119. Number of embryos in brood pouch: ?= inapplicable (brood pouch absent); 1= up to 20 (*Aylacostoma* spp); 2= about 100 (*Melanoides tuberculatus*); 3= about 1000 (*Supplanaxis nucleus*) (CI= 100, RI= 100, not additive).

In the case of planaxids and thiarids, the ciliated groove that commences at the anterior extremity of the oviduct does not finish in at an ovopositor, but at the aperture of an inner brood pouch. Except for this feature, no other similarity is found upon examination of the brood pouch of both groups. In planaxids, the brood pouch is double, runs ventral to the esophagus, and stays in the dorsal region of the foot, and contains about a thousand embryos at the same level of development (see also Houbrick. 1987a, 1990). In contrast, the brood pouch of thiarids is single, runs dorsal to the esophagus, stays free in the posterior region of the haemocoel, and contains up to a hundred (in case of *Melanoides* or less than 20 in *Aylacostoma* spp.) young specimens in different growth stages (from one to five whorls). Scott (1953: 443) found only about 3 young specimens in the brood pouch of *Aylacostoma guaratinica*. Berry and Kadry (1974) found an average of 29 - 48 in different samples of *M. tuberculatus*. In the present analysis, the character brood pouch was divided into 2, an entrance in right side of head, at the end of ciliated furrow, and the remainder of the brood pouch. Even with this supposed non-homology, the proximity of the planaxid and thiarids in the obtained tree suggests that these structures may be homologue.

120. Pallial sperm groove: 0= non-glandular; 1= glandular (prostate) (all cerithioideans, **except** thiarids, with no male examined); 2= which a chamber in inner lamina (pleurocerids) (CI= 100, RI= 100, additive).

The aphalate condition of cerithioidean males is controversial. This had been regarded as secondary, i.e., originating from lost of a pre-existent penis (Fretter, 1951: 584; Houbrick 1988), but the same reasoning as for character 113 can be applied here. Aphaly is the condition of the archaeogastropods, but also occurs in some Ctenoglossa (among Caenogastropoda) and in Allogastropoda. Based on parsimony and comparisons with the archaeogastropods, the aphalate condition is also regarded as plesiomorphic. This agrees with Haszprunar (1988) and Ponder & Lindberg (1997).

121. Parthenogenesis. 0= absent; 1= present (thiarids) (CI= 100, RI= 100).

The supposed parthenogenesis is based on the lack of males and on the data of the literature.

Ecology

122. Environment: 0= marine; 1= freshwater (thiarids and pleurocerids) (CI= 50, RI= 85).

Cladistic Analysis

Discussion of cladogram

Comparing the tree obtained in the present study with that shown by Houbrick (1988, fig. 2) for the phylogeny of Cerithioidea at the family level, it is clear that they have little in common. This is probable largely due to the outgroup choice. Houbrick chose Hydrobiidae and Strombidae (Caenogastropoda), while mainly the archaeogastropods were chosen herein (see explanation above). This choice resulted in the inversion of polarization of several important characters. The data of the Houbrick (1988: 102-105) were reanalyzed using the archaeogastropods as outgroup, the inversion of the polarization of the following characters was detected: 1, 2, 7, 8, 9, 10, 11, 14, 19, 20, 26, 28, 33, 35, 37, 40, 42, 43, 49, 50 and 51. The table was copied without any modification, although, some few modifications would be possible to be done with the results of other species analyzed here. The obtained tree (Fig. 442) is the consensus of 4 equal-parsimonious trees. The Turritellidae-Vermetidae inverted their position to the base, with Campanilidae as second branch. This new tree is more or less compatible with the obtained in this study. However, the position of the Modulidae and Batillariidae is quite different (may be the result of the insertion of the study of the other structures such as buccal mass muscles). The cerithioidean synapomorphies of this new tree based on Houbrick data are the following: character #1 (elongate shell), #15 (ciliated groove on right of foot), #43 (sub-esophageal ganglion close from pleural ganglion), #47-48 (sperm details), #53 (seminal receptacle) and #54 (bursa copulatrix).

Comments on nodes

From the nodes, only some with interesting, polemic or dubious data are chosen for some comments.

Node 1. In this study, 23 cerithioidean synapomorphies were detected, these are important for the comprehension and establishment of the superfamily among the Caenogastropoda. Up to present, this taxon was only united by shared plesiomorphies. The great difficult is, however, that most synapomorphies were not maintained in all its representatives, but so modified or even lost at least in one, and sometimes in several groups. However, the odontophoric muscle m11 free from the m4 (character 75) and the muscle m12 (79) are maintained in all examined species, inclusive *Campanile*. From the synapomorphies, those regarded as more important are: papillate mantle border (23), aortas attached directly in stomach (separated only by pericardium membrane) (56), the migration of m11 to median region and detachment from m4 (75), the m8 (72), the m12 (79), the gastric central pad (93) and the ovopositor (114). With a list of cerithioidean synapomorphies known, it is possible do reevaluate some *incertae sedis* taxa with probable close affinity with cerithioideans. Some examples are Abyssochrysidae Houbrick, 1979; Plesiotrochidae Houbrick, 1990b and Provannidae Warén & Ponder, 1991.

Modulus modulus. From those analyzed cerithioideans, *M. modulus* is that which brings the larger quantity of plesiomorphies, including the turbinoid shell shape. However, this species presents an interesting group of highly modified characters, such as more distal position of eyes in tentacles (18), anterior extremity of osphradium with a strong zigzag (31) and the total separation of style sac from intestine (98).

Node 2. This branch reunites all other

Table 1. Character table of examined cerithioideans and outgroups. Abbreviations: Aylac1, *Aylacostoma exoplicata*; Aylac2, *A. ci*; Aylac3, *A. tenuilabris*; Melanoide, *Melanoides tuberculatus*; Planaxis. *Supplanaxis nucleus*; Doryssa1, *Doryssa ipupiara*; Doryssa2 *D. atra*; Doryssa3, *D. macapa*; Pachychil, *Pachychilus* sp.; Turritell, *Turritella hookeri*; Modulus, *Modulus modulus*; Cerithium, *Cerithium atratum*; Bittium, *Bittium varium*; Finella, *Finella dubia*; Alaba, *Alaba incerta*; Batillari, *Batillaria minima*; Cerithidea, *Cerithidea costata*; Campanile, *Campanile symbolicum*; Serpulorbis, *Serpulorbis decussatus*; Potamolith, *Potamolithus ribeirensis*; Viviparus, *Viviparus acerosus*; Littorina, *Littorina flava*; archarogast, pool of archaeogastropods.

taxon	**1 2 3 4 5 6**
	1234567890123456789012345678901234567890123456789012345678901
Aylac1	1011000110000022210000200000020010100000100011111103111111001
Aylac2	1011000110000022210000200000010000100000000001111003111111001
Aylac3	1011000110000022210000200000000000100000000011111002111111000
Melanoide	1011000010000022210000200000010000100000000001111001111111000
Planaxis	1111000010000022210100000000120000100000100001011010000111200
Doryssa1	1011000110000000010200000000010001100001010001211000222111000
Doryssa2	1011000110002000010200000000012001102001010011211000222111000
Doryssa3	1111000110000000010200000000012001102001010011211000222111000
Pachychil	1011000010000000010200010000010000100001010001211000222111000
Turritell	1000000000100000010001101000020000001111101001011010000110010
Modulus	0111000000000000020100100000021000000001002000011010000110000
Cerithium	1011000011000011110110100011020100102000000001011010000111020
Bittium	1012011012100111110020100012020020100000000101021010000111020
Finella	1012011012000111110020100012020020100000020101020010000111020
Alaba	1012001012003111110020000012100120100000000101021010000111020
Batillari	1111000010000000020100100000000000000000000101011010000111200
Cerithidea	1012000010000000010000101100010000100000000101011010000111000
Campanile	11101000000100000211011010 2?0100000120000000110100103300101 10
Serpulor	2000000003201003012011101000100100000111001101011010000110010
Potamolith	0000001000000010001000000000000000000000000000000000000010000
Viviparus	0000000000000011010100000000000000000010100100000000000?010010
Littorina	1000000000000000000000000000000001000000001000000010000010000
archaogast	000000000000100000000000000??0??0000000000000000000000000000 0

taxon	**7 8 9 10 11 12**
	2345678901234567890123456789012345678901234567890123456789012
Aylac1	0110001100010101110010000122011201012111101011110101011111?11
Aylac2	0110001000010101110010000122011201012111101011110101011111?11
Aylac3	0110001010010101010010000122011201012111101011110001011111?11
Melanoide	0110001110010101012010001122011202012110101011110102011112?11
Planaxis	0110000000010111010000101100011200?10000101021110200011123100
Doryssa1	0110011202200111011100110111011201011000101011111000010 00?201
Doryssa2	0110011202200111011100211111011301011200101011111000010 00?201
Doryssa3	0110011202200101011100100111011301011200101011111000110 00?201
Pachychil	0110010202200101010100100111011201011200101011111000110 00?201
Turritell	0110000001111101010011000000 0111?0?11000101010110000110 00?100
Modulus	0100000101100101010010100000 0011?0?12000101000110000110 00?100
Cerithium	0110001000010101010010000100011202011000101011111210110 00?100
Bittium	0110001010010101010011000132011211111000101011110200110 00?100
Finella	0110001000010101010011000132011211111000101011110100010 00?100
Alaba	0110001000010101010011000140011211111000100011110000110 00?100
Batillari	0110000012210101010000010100011200?11000100010110000010 00?100
Cerithidea	0110000110010101010010000132011201012000111011111000110 00?100
Campanile	0111000001110101010011100002 1111?0?00110120000?1112001000?100
Serpulor	1110101001111101010011000053 0111?0?00000122100110100010 00?100
Potamolith	0000000000000000000010000052010000?02000000020010?0200000?101
Viviparus	0000000100000000010010000002000000?000000200000 10?0200000?101
Littorina	10001000000000000000000000000000?0?000000000000???0200000??00
archaogast	0??000???0000??000000?000000000000?000000 2000000??0000000?000

cerithioideans except *Modulus*. The main character is the modification of shell in a turriform shape (1); there are also the loss of glandular tissue in esophagus (91) and the simplification of hypobranchial gland (46), among other characters.

Node 3. It was a surprise to reunite *Campanile* with *Serpulorbis* and *Turritella*, occurred by 8 synapomorphies, being the most important the loss of determinate growth in shell (4) and loss of m2 (60). There is also the possibility of duplication of ducts to digestive gland (a reversion), but this character was not found in *T. hookeri*. There are two possibilities, the preferred here is that *T. hookeri* lost, tertiarily, the second duct. The other possibility is that *Campanile* and *Serpulorbis* duplicated it independently with each other. Both explanations are equally parsimonious. Other more remote possibility, but also considered, is that the single duct to digestive gland appeared in node 5, and *Modulus* and *Turritella* converged to this condition too. Further studies of more species and on ontogeny could clarify this question.

Campanile symbolicum. This species presents a great reunion of autapomorphies, but comparable to other branches of the tree. The Australian *Campanile* was included in present analysis (mainly of South American species) with the objective of clarifying its relation with the cerithioideans. Houbrick (1981a, 1988, 1989) and Haszprunar (1988) cast doubts on its systematic position. This allowed the separation in its own superfamily (Houbrick, 1989), but the present analysis reveals that *Campanile* can be perfectly regarded as cerithioidean, inclusive with some close relation to vermetids and turritellids. Some of the polemic characters in *Campanile* are also found in other groups of never questioned cerithioideans, like, e.g., the pectinate osphradium (node 12) and the double duct to digestive gland (*Serpulorbis*). The inclusion of *Campanile* within the Cerithioidea agrees also with results on paraspermatozoa (Healy, 1986) (see also Ponder & Warén, 1988). In the consensus tree obtained by Ponder & Lindberg (1997:182), Campanilidae occupies a position between the Cerithidae and remain caenogastropods. That position, in certain point of view, is compatible with the result obtained herein.

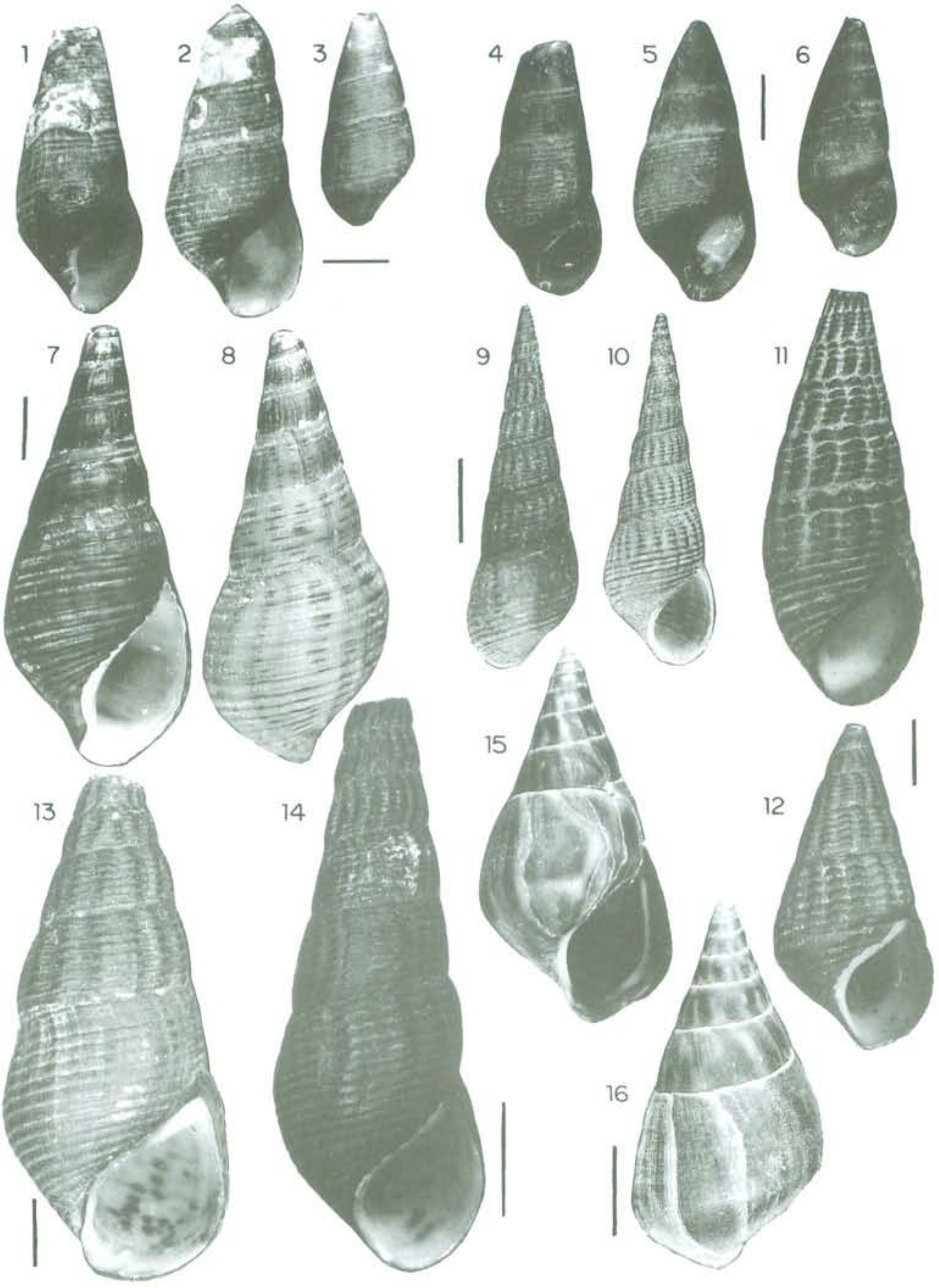
Node 4. The close relation between turritellids and vermetids was expected, and also found by Houbrick (1988). From 6, 2 important synapomorphies unite both groups: the food groove (38) and the tall gill filaments (43).

Node 5. This branch unites those species with dorso-ventrally flattened snout (9) and a large central pad in stomach (93), among 7 synapomorphies.

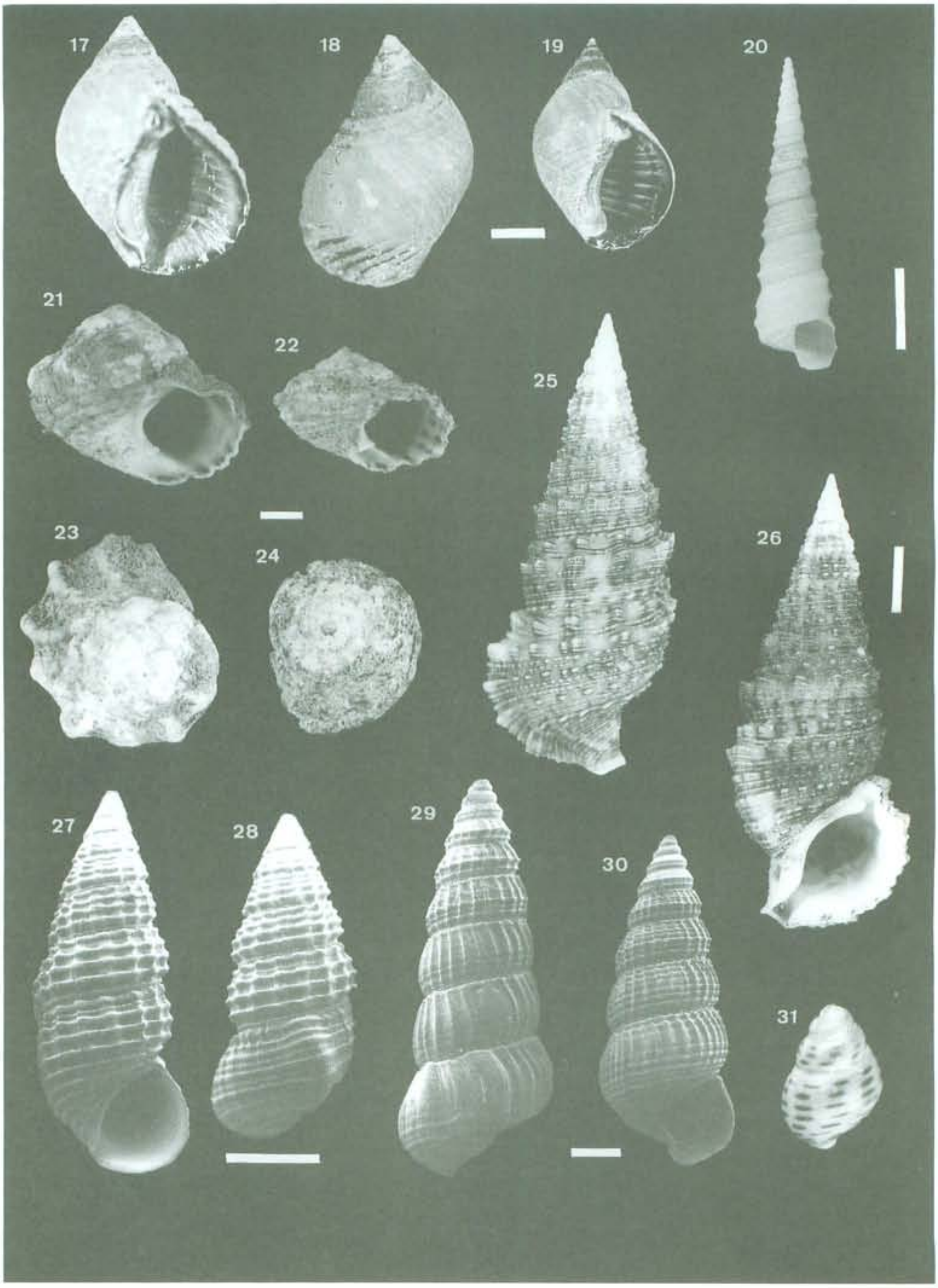
Node 12. There is a problem in choosing *C. atratum* as the single representative of genus *Cerithium*. This taxon is a very heterogeneous group, with monophyly uncertain (Houbrick, 1992a). Surely when more *Cerithium* will be known in more detail, several species attributed to this genus probably will be replaced. From 4, an important synapomorphy unites the species of this branch: the pectinate and ridge-like (in a overview) osphradium (27).

Node 13. The miniaturized forms *Bittium, Finella* and *Alaba* are united by 17 synapomorphies, which indicated more than single convergence due to miniaturization. Some characters, such as satellite osphradium fold (33), rectum narrow (48), crescentic ridge similar to central pad (96) and posterior furrow of pedal sole (14), among others, are notable synapomorphies.

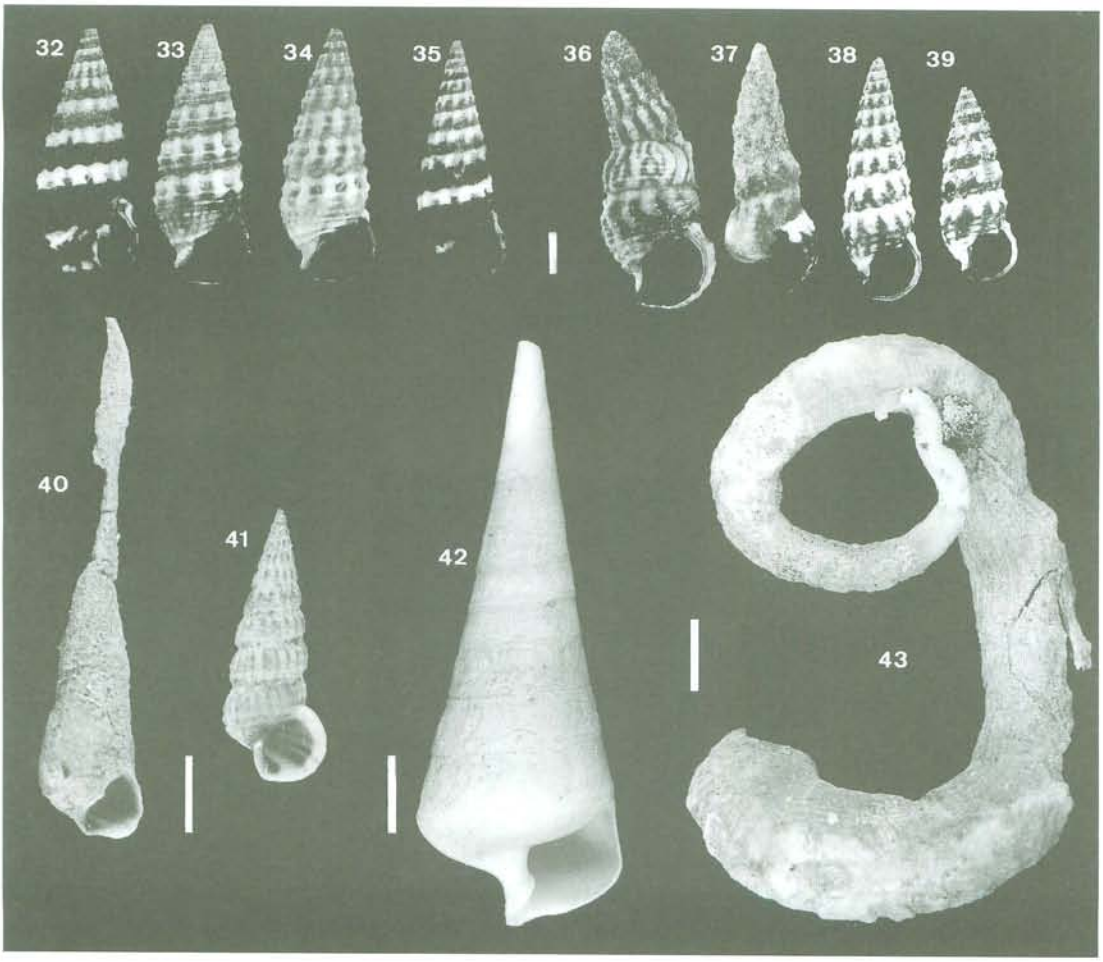
Node 15. The union between planaxids and thiarids is not a surprise, already Morrison (1954) pointed out the close relationship of both groups under the light of the presence of a brood pouch. In the present analysis, the brood pouch of both groups, were not considered homologues, based on data discussed above. Even so, both groups were maintained united due the remainder 6 characters. The genera of planaxids were analyzed phylogeneticly by Houbrick (1987a), dispensing any complementary comment. *Faunus*, like other Melanopsinae, has been related to Thiaridae (Houbrick, 1991b), at least the operculum has some similarity in being eccentric nucleate (Houbrick, 1991b: 40-41, fig. 16). On the other hand, they are gonochoristic, lack tentacles in mantle border and lack brood pouch, which indicates that the relationship of these groups merits revaluation. Some different arrangement of the Thiaridae is presented by Starobogatov & Izzatullaev (1980), based mainly on pallial gonoducts. *Simulathena papuensis* Houbrick, 1992b, described in Planaxidae, appears to be better placed in Thiaridae in spite of marine habitat, since presents tentacles in mantle border and dorsal placed brood pouch.



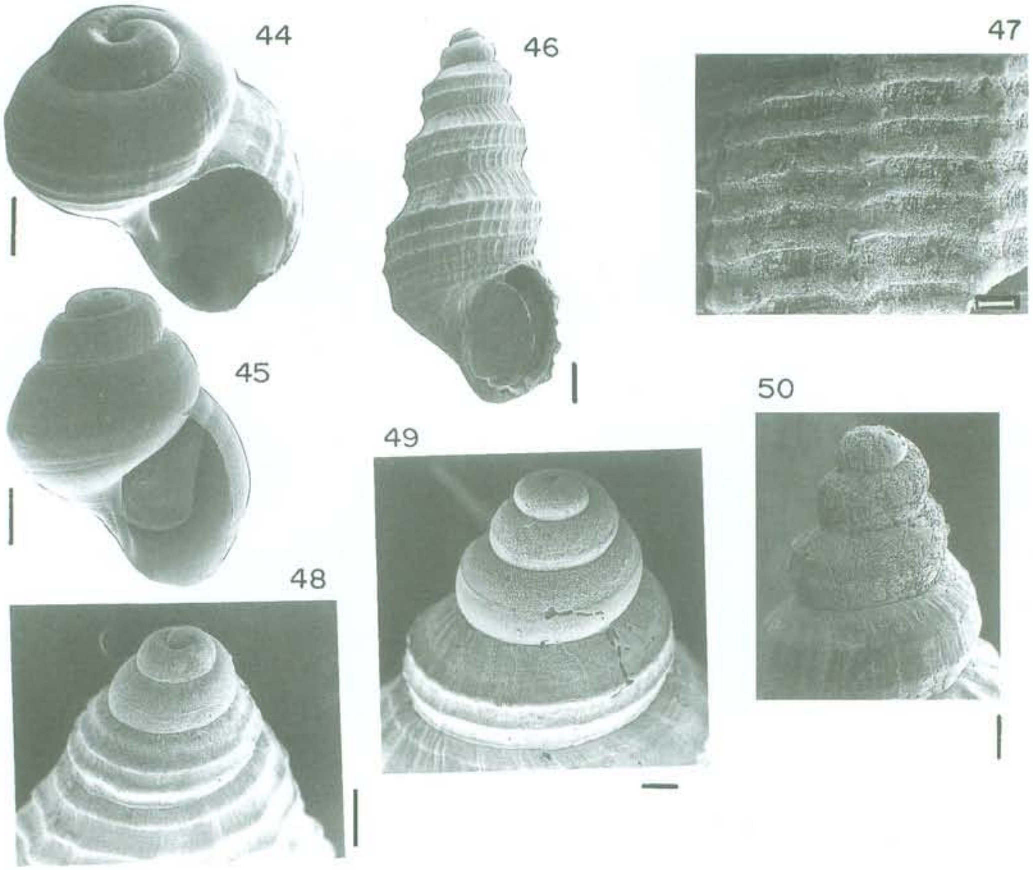
Figs 1-16 Shells: **1-3)** *Aylacostoma exoplicata* from Tucurui, Pará, **1-2)** frontal view of holotype and a paratype, **3)** dorsal view of a younger paratype, scale = 5 mm; **4-6)** *Aylacostoma ci* from Jamari River, Roraima, three specimens in frontal view (holotype and two paratypes), scale = 5 mm; **7-8)** *Aylacostoma tenuilabris* from Avaré, São Paulo, **7)** frontal and **8)** dorsal view, scale = 5 mm; **9-10)** *Melanoides tuberculatus* (Müller), Eurasian species found in Pantanal, Mato Grosso do Sul, **9)** dorsal, **10)** frontal view, scale = 5 mm; **11)** *Doryssa macapa* from Araguari River, Amapá, frontal view, scale = 10 mm; **12)** *Doryssa ipupiara* (holotype) from Apui, Roraima, frontal view; **13)** *Doryssa transversa* (Lea) from Roraima; **14)** *Doryssa atra* (Bruguière) from French Guyana, frontal view, scale = 5 mm; **15-16)** *Pachychilus sp* from Chiapas, Mexico, **15)** frontal, **16)** dorsal view, scale = 5 mm.



