ZOOTAXA

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Magnolia Press
Auckland, New Zealand

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(*Zootaxa* 1112)

64 pp.; 30 cm.

20 Jan. 2006

ISBN 1-877407-54-2 (paperback)

ISBN 1-877407-55-0 (Online edition)

FIRST PUBLISHED IN 2006 BY

Magnolia Press

P.O. Box 41383

Auckland 1030

New Zealand

e-mail: zootaxa@mapress.com

http://www.mapress.com/zootaxa/

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Zootaxa 1112: 1–64 (2006)
www.mapress.com/zootaxa/

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Morphological and phylogenetic study of the Western Atlantic *Crepidula plana* complex (Caenogastropoda, Calyptraeidae), with description of three new species from Brazil

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Accepted by D. Geiger: 8 Oct. 2005; published: 20 Jan. 2006

Abstract

A detailed morphological study was performed in the following species of *Crepidula*: 1) *C. margarita* new species from Venezuela; 2) *C. plana* Say, 1822; 3) *C. atrasolea* Collin, 2000; 4) *C. depressa* Say, 1822, from Florida, USA; 5) *C. pyguaia*, new species from Santa Catarina coast, Brazil; 6) *C. carioca*, new species from Rio de Janeiro coast, Brazil. Additionally, five other species anatomically studied in Simone (2002) were also included: 7) *C. argentina* Simone, Pastorino & Penchaszadeh, 2000, from Argentina; 8) *C. glauca* Say, 1822, from Venezuela; 9) *C. fornicata* (Linné, 1758), from Mediterranean and Florida; 10) *C. protea* Orbigny, from S.E. Brazil; 11) *C.* aff. *plana*, here described as *C. intratesta* new species, from S.E. Brazil; 12) *C. cachimilla* Cledón Simone & Penchaszadeh, 2004, from Patagonia. The 46 characters (106 states) for these species were phylogenetically analyzed and a single cladogram was obtained (length: 93, CI: 65; RI: 64) as follows: (*Crepidula cachimilla* (*C. argentina* ((*C. carioca C. pyguaia*) ((*C. fornicata* (*C. intratesta C. protea*)) ((*C. glauca C. margarita*) (*C. plana* (*C. atrasolea C. depressa*))))))). Two outgroups were used: *Bostrycapulus aculeatus* (Gmelin, 1791), which most authors consider a *Crepidula* (operationally analyzed as part of the ingroup), and the remaining calyptraeoideans studied by the author. The monophyly of the ingroup is confirmed, supported by 25 morphological synapomorphies. Although the ingroup is fully resolved, no clades are formally named, because the phylogeny is still considered provisional. Most studied species belong to an informal group called "*Crepidula plana*-complex", but it is not monophyletic, since *C. fornicata*, which does not belong to this complex, is part of the ingroup. This study demonstrates that detailed morphological data are useful in phylogenetic studies even at the level of closely related/sibling species, resulting in cladogram with good resolution and a good number of shared, analyzable characters. A biogeographic analysis is also performed considering the distribution of each species under the light of the obtained cladogram, a clear ascension from south to north is the main pattern of the evolutionary history of these species. Further comments on the systematics of *Crepidula aplysioides* Reeve and *C. convexa* Say is also performed.

Key words: Gastropoda, Caenogastropoda, Calyptraeidae, West Atlantic, Phylogeny, Biogeography, new species

Introduction

The *Crepidula plana* complex is defined here as a set of species that occurs in the Western Atlantic. This group of species is difficult to separate by means of shell characters alone and, sometimes, even by anatomical characters. The status of those species, at least the known ones, varies from truly separated species to synonyms of *C. plana* Say, 1822. Collin (2000) was the first to use the term, encompassing Florida species with pale, smooth, flat shell. The concept is extended here for the Western Atlantic that possibly sets closey related species, and to differentiate from the "*C. plana* group" as mentioned by Hoagland (1977) that sets convergent whitish species.

The more we know about those populations, the more the result is the fragmentation in several species. Further studies of those populations indicates/suggests that multiple species are involved. The anatomical studies Simone *et al.* (2000) and Simone (2002), have revealed that differences of several anatomical characters allows species-level separations. Molecular approaches, on the other hand, have identified sympatric and cryptic (with respect to shell) species (Collin, 2000).

This paper is another step to better understand 12 species in this enigmatic group. One of them, *Crepidula fornicata* Linné, 1758, does not belong in the *C. plana* complex proper, since it differs clearly in conchological characters. Its inclusion in this paper has two reasons: 1) it is the type species of the genus *Crepidula* Lamarck, 1799; 2) to test the monophyly of the *C. plana*- complex, i.e., if this group is monophyletic, *C. fornicata* will be found as an external branch of the remaining ingroup species.

This study is part of a larger project concerning to a phylogenetic revaluation of the Caenogastropoda relationship, based mainly on morphology. The project has produced some phylogenetic studies based on heterogeneous samples of each superfamily. The results have been single or few cladograms (e.g., Simone 2001 on Cerithioidea; Simone 2002 on Calyptraeoidea). The reason for obtaining few cladograms has been pointed out as the sample is composed of distantly related species. This paper has also the objective of testing the methodology in a sample of closer related species, supposedly belonging to a single genus, occurring in the same geographic area, and which can not be separated easily by conchology. The research methodology consists of a detailed morpho-anatomical study, developed under a comparative approach.

Material and Methods

The specimens examined here belong to institutional collections or were collected specifically for this study. The specimens were dissected by standard techniques, under the microscope, with the specimens immersed in fixative. Some organs such as oviduct and foregut were processed by standard histological technique for serial sections of 5 µm. Hard structures, such as shells, radulae and jaws were examined by SEM in the Museu de Zoologia da Universidade de São Paulo (MZSP). The descriptive part of this paper provides a complete description of the first species, the remaining species are described under a comparative aspect, with most of similar features omitted. The same approach is adopted in the figures. A detailed list of examined specimens follows each species description.

The section of comparative morphology is organized as a phylogenetic analysis. The account of each character begins with abbreviated descriptive sentence followed by plesiomorphic and derived conditions(s), as identified by subsequent phylogenetic analysis; also included CI and RI (consistency and retention indices, respectively, autapomorphies included), values for the character under the most parsimonious hypothesis. Following the apomorphic state(s), a list of terminal taxa with the apomorphic condition is presented. Characters with high intraspecific variability or with overlapping character stated were excluded from the cladistic analysis. Characters were polarized by outgroup comparison.

The cladistic analysis has as scenario the paper Simone (2002), in such 11 calyptraeids have been anatomically studied. In the present paper focusing the *Crepidula plana* complex, three calyptraeids that do not belong to the complex are included: *Bostrycapulus aculeatus* (Gmelin, 1791) (Simone 2002, figs. 1–3, 54, 98–118), *Crucubulum auricula* (Gmelin, 1791) (figs. 15–17, 58, 59, 185–206 of that paper) and *Crepidula fornicata* (Linné, 1758) (Figs. 10, 11, 71, 72, 160–164 of that paper). In the computer analysis, the root was only made with *Cr. auricula*.

The discussion of each character is also based on the analysis of the obtained cladogram (Figs. 116, 117). The matrix of characters (Table 1) and the subsequent tree are shown only in the following section.

Some multistate characters are analyzed here under an additive (ordered) approach. In each case, the additive concept is justified in the discussion and is always based on the ontogeny or on the fact that each state is a clear modification of the preceding one. Additionally, each additive multistate character was also analyzed as non-additive, and any change in the result and/or indices is also reported. In the discussion of the characters, where mentioned "all species" only the ingroup species are included, i.e, excluding *B. aculeatus and Cr. auricula*.

The cladistic analysis was performed with the computer program "Tree Gardner 2.2" (Ramos 1997), which works as an interface of Hennig86 (Farris 1988). The "ie" algorithm was applied. The computer programs PAUP 3.1 (Swofford 1991) and Winclada (Nixon 2000) were also used. All programs produce the same result.

In the figures, the following abbreviations are used: **aa**, anterior aorta; **ab**, auricle region beyond ventricle connection; **ac**, anterior extremity of gill on mantle border; **ad**, adrectal sinus; **af**, afferent gill vessel; **ag**, albumen gland; **an**, anus; **ap**, aperture of visceral vas deferens into pallial cavity; **au**, auricle; **bg**, buccal ganglion; **cg**, capsule gland; **cm**, columellar muscle; **cv**, ctenidial vein; **dd**, duct to digestive gland; **df**, dorsal fold of buccal mass; **dg**, digestive gland; **di**, septum separating haemocoel from visceral mass; **dm**, dorsal shell muscle; **dp**, posterior duct to digestive gland; **en**, endostyle; **es**, esophagus; **ey**, eye; **fd**, foot dorsal surface; **fg**, food groove; **fl**, female papilla; **fp**, female pore; **ga**, parietal ganglion; **gc**, cerebral ganglion; **gd**, gonopericardial duct; **ge**, sub-esophageal ganglion; **gf**, gastric fold; **gi**, gill; **gp**, pedal ganglion; **gr**, thick tip of gill filament; **gs**, gastric shield; **hg**, hypobranchial gland; **in**, intestine; **ir**, insertion of m4 in "br"; **is**, insertion of m5 in radular sac; **iu**, "U"-shaped loop of intestine on pallial roof; **jw**, jaw; **kc**, kidney chamber; **ki**, kidney; **km**, membrane between kidney and pallial cavity; **kv**, ventral lobe of kidney attached to intestine; **ll**, left lateral expansion (flap) of neck; **lm**, lateral shell muscle; **m1** to **m14**, odontophore muscles; **mb**, mantle border; **mc**, circular muscle (sphincter) of mouth; **mj**, muscles of jaws and mouth; **ml**, mantle region restricting pallial cavity; **mo**, mouth; **mt**, transversal dorsal muscle of odontophore; **ne**, nephrostome; **ng**, nephridial gland; **nr**, nerve ring; **oc**, odontophore cartilage; **od**, odontophore; **os**, osphradium; **ov**, pallial oviduct; **oy**, ovary; **pc**, pericardium; **pd**, penis sperm groove; **pe**, penis; **pg**, pedal gland anterior furrow; **pp**, penis papilla; **pr**, propodium; **ra**, radula; **rg**, repugnatorial gland; **rl**, right lateral expansion (flap) of neck; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **sa**, salivary gland aperture; **sc**, subradular cartilage; **se**, septum between odontophore and esophageal portions of buccal mass; **sg**, salivary gland; **si**, siphon-like fold; **sn**, snout-proboscis; **sr**, seminal receptacle; **ss**, style sac; **st**, stomach; **sv**, seminal vesicle; **sy**, statocyst; **te**, cephalic tentacle; **tg**, integument; **tm**, net of transversal muscles of haemocoel; **to**, tissue covering middle region of radula before its in use part; **ts**, testis**, vc**, visceral connection with haemocoel; **vd**, pallial vas deferens (furrow); **ve**, ventricle; **vg**, vaginal duct; **vm**, visceral mass; **vo**, visceral oviduct; **vt**, vestigial pallial oviduct; **vv**, visceral vas deferens (duct).

Institutional abbreviations: **ANSP**, Academy of Natural Sciences of Philadelphia, Pennsylvania, USA; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **IOUSP**, Intituto Oceanográfico da Universidade de São Paulo, Brazil; **MNRJ**, Museu Nacional da Univesidade Federal do Rio de Janeiro, Brazil; **MZSP**, Museu de Zoologia da Universidade de São Paulo, Brazil.

Systematics

Crepidula margarita **new species**

(Figs. 10–12, 26, 27, 35–51)

Crepidula aplysioides, Hoagland 1977: 369; Simone et al. 2000: 140. (non Reeve, 1859).

Types: Holotype MZSP 36329 ♀. Paratypes: MZSP 50892, 11 specimens from type locality.

Type locality: VENEZUELA; **Nueva Esparta State**; Margarita Island; La Restinga lagoon, 64°02'–64°12'W 10°90'–11°02'N (P. Penchaszadeh col.).

Description:

Shell (Figs. 10–12): Wide, somewhat flat, concave, outline oval; walls thin, transparent. Color cream, with pale brown, narrow, irregular spiral, radial bands. Periostracum absent, except very narrow portions in shell edges. Outer surface with weak growth lines. Anterior edge of septum with broad and shallow central notch, with edges almost straight, and another shallow notch in left end, narrower (Fig. 11). Inner surface glossy.

Head-foot (Figs. 36, 42): Head differentiated, preceded by long, dorso-ventrally flattened, neck region, about half as long as foot. Proboscis short, cylindrical, can be entirely retracted within haemocoelic cavity (Fig. 36). Tentacles long, stubby, apex somewhat bifid. Eyes dark, small, located on very short ommatophores in basal region of tentacles lateral margin. Neck with pair of lateral, flattened lappets (nuchal lobes); left expansion narrower than right one; right expansion bringing low food groove along its dorsal-medial limit (Fig. 36: fg). Foot wide (occupies about 3/4 of shell ventral area, dorso-ventrally greatly flattened, thin; distinct longitudinal inner sinus runs in median line; shell septum as dorsal foot limit. Mantle fuses with dorsal surface of foot and protrudes beyond its borders. Furrow of pedal glands transverse, in anterior margin of foot; this anterior margin of foot covered dorsally by posterior region of neck ventral surface. Columellar muscle reduced, very small, contours anterior border of shell septum, more pronounced on right (Fig. 36: cm) in smaller specimens and almost absent in larger ones. Inner haemocoel cavity narrow, running approximately in center of neck region. Inner space almost all filled by great quantity of transverse, very slender muscular fibers; these fibers connect ventral surface of dorsal haemocoel wall with dorsal surface of its ventral wall, contouring salivary glands and esophagus (Fig. 42: tm). No vestiges of operculum even in very young specimens (smaller than 1 mm) inside egg capsules.

Mantle organs (Figs. 35, 37–40): Mantle border thick, slightly hollow due broad collar sinuses (Fig. 40). Mantle border surrounds entire ventral margin of shell, free in anterior third and attached to foot margins in posterior 2/3, situated slightly away from foots edge, connected to it by a thin, semi-transparent portion. Mantle border without appendages, but filled entirely by series of minute repugnatorial glands, aligned inside mantle edge. Mantle border with special arrangement of folds in middle region of opening of pallial cavity, broad fold starting at anterior end of gill, running towards left, decreasing in width, disappearing abruptly at level of osphradium; its broader region possesses a central, broad furrow, its posterior edge expands beyond mantle border covering ventrally anterior region of gill, its anterior edge slightly projected outside (Fig. 37). Dorsal shell muscle well developed (Fig. 35: dm), origin small, in about middle-right region of shell, just anterior to septum; their fibers run fan-like anteriorly, insertion in adjacent anterior region of dorsal surface of pallial cavity. Lateral shell muscle (Figs. 35: lm) very small, fan-like, located close to mantle border on right side, just in region where pallial cavity penetrates shell septum chamber. Opening of pallial cavity occupies about 2/3 of anterior half of shell margin turned to right (if shell compared with a clock, in dorsal view and with head occupying 12 oclock, pallial aperture begins in 10 and finishes in 2 oclock) (Fig. 38). Pallial cavity deep, broad, triangular, arched and dorso-ventrally flattened. Anterior extremity of pallial cavity slightly larger than its opening due to closure in left and right extremities produced by fusion of mantle and foot (Figs. 38, 39: ml). Gradually, pallial cavity narrows towards posterior, extending at left of visceral mass (described below); cavity length about 2/3 of total length of animal (Figs. 35, 38, 39). Osphradium very small, monopectinate, located between anterior half of gill and mantle border, at some distance from gill anterior end, located about in left region of pallial aperture somewhat perpendicular to longitudinal axis of animal body (Figs. 38). Length of osphradium slightly more than 1/6 of length of pallial opening, shaped like a small fold, attached to mantle, separated from gill structures. Osphradium leaflets cylindrical, separated from each other, somewhat thick and tall, approximately 9 in number (Fig. 37). Osphradial ganglion narrow. Gill very large, its base somewhat narrow, surrounding anterior and left margin of pallial cavity [almost entire length of this cavity; anterior tip of gill in right-anterior region of opening of pallial cavity, close to its right limit, on thick mantle border; posterior margin of gill in posterior end of pallial cavity (Fig. 39). Basal region of gill filaments triangular, with very long, almost straight, narrow, stiff rod turned to right (Fig. 40); rods about three times as long as their triangular, membranous base; rods begin in ctenidial vein region, in left margin of cavity roof, touching food groove of head-foot, in right margin of cavity floor; rod apex rounded and preceded by thicker region. Gill filaments stay connected with each other by cilia, mainly of their thicker apical region, maintaining them in somewhat firm position. Gill filaments longer in central gill region, shortening gradually in both extremities; anterior tip of gill, with short filaments, suddenly turning forwards, located on mantle border (Figs. 37–39). Ctenidial vein narrow, of uniform width along its length. Endostyle well-developed (Figs. 37, 39: en), yellowish, in form of broad and flat glandular ridge located in middle level of ventral surface of ctenidial vein all along its length. Hypobranchial gland whitish, thin, weakly developed, surface smooth; occupies area between gill and visceral mass. About 1/3 of visceral mass encroaching on pallial cavity roof (Fig. 39), occupying about 1/3 of this cavity in posterior-right region; pericardium and kidney posteriorly; intestinal loop long, anus and pallial oviduct anteriorly (described below).

Visceral mass (Figs. 35, 38, 39): Dorso-ventrally flattened, cone-shaped, housed in shell chamber produced by thin calcareous septum (Fig. 35); separating visceral mass from dorsal surface of foot. Left and anterior region of visceral mass occupied by pallial cavity (Figs. 35, 39). Remaining regions of visceral mass with stomach as central structure, immediately surrounded by digestive gland (except in some ventral and dorsal areas). Gonad surrounds externally digestive gland, more concentrated anteriorly. All structures described in more details below. Visceral mass also lies on right-posterior region of pallial cavity roof as described above, and possesses another ventral flap forming floor of pallial cavity. Anterior extremity of visceral mass ventral flap stays just in shell septum anterior border, covering columellar muscle (Figs. 38, 39).

Circulatory and excretory systems (Figs. 39, 41): Pericardium somewhat triangular and broad, situated obliquely to longitudinal axis of animal (Fig. 35: pc). Left region of pericardium very narrow, forming a vein connecting gill with auricle, beginning just at posterior end of gill, in posterior-left end of pallial cavity; running along anterior margin of visceral mass (its portion in pallial roof), about in middle level of this region of visceral mass it connects to auricle, near median line. Remaining pericardium limits: 1) anterior and ventral pallial cavity; 2) posterior visceral mass (gonad generally); 3) dorsal mantle; 4) right kidney. Auricle thin-walled, long, narrow, runs all along broader region of pericardium, attached to its anterior and dorsal inner surfaces (Fig. 41); connecting with ventricle approximately in its middle portion; auricle having broad portion beyond ventricle connection as blind sac (Fig. 41: ab), bearing orifice to nephridial gland. Ventricle elliptical, very muscular; its connection with auricle located about in middle region of its anterior surface; on opposite side bears origin of aortas. Anterior aorta broad, running towards opposite side than posterior aorta. Anterior aorta running towards right, adjacent to posterior inner pericardium surface; penetrating head haemocoel. Kidney occupying about half of visceral mass within pallial cavity (Figs. 39, 41). Kidney limits: 1) dorsal mantle; 2) ventral pallial cavity; 3) posterior-right visceral mass (gonad generally); 4) posterior-left pericardium; 5) anterior an intestinal loop; 6) lateral-right intestine and oviduct (when present). Kidney central region hollow, with single lobe (Fig. 41). Kidney lobe slightly uniform, covers dorsal surface, intestinal region passing through kidney chamber, and about 1/4 of inner space of kidney adjacent to intestine. Nephridial gland in renal limit with pericardium, very small, presenting a series of triangular, transversal, narrow folds connected with dorsal renal lobe (Fig. 41: ng). Nephrostome a very small slit in left-anterior region of ventral wall (Figs. 39, 41), in anterior region of hollow portion of kidney; no inner glandular folds close to it. Adrectal sinus very broad, adjacent to externally intestine loop exposed in pallial cavity, connected to main kidney chamber by a narrow region presenting a branch of renal lobe; this branch runs a short distance inside adrectal sinus (Fig. 41).

Digestive system (Figs. 42–49, 51): Proboscis short and broad, with capacity of retraction inside haemocoel in small rhynchocoel (Figs. 36, 42), but a short snout remains. Pair of narrow ventral proboscis retractor muscles very thin, immersed in proboscis wall. Mouth longitudinal, in center of anterior proboscis surface. Buccal mass very large, occupying most of proboscis inner space and short portion of haemocoel posterior to it. Jaw plates in dorsal wall of buccal mass, thin, almost vestigial, broad laterally, short longitudinally (Fig. 44). Pair of dorsal folds broad and tall, begin at some distance posterior to jaws; dorsal chamber between both folds shallow. Odontophore occupying about 1/4 of haemocoelic space, and most of buccal mass volume. Odontophore muscles (Figs. 43, 45–49: **m1**) jugal muscles, several very narrow muscles connecting buccal mass with adjacent wall of snout, more concentrated anteriorly around mouth; **m1a**) pair of dorsal protractor muscles, narrow, thin and superficial, origin in anterior-dorsal region of mouth, close to median line, inserting in posterior-dorsal-lateral region of odontophore; **m2**) pair of retractor muscle of buccal mass (retractor of pharynx), broad, origin in lateral-ventral region of haemocoel just posterior to snout, run towards anterior, insertion in lateral-posterior-dorsal region of odontophore cartilages; **m2a**) pair of dorsal tensor muscles of radula, continuation of m2 after insertion in cartilages, run towards anterior, insertion in subradular cartilage in middle region of its dorsal inner surface; **mt**) dorsal transversal muscle or approximator muscle of cartilages, connects dorsally both posterior-dorsal-lateral surfaces of cartilages, lies between superficial membrane which covers odontophore and tissue on middle region of radula (to); **m4**) pair of median dorsal tensor muscle of radula, very large and thick, origin in ventral-middle-posterior region of odontophore cartilages, run towards medial, contours medial-ventral surface of cartilages, run on their dorsal surface, insertion in subradular cartilage dorsal-posterior-medial extremities; **m5**) pair of median radular tensor muscle, thick, origin in median-posterior-dorsal region of odontophore cartilages, just by side of m2 insertion and m2a origin, cover perpendicularly m4 middle region, run towards medial, insertion along radular sac in its both sides (each m5 branch covers a side of radular sac, medially and dorsally); **m6**) horizontal muscle, very thin, unites anterior half of odontophore cartilages, inserting on their dorsal margin; **m7**) pair of ventral tensor muscle of radula, thin and narrow, origin inside radular sac ventral surface close to each other, run towards anterior separating gradually from each other, insertion in radula ventral border; **m8**) pair of strong muscles origin in posterior-dorsal-lateral regions of odontophore cartilages just by side of insertion of m2, run attached to dorsal margin of odontophore cartilages, insert in their anterior-dorsal region close to horizontal muscle (m6); **m9**) pair of dorsal-medial tensor muscle of radula, broad and thin, origin along dorsal-median surface of radular sac (in its region internal to odontophore), cross to dorsal surface, insert in dorsal-ventral border of subradular cartilage; **mj**) jaws and peribuccal muscles, of moderate thickness, surround lateral and dorsal wall of buccal mass, origin around mouth, insertion in middle level of lateral and dorsal wall of odontophore; **m11**) absent; **m14**) pair broad and thin, origin in posterior-dorsal region of odontophore, close to m2 and m5 origins, runs towards ventral and anterior, insertion in snout inner ventral surface in about middle level of odontophore; **to**) tissue covering middle region of radula within odontophore, in its dorsal surface. Radula short, little longer than odontophore. Radula (Figs. 26, 27): rachidian tooth tall, narrow, strongly curved inwards, central cusp large and sharp, 3 to 4 similar sized pairs of secondary cusps, pair of lateral reinforcements on its borders somewhat weak; lateral tooth about 3 times as broad as rachidian, curved internally, with about 12 triangular cusps, fifth cusp larger, apical, turned towards median, cusps decrease towards lateral, disappear about in middle region of tooth, remaining a slight thick and arched border; inner marginal tooth long, curved, tall, tip sharp pointed, about 9 sub-terminal cusps along its inner-apical margin and up to 6 very small cusps along outer margin; outer marginal tooth similar to inner marginal tooth, except in being slender, and with 2–3 small cusps along its inner margin only. Pair of buccal ganglia large, close with each other near median line (Fig. 43), located between buccal mass and adjacent esophagus. Salivary glands narrow, slender, long; length about half of that of haemocoel (Figs. 42). Salivary glands do not pass through nerve ring. Ducts of salivary glands broad, run in dorsal surface of buccal mass, penetrate in adjacent buccal mass wall a short distance, openings small in anterior region of dorsal folds of buccal mass (Figs. 44). Esophagus (Figs. 42, 43, 51) narrow, long and somewhat coiled; inner surface of anterior esophagus with pair of broad folds. Stomach (Fig. 51) slightly conical, large, occupying about half of visceral mass size; esophagus inserting in left side of its posterior-left region, close to shell apex. Anterior duct to digestive gland about in middle region of stomach ventral surface; highly branched. Posterior duct to digestive gland very narrow, located in ventral region of stomach posterior end, turned posteriorly. Stomach gradually narrowing towards anterior and left, arriving close to left-posterior extremity of pallial cavity. Stomach inner surface with pair of longitudinal folds, posterior to esophagus insertion, separating intestine from style sac region of stomach. Digestive gland pale brown in color, surrounding stomach except some areas in dorsal and ventral surfaces. Intestine narrow and sinuous (Fig. 51); running along anterior border of visceral mass from left to right, initially in its ventral region, slightly near median line cross to its dorsal region and runs up to right-anterior extremity of visceral mass (Fig. 51); running towards left in this region, becoming broader and exposed in pallial cavity, surrounds right and anterior border of kidney, suddenly runs towards right in a U-shape, parallel to preceding loop. Anus small, siphoned, located in right region of pallial cavity close to mantle border. Intestine last loops replete of several somewhat small, elliptical fecal pellets.

