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Comparative anatomy of the fasciolariids *Pustulatirus ogum* and *Hemipolygona beckyae* from Brazil (Gastropoda: Buccinoidea: Peristerniinae)

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Summary: The Brazilian species *Pustulatirus ogum* and *Hemipolygona beckyae* were examined, and certain morphological characters were described. Both species were originally assigned to the genus *Latirus*, considered as a heterogeneous complex. The radulae of both species are like that which characterizes *Latirus*, in which the innermost cusp of the rachidian tooth is well developed but always smaller than the other cusps. This feature differs from *Leucozonia,* in which this cusp is reduced or absent. The penis tapers terminally, and the tapered part may be long (more than half the total penis length), as in *H. beckyae*, or very short (less than half the total penis length), as in *P. ogum*. The anatomical data observed in both species are discussed under the framework of fasciolariid systematics and they appear to be widespread among other fasciolariid species. For this reason, to date, the soft-part features here provided and those known from previously studied species of *Latirus* are not useful for delineating precise generic diagnoses.

Keywords: morphology; Caenogastropoda; Fasciolariidae; *Latirus*; western Atlantic.

Anatomía comparada de los fasciolláridos *Pustulatirus ogum* y *Hemipolygona beckyae* de Brasil (Gastropoda: Buccinoidea: Peristerniinae)

Resumen: Se describe la morfología y anatomía de las especies brasileñas *Pustulatirus ogum* y *Hemipolygona beckyae*. Ambas especies han sido tradicionalmente asignadas al género *Latirus*, que en la actualidad se considera que agrupa a un conjunto heterogéneo de especies. Las rádulas de ambas especies son como la que caracteriza a *Latirus*, con la cúspide más interna del diente raquídeo bien desarrollada y siempre menor que las otras cúspides. Esta característica difiere de la que presentan las especies del género *Leucozonia*, en las que esta cúspide está reducida o ausente. El pene se estrecha en su parte terminal, y la parte cónica puede ser larga (más de la mitad de la longitud total del pene), como en *H. beckyae*, o muy corta (menos de la mitad de la longitud total del pene), como en *P. ogum*. Los caracteres morfológicos observados en ambas especies se discuten en el marco de la sistemática de los Fasciolariidae y parecen estar ampliamente distribuidos en otras especies de fasciolláridos. Por ello, hasta la fecha, las características de las partes blandas del animal aquí descritas y las conocidas previamente de otras especies de *Latirus* no se consideran de utilidad para la diagnosis de los géneros en esta familia.

Palabras clave: morfología; Caenogastropoda; Fasciolariidae; *Latirus*; Atlántico occidental.

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INTRODUCTION

The neogastropod family Fasciolariidae comprises more than 1300 living species, distributed in the tropics and subtropics (Gofas 2014), and divided into three subfamilies, Fasciolariinae, Fussininae and Peristerniinae. Members of the subfamily Peristerniinae inhabit hard bottoms, although other fasciolariids dwell mostly in soft and muddy substrates (Harasewych 1998, Vermeij and Snyder 2006).

Members of the Peristerniinae are represented in Brazil by at least 16 species, in the genera *Polygona*

Schumacher, 1817 (7 spp.), *Hemipolygona* Rovereto, 1899 (2 spp.), *Pustulatirus* Vermeij and Snyder, 2006 (3 spp.) and *Leucozonia* Gray, 1847 (4 spp.) (Rosenberg 2009). Most species included in *Hemipolygona* and *Pustulatirus* were previously grouped in *Latirus*. However, this genus is now restricted to the Indo-West Pacific (Vermeij and Snyder, 2006); it was previously regarded as a heterogeneous assemblage, and was recently the target of some taxonomic revisions (Vermeij and Snyder 2002, 2006).

Pustulatirus ogum and *Hemipolygona beckyae,* which occur in Brazilian waters, were treated in the most recent bibliographic records as subgenera of *Latirus* (Rios 1994, 2009).The former species occurs from Espírito Santo to Bahia state, and the latter only in Espírito Santo; *P. ogum* inhabits tide pools, while *H. beckyae* occurs at depths of about 30 m.

Kosyan et al. (2009) studied the anatomy of some species of Fasciolariidae, including *Turrilatirus turritus* (Gmelin, 1791), *Pustulatirus mediamericanus* (Hertlein and Strong, 1951) and *Latirus polygonus* (Gmelin, 1791), all of which were previously regarded as members of *Latirus*. In Brazil, only the anatomy of species belonging to *Leucozonia* has been studied: *L. nassa* (Gmelin, 1791) by Marcus and Marcus (1962); *L. nassa* (Gmelin, 1791), *L. ocellata* (Gmelin, 1791) and *L. ponderosa* (Vermeij and Snyder 1998) by Couto and Pimenta (2012); and *Teralatirus roboreus* by Simone et al. (2013).

Fraussen et al. (2007) reported that a combination of traits is diagnostic for Fasciolariidae: multicuspidate lateral teeth and straight rachidian teeth, proboscis retractor muscle as a single or paired tuft of fibres, ducts of the salivary glands embedded in the esophagus wall, and a stomach without a posterior mixing area. Kosyan et al. (2009) studied the anatomy of eight fasciolariid species belonging to seven genera. These authors distinguished fasciolariids from buccinids studied by them and by Kosyan and Kantor (2009), based on the stomach morphology: low folds with transverse striations, absence of differentiation of the gastric chamber, absence of a posterior mixing area (Kantor 2003), and proboscis retractor muscles as a single muscle or paired (Fraussen et al. 2007). The orange-red colour of the foot and head-foot mass is typical for fasciolariids.

Morphological characters may prove useful in validating phylogenetic relationships and may help to resolve internal clades (Strong 2003, Simone 2011). However, no formal anatomical characterization within *Latirus* and related species exists. They are presently distinguished solely on shell features (Vermeij and Snyder 2006, Lyons and Snyder 2013), and hence prone to hypotheses of polymorphism and convergence. The present contribution provides morphological descriptions and comparisons of *Pustulatirus ogum* and *Hemipolygona beckyae*.

MATERIALS AND METHODS

The material used for this study is deposited in the Museu Nacional / Universidade Federal do Rio de Janeiro (MNRJ) and Museu de Zoologia / Universidade de São Paulo (MZSP).

The specimens collected were fixed in 70% ethanol. Shells were measured with a caliper, and photographs of individuals were taken with a digital camera. The anatomical dissections were done under a stereomicroscope. All drawings were made using a camera lucida. Radulae were manually extracted and prepared by immersion in KOH, followed by ultrasonic cleaning and subsequent immersion in distilled water for scanning electron microscope photography.

RESULTS

Genus *Pustulatirus* Schumacher, 1817

Pustularitus Vermeij and Snyder, 2006. Type species: *Latirus mediamericanus* Hertlein and Strong, 1951 by original designation.

Diagnosis. See Vermeij and Snyder (2006).

Pustulatirus ogum (Petuch, 1979) (Figs 1-5)

Latirus ogum: Petuch 1979: 519 (Figs 3A-B); Rios 1985: 107 (pl. 36, Fig. 470); Mallard and Robin 2005: 18 (pl. 47).
Latirus (*Polygona*) *ogum*: Petuch 1987: 140 (pl. 27, Figs 1-2); Rios 1994: 133, (pl. 42, Fig. 574); Snyder 2003: 152, 306; Rios 2009: 253.
Benimakia ogum: Vermeij and Snyder 2003: 17 (Figs 6A-B).
Polygona ogum: Rosenberg 2009.
Pustulatirus ogum: Landau and Vermeij 2012: 88; Lyons and Snyder 2013: 49 (Figs 52-62).

Type locality. West of Coroa Vermelha, in tide pool, Abrolhos reef, Bahia state, Brazil, 17°57'S, 39°13'W.

Types. Holotype: USNM 780654.

Examined material. Brazil: Bahia, Alcobaça (20-25 m), MZSP 68475, 16 specimens (vi/2006), MZSP 68835, 1 specimen (viii/2005); Espírito Santo, Guarapari (A. Bodart col., 20-25 m, i/2006), MZSP 69477, 6 especimens, MZSP 69481, 10 specimens; Rio de Janeiro, Arraial do Cabo, 30-35 m, MZSP 69301, 2 specimens (P. Conçalves col., i/2005).

Distribution. Abrolhos reef, Bahia state; Espírito Santo to Rio de Janeiro states, southeast coast of Brazil.

Shell (Fig. 1A-F). Shell elliptical, fusiform, height up to 39.2 mm, width 2/5-1/2 of height. Colour chestnut to dark brown. Spire high, angle 45°-50°, ~1/2 of total shell height. Protoconch small with 2 whorls, smooth, terminal varix low. Teleoconch with 7-8 rounded whorls; subsutural ramp slightly concave, suture deep, base of shell concave. Spiral sculpture of 6-7 continuous spiral cords along entire teleoconch, 3 in abapical half of each whorl, more evidenced in first whorls, 3-4 strong spiral cords marking siphonal canal; several secondary spiral cords along entire teleoconch. Axial sculpture of 7-8 strong rounded ribs. Aperture elliptical to pyriform, height ~3× width. Columella bearing 3 folds medially. Outer lip crenulated, marked internally by 10 discontinuous lirae. Siphonal canal moderately long, length ~1/2 of length of aperture. Siphonal fasciole indistinct. Pseudoumbilicus as shallow slit.