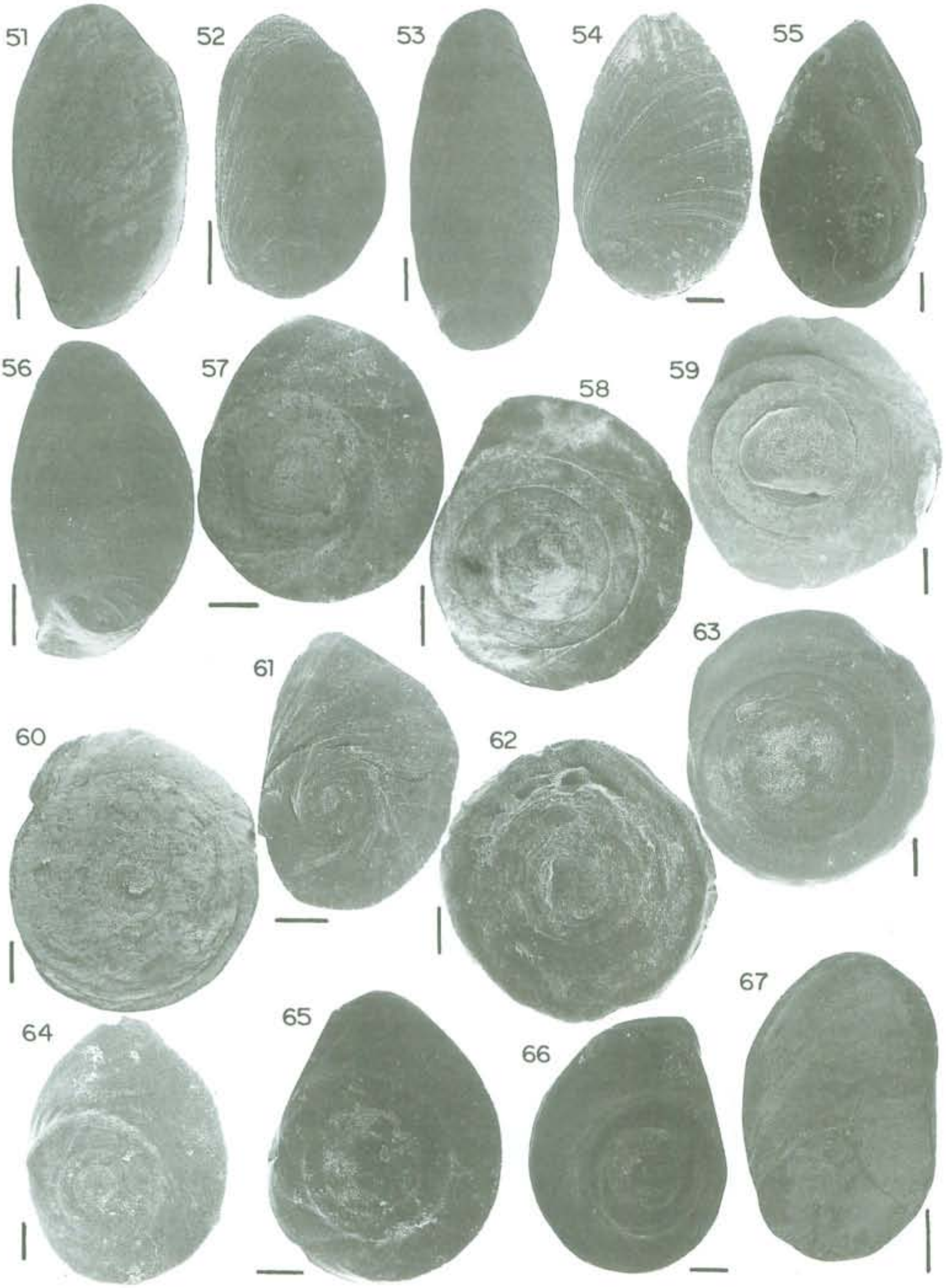
Figs 17-31 Shells: **17-19)** *Supplanaxis nucleus* (Bruguière) from Margarita Island, Venezuela, **17)** frontal view of a adult specimen, **18)** dorsal view of same, **19)** frontal view of a younger specimen, scale = 2 mm; **20)** *Turritella hookeri* (Reeve) from off Campos Bay, Rio de Janeiro, frontal view, scale = 5 mm; **21-24)** *Modulus modulus* (Linné), **21)** frontal view of a specimen from Ilha Bela, São Paulo, **22)** frontal view of a specimens from Margarita Island, Venezuela; **23)** apical view of specimen of fig. 21, **24)** same for specimen of fig. 22, scale = 2 mm;**25-26)** *Cerithium atratum* (Born) from São Sebastião, São Paulo, **25)** dorsal view, **26)** frontal view, scale = 5 mm; **27-28)** *Bittium varium* (Pfeiffer) from Angra dos Reis, Rio de Janeiro, SEM, **27)** frontal, **28)** dorsal view, scale = 1 mm; **29-30)** *Finella dubia* (Orbigny) from Ubatuba, São Paulo, SEM, **29)** dorsal, **30)** frontal view, scale = 0.5 mm; **31)** *Aylacostoma tenuilabris*, young specimen found in brood pouch, dorsal view, scale = 0.5 mm.



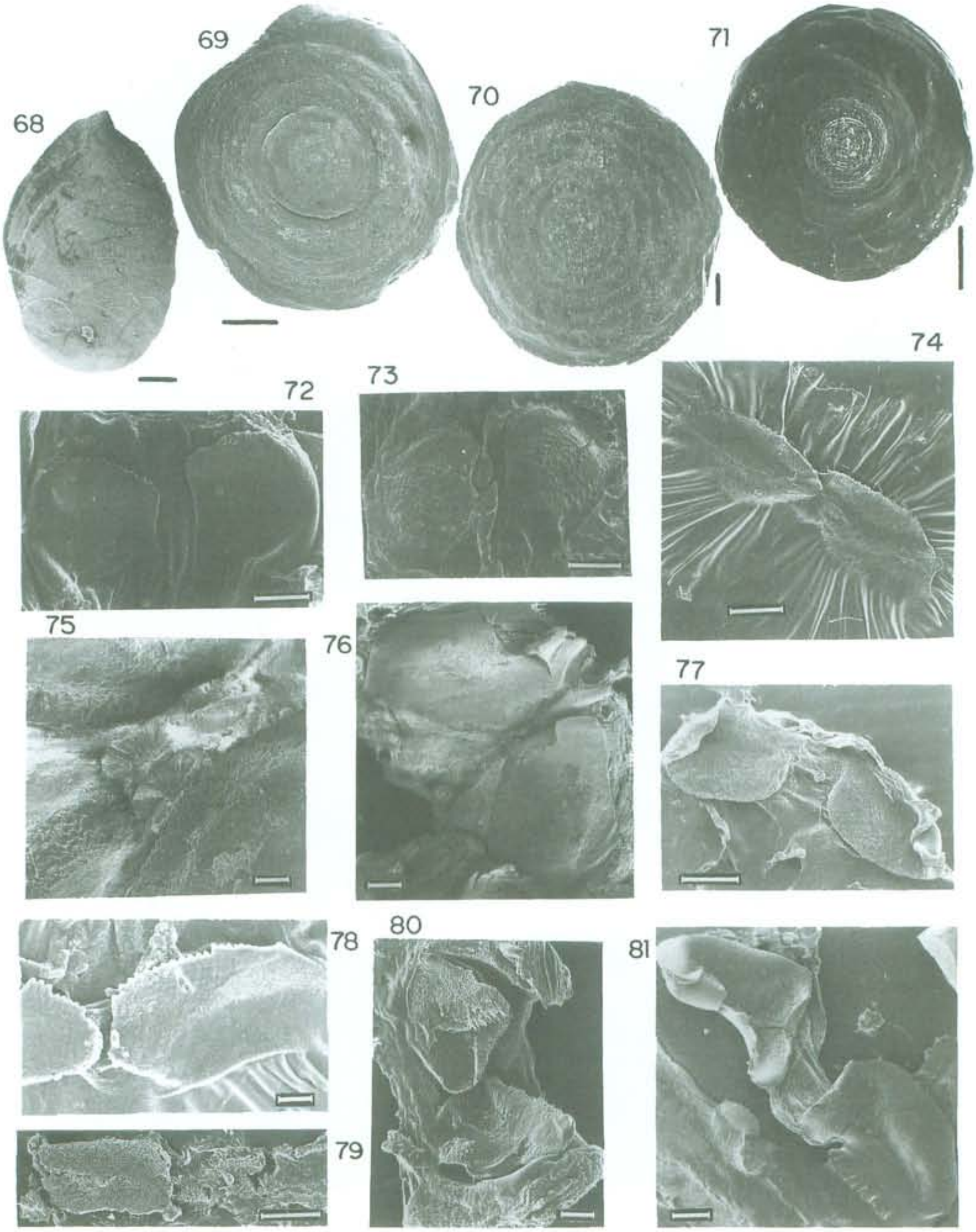
Figs 32-43 Shells: **32-39)** *Batillaria minima* (Gmelin) from Margarita Island, Venezuela, collection of main variation and anomalies samples, all frontal view, scale = 2 mm; **40-41)** *Cerithidea costata* from Margarita Island, Venezuela, frontal view, **40)** specimen as found in Nature, **41)** cleaned specimen, scale = 5 mm; **42)** *Campanile symbolicum* Iredale from Western Australia, frontal view, scale = 10 mm; **43)** *Serpulorbis decussatus* (Gmelin) from Guarapari, Espirito Santo, dorsal view, scale = 5 mm.



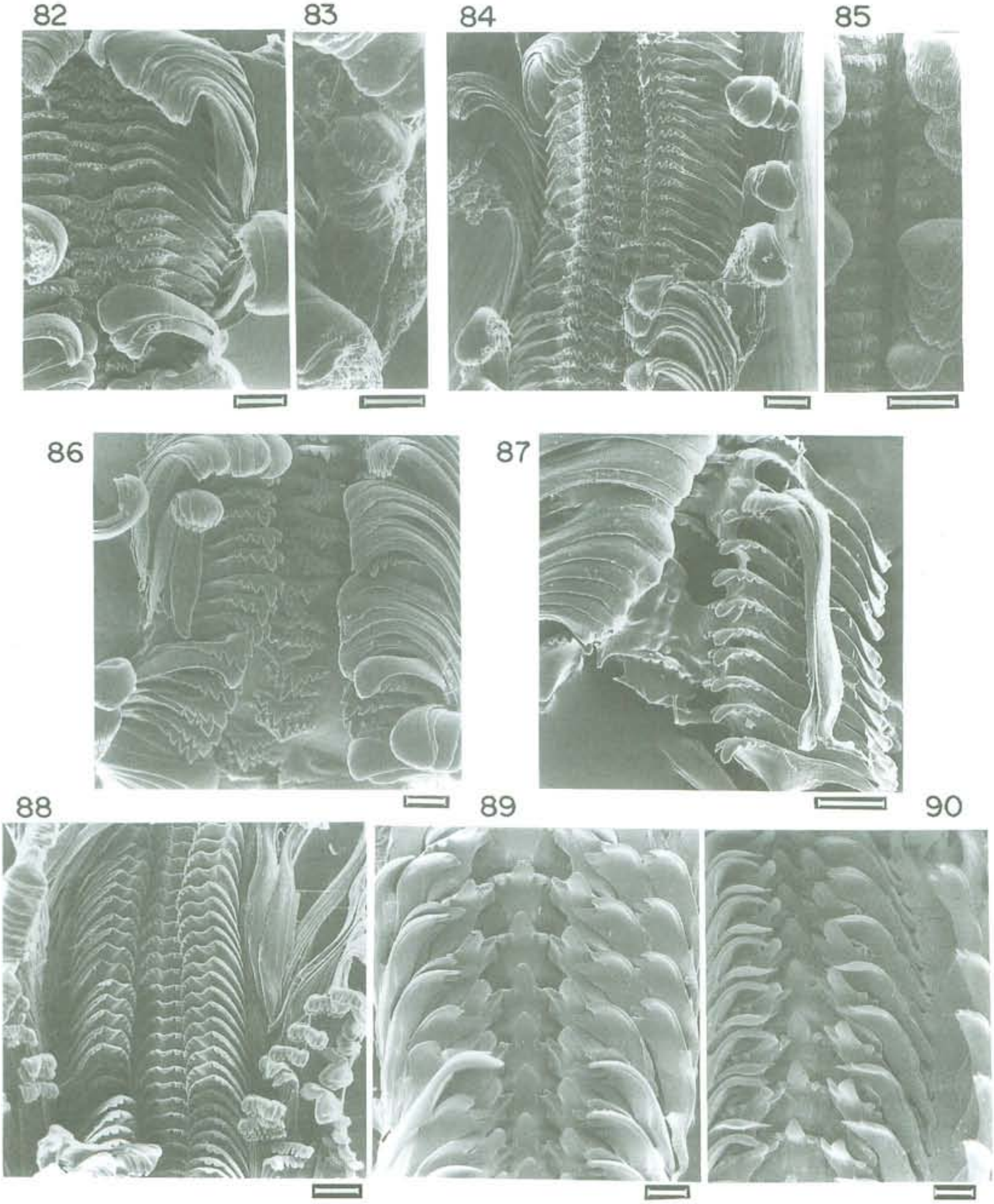
Figs 44-50 Protoconchs and shell details in SEM: **44-46)** young shells found in brood pouch, frontal view, **44)** *Aylacostoma ci,* scale = 0.2 mm, **45)** *Aylacostoma tenuilabris*, scale = 0.5 mm, **46)** *Melanoides tuberculatus*, scale = 0.2 mm; **47)** *M. tuberculatus* detail of teleoconch sculpture, scale = 0.2 mm; **48-50)** detail of shell apex in profile, **48)** *Bittium varium*, scale = 0.1 mm, **49)** *Finella dubia*, scale = 0.05 mm; **50)** *Cerithidea costata*, scale = 0.1 mm.



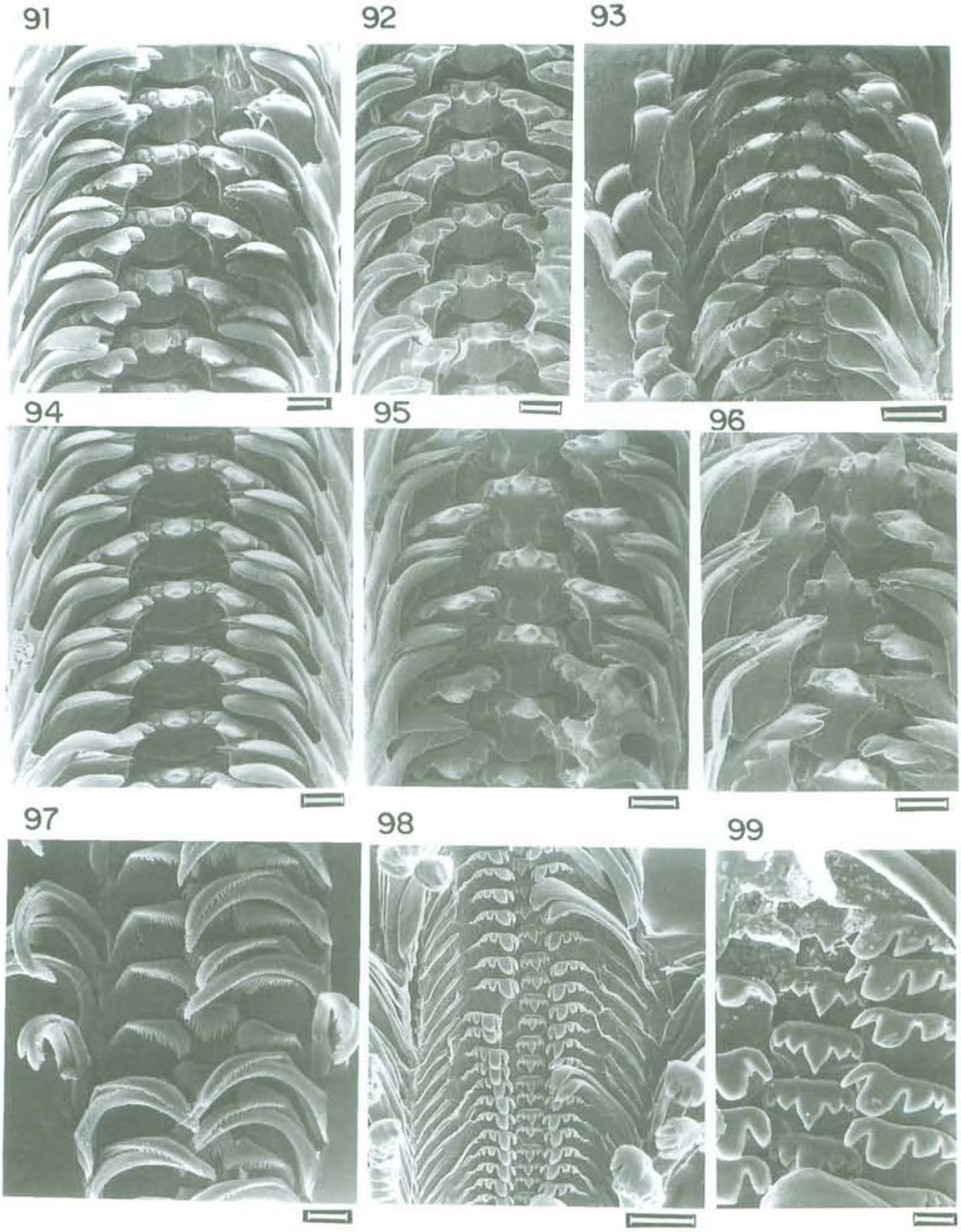
Figs 51-67 Opercula in SEM (outer view except those indicated): **51)** *Aylacostoma exoplicata*, scale = 1 mm; **52)** *A. ci*, scale = 1 mm; **53)** *A. tenuilabris*, scale = 1 mm; **54)** *Melanoides tuberculatus*, scale = 0.5 mm; **55)** same, inner view, scale = 0.5 mm; **56)** *Supplanaxis nucleus*, scale = 1 mm; **57)** *Doryssa ipupiara*, scale = 1 mm; **58)** same, other specimen, scale = 1 mm; **59)** *D. atra*, scale = 1 mm; **60)** *D. macapa*, scale = 1 mm; **61)** *Pachychilus sp*, scale = 1 mm; **62)** *Turritella hookeri*, scale = 0.2 mm; **63)** *Modulus modulus*, scale = 0.5 mm; **64)** *Bittium varium*, scale = 0.1 mm; **65)** *Finella dubia*, scale = 0.1 mm; **66)** same, inner view, scale = 0.1 mm; **67)** *Cerithium atratum*, scale = 1 mm.



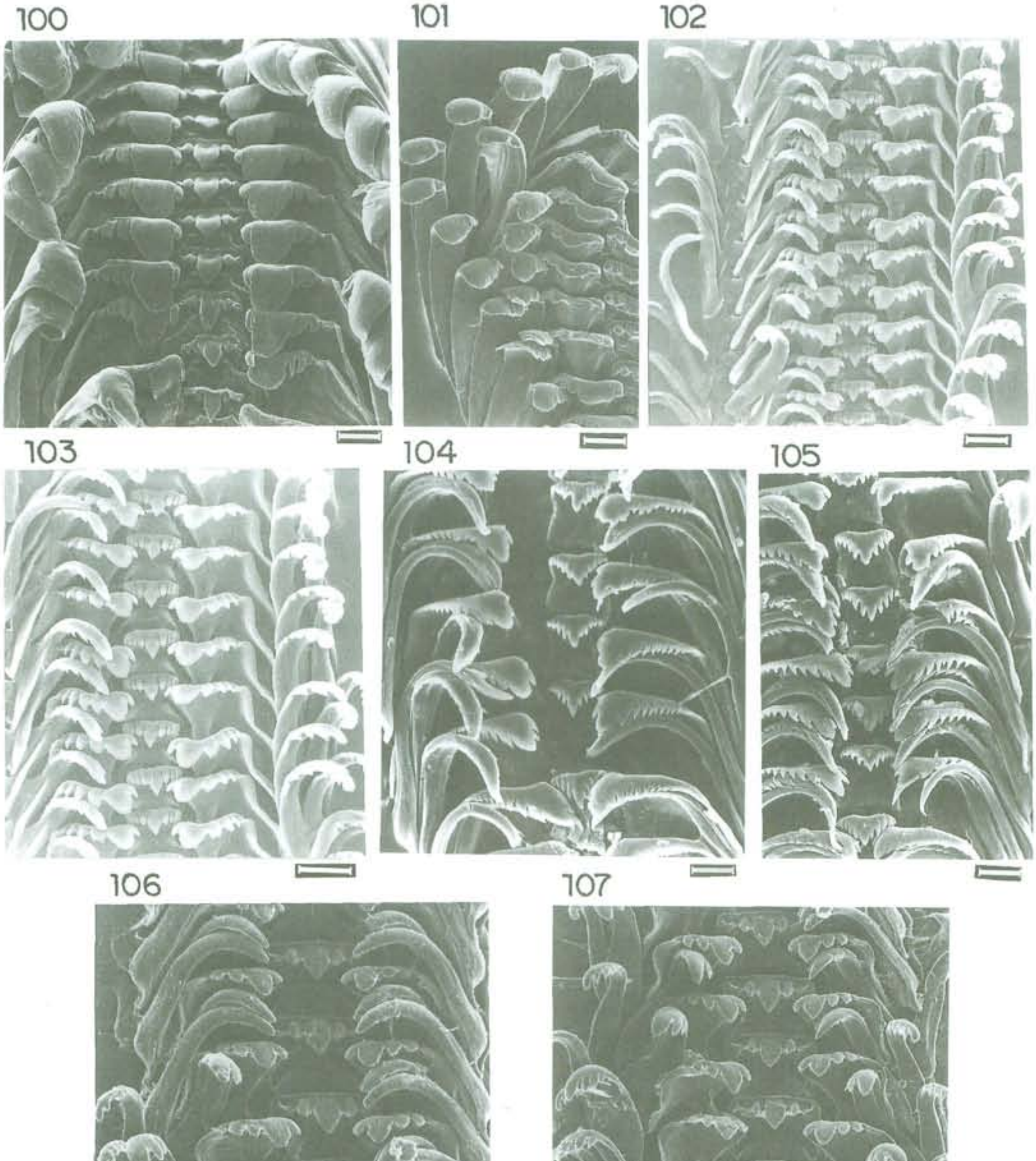
Figs 68-81 Opercula and jaws in SEM: **68-70)** opercula, outer view, **68)** *Alaba incerta*, scale = 0.2 mm; **69)** *Batillaria minima*, scale = 0.5 mm; **70)** *Cerithidea costata*, scale = 0.2 mm; **71)** same, inner view, scale = 0.5 mm; **72-81)** jaws: **72)** *Aylacostoma exoplicata*, scale = 0.1 mm; **73)** *A. ci*, scale = 0.1 mm; **74)** *Supplanaxis nucleus*, scale = 0.1 mm; **75)** *Doryssa ipupiara*, scale = 0.02 mm; **76)** same, scale = 0.1 mm; **77)** *D. atra*, scale = 0.2 mm; **78)** *Bittium varium*, scale = 0.02 mm; **79)** *Serpulorbis decussatus*, scale = 0.2 mm; **80)** *Alaba incerta*, Scale = 0.05 mm; **81)** *Campanile symbolicum*, Scale = 0.5 mm.



Figs 82-90 Radulae in SEM: **82-83)** *Aylacostoma exoplicata*; **84-85)** *A. ci*; **86)** *A. tenuilabris*; **87)** *Melanoides tuberculatus*; **88)** *Supplanaxis nucleus*; **89-90)** *Doryssa ipupiara*. Scales = 50 mm.



Figs 91-99 Radulae in SEM: **91-92)** *Doryssa atra*, scale = 50 mm; **93-94)** *D. macapa*, scale = 100 mm (93), 50 mm (94); **95-96)** *Pachychilus sp*, scales = 50 mm; **97)** *Turritella hookeri*, scale = 10 mm; **98-99)** *Modulus modulus*, scale = 100 mm (98), 20 mm (99).



Figs 100-107 Radulae in SEM: **100-101)** *Cerithium atratum*, scales = 50 mm; **102-103)** *Bittium varium*, scales = 20 mm; **104-105)** *Finella dubia*, scales = 10 mm; **106-107)** *Alaba incerta*, scales = 10 mm.

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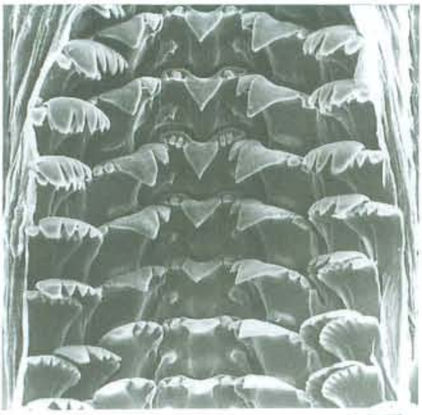

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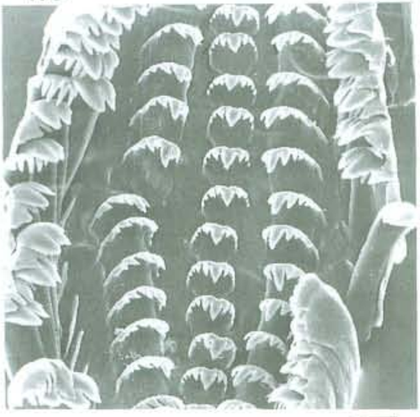

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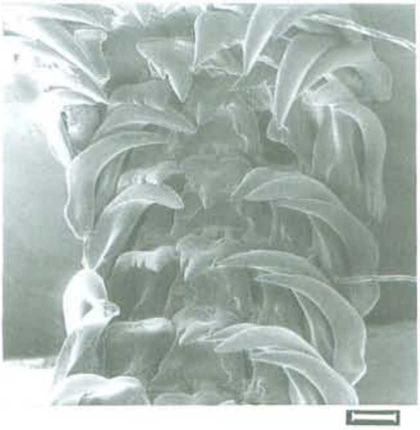

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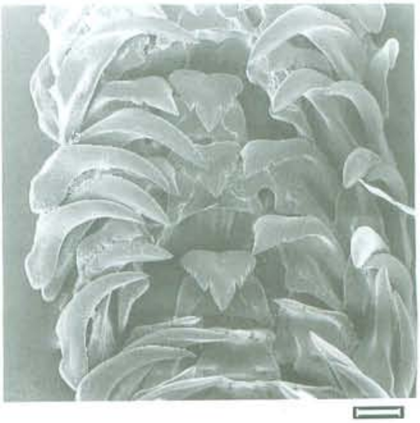
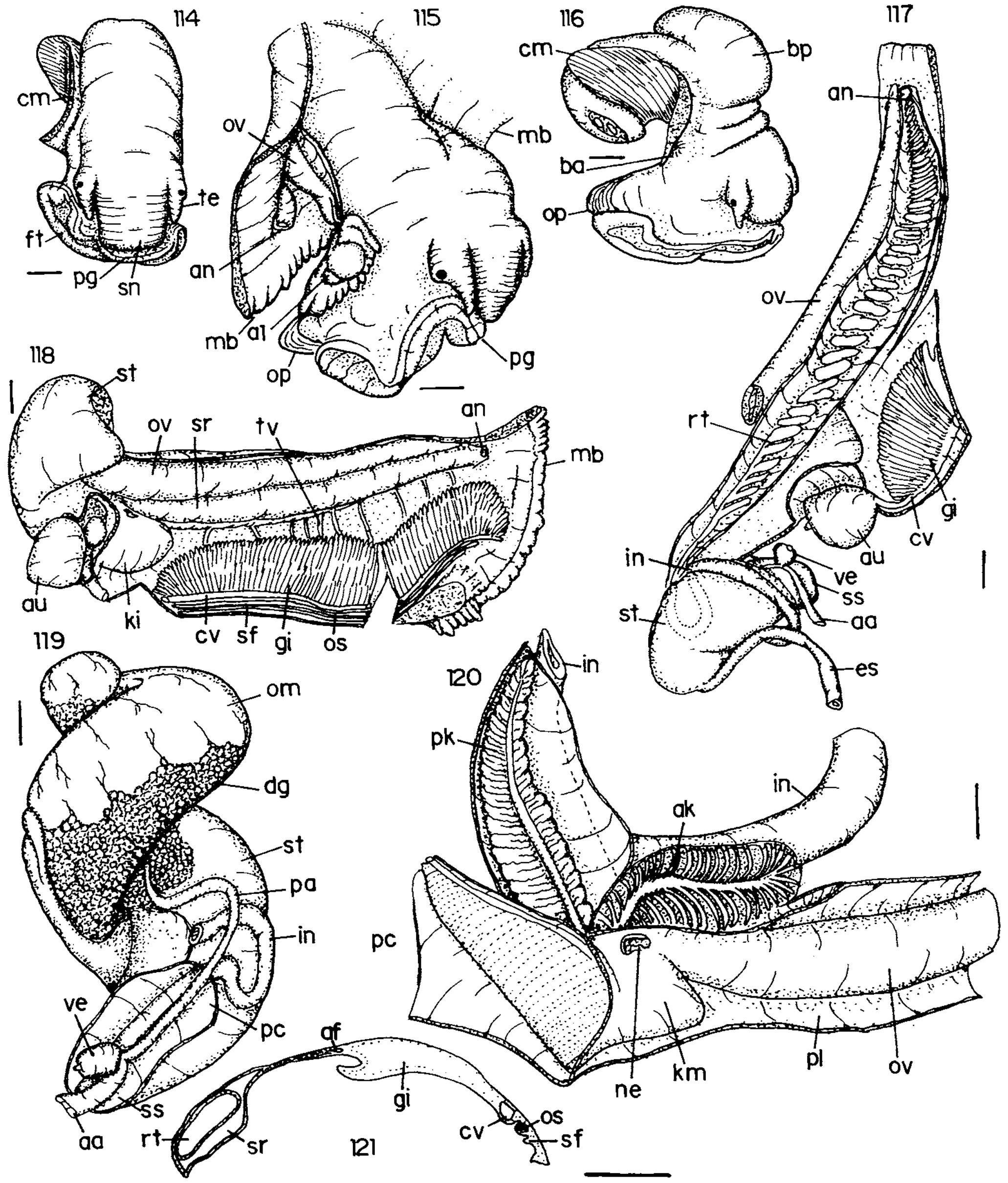
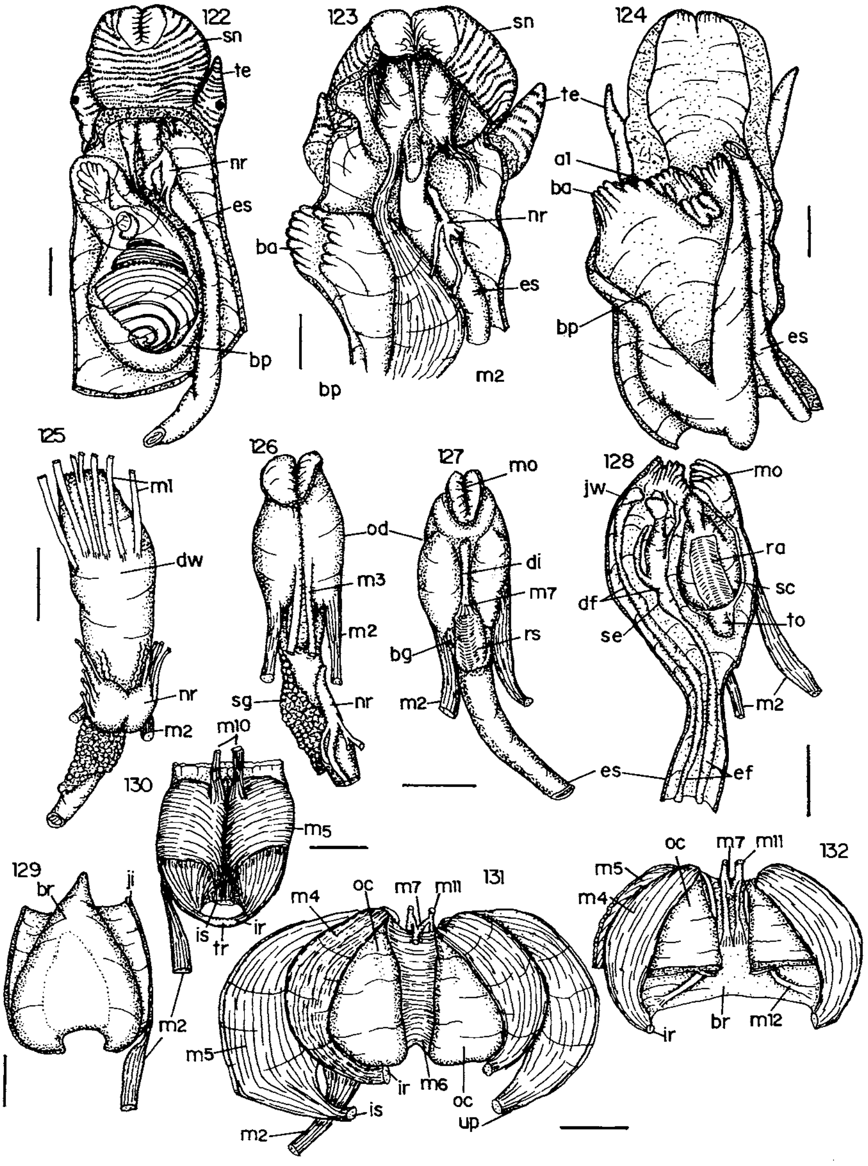