Genital system: **Development**: Protandric hermaphrodite, further details in Miloslavich & Penchaszadeh (2001). No male examined herein.

Female (Fig. 50): Ovary yellow, surrounds digestive gland, more concentrated in anterior region of visceral mass (Fig. 38). Visceral oviduct formed by gradual decrease from right-anterior end of ovary. Gonopericardial duct narrow; origin in right-ventral extremity of pericardium, running ventral to visceral glands encroached in pallial cavity, inserting in posterior extremity of pallial oviduct joined with insertion of visceral oviduct. Pallial oviduct relatively small, located in right-anterior end of pallial cavity (Figs. 35, 38). Visceral oviduct preceding pallial oviduct somewhat broad. A pair of seminal receptacles located in right side of last portion of visceral oviduct; each one as a small sac; duct very narrow and long; their insertion preceding albumen gland, in right surface. Albumen gland long, narrow, whitish, walls thick glandular; located in anterior-right extremity of visceral mass. Capsule gland as continuation of albumen gland, broad, spherical; walls thick glandular, pale brown; inner duct narrow, U-shaped. Genital pore in form of tall, long papilla close to mantle border and at right of anus. This papilla has a broader base and a somewhat conical form; a pair of low folds runs close to each other along its posterior side; both start gradually in papilla base and finish at some distance from pore; right fold slightly longer than left one.

Habitat: Attached to the mangrove oyster *Crassostrea rhizophorae* (Guilding, 1828), that is attached to mangrove roots of *Rhizophora mangle* Linné, 1753, from 0.5 to 1.0 m depth.

Distribution: Venezuela.

Measurements of shells (in mm): MZSP 36329, ♀: 1: 17.8 by 12.0; ♀2: 16.3 by 10.6.

Material examined: types.

Discussion: *Crepidula margarita* was previously identified as *C. aplysioides* Reeve, 1859 in some previous papers (Hoagland, 1977; Simone et al. 2000; Miloslavich et al.

2001, 2003). However, further examination of the type specimens of *C. aplysioides* at BMNH revealed some important conchological differences. They share the external fashion, flat, wide, with terminal apex (Figs. 119–121). However, *C. aplysioides* type specimens (Figs. 119–122) possess a large muscle scar just dorsal to the right insertion of the septum (Figs. 119, 122 arrow). This feature is not found in the *Crepidula plana* complex, with normally has this muscle scar small and inconspicuous. Larger dorsal muscle scars are found in the western Atlantic species only in *C. convexa* (commented below) and *Bostrycapulus aculeatus* that I have examined. *C. margarita* additionally differs from *C. aplysioides* in having longitudinal colored bands, by apex closer to the posterior shell edge, and by loss of periostracum.

The type locality of *C. aplysioides* is Rio de Janeiro. However, the imprecision of the South American localities in the middle of 19th century is well known, and “Rio de Janeiro” can be any city located in Atlantic coast of that mainland. Hoagland (1977) had commented on the systematic problems related to *C. aplysioides*, but she could not resolve them because of the absence of the types. Anyway, based on the description, the examined species of that paper appears to be of *C. margarita*.

C. aplysioides has the shell apex somewhat projected posteriorly and slightly away from the shell base, which approaches it from *C. convexa* (see below). On the other hand, *C. aplysioides* has a well developed beige periostracum, that show some similarity with *C. carioca* and *C. pyguaia* described below.

Crepidula plana **Say, 1822**

(Figs. 1, 2, 28, 29, 52–67)

Synonymy part in Hoagland (1977: 389). Complement:
Crepidula plana: Collin 2000: 1500–1512 (figs. 1, 2, 3A–B, 4, 5A, D, 6 left); 2001 (fig. 5).

Type: Neotype ANSP 19186 (designed by Collin [2000]); UNITED STATES OF AMERICA, **Massachusetts**, Woods Hole, 41º30'N 70º40'W.

Differential Diagnosis: Shell (Figs. 1, 2): Wide and flat, convex or concave, outline oval. Color white. Outer surface smooth except for weak growth lines. Septum deep and bulged ventrally; anterior edge with a broad median notch and others in each side, just in insertion in the remaining shell. Other details in Collin (2000).

Head-foot (Figs. 53, 58, 63): Tip of tentacles simple. Eyes dark, small, located on very small ommatophores between basal and middle third of tentacles lateral margin. Left neck lappet (nuchal lobe) broader than right one; right lappet brings low food groove along its dorsal limit with head; sperm groove of males (described below) running externally along food groove (Fig. 63). Foot occupying about 3/4 of shell concavity. Columellar muscle very small, contouring anterior border of shell septum, more concentrated at right (Figs. 53, 63) in smaller specimens and almost absent in larger ones.

Mantle organs (Figs. 52, 54–57): Mantle border thick, slight hollow due broad collar sinuses (Fig. 56). Mantle border without appendages, but entirely surrounded by series of minute repugnatorial glands; these glands arranged in elliptical form. Mantle border with special arrangement of folds in middle region of pallial cavity opening, a broad fold located from gill anterior end running towards left, decreasing and disappearing suddenly at level of osphradium; its broader region possessing a central furrow, its posterior edge expanding beyond mantle border covering ventrally anterior region of gill, its anterior edge slightly projecting outside (Fig. 57); a central, low fold, beginning in median region of above described fold, appearing gradually, becoming gradually weak at level of osphradium, producing a narrow furrow with posterior edge of main fold. Dorsal shell muscle well developed (Fig. 52: dm), origin small, in about middle-right region of shell, just anterior to septum; its fibers run anteriorly like a fan, insertion in adjacent anterior region of dorsal surface of pallial cavity. Lateral shell muscle (Fig. 52: lm) very small, fan-like, located close to mantle border right side, just in region where pallial cavity penetrates shell septum chamber.

Pallial cavity aperture occupies about 2/3 of anterior half of shell border turned to right (if shell compared with a clock, in dorsal view and with head occupying 12 oclock, pallial aperture begins in 10 and finishes in 2 oclock) (Fig. 54). Pallial cavity length about 2/3 of total length of animal (Figs. 52, 55). Osphradium very small, monopectinate, located between anterior half of gill and mantle border, at some distance from gill anterior end, located about in left region of pallial aperture somewhat perpendicular to longitudinal axis of animal body (Figs. 54, 55, 57). Osphradium length little more than 1/10 of pallial aperture length, in form of a small fold, attached to mantle, separated from gill structures. Osphradium leaflets rounded, close to each other, somewhat thick and tall, varying around 8 in number (Fig. 57). Osphradium ganglion narrow. Gill filaments triangular in their base and with very long, almost straight, narrow, stiff rod turned to right (Fig. 56); rods extend about three times longer than their triangular, membranous base; these rods begin in ctenidial vein region, in left margin of cavity roof and touches food groove of head-foot, in right margin of cavity floor; rod apex rounded and preceded by thicker region. Ctenidial vein narrow, with uniform width along its length. Endostyle (Figs. 55, 57: en) yellowish, in form of somewhat narrow glandular ridge located in middle level of ventral surface of ctenidial vein all along its length. Endostyle divided along its length by a narrow, middle furrow, into 2 similar ridges (Fig. 57). Hypobranchial gland whitish, thin, weakly developed, surface smooth; occupies area between gill and visceral mass. About 1/3 of visceral mass encroaches in pallial cavity roof (Fig. 55), occupying about 1/3 of this area in posterior-right region; pericardium and kidney posteriorly; a long intestinal loop, anus and pallial oviduct anteriorly (described below).

Visceral mass (Figs. 52, 54, 55): Morphological attributes similar to those of *C. margarita*, proportionally longer only.

Circulatory and excretory systems (Fig. 59): Pericardium very long, situated oblique to longitudinal axis of animal (Fig. 52); begins very narrow, just in posterior extremity of gill, in posterior-left end of pallial cavity; runs edging anterior margin of visceral mass part encroached in pallial roof, gradually enlarges; finishes in about middle level of this region of visceral mass, near median line. Auricle thin walled and very long, runs all along pericardium length attached to its anterior and dorsal inner surfaces (Fig. 59); connecting with ventricle approximately between its middle and right third parts; auricle has, then, broad portion beyond ventricle connection (Fig. 59: ab). Kidney occupying about half of area of visceral mass within pallial cavity (Figs. 55, 59). Kidney central region hollow, with single, irregular lobe (Fig. 59). Kidney lobe rich in transversal, folds not uniform in size, covering entire intestinal region passing through kidney chamber, and about half of inner space of kidney adjacent to intestine. Nephridial gland in renal limit with pericardium, very small, presenting a series of triangular, transversal, narrow folds connected with dorsal renal lobe. Nephrostome a very small slit in left region of ventral wall (Fig. 59), in middle region of hollow portion of kidney; no inner glandular folds close to it. Adrectal sinus narrow, edging externally intestine loop exposed in pallial cavity, becoming slightly broader towards posterior; connecting directly to kidney chamber anterior-left edge.

Digestive system (Figs. 60–62): Buccal mass very large, occupying most of proboscis inner space and about 1/3 of haemocoel posterior to it. Jaw plates thinner. Pair of dorsal folds broad and tall. Odontophore muscles (Figs. 60, 61): **mj**) jaws and peribuccal muscles, somewhat thick, surround lateral and dorsal wall of buccal mass, origin around mouth, insertion in middle level of lateral and dorsal wall of odontophore; **m10**) pair of ventral protractor muscles of odontophore, forming median edge of mj and fused with these; **m14**) pair narrow and thin. Radula short, little more than odontophore length. Radula (Fig. 28, 29) : rachidian tooth secondary cusps vary from 3 to 6 pairs, considerably smaller than central cusp; lateral tooth with about 12 triangular cusps, fifth cusp very larger; inner marginal tooth with about 8 cusps in its inner-subapical margin and 4–6 in its outer-subapical margin; outer marginal tooth with about 4 small cusps in inner margin. Salivary glands long, slender, coiled (Fig. 58), with about 2/3 of haemocoel length, do not pass through nerve ring. Ducts of salivary glands broad, running in dorsal surface of buccal mass, penetrating in adjacent buccal mass wall in short distance, apertures small in middle region of dorsal folds of buccal mass. Esophagus (Figs. 54, 58, 62, 65) narrow, long and coiled; anterior esophagus inner surface with pair of broad folds as continuation of those of buccal mass dorsal wall, located in opposite side from each other. Middle and posterior esophagus inner surface with only 4–5 longitudinal, narrow, similar sized folds. Stomach (Figs. 62, 65) somewhat slender. Anterior duct to digestive gland about in middle region of stomach ventral surface; highly dichotomic. Stomach gradually narrowing towards anterior and left, arriving close to left-posterior extremity of pallial cavity. Posterior duct narrow, strongly turned posteriorly. Stomach inner surface (Fig. 62) with square gastric shield located in right-posterior region, opposite to esophageal insertion; a narrow fold starts in right side of esophageal insertion and runs towards anterior, surrounding left and anterior edges of gastric shield; another fold, transversal, somewhat tall, located just anterior to posterior duct to digestive gland; this fold suddenly runs towards anterior in left gastric surface originating a pair of longitudinal folds dividing gastric surface into intestinal and style sac portions. No preserved crystalline style found. Digestive gland greenish brown in color, surrounding stomach except some areas in dorsal and ventral surfaces (Figs. 52, 65). Intestine narrow and sinuous (Fig. 62) differing by ampler middle loop, approaching first free portion of intestine from style sac, and renal portion from rectum. Anus small, siphoned, located in right region of pallial cavity close to mantle border.

Genital system. **Development**: See Collin (2000).

Male (Figs. 63–65, 67): Larger examined male with 9.7 mm. Testis pale yellow in color, located in anterior region of visceral mass (Fig. 65). Seminal vesicle convoluted, thick, broad, cream in color, located in anterior-right extremity of visceral mass, gradually narrows and becomes very slender tube that opens in right-posterior-ventral region of pallial cavity (Figs. 64, 65); in this portion, passing close to vestigial pallial oviduct. Shallow groove running from this aperture up to penis base, in pallial floor near right margin of head. Sperm groove more clear and deep anteriorly. Penis large (several times tentacle length and width), curved; suddenly narrows before tip producing a very long papilla (Figs. 63, 67), with about half of penis length and about 1/10 of its width. Penis duct opened (groove), running about in middle region of penis ventral surface until papilla tip. A small, somewhat spherical, incipient oviduct found in some males (Figs. 64, 65: vt), in region preceding aperture of visceral vas deferens in pallial cavity.

Female (Fig. 66): Ovary yellow, surrounding digestive gland, more concentrated in anterior region of visceral mass (Fig. 54). Visceral oviduct very narrow, running from left to right in anterior border of visceral mass. Gonopericardial duct well-developed, weakly broader than visceral oviduct; originating in right-ventral extremity of pericardium, running ventral to visceral glands encroached in pallial cavity, inserting in posterior extremity of pallial oviduct joined with insertion of visceral oviduct. Pallial oviduct relatively small, located in right-anterior end of pallial cavity (Figs. 52, 55). Albumen gland long, slight broad, whitish, walls thick glandular; located in anterior-right extremity of visceral mass. About 5 seminal receptacles inserted in right side of albumen gland, successively larger towards anterior. Seminal receptacles duct broad and very short. Capsule gland broad, thick, occupying about half of pallial oviduct volume; walls thick glandular; inner duct narrow, flat, straight. Vaginal tube originating from anterior-left corner of capsule gland; running towards left, after a short distance suddenly twist and runs towards right, parallel to capsule gland; form somewhat thick and broad (about ¼ of capsule gland width); length about same of that of capsule gland. Genital papilla very tall, situated close to anterior region of albumen gland, at some distance from anus. Papilla with a pair of longitudinal folds along posterior surface; left fold longer, starts gradually in papilla base, and finishes in a conspicuous fold situated parallel to pore; right folds short, starts as a low fold of middle region of papilla, finishes in posterior edge of pore. Genital pore a small, transversal, terminal slit.

Habitat: See Collin (2000), subtidal, in shells occupied by hermit crabs.

Distribution: East coast of North America, from New Brunswick (Canada) to Georgia (USA).

Measurements of shells (in mm) MZSP 36327 ♀1: 19.4 by 12.2; ♀2: 16.5 by 9.5; ♀3: 8.4 by 6.0 (immature); ♀4: 17.0 by 13.5; ♂5: 8.7 by 6.8; ♀6: 8.8 by 6.3 (mature); ♂7: 9.7 by 6.0; ♂8: 6.1 by 6.3; ♂9: 9.0 by 7.3.

Material examined: UNITED STATES OF AMERICA; **Georgia**; Saint Catherines Island, MZSP 36327, 4♀, 5♀ (R. Collin col.). **South Carolina**, ANSP 19495. 3 shells (Mrs. Say col.)

Crepidula atrasolea Collin, 2000

(Figs. 3, 4, 30, 31, 68–82)

Crepidula atrasolea Collin 2000: 1500–1512 (figs. 12, 3E–F, 4, 5C, F, 6 right); 2001 (fig. 5).

Type: Holotype ANSP 19188; UNITED STATES OF AMERICA; **Florida**, Sanibel Island, Wolfert Point, 26º29'N 82º10'W. Paratypes FMNH 282203, 282206, 282217.

Differential diagnosis: Shell (Figs. 3, 4): growth lines stronger, producing a rougher outer surface. Other details in Collin (2000).

Head-foot (Figs. 69, 75, 79): Color darker, with grey or black spots in foot sole and neck ventral surface. Tentacles tip weakly bifid. Eyes dark, very small, located on very short ommatophores in level between basal and middle thirds of tentacles lateral margin. Head and neck little shorter than foot length. Columellar muscle reduced, contours anterior border of shell septum, more concentrated at right (Fig. 69, 79), as in smaller specimens as in larger ones.

Mantle organs (Figs. 68, 71–73): Mantle border special arrangement of folds in middle region of pallial cavity aperture with main fold narrower, located from gill anterior end running towards left, decreasing and disappearing gradually; anterior edge of this fold short, disappearing at short distance from gill anterior end; posterior edge continuing with inner edge of mantle border (Fig. 73). This broader fold with a weak central furrow. Dorsal shell muscle well developed (Fig. 68: dm), although thin. Lateral shell muscle (Figs. 68: lm) very small, located slightly posteriorly. Pallial cavity aperture occupies about 2/3 of anterior half of shell border turned to right (if shell compared with a clock, in dorsal view and with head occupying 12 oclock, pallial aperture begins in 9:30 and finishes in 2:30 oclock) (Fig. 70). Pallial cavity length about 4/5 of total length of animal (Figs. 68, 71). Osphradium very small, monopectinate, located between anterior half of gill and mantle border, at some distance from gill anterior end (Figs. 71, 73). Osphradium length about 1/

10 of pallial aperture length, in form of a small fold, attached to mantle, separated from gill structures. Osphradium leaflets rounded, close to each other, somewhat thick and tall, varying around 7 in number (Fig. 73). Gill filaments triangular base somewhat longer, extending by about half of filament length (Fig. 72). Endostyle (Figs. 71, 73: en) yellowish, divided along its length by a narrow, middle furrow, into 2 similar ridges. Hypobranchial gland very thin, almost absent.

Visceral mass (Figs. 68, 70, 80): broader and longer area of pallial cavity.

Circulatory and excretory systems (Figs. 74, 77): Kidney central region mostly hollow, with single, irregular lobe, rich in longitudinal vessels (Fig. 77). A very broad vessel running in center, coming from adrectal sinus; a ventral branch coming from haemocoel; also several other smaller vessel branches covering dorsal, anterior and left surface of renal chamber, and local portion of intestine. Nephridial gland in renal limit with pericardium, very small, presenting a series of triangular, transversal, narrow folds connected with dorsal renal lobe (Fig. 77: ng) in anterior region, and longitudinal folds in posterior region. Nephrostome a very small slit in left region of ventral wall (Fig. 74), in middle region of hollow portion of kidney, protected at left by larger longitudinal vessel. Adrectal sinus broad, edging externally intestine loop exposed in pallial cavity almost all along its length; connecting directly to kidney chamber anterior-left edge.

Digestive system (Figs. 76, 78): Buccal mass occupying most of proboscis inner space and a short portion of haemocoel posterior to it. Pair of dorsal folds broad, their inner edge closer to median line. Odontophore muscles (Fig. 76): **m11**) pair of ventral tensor muscles of radula, originating in haemocoel ventral surface in region of proboscis base, running towards anterior, penetrating in odontophore ventral, middle region; inserting in subradular membrane in ventral end of radula. Radula extending little beyond odontophore length. Radula (Figs. 30, 31) similar to that of *C. margarita*, distinction and notes: rachidian tooth secondary cusps varying from 4 to 6 pairs; lateral tooth with about 14–16 triangular cusps, fifth cusp very larger; inner marginal tooth with 6–10 cusps along its inner-subapical margin and about 4 in outer subapical margin; inner marginal tooth with about 4 very small cusps along its inner subapical margin. Salivary glands very narrow and small (Fig. 75), with about 1/6 of haemocoel length. Salivary glands aperture a transversal slit in anterior region of dorsal folds of buccal mass. Esophagus (Figs. 75, 78, 80) narrow, long; anterior esophagus inner surface with pair of broad folds as continuation of those of buccal mass dorsal wall, located in opposite side from each other. Stomach (Fig. 78) somewhat more curved. Anterior duct to digestive gland about in middle region of stomach ventral surface; highly dichotomic. Stomach gradually narrowing towards anterior and left, arriving close to left-posterior extremity of pallial cavity. Posterior duct narrow, strongly turned towards posterior. Stomach inner surface (Fig. 78) with a very small gastric shield located in middle-right region of right surface of stomach, by side of esophageal insertion; a narrow fold starting in right side of posterior duct to digestive gland insertion, running towards anterior, along gastric ventral surface; bifurcating in a Yshape in region just anterior, and right of posterior duct to digestive gland, raising a transversal fold separating gastric chamber from style sac chamber; on opposite side, this transversal fold suddenly runs towards anterior in left gastric surface, originating a pair of longitudinal folds dividing gastric surface into intestinal and style sac portions. No preserved crystalline style found. Digestive gland pale beige in color. Intestine narrow (Fig. 78) differing by ampler and more separated loops. Anus small, siphoned, located in right region of pallial cavity close to mantle border.

Genital system: **Development**: See Collin (2000).

Male (Figs. 79–81): Largest male examined was 6.6 mm. Testis white in color, located in anterior and left regions of visceral mass. Seminal vesicle convoluted, narrow, cream in color, located in anterior-right extremity of visceral mass (Fig. 80). Penis large (about 4 times tentacle length, and about double width), curved; suddenly narrows before tip producing a very long papilla, with about 1/3 of penis length, papilla base somewhat broad, narrowing gradually towards distal (Figs. 79, 81). Penis furrow runs about in middle region of penis ventral surface until papilla tip.

Female (Fig. 82): Ovary cream in color. Albumen gland narrower. About 5 seminal receptacles inserted in right side of albumen gland, successively smaller towards anterior. Seminal receptacles duct broad and short. Capsule gland narrower, inner duct narrow, flat, straight. Vaginal tube originating from anterior-left corner of capsule gland; running parallel to capsule gland towards right; form somewhat thick and broad (about 1/2 of capsule gland width); length about same as that of capsule gland. Genital papilla very tall, situated close to anterior region of albumen gland, at some distance from anus. Papilla with a single longitudinal fold along posterior surface, starting gradually in papilla base, finishing surrounding pore. Genital pore a small, transversal, terminal slit.

Habitat: See Collin (2000), on oyster shells near mangrove roots, up to 1 m depth.

Distribution: North Carolina, Gulf and Atlantic coast of Florida, Florida Keys.

Measurements of shells (in mm): MZSP 36328 ♀1: 15.2 by 11.7; ♂2: 4.9 by 4.6; ♀3: 15.0 by 11.8; ♂4: 6.5 by 3.4; ♀5: 6.6 by 5.4 (mature).

Material examined: UNITED STATES OF AMERICA; **Florida**; Harbor Branch, MZSP 36328, 2♂, 3♀ (R. Collin col.)

Crepidula depressa Say, 1822
(Figs. 5, 6, 32, 83–96)

Crepidula depressa: Collin 2000: 1500–1512 (figs. 1, 2, 3C–D, 4, 5B, E, 6center); 2001 (fig. 5).

Neotype: ANSP 19187; UNITED STATES OF AMERICA; **Florida**, Sanibel Island, Sanibel Marina, 26º27'N 82º02'W.

Differential diagnosis: Shell (Figs. 5, 6): growth lines stronger, producing a rougher outer surface. Color entirely white. Anterior edge of septum with a deeper notch in left side. Other details in Collin (2000).

Head-foot (Figs. 84, 89, 91): Tentacles tip simple. Eyes dark, very small, located on very short ommatophores in level between basal and middle thirds of tentacles lateral margin. Head and neck with about same foot length. Columellar muscle reduced, contours anterior border of shell septum, more concentrated at right (Fig. 84). Anterior edge of foot, with pedal gland furrow, presenting projected edges in both sides.