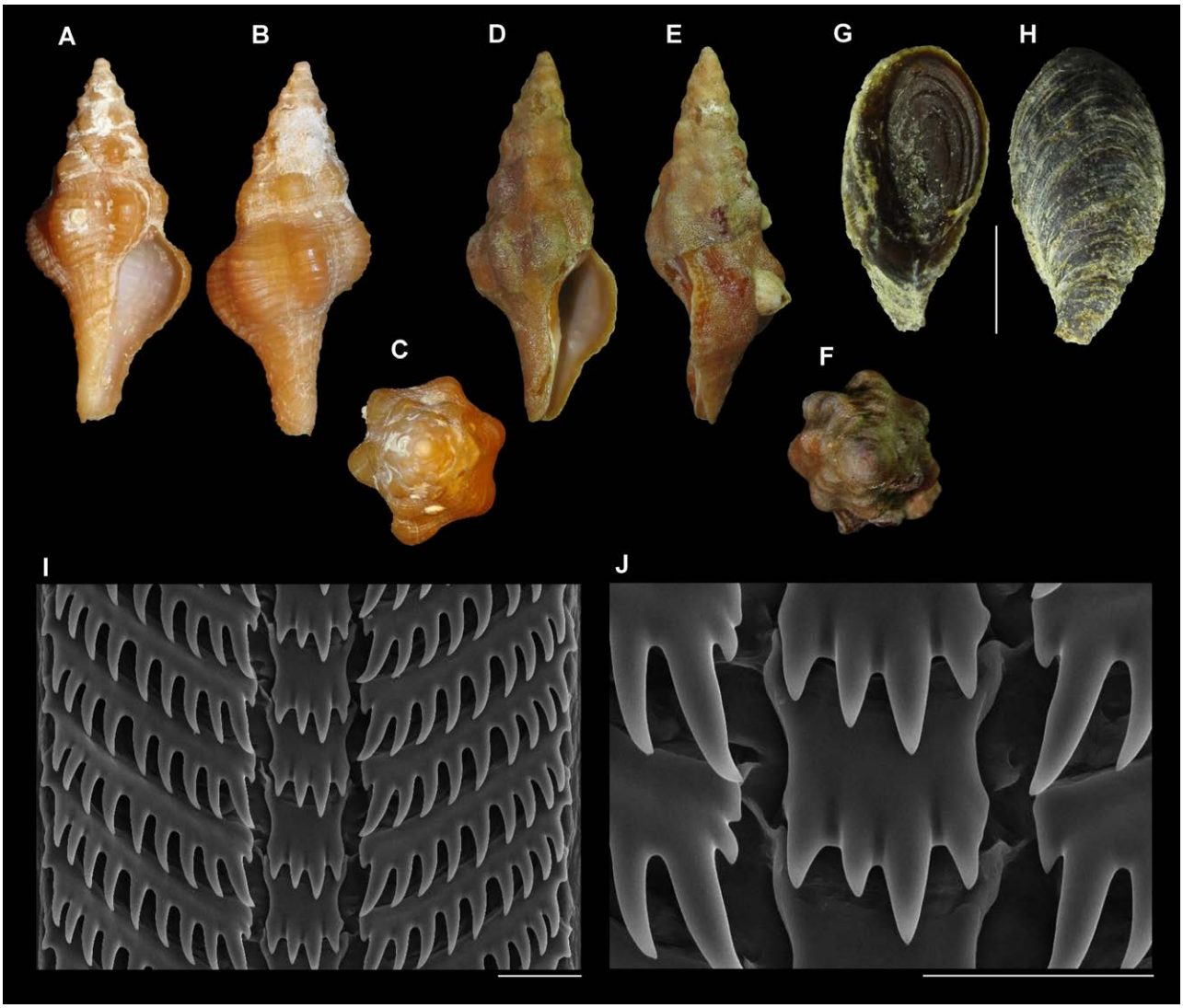

Fig. 1. – *Pustulatirus ogum*. A-C, 22.2 mm (MZSP 68475); D-F, 39.2 mm (MZSP 69301); G, operculum internal view; H, operculum external view; I, radula; J, detail of rachidian tooth. Scale bars: G-H, 3 mm; I-J, 30 mm.

Head-foot (Fig. 2A-B). colour cream in fixed species. Head prominent, of medium size (width ~1/3 of adjacent width of head-foot), cephalic tentacles blunt and short (length ~1/2 of anterior width of head), situated very close to each other; bases lying side by side. Eyes dark, small, rounded, situated in middle region of outer edge of tentacles. Foot short, rounded, anterior region bifid. Pedal gland as shallow median anterior slit, with anterior furrow extending along entire anterior edge. Columellar muscle thick, with ~1.25 whorls in length.

Operculum (Fig. 1G-H). Operculum corneous, unguiculate (width ~2/3 of length), filling entire aperture; outer surface opaque, with anterior nucleus inner surface with attachment scar elongated, elliptical, situated posteriorly, occupying ~2/3 of inner area.

Pallial complex (Fig. 2C-D). Pallial cavity wide, of one whorl. Mantle border simple, thickened. Siphon short (length about 1/4 of free portion of mantle edge), its margin smooth; right fold of siphon base extending into pallial cavity, ending close to anterior end of ctenidium. Osphradium elongated, tapering anteriorly; length ~1/2 of ctenidium; almost symmetrical longitudinally; osphradium leaflets rounded, short (height ~1/2 of ctenidial filament height at middle region of pallial cavity), ~equal in size. Ctenidium curved, ~1/4 of total pallial cavity area, width slightly larger than osphradium; anterior and posterior region pointed, posterior end situated close to pericardium; filaments triangular; ctenidial vein (efferent branchial vessel) uniformly narrow along its length. Hypobranchial gland thin and loosely fixed, situated between gill and rectum, except for posterior 1/2 of pallial cavity. Rectum elongated. Anus elliptical, situated at 1/4 of mantle edge.

Circulatory and excretory systems (Fig. 4G). Pericardium spanning ~1/5 of total renal cavity area. Auricle pyriform, wall thin, translucent; ventricle large and rounded (~larger than auricle), triangular in shape, with thick walls. Aorta bifurcate immediately after leaving ventricle; posterior aorta following visceral mass close to stomach; anterior aorta crossing diaphragmatic sep-