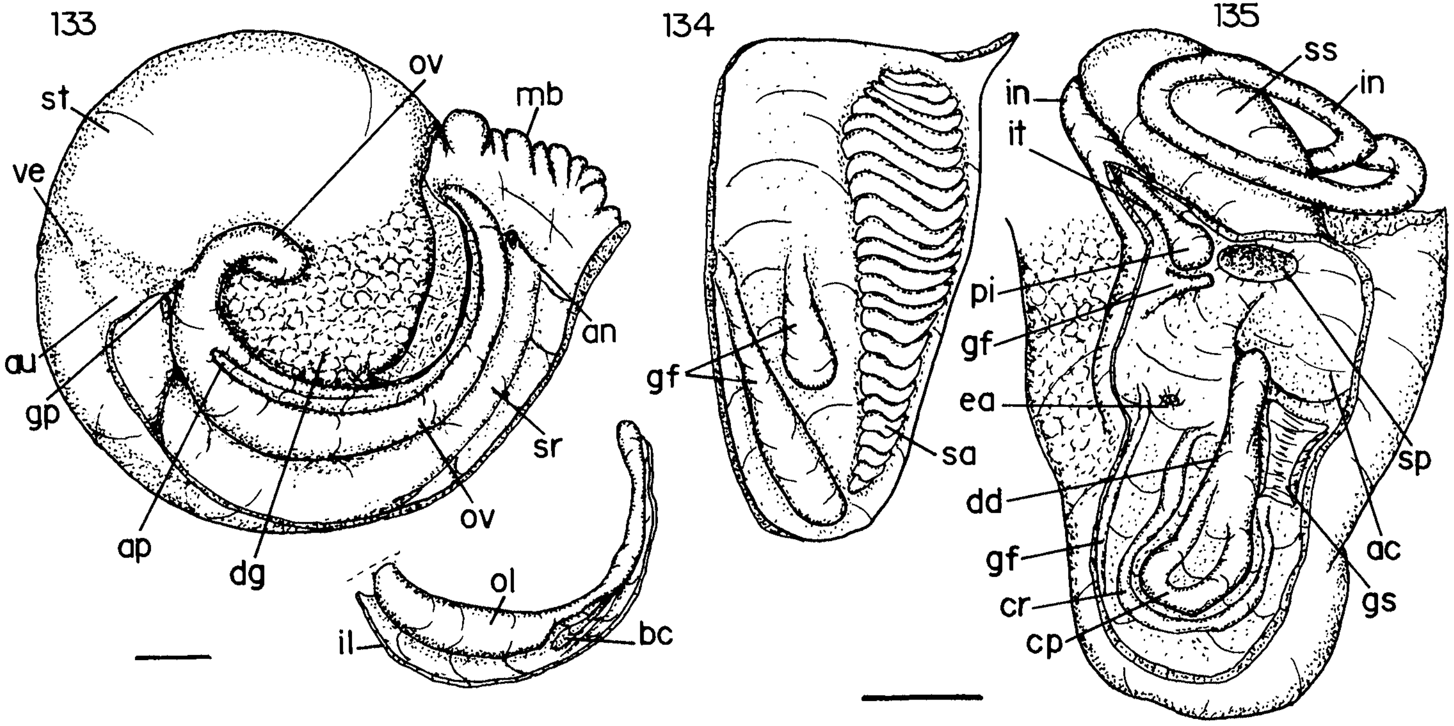
Figs 108-113 Radulae in SEM: **108)** *Batillaria minima*, scale = 20 mm; **109-110)** *Cerithidea costata*, scales = 20 mm; **111)** *Campanile symbolicum*, scale = 200 mm; **112-113)** *Serpulorbis decussatus*, scales = 100 mm.



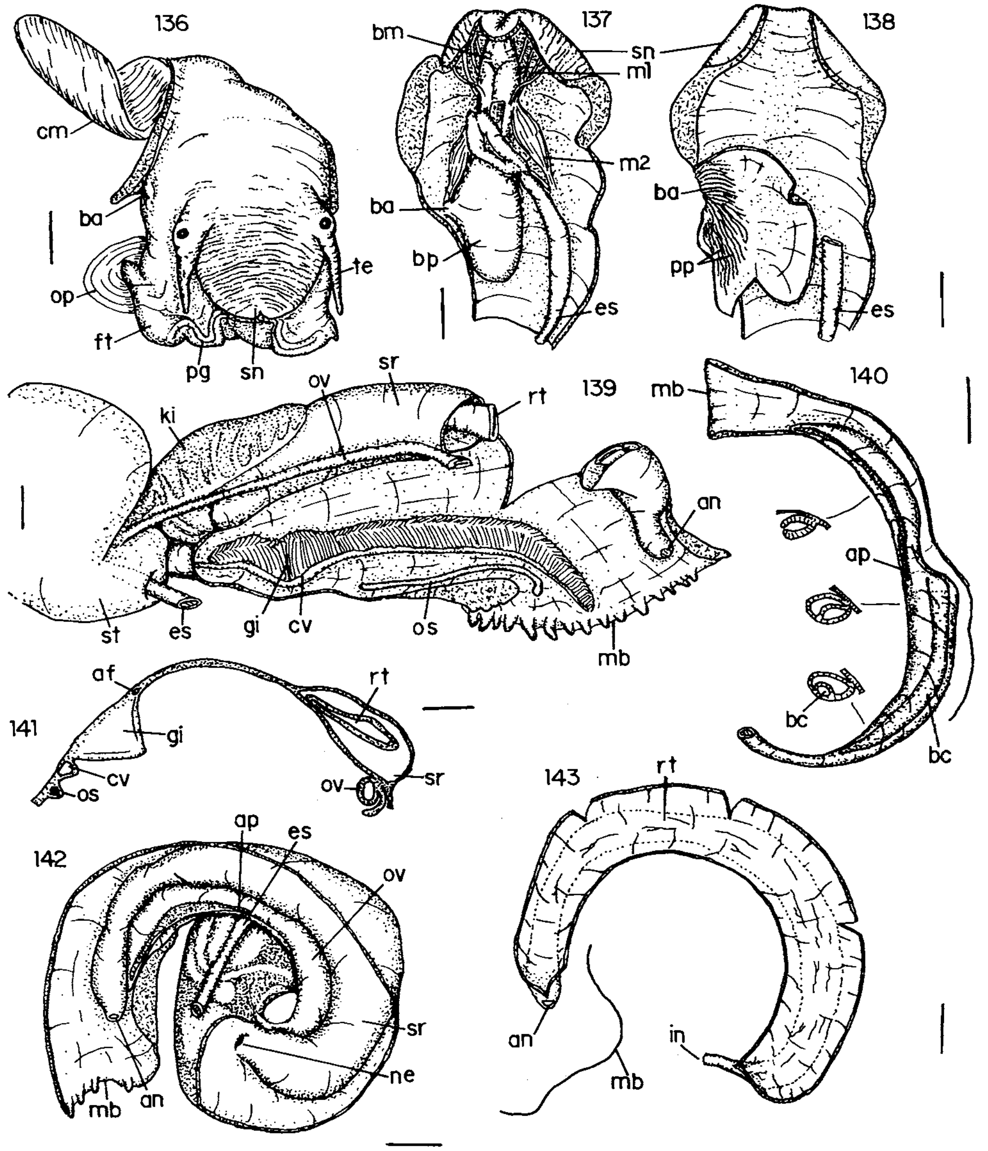
Figs 114-121 *Aylacostoma exoplicata* anatomy: **114)** head-foot in frontal view; **115)** head-foot and part of mantle (sectioned) of a specimen preserved with brood pouch fold protracted, lateral-right view; **116)** head-foot, lateral-right view, specimen with replete brood pouch; **117)** detail of right and posterior regions of pallial cavity and anterior region of visceral mass, pericardium dissected, inner view; **118)** pallial cavity and part of visceral mass, inner-ventral view; **119)** extracted visceral mass, profile; **120)** kidney opened by longitudinal section; **121)** transversal section in middle of pallial cavity. Scales = 1 mm; a1 = brood pouch fold.



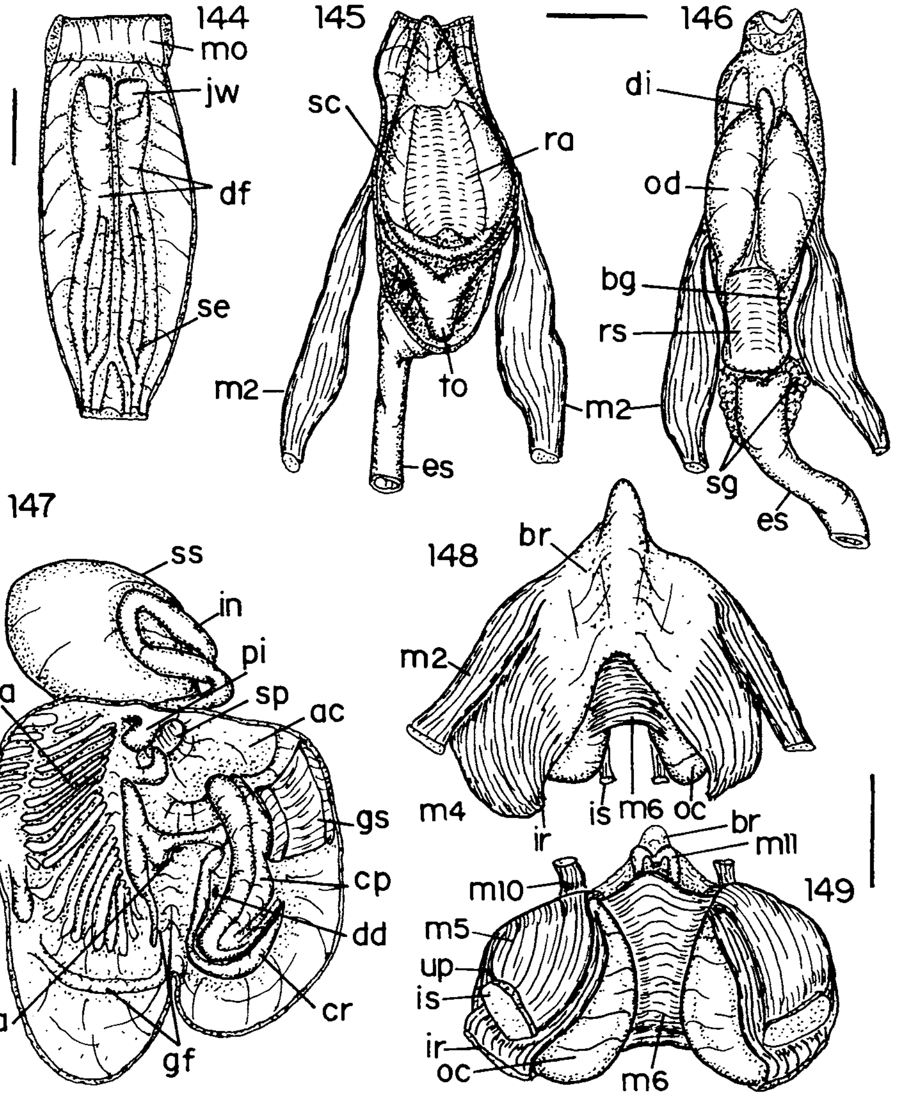
Figs 122-132 *Aylacostoma exoplicata* anatomy: **122)** head and haemocoel, ventral view, foot extracted; **123)** same, snout sectioned longitudinally, buccal mass exposed; **124)** same, all organs extracted except esophagus and brood pouch, brood pouch partially opened longitudinally; **125)** buccal mass extracted, dorsal view; **126)** same, ventral view; **127)** same with jugal muscles, nerve ring and salivary glands extracted, ventral view; **128)** buccal mass opened by a lateral-right longitudinal section, showing inner surface; **129)** odontophore, radula extracted, dorsal view; **130)** same, ventral view; **131)** same, all muscles deflected showing inner cartilages, ventral view; **132)** same with more external muscles and posterior part of cartilages extracted. Scales (122-128)= 1 mm (129-132)= 0.5 mm; al = brood pouch fold.



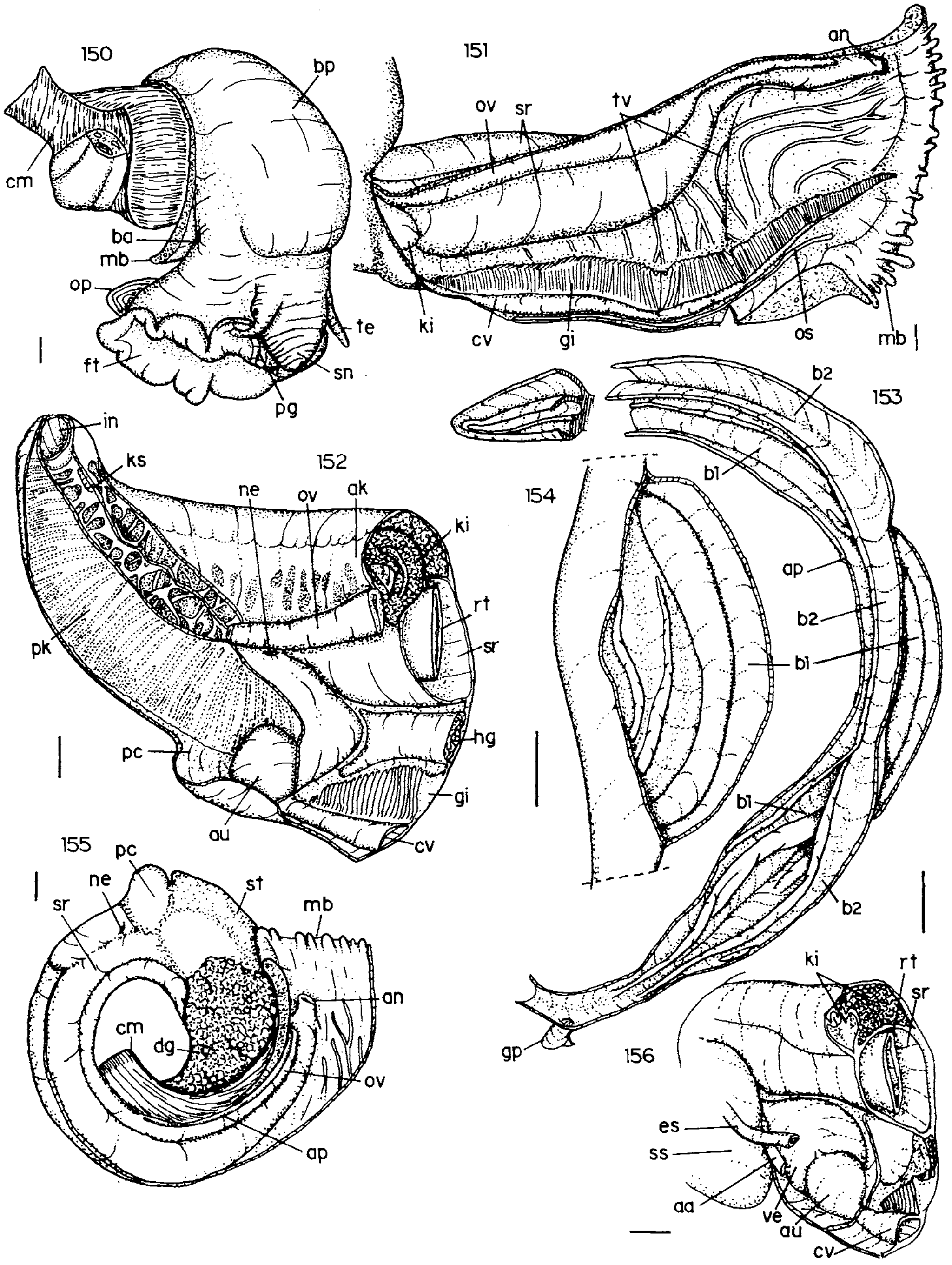
Figs 133-135 *Aylacostoma exoplicata* anatomy: **133)** right region of pallial cavity and anterior region of visceral mass, showing pallial oviduct, lateral-right view, with a detail (down) of extracted pallial oviduct with inner lamina (il) partially extracted, same position; **134)** dorsal face of stomach extracted, inner surface; **135)** stomach, dorsal view, dorsal face removed showing inner surface. Scale = 1 mm.



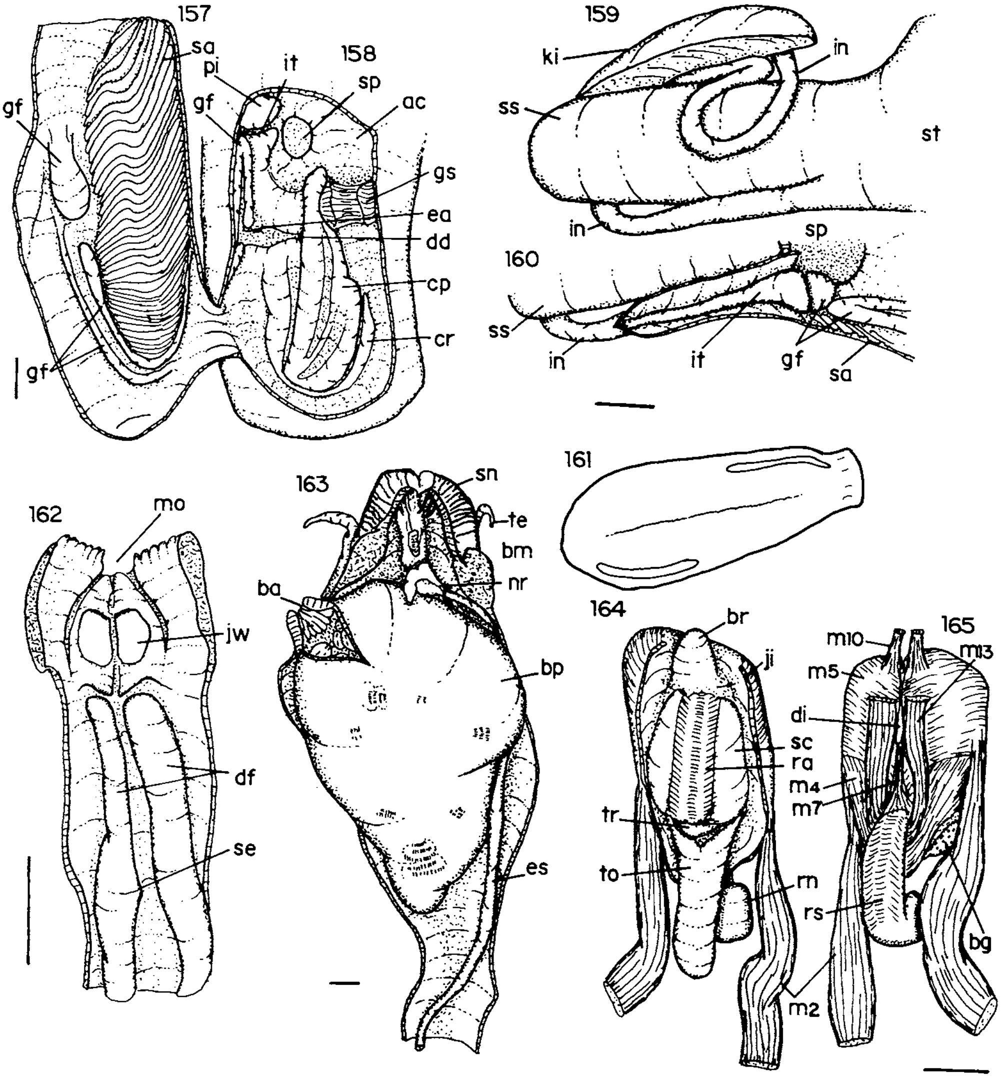
Figs 136-143 *Aylacostoma ci* anatomy: **136)** head-foot, frontal view; **137)** head and haemocoel, ventral view, foot removed, snout sectioned longitudinally; **138)** same with all organs removed except part of esophagus and brood pouch, brood pouch opened longitudinally; **139)** pallial cavity and part of visceral mass, inner view; **140)** pallial oviduct extracted, with scheme of transversal section in three indicated levels; **141)** transversal section in middle region of pallial cavity; **142)** right region of pallial cavity and anterior region of visceral mass, showing pallial oviduct and rectum, lateral right view; **143)** rectum extracted and opened longitudinally, lateral-right view. Scales = 1 mm, except 141 = 0.5 mm.



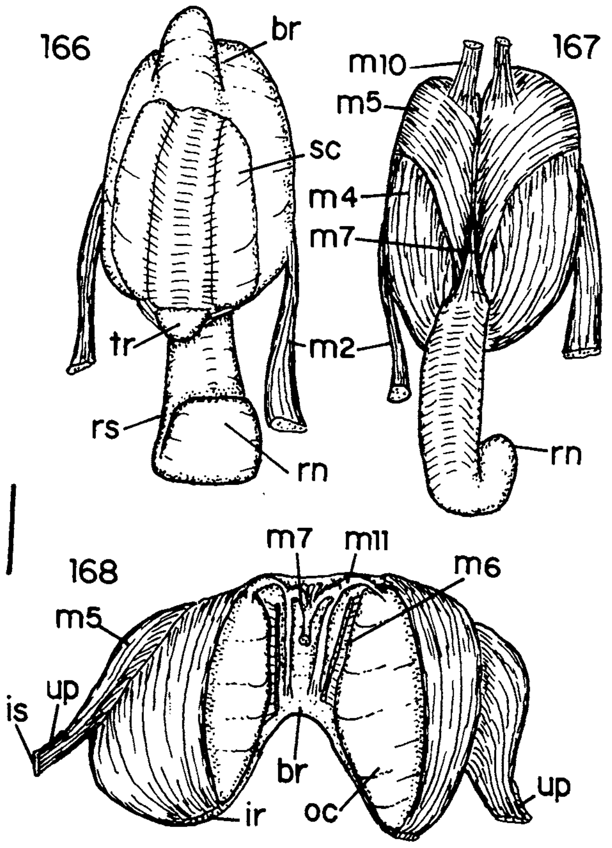
Figs 144-149 *Aylacostoma ci* anatomy: **144)** dorsal face of buccal mass extracted, ventral view, inner surface exposed; **145)** buccal mass, dorsal view, dorsal face and esophagus extracted; **146)** same, ventral view; **147)** Stomach, dorsal view, dorsal face opened by a section in right margin and deflected to show inner gastric surface; **148)** odontophore dissected, dorsal view, radula extracted; **149)** same, ventral view, muscles partially deflected to shown cartilages. Scales = 0.5 mm.



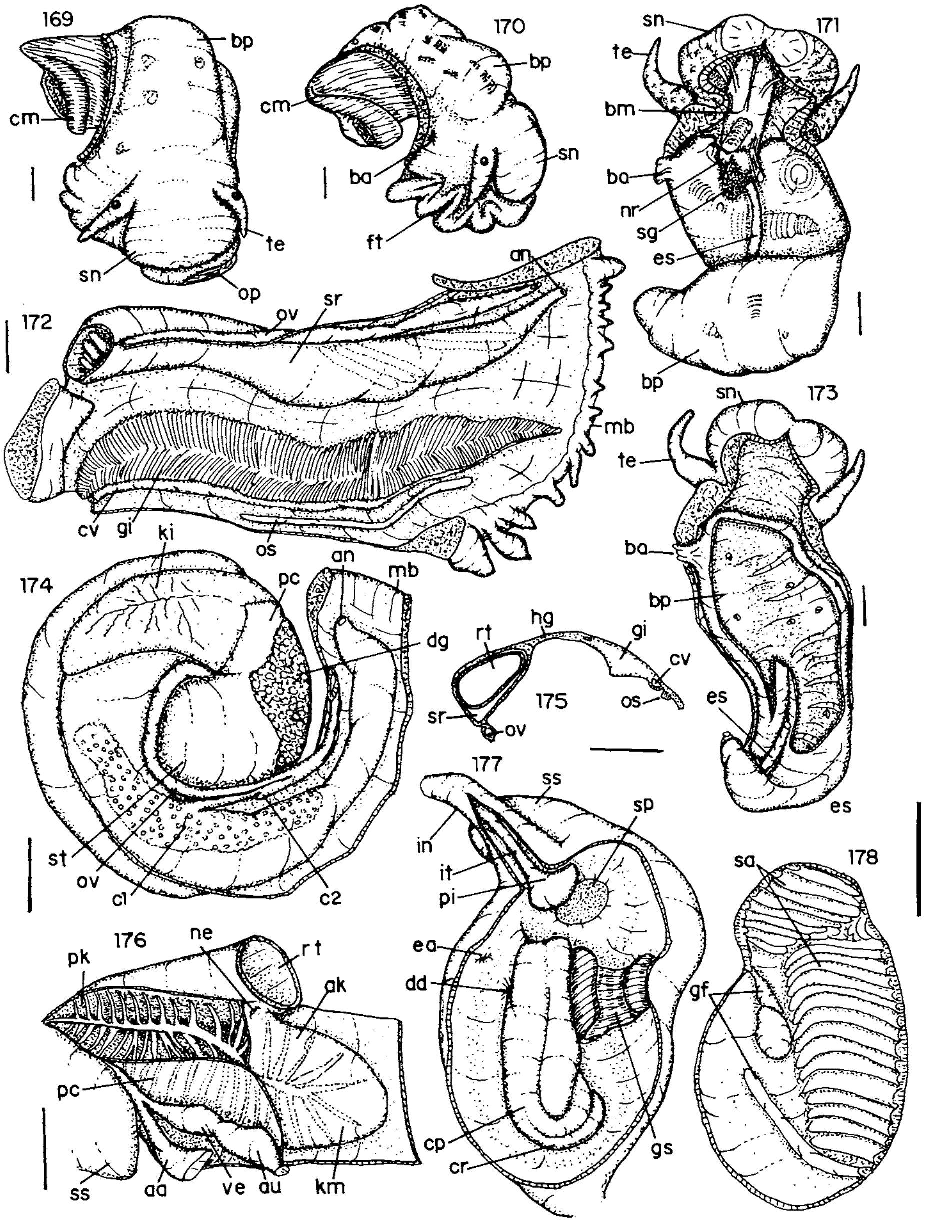
Figs 150-156 *Aylacostoma tenuilabris* anatomy: **150)** head-foot, lateral-right view; **151)** pallial cavity, inner-ventral view; **152)** detail of posterior end of pallial cavity and anterior region of visceral mass, pericardium almost all extracted; **153)** pallial oviduct, ventral view, most of laminae deflected to show inner surface; **154)** same, detail of middle region with ventral chamber (b2) deflected; **155)** right region of pallial cavity and anterior region of visceral mass, right view; **156)** detail of anterior region of visceral mass, pericardium opened, heart exposed. Scales = 1 mm; b1 = dorsal chamber of pallial oviduct; b2 = ventral chamber of pallial oviduct.