Mantle organs (Figs. 83, 85–88): Mantle border special arrangement of folds in middle region of pallial cavity aperture with very broad main fold, located from gill anterior end running towards left, decreasing gradually (Figs. 87, 88); both edges of this fold unite at level of osphradium by a short distance, and connect to mantle border. This fold possesses a broad and shallow central furrow. Dorsal shell muscle well developed (Fig. 83: dm), relatively large. Lateral shell muscle (Figs. 83: lm) very small, almost absent. Pallial cavity aperture occupies about 2/3 of anterior half of shell border turned to right (if shell compared with a clock, in dorsal view and with head occupying 12 oclock, pallial aperture begins in 9:30 and finishes in 3 oclock) (Fig. 86). Pallial cavity length about same of total length of animal (Figs. 83, 87). Osphradium very small, length about 1/10 of pallial aperture length. Osphradium leaflets rounded, slightly far from each other, somewhat thick and tall, varying around 8 in number (Fig. 88). Gill filaments triangular base somewhat longer, extending by about half of filament length, but narrower than that of *C. atrasolea*. Endostyle (Figs. 87, 88: en) divided along its length by a narrow, middle furrow, into 2 similar ridges. Hypobranchial gland very thin.

Visceral mass (Figs. 83, 93): relatively shorter.

Circulatory and excretory systems (Figs. 87): renal lobe slightly thicker attached to intestine.

Digestive system (Figs. 89, 90, 92): Buccal mass occupying most of proboscis inner space and a short portion of haemocoel posterior to it. Pair of dorsal folds somewhat notched (Fig. 90) and narrow. Odontophore muscles: **m7** pair with insertion inside radular sac strongly connected with each other; **m11** pair also present; **m14**, very narrow, almost filiform. Radula extending little beyond odontophore length. Radula (Fig. 32): rachidian tooth with 3–4 secondary cusps; lateral tooth with about 12 triangular cusps, forth cusp very larger; inner marginal tooth with about 8 cusps along its inner-subapical margin and 4 in along its outer subapical margin; inner marginal tooth with about 3 small and pointed cusps long its inner subapical margin. Salivary glands very narrow (Figs. 89), length little longer that half of haemocoel length. Salivary glands aperture an oblique slit in anterior region of dorsal folds of buccal mass (Fig. 90). Esophagus (Figs. 89, 92) very narrow, long. Stomach (Fig. 92) very similar to that of *C. atrasolea*, except for anterior and posterior ducts to digestive gland dichotomic at their base, practically double. Digestive gland greenish beige in color. Intestine very similar in attributes to that of *C. atrasolea* (Fig. 92).

Genital system: **Development**: See Collin (2000).

Male (Figs. 91, 93): Testis cream in color, located in anterior and left regions of visceral mass. Seminal vesicle proportionally larger, highly convoluted, narrow, cream in color, located in anterior-right extremity of visceral mass. Penis large (about 5 times tentacle length, and about 3 times its width), curved; narrowing gradually towards tip, lacking a clear separation with terminal papilla. Penis furrow runs in middle region of penis ventral surface until papilla tip.

Female (Figs. 95, 96): Ovary pale yellow in color. Albumen gland narrower. About 4 seminal receptacles inserted in right side of albumen gland, successively larger towards anterior. Seminal receptacles duct narrow and long. Capsule gland narrower, inner duct narrow, flat, straight. Vaginal tube originating from left region of capsule gland; running parallel to capsule gland towards right; form very thick and broad (little slender than capsule gland width); length about same as that of capsule gland; vaginal tube inner surface with 7–8 longitudinal, irregular folds, starting just in region after capsule gland. Genital papilla very tall, situated close to anterior region of albumen gland (part covering it), at some distance from anus; its inner surface with vaginal tube folds converging and becoming only 3 broad longitudinal folds. Papilla with about 5 longitudinal folds along posterior and left surfaces, starting gradually in papilla base, finishing at short distance from pore; those more posterior folds taller, forming a deep furrow between their distal end as genital pore lips. Genital pore a small, transversal, terminal slit.

Central nervous system (Figs. 89, 94): With normal characters as in other described *Crepidula* (Simone 2002), located posterior, far removed from buccal mass, ganglia somewhat concentrated, statocyst with statolith.

Habitat: See Collin (2000), on oyster shells and shells occupied by hermit crabs, 3–5 m depth.

Distribution: Gulf coast of Texas, Gulf and Atlantic coasts of Florida.

Measurements of shells (in mm): MZSP 36326 ♀1: 14.1 by 10.5; ♂2: 4.8 by 3.6; ♀3: 9.7 by 7.2.

Material examined: UNITED STATES OF AMERICA; **Florida**; Sanibel Marina, MZSP 36326, 10 specimens (R. Collin col.); St. Petersberg, MZSP 35844, 16 specimens (T. Bert col. 1977, R. Collin leg & id.).

***Crepidula intratesta*, new species**

(Figs. 13–15, 112)

Crepidula plana: Rios 1985: 59 (pl. 21, fig. 267); Rios 1994: 71 (pl. 24, fig. 272). (Non Say 1822.)
Crepidula (*Ianacus*) *plana:* Rios 1970: 56; 1975: 65 (pl. 17, fig. 260); Oliveira et al. 1981: 112. (Non Say 1822.)
Crepidula aff. *plana:* Simone 2002 (figs. 4, 7, 60–62, 119–140).

Types: Holotype ♀ MZSP 30791 (19.5 by 14.8 mm). **Paratypes**: BRAZIL. **Espírito**

Santo; off Vitória, MNRJ 8989, 5 shells (P.M.Costa col. otter trawl, 2001). RIO DE JANEIRO; **Rio de Janeiro**, Governador Island, Centro de Instrução da Marinha, MNRJ 2338, 1♀ (Adolfo Emigdio col. Iii/1957). **São Paulo**; off Ubatuba (Integrated Project IOUSP, R.V. Veliger II col.), 23°30'S 44°54'W, 42m depth, MZSP 30790, 5 specimens (Sta. 26, 21/iv/1986); 23°25'S 44°52'W, 21 m depth, MZSP 30803, 13 specimens (Sta. 27, 21/iv/1986); 23°29'S 44°52'W, 38 m depth, MZSP 30798, 2 specimens (Sta. 8, 28/x/1985); 23°33'S 44°50.5'W, 43 m depth, MZSP 30799, 2♀ (Sta. 7, 28/x/1985); 23°34'S 44°48'W, 44 m depth, MZSP 30801, 4 specimens (Sta. 17, 22/i/1986); 23°34'S 45°06'W, 21 m depth, MZSP 30802, 24 specimens (Sta. 12, 20/i/1986), 20 m depth, MZSP 30800, 1 specimen (Sta. 39, 21/x/1986); 23°34'S 45°07'W, 20 m depth, MZSP 30797, 2 specimens (Sta. 21, 18/iv/1986); 23°38'S 44°49'W, 47 m depth, MZSP 30795, 1♀ (Sta. 16, 22/i/1986); 23°38'S 45°14'W, 16 m depth, MZSP 30805, 1 specimen (Sta. 42, 22/x/1986); 23°39'S 45°04'W, 36m depth, MZSP 30792, 2♂ (Sta. 11, 20/i/1986); 23°44'S 45°00'W, 42 m depth, MZSP 30796, 2♀ (Sta. 37, 21/x/1986); 23°44'S 45°15'W, 32 m depth, MZSP 30804, 10♀, MZSP 36325, 2♀ (sta. 5, 27/x/1985); 23°47'S 45°10'W, 35 m depth, MZSP 30793, 2♂, 1♀ (Sta. 14, 21/i/1986). **Rio Grande do Sul**, off Albardão, 33°32'S 52°18'W, 35 m depth, MZSP 19034, 10♀ (GEDIP-RS, R. V. W.Besnard sta. 571, 13/iii/1969).

Type locality: BRAZIL; **São Paulo**; off Ubatuba, 23°29'S 44°52'W, 38 m depth (Integrated Project IOUSP, R.V. Veliger II, Sta. 8, 28/x/1985).

A complete conchological and anatomical description of this species is provided elsewhere (Simone 2002). In present paper only a formal description for naming this species is presented.

Description: Shell (Figs. 13–15): Medium to large size (up to 40 mm), color white, periostracum deciduous. Dorsal surface plane to concave, arched, opaque. Sculpture lacking, except for concentric, low, narrow somewhat uniform undulations and growth lines. Protoconch 1 whorl, inlaid, located approximately in center of posterior edge. Borders sharp, fragile, with weak remains of pale brown, hairy periostracum. Ventral surface smooth, glossy, white. Septum triangular, protruding ventrally; lateral edges almost straight, at some distance from shell edges; posterior end normally with a shallow concavity and at some distance from shell posterior end. Septum anterior free edge concave, presenting a shallow central notch from which edges diverge gradually towards anterior and lateral, somewhat straight; left insertion in shell simple; right insertion marked by a somewhat deep and narrow notch. No clear muscle scar.

Inner anatomy: Already described in Simone (2002). The some complements follows. 1) Odontophore muscle **m12**, a small pair of muscles, originating in odontophore cartilages in a small portion by side of m6 (horizontal muscle) anterior region, running free towards ventral and lateral, inserting in short distance in subradular membrane inner surface. 2) Female genital papilla somewhat tall, in posterior surface a pair of broad folds running longitudinally close from each other, between both a narrow furrow, each one surrounding distal, narrow genital pore; an additional left-dorsal, longitudinal, low fold, originating gradually in papilla base, disappearing gradually at some distance lateral from genital pore (Fig. 112).

Habitat: Almost invariably within empty gastropod (bivalve sometimes) shells, from intertidal to 73 m depth.

Distribution: Central and Southeast coast of Brazil (Bahia to Rio Grande do Sul).

Measurements of shells (in mm): MZSP 36325: 1) 18.4 by 14.0, 2) 19.1 by 15.3; MZSP 30795: 24.1 by 18.0; MZSP 30790: 27.3 by 20.0. Holotype see type list.

Etymology: The specific epithet refers on the living habit inside empty shells, being *intra* meaning inside, and *testa* meaning shell from the Latin.

Material examined: Types and those listed in Simone (2002).

Discussion: *Crepidula intratesta* has been considered as the Brazilian occurrence of *C. plana*. However, based on the anatomical difference with the *C. plana* specimens collected from the neotype locality, and further arguments given by Collin (2000), the specific separation becomes necessary. This description was considered premature in by Simone (2002), but is provided here. A more complete morphological differentiation is given in the section of discussion of characters. However, the more outstanding differences are the *C. intratesta* longer osphradium, with more filaments; endostyle simple (not divided along its length); kidney with larger hollow chamber, lacking solid dorsal lobe; the thinness of the peri-oral and jaw muscles (mc); the presence of an auxiliary ventral tensor muscle of the radula (m7a); salivary gland very shorter, forming a single mass (instead of being coiled); a different arrangement of gastric inner folds; the penis with shorter terminal papilla; pallial oviduct with fewer seminal receptacles; papilla of female pore with different folds (Figs. 66, 112).

Although all species of the “*C. plana* complex” potentially can show a concave dorsal surface, this apparently is rare. I have not seen any specimen with this shell morphology, except some specimens of *C. plana*. *Crepidula intratesta* almost invariably has the concave dorsal surface, which easily differentiate it from the other species. This shell morphology has the shell septum protruding by the ventral shell surface. It is undoubtedly a consequence of the habitat inside empty shells (mostly gastropods).

Further anatomical discussion and distinction is provided by Simone (2002) and herein, in the following section. However, it is interesting to establish that the anatomical difference between *C. intratesta*, and particularly with *C. protea*, is relatively small. The differences remain in the conchological features and in developmental attributes (*C. protea* most probably is not a protandric hermaphrodite, but a dioic).

Crepidula pyguaia new species

(Figs. 7–9, 34, 97–106)

Crepidula protea: Rios 1994: 71 (part).

Types: *Holotype:* MZSP 35831 ♀. *Paratypes:* BRAZIL; **Santa Cataria**; Bombinhas, 0–1 m depth, MZSP 35832, 2♀ (Tarasconi col., 22/vii/1993), Trapiche and Embrulho beaches, MZSP 34640, 2♀, 2 shells, 9 young (Simone col. 20/ii/2002); Camburiu, Central beach, MZSP 34603, 2 shells (Simone col. 21/ii/2002); Itapema, Canto da Praia, MZSP 35842, 2♀, 1 shell (Tarasconi col., 28/xii/1999).

Type locality: BRAZIL; **Santa Catarina**; Bombinhas, Enseada de Zimbros 27º06S 48º 30W (otter trawl, 2–5 m depth, xii/1993, Tarasconi leg.).

Diagnosis: Shell occurring intertidal in Santa Catarina coast. Shell whitish, with periostracum persistent covering most of shell. Siphonal pallial fold broad and wide. Pericardium constricted in middle portion, being narrow in its posterior half. Osphradium occupying about 5% of pallial aperture, bearing about 10 filaments close from each other. Pallial oviduct having 7 seminal receptacles connected to albumen gland almost in same region. Female genital papilla lacking folds, broad, irregular, inflated.

Description: Shell (Figs. 7–9): Of medium size (up to 20 mm), white, convex, flat, surface opaque. Protoconch not seen (eroded). Periostracum heavy, rich in hair, color pale brown, lost in older regions but generally covering most of shell. Sculpture lacking, except concentric undulations and growth lines. Septum somewhat short, wide, triangular, curved septum lateral insertions slightly far from shell outer edges, mainly at right. Septum anterior edge with a wide central notch, its right edge almost straight, its left edge curved, convex; another narrower notch in left end weakly deeper. Inner surface glossy, white, smooth.

Head-foot (Figs. 97, 103): General characters similar to those of *C. margarita*, differences and notable features following. Tentacles tip weakly bifid. Eyes dark, very small, located on very short ommatophores in level between basal and middle thirds of tentacles lateral margin. Head and neck little shorter than foot length. Columellar muscle very reduced, contours anterior border of shell septum, more concentrated at right (Fig. 97). Anterior edge of foot, with pedal gland furrow, simple.

Mantle organs (Figs. 98–101): Characters similar to those of *C. plana*, remarks following. Mantle border special arrangement of folds (in middle region of pallial cavity aperture) very broad, covering anterior end of gill, and exceeding beyond mantle border (Figs. 99, 100); decreasing gradually towards left, disappearing in middle level of osphradium. This fold possesses a broad and shallow central furrow. Dorsal shell muscle well developed (Fig. 98: dm), relatively large. Lateral shell muscle reduced, almost absent. Pallial cavity aperture occupies almost half of anterior half of shell border turned to right (if shell compared with a clock, in dorsal view and with head occupying 12 oclock, pallial aperture begins in 9:30 and finishes in 3 oclock) (Figs. 98, 99). Pallial cavity length about same of total length of animal (Figs. 98). Osphradium small, length about 1/6 of pallial aperture length. Osphradium leaflets tall, tip rounded, close from each other, somewhat thick, varying around 11 in number (Fig. 100). Gill filaments triangular base short, extending by about 1/5 of filament length (Figs. 100, 101). Endostyle (Figs. 99, 100: en) simple. Hypobranchial gland thin, white, more developed in left side of intestine.

Visceral mass (Figs. 98, 99): Shorter and broader than that of *C. margarita*.

Circulatory and excretory systems (Fig. 102): Characters very similar to those of *C. atrasolea*, remarks following. Pericardium right region broader, with auricle curved, possessing a blunt angle in its middle anterior region. Kidney posterior-right region with 2–3 broad, tall, longitudinal folds in dorsal surface; these folds running towards anterior covering left surface of rectum, bearing longitudinal folds; in anterior-left region renal issue covering only dorsal surface, having oblique folds, some penetrating in adrectal sinus. Adrectal sinus continuous to kidney, surrounding rectum up to short distance of anus, gradually decreasing.

Digestive system (Figs. 103–105): . Buccal mass extending little posterior to proboscis. Odontophore muscles (Fig. 104): **m7** pair with insertion inside radular sac, connected with each other by about half of their length; **m11** pair present. Radula extending little beyond odontophore length. Radula (Fig. 34): rachidian tooth tall, narrow, central cusp large and sharp, single secondary cusps, no basal cusps but pair of lateral reinforcements on its borders; lateral tooth broad, curved internally, with about eight triangular cusps, medial cusp larger, apical, turned towards median, cusps somewhat similar sized, disappearing about in middle region of tooth, remaining a slight thick border; both marginal teeth long, curved, tall, sharp pointed tip, about seven cusps in their inner-apical margin; inner marginal tooth with about double width than outer marginal tooth. Salivary glands narrow, (Fig. 103), length longer than of haemocoel length, running almost straight along haemocoel, becoming broader in region posterior to nerve ring. Stomach (Fig. 105) similar to that of *C. atrasolea*, except for 1) insertion of esophagus somewhat close to posterior end of stomach; 2) posterior duct to digestive gland very much narrow, simple, running towards posterior; 3) anterior duct to digestive gland broad, dichotomic only after some distance. Stomach inner surface with a single, narrow, pair of folds running along ventral surface of style sac; these folds running in opposite side from each other in region just anterior to anterior duct to digestive gland, surrounding origin of style sac, fading in dorsal surface. Digestive gland pale beige in color. Intestine similar in attributes than that of *C. atrasolea*, except for strongest U-shaped loop of rectum exposed in pallial cavity (Figs. 100, 105).

Genital system: **Development**: All examined specimens females and larger than 15 mm. No males available.

Female (Fig. 106): Albumen gland narrower, differing little from visceral oviduct. About 7 seminal receptacles inserted in right side of albumen gland, reunited in a short region. Seminal receptacles duct slender and long. Capsule gland narrower, somewhat triangular, inner duct broad, flat, straight; walls slightly thin. Vaginal tube originating from anterior-left region of capsule gland; running obliquely to capsule gland towards right, narrow; length little shorter of that of capsule gland; vaginal tube inner surface with 7–8 longitudinal, very narrow folds. Genital papilla tall, situated at sort distance of anterior region of albumen gland, at long distance from anus; its inner surface continuous with vaginal tube folds. Papilla broad, blunt, anterior half semispherical, posterior surface with irregular folds Genital pore a transversal, terminal slit with edges tall and thick.

Central nervous system: With normal characters as remainder known *Crepidula* (Simone 2002), located posterior, far removed from buccal mass, close to visceral mass.

Habitat: Intertidal rocks.

Distribution: Brazilian coast of Santa Catarina.

Measurements of shells (in mm): MZSP 35831: 16.3 by 14.0; MZSP 35832, ♀2: 16.0 by 13.4; ♀3: 19.4 by 14.0.

Etymology: The specific epithet came from the Tupy language, *pyguaia*, meaning concave, and allusion to the possible extreme form of some specimens.

Material examined: Types.

Discussion: *Crepidula pyguaia* is similar to the other congeneric species from Western Atlantic. Differs mainly in flat, concave shell, somewhat rounded outline, and by heavy periostracum preserved in youngest region. The characteristic uniform white color is also distinctive, since the remaining species are usually brownish. The anatomical characters also corroborate with the specific separation, mostly explored above. The most important are the longer osphradium, with filaments closer to each other; the shorter triangular base of the gill filaments; the curved fashion of the auricle; the longer salivary glands; the different conformation of gastric ducts to digestive gland (simpler and narrower); and the strongest curve of the U-shaped portion of rectum. However, the deeper differences are in the characters of the pallial oviduct, such as the narrow albumen gland situated almost perpendicularly to the capsule gland; the seminal receptacles in a larger number, reunited forming a single mass, and the genital papilla blunt, almost spherical.

C. pyguaia has been identified as *C. protea*, a species re-described in Simone (2002) occurring in deeper waters (generally on other shells), with taller and more convex shell, lacking periostracum, and more colorful.

Crepidula carioca new species
(Figs. 22–25, 33, 107–110)

Crepidula protea: Rios 1994: 71 (part).

Types: *Holotype:* MNRJ 7464, ♀. From type locality.

Paratypes: BRAZIL. **Rio de Janeiro**; ANSP 19462, 1 shell (ex-Smithsonian, USEE); Casemiro de Abreu, Rio das Ostras, Joana beach, MNRJ 9517, 5 specimens (A. Coelho col. ii/1971); Búzios, Raza beach, MNRJ 9516, 1 shell (L.R. Tostes & A. Coelho col., xii/1974); Cabo Frio, Arraial do Cabo, MNRJ 3366, 4 shells (H.S. Lopes col., iii/1950), Forno Beach, MNRJ 2337, 2♀ (A. Coelho & S. Ypiranga col., i/1960), Prainha, MZSP 42053, 10♀ (Simone & Costa col., 18/iii/2003); Niterói, Boa Viagem beach, MNRJ 5480, 1 shell (H.S. Lopes col.), MNRJ 7464, 18♀ (H. Travassos & H.S. Lopes col., 9/iii/1953), Itaipu beach, MNRJ 2336, 1 ♂, 4♀ (A. Coelho col., 1959), MZSP 28737, 1♀ (Simone col., 12/

vii/1997); Rio de Janeiro, off Santana Island, 22º30'S–41º23'W 22º43'S–41º40'W, 48 m depth, MNRJ 9518 (B. Prazeres & O. Silva col. 15–25/x/1963).

Type locality: BRAZIL; **Rio de Janeiro**; Niterói, Boa Viagem beach, 22°56'S 43°12'W.

Diagnosis: Shell occurring intertidal in Rio de Janeiro coast. Shell whitish, with periostracum persistent covering most of shell. Siphonal pallial fold low and narrow. Pericardium constricted in middle portion, being narrow in its posterior half. Osphradium occupying about 15% of pallial aperture, bearing about 20 filaments close from each other. Pallial oviduct with 5 seminal receptacles connected to albumen gland almost in same region. Female genital papilla with a pair of folds in posterior side, disappearing at some distance from pore; papilla tip pointed.

Description: Shell (Figs. 22–25): Of medium size (up to 20 mm), white, convex, flat, surface opaque. Protoconch eroded. Periostracum heavy, rich in hair, color pale brown, lost in older regions but generally covering most of shell. Sculpture lacking, except shallow concentric undulations and growth lines. Septum somewhat short, wide, triangular, curved septum lateral insertions slightly far from shell outer edges, mainly at right. Septum anterior edge with a wide central notch, its right edge almost straight, its left edge curved, convex; another narrower notch in left end weakly deeper. Inner surface glossy, white, smooth.

Head-foot (Fig. 108): Similar features to those of *C. pyguaia*, tentacles more clearly bifurcated, having a somewhat deep furrow at tip.

Mantle organs (Fig. 107): Characters closely similar to those of preceding species. Remarkable features following. Pallial cavity length of larger specimens about 90% of total animal length. Siphonal fold at mantle border shorter and narrower, its right end low, fused with remaining mantle edge. Osphradium with about 20 filaments; length about 15% of pallial cavity aperture; each filament slightly cylindrical, close with each other. Endostyle posterior half running separated from ctenidial vein, running along mantle surface adjacent to it, slightly ventral to ctenidial vein up to gill end.

Visceral mass and circulatory-excretory systems: Same characters than those of *C. pyguaia*, including sudden narrowing in its left half.

Digestive system: Morphological attributes similar to those of *C. pyguaia*. Radula (Fig. 33) also similar, except by rachidian slightly narrower, having two pairs of secondary cusps; marginal with seven cusps, second cusp larger and terminally disposed; marginal teeth with six secondary cusps in sub-terminal inner edge.

Genital system: **Male** (Figs. 108, 109): General features similar to those of preceding *Crepidula*. Remarkable characters following. Testis whitish, located in anterior region of ventral branch of visceral mass, additionally extending towards posterior along its left side, this region forming successive and decreasing digitiform acina. Seminal vesicle slightly small, bearing 3–4 whorls, narrowing gradually. Penis somewhat long, terminal papilla slender and long, with about half of remaining penis length (Fig. 108).

Female (Fig. 110): General organization similar to those of preceding species. Remarks following. Albumen gland narrow and short. Seminal receptacles rounded, number of 5 decreasing towards anterior; ducts very narrow, connected to albumen gland anterior-right side almost in same region. Capsule gland narrow. Vaginal tube broad and long. Internally low longitudinal, narrow folds. Genital papilla tall, with a pair of longitudinal folds running at some distance from each other along posterior surface, finishing at some distance from pore. Papilla tip somewhat pointed. Genital pore a narrow, sub-terminal slit. Anus in basal level of pallial oviduct.