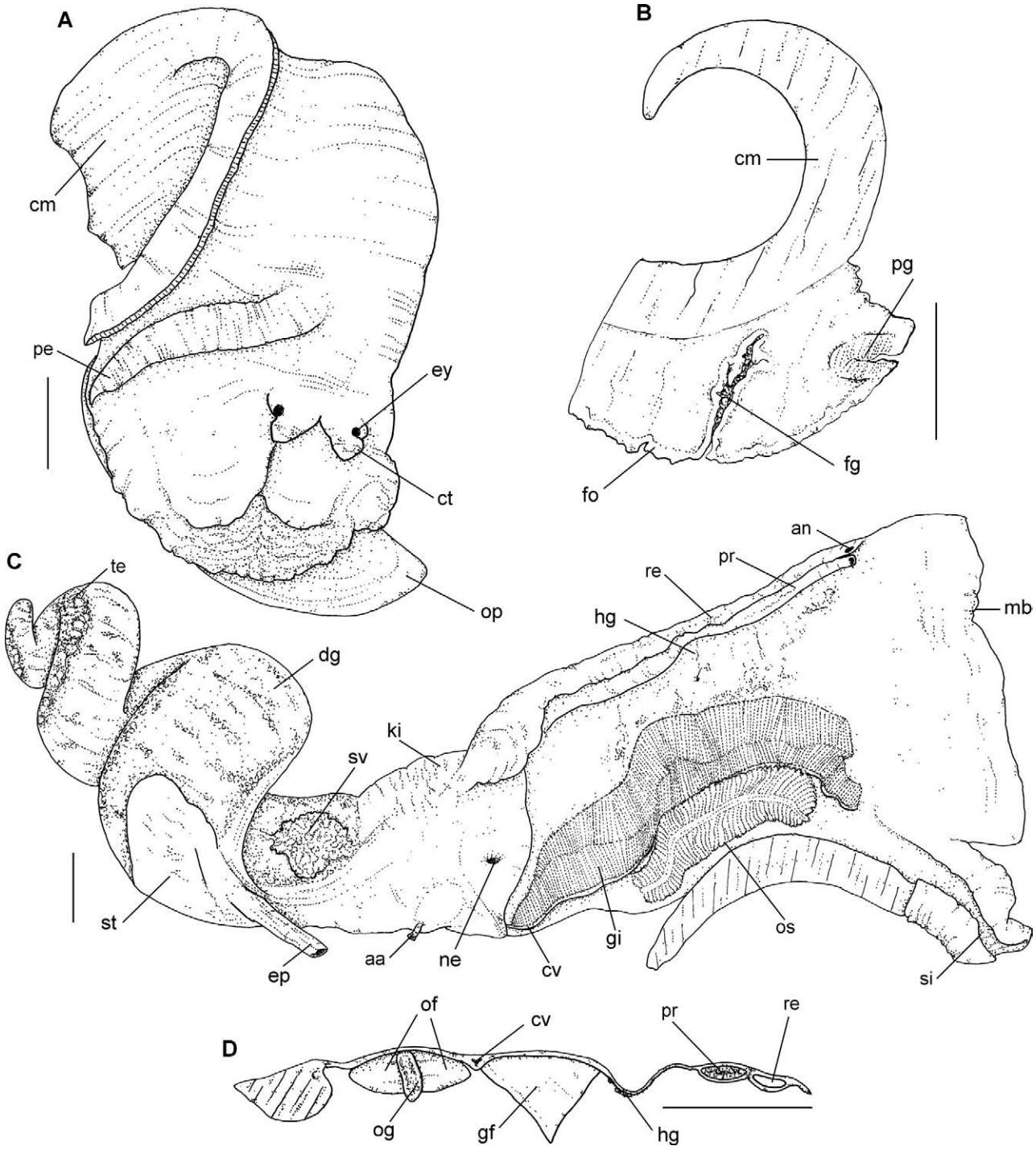

Fig. 2. – *Pustulatirus ogum*. A, head-foot mass in dorsal view; B, longitudinal section of head-foot mass, female; C, roof of pallial cavity in ventral view, male; D, transverse section of roof of pallial cavity. Abbreviations: aa, anterior aorta; an, anus; cm, columellar muscle; ct, cephalic tentacle; cv, ctenidial vein; dg, digestive gland; ep, posterior esophagus; ey, eye; fg, female cement gland; fo, foot; gf, gill filament gi, gill; hg, hypobranchial gland; ki, kidney; mb, mantle border; ne, nephrostome; of, osphradium filament; og, osphradium ganglia; op, operculum; os, osphradium; pe, penis; pg, pedal gland; pr, prostate; re, rectum; si, siphon; st, stomach; sv, seminal vesicle; te; testis. Scale bars: 2 mm.

tum anteriorly. Anterior aorta running anteriorly along whole length of posterior esophagus, crossing gland of Leiblein in mid-esophagus, with branches forming sinus surrounding nerve ring. Anterior aorta bifurcating anteriorly to nerve ring; one branch following anteriorly to pedal ganglia as pedal aorta, another branch accompanying anterior esophagus, following anteriorly to buccal mass and odontophore. Kidney bearing ventral and dorsal lamellar lobes similar in shape; nephridial gland situated on dorsal side of membrane between renal cavity and pericardium; renal aperture as slit in membrane between pallial and renal cavities, flanked on its right side by transversal folds, longitudinal to roof of pallial cavity. Part of intestine running longitudinally on inner side of kidney, ventrally adhered to its membrane

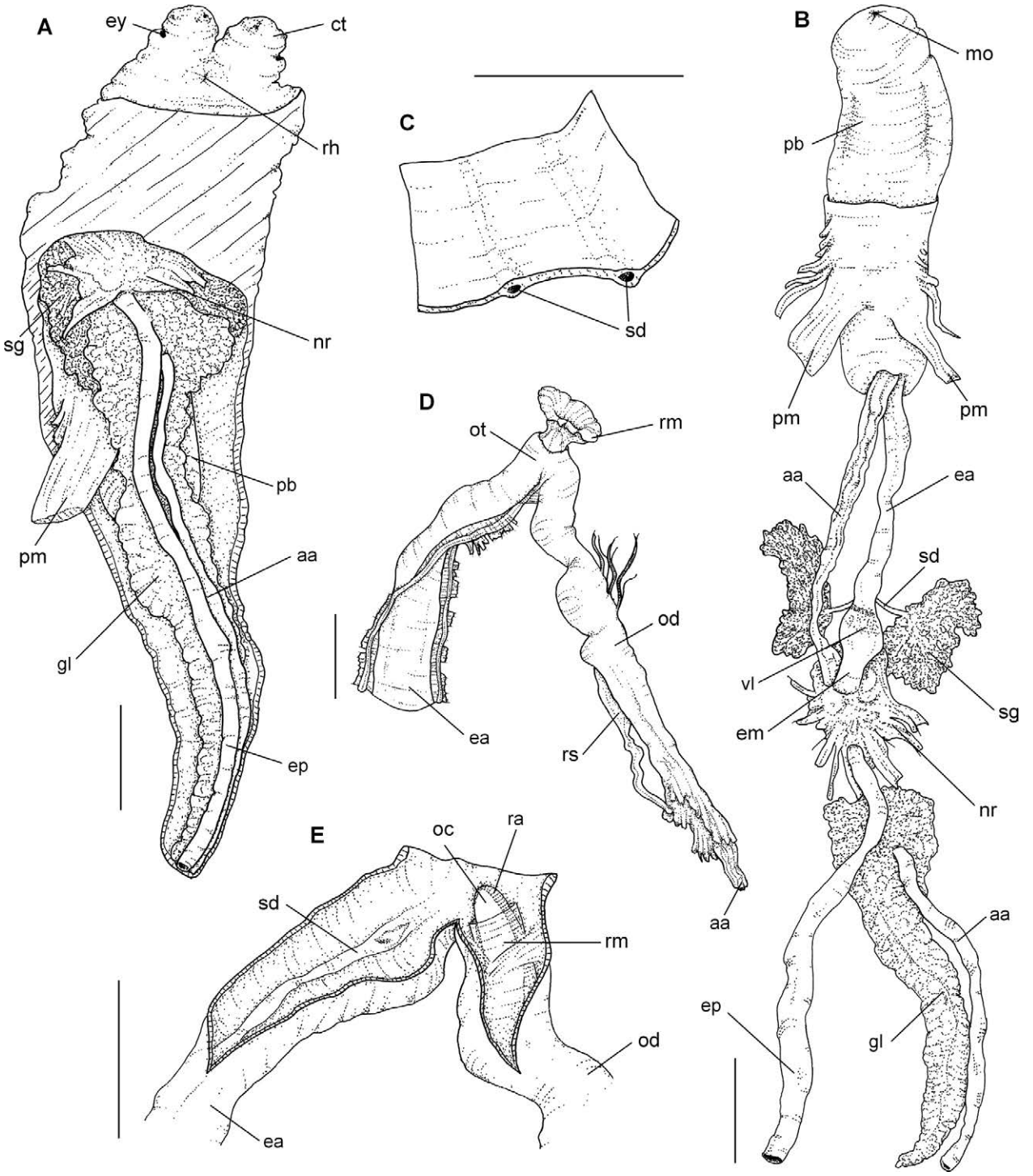

Fig. 3.- *Pustulatirus ogum*. A, haemocoel in ventral view; B, anterior digestive system; C, lumen of anterior esophagus; D, buccal mass in lateral view; E, buccal mass in lateral view, opened longitudinally. Abbreviations: aa, anterior aorta; ct, cephalic tentacle; ea, anterior esophagus; ep, posterior esophagus; ey, eye; gl, gland of Leiblein; mo, mouth opening; nr, nerve ring; oc, odontophore cartilage; od, odontophore tube; ot, oral tube; pb, proboscis; pm, proboscis retractor muscles; ra, radula; rh, rhynchostoma; rm, subradular membrane; rs, radular sac; sd, salivary gland duct; sg, salivary gland; vl, valve of Leiblein. Scale bars: A-B, 2 mm; C-E, 1 mm.