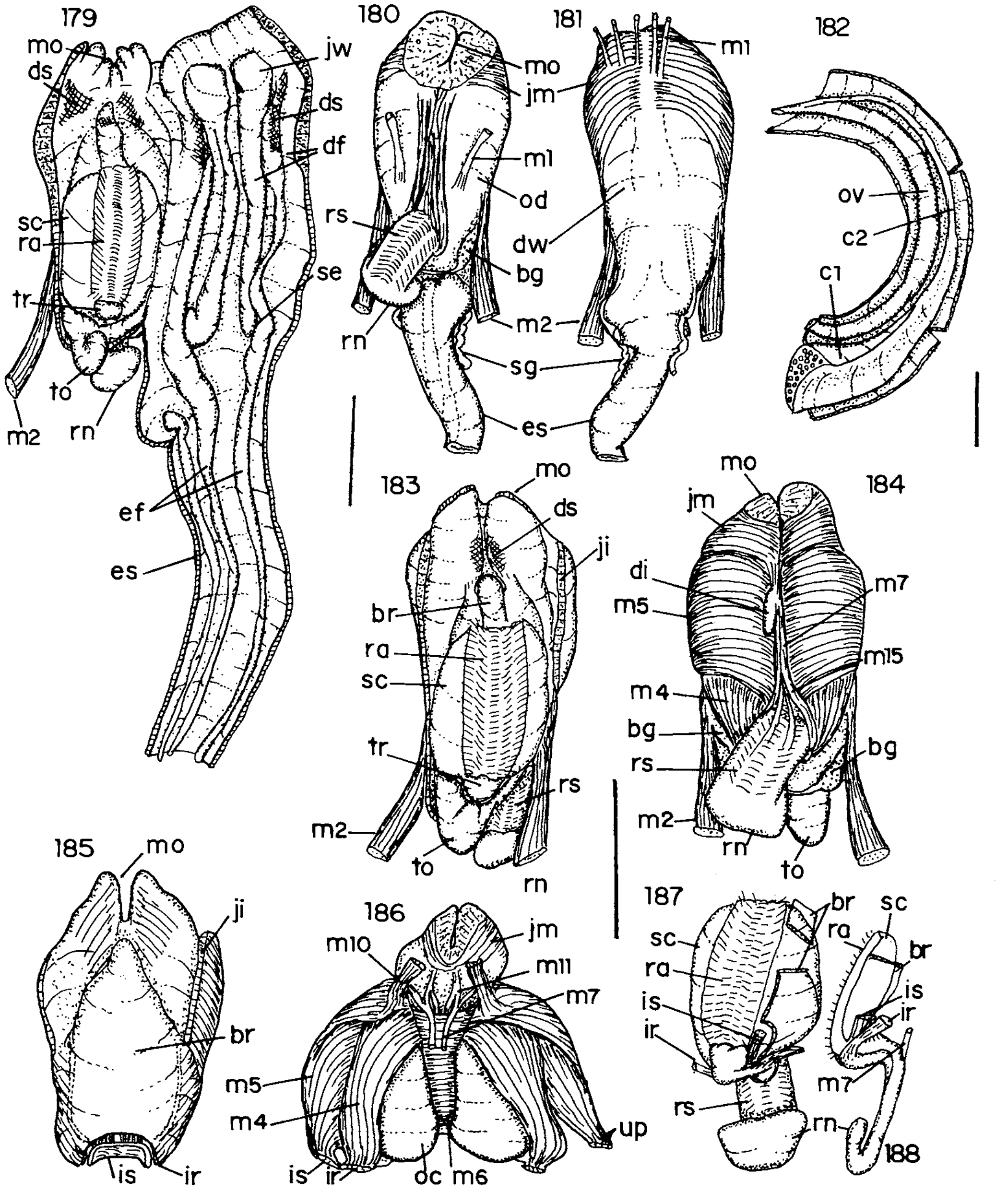
Figs 157-165 *Aylacostoma tenuilabris* anatomy: **157)** dorsal wall of stomach partially extracted and deflected to show its inner surface; **158)** stomach, dorsal wall removed, dorsal view; **159)** detail of anterior region of stomach, lateral-left view, gonad and digestive gland removed; **160)** same, detail of intestine origin opened longitudinally; **161)** crystalline style extracted from gastric style sac; **162)** dorsal wall of buccal mass and anterior esophagus extracted from odontophore, ventral view, inner surface exposed; **163)** head and haemocoel, ventral view, foot removed, snout opened longitudinally; **164)** odontophore extracted from buccal mass, dorsal view; **165)** same, ventral view. Scales (157-163) = 1 mm, (164-165)= 0.5 mm.



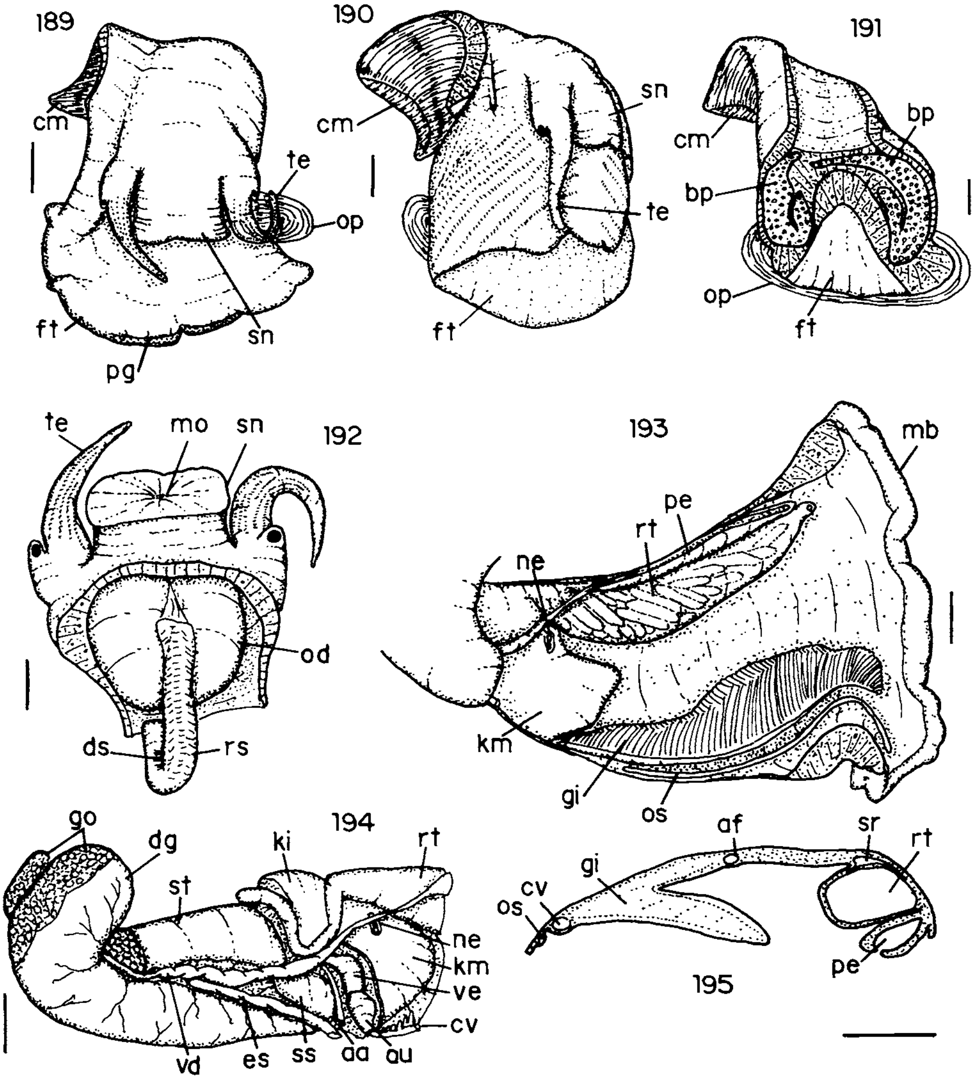
Figs 166-168 *Aylacostoma tenuilabris* anatomy: **166)** odontophore, outer layer of muscles and membranes removed, dorsal view; **167)** same, ventral view; **168)** same, ventral view, most of muscles deflected and horizontal muscle sectioned to show inner structures. Scales = 0.5 mm.



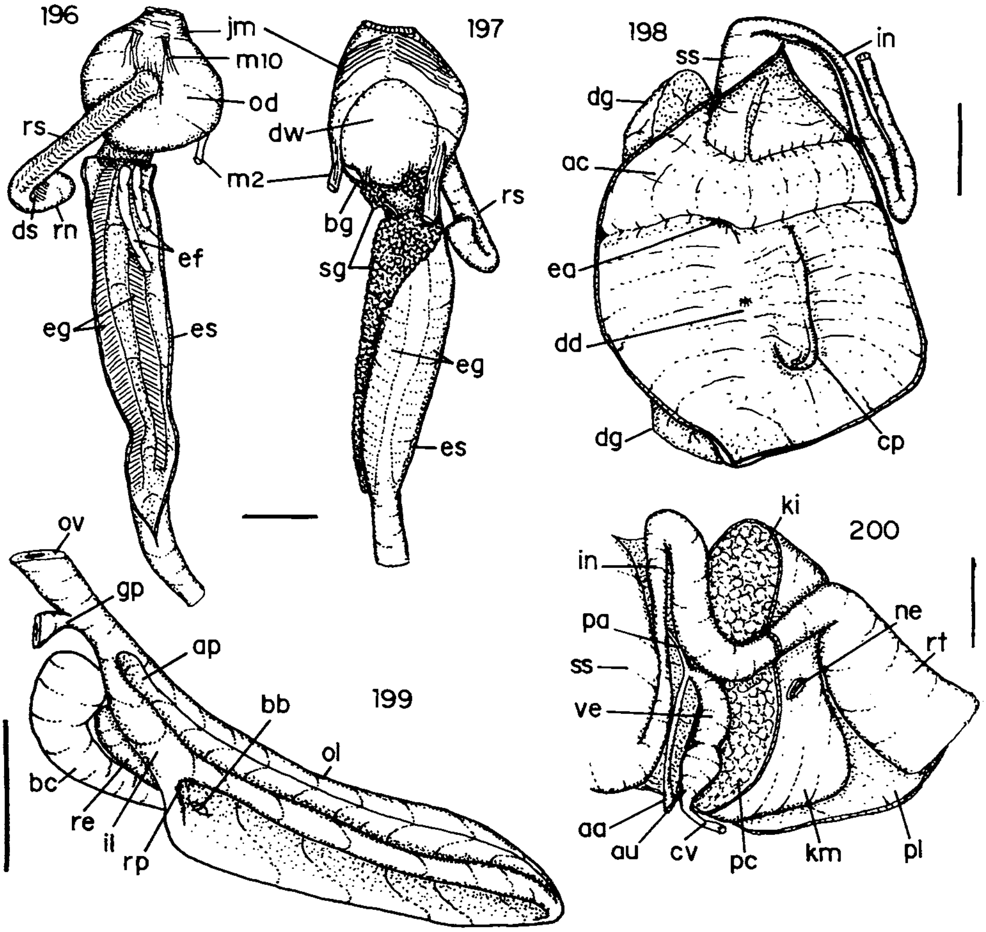
Figs 169-178 *Melanoides tuberculatus* anatomy: **169)** head-foot, frontal view; **170)** same, lateral-right view, some young specimens seen by transparency in brood pouch; **171)** head and haemocoel, ventral view, foot removed, snout opened longitudinally; **172)** pallial cavity, ventral-inner view; **173)** same than fig 171, inner organs removed except brood pouch and part of esophagus, brood pouch opened longitudinally, inner young specimens most removed; **174)** right region of pallial cavity and anterior region of visceral mass, right view; **175)** transversal section of middle region of pallial cavity; **176)** anterior region of visceral mass, pericardium and part of kidney opened to show their inner structures; **177)** stomach, dorsal view, dorsal wall removed, part of intestine opened longitudinally; **178)** dorsal wall of stomach, ventral view to show its inner surface. Scales = 1 mm; c1 = chamber with ova surrounding rectum; c2 = duct of chamber.



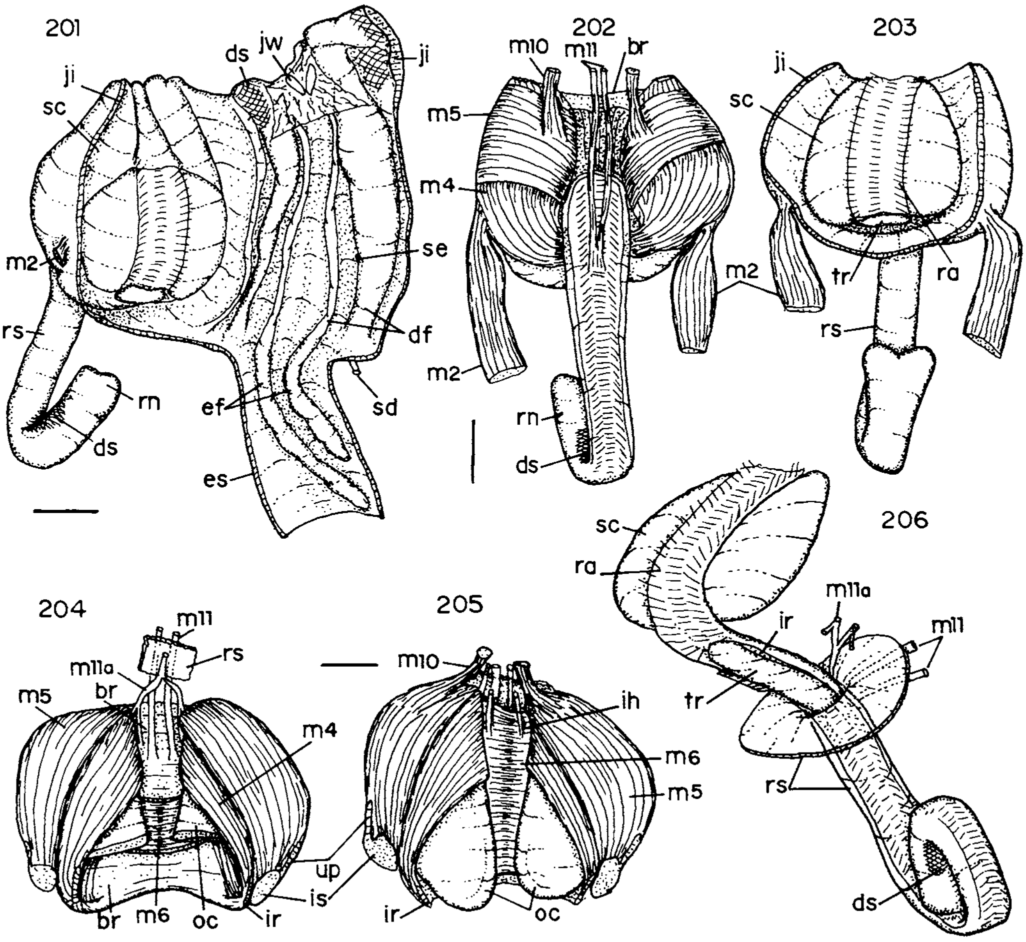
Figs 179-188 *Melanoides tuberculatus* anatomy: **179)** buccal mass and esophagus opened by a longitudinal section in left side, lateral-left view; **180)** buccal mass, ventral view; **181)** same, dorsal view; **182)** pallial oviduct extracted from rectum, right view, part of mantle also shown, **183)** buccal mass, dorsal view, dorsal wall and esophagus removed; **184)** odontophore, ventral wall, first layer of muscles and membranes removed; **185)** same, dorsal view, radula and subradular cartilage removed; **186)** same, most of muscles deflected to show inner structures, part of peribuccal muscles also shown; **187)** radula and subradular cartilage removed, dorsal view, part of adjacent muscles shown; **188)** same, lateral-right view. Scales = 1 mm; c1 = chamber with ova surrounding rectum; c2 = duct of chamber.



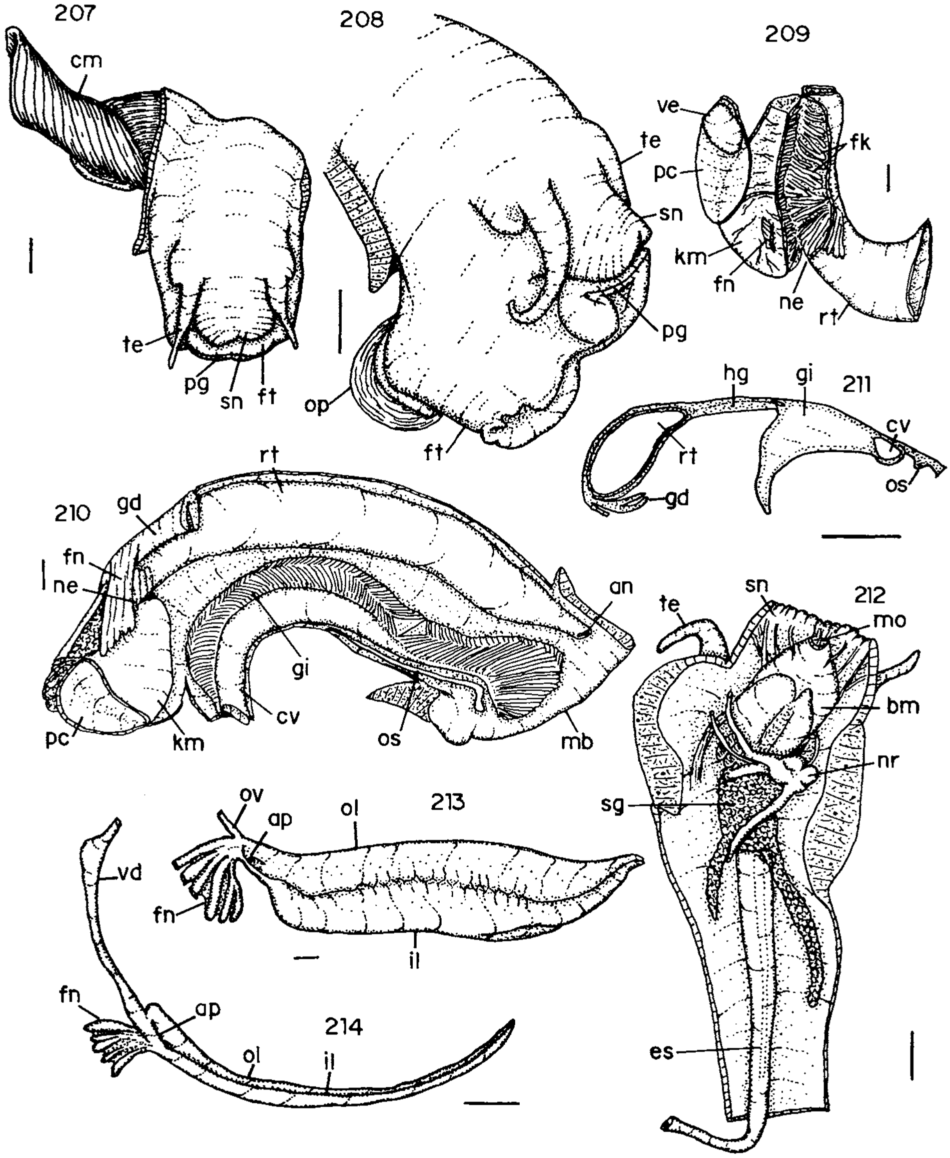
Figs 189-195 *Supplanaxis nucleus* anatomy: **189)** Head-foot of male, frontal view; **190)** head-foot of female, lateral-right view; **191)** posterior region of foot after frontal section of head-foot in middle region, anterior view, to show brood pouch immerse in foot; **192)** Head and part of haemocoel, ventral view, foot removed; **193)** pallial cavity, ventral-inner view; **194)** posterior limit of pallial cavity and entire visceral mass, lateral-right view, pericardium opened; **195)** transversal section of middle region of pallial cavity. Scales = 1 mm.



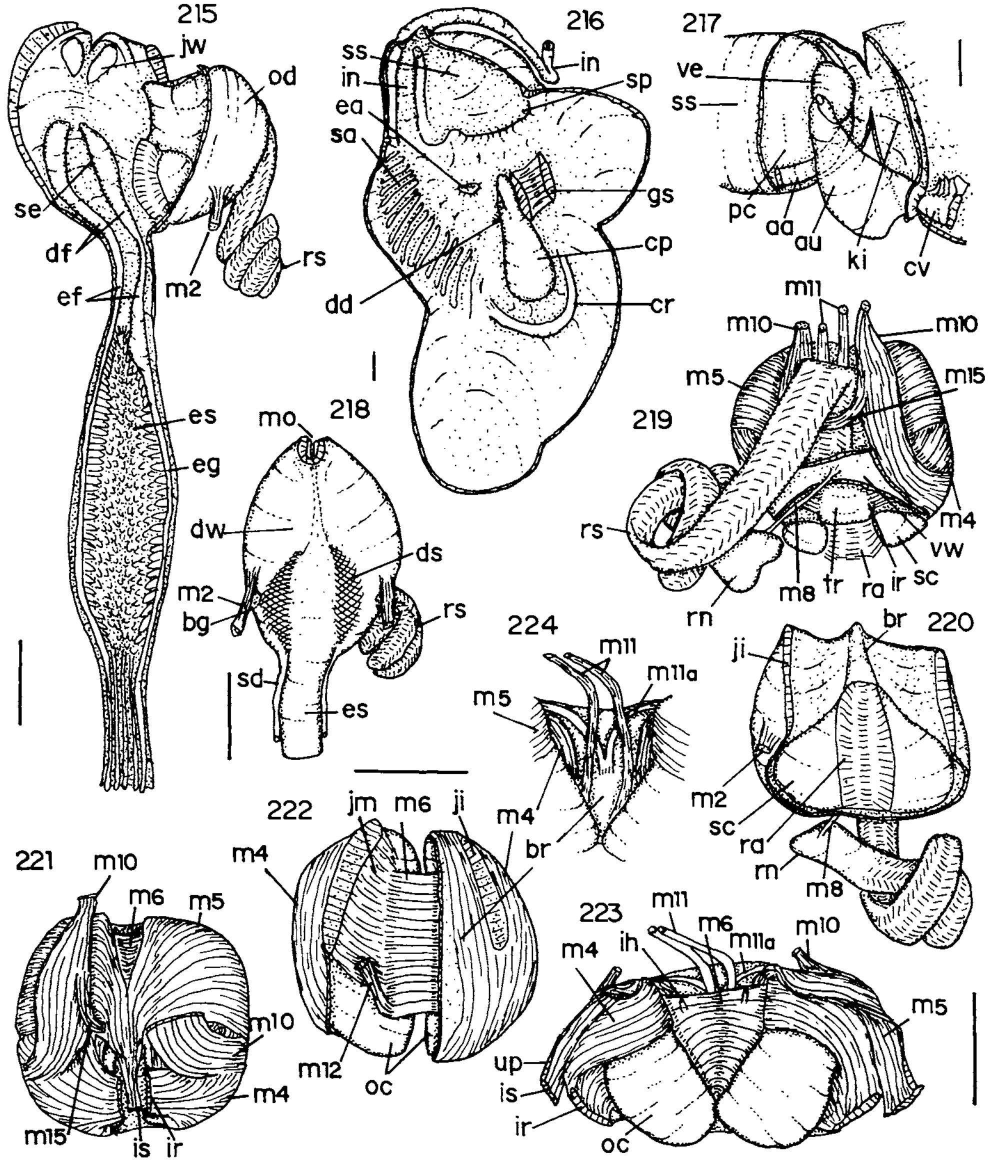
Figs 196-200 *Supplanaxis nucleus* anatomy: **196)** buccal mass and esophagus, ventral view, esophagus opened longitudinally; **197)** same, dorsal view; **198)** stomach opened by a longitudinal section in its middle region, dorsal view; **199)** pallial oviduct extracted, ventral view; **200)** posterior limit of pallial cavity and anterior region of visceral mass, ventral view, pericardium and kidney chamber opened. Scales = 1 mm.



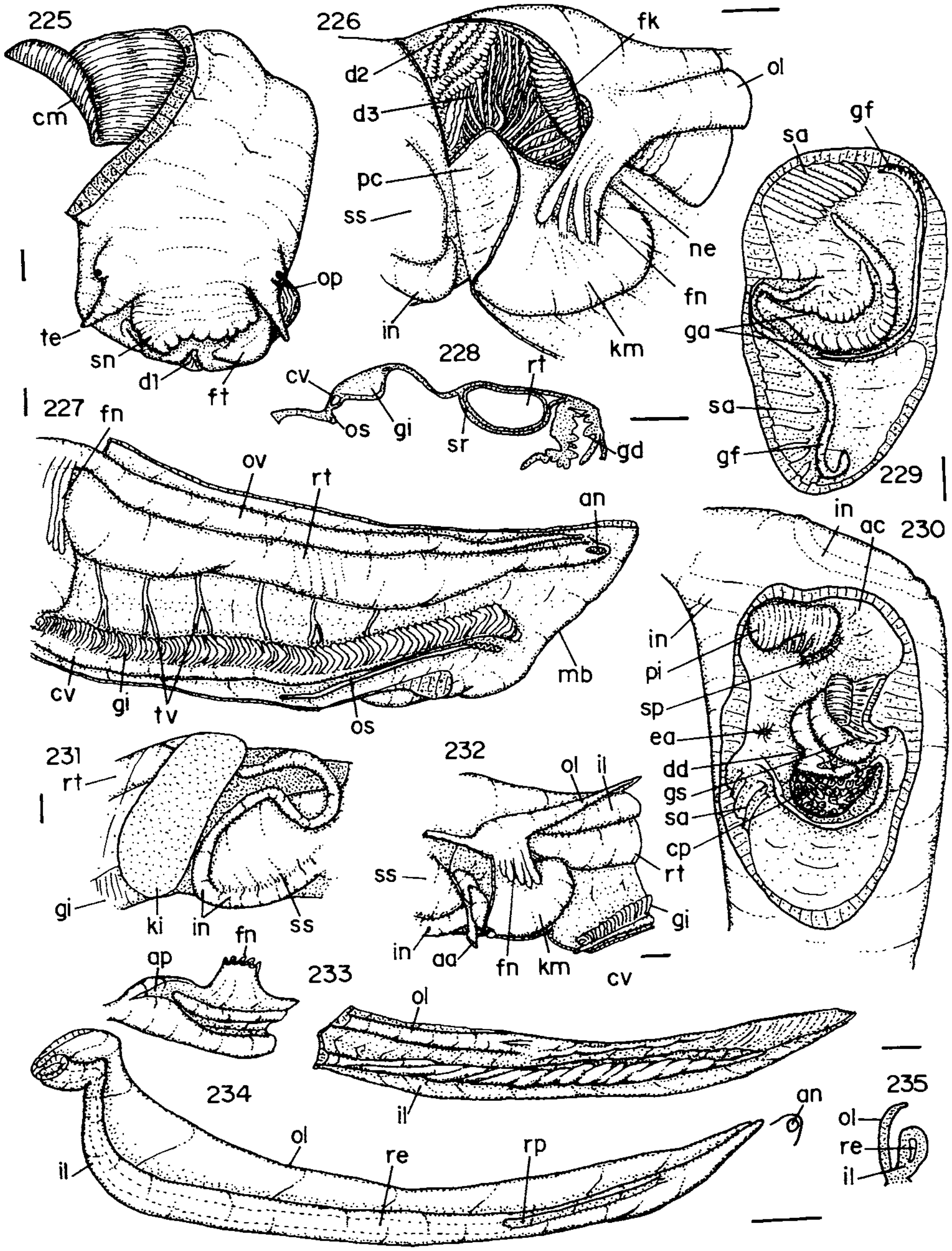
Figs 201-206 *Supplanaxis nucleus* anatomy: **201)** buccal mass and anterior esophagus opened by a longitudinal section in right region; **202)** odontophore, ventral view, first layer of muscles and membranes removed; **203)** same, dorsal view; **204)** same, ventral view, most of muscles deflected and part of horizontal muscle and cartilages removed to show inner structures; **205)** same, before extraction of part of horizontal muscle and cartilages; **206)** radula, subradular cartilage and radular sac extracted from odontophore, lateral right view. Scales = 0.5 mm.



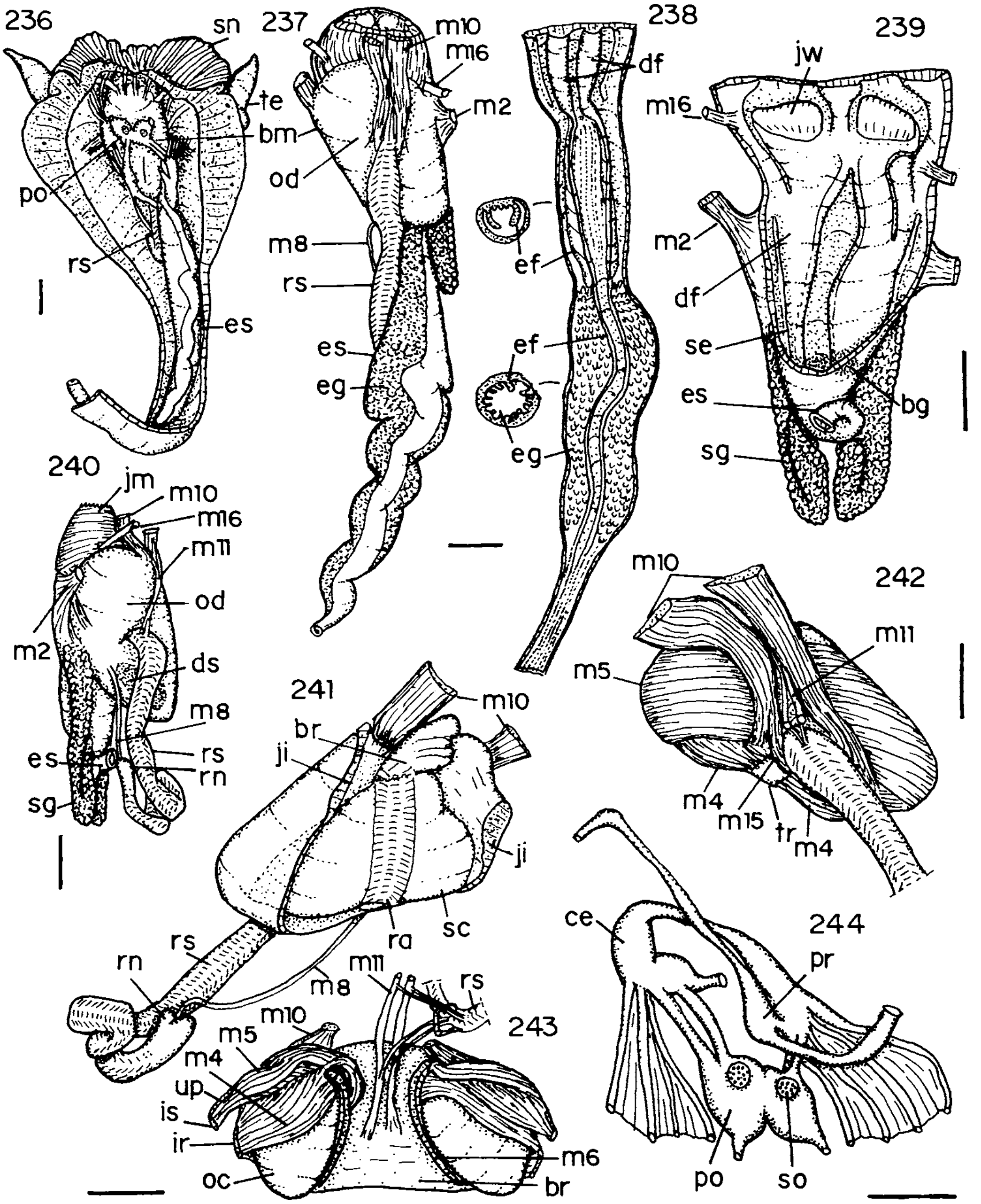
Figs 207-214 *Doryssa ipupiara* anatomy: **207)** head-foot, frontal view; **208)** same, lateral-right view; **209)** kidney extracted and opened longitudinally in its ventral region close rectum, part of pericardium and rectum also shown; **210)** pallial cavity, inner-ventral view, pallial gonoduct partially extracted; **211)** transversal section in middle region of pallial cavity; **212)** head, ventral view, foot extracted, snout opened longitudinally; **213)** pallial oviduct, extracted, ventral view; **214)** pallial spermoduct, extracted, ventral view. Scales = 1 mm.