Measurements (in mm): MNRJ 7464 >♀: 34.0 by 23.5; <♀: 11.0 by 9.0; >♂: 15.0 by 9.7; ♂3: 12.9 by 10.0; ♂4: 22.7 by 17.4.

Distribution: Known for coast of Rio de Janeiro.

Habitat: Intertidal rocks up to 48 m depth.

Etymology: The specific epithet refers to the geographic occurrence of the species, i.e., the region of the Rio de Janeiro. The people from the city of Rio de Janeiro are known as “carioca”.

Material examined: Types.

Discussion: *Crepidula carioca* is closely similar to *C. pyguaia*, both, in conchological and anatomical features. In the shell they are almost indistinguishable. *Crepidula carioca* normally has less periostracum, but this feature disappears in dead samples. The number and type of anatomical character, most explored above, based the specific separation of *C. carioca* from *C. pyguaia*. The considered more important are: 1) the longer osphradium (about 15% of pallial cavity aperture in *C. carioca*, wile *C. pyguaia* has about 5%); 2) osphradium bearing more filaments (about 20 in *C. carioca* and about 10 in *C. pyguaia* in larger specimens of equivalent size); 3) fewer seminal receptacles (5, while *C. pyguaia* has 7); 4) anus closer to pallial oviduct; 5) female genital papilla with different fashion, having a pair of longitudinal papillae in posterior surface and a pointed tip. *Crepidula pyguaia* and *C. carioca* are close related species, but they are apparently separated geographically, since no *Crepidula* of similar feature occur in São Paulo coast, as I have consulted in all local collections.

Crepidula pyguaia and *C. carioca* differ from the other congeneric species in having a persistent periostracum, whitish shell color, and in occurring in shallow waters (intertidal), these characters can easily and quickly identify any sample. But for differentiating both only based on shell samples it is necessary taking into consideration the locality.

***Crepidula protea* Orbigny, 1841**

(Figs. 16–18, 111)

Synonymy see Simone (2002: 32). Complement:

Crepidula protea: Simone et al. 2000: 139–140 (figs. 22–27); Simone 2002: 32–36 (Figs. 5, 6, 63, 64, 141–151).

The description of this species is accurate in Simone (2002), including the synonymy. The single addition is the presence of the odontophore muscle pair m12, and the female genital papilla folds fashion (Fig. 111), both similar to those described by *C. intratesta*.

Additional material examined: BRAZIL; **Rio Grande do Sul**; off Sarita, ANSP 244118. 5 shells (Fishing boats col. 1959. E.C. Rios leg.); off Rio Grande, 32º30S 52º00W, ANSP 355327, 35 specimens (voucher material of Hoagland; Hoagland, Hoagland & Davis col., 20/xii/1981). URUGUAY; **Rocha;** La Paloma, 34º40S 54º09W, ANSP 410440, 2 shells (Naide & Naide col., iii/1959; E.I.Duarte leg.); off Maldonado, ANSP 220712, 1 shell (B.R. Bales col.; 1958).

Crepidula argentina Simone, Pastorino & Penchaszadeh, 2000
(Fig. 115)

Crepidula argentina Simone, Pastorino & Penchaszadeh 2000: 127–140 (figs. 1–21, 28–46); Cledón & Penchaszadeh 2001: 15–20; Simone 2002: 36, 118–125 (figs. 65, 437, 438).

The description provided by Simone et al. (2000) is sufficiently precise, the single addition is in the female genital papilla (Fig. 115). This structure present a pair of longitudinal folds in posterior side, originating convergently in papilla base, running close from each other with a very narrow furrow between both, finishing in posterior side of genital pore, becoming its lips. Remainder surface smooth.

Additional material examined: ARGENTINA; off Mar del Plata, on commercial mussel banks, 20–30 m depth, ANSP 338926, 2 shells (Victor Scarabino col. vi/1975; E. Hoagland leg.)

Crepidula glauca Say, 1822
(Figs. 19–21, 113, 123–125)

Synonymy see Simone (2002). Complement:

Crepidula convexa: Collin 2001 (figs. 2, 3); Simone 2002: 36–38 (figs. 8, 9, 66, 67, 152–159). [non Say, 1822]

The anatomical description by Simone (2002) is accurate. The shell is similar to *C. margarita* (Figs. 19–21). The single addition is the confirmation that the female genital papilla has smooth outer surface, lacking any kind of folds (Fig. 113).

The examined specimens have been erroneously identified as *Crepidula convexa* Say, 1822 in my previous paper (Simone, 2002), which is here corrected. The change of the concept was based on the examination of voucher specimens at BMNH as explained following.

There are some samples of *Crepidula convexa* in the visited museums; however, coincidently few them have precise locality data. Voucher material of Reeve (1859)

(BMNH 1829) has no locality at the label. Some samples (BMNH, ANSP 357830) show that the species occur in the north-western Atlantic, sometimes referred for estuary. The shell of *C. convexa* is very characteristic (Figs. 126–1295) in being small (about 10 mm), dark reddish colored, highly convex (tall for the genus) and with a projected posterior beak, keeping the protoconch away from substrate and normally distant from the posterior shell border (Fig. 127). The shell septum is weakly and centrally concave at its edge (Fig. 128). Additionally, a conspicuous feature is the large muscle scar present in right side, just dorsal to right septum insertion (Fig. 126). A sample with soft parts was examined (BMNH from New Jersey), revealing a huge dorsal muscle. These characters show that *C. convexa* is not actually close to the *C. plana* complex, and some distinctive anatomical attributes are present.

On the other hand, *Crepidula glauca*, which has been considered a form of *C. convexa* (e.g., Warmke & Abbott, 1961; Abbott, 1974), appears to be a separated species. This conclusion is based on the examination of voucher lot of Reeve (1859) (BMNH no locality) (Figs. 123–125). The shells are flat, wide, whitish, with apex fused with shell edge, sigmoid septum edge, and with the muscle scar shallow and small. These characters are common in the *C. plana* complex. In being the examined specimens virtually identical to the Reeves lot, the systematics of these species can be resolved, considering *C. glauca* a valid species, separated from *C*, *convexa*, possessing the shell and anatomical attributes described here and by Simone (2002).

Additional material examined: No locality, BMNH, 4 shells (voucher of Reeve, 1859). VENEZUELA; **Isla Margarita**, off Morro de Pto. Moreno, 13–17 m depth, ANSP 240085, 1 dry specimen (Wesley M. Heilman leg. 16/ii/1959; sta. 28).

Material examined of ***Crepidula convexa***: No locality; BMNH 1829, 4 shells (Voucher of Reeve, 1859); BMNH, 3 shells (Van Couvers Lsd); BMNH, 4 shells (figured specimen; H. Cuming collection). UNITED STATES OF AMERICA; **Massachusetts**; Plymouth, BMNH, 12 shells. **Connecticut**; Bridgeport, Fairfield county, Long Island sound, St. Marys estuary, 41°10N 73°10W, ANSP 357830, 1 shell (Hoagland & Hoagland col. 1982). **New York**; Northport, BMNH 1838, 9 shells (Winckworth colln.). **New Jersey**; Cape May, Wildwood, BMNH 20020070, 6 specimens (R. Collin col. 13/vi/1999).

Crepidula fornicata (Linné, 1758)

(Fig. 114)

Synonymy see Simone (2002: 38). Complement:
Crepidula fornicata: Collin 1995: 815–829 (fig. 1); 2001 (fig. 4); Simone 2002: 38–40 (figs. 10, 11, 71, 72, 160–164).

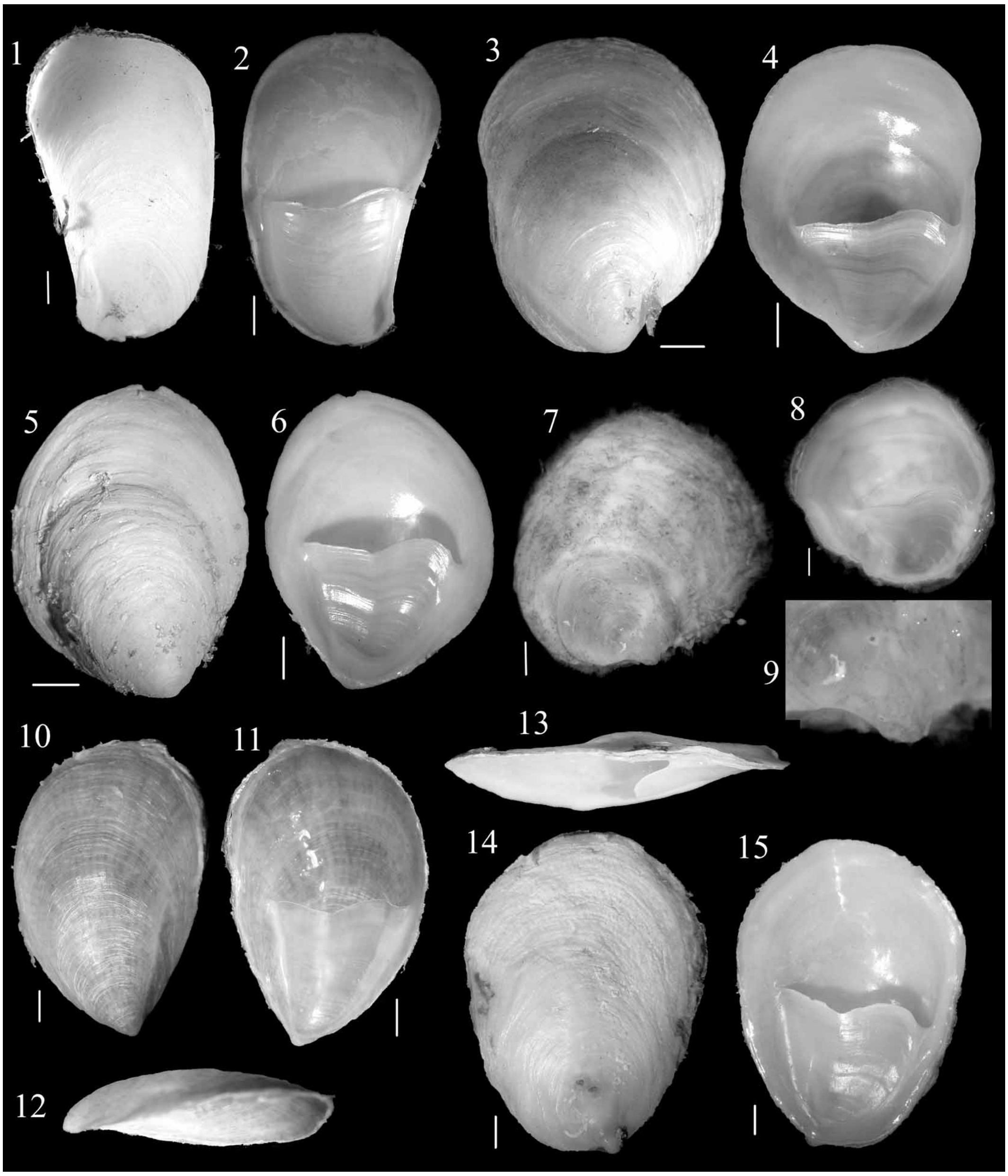
The anatomical description provided by Simone (2002) is appropriate. The single addition is the female genital papilla. This structure is broader than those of remaining species; a pair of broad, longitudinal folds running in posterior side close from each other, with a shallow and narrow furrow between both, both finishing at some distance from genital pore (Fig. 114). Another longitudinal fold running in right side, narrow, slightly sinuous, starting gradually in base of papilla, finishing also gradually far from pore. Genital pore with thick edges, marked by deep, radial furrows.

Additional material examined. UNITED STATES OF AMERICA; **Florida**; St. Petersberg, MZSP 35843, 14♀ (T. Bert col. 1997, R. Collin leg. & id.).

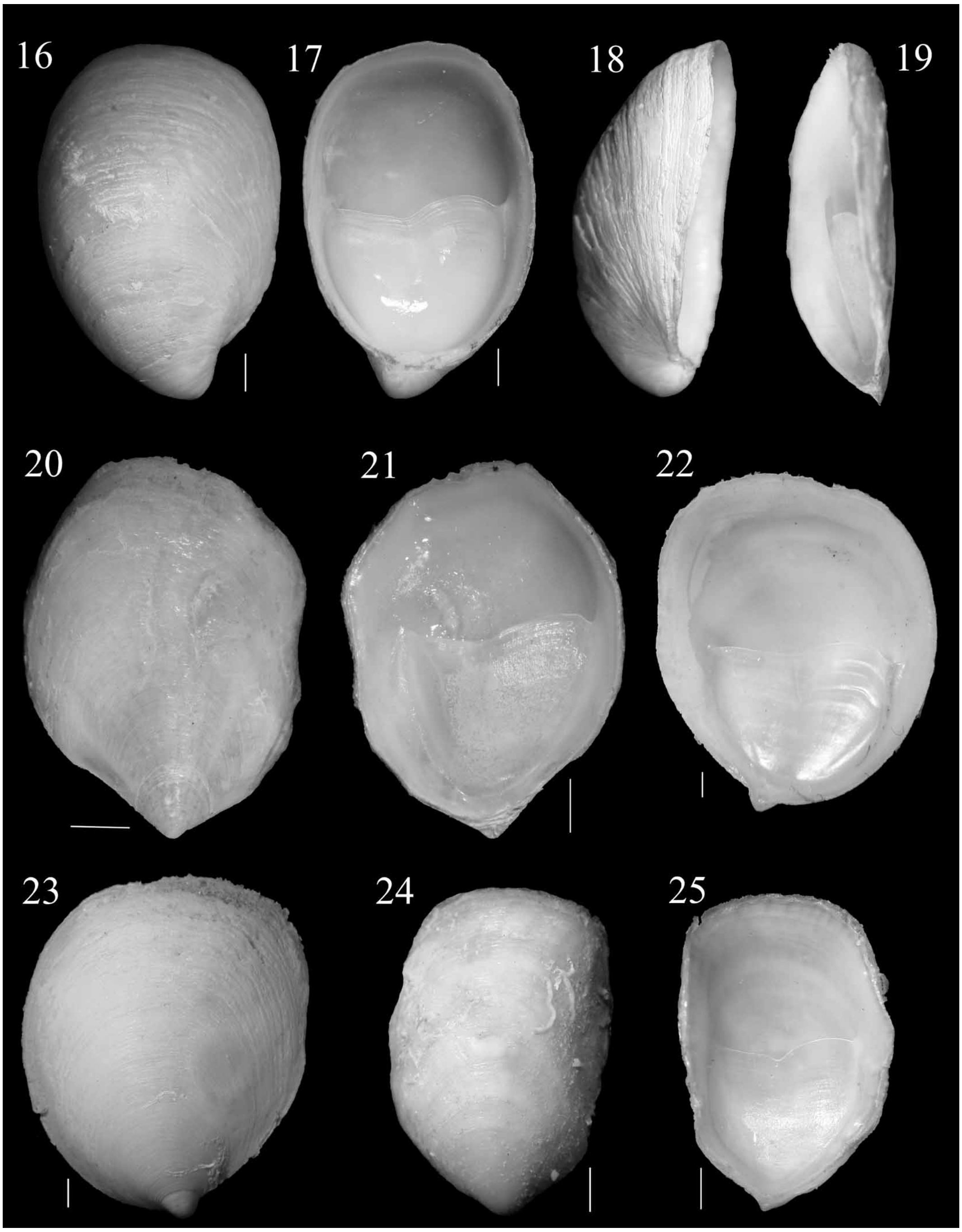
N.B.: The lot ANSP 411047 is 3 shells almost certainly of *C. fornicata*, however, the collect data is URUGUAY; Rocha, La Paloma 34º40S 54º09W (E. Duarte leg iii/1959). It is possible that some change of data happened and this species does not occur in the south Atlantic.

Crepidula cachimilla Cledón, Simone & Penchaszadeh (2004)

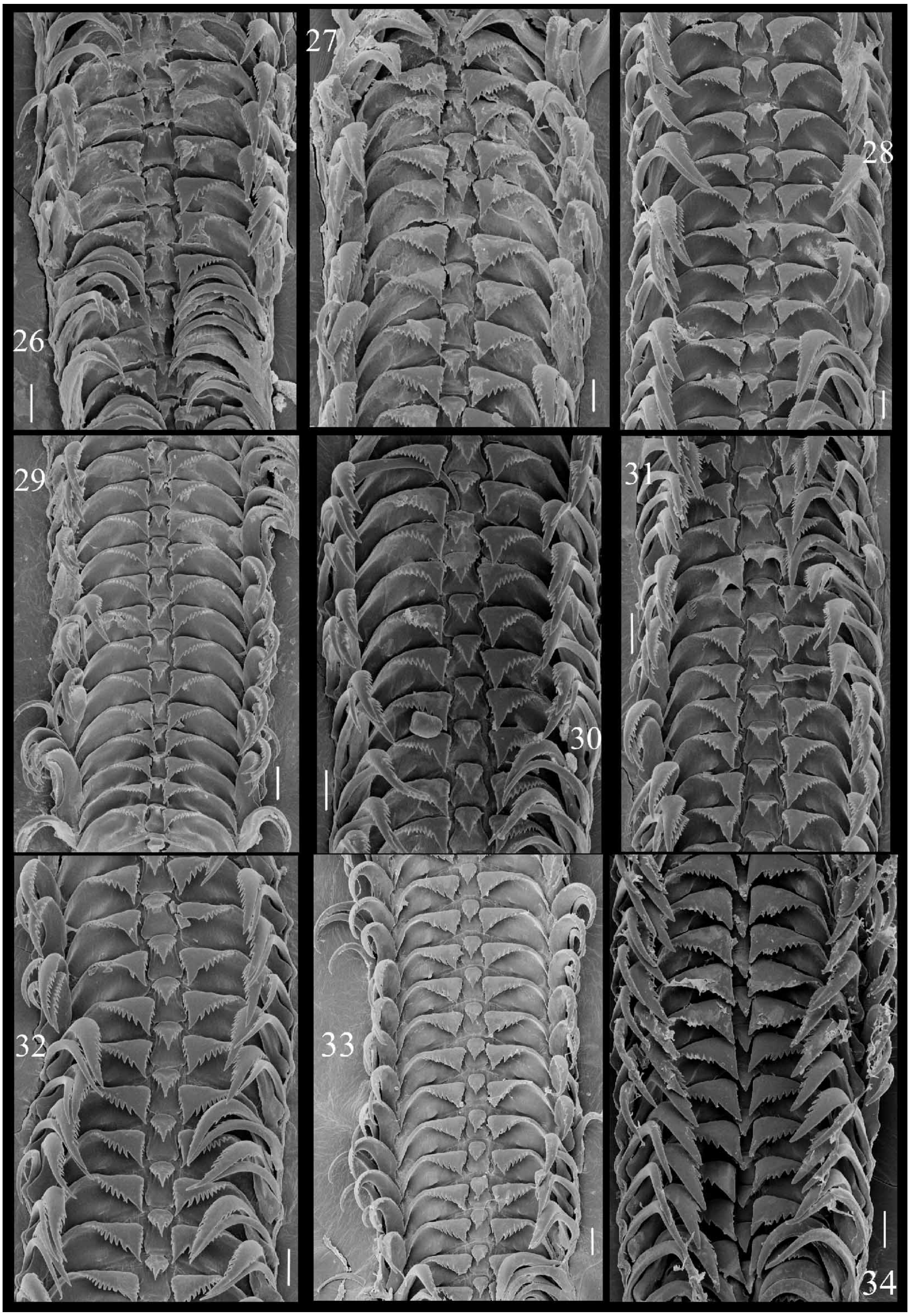
The anatomical description provided by Cledón, Simone & Penchaszadeh (2004) is appropriate. All descriptive and taxonomic treatment is given in that paper.



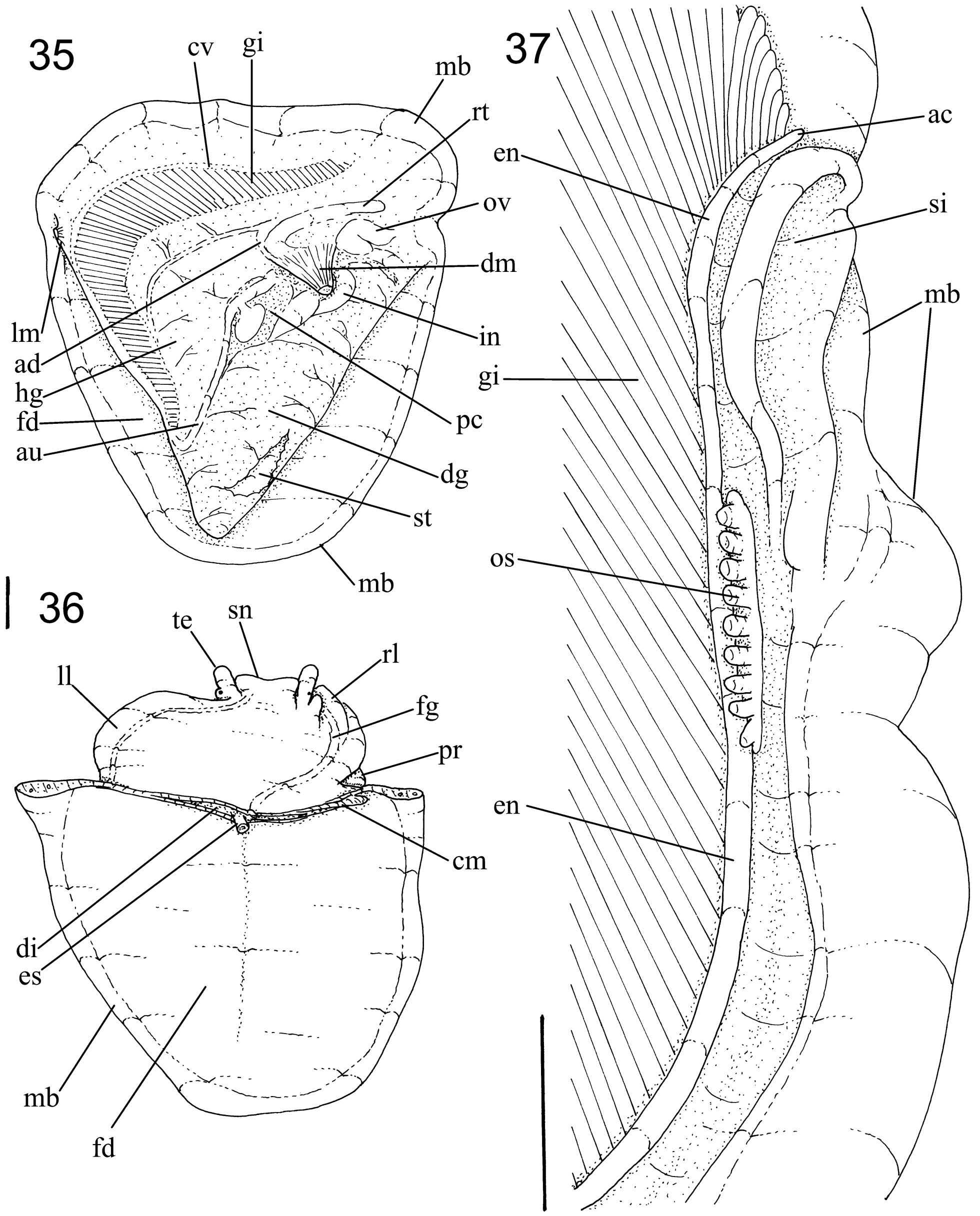
FIGURES 1–15, Shells. Figs.1–2: *Crepidula plana*, dorsal and ventral views, MZSP 36327. Fig.3:4: *C. atrasolea*, dorsal and ventral views, MZSP 36328. Figs.5–6: *C. depressa*, dorsal and ventral views, MZSP 36326. Figs.7–9: *C. pyguaia*, dorsal, ventral views and detail of the protoconch, MZSP 35831 (Holotype). Figs.10–12: *C. margarita*, MZSP 36329, dorsal, central and right views. Fig.13–15: *C. intratesta*, MZSP 30791 (Holotype), left, dorsal and ventral views. Scale bars = 2 mm.