Digestive system (Figs 3A-E, 4A-E). Rhynchostome as small longitudinal slit, located between and below cephalic tentacles. Proboscis straight, of moderate length (~2/3 of haemocoel length), with thick muscular walls bearing 2 lateral grooves. Pair of proboscis retractor muscles originating in ventral posterior wall of proboscis; series of short lateral muscle fibres connected to inner walls of haemocoel. Mouth small, circular. Odontophore long, slender (~same length as proboscis), pair of odontophore cartilages dorsally concave, fused anteriorly at ~1/4 of total cartilage length. Series of transversal muscle fibres connecting odontophore tube with anterior esophagus; superficial circular muscles (m3) enveloping entirely odontophore, except for most posterior end; horizontal muscle (m6), originating on ventral surface of odontophore

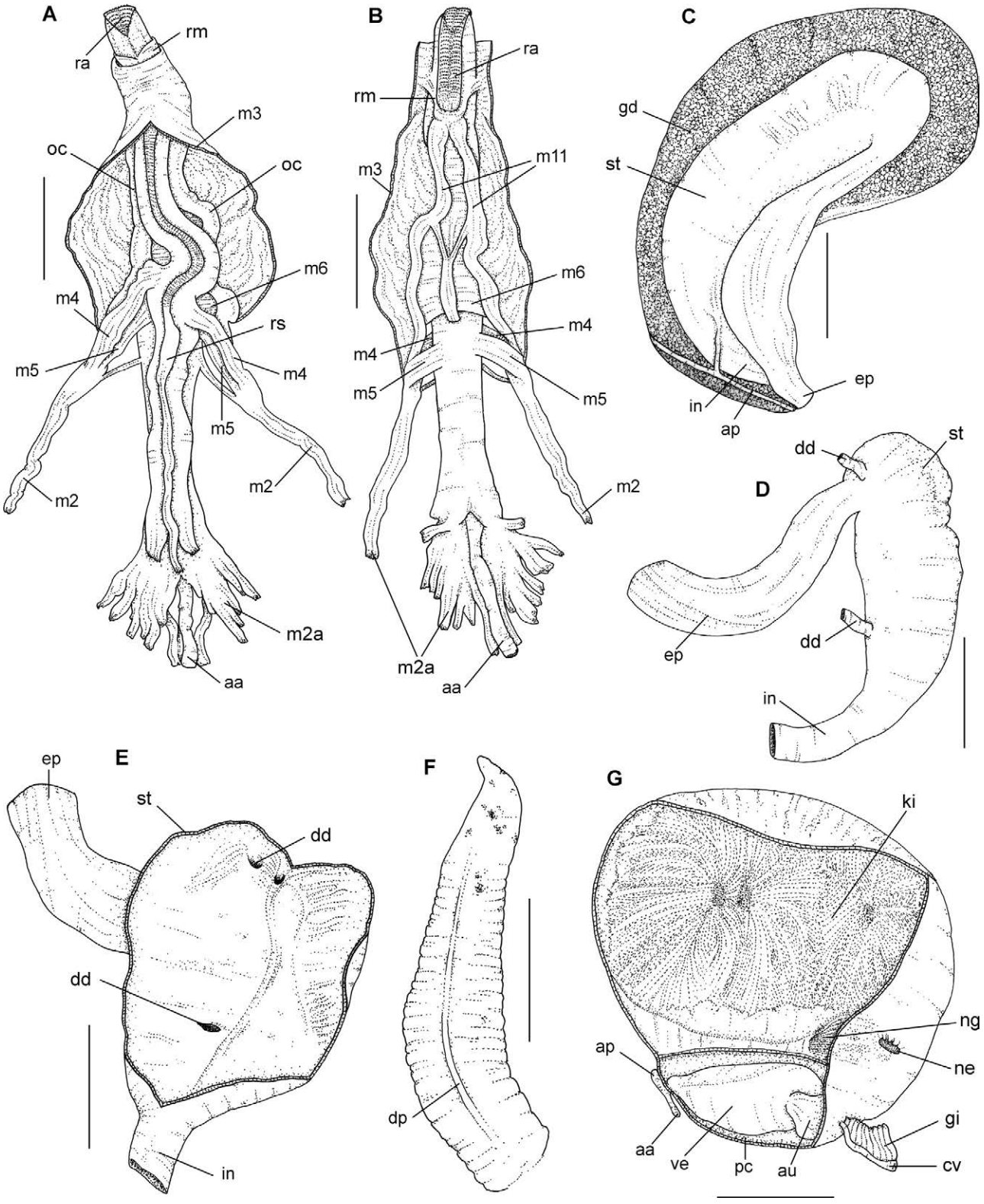

Fig. 4. – *Pustulatirus ogum*. A, odontophore in dorsal view; B, odontophore in ventral view; C, stomach in dorsal view; D, stomach in ventral view; E, stomach shown internally; F, penis in dorsal; G, renal cavity and pericardium in ventral view. Abbreviations: aa, anterior aorta; ap, posterior aorta; au, auricle; bu, bursa; cv, ctenidial vein; dd, duct of digestve gland; dg, digestive gland; dp, duct of penis; ep, posterior esophagus; in, intestine; ki, kidney; m11, ventral tensor muscles of radula; m2, odontophore retractor muscles; m2a, accessory odontophore retractor muscles; m3, superficial circular muscles; m4, dorsal tensor muscles of radula; m5, auxiliary dorsal tensor muscles of radula; m6, horizontal muscle; ne, nephrostome; ng, nephridial gland; oc, odontophore cartilage; pc, pericardium; ra, radula; re, rectum; rm, subradular membrane; rs, radular sac; ve, ventricle. Scale bars: A-B, 1 mm; C-G, 2 mm.

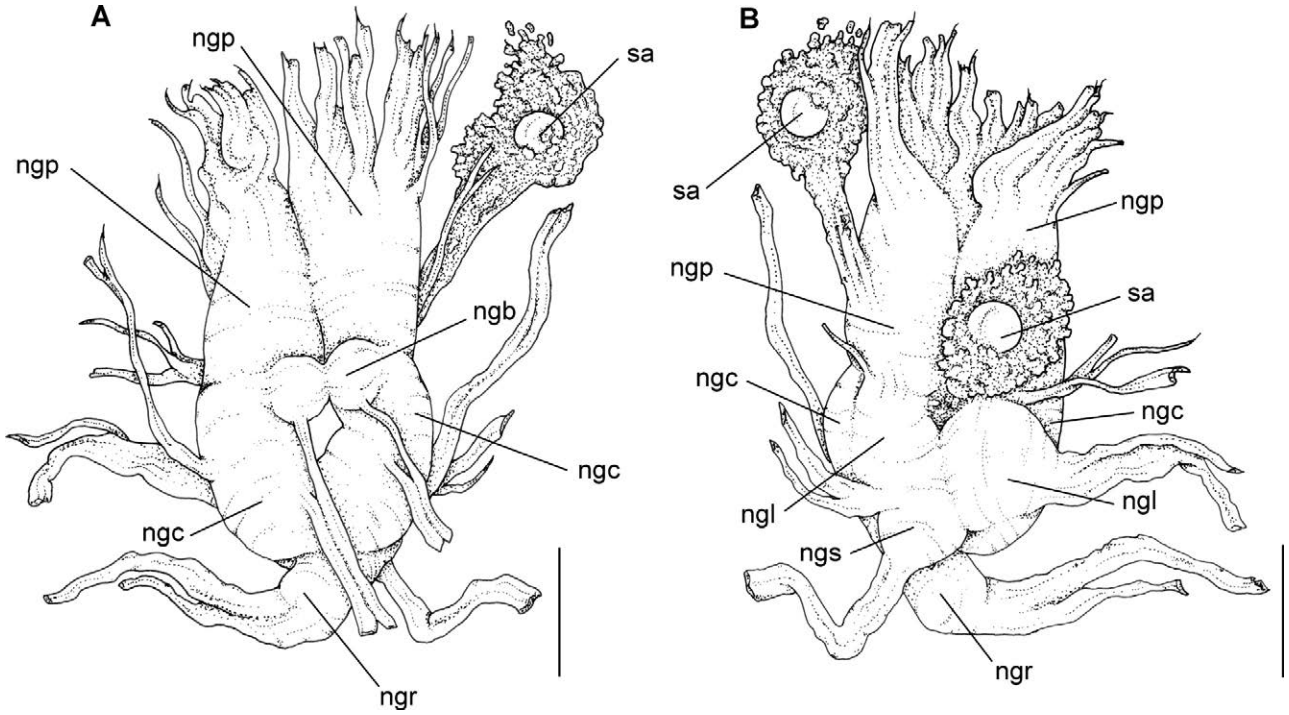

Fig. 5. – *Pustulatirus ogum*. A, nerve ring in dorsal view; B, nerve ring in ventral view. Abbreviations: ngb, buccal ganglion; ngc, cerebral ganglion; nbl, pleural ganglion; ngp, pedal ganglion; ngr, supra-esophageal ganglion; ngs, subesophageal ganglion; sa, statocyst. Scale bars: 0.5 mm.