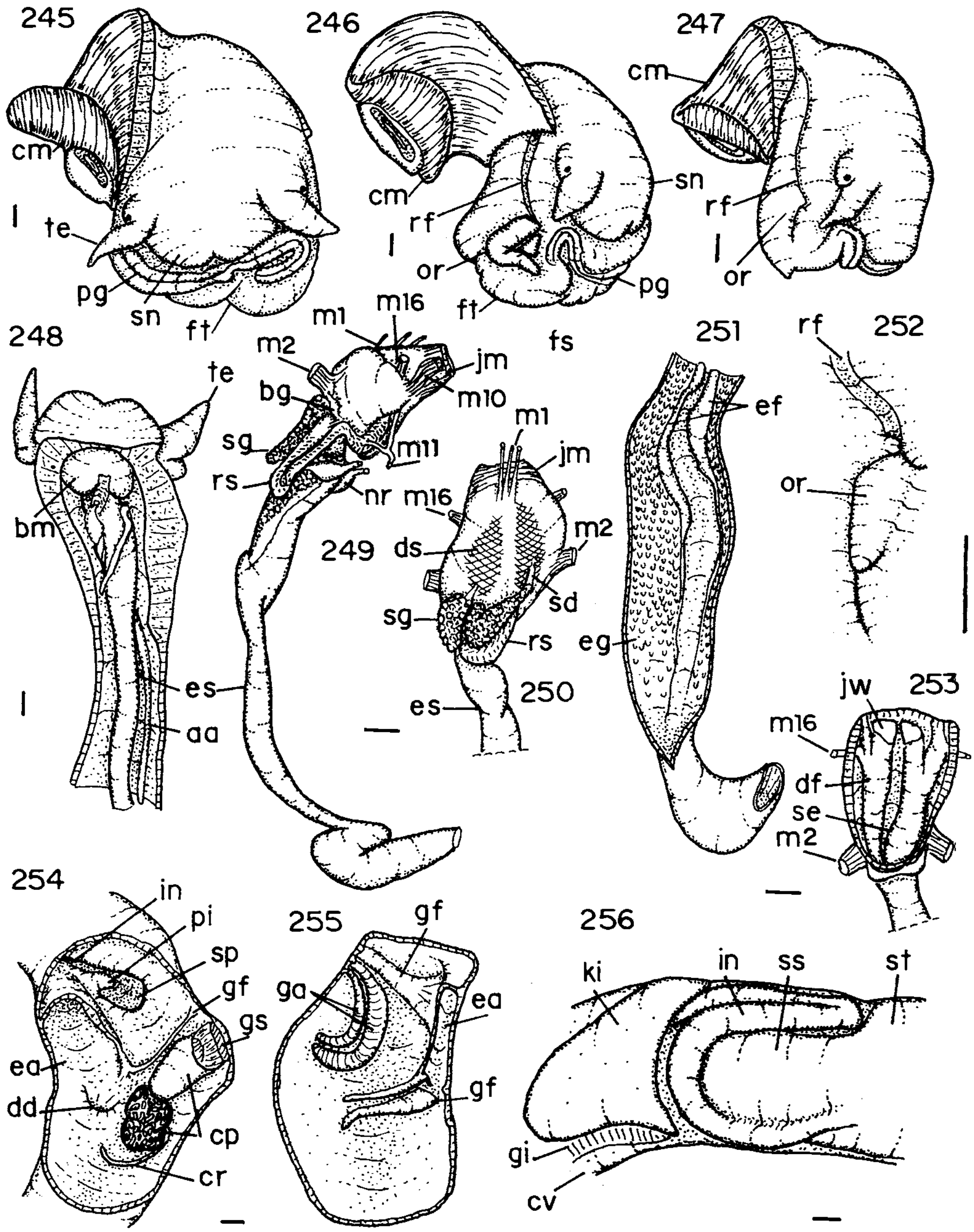
Figs 215-224 *Doryssa ipupiara* anatomy: **215)** buccal mass and esophagus, both opened longitudinally by means of a section in their right side, inner surface exposed; **216)** stomach, dorsal view, inner surface exposed by means of a median longitudinal section; **217)** pericardium dissected, ventral view; **218)** buccal mass, dorsal view; **219)** odontophore with first layer of muscles and membranes partially extracted, ventral view; **220)** same, dorsal view; **221)** same, ventral view, radula and subradular cartilage extrected, right m10 partially sectioned; **222)** same, dorsal view, left part of subradular membrane and m4 extracted to show inner structures; **223)** same, ventral view, most of muscles deflected to show inner structures; **224)** detail of fig. 223 with horizontal muscle extracted. Scales = 1 mm.



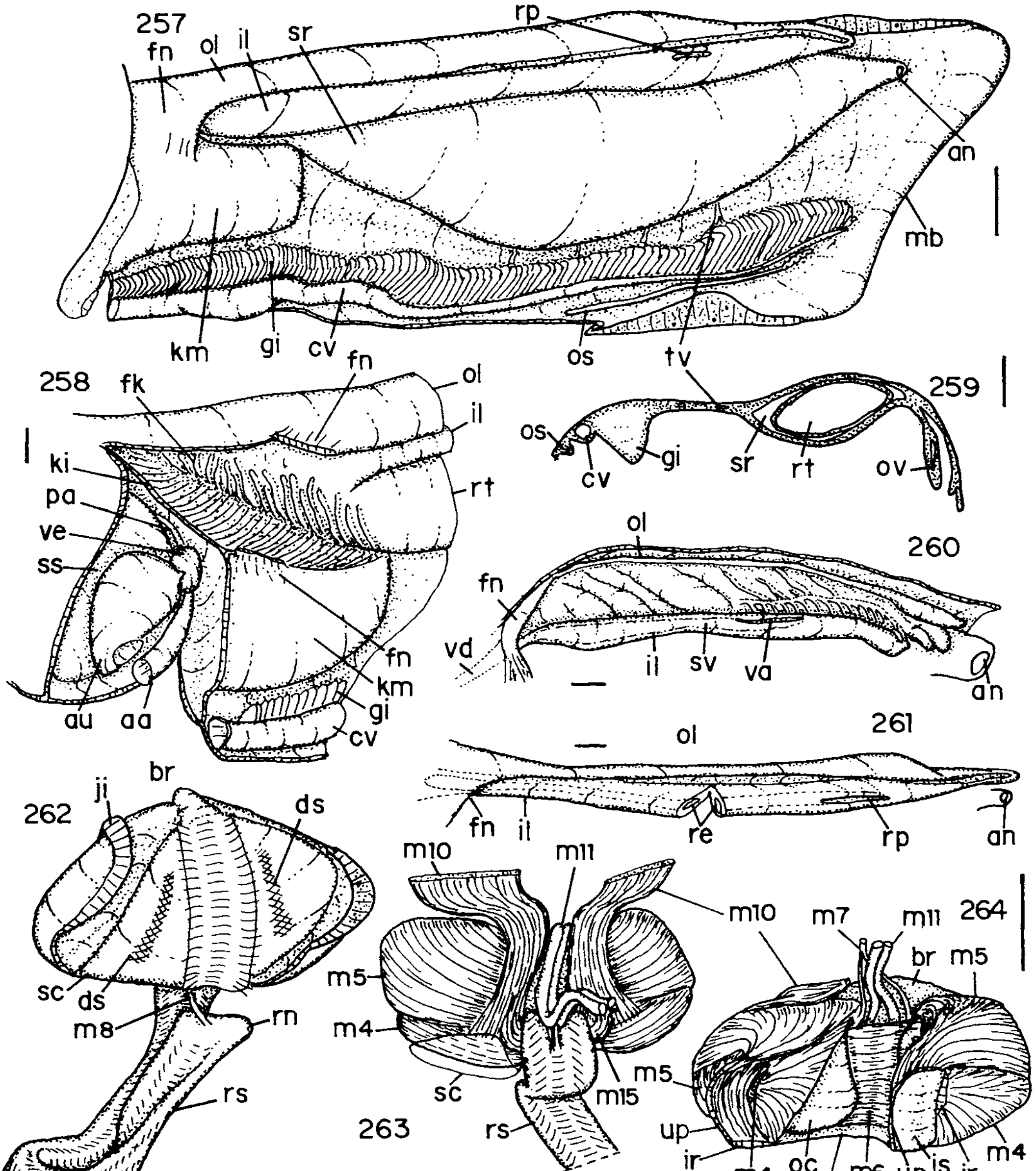
Figs 225-235 *Doryssa atra* anatomy: **225)** head-foot, frontal view; **226)** posterior end of pallial cavity and anterior region of visceral mass, ventral view, kidney opened by a transversal section, its inner surface exposed; **227)** pallial cavity, ventral-inner view; **228)** transversal section in middle region of pallial cavity; **229)** dorsal wall of stomach, ventral-inner view; **230)** stomach, dorsal view, dorsal wall extracted to show its inner surface; **231)** anterior region of visceral mass, dorsal-outer view; **232)** same region. ventral-inner view, pericardium opened transversally; **233)** pallial spermoduct, extracted, ventral view; **234)** pallial oviduct, extracted, ventral view; **235)** same, transversal section in its middle region. Scales = 1 mm; d1 = mesopodial tentacle; d2 = large folds of kidney posterior to rectum; d3 = kidney septate face.



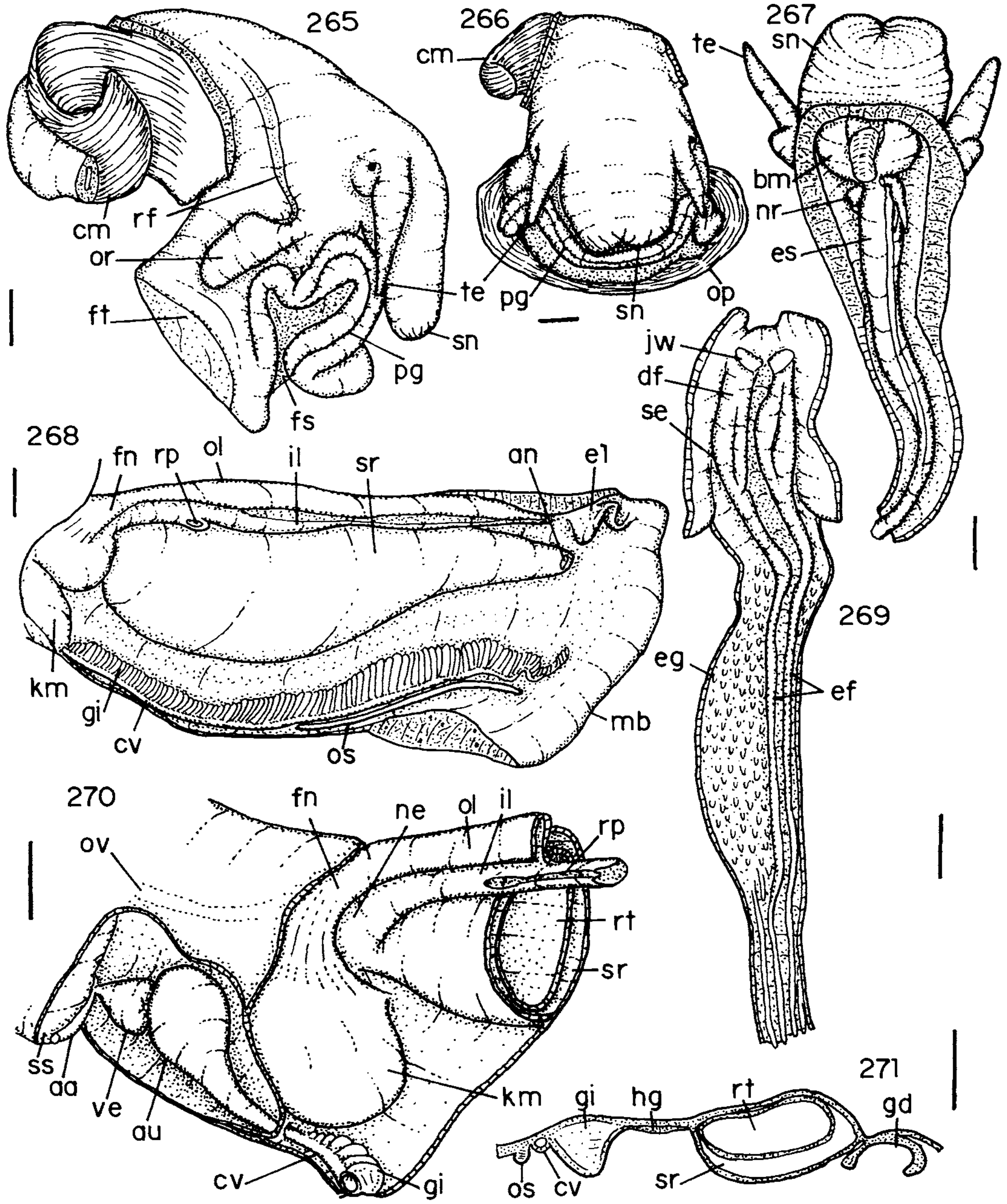
Figs 236-244 *Doryssa atra* anatomy: **236)** head and haemocoel, ventral view, foot extracted, snout opened longitudinally; **237)** buccal mass and esophagus extracted, dorsal view; **238)** dorsal wall of buccal mass and esophagus opened longitudinally, ventral view, inner surface exposed, with two transversal sections of indicated level shown; **239)** dorsal wall of buccal mass, ventral view, odontophore extracted, inner surface exposed; **240)** buccal mass, lateral-right view, note salivary glands only anterior to nerve ring level (nerve ring extracted, but its site indicated); **241)** odontophore, dorsal view; **242)** same, ventral view, first layer of muscles and membranes extracted; **243)** same, ventral view, most of muscles deflected and horizontal muscle sectioned to show inner structures; **244)** central nervous system, ventral view. Scales = 1 mm.



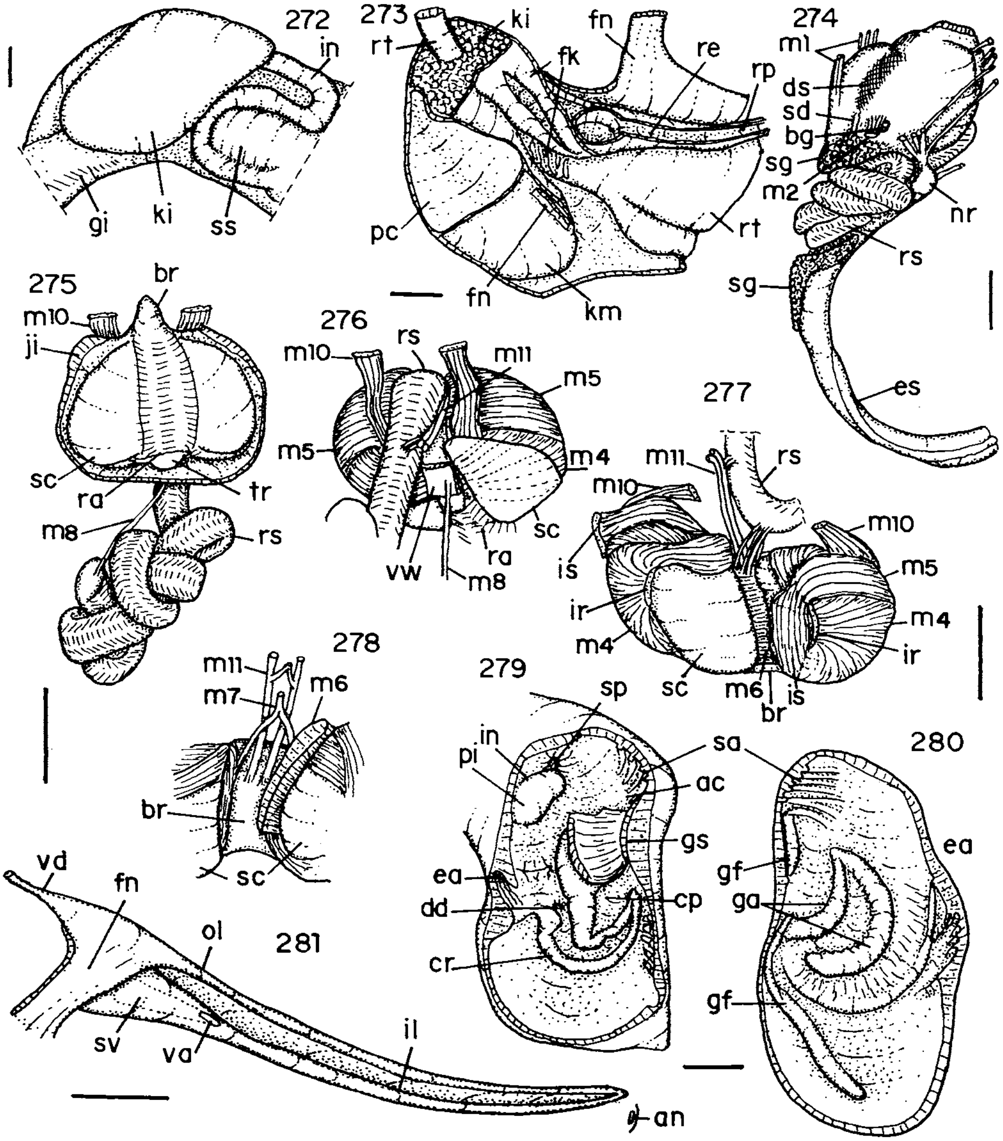
Figs 245-256 *Doryssa macapa* anatomy: **245)** head-foot, male, frontal view; **246)** head-foot, mature female, lateral-right view; **247)** head-foot, immature female, lateral-right view; **248)** head and haemocoel, ventral view, foot extracted; **249)** buccal mass and esophagus, lateral-right view; **250)** buccal mass, dorsal view; **251)** esophagus, dorsal view, anterior and middle region opened longitudinally, inner surface exposed; **252)** detail of immature female (fig. 247) ovopositor, dorsal view; **253)** dorsal wall of buccal mass, odontophore extracted, ventral view inner surface exposed; **254)** stomach, dorsal view, dorsal wall extracted, inner surface exposed; **255)** dorsal wall of stomach, ventral view; **256)** anterior region of visceral mass, dorsal-outer view, anterior region at left. Scales = 1 mm.



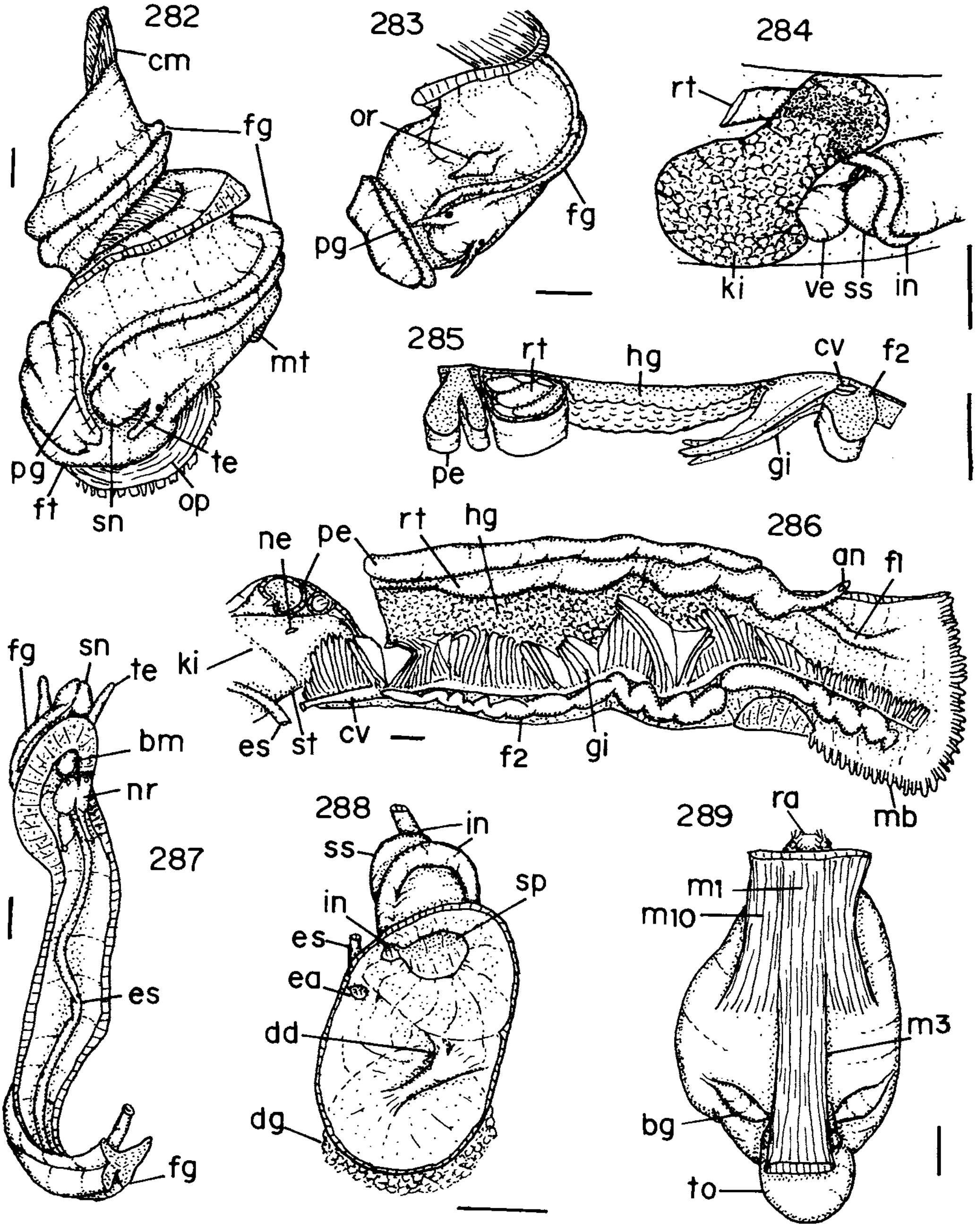
Figs 257-264 *Doryssa macapa* anatomy: **257)** pallial cavity, ventral-inner view; **258)** detail of posterior end of pallial cavity, ventral-inner view, pericardium and kidney opened, inner surface exposed; **259)** transversal section in middle region of pallial cavity; **260)** pallial spermoduct, ventral view, inner lamina partially deflected to show inner surface, part of mantle also shown; **261)** same for pallial oviduct; **262)** odontophore, dorsal view; **263)** same, ventral view, first layer of muscles and membranes extracted; **264)** same, ventral view, right muscles (left in figure) deflected to show inner structures. Scales = 1 mm.



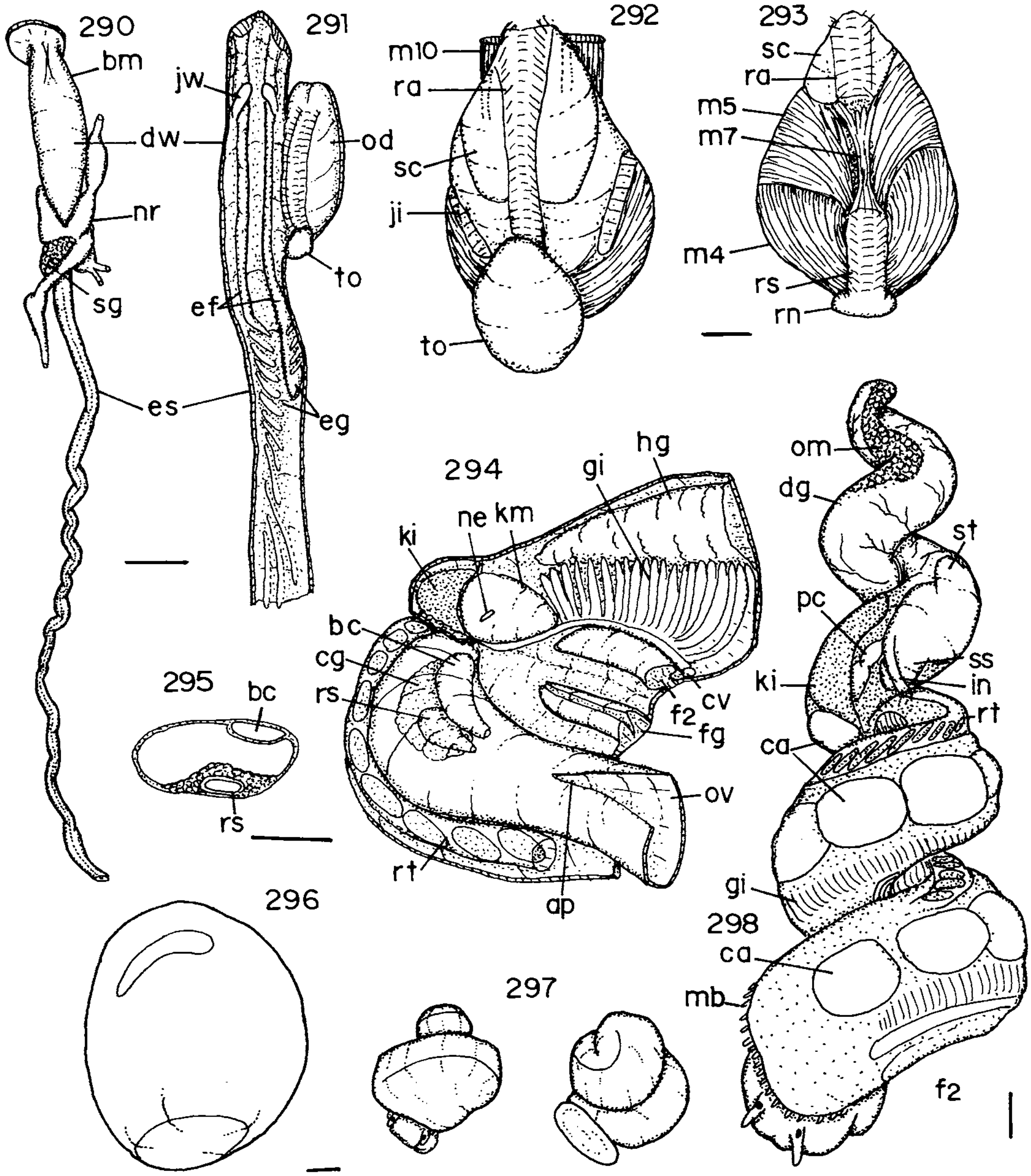
Figs 265-271 *Pachychilus* sp. anatomy: **265)** head-foot of female, lateral right view; **266)** same, frontal view; **267)** Head and haemocoel, ventral view, foot extracted; **268)** pallial cavity, ventral-inner view; **269)** Dorsal wall of buccal mass and esophagus opened longitudinally, ventral view, odontophore extracted; **270)** posterior end of pallial cavity and anterior region of visceral mass, ventral-inner view, pericardium opened longitudinally; **271)** transversal section in middle region of pallial cavity. Scales = 1 mm; e1 = pallial flap.



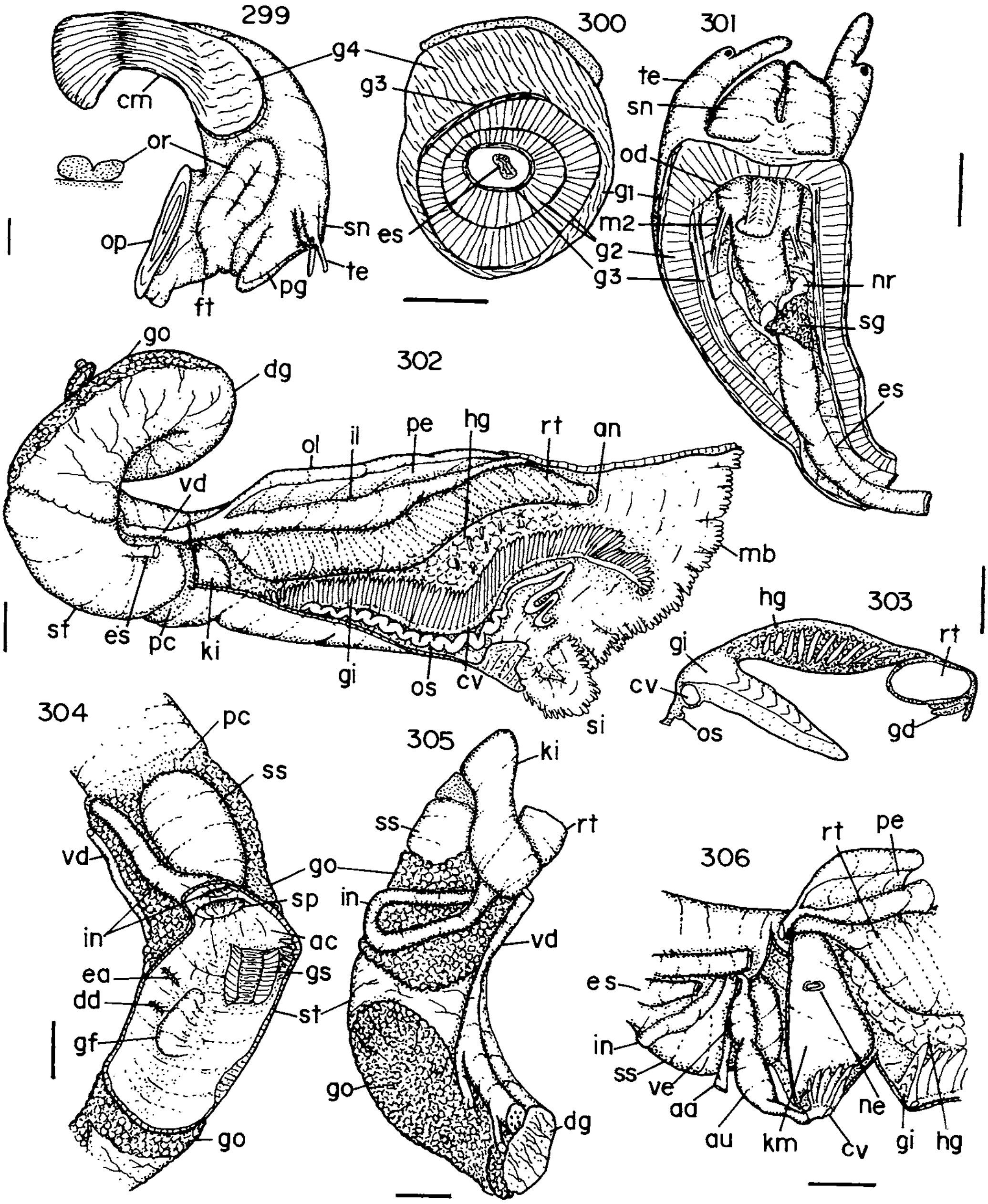
Figs 272-281 *Pachychilus* sp. anatomy: **272)** anterior region of visceral mass, dorsal-outer view, anterior region at left; **273)** posterior end of pallial cavity, ventral-inner view; **274)** buccal mass and esophagus, lateral-right view; **275)** odontophore, dorsal view; **276)** same, ventral view, first layer of muscles and membranes partially removed; **277)** same. ventral view, right muscles (left in figure) deflected to show inner structures, radular ribbon also deflected; **278)** same, ventral view, detail of middle region with horizontal muscle sectioned to show inner structures; **279)** stomach, dorsal view, dorsal wall extracted, inner surface exposed; **280)** dorsal wall of stomach, ventral view; **281)** pallial spermoduct extracted, ventral view. Scales = 1 mm.