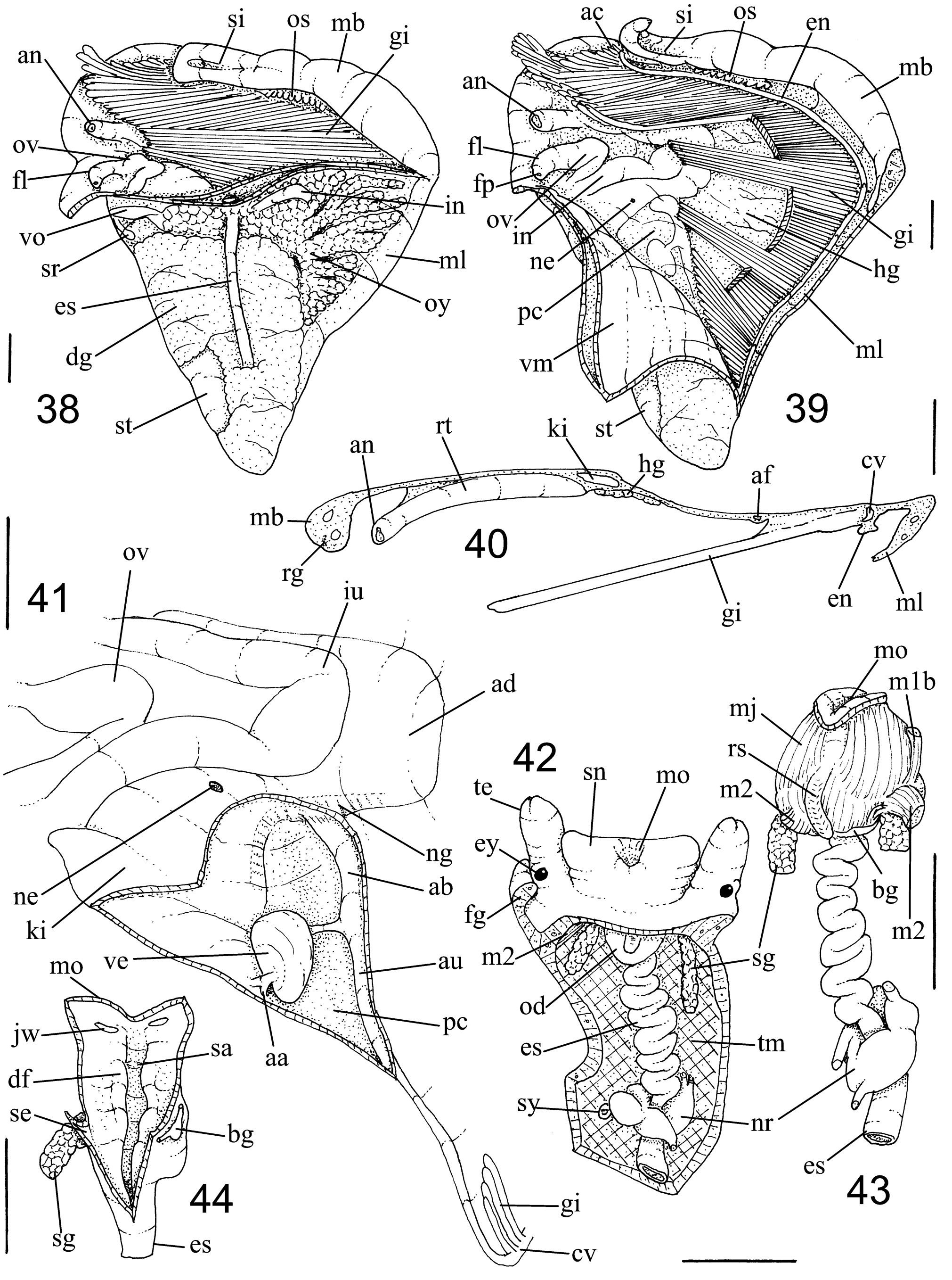
FIGURES 16–25, Shells. Figs.16–18: *Crepidula protea*, MZSP 30780, dorsal, ventral and right views. Figs. 19–21: *C. glauca*, MZSP 30810, left, dorsal and ventral views. Fig. 22–25: *C. carioca*. Figs. 22–23: Holotype, ventral and dorsal views. Figs. 24–25, paratype 1, MNRJ 7464, dorsal and ventral views. Scale bars = 2 mm.



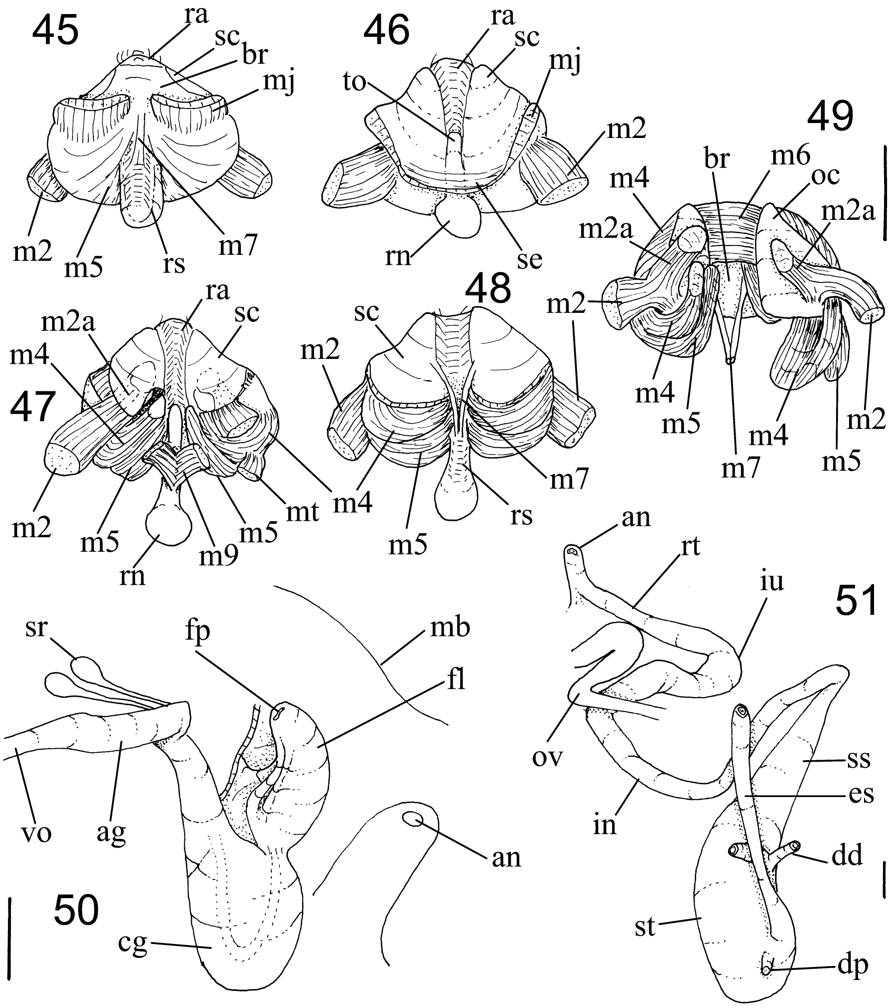
FIGURES 26–34, Radulae in SEM: Figs.26–27: *Crepidula margarita*. Figs. 28–29: *C. plana*. Figs.30–31: *C. atrasolea*. Fig. 32: *C. depressa*. Scale bars = 30 “m, except Fig. 11 = 20 “m. Fig. 33: C. carioca. Fig.34: *C. pyguaia*.



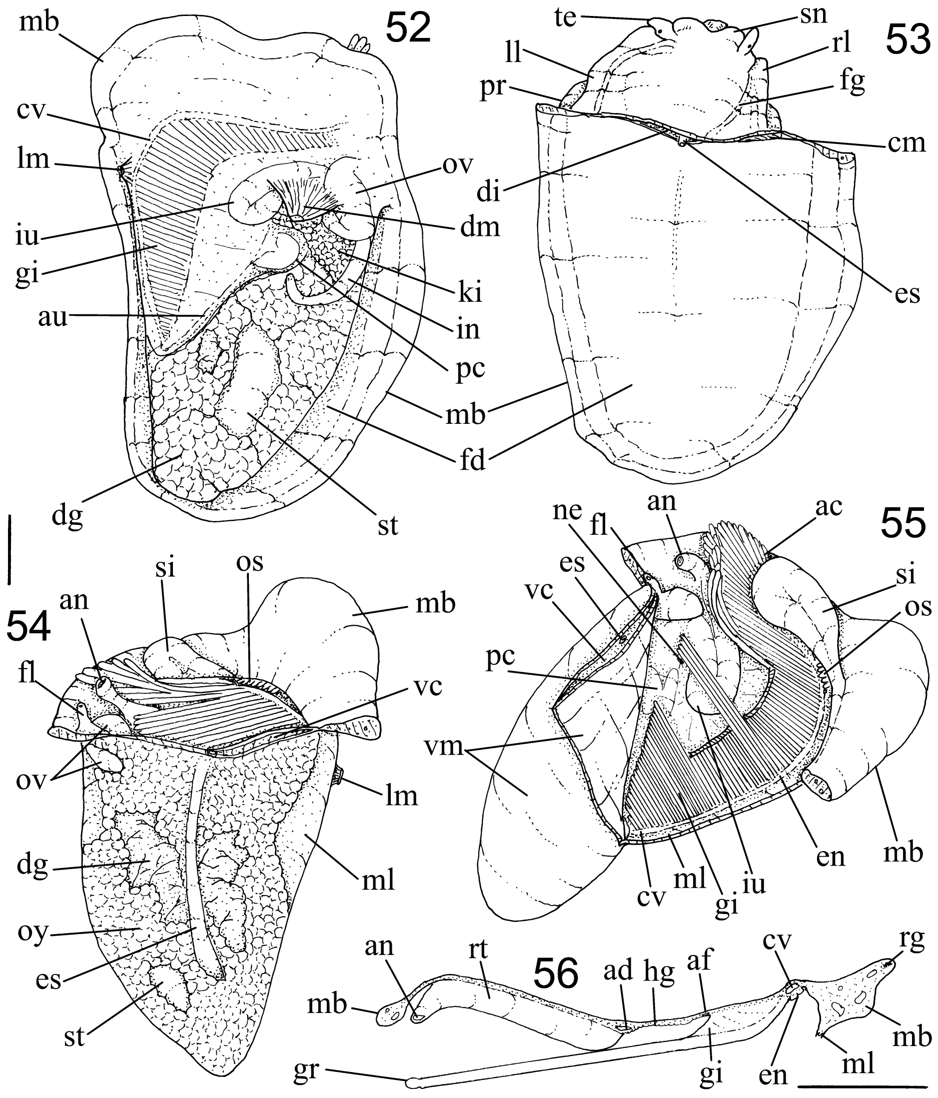
FIGURES 35–37, *Crepidula margarita* anatomy. Fig. 35: whole view of a specimen removed from shell, female, dorsal view. Fig. 36: head:foot, female, dorsal view, pallial cavity and visceral mass removed. Fig. 37: pallial cavity roof, detail of region of osphradium and anterior end of gill, ventral view. Scale bars = 1 mm.



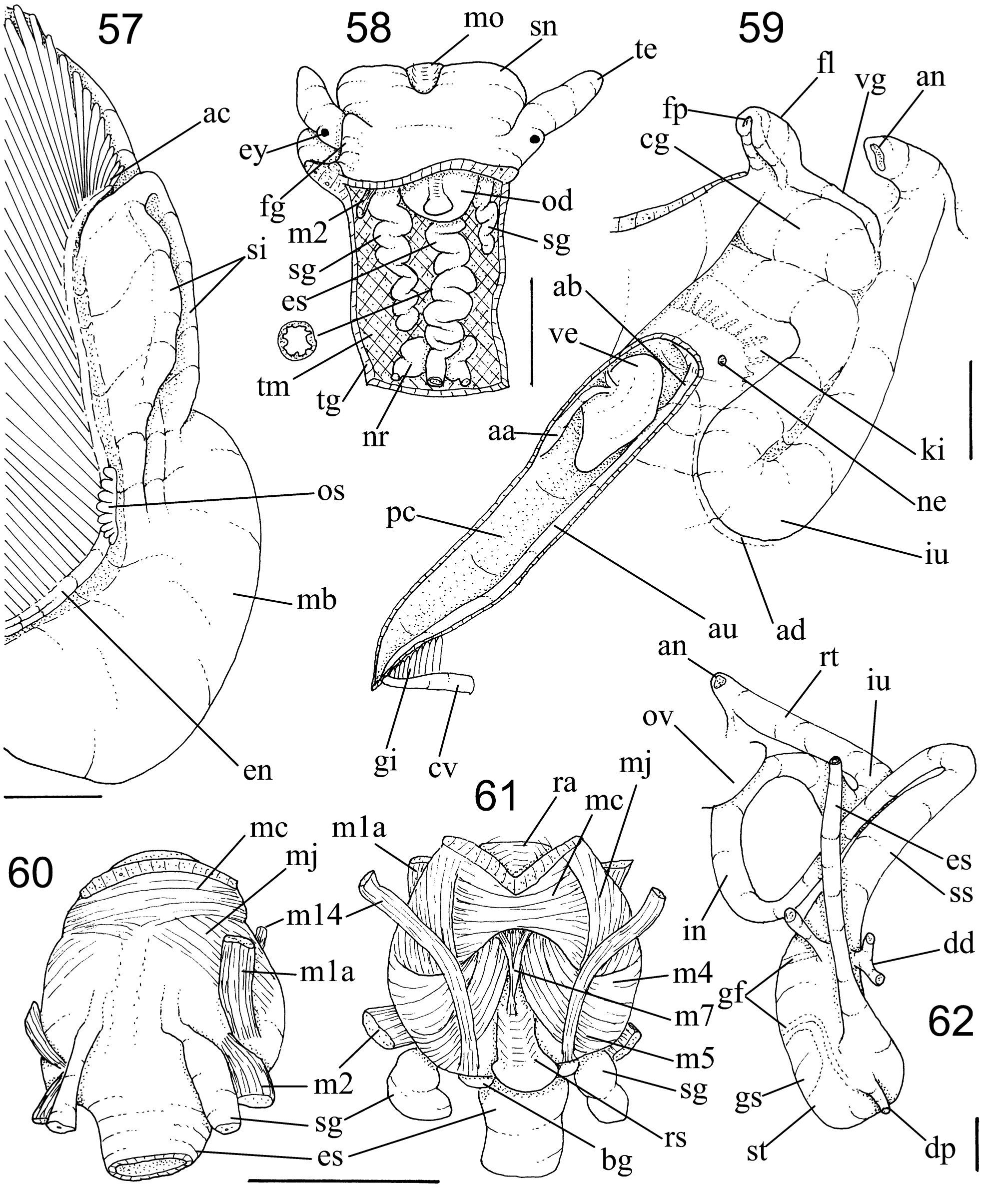
FIGURES 38–44, *Crepidula margarita* anatomy. Fig. 38: visceral mass and pallial cavity separated from head-foot, ventral view. Fig. 39: same, ventral portion of visceral mass (floor of pallial cavity) sectioned longitudinally at left (right in Fig.) and deflected, some portions of gill filaments partially removed, pallial roof exposed. Fig. 40: pallial cavity roof, transversal section tangent to rectum. Fig. 41: visceral mass portion encroaching in pallial roof, ventral view, ventral membrane of pericardium mostly removed, only a short portion of gill shown. Fig. 42: head and haemocoel, ventral view, foot removed. Fig. 43: foregut, ventral-slightly left view, nerve ring shown as in situ. Fig. 44: dorsal portion of buccal mass, ventral view, odontophore removed, anterior esophagus partially sectioned longitudinally and part deflected. Scale bars = 1 mm.



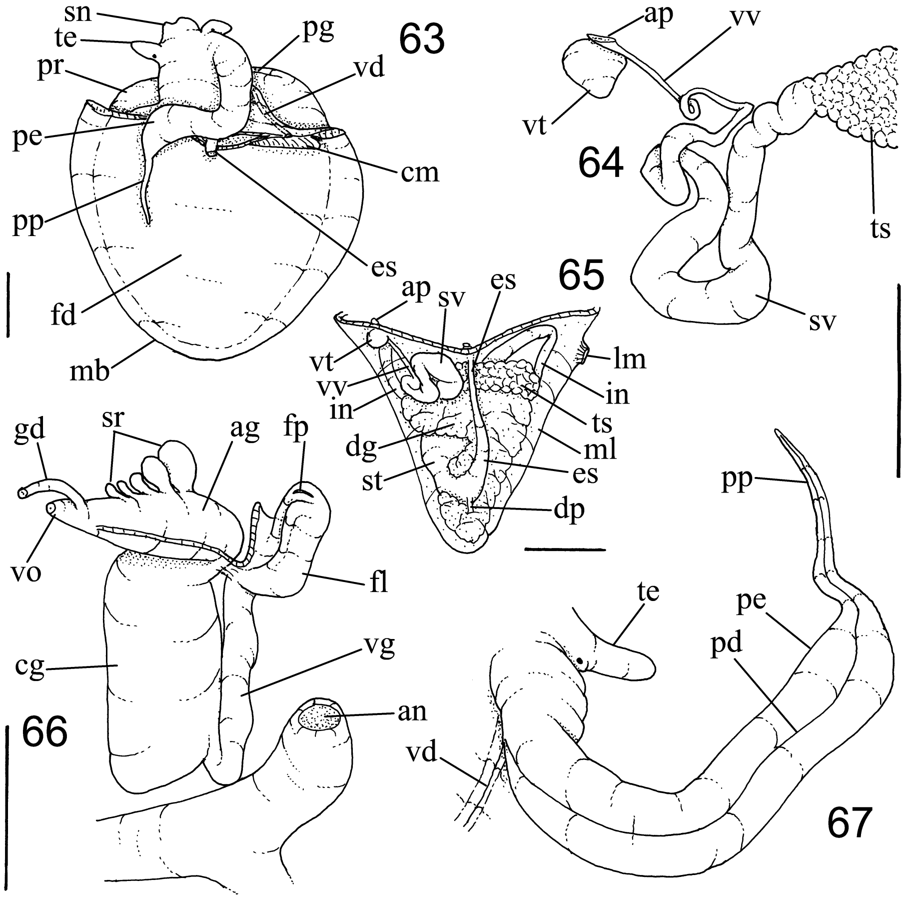
FIGURES 45–51, ***Crepidula margarita*** **anatomy**. Fig. 45: isolated odontophore, ventral view. Fig. 46: same, dorsal view. Fig. 47: same, ventral view, superficial membrane removed, some muscles sectioned transversally, insertion of some muscles shown by transparency. Fig. 48: same, dorsal view. Fig. 49: odontophore, ventral view, subradular membrane removed, both cartilages strongly deflected, right m4 and m5 deflected. Fig.50: pallial oviduct and adjacent structures, ventral view. Fig. 51: digestive tubes as in situ, ventral view, topology of pallial oviduct also shown. Scale bars= 0.5 mm.



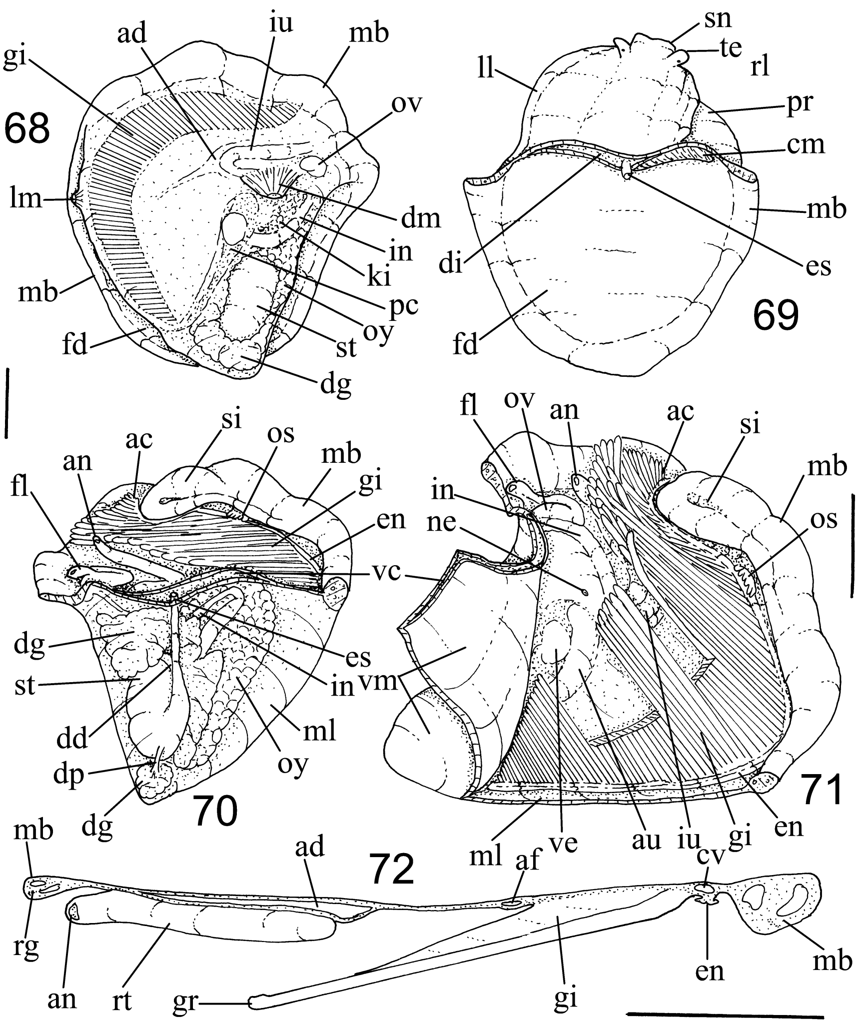
FIGURES 52–56, *Crepidula plana* anatomy. Fig. 52: whole view of a specimen removed from shell, female, dorsal view. Fig. 53: head-foot, female, dorsal view, pallial cavity and visceral mass removed. Fig. 54: visceral mass and pallial cavity separated from head-foot, ventral view. Fig. 55: same, ventral portion of visceral mass (floor of pallial cavity) sectioned longitudinally at left (right in fig.) and deflected, some portions of gill filaments partially removed, pallial roof exposed. Fig. 56: pallial cavity roof, transversal section tangent to rectum. Scale bars = 2 mm.



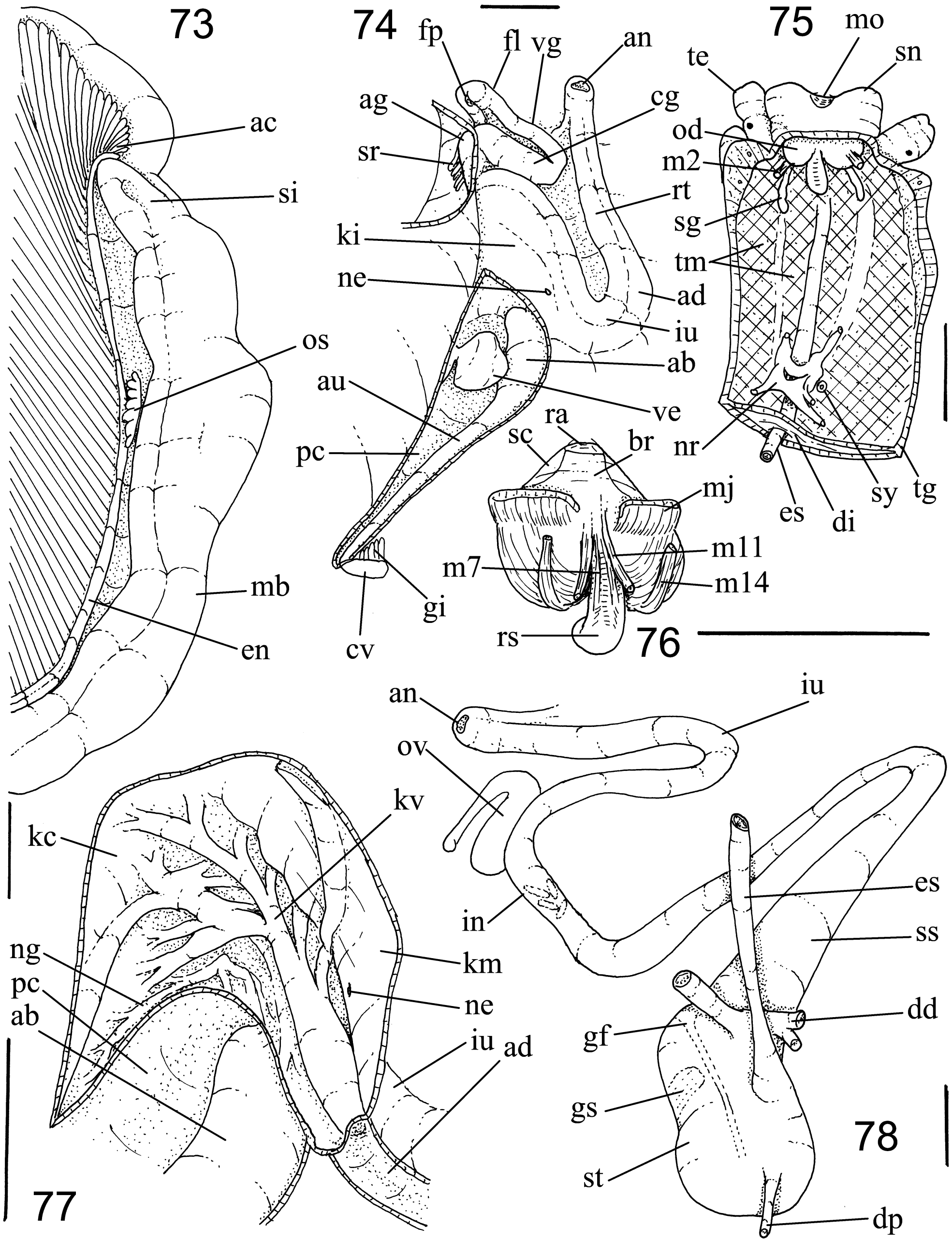
FIGURES 57–62, *Crepidula plana* anatomy. Fig. 57: pallial cavity roof, detail of region of osphradium and anterior end of gill, ventral view. Fig. 58: head and haemocoel, ventral view, foot removed. Fig. 59: visceral mass portion encroaching in pallial roof, ventral view, ventral membrane of pericardium mostly removed, only a short portion of gill shown. Fig. 60: isolated odontophore, dorsal view. Fig. 61: same, ventral view. Fig. 62: digestive tubes as in situ, ventral view, topology of pallial oviduct also shown, some inner gastric structures seen by transparency. Scale bars = 1 mm.