cartilages, except for most posterior region (~1/5 of total odontophore length). Pair of odontophore retractor muscles (m2) originating from posterior end of odontophore cartilages, near to radular sac, inserted in inner wall of proboscis; pair of accessory odontophore retractor muscles (m2a), originating from inner surface of proboscis, near origin of m2, runnind adjacent to esophagus, insertion enveloping enveloping radular sac; pair of secondary, long branch of m2a accompanying anterior aorta reaching up to posterior level of nerve ring. Pair of dorsal tensor muscles of radula (m4) originating from posterior dorsal end of odontophore, covering its dorsal surface, inserting m2a; pair of auxiliary dorsal tensor muscles of radula (m5) originating from posterior end of odontophore, covering its ventral surface, inserting in m2a; pair of ventral tensor muscles of radula (m11), inserting anteriorly in subradular membrane, running, ventrally adhered (~3/4 of total odontophore length), origin bifid: main branch originating in ventral posterior cartilage of odontophore near origin of m2, secondary branch originating ventrally in m2a, crossing dorsally m6, connecting in main branch (at ~1/2 of total m11 length). Radula long and thin; radular sac extending beyond posterior end of odontophore; Radular teeth (Fig. 1I-J): rachidian tooth straight, slightly rectangular, their base with concave outline, cusped margin convex, bearing 4 sharp cusps of ~equal size, except for right central, slightly larger than others; lateral tooth wider than long, bearing 11 prominent, centrally recurved cusps of approximately same size, except for innermost ~1/5 smaller, and outermost ~1/4 smaller and separated from rest. Anterior esophagus moderately long and broad (~2× proboscis length), dorsally-ventrally compressed, originating in oral tube. Valve of Leiblein pyriform, forming orange ring around esophagus, ~1.5 of esophagus width. Salivary glands just anterior to valve of Leiblein, forming pair of branching and amorphous masses; free portion of salivary ducts short, extending along esophagus, anteriorly to valve of Leiblein, becoming embedded with esophageal wall, running immersed anteriorly, opening in oral lumen, immediately before oral tube. Accessory salivary glands absent. Middle esophagus short. Duct of gland of Leiblein short and narrow, inserted posterior to nerve ring. Gland of Leiblein brownish, long, of ~same length as posterior esophagus, posterior end acute. Posterior and anterior esophagus of ~same width. Inner wall of anterior esophagus smooth, salivary ducts immersed in marked lateral folds. Stomach wide, walls thin, bearing many internal folds. Digestive gland dark brown, occupying all whorls of visceral mass, from apex to kidney/pericardium area, surrounding stomach, emitting two narrow, branching ducts discharging near esophagus and intestine apertures. Intestine bearing expansion near posterior region of pallial cavity in region preceding rectum, internally bearing many longitudinal folds.

Male genital system (Fig. 4F). Testis brownish, occupying all whorls of visceral mass, except for last one; surrounding apically entire length of digestive gland. Visceral vas deferens running from testis. Seminal vesicle coiled, located on mid-ventral region of last whorl of visceral mass; vas deferens narrow, simple, running along ventral wall of kidney. Prostate thin and long, tubular, located along right side of roof of pallial cavity, next to rectum and ~equal in width. Penis long, close to head-foot, ~circular in transverse section; penis becoming narrower at middle of its length, terminating in extension of ~1/2 of total penis length; duct of penis linear, simple.

Female genital system (Fig. 2B). Ovaries brownish, with same texture and length as testis. Female cement gland opening at ~1/2 from anterior edge of foot, forming somewhat elongated and deep sac of ~same depth as foot thickness, recurved anteriorly. Pallial oviduct not observed.

Nervous system (Fig. 5A-B). Nerve ring highly concentrated, occupying ~1/6 of total haemocoel area, surrounding mid-esophagus posteriorly. All commissures internal. Cerebral ganglia bean-shaped, occupying ~1/2 of total nerve ring volume, right ganglion slightly larger and more dorsal than left ganglion, its posterior halves broadly connected with each other; pair of lateral tentacular nerves following anteriorly to pedal aorta. Pleural ganglia as pair of bulges ventral to cerebral ganglia, strongly attached to these; left pleural ganglia emitting thick nerve accompanying proboscis anteriorly. Pedal ganglia anterior, elongated, ~1/2 of total nerve ring volume; bearing anterior nerves; right pedal ganglion slightly larger and dorsal than left pedal ganglion. Buccal ganglia circular, small, ~1/5 of cerebral ganglia and dorsal to these, emitting pair of cerebro-buccal nerves, following anteriorly to anterior aorta. Supra-esophageal ganglion posterior to cerebro-pleural ganglia complex, slightly larger than buccal ganglia, emitting thick osphradial nerve. Subesophageal ganglion as ventral bulge in left cerebro-pleural ganglia complex emitting thick pallial-siphon nerve. Pair of vitreous statocysts with one anterior and associated with right pedal ganglion; and one posterior, associated with left pedal ganglion.

Genus *Hemipolygona* Rovereto, 1899

Hemipolygona Rovereto, 1899: 104. New name for *Chascax* Watson, 1873, *non* Ritgen 1828 (Reptilia). Type species: *Chascax maderensis* Watson, 1873 by monotypy.

Diagnosis. Shell extremely nodulose with blunt to sharp nodes where axial ribs cross spiral cords, especially on shoulder angulation and central cord, but also on base of shell and subsutural ramp; columella bearing up to 3 weak to strong folds medially; outer lip crenulated, marked internally by several beaded lirae; siphonal fasciole and pseudoumbilicus usually present.

Hemipolygona beckyae (Snyder, 2000) (Figs 6-9)

Latirus beckyae: Snyder 2000: 161 (Figs 1-2); Snyder 2003: 48, 300; Mallard and Robin 2005: 17 (pl. 40).
Hemipolygona beckyae: Vermeij and Snyder 2006: 417 (Fig. 2D); Rosenberg 2009.

Type locality. Off Vitória, 30-50 m depth, Espírito Santo state, Brazil.

Types. Holotype: USNM 880231; Paratypes: USNM 880232; IBUFRJ 9121; MORG 39008; MNRJ 7696.

Examined material. Brazil: Espírito Santo, Vitória (30-50 m, v/1994), MNRJ 7696, paratype, 1 shell; (viii/2005) MZSP 68835, 1 specimen; Vitória (viii/2003, 30-35 m), MZSP 69482, 3 specimens; Guarapari, MZSP 57053, 1 specimen, (30-35 m, viii/2000), MZSP 69764, 1 specimen.

Distribution. Espírito Santo to São Paulo states, southeast coast of Brazil.

Shell (Fig. 6A-G). Shell elliptical, fusiform, height up to 55.4 mm, width ~1/3 of height. Colour light orange with spiral cords whitish. Spire high, angle 50°-55°, ~1/2 of total shell height. Protoconch small with 1,5 whorls, smooth, terminal varix low. Teleoconch with 6-9 rounded whorls; suture raised, subsutural lamellar spiral cord, base of shell concave. Spiral sculpture of 8-9 continuous whitish spiral cords per whorl, more prominent in shoulder angulation; 14-18 whitish spiral in base; several secondary spiral cords along teleoconch. Axial sculpture of 7-8 strong, wide, rounded ribs; lamellar striae occurring between spiral cords, eroded in early whorls. Aperture elliptical, height ~3× width. Columella bearing 3 folds medially. Outer lip crenulated, marked internally by 10-11 discontinuous lirae, not present where they cross outer lip growth scars. Siphonal canal moderately long, length ~1/2 of length of aperture. Siphonal fasciole present. Pseudoumbilicus as shallow slit.

Head-foot (Fig. 7A-B). Colour cream in fixed species, Head prominent, small (width ~1/4 of adjacent width of head-foot), cephalic tentacles blunt and of medium size (length ~same as anterior width of head), situated very close to each other, bases lying side by side. Eyes dark, small, rounded, situated in middle region of outer edge of tentacles. Foot short, rounded, its anterior region bifid. Pedal gland as shallow median anterior slit, with anterior furrows extending along entire anterior edge.

Operculum (Fig. 6H-I). Corneous, unguiculate (width ~2/3 of length), filling entire aperture; outer surface opaque, with anterior nucleus; inner surface with attachment scar elongated, elliptical, situated posteriorly, occupying ~2/3 of inner area. Columellar muscle thick, with ~1 whorl in length.

Pallial complex. Pallial cavity of 3/4 whorl; mantle border simple, thickened. Siphon short (length about 1/4 of free portion of mantle edge), margin smooth. Gill, hypobranchial gland osphradium and pallial portion of digestive system not observed.

Circulatory and excretory systems. Not analysed.