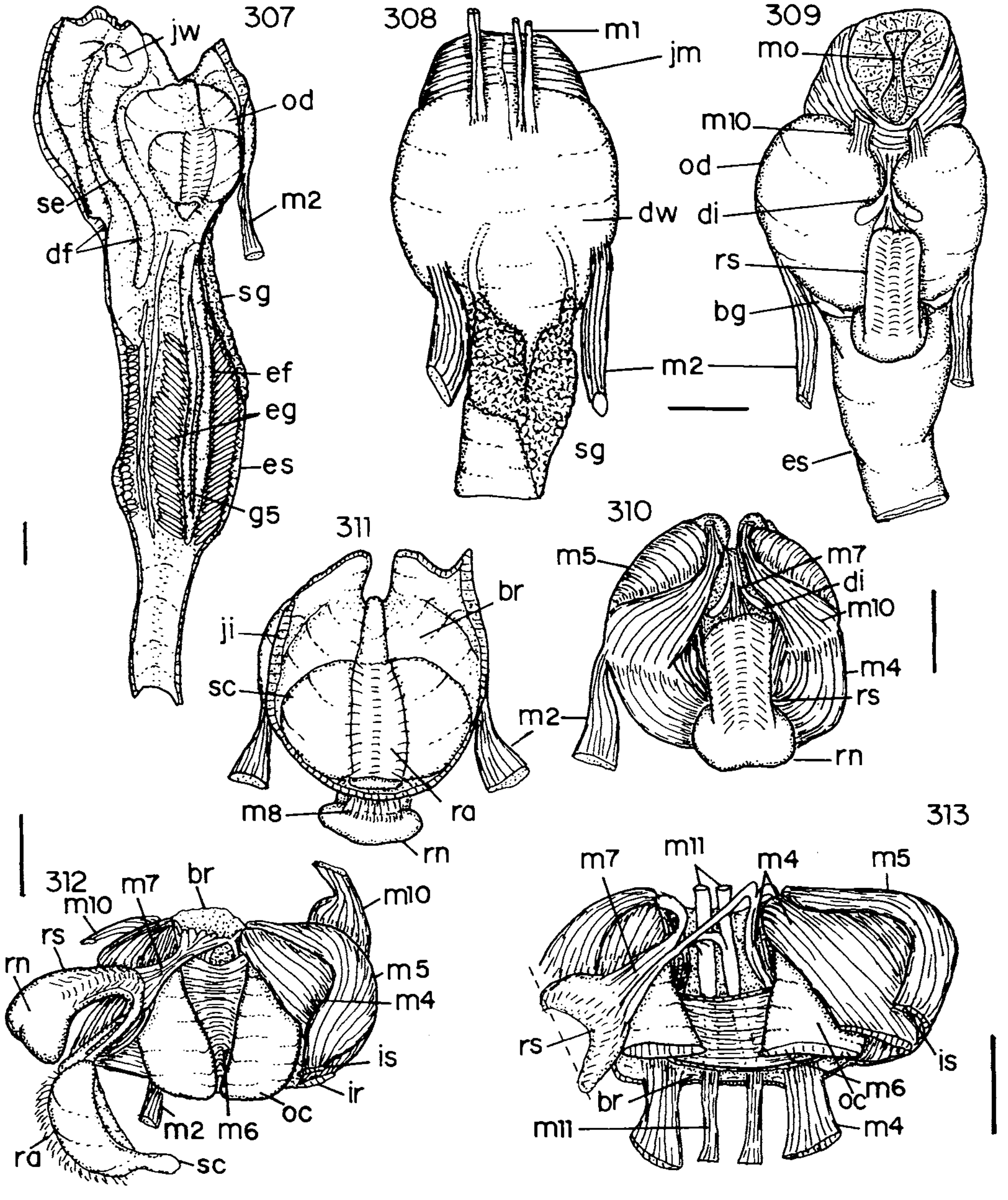
Figs 282-289 *Turritella hookeri* anatomy: **282)** head-foot, male, frontal view; **283)** head-foot, female, frontal view, only last whorl shown; **284)** anterior region of visceral mass, dorsal-outer view, anterior to left; **285)** transversal section of middle region of pallial cavity; **286)** pallial cavity, ventral-inner view; **287)** head and haemocoel, ventral view, foot extracted; **288)** stomach, dorsal view, dorsal wall extracted, inner surface exposed; **289)** odontophore, ventral view. Scales 282-288 = 0.5 mm, 289 = 0.1 mm; f1 = mantle fold from region of anus to near border; f2 = endostyle.



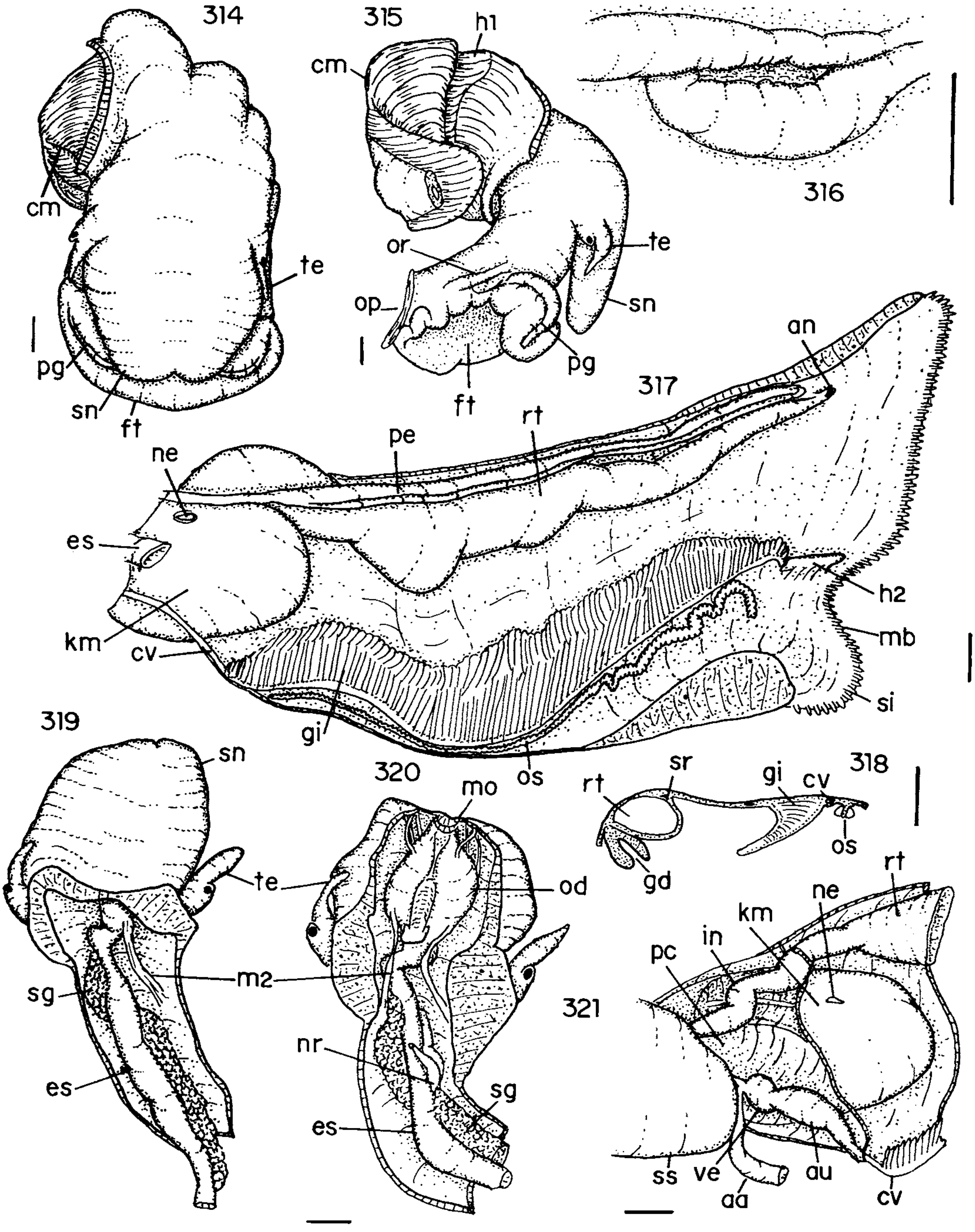
Figs 290-298 *Turritella hookeri* anatomy: **290)** buccal mass and esophagus, dorsal view; **291)** same, opened by means of longitudinal section in their right side; **292)** odontophore, dorsal view; **293)** same, ventral view, first layer of muscles and membrane extracted; **294)** posterior region of pallial cavity, ventral-inner view; **295)** transversal section in posterior region of pallial oviduct; **296)** capsule extracted from pallial cavity; **297)** two young specimens extracted from capsule; **298)** mature female, whole outer view, showing disposition of capsules within pallial cavity. Scales 290-291, 294-295, 298 = 0.5 mm; 292-293, 296-297 = 0.1 mm; f2 = endostyle.



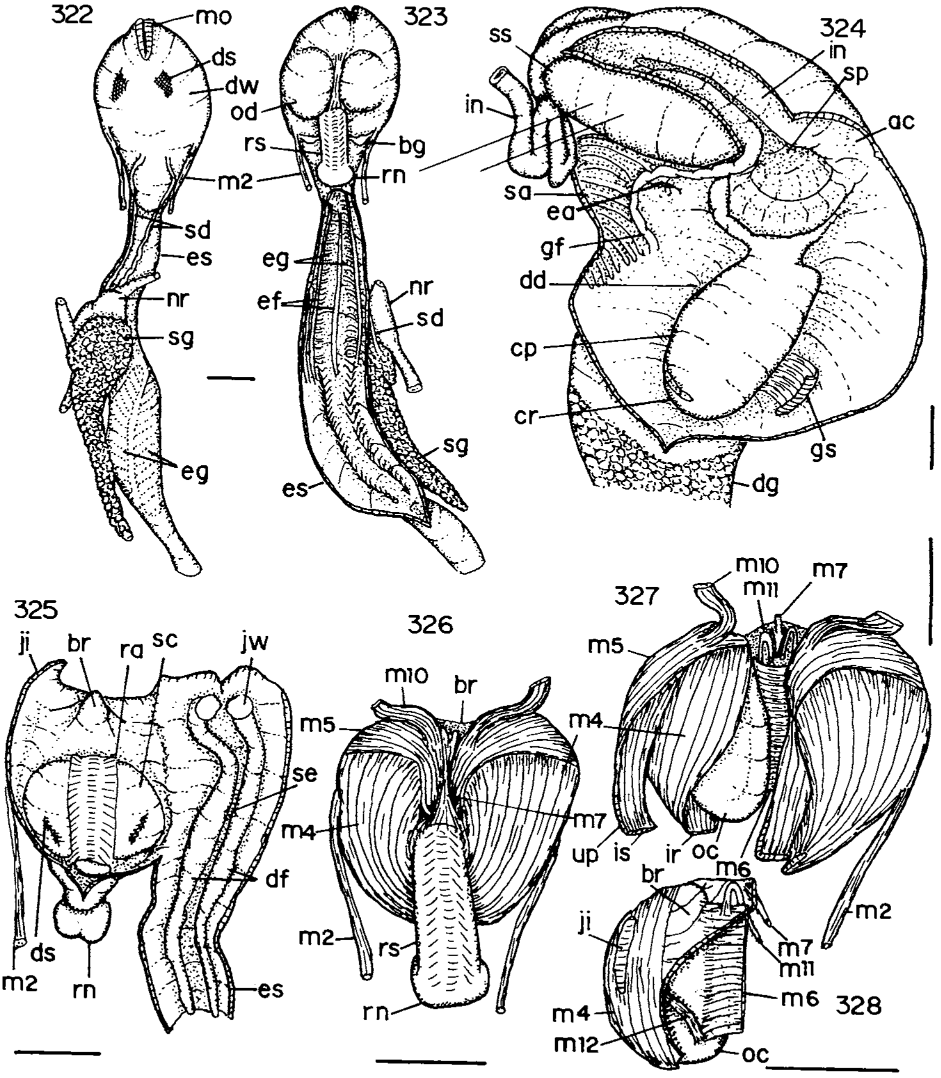
Figs 299-306 *Modulus modulus* anatomy: **299)** head-foot, female, lateral-right view; **300)** transversal section in middle region posterior to head showing muscle layers; **301)** head, ventral view, foot extracted; **302)** pallial cavity, ventral-inner view, whole visceral mass also shown; **303)** transversal section in middle region of pallial cavity; **304)** stomach and adjacent structures, dorsal view, dorsal wall of stomach extracted to show inner surface; **305)** same region, ventral view; **306)** posterior end of pallial cavity and anterior region of visceral mass, ventral-inner view, pericardium opened transversally. Scales = 1 mm; g1 = longitudinal muscle fibers; g2 = transversal muscle fibers; g3 = circular muscle fibers; g4 = thickness of columellar muscle.



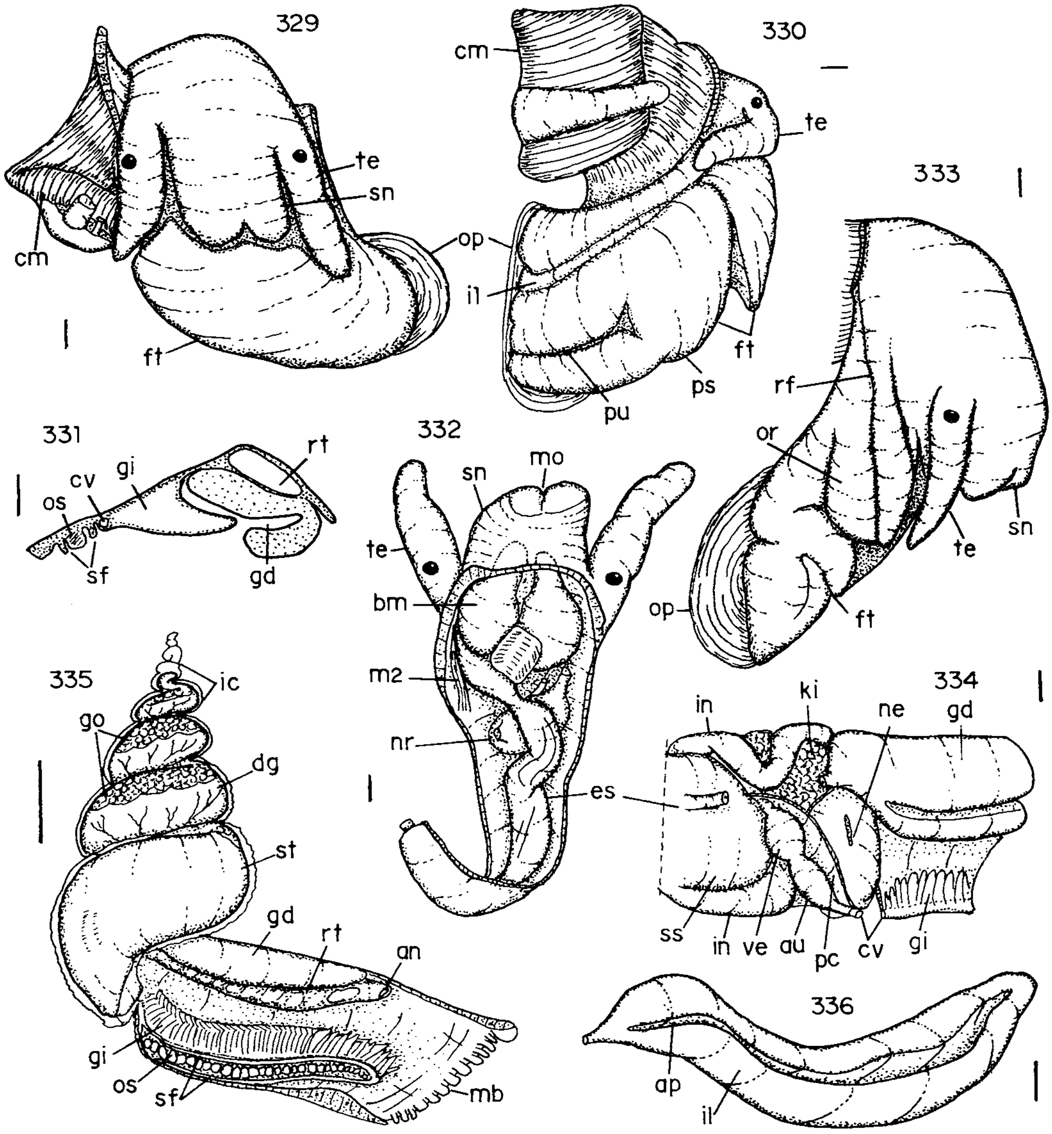
Figs 307-313 *Modulus modulus* anatomy: **307)** buccal mass, ventral view; **308)** same, dorsal view; **309)** buccal mass and esophagus opened longitudinally by means of a section in their left region; **310)** odontophore, ventral view, first layer of muscles and membranes extracted; **311)** same, dorsal view; **312)** same, ventral view, most of muscles deflected to show inner structures, cartilages, horizontal muscle, m4 and subradular membrane partially sectioned; **313)** same before section of structures. Scales = 0.5 mm; g5 = annex third esophageal pouch resulting from a deep furrow of large esophageal fold in its middle region.



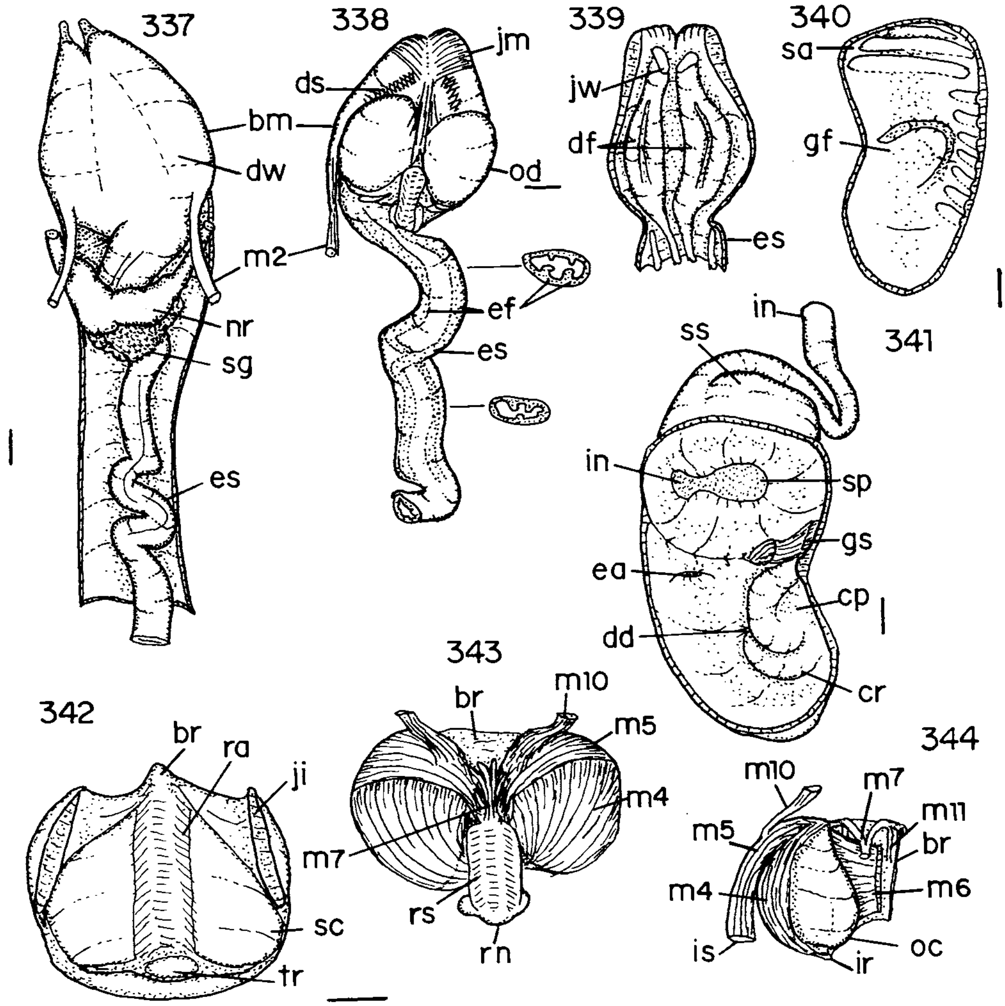
Figs 314-321 *Cerithium atratum* anatomy: **314)** head-foot, male, frontal view; **315)** head-foot, female, lateral-right view; **316)** detail of ovopositor of fig. 315; **317)** pallial cavity, ventral-inner view; **318)** transversal section in middle region of pallial cavity; **319)** head and haemocoel, ventral view, foot extracted; **320)** same, snout opened longitudinally; **321)** posterior end of pallial cavity and anterior region of visceral mass, ventral-inner view, pericardium opened. Scales = 1 mm; h1 = transversal furrow of columellar muscle, found in some specimens.



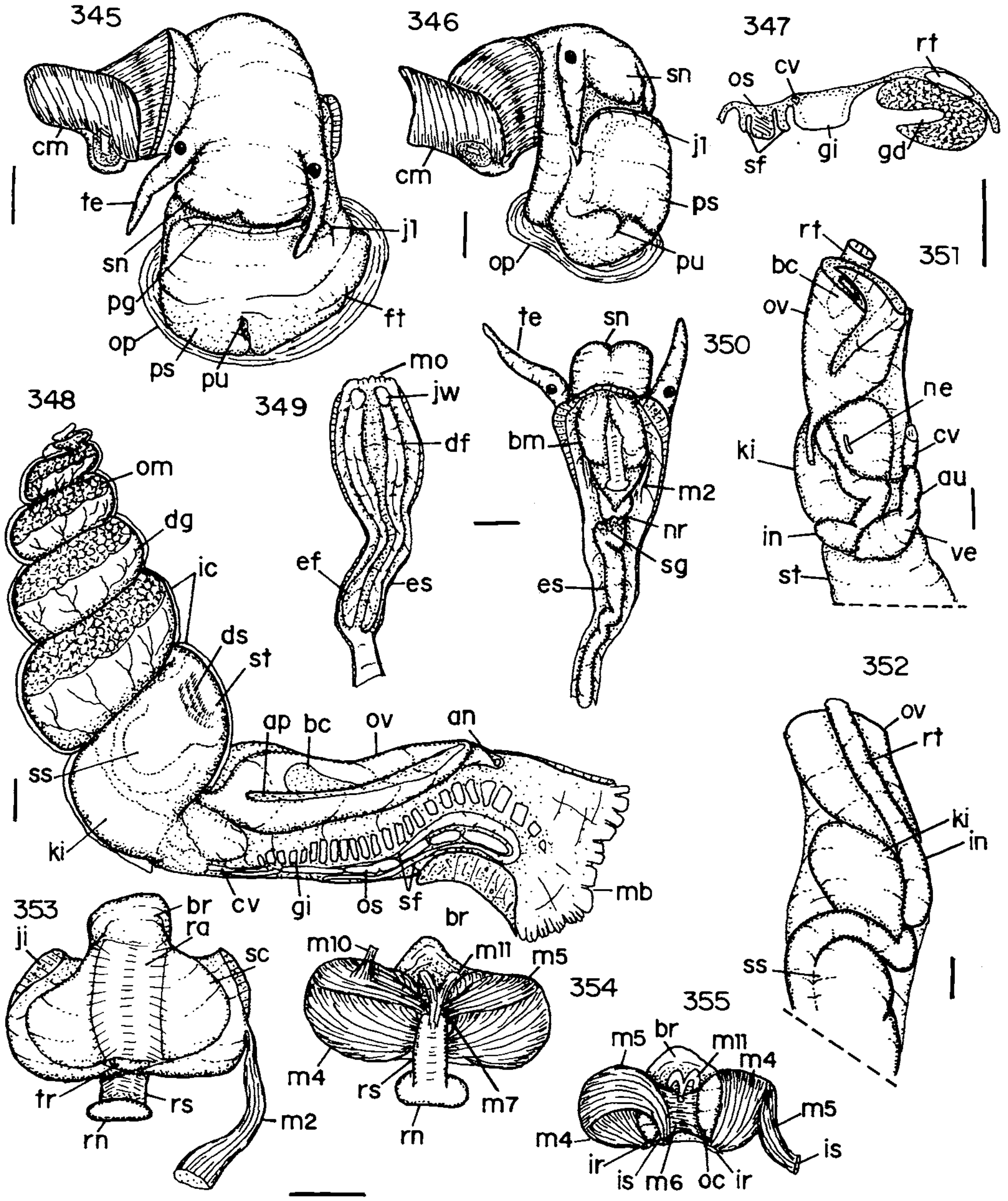
Figs 322-328 *Cerithium atratum* anatomy: **322)** buccal mass and esophagus, dorsal view; **323)** same, ventral view; **324)** stomach, dorsal view, inner surface exposed by means of a longitudinal section in its median region; **325)** Buccal mass opened by means of a longitudinal section in their left side; **326)** odontophore, ventral view, first layer of muscles and membranes extracted; **327)** same, ventral view, radula extracted, right muscles (left in figure) deflected to show inner structures; **328)** same, left half, dorsal view, subradular membrane partially extracted to show inner structures. Scales = 1 mm.



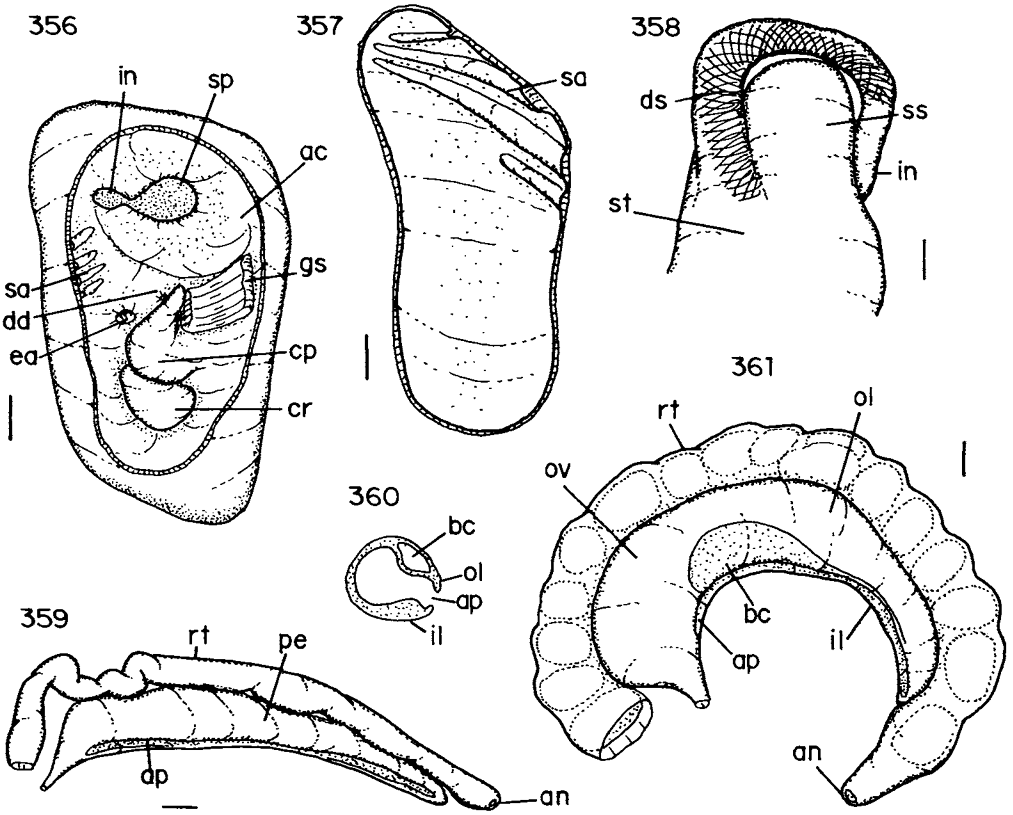
Figs 329-336 *Bittium varium* anatomy: **329)** head-foot, male, frontal view; **330)** same, lateral-right view; **331)** transversal section in middle region of pallial cavity; **332)** head, ventral view, foot extracted; **333)** head-foot, female, lateral-right view; **334)** posterior region of pallial cavity and anterior region of visceral mass, ventral-inner view, pericardium and part of kidney opened, anterior region at right; **335)** pallial cavity, ventral-inner view, whole visceral mass also shown; **336)** pallial spermoduct extracted, ventral view, anterior region at right. Scales = 0.1 mm, except 335 = 0.5 mm; i1 = furrow between mesopodium and metapodium.