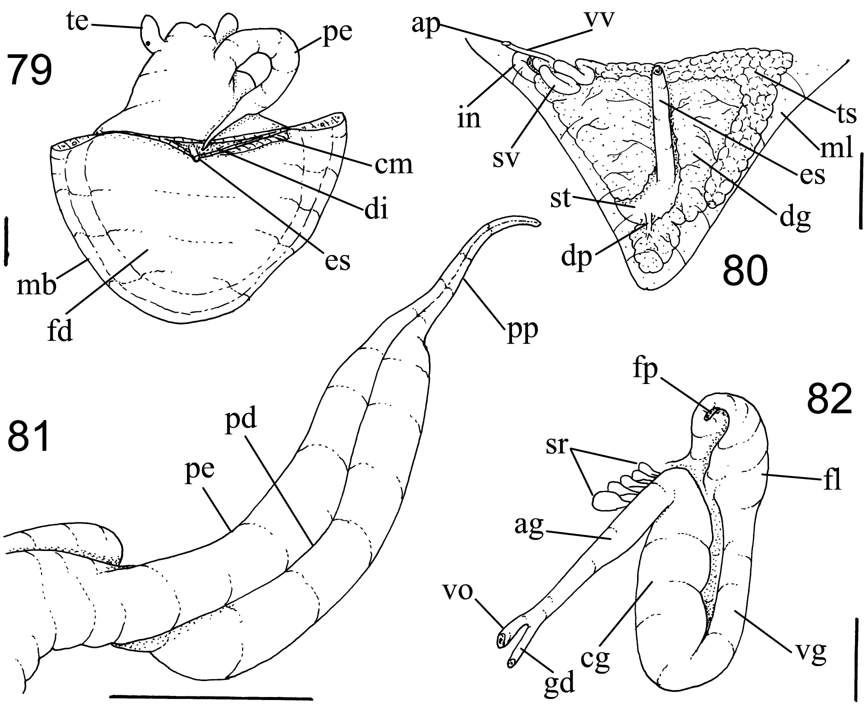
FIGURES 63–67, ***Crepidula plana*** **anatomy**. Fig. 63: head-foot, male, dorsal view, pallial cavity and visceral mass removed. Fig. 64: visceral organs of male genital system, ventral view, seminal vesicle partially uncoiled, remainder as in situ. Fig. 65: isolated visceral mass, male, ventral view, structures seen by transparency. Fig. 66: pallial oviduct and adjacent structures, ventral view. Fig. 67: penis and some adjacent structures, ventral view. Scale bars = 1 mm.



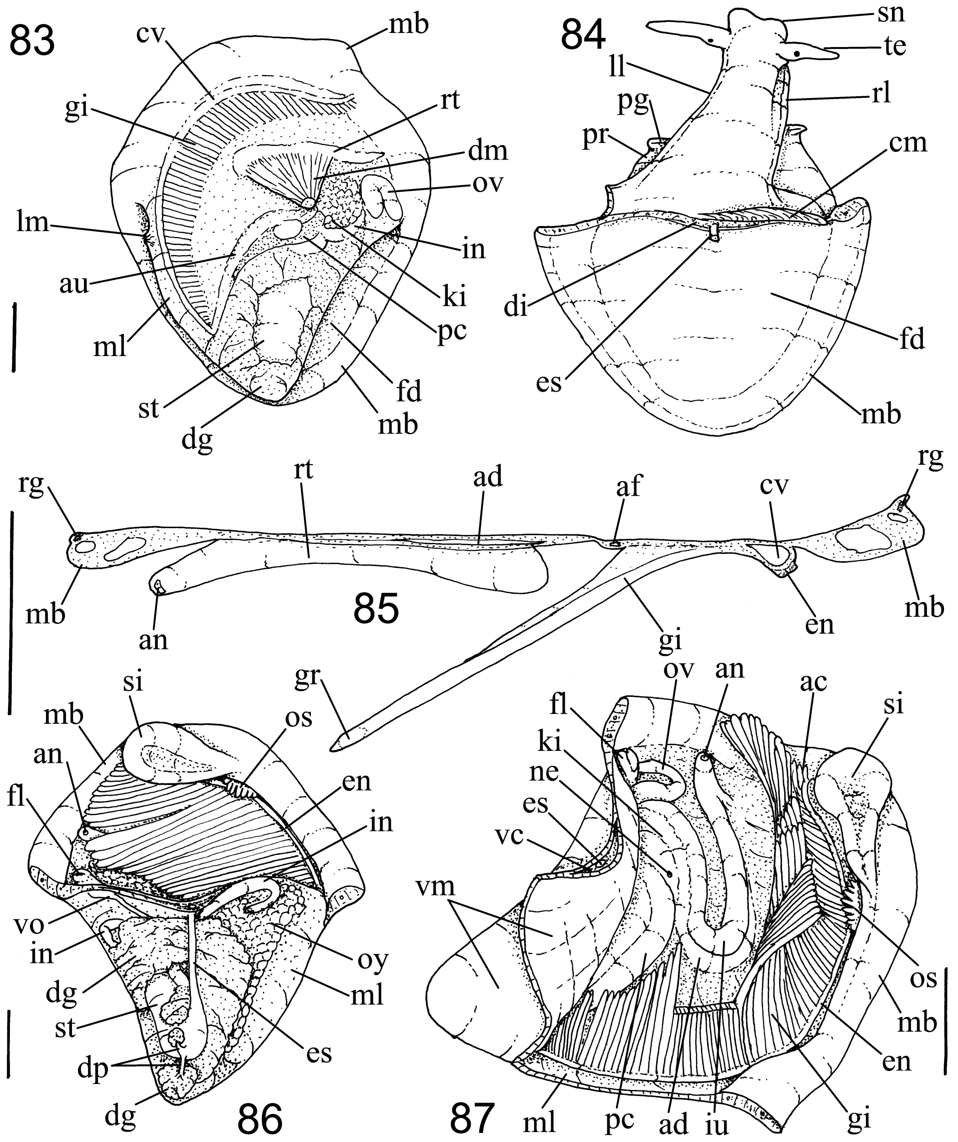
FIGURES 68–72, *Crepidula atrasolea* anatomy. Fig. 68: whole view of a specimen removed from shell, female, dorsal view. Fig. 69: head-foot, female, dorsal view, pallial cavity and visceral mass removed. Fig. 70: visceral mass and pallial cavity separated from head-foot, ventral view. Fig. 71: same, ventral portion of visceral mass (floor of pallial cavity) sectioned longitudinally at left (right in fig.) and deflected, some portions of gill filaments partially removed, pallial roof exposed. Fig. 72: pallial cavity roof, transversal section tangent to rectum. Scale bars = 2 mm.



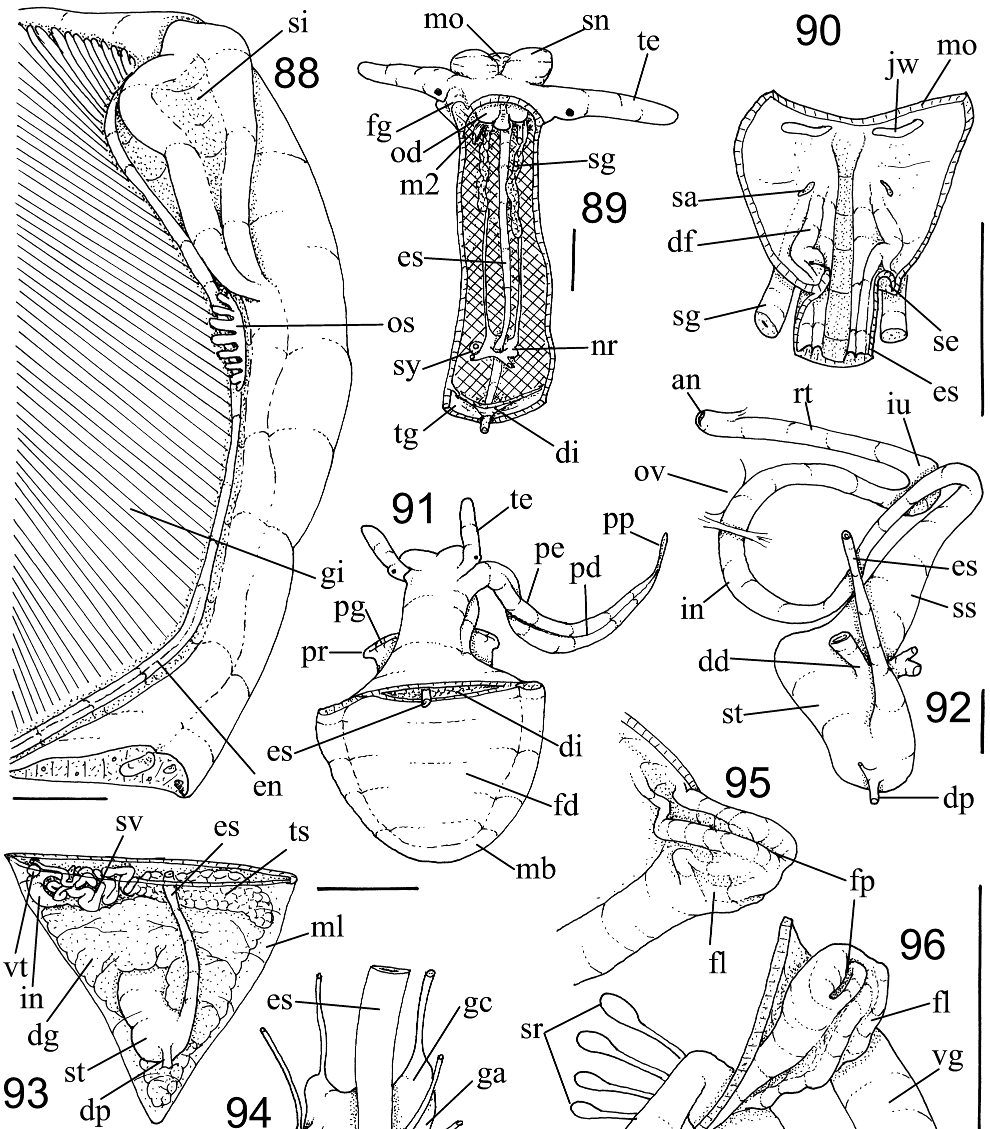
FIGURES 73–78, *Crepidula atrasolea* anatomy. Fig. 73: pallial cavity roof, detail of region of osphradium and anterior end of gill, ventral view. Fig. 74: visceral mass portion encroaching in pallial roof, ventral view, ventral membrane of pericardium mostly removed, only a short portion of gill shown. Fig. 75: head and haemocoel, ventral view, foot removed. Fig. 76: isolated odontophore, ventral view. Fig. 77: visceral mass portion encroaching in pallial roof, ventral view, details of renal area, ventral membrane of pericardium removed, renal ventral wall sectioned longitudinally and deflected, inner structures exposed. Fig. 78: middle and distal digestive tubes, ventral view, seen as in situ, some adjacent structures also shown. Scale bars = 1 mm.



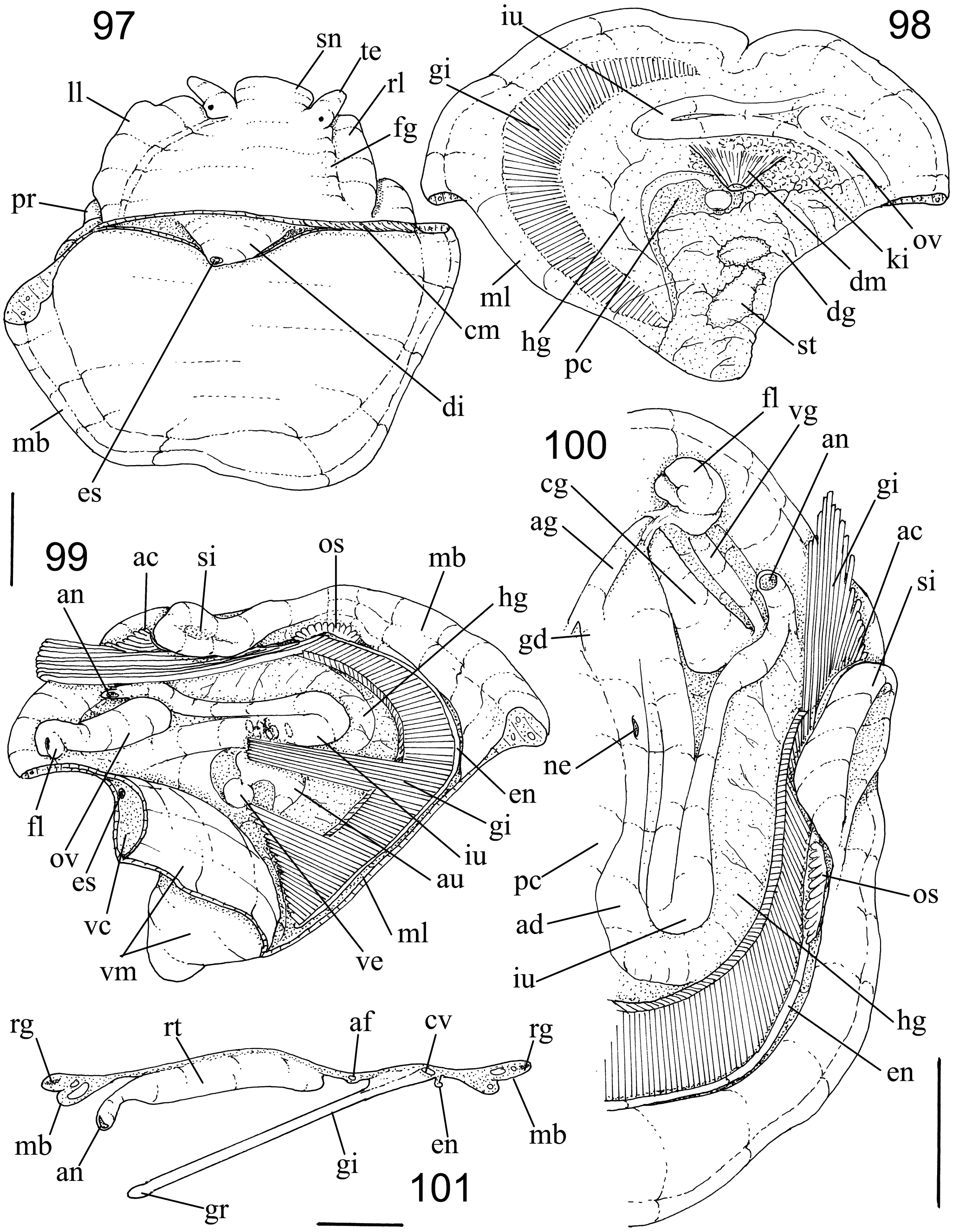
FIGURES 79–82, *Crepidula atrasolea* anatomy. Fig. 79: head-foot, male, dorsal view, pallial cavity and visceral mass removed. Fig. 80: isolated visceral mass, male, ventral view, structures seen by transparency. Fig. 81: penis, ventral view. Fig. 82: pallial oviduct as in situ, ventral view. Scale bars = 0.5 mm.



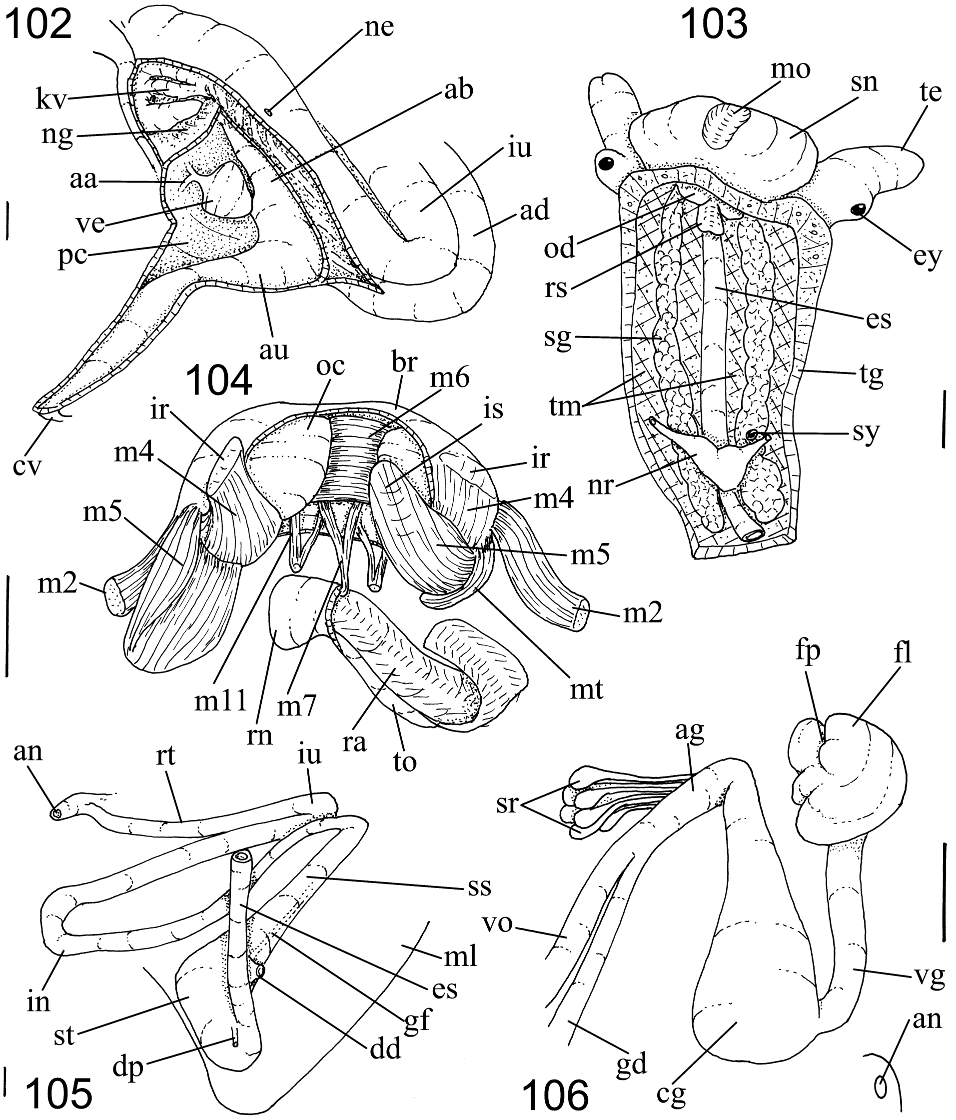
FIGURES 83–87, *Crepidula depressa* anatomy. Fig. 83: whole view of a specimen removed from shell, female, dorsal view. Fig. 84: head-foot, female, dorsal view, pallial cavity and visceral mass removed. Fig. 85: pallial cavity roof, transversal section tangent to rectum. Fig. 86: visceral mass and pallial cavity separated from head-foot, ventral view. Fig. 87: same, ventral portion of visceral mass (floor of pallial cavity) sectioned longitudinally at left (right in Fig.) and deflected, some portions of gill filaments partially removed, pallial roof exposed. Scale bars = 2 mm.



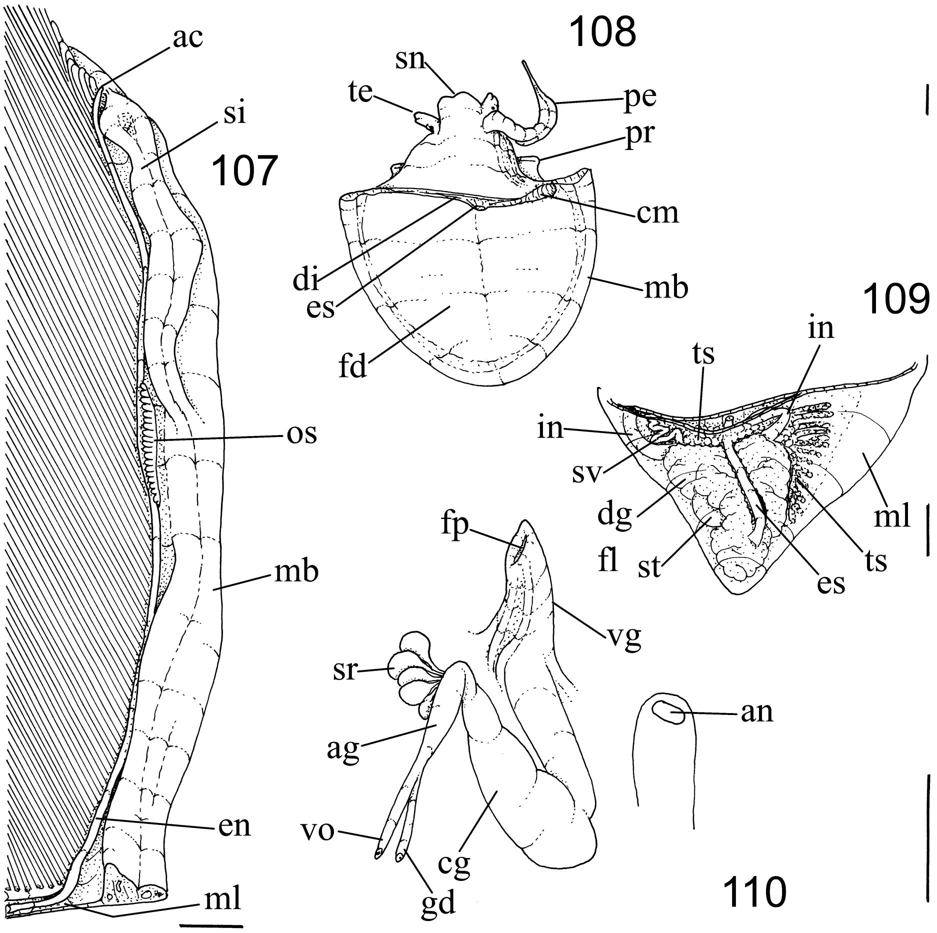
FIGURES 88–96, *Crepidula depressa* anatomy. Fig. 88: pallial cavity roof, detail of region of osphradium and anterior end of gill, ventral view. Fig. 89: head and haemocoel, ventral view, foot removed. Fig. 90: dorsal region of buccal mass, ventral view, odontophore removed, anterior esophagus sectioned longitudinally, inner surface exposed. Fig. 91: head-foot, male, dorsal view, pallial cavity and visceral mass removed. Fig. 92: digestive tubes as in situ, ventral view, topology of pallial oviduct also shown. Fig. 93: isolated visceral mass, male, ventral view, structures seen by transparency. Fig. 94: central nervous system, ventral view, adjacent portion of esophagus also shown, a single statocyst shown. Fig. 95: detail of female genital papilla, posterior view. Fig. 96: pallial oviduct as in situ, ventral view. Scale bars = 1 mm.