Digestive system (Figs 7C-D, 8, 9A-C). Rhynchostome as transversal slit, located slightly below right cephalic tentacle. Proboscis straight, of moderate length (~2/3 of haemocoel length), with thick muscular walls; strong proboscis retractor muscles originating in right ventral posterior wall of proboscis; laterally to proboscis, series of short muscle fibres connect to inner walls of haemocoel. Mouth small, circular. Odontophore long, very slender (~1/2 total length of proboscis). Pair of odontophore cartilages dorsally concave, fused anteriorly at ~1/5 of total cartilage length; series of transversal muscle fibres connect odontophore tube with anterior esophagus, and series of

Fig. 6. – *Hemipolygona beckyae*. A-B, 55.4 mm (MZSP 69764); C-E, 52.4 mm (MZSP 57053); F-G, 38.2 mm (MZSP 69482); H, operculum internal view; I, operculum external view; J, radula; K, detail of rachidian tooth. Scale bars: H-I, 3 mm; J-K, 30 mm.

thin muscle fibres, superficial circular muscles (m3) entirely envelope odontophore, except for most posterior end. Horizontal muscle (m6), on ventral surface of odontophore cartilages, except for most posterior region (~1/6 of total odontophore length). Pair of odontophore retractor muscles (m2) originating from posterior end of odontophore cartilages, near to radular sac, inserted in inner wall of proboscis. Pair of accessory odontophore retractor muscles (m2a), originating from inner surface of proboscis, near origin of m2, running adjacent to esophagus, insertion enveloping radular sac; pair of secondary, long branches of m2a accompanying anterior aorta reaching up to posterior level of nerve ring. Pair of dorsal tensor muscles of radula (m4) originating from posterior dorsal end of odontophore, covering its dorsal surface, inserting m2a. Pair of auxiliary dorsal tensor muscles of radula (m5) originating from posterior end of odontophore, covering its ventral

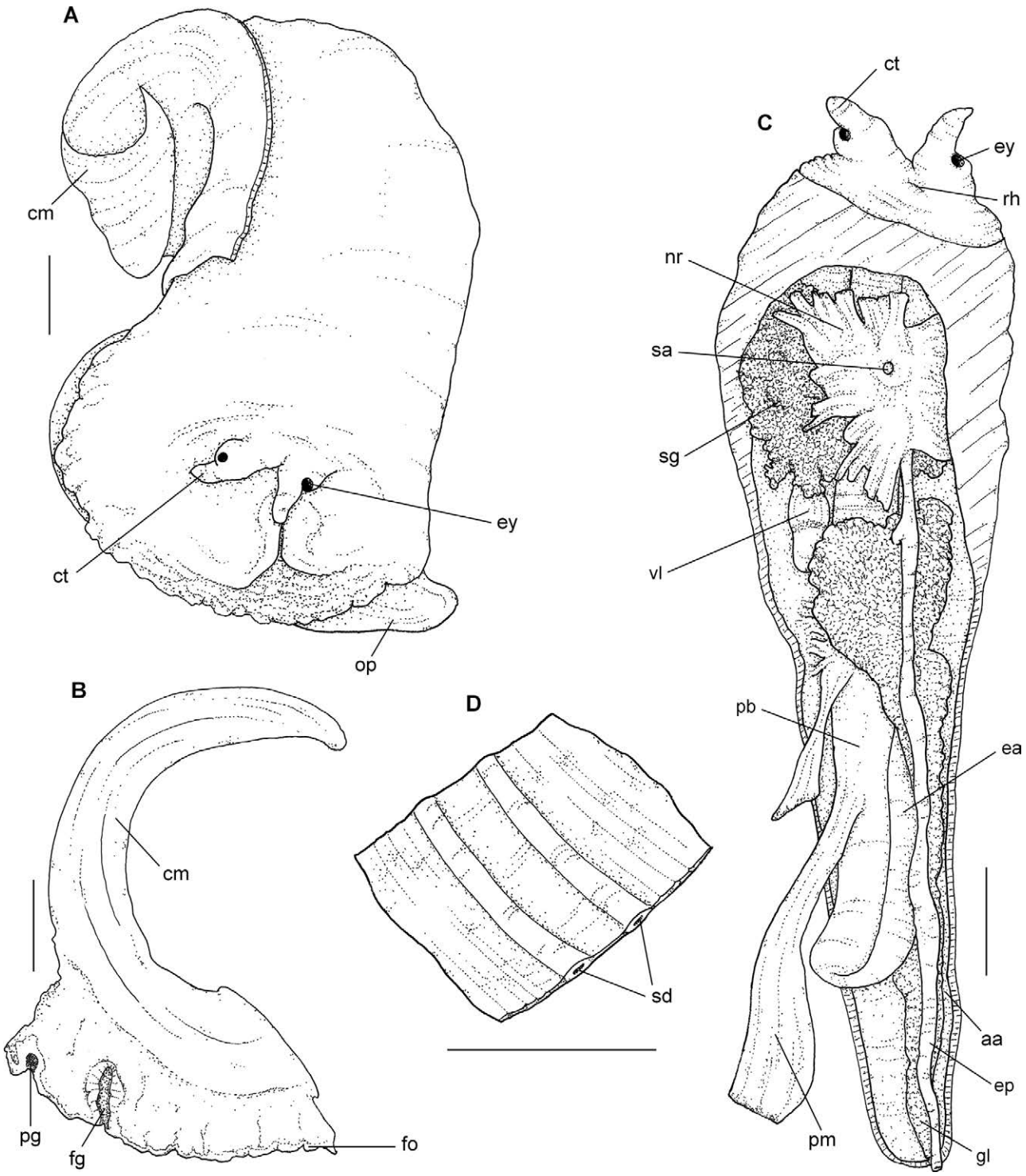

Fig. 7. – *Hemipolygona beckyae*. A, head-foot mass in dorsal view; B, longitudinal section of head-foot mass, female; C, haemocoel in ventral view; D, lumen of anterior esophagus. Abbreviations: aa, anterior aorta; cm, columellar muscle; ct, cephalic tentacle; ea, anterior esophagus; ep, posterior esophagus; ey, eye; fg, female cement gland; fo, foot; gl, gland of Leiblein; nr, nerve ring; op, operculum; pb, proboscis; pg, pedal gland; rh, rhynchostoma; sa, statocyst; sd, salivary gland duct; sg, salivary gland. Scale bars: A-C, 2 mm; D, 0.5 mm.

surface, inserting in m2a. Pair of ventral tensor muscles of radula (m11), inserting anteriorly in subradular membrane, running ventrally adhered (~2/3 of total odontophore length), their origin bifid: main branch originating in ventral posterior cartilage of odontophore near origin of m2; secondary branch originating ventrally in m2a, crossing m6 dorsally, connecting in main branch, (at ~2/3 of total m11 length). Radula long and thin; radular sac extending beyond posterior end of odontophore. Radular teeth (Fig. 6J-K): rachidian tooth straight, rectangular, its base with concave outline and its cusped margin slight convex outline, with 3 sharp cusps of equal size; lateral tooth wider than long, bearing 8-9 prominent and centrally recurved cusps of