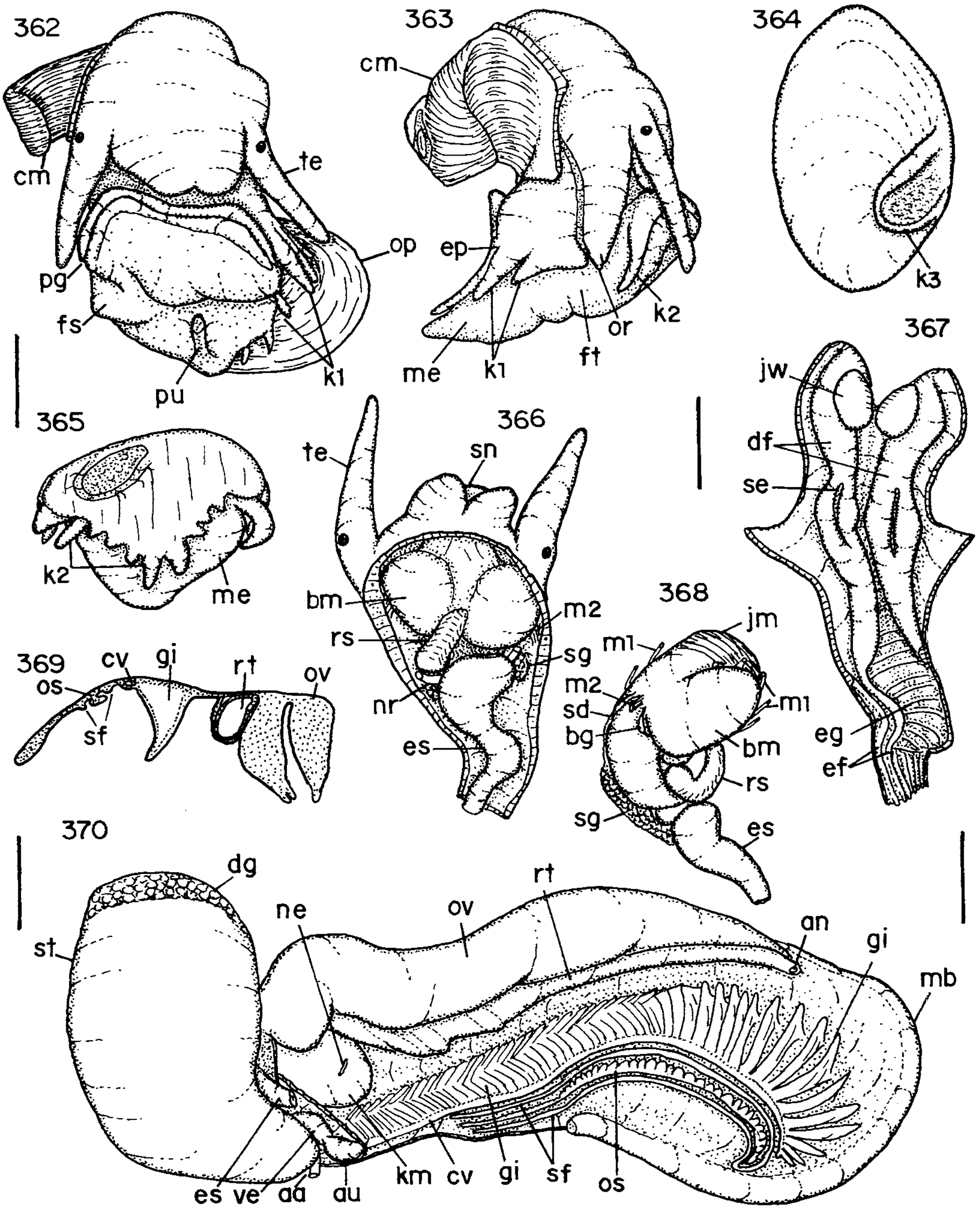
Figs 337-344 *Bittium varium* anatomy: **337)** buccal mass and esophagus, dorsal view, part of haemocoel floor also shown; **338)** same, ventral view, with transversal sections in two indicated esophageal levels; **339)** dorsal wall of buccal mass, ventral view, odontophore extracted; **340)** dorsal wall of stomach, ventral view; **341)** stomach, dorsal view, dorsal wall extracted, inner surface exposed; **342)** odontophore, dorsal view; **343)** same, ventral view, first layer of muscles and membranes extracted; **344)** same, left half, most of muscles deflected to show inner structures. Scales = 0.1 mm.



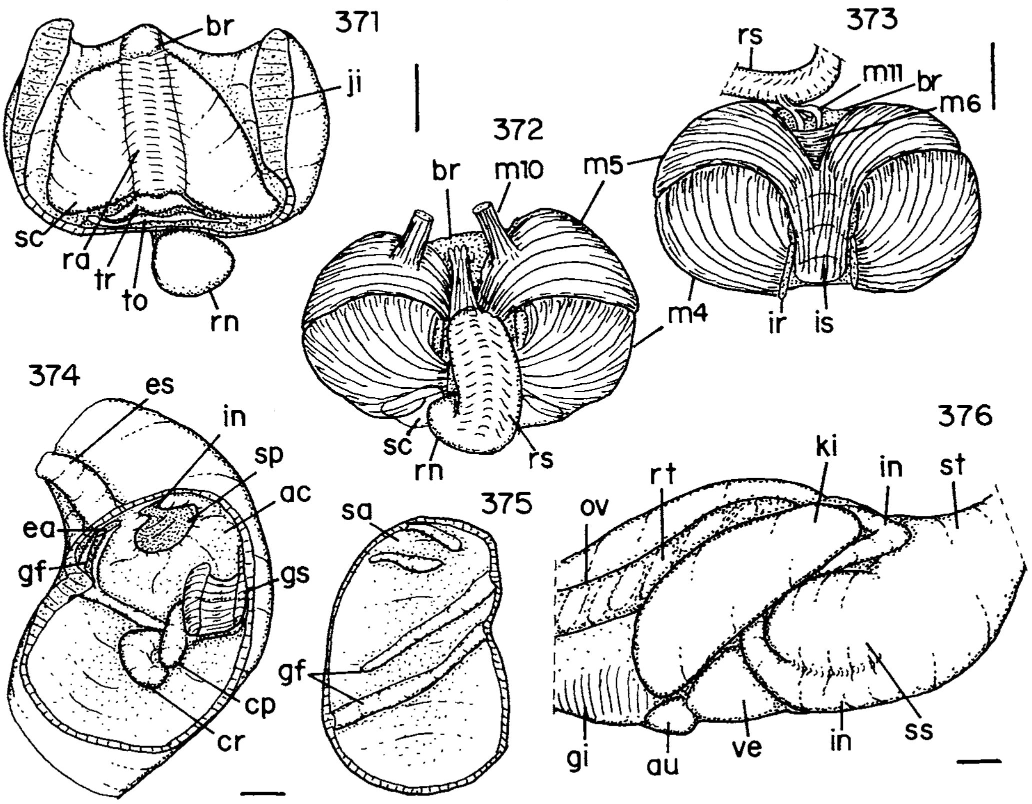
Figs 345-355 *Finella dubia* anatomy: **345)** head-foot, male, frontal view; **346)** head-foot, female, lateral-right view; **347)** transversal section in middle region of pallial cavity; **348)** pallial cavity, ventral-inner view, entire visceral mass also shown; **349)** dorsal wall of buccal mass, ventral view, inner surface exposed; **350)** head and haemocoel, ventral view, foot removed; **351)** posterior region of pallial cavity and anterior region of visceral mass, ventral-inner view; **352)** same, dorsal-outer view; **353)** odontophore, dorsal view; **354)** same, ventral view, first layer of muscles and membranes extracted; **355)** same, ventral view, radula and subradular cartilage extracted, left muscles (right in figure) deflected to show inner structures. Scales (345-352) = 0.2 mm, (353-355)= 0.1 mm; j1 = anterior flap of foot.



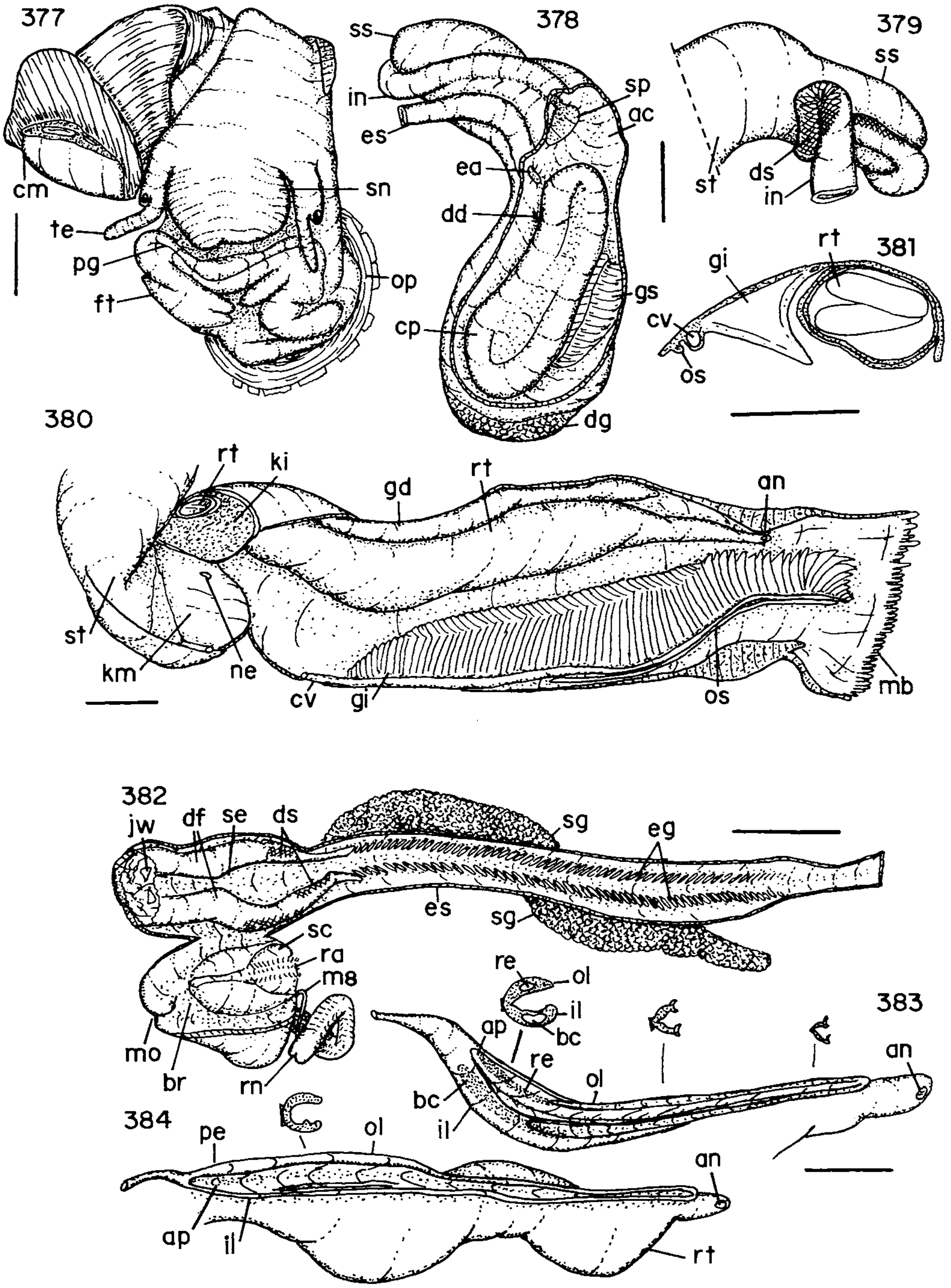
Figs 356-361 *Finella dubia* anatomy: **356)** stomach, dorsal view, dorsal wall extracted, inner surface exposed; **357)** dorsal wall of stomach, ventral surface; **358)** anterior region of stomach, dorsal view, digestive gland and kidney extracted; **359)** pallial spermoduct and rectum, ventral view; **360)** transversal section in middle region of pallial oviduct; **361)** pallial oviduct and rectum, ventral view. Scales = 0.1 mm.



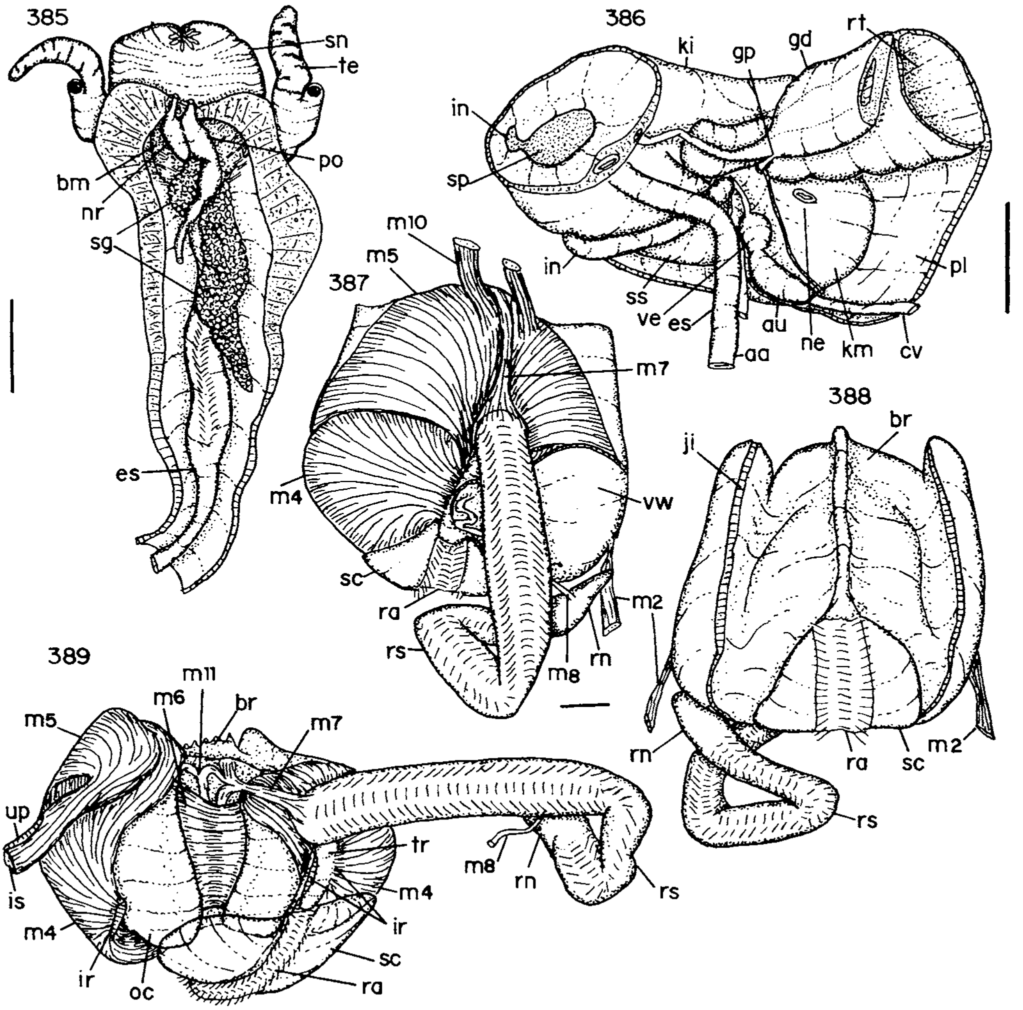
Figs 362-370 *Alaba incerta* anatomy: **362)** head-foot, male, frontal view; **363)** head-foot, female, lateral-right view; **364)** operculum, inner view; **365)** opercular pad and dorsal-posterior region of foot, dorsal view, operculum extracted; **366)** head and haemocoel, ventral view, foot removed; **367)** dorsal wall of buccal mass and esophagus, ventral view, inner surface exposed; **368)** buccal mass and esophagus, lateral-right view; **369)** transversal section in middle region of pallial cavity; **370)** pallial cavity, ventral-inner view, last visceral whorl also shown. Scales = 0.5 mm; k1 = epipodial tentacle; k2 = propodial tentacle; k3 = ridge surrounding opercular scar.



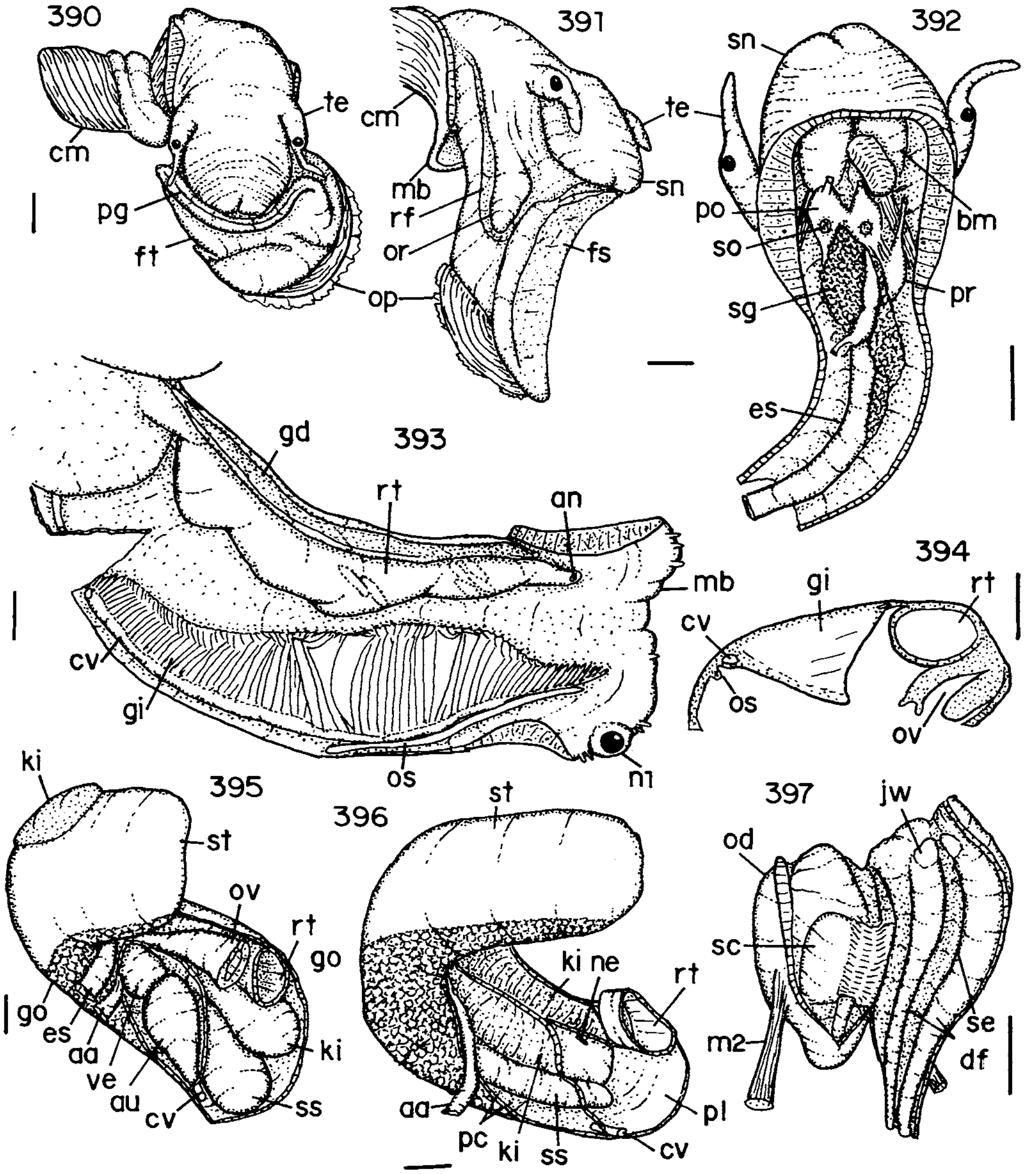
Figs 371-376 *Alaba incerta* anatomy: **371)** odontophore, dorsal view; **372)** same, ventral view, first layer of muscles and membranes extracted; **373)** same, ventral view, radula and subradular cartilage extracted and deflected; **374)** stomach, dorsal view, dorsal wall extracted, inner surface exposed; **375)** dorsal wall of stomach, ventral view; **376)** posterior region of pallial cavity and anterior region of visceral mass, dorsal-outer view, anterior region at left. Scales = 0.2 mm.



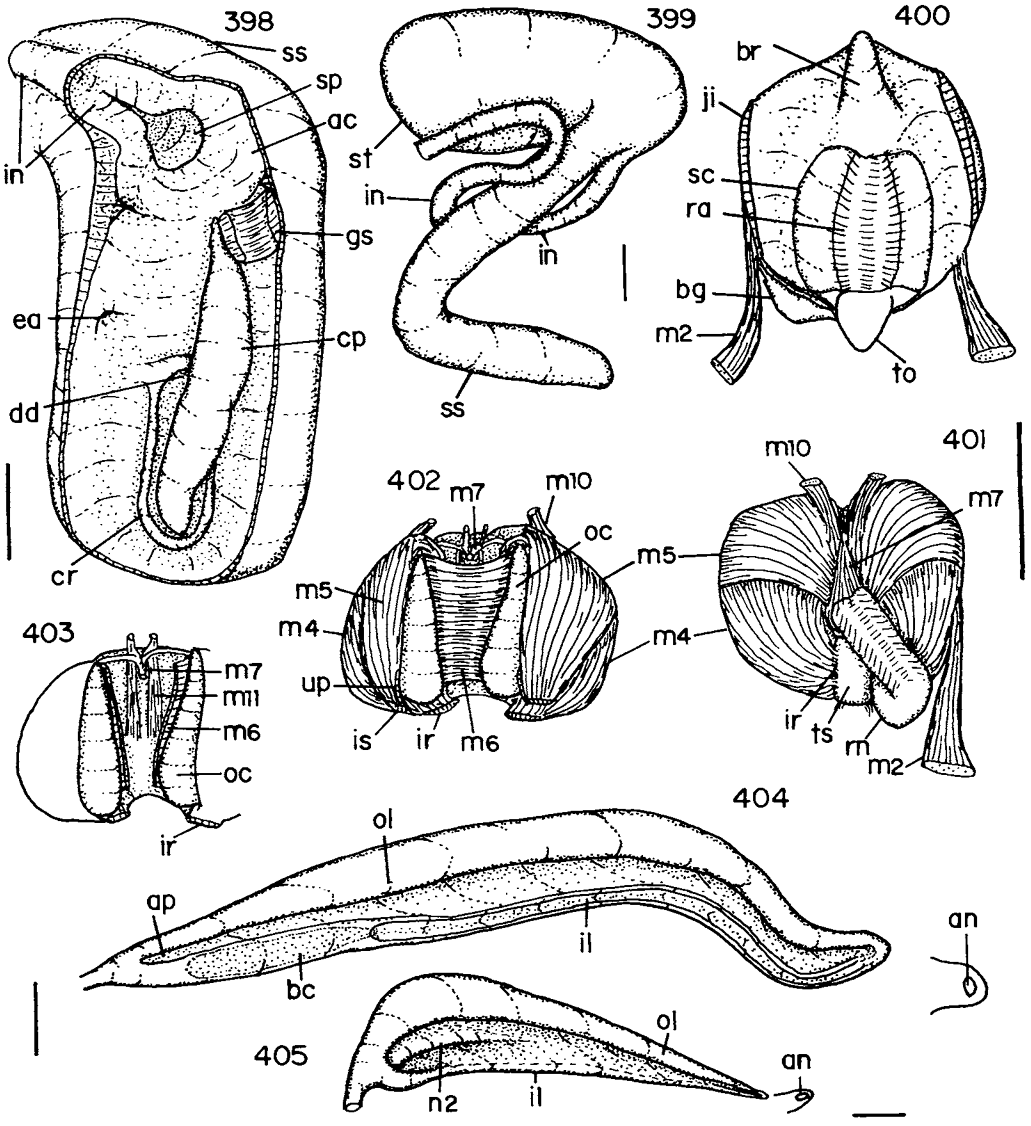
Figs 377-384 *Batillaria minima* anatomy: **377)** head-foot, frontal view; **378)** stomach, dorsal view, dorsal wall extracted, inner surface exposed; **379)** anterior region of stomach, lateral-right view, digestive gland and kidney extracted; **380)** pallial cavity, ventral-inner view; **381)** transversal section in middle region of pallial cavity; **382)** buccal mass and esophagus, both opened by means of a longitudinal section in their left side, anterior region at left; **383)** pallial oviduct, ventral view, with transversal section in three indicated levels; **384)** pallial spermduct and rectum, ventral view, with a transversal section in indicated level; Scales = 1 mm.



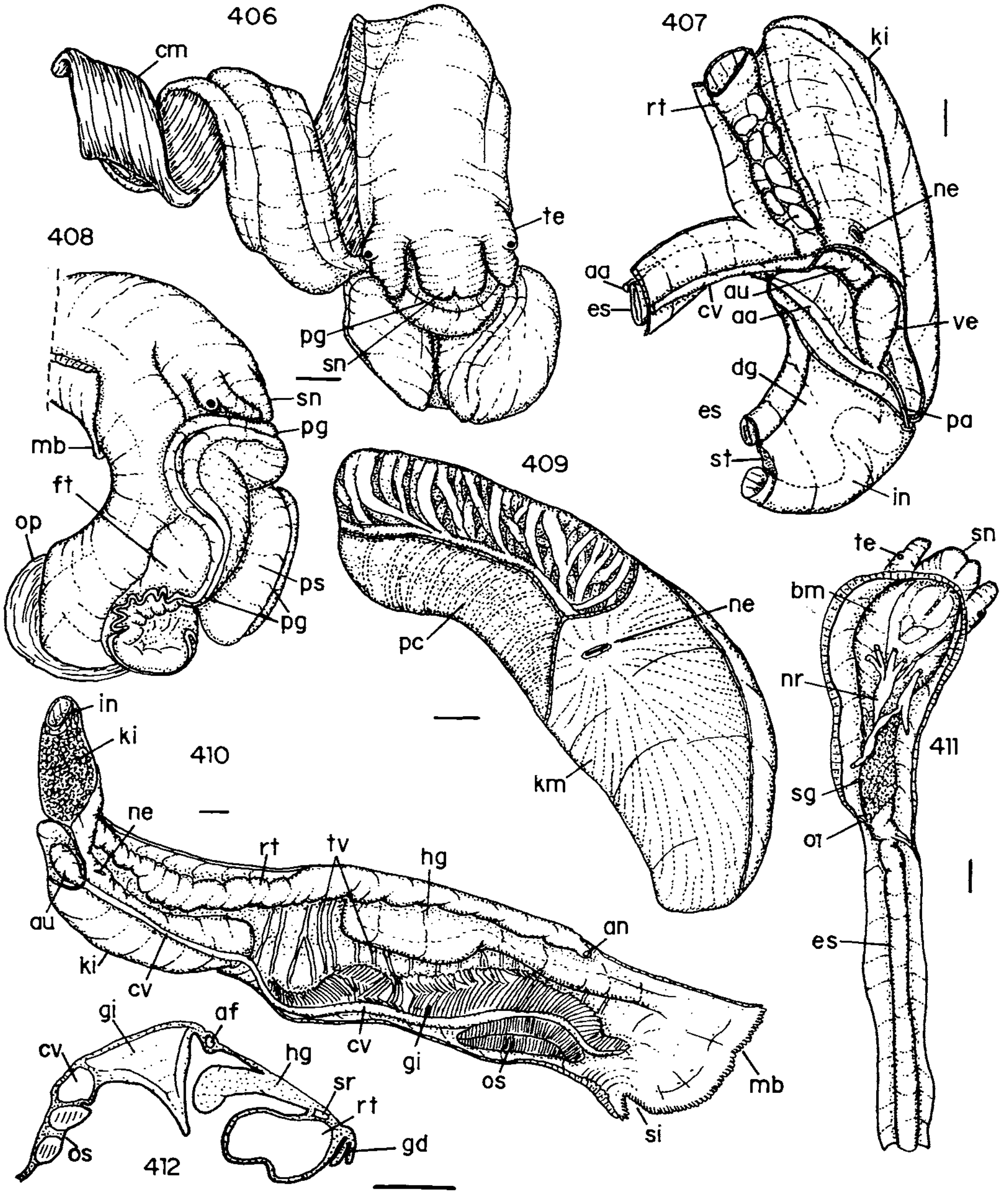
Figs 385-389 *Batillaria minima* anatomy: **385)** head and haemocoel, ventral view, foot removed; **386)** posterior end of pallial cavity and anterior region of visceral mass, ventral-inner view, pericardium opened longitudinally; **387)** odontophore, ventral view, first layer of muscles and membranes partially removed; **388)** same, dorsal view; **389)** same, ventral view, radula and subradular cartilage extracted and deflected. Scales 385-386 = 1 mm; 387-389 = 0.2 mm.