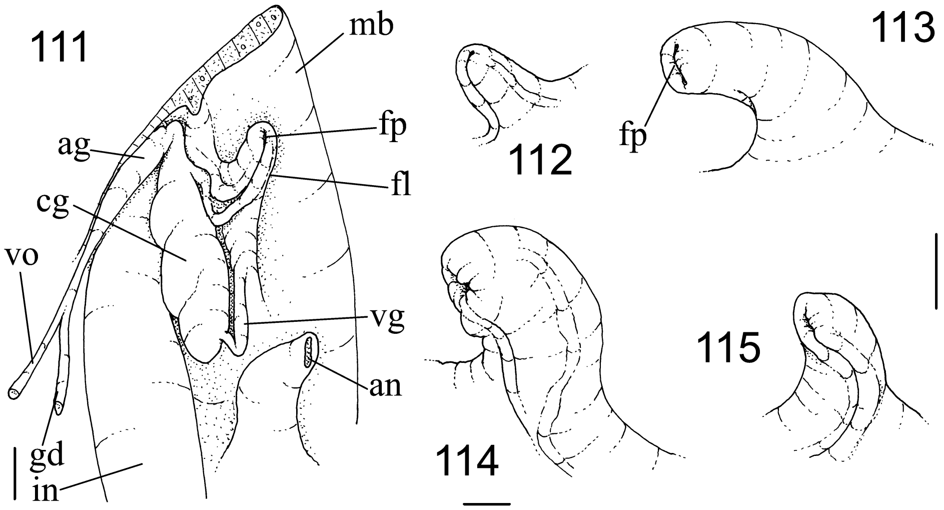
FIGURES 97–101, *Crepidula pyguaia* anatomy. Fig. 97: head-foot, female, dorsal view, pallial cavity and visceral mass removed. Fig. 98: pallial cavity roof and visceral mass, dorsal view, head-foot removed. Fig. 99: visceral mass and pallial cavity separated from head-foot, ventral view, ventral portion of visceral mass (floor of pallial cavity) sectioned longitudinally at left (right in Fig.) and deflected, some portions of gill filaments partially removed, pallial roof exposed. Fig. 100: pallial cavity roof, detail of region of osphradium and anterior end of gill, ventral view. Fig. 101: pallial cavity roof, transversal section tangent to rectum. Scale bars = 2 mm.



FIGURES 102–106, *Crepidula pyguaia* anatomy. Fig. 102: visceral mass portion encroaching in pallial roof, ventral view, ventral membrane of pericardium removed, renal ventral wall sectioned longitudinally and deflected, inner structures exposed. Fig. 103: head and haemocoel, ventral view, foot removed. Fig. 104: odontophore, ventral view, both cartilages deflected, left m5 deflected, radular ribbon removed and deflected downwards. Fig. 105: digestive tubes as in situ, ventral view, topology visceral mass shown. Fig. 106: pallial oviduct as in situ, ventral view, topology of anus also shown. Scale bars = 0.5 mm.



FIGURES 107–110, *Crepidula carioca* anatomy. Fig. 107: pallial cavity roof, detail of region of osphradium and anterior end of gill, ventral view. Fig. 108: head-foot, male, dorsal view, pallial cavity and visceral mass removed. Fig. 109: isolated visceral mass, male, ventral view, structures seen by transparency. Fig. 110: pallial oviduct as in situ, ventral view, topology of anus also shown. Scale bars = 1 mm.



FIGURES 111–115, Female genital structures. Fig. 111: *Crepidula protea*, detail of pallial oviduct, ventral view, adjacent structures also shown, genital papilla somewhat deflected. Figs. 112–115: detail of genital papilla, ventral-slightly left view: Fig. 112: *C. intratesta*. Fig. 113: *C. glauca*. Fig. 114: *C. fornicata*. Fig. 115: *C. argentina*. Scale bars = 0.25 mm (Fig. 112, same scale than 113).

Discussion of the characters

Shell

1. Shell color in larger specimens: 0= brownish; 1= whitish (*C. intratesta, C. plana, C. atrasolea, C. depressa, C. pyguaia, C. carioca*); 2= with narrow spiral bands (*C. margarita, C. glauca*) (CI= 0.5; RI= 0.6, not additive).

2. Spiral bands in early development: 0= weak or continuous; 1= interrupted (*C. margarita, C. glauca*) (CI= 1; RI= 1).

The shell color is naturally variable in all species, however, in those above mentioned, there is a clear tendency to the pure white, a rare tendency in the other species. Nevertheless, it is possible to found some specimens of above mentioned species with some scarce radial bands, mainly in the young ones. This is the reason for separating the color pattern into two characters. The character 1 refers to the presence of spiral bands in large specimens (mature females normally), which sometimes are present in young specimens of those species that are coded as having state 1, but disappear along the growth. On the other hand, all specimens that have spiral bands, have them continuous in the early development, including those listed in the character 2. The bands become interrupted (irregularly dotted) further, allowing as a separated phenomenon.

3. Shell form: 0= weakly spiral; 1= unguiform (all) (CI= 1; RI= 1).
The closer outgroup, *B. aculeatus*, has not the same degree of spiralization of the remaining, non-*Crepidula* calyptraeoideans, as have been demonstrated in Simone (2002). However, the ingroup species reduced still more the spiralization if compared with *B. aculeatus*, becoming almost symmetrical.

4. Periostracum: 0= thick; 1= deciduous (all except *C. pyguaia, C. carioca*) (CI= 0.5; RI= 0.5).

A hairy periostracum is one of the calyptraeoideans synapomorphy (Simone 2002). However, most ingroup species have a deciduous periostracum, hardly present only in the younger portion of the shell, surrounding the aperture.
According to the result, the loss of the periostracum is one of the ingroup synapomorphy, reverting in *C. pyguaia*.

5. Shell septum left notch: 0= very shallow; 1= well marked (all); 2= deep (*C. intratesta, C. protea*); 3= shallow, but associated to a very thin, transparent shell (*C. margarita, C. glauca*) (CI= 1; RI= 1; not additive).

The shell septum has a well-marked notch in the left side in the ingroup species, particularly deep in *C. intratesta* and *C. protea*. The ventral septum of *B. aculeatus* has a very shallow notch, as well as other Pacific species I have examined.

It is possible to consider this character in an additive optimization, based on the ontogeny, since the very young specimens of both listed species have a shallower notch. Notwithstanding, both kinds of optimization nothing change in the results or in the indices.

Head-foot

6. Ommatophore: 0= present; 1= absent (*C. intratesta, C. protea, C. atrasolea, C. depressa*) (CI= 0.5; RI= 0.66).

Ommatophore is defined as a small stalk for the eye, keeping it somewhat away from the tentacle axis. An ommatophore, even very short, is characteristically present in the calyptraeoideans (Simone 2002), and absent, as an apomorphy, in above listed species.
According to obtained cladogram, the state 1 is a convergence between the nodes 7 and 10.

7. Tentacles: 0= simple; 1= bifid (*C. intratesta, C. protea, C. fornicata, C. margarita, C. atrasolea, C. pyguaia, C. carioca, C. cachimilla*) (CI= 0.25; RI= 0).
The here called “bifid” tentacles is mainly notable in the retracted condition, and is marked by a shallow furrow dividing the tentacle tip in the middle portion.

8. Foot thickness: 0= thick, form cylindrical, thickness equivalent to half of shell dorso-ventral height; 1= very thin, form flat, thickness equivalent to 1/5 of shell dorso-ventral height (all) (CI= 1; RI= 1).

The larger portion of the foot of the ingroup species is a somewhat thin platform, thinner than the homologous portion of the outgroups.

9. Columellar muscle: 0= developed, part attached to shell dorsal surface; 1= very small, almost absent, only attached to shell septum edge (all except *C. cachimilla*) (CI= 1; RI= 1).

The columellar muscle of the *Crepidula* species is very reduced, its homology with the columellar muscle is suggested by the previous comparative analysis (Simone 2002). *Bostrycapulus aculeatus* has it already reduced, but still discernible. In the ingroup species, however, it is still more reduced, hardly visible except for a thin muscular layer connected to the right edge of the shell septum. After all, the younger specimens of these species present a larger columellar muscle.

10. Dorsal shell muscle: 0= thick; 1= thin, reduced (all except *C. cachimilla*); 2= absent (*C. glauca*) (CI= 1; RI= 1; additive).

The small dorsal shell muscle has been demonstrated to be also evolved from the columellar muscle (Simone 2002). It keeps a small scar inside the shell cavity produced by the septum, dorsal, in level of the septum edge.

The additive optimization is based on comparison, as suggestion in being a single evolutionary strain towards the loss of the muscle, however, if considered not additive nothing changes (result or indices).

Pallial organs

11. Approximate length of pallial cavity in relation to visceral mass: 0= 60%; 1= 75% (*C. glauca, C. fornicata, C. margarita, C. plana, C. atrasolea, C. depressa, C. pyguaia*); 2= 90% (*C. intratesta, C. protea, C. argentina, C. carioca*) (CI= 0.50; RI= 0.33; additive).

There is a clear tendency in the ingroup species for increasing the length of the pallial cavity, if compared with the calyptraeoideans outgroups. Although, some of them are also filter feeding organisms.

The state 1 revealed to be one of the ingroup synapomorphy, passing to the state 2 in *C. argentina*, *C. carioca* and node 7 as convergence. The additive optimization is based on the ontogeny, since the very young specimens present a shorter pallial cavity. It becomes proportionally longer during the animals growth. However, the result and indices are the same if the optimization is not additive.

12. Siphonal fold: 0= restrict to a median portion; 1= extending towards left by mantle border (all except *C. cachimilla*) (CI= 1; RI= 1).

13. Siphonal fold: 0= protruding left; 1= not protruding left (*C. intratesta, C. protea*) (CI= 1; RI= 1).

The special fold of the mantle border in the middle portion of the pallial cavity aperture, also called food pouch, is mostly probably homologous to the siphon present in remaining calyptraeoideans and caenogastropods (Simone 2002). It is an auxiliary structure in the ciliar flow of the filter feeding activity. The two characters explored above (11 and 12) are based on differences with *B. aculeatus*.

14. Osphradium: 0= bipectinate; 1= monopectinate (all) (CI= 1; RI= 1).

15. Osphradium length: 0= more than half of pallial cavity aperture; 1= about 15% of pallial cavity aperture (all); 2= 5% of pallial cavity aperture (*C. glauca, C. plana, C. atrasolea, C. depressa*) (CI= 0.66; RI= 0.66; additive).

The additive optimization is based on ontogeny, since the very young specimens have respectively the preceding states, i.e., a proportionally longer osphradium. If considered non-additive the indices and the result are the same.

The state 2 has two equally parsimonious optimizations, as a node 8 synapomorphy with a reversion (to state 1) in *C. margarita*, or a convergence between *C. glauca* and the node 10, the first hypothesis is shown in Figure 116.

16. Osphradium filaments attachment: 0= partially to adjacent mantle; 1= only to osphradium ganglion, projected ventrally (all) (CI= 1; RI= 1).

The osphradia of the ingroup species are different fashioned in relation to those of remaining calyptraeoideans, including *B. aculeatus*, not only in being monopectinate (character 13), but also in having a different form of the filaments. They are digitiform, cylindrical, with tip rounded, decreasing gradually towards both ends.

17. Number of osphradium filaments: 0= thousand; 1= about 20 (*C. intratesta, C. protea, C. fornicata, C. argentina, C. carioca, C. cachimilla*); 2= less than 10 (*C. glauca, C. margarita, C. plana, C. atrasolea, C. depressa, C. pyguaia*) (CI= 0.66; RI= 0.8; additive).

The additive optimization is based on ontogeny, since the number of osphradium filaments increases with the animals growth. The present character is only concerned with mature female specimens. If considered not additive, the resulted cladogram is the same, from the indices, only RI changes to 0.75.

18. Osphradium filaments: 0= close from each other; 1= somewhat separated (*C. glauca, C. margarita*) (CI= 1; RI= 1).

The analysis of the osphradium characters (13–17) shows a tendency towards a reduction and a different fashioned structure (both explained above). The ingroup osphradium, in fact, is the most conspicuous anatomical feature of the taxon, showing great difference in relation to remaining calyptraeoideans, as well as the caenogastropods. Nevertheless, the osphradium constitution of other *Crepidula* species is still unclear, precluding any further analysis with the species studied herein.

19. Endostyle: 0= simple; 1= double in middle and posterior thirds (*C. plana, C. atrasolea, C. depressa*) (CI= 1; RI= 1).

20. Endostyle: 0= narrow; 1= covering ctenidial vein (*C. margarita, C. plana, C. atrasolea, C. depressa*); 2= running in lateral surface of mantle (*C. carioca*) (CI= 1; RI= 1; not additive).

The presence of the endostyle was further discussed in the preceding paper (Simone 2002). It is a glandular ridge surrounding the left edge of the gill, possibly helping in the extra necessity of mucus production, for filter feeding. The ingroup species present two characters (18, 19) suitable for comparative analysis, both resulting synapomorphy respectively of the node 10 and 8.

21. Hypobranchial gland: 0= slightly hick; 1= very thin (all) (CI= 1; RI= 1).

Contrasting with the presence of the endostyle, the hypobranchial gland, which is located in the opposite side of the gill in relation to endostyle, is very thin, almost absent in the ingroup species. This reduction is one of the ingroup synapomorphies.

Circulatory and excretory systems

22. Pericardium sudden narrowing in its left half: 0= absent; 1= present (*C. margarita, C. pyguaia, C. carioca*) (CI= 0.5; RI= 0.5).

The normal fashion of the pericardium, which in the calyptraeoideans is already a highly modified structure, is of a long, cylindrical tube. The presence of a middle constriction in above mentioned species was interpreted as homologous. However, the state 1 resulted as 2 convergences between node 4 and *C. margarita*.

23. Number of renal lobes: 0= 2; 1= 1 (all) (CI= 1; RI= 1).

24. Nephridial gland; 0= with transversal folds; 1= irregular, mostly longitudinal folds (all except *C. cachimilla*) (CI= 1; RI= 1).

25. Nephrostome: 0= protected inside by a glandular fold from real lobe; 1= no close fold protecting it (all) (CI= 1; RI= 1).

The ingroup species show a clear tendency to decreasing the kidney, reflecting in its morphology. These aspects were explored in the characters 22 to 24.

26. Adrectal sinus: 0= separated from kidney by a membrane; 1= continuous to kidney (all except *C. cachimilla*) (CI= 1; RI= 1).

27. Connection of adrectal sinus with kidney: 0= inconspicuous; 1= surrounding intestine (*C. argentina, C. margarita, C. plana, C. atrasolea, C. depressa, C. pyguaia, C. carioca,*

C. cachimilla); 2= separated from intestine (*C. intratesta, C. protea, C. fornicata*) (CI= 1; RI= 1; not additive).

The adrectal sinus is a hollow pallial region running along rectum. The blood inside caenogastropods adrectal sinus normally flows towards kidney, however frequently there is separation between both by a permeable septum. The ingroup species, unlike this normal fashion, no septum separating both is found, representing another ingroup synapomorphy (character 25). The species reunited by the node 6 additionally modified the condition to a separated vessel, running slightly away from the rectum.

Digestive system

28. Radular lateral tooth basal cusp: 0= low; 1= well marked (*C. plana, C. depressa, C. atrasolea*) (CI= 1; RI= 1).

The increment of the lateral tooth basal pair of cusps shown as another synapomorphy of the node 10.

29. Radular inner marginal tooth: 0= sharp pointed tip; 1= blunt pointed tip (*C. intratesta, C. protea*) (CI= 1; RI= 1).

Several radular characters were researched, but all them, but the two above (27, 28), resulted autapomorphic and were omitted. The general aspect of the ingroup radula is very similar, as well as of the closer outgroups, and, consequently, with weak comparative interest.

30. M11: 0= present; 1= absent (*C. fornicata, C. intratesta, C. protea, C. glauca, C. margarita, C. plana, C. depressa*) (CI= 0.5; RI= 0.75).

This character represents the single extracted from the odontophore muscles, which presented conservative. The m11 is the pair of ventral tensor muscle of the radula, its presence is plesiomorphic. Its loss showed as a convergence between the node 5 and *C. glauca*, being further reversed by *C. atrasolea*.

31. Length of salivary gland: 0= about same of haemocoel (*C. pyguaia, C. cachimilla*); 1= less than half of haemocoel (*C. intratesta, C. protea, C. glauca, C. fornicata, C. margarita, C. atrasolea, C. depressa*) (CI= 0.5; RI= 0.8).

32. Salivary gland form: 0= broad; 1= slender (all); 2= filiform, small (*C. atrasolea, C. depressa*) (CI= 1; RI= 1; additive).

The salivary gland of the ingroup species is very different from that of *B. aculeatus*. It is long and narrow, running along the haemocoel, parallel to the esophagus. Two most important differences are explored in the above characters (30, 31). The states of the character 31 are considered additive, as a single tendency of simplification and reduction of the structures. If they are considered not additive nothing changes (result and indices).

33. Stomach posterior duct to digestive gland: 0= bifurcating shortly; 1= long, narrow simple in base (all except *C. fornicata, C. argentina, C. depressa, C. cachimilla*) (CI= 0.33; RI= 0.5).

The posterior duct to digestive gland in the stomach is very reduced in the ingroup species. The closer outgroup, *B. aculeatus*, in fact lost it. The polarization of this character was, then, based on the other calyptraeoideans, as the loss of the posterior duct to the digestive gland is a *B. aculeatus* autapomorphy (Simone 2002). The normal fashion of the posterior duct is highly dichotomic, some of the ingroup species, however, have it modified to a long and narrow duct, running towards posterior.

34. Intestinal U-shaped portion exposed in pallial cavity: 0= short (far from stomach anterior end); 1= long (close to stomach anterior end) (all except *C. margarita, C. depressa*) (CI= 0.33; RI= 0).

The polarization of this character is based on the condition found in *B. aculeatus*, in such U-shaped intestinal portion in the pallial cavity is shorter. According to the cladogram, the state 1 is one of the ingroup synapomorphies, being further reverted in the above listed species.

Genital system

35. Penis distal papilla: 0= broad (about half of penis width) and short; 1= long, slender, filiform (*C. intratesta, C. protea, C. fornicata, C. argentina, C. plana, C. atrasolea, C. depressa, C. carioca, C. cachimilla*) (?= *C. margarita, C. pyguaia*) (CI= 1; RI= 1).

36. Coiling of seminal vesicle: 0= intense (about 1/10 of visceral mass); 1= weak (about 1/20 of visceral mass) (all except *C. cachimilla*) (CI= 1; RI= 1).

This is the only character of the male genital system suitable for comparative analysis, however, no male of *C. margarita* and *C. pyguaia* was examined.

37. Number of seminal receptacles: 0= 8–10 (*C. pyguaia, C. glauca*); 1= 7–6 (*C. fornicata*); 2= 5 (*C. atrasolea, C. plana, C. carioca, C. cachimilla*); 3= 3–4 (*C. intratesta, C. protea, C. argentina, C. depressa*); 4= 2 (*C. margarita*) (CI= 0.5; RI= 0.2; not additive).

The states of this character are standardized according to the mature female average number of seminal receptacles. However, it was observed that the number of receptacles varies little in each species, making the states division sufficiently secure for the presented analysis. Although considered not additive, the analysis of the allocation of the states in the cladogram shows a general tendency to a reduction of the number of seminal receptacles in the ingroup species.

38. Seminal receptacles: 0= distributed along albumen gland; 1= united in a single region (*C. glauca, C. pyguaia, C. margarita, C. fornicata, C. carioca*) (CI= 0.33; RI= 0.5).

39. Seminal receptacles duct: 0= long, slender; 1= short, broad (*C. argentina, C. plana*) (CI= 0.5; RI= 0).

The female seminal receptacles characters (35–37) are polarized according to the condition found in *B. aculeatus*, as well as those of remainder calyptraeoideans.

In the character 37, the state 1 resulted as two convergent autapomorphies between both listed species.

40. Vaginal tube: 0= absent; 1= present very short (*C. margarita*); 2= long (remainder) (CI= 0.66; RI= 0; additive).

The vaginal tube is another exclusive feature of the ingroup, modifying the V-shaped fashion of the pallial oviduct (the pore is located in the vertex of this “V”) found in the other calyptraeoideans, including *B. aculeatus*. The fashion of the ingroup oviduct is N-shaped, with the pore located at the end. The additive optimization is because of ontogeny, in such immature specimens present a short vaginal tube. However, the result is the same if the states are optimized as not additive, both indices, however, change to 100. Two of the indices of the cladogram also change, the length becomes 88 and the CI 0.67. In fact, the short vaginal tube of *C. margarita* revealed to be a reversion, and I have observed some rare specimens of this species with a longer structure.

41. Genital papilla pair of longitudinal folds at posterior surface: 0= absent; 1= present (all except *C. glauca, C. pyguaia*) (CI= 0.33; RI= 0).

42. Genital papilla dorsal fold: 0= absent; 1= present (*C. intratesta, C. protea, C. fornicata, C. depressa*) (CI= 0.5; RI= 0.75).

The state 1 resulted as a convergent synapomorphy between nodes 6 and 11.

43. Genital papilla: 0= at end of capsule gland; 1= at end of vaginal tube (all) (CI= 1; RI= 1).

44. Genital papilla: 0= low; 1= tall (all) (CI= 1; RI= 1).

45. Female aperture: 0= close to anus; 1= far from anus (all except *C. margarita*) (CI= 0.5; RI= 0).

The pallial oviduct of the ingroup species are different from the other calyptraeoideans (Simone 2002) not only for the distinct fashion (see discussion after character 38), but also for the development of a tall papilla as a stalk for the female genital pore. This papilla is relatively complex, possessing folds and furrows, probably with function during the copulation and ovoposition. The distinction between these folds has been used by Collin (2000) as additional data of the Florida species.

Environment

46. Habit: 0= rocky; 1= on gastropod shells (*C. intratesta*, *C. protea*, *C. plana*, *C. atrasolea*, *C. depressa*); 2= on bivalve shells (*C. argentina*, *C. cachimilla*) (CI= 0.5; RI= 0.6; not additive).

Despite all calyptraeoideans occur in hard substrates (except, maybe, the trichotropids), the obtained cladogram demonstrated another tendency towards the occupation of other mollusks shells, gastropod shells in particular. *C. intratesta*, specifically, occurs exclusively inside gastropod (rarely bivalve) shells, normally occupied by hermit crabs. Still, the state 1 resulted as convergence between the nodes 7 and 10. Of course this character is very variable, as we sometimes found specimens if other kind of substrata. However, the point is to show environmental tendencies and to test the value of habit characters in cladistic analyses. Collin (personal communication) inform me that *C. atrasolea* is also common on bivalve shells.

Cladistic analysis

Matrix of characters:

TABLE 1: matrix of characters of the ingroup *Crepidula* species and the closer outgroup (last row)

Character	1 2 3 4
	12345 67890 12345 67890 12345 67890 12345 67890 12345 6
C. intratesta	10112 11111 21111 11000 10111 12011 11111 13002 11111 1
C. protea	00112 11111 21111 11000 10111 12011 11111 13002 11111 1
C. glauca	21113 01112 11012 12101 10111 11001 11111 10102 00111 0
C. fornicata	00111 01111 11011 11000 10111 12001 11011 11102 11111 0
C. argentina	00111 00111 21011 11000 10111 11000 01011 13012 10111 2
C. margarita	21113 01111 11011 12101 11111 11001 1110? 14101 10110 0
C. plana	10111 00111 11012 12011 10111 11101 01111 12012 10111 1
C. atrasolea	10111 11111 11012 12011 10111 11100 12111 12002 11111 1
C. depressa	10111 10111 11012 12011 10111 11101 12001 13002 11111 1
C. pyguaia	10101 01111 11010 12000 11111 11000 0111? 10102 00111 0
C. carioca	10101 01111 21011 11002 11111 11000 01111 12102 10111 0
C. cachimilla	00111 01100 10010 11000 10101 01000 01011 02002 10111 2
B. aculeatus	00000 00000 00000 00000 00000 00000 00000 00000 00000 0
Cr. auricula	00000 00000 00000 00000 00000 00000 00000 00000 00000 0

Abbreviations: *B.*, *Bostrycapulus*; *C.*, *Crepidula*, *Cr. Crucibulum*.