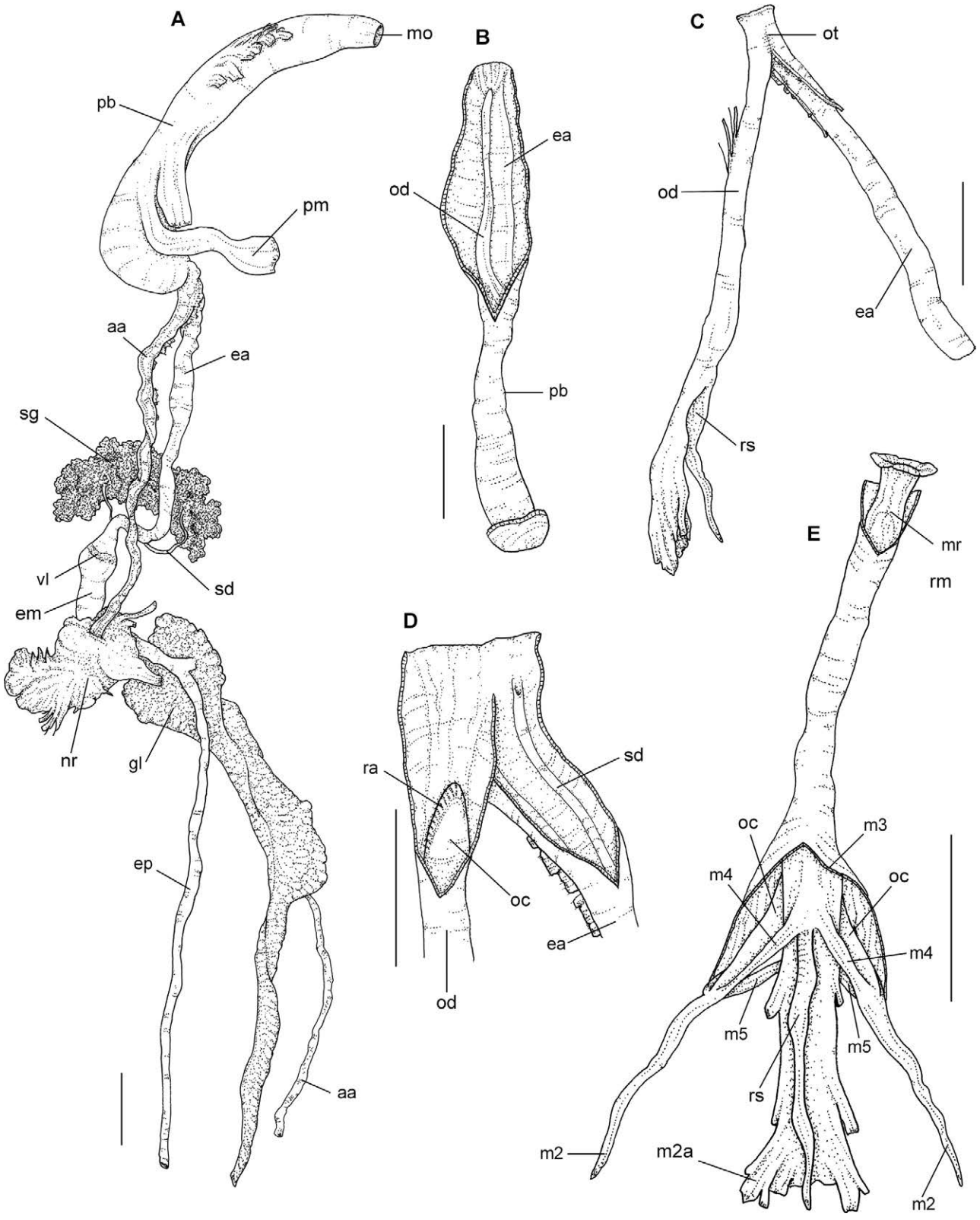

Fig. 8. – *Hemipolygona beckyae*. A, anterior digestive system; B, proboscis opened anteriorly in lateral view; C, buccal mass in lateral view; D, buccal mass in lateral view, opened longitudinally; E, odontophore in dorsal view. Abbreviations: aa, anterior aorta; ea, anterior esophagus; ep, posterior esophagus; gl, gland of Leiblein; m2, odontophore retractor muscles; m2a, accessory odontophore retractor muscles; m3, superficial circular muscles; m4, dorsal tensor muscles of radula; m5, auxiliary dorsal tensor muscles of radula; m6, horizontal muscle; mo, mouth opening; nr, nerve ring; oc, odontophore cartilage; od, odontophore tube; ot, oral tube; ra, radula; rm, subradular membrane; rs, radular sac; sd, salivary gland duct; sg, salivary gland; vl, valve of Leiblein. Scale bars: A-B, 2 mm; C-E, 1 mm.

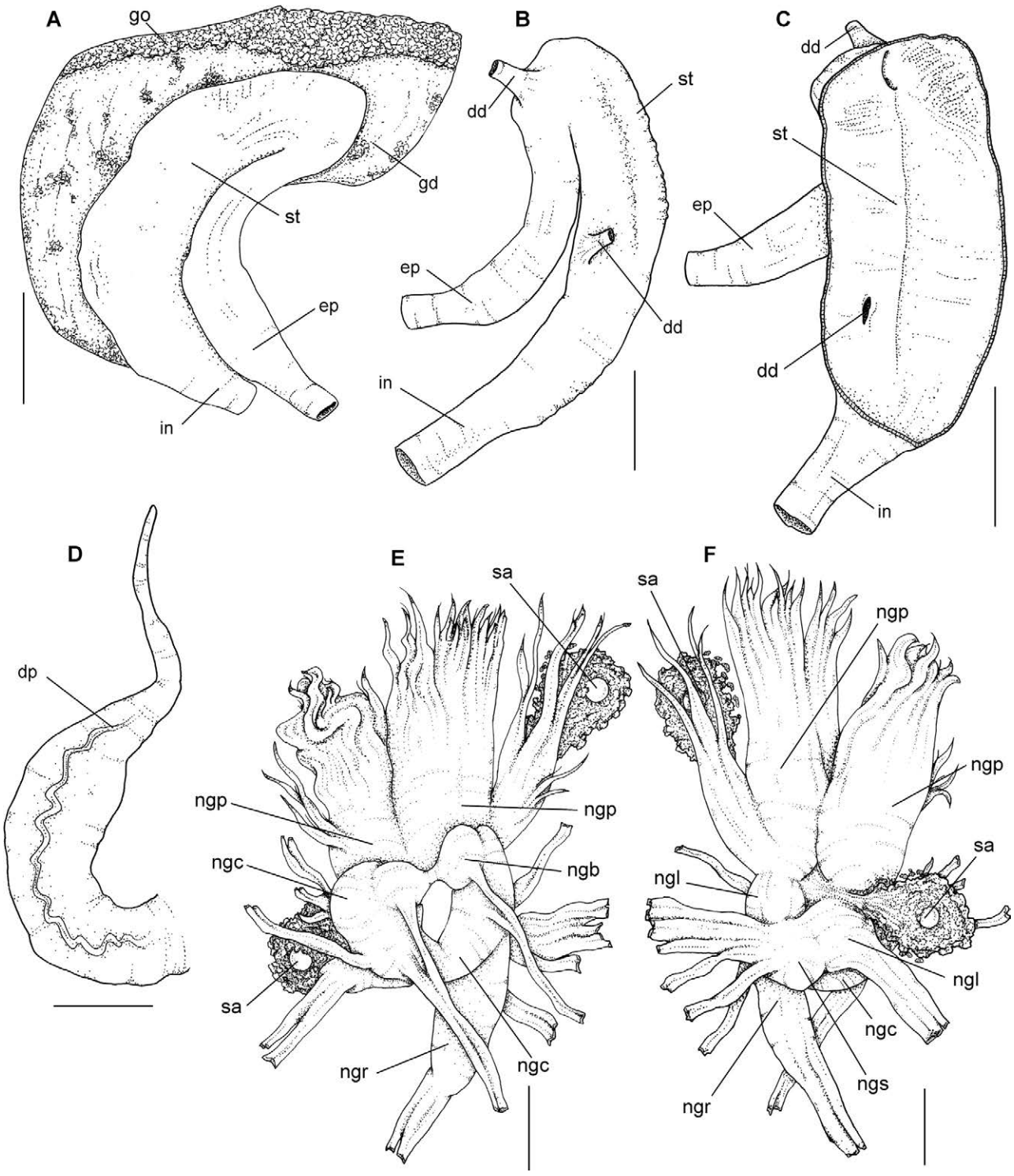

Fig. 9. – *Hemipolygona beckyae*. A, stomach in dorsal view; B, stomach in ventral view; C, stomach shown internally; D, penis in dorsal; E, nerve ring in dorsal view; F, nerve ring in ventral view. Abbreviations: dd, duct of digestive gland; dp, duct of penis; ep, posterior esophagus; in, intestine; nbl, pleural ganglion; ngb, buccal ganglion; ngc, cerebral ganglion; ngp, pedal ganglion; ngr, supra-esophageal ganglion; ngs, subesophageal ganglion; sa, statocyst. Scale bars: A-D, 2 mm; E-F, 0.5 mm.

approximately same size, except for innermost ~1/2 smaller than rest, lateral margin acute, terminating in external cusp. Anterior esophagus moderately long and broad (~2× proboscis length), dorsally-ventrally compressed, originating in oral tube. Valve of Leiblein pyriform, as an orange ring around esophagus, ~2× esophagus width. Salivary glands just anterior to valve of Leinblein, as pair of amorphous masses; free portion of salivary ducts short, extending to esophagus anteriorly to valve of Leiblein, where ducts become embedded with esophagus wall, following anteriorly and opening in esophagus lumen, immediately before

oral tube. Accessory salivary glands absent. Middle esophagus short; duct of gland of Leiblein short, situated after nerve ring. Gland of Leiblein brownish, long, of ~same length as posterior esophagus, posterior end acute. Posterior and anterior esophagus of ~same width. Inner wall of anterior esophagus with thin dorsal longitudinal folds, salivary ducts immersed in marked lateral folds. Stomach as wide sac with thin walls bearing many internal folds. Digestive gland dark brown, occupying all whorls of visceral mass, from apex to kidney/pericardium area, surrounding stomach and emitting two narrow ducts that discharge into stomach near esophagus and intestine apertures. Pallial portion of digestive system not analysed.

Male genital system (Fig. 9D). Testis brownish. Visceral and pallial portion of male genital system not observed. Penis long and thin, close to head-foot mass, ~circular in transverse section; at ~2/3 of its length penis becomes narrower (~1/4 diameter), terminating in short, blunt extension; duct of penis linear.

Female genital system (Fig. 7B). Ovaries same colour and texture as testis. Female cement gland opening at ~1/3 from anterior edge of foot, forming shallow sac (~1/2 foot thickness).

Nervous system (Fig. 9E-F). Nerve ring highly concentrated, occupying ~1/4 of total hemocoel area, surrounding mid-esophagus posteriorly. All commissures and internal. Cerebral ganglia bean-shaped, occupying ~1/3 of total nerve ring volume, of about same size, posterior halves broadly connected; pair of lateral tentacular nerves follow pedal aorta anteriorly. Pleural ganglia as pair of bulges ventral to cerebral ganglia, strongly attached to these; left pleural ganglia emits thick nerve that accompanies proboscis anteriorly. Pedal ganglia anterior, elongated, ~1/2 of total nerve ring volume, emitting anterior zigzag nerves; right pedal ganglion slightly larger and dorsal than left. Buccal ganglia subcircular, ~1/3 of cerebral ganglia and dorsal to these, emitting pair of nerves that form cerebro-buccal nerves, that follow anterior aorta anteriorly. Supra-esophageal ganglion posterior to cerebro-pleural ganglia complex, elongated, ~same volume as cerebral ganglion, emitting thick osphradial nerve. Subesophageal ganglion as ventral bulge in left cerebro-pleural ganglia complex that emits thick branching pallial-siphon. Pair of vitreous statocysts with one anterior and associated with right pedal ganglion, and one posterior, associated with left pedal ganglion.