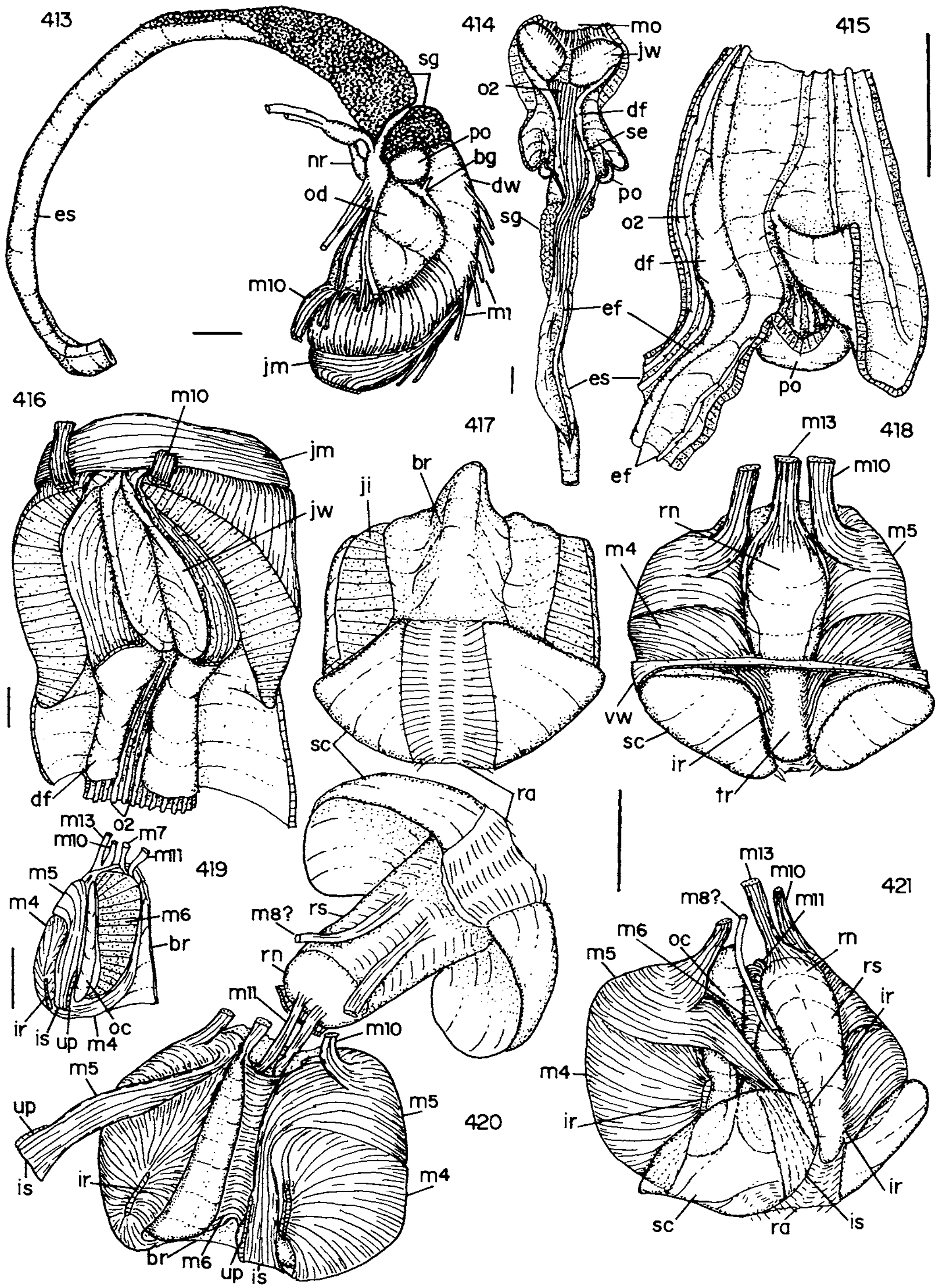
Figs 390-397 *Cerithidea costata* anatomy: **390)** head-foot, male, frontal view; **391)** head-foot, female, lateral-right view; **392)** head and haemocoel, ventral view, foot removed; **393)** pallial cavity, ventral-inner view; **394)** transversal section in middle region of pallial cavity; **395)** anterior region of visceral mass, ventral view, pericardium opened longitudinally; **396)** same, heart and part of rectum extracted; **397)** buccal mass, opened in left side, lateral-left view, inner surface exposed. Scales = 0.5 mm; n1 = pallial eye.



Figs 398-405 *Cerithidea costata* anatomy: **398)** stomach, dorsal view, dorsal wall removed, inner surface exposed; **399)** stomach and intestine, isolated from other organs, left view; **400)** odontophore, dorsal view; **401)** same, ventral view, first layer of muscles and membranes removed; **402)** same, ventral view, most of muscles deflected to show inner structures; **403)** detail of fig. 402 with horizontal muscle sectioned; **404)** pallial oviduct, ventral view; **405)** pallial spermduct, ventral view. Scales = 0.5 mm; n2 = posterior-middle lamina of pallial spermduct.



Figs 406–412 *Campanile symbolicum* anatomy: **406)** head-foot, frontal view; **407)** posterior region of pallial cavity and anterior region of visceral mass, pericardium opened longitudinally; **408)** head-foot, lateral-right view; **409)** Kidney extracted, ventral view, pericardium and intestine removed; **410)** pallial cavity, ventral-inner view; **411)** head and haemocoel, ventral view, foot removed; **412)** transversal section in middle region of pallial cavity, the tall fold of hypobranchial gland is found only in some specimens. Scales = 1 mm; o1 = septum separating anterior and posterior regions of haemocoel.



Figs 413-421 *Campanile symbolicum* anatomy: **413)** buccal mass and esophagus, lateral-right view; **414)** dorsal wall of buccal mass and esophagus opened longitudinally, ventral view, inner surface exposed; **415)** detail of fig 414 just in region of right esophageal pouch, which is partially opened by a longitudinal section; **416)** buccal mass, ventral view, odontophore extracted, inner surface exposed; **417)** odontophore, dorsal view; **418)** same, ventral view, first layer of muscles and membranes partially extracted; **419)** same sagital section, right half in lateral-left view; **420)** same, ventral view, radula and subradular cartilage extracted and deflected; **421)** same, ventral view, radula and subradular cartilage only partially deflected. Scales = 1 mm; o2 = dorsal folded chamber of buccal mass.

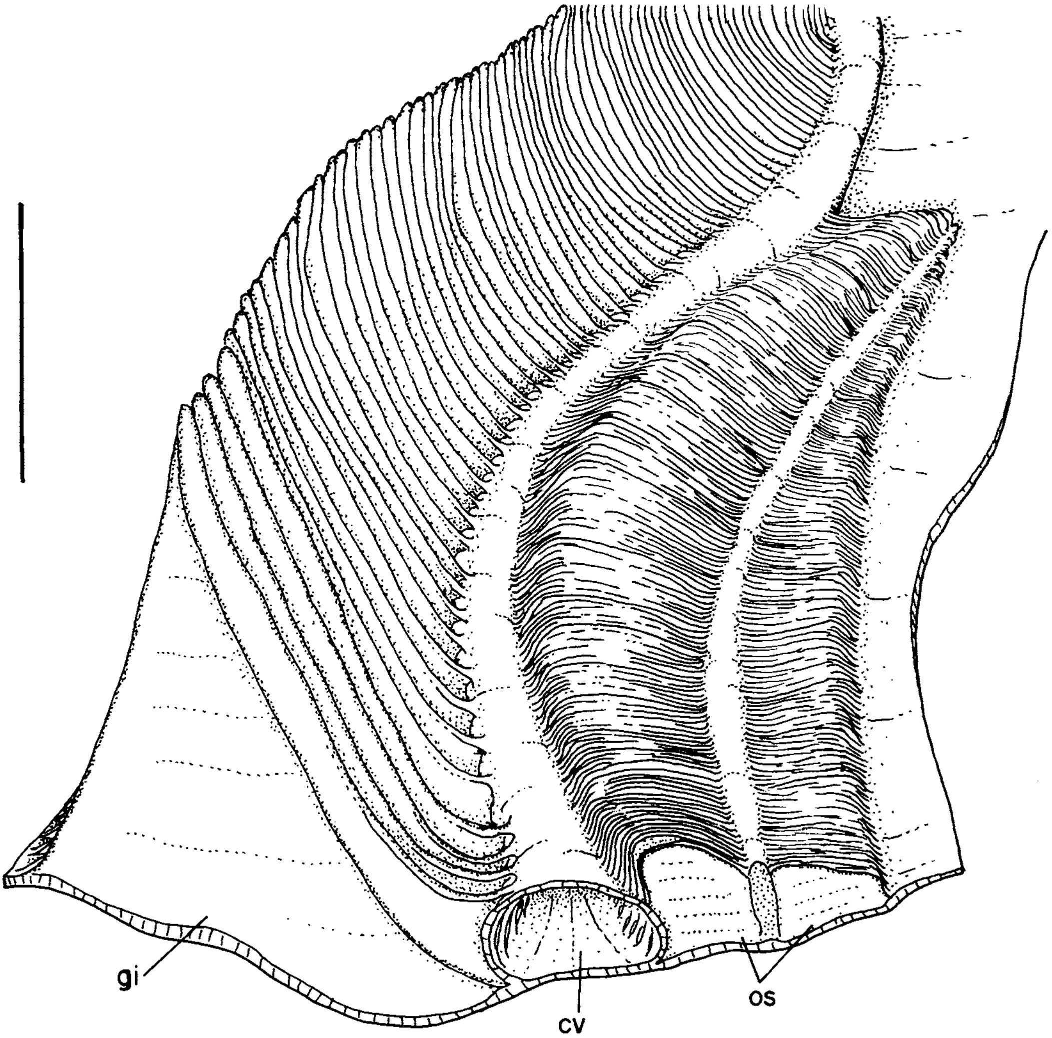
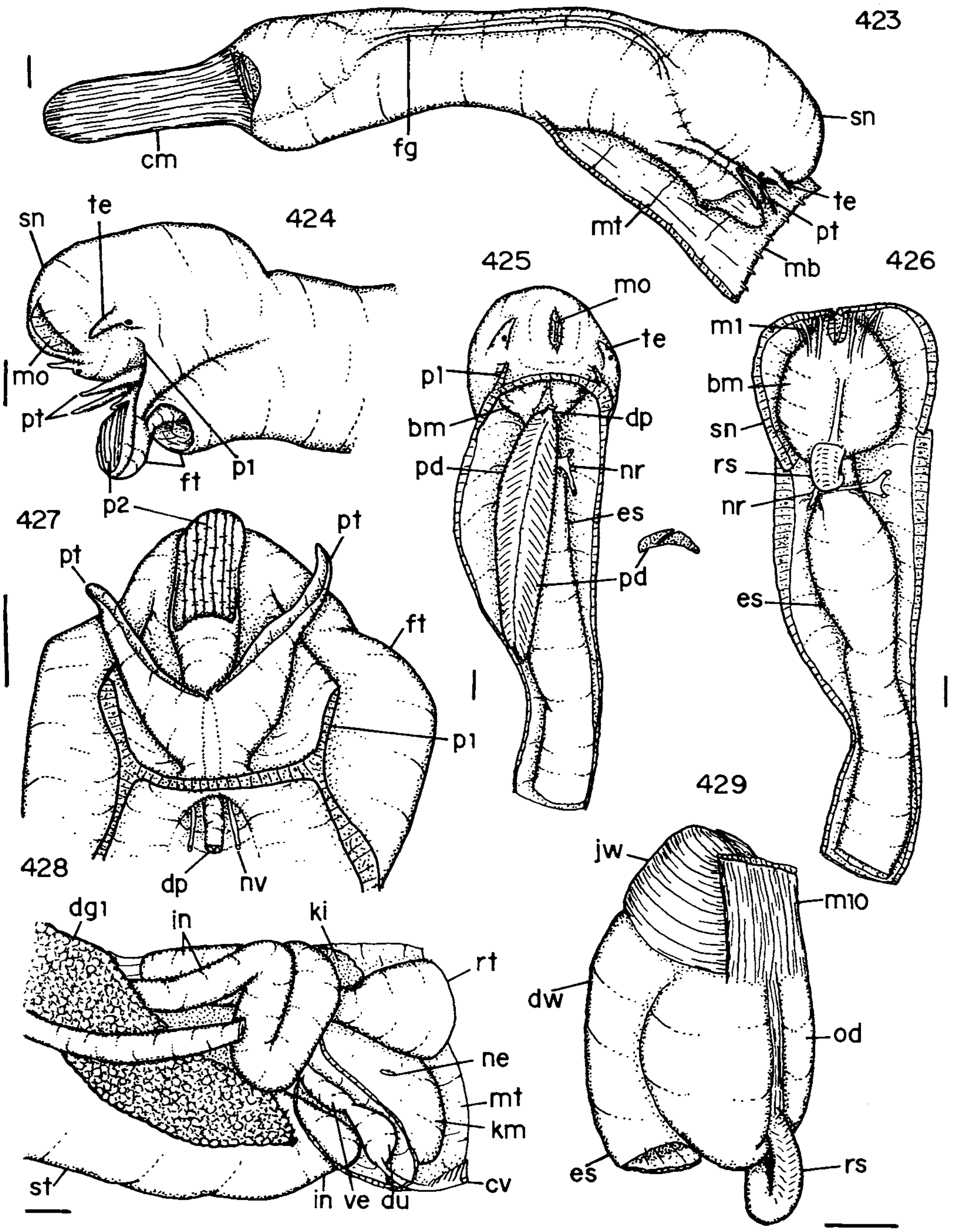
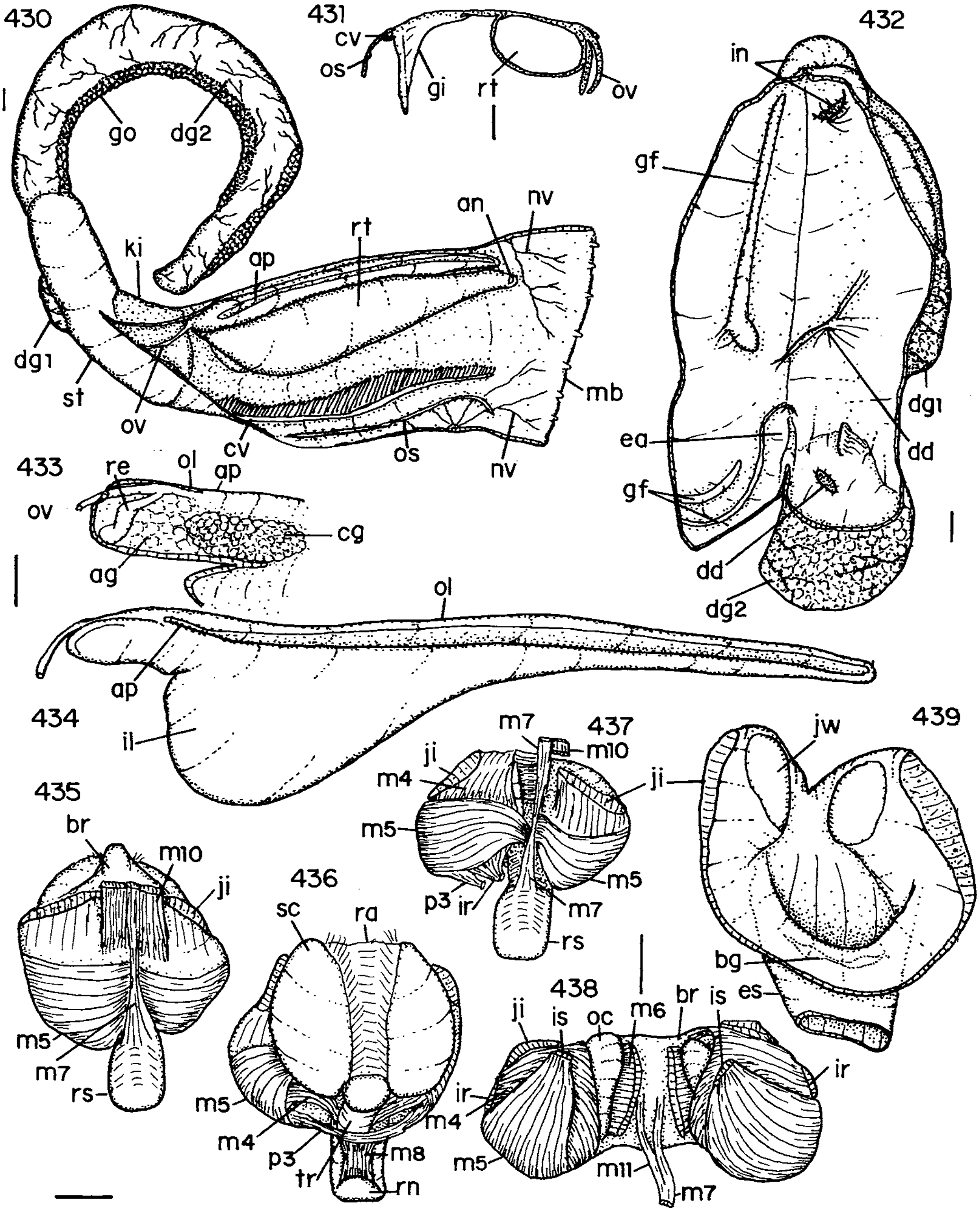


Fig. 422: *Campanile symbolicum*, detail of osphradium and adjacent structures sectioned in its posterior third part, ventral view. Scale = 1 mm.



Figs 423-429 *Serpulorbis decussatus* anatomy: **423)** head-foot, lateral-right view; **424)** head-foot, detail of anterior region, lateral-left view; **425)** head and haemocoel, ventral view, foot and columellar muscle removed; **426)** same, snout opened by a longitudinal-ventral section; **427)** detail of anterior region of foot, dorsal view, head removed; **428)** posterior end of pallial cavity and anterior region of visceral mass, ventral-inner view; **429)** buccal mass, lateral-right view. Scales = 1 mm; p1 = flaps uniting head with lateral region of foot; p2 = glandular pad of foot; dg1 = anterior digestive gland; dg2 = posterior digestive gland.



Figs 430-439 *Serpulorbis decussatus* anatomy: **430)** pallial cavity, ventral-inner view, whole visceral mass also shown; **431)** transversal section in middle region of pallial cavity roof; **432)** stomach, dorsal view, dorsal wall sectioned in its lateral-right limit and deflected to show inner surface; **433)** detail of posterior region of pallial oviduct, ventral view, inner lamina removed; **434)** pallial oviduct, ventral view; **435)** odontophore, ventral view, first layer of muscles and membranes partially removed; **436)** same, dorsal view; **437)** same, ventral view, right muscles (left in figure) deflected to show inner structures; **438)** same, ventral view, most of muscles deflected and horizontal muscle sectioned; **439)** dorsal wall of buccal mass, ventral-inner view. Scales = 1 mm; p3 = accessory muscular bridge of m4.

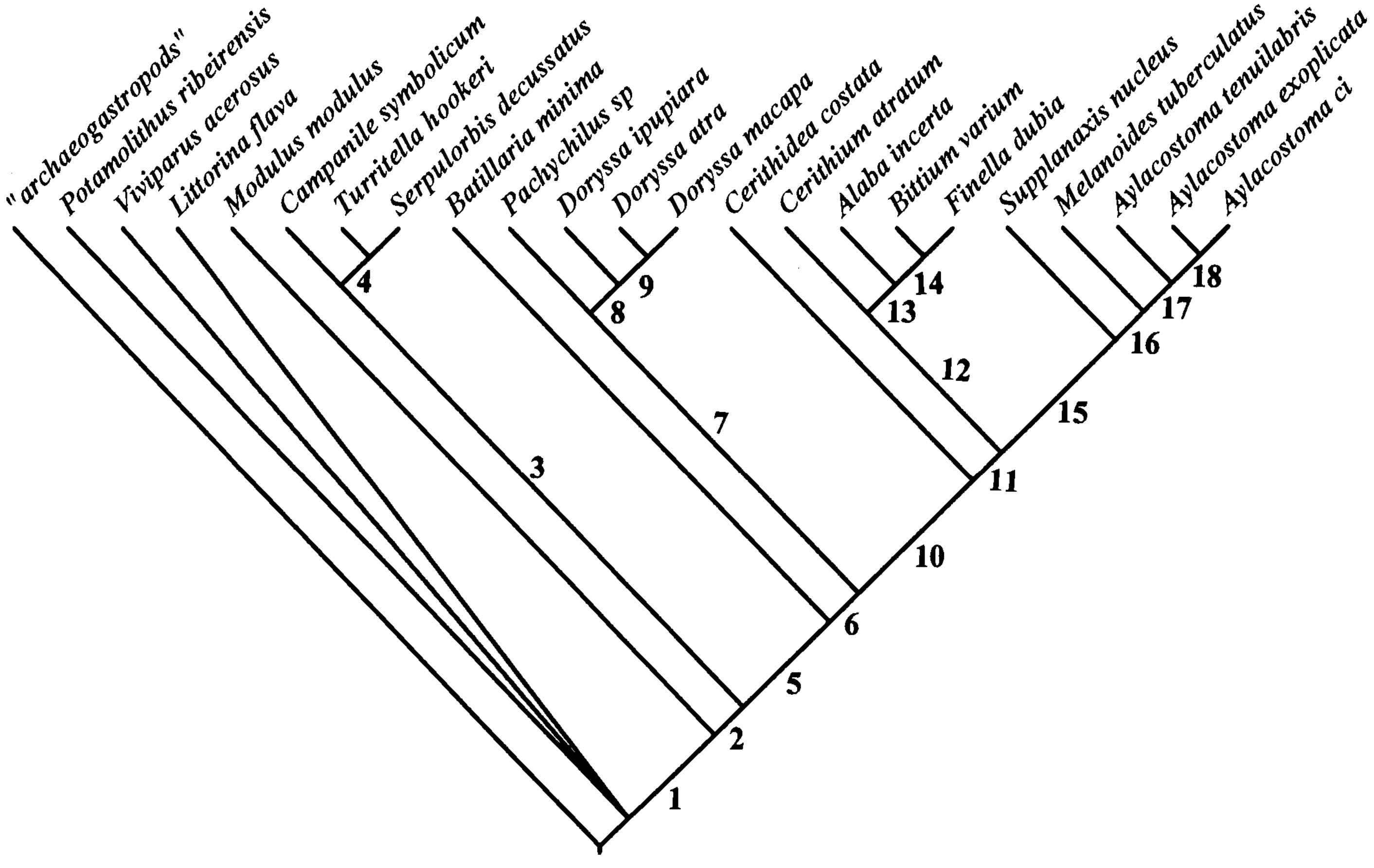


Fig. 440. Cladogram illustrating phylogeny of studied Cerithioidea and outgroups (length: 331; CI: 55; RI: 73). Consensus of 3 trees.

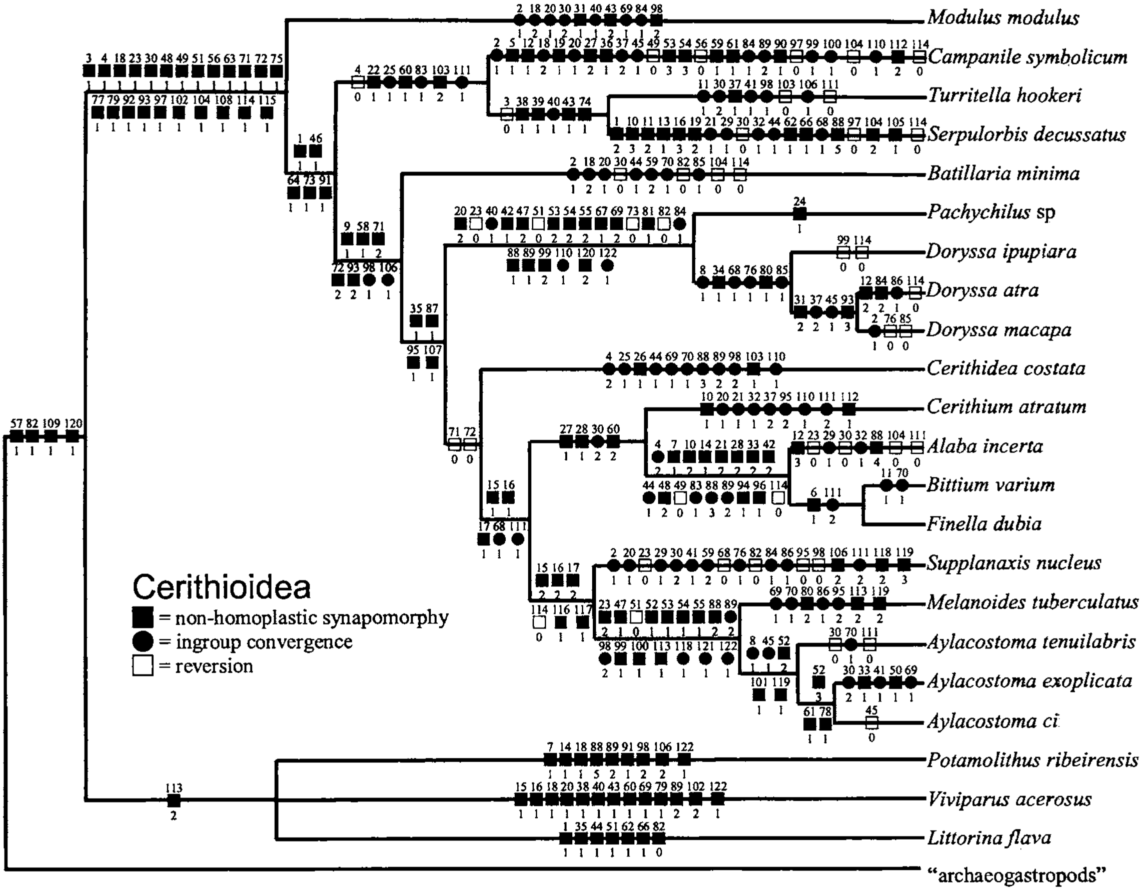


Fig. 441. Same tree as in fig. 440 with insertion of the apomorphics of each ingroup node. Convergent characters with outgroups also indicated. Key for symbols: squarc, exclusive synapomorphy; black circle, convergence; empty circle, reversion.

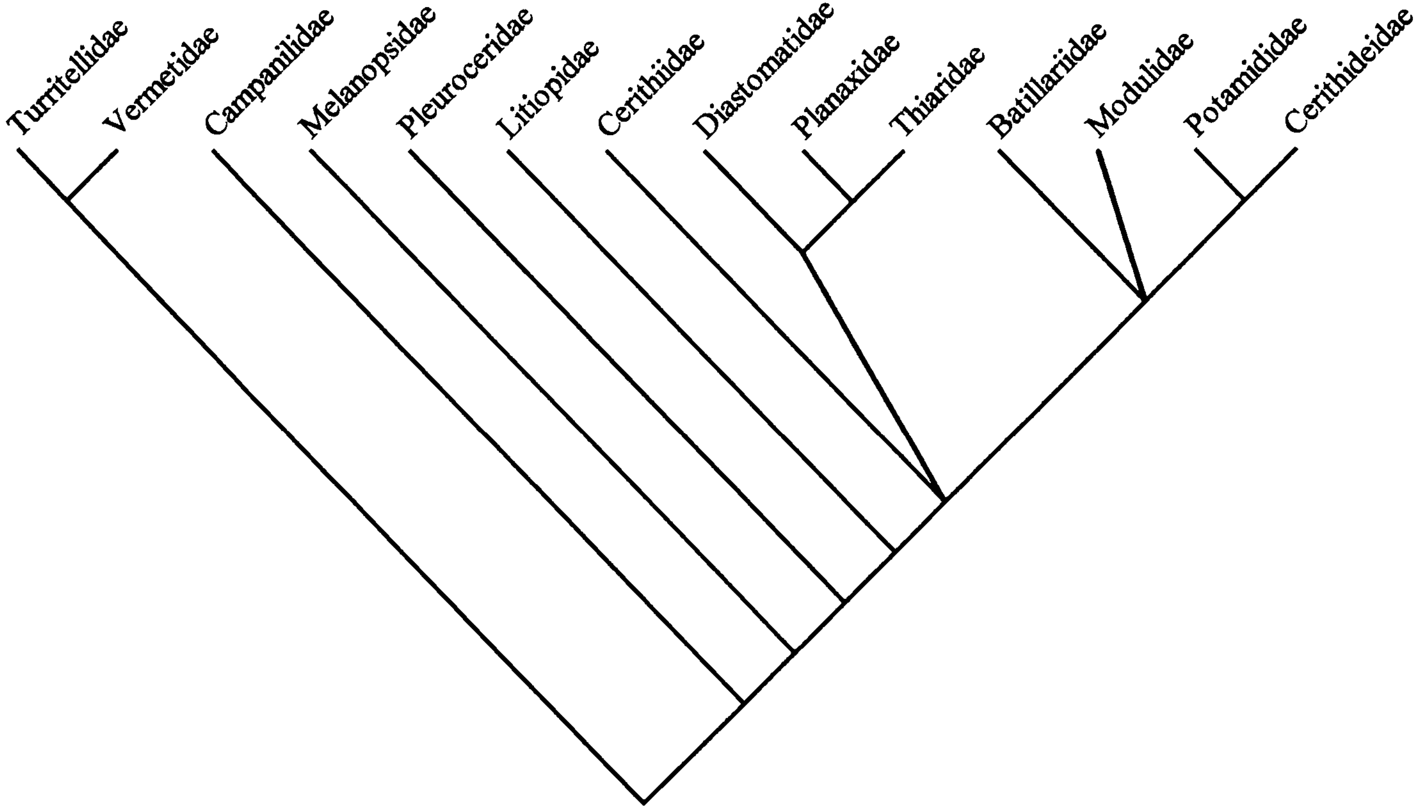


Fig. 442. Consensus of 4 trees obtained polarizing the data of Houbrick (1988) with archaeogastropods as outgroups (length 155, CI= 50, RI= 47). See text for more details.

The result of only one tree demonstrates the high degree of morphological differences in the cerithioidean sample analyzed. The superfamily probably evolved a long time ago, since late Devonian (Houbrick, 1988), inducing the differentiation among its branches. However, a relatively high degree of homoplasies was detected, reflecting in the presented (retention and consistence) indices. The indices level, nevertheless, are regarded as of a good level.

The obtained tree was not performed to be regarded as a "phylogeny of the superfamily Cerithioidea". Although it is totally resolved, the insertion of much other taxa is necessary to obtain an actually well-represented sample of the superfamily. Most nodes are well supported by several synapomorphies, but, e.g., only a pair of reversions supports the node 10. A lot of characters and states were not included in the present analysis due its autapomorphic condition in the studied level. However they surely would be suitable data if the analysis included more species of a single group. On the other hand, the results were considered enough for interpreting the main purpose of this paper: to test the cerithioidean monophyly.

CONCLUSIONS

1. The superfamily Cerithioidea is a monophyletic group, defined by 23 synapomorphies.
2. Most synapomorphies were modified or lost among its representatives.
3. A phylogenetic organization was obtained based in characters in almost all organs, some of them never previously analyzed, and differs from other previous analyzes.
4. The Cerithioidea appears to be a basal taxon among Caenogastropoda and several characters are better comparable with archaeogastropod, rather than other caenogastropod outgroups.
5. The holistic, detailed morphological analysis is enough for phylogenetic and systematic analysis in cerithioideans at all levels.

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