Cladogram:

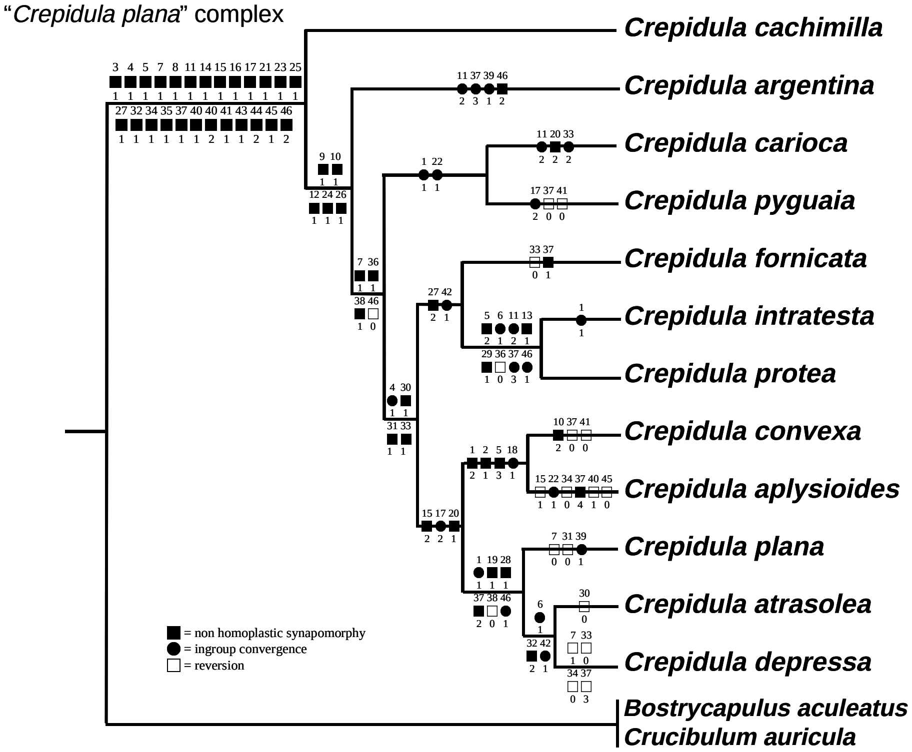


FIGURE 116. Single most parsimonious tree based on data searched in the present study, synapomorphies of each branch shown. In each symbol, superior number means the character, inferior number the state. Symbol key also shown in the tag. Length: 89; CI: 66; RI: 60. The closer outgroup also represented in the bottom of the Figure.

Analysis of the cladogram:

The 12 species of the ingroup are part of a monophyletic group (**node 1**), supported by 25 morphological synapomorphies, seven of them (characters 11, 15, 34, 37, 40, 41) suffer reversion inside cladogram. The most important synapomorphies are: the unguiform shell form (character 3), the notch of the shell septum (5), the decreasing foot and muscles connecting to the shell (8), the decreasing osphradium, becoming monopectinate (14, 15), the modification of the osphradium filaments from a septum to digitiform (16), the decreasing number of osphradium filaments (17), further modification of the kidney (23, 25, 27), the elongation of the intestine portion exposed in pallial cavity (34), and further modification of the pallial oviduct (40, 43–45). However, it is important to establish that several other species also presently belonging to the genus *Crepidula* were not included in this study. The list of 25 characters that support the ingroup most probably would be reduced if those species were included, if they are closer to ingroup than to *Bostrycapulus aculeatus*. Character 40 appears twice in the synapomorphies list because of its additive optimization, counting as two steps. Only the state 2 of this character is synapomorphic if the optimization was non-additive.

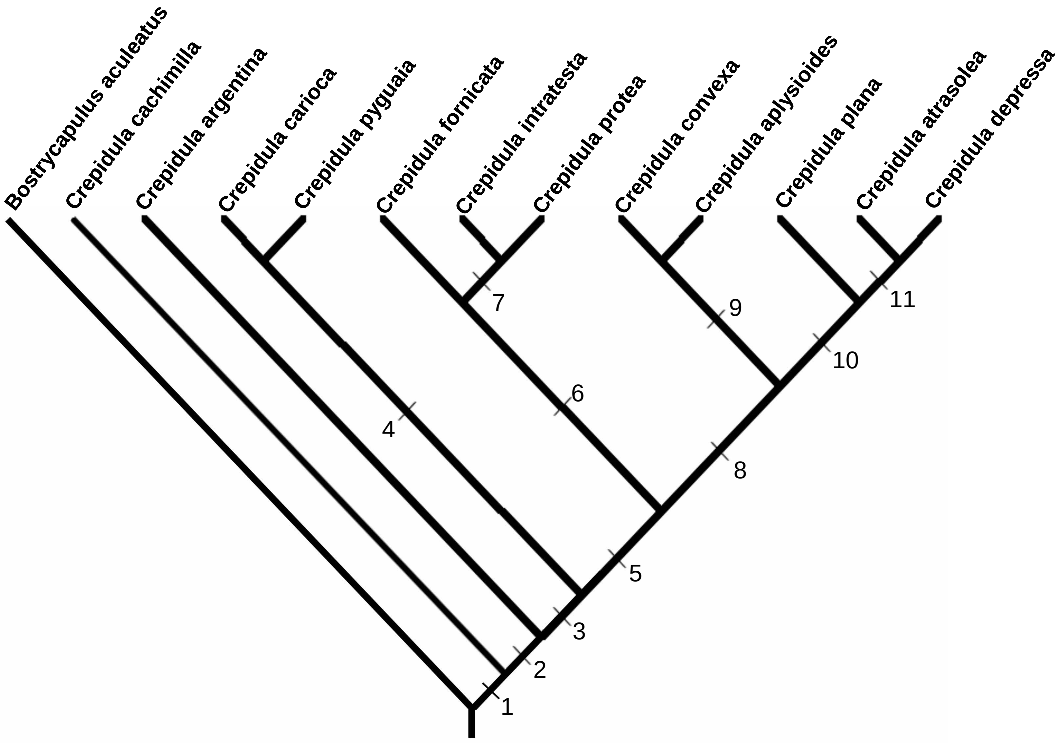


FIGURE 117: Single most parsimonious tree based on data searched in the present study, each node numbered. Length: 89; CI: 66; RI: 60. The closer outgroup also represented at left.

Node 2 is a set of all ingroup species excluding the Patagonian *C. cachimilla*. Five synapomorphies support this node, being two of them (characters 9, 10) result of the thickness of the shell muscles derived from the columellar muscle (lateral and dorsal muscles) (Simone 2002) in that species. The others are the development of the siphonal fold (12), the modification of the fashion of the nephridial gland (24), and connection kidney-adrectal sinus (26).

Node 3 groups all *Crepidula* except *C. argentina* and *C. cachimilla*, which are the more basal species. This node is supported by four synapomorphies, such as the bifid condition of the cephalic tentacles (character 7), the decrease of the male seminal vesicle coiling (36), the reunion of the seminal receptacles in a close point of albumen gland (38).

Node 4 is supported by two synapomorphies; it groups the South West Brazilian coast species with persistent periostracum (considered here a plesiomorphy), *C. carioca* and *C. pyguaia*. The two synapomorphies are convergent with other ingroup branches, the characters 1 (whitish shell color) and 22 (pericardium constricted in middle portion). These two shallow water new species, as already commented above, were misidentified with *C. protea*, due to their convex and somewhat smooth shell. The descriptions are result of the comparative analysis of their anatomy.

Node 5 groups remaining species excluding the four above mentioned species. This node is supported by four synapomorphies, with a single convergence. The synapomorphies include the deciduous periostracum (character 4), the loss or odontophore muscle m11 (ventral tensor muscle of radula) (30), decreasing of salivary glands (31), the long posterior duct to digestive gland (33).

Two synapomorphies support **node 6**, grouping three of the ingroup species. The synapomorphies are the adrectal sinus separated from the rectum (character 27, state 2) and a dorsal fold in the female genital papilla (42). The first branch of this clade is the *C. fornicata*, the type species of the genus *Crepidula*. According to further studies on other *Crepidula*, it is quite possible that this branch (node 6) be the single truly *Crepidula*, being necessary to designate generic names for the remaining clades. However, this procedure is considered still premature. The other branch is **node 7**, grouping *C. intratesta* and *C. protea*. This node is supported by eight synapomorphies, including four convergences, the more important ones are: notch of the shell septum further deeper (character 5, state 2), the radular inner marginal tooth with a blunt pointed tip (29), and the habit of living in gastropod shells (46). These two species have practically no anatomical differences (Simone 2002), the single differences found were the concavity of the shell (*C. protea* dorsally convex; *C. intratesta* concave), and the fact of *C. protea* is the single calyptraeoidean species lacking protandric hermaphroditism.

Node 8, supported by three synapomorphies, groups five species, being the first branch Venezuelan species (node 9) and the remaining species from Florida. The three synapomorphies are the further decreasing of osphradium length (character 15) decreasing of osphradium filaments (17), and the broader fashion of the endostyle (20). Maybe the five species of this branch could have the generic attribution as *Janacus* Mörch, 1852, since they are conchologically similar to the type species of this genus, *C. unguiformis* Lamarck.

Node 9, supported by four synapomorphies, encompasses the two Venezuelan species (*C. glauca* and *C. margarita*). The synapomorphies are the color of shell as narrow spiral bands (character 1, state 2; character 2), the thin-transparent shell septum (5, state 3), and the separation of the osphradium filaments (17).

Node 10 has six synapomorphies and groups the three species from Florida studied by Collin (2000), with samples sent by her. From the synapomorphies the more important are: colorless shell (character 1), the duplicated middle and posterior portions of the endostyle (19), the increasing of basal cusp of radular lateral tooth (28), the number of seminal receptacles equal to 5 (37), and the habit in gastropod shells (46). Interestingly, the result of this paper is comparable with that presented by Collin (2000: fig. 2), majority-rule consensus tree of 267 phylograms obtained by the analysis of 614 base pairs of the mitochondrial cytochrome oxidase I sequence data.

In that study, *C. depressa* and *C. atrasolea*, were found closer related to each other than *C. plana*. In the present study, three synapomorphies support **Node 11**, which groups *C. depressa* and *C. atrasolea*, separating them from *C. plana*. A similar result has been reported by Collin (2001: fig. 5). The synapomorphies are: presence of an ommatophore in the cephalic tentacles (character 6), the filiform fashion of the salivary gland (32), and the dorsal fold of female genital papilla (42). It is interesting to note the number of detected reversions in these 3 species as autapomorphies, 2 in *C. plana*, 1 in *C. atrasolea* and 4 in *C. depressa*.

The present cladogram shows that the 12 species studied herein, belonging to the *Crepidula plana* complex plus *C. fornicata*, are part of a monophyletic taxon, separated from *Bostrycapulus aculeatus*, which most authors consider also as *Crepidula*, by 25 morphological synapomorphies. One of the objectives of this paper to test whether morphological data are useful in the phylogenetic reconstructions of closely related species (see Introduction) was carried out, and showed that it is possible to obtain a good number of characters (46 in present study on 11 species) and few cladograms (single in present study) even at this taxonomic level. However, the relationships of the sampled species is considered still provisional; other species should be included to obtain a wider phylogeny. For this reason no changes in classification has been proposed. On the other hand, it is expected that the relationship among these 12 species remains the same even with the inclusion of more species, and it is expected that most of the Western Atlantic *Crepidula* species has been studied, being necessary to expand the same level of knowledge to species from other areas. On the other hand, the “complex *Crepidula plana*” was not found to be monophyletic, since *C. fornicata* was part of if.

The suspicion that the relationships among the studied species remains the same even with inclusion of more species is intuitive, but is also sustained by the comparison of the result of the present study with that of Simone (2002). That study included five of the species considered here and the same relationships among these five species are obtained in this study. The same happened in comparison of the three Floridian species studied by Collin (2000).

The biogeography of marine species is very difficult to be reconstruct. However, comparing the cladogram with the geographic distribution of the ingroup species, it is possible to see that there is a correlation between the two. With few exceptions, the cladogram shows ascension from south to north. The more basal species, *Crepidula cachimilla*, occurs in Patagonia (South Argentina), *C. argentina*, occurs in the northern Argentine coast, the other four species (except *C. fornicata*), are from the south-west coast of Brazil (*C. pyguaia*, *C. carioca, C. intratesta*, *C. protea*). The further-derived two species (*C. glauca* and *C, margarita*) are from Venezuela. The three most derived species are from Florida (*C. plana, C. atrasolea, C. depressa*), the northernmost species examined.

Crepidula fornicata is the single exception of this pattern, occurring in the both sides of the North Atlantic and in the Mediterranean. A synopsis of this pattern is shown in the Fig. 118, supporting a theory that the ingroup evolved by successive invasions from south to north; as well as the evolve scenario can be based on a wide sprayed ancestral species (occurring from Florida to Patagonia) and that the speciation occurred via vicariance from south to north events.

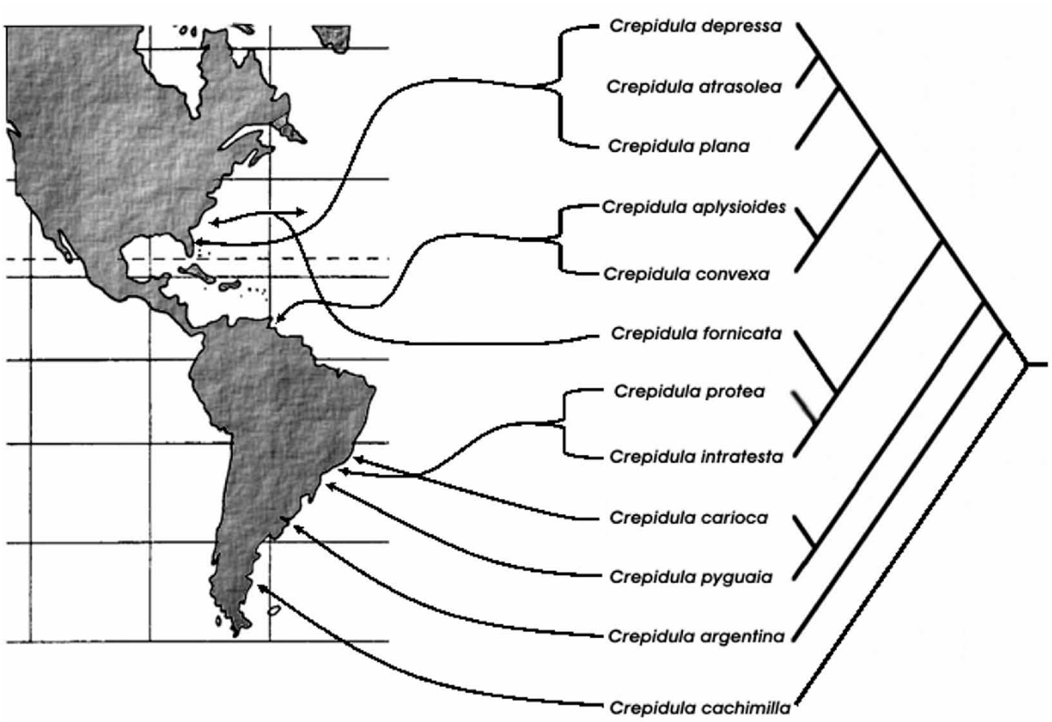


FIGURE 118: Biogeographic mapping between obtained cladogram (right) and geographic occurrence of each studies species (left), showing a general evolutionary ascension from south to north of the ingroup species..

Conclusions

1) There is a pool of 11 *Crepidula* species that perform a monophyletic taxon, supported by 27 morphological synapomorphies if the closer outgroup is *Bostrycapulus aculeatus*, a species that most authors consider belonging to *Crepidula* and *Crucibulum auricula.*

2) This monophyletic taxon encompasses the *Crepidula* flat shelled species from the western Atlantic, informally called “complex *Crepidula plana*”, but it is not a monophyletic taxon, since also encompasses *C. fornicata*.

3) A biogeographic analysis suggests that the ingroup species probably evolved by successive invasions, or vicariance of a wider ranged species, from south to north of Western Atlantic coast.

4) The methodology of studying detailed morphology is demonstrated to be useful at all levels, from high ranks, to species belonging to same genus, occurring in same geographical area and hardly separated in shell characters.

Bibliography

Cledón, M. & Penchaszadeh, P.E. (2001) Reproduction and brooding of *Crepidula argentina*, Simone, Pastorino and Penchaszadeh, 2000 (Gastropoda: Calyptraeidae). *Nautilus,* 115, 15–21.

Cledón, M., Simone, L.R.L. & Penchaszadeh, P.E. (2004) *Crepidula cachimilla* (Mollusca: Gastropoda) a new species from Patagonia, Argentina. *Malacologia,* 46, 1–18.

Collin, R. (1995) Sex, size, and position: a test of models predicting size at sex change in the protandrous gastropod *Crepidula fornicata*. *The American Naturalist,* 146: 815–831.

Collin, R. (2000) Phylogeny of the *Crepidula plana* (Gastropoda: Calyptraeidae) cryptic species complex in North America. *Canadian Journal of Zoology,* 78, 1500–1514.

Collin, R. (2001) The effects of mode of development on phylogeography and population structure of North Atlantic *Crepidula* (Gastropoda: Calyptraeidae). *Molecular Ecology,* 10: 2249–2262.

Hoagland, K.E. (1977) Systematic review of fossil and recent *Crepidula* and discussion of evolution of the Calyptraeidae. *Malacologia*, 16, 353–420.

Miloslavich, P. & Penchaszadeh, P.E. (2001) Reproduction of *Crepidula aplysioides* Reeve (Caenogastropoda) from La Restinga Lagoon, Venezuela; pg. 224. *Abstracts, World Congress of Malacology 2001*. Salvini-Plawén, L.; Voltzow, J.; Sattmann, H. & Steiner, G. [eds.]. Unitas Malacologica. Vienna, Austria, 417 pp.

Miloslavich, P.; Klein E. & Penchaszadeh, P.E. (2003) Reproduction of *Crepidula navicula* Mørch, 1877 and *Crepidula aplysioides* Reeve, 1859 (Caenogastropoda) from Morrocoy and La Restinga Lagoon, Venezuela. *Nautilus,* 117(4), 121–134.

Nixon, K.C. (2000) Winclada Version 0.9.9. Computer program published by the author. Ithaca, NY.

Oliveira, M.P.; Rezende, G.J.R. & Castro, G.A. (1981) *Catálogo dos moluscos da Universidade Federal de Juiz de Fora*. MEC, UFJF. Juiz de Fora, 520 pp.

Reeve, L.A. (1859) Monograph of the genus *Crepidula*. *Conchologia Iconica*, 11, 5 pls.

Rios, E.C. (1970) *Coastal Brazilian seashells*. Fundação Cidade do Rio Grande. Rio Grande, 255 pp. + 4 maps + 60 pls.

Rios, E.C. (1975) *Brazilian marine mollusks iconography.* Fundação Cidade do Rio Grande. Rio Grande, 331 pp. + 91 pls.

Rios, E.C. (1985) *Seashells of Brazil*. Fundação Cidade do Rio Grande. Rio Grande, 328 pp. + 102 pls.

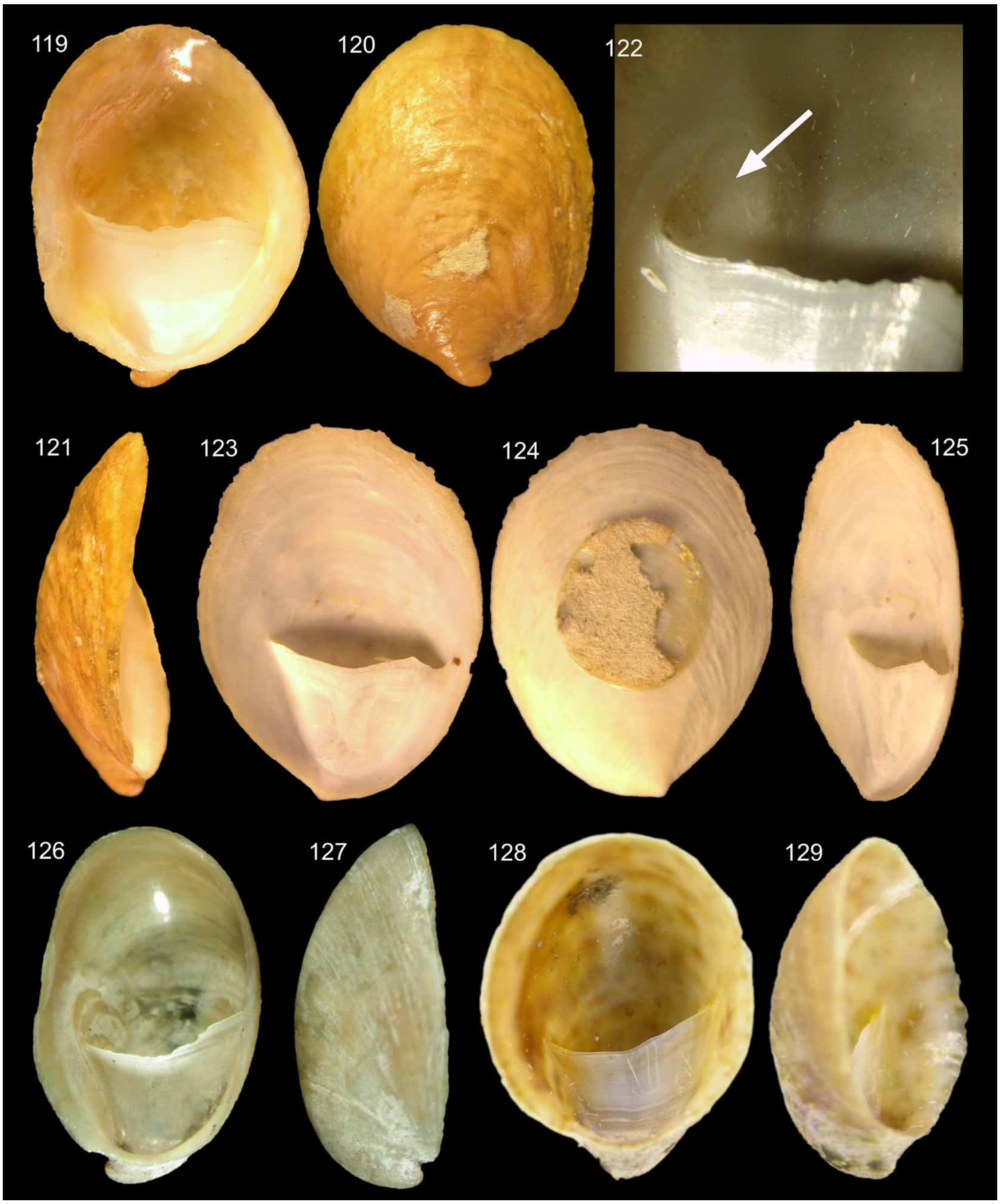
Rios, E.C. (1994) *Seashells of Brazil,* second edition. Fundação Universidade do Rio Grande. Rio Grande, 368 pp. + 113 pls.

Simone, L.R.L. (2001) Phylogenetic analyses of Cerithioidea (Mollusca, Caenogastropoda) based on comparative morphology. *Arquivos de Zoologia,* 36, 147–263.

Simone, L.R.L. (2002) Comparative morphological study and phylogeny of representatives of the Superfamily Calyptraeoidea (including Hipponicoidea), (Mollusca, Caenogastropoda). *Biota Neotropica*, 2: 1–137.

Simone, L.R.L.; Pastorino, G. & Penchaszadeh, P.E. (2000) *Crepidula argentina* (Gastropoda: Calyptraeidae), a new species from the littoral of Argentina. *Nautilus*, 114, 127–141.

Swofford, D.L. (1991) PAUP (Phylogenetic Analysis Using Parsimony) Version 3.1. Computer program distributed by the Illinois Natural History Survey. Champaign, USA.



FIGURES 119–129, Type and voucher specimens of some *Crepidula* worthy for this study. Fig. 119–122: *Crepidula aplysioides*, one of four syntypes, BMNH 1977137 (length= 23 mm); Figs 119–121: ventral, dorsal and right views respectively; Fig. 122: detail of region of right side of septum insertion, showing large muscle scar (arrow). Figs. 123–125: *Crepidula glauca* voucher specimen (one of four) from Reeve (1859), BMNH 1829 (length= 20 mm), ventral, dorsal and left views respectively. Figs 126–129: *Crepidula convexa* voucher specimens; Figs. 126–127: specimen figured by Reeve (1859), BMNH 1829 (length= 10 mm), ventral and right views. Figs. 128–129: voucher of Hoagland (1977), ANSP 357830 (length= 11 mm), ventral and right-slightly oblique views.