DISCUSSION

Ponder (1973) pointed out the anatomical similarity among members of the Buccinoidea, concluding that there are no consistent differences among the families; hence they could be treated as subfamilies (e.g. Buccininae, Fasciolariinae). However, later taxonomic studies (e.g. Bouchet and Rocroi 2005) recognized family entities within the superfamily Buccinoidea. The morphological results obtained in this study are in agreement with the diagnostic characteristics established by Fraussen et al. (2007) for Fasciolariidae. These are the multicuspidate lateral teeth, the straight shape of the rachidian teeth of the radula, the proboscis retractor muscle as a single or paired tuft of fibres, ducts of the salivary glands embedded in the esophagus wall, and the stomach without a posterior mixing area.

The taxonomy of fasciolariids is based on the shell and radula (e.g. Tryon 1880, Thiele 1929-1935, Vermeij and Snyder 2002, 2006), and taxonomic approaches based on soft-part anatomy are few. Anatomical data for the buccinoideans, particularly the stomach (e.g. Kosyan and Kantor 2013, Kantor 1996, Strong 2003), the anterior digestive system including the radula (e.g. Kosyan et al. 2009, Simone 1996) and the reproductive system (Fraussen et al. 2007), suggest that they are highly advanced Neogastropoda that lack accessory salivary glands and anal glands.

The accessory salivary glands and anal glands are synapomorphic to neogastropods (Ponder and Lindberg 1997, Harasewych 1998, Strong 2003, Simone 2011), although these organs are lacking in buccinoideans. Kantor and Fedosov (2009) asserted the dual appearance of the valve of Leiblein in Buccinoidea; therefore, this clade shares none of the previously hypothesized autapomorphies with other neogastropods; and in this case, Neogastropoda is a paraphyletic group.

Historically, the taxonomy of the subfamily Peristerniinae, especially that of *Latirus*, has been confused, because the genus was used indiscriminately to include several species, some of them doubtfully related. *Latirus* was initially considered to have a worldwide distribution. However, Vermeij and Snyder (2006) considered the known geographic range of the genus to be restricted to the western Indo-Pacific, and consequently raised several taxa previously considered as subgenera to genus rank (e.g. *Hemipolygona*) and proposed new genera (e.g. *Pustulatirus, Turrilatirus*).

Vermeij and Snyder (2003) transferred several species to the genus *Benimakia* Habe, 1958, including *Benimakia ogum*, originally described in *Latirus*. These authors characterized *Benimakia* as high-spired fasciolariids with prominent axial ribs and a labral tooth at the end of the central cord of the outer lip. *Benimakia ogum* differs from other species of the genus in having a discontinuous beaded lira on the inner side of the outer lip (Fig. 1A, D), in this respect resembling *Latirus* (Vermeij and Snyder 2003) and *Pustulatirus* (Vermeij and Snyder 2006). Species included in *Benimakia* by Habe (1958) and Vermeij and Snyder (2003) occur in the western Pacific, with the exception of *B. ogum*, which putatively differs from other members of Peristerniinae related to *Latirus* in having a small labral tooth at the end of the basal cord. However, the presence of this tooth is questionable. A labral tooth is not mentioned in the original description by Petuch (1979), nor was it found in the present study (Fig. 1A-F). A pseudoumbilicus is also present, differentiating it from *Benimakia*, although it occurs in *Pustulatirus*. Therefore *B. ogum* clearly belongs to the genus *Pustulatirus*, in agreement with Landau and Vermeij (2012) and Lyons and Snyder (2013).

Table 1. – Main comparative radular features of the Peristerniinae based on our data and those of [1] Couto and Pimenta (2012), [2] Kosyan et al. (2009), [3] Bandel (1984) and [4] Snyder and Bouchet (2006).

	Raquidian		Lateral	
	format	cusps	first cusp	cusps
Pustulatirus ogum	square, base broad	4	developed	11 curved
Hemipolygona beckyae	rectangular, thin, base broad	3	developed	8-9 somewhat curved
Leucozonia nassa [1]	square, broad, base broad	3	vestigial	7-8 curved
Leucozonia ocellata [1]	square, broad, base broad	3	reduced	5-6 curved
Pustulatirus mediamericanus [2]	square, broad, base broad	4	developed	11-12
Peristernia nassatula [2]	Trapezoidal, thin, base thin	3 laterally recurved	well developed	11-12 alternating smaller/larger
Peristernia ustulata [2]	Trapezoidal, thin, base thin	3 laterally recurved	well developed	11-12 alternating smaller/larger
Opeatostoma pseudodon [2]	square, broad, base broad	5	absent	8, central larger
Tarantinae lignaria [2]	square, broad, base broad	3	developed	9 curved
Latirus polygonus [2,3]	square, broad, base broad	3, central longer	developed	11-12 curved
Turrilatirus turritus [2,3]	rectangular, base broad	3	well developed	7 curved
Latirus infundibulum [3]	rectangular, thin, base broad	3 centrally recurved	well developed	7-8 curved
Latirolagena smaragdula [3]	square, base broad	3, central longer	reduced	15-16
Polygona angulata [3]	Trapezoidal, thin, base thin	3	well developed	8-9 curved
Fusolatirus elsiae [4]	Trapezoidal, thin, base thin	3	well developed	12-13 alternating smaller/larger

Hemipolygona beckyae was originally included in *Latirus* by Petuch (1979), and was later allocated to *Hemipolygona* by Snyder (2003), as agreed to by Vermeij and Snyder (2006), due to the highly nodulose shell with a deep slit-like pseudoumbilicus and whitish spiral cords (Fig. 6A-G).

The morphology of the two species is similar and in accordance with other descriptions of fasciolariids (Fraussen et al. 2007, Kosyan et al. 2009, Couto and Pimenta 2012), with the main differences occurring in the anterior digestive and male reproductive systems. Details of the anatomy, histology and ultrastructure of the anterior digestive system (including the radula) have been noted as useful traits for phylogenetic analyses (Ponder and Lindberg 1997), and the anterior structures of the foregut are generally used to distinguish neogastropod families (Fraussen et al. 2007). A recent phylogenetic analysis based on comparative morphology (Simone 2011) consistently recovered all the major caenogastropod clades.

The rhynchostome occurs as a lip-like slit bearing longitudinal lamellar folds, which may be longitudinal to the adjacent head-foot mass as in *P. ogum* (Fig. 3A) or transverse, although located slightly to the right side of the animal, not between its cephalic tentacles as in *H. beckyae* (Fig. 7C).

Golding et al. (2009a) studied the snout and proboscis morphology in species belonging to 33 caenogastropod families, among them a buccinoidean (Columbellidae), but included no fasciolariid. In their study they reported the ventro-lateral insertion of the proboscis retractor muscles as occurring in all Neogastropoda, and the presence of aortic muscles that flank the aorta in the anterior esophagus; both characters are confirmed for members of Fasciolariidae so far studied. On the other hand, Goulding et al. (2009b) studied the anatomy of odontophoral cartilages in Caenogastropoda through the use of micro-CT scanning, although none of the species studied were buccinoideans. This method allows observation of the cartilages in their natural orientation, without anatomical dissections that would otherwise cut or displace structures. Despite the methodological differences, *Pustulatirus ogum* and *H. beckyae* showed a close resemblance to the muricoidean studied by Golding et al. (2009b) in having greatly elongated anterior cartilages and lacking subradular cartilages. As noted by these authors, the Neogastropoda possess the most dramatic modifications of the plesiomorphic odontophoral cartilage morphology. Also, the morphology of the odontophoral cartilages may be conserved within families and superfamilies: hence the resemblance of these structures among the Fasciolariidae (Couto and Pimenta 2012) and to other buccinoideans (Simone 1996, 2011)

The lateral teeth of the radula of the Peristerniinae observed in this study and in *Leucozonia* (Couto and Pimenta 2012) have the innermost cusp (defined as a 'denticle' by Bullock, 1974) as a small projection at its base, next to the rachidian tooth. This projection may vary considerably in size and shape. In *Leucozonia*, it is reduced or even absent (Couto and Pimenta 2012: 1Q, 5G and 9O), while in *P. ogum* (Fig. 1A-J) and *Hemipolygona beckyae* (Fig. 6J-K) it is developed, although smaller than the outer cusps, and recurved outward. All species of Peristerniinae studied by Bullock (1974) and Bandel (1984) have this same conformation, and Bullock (1974) also noted that this feature distinguishes *Latirus* and related species from *Leucozonia*.

Within the Fasciolariidae, members of Peristerniinae possess fewer cusps of the lateral teeth than members of other subfamilies (Bandel 1984, Taylor and Lewis 1995, Snyder and Bouchet 2006). However, recent findings from moderate/deep-sea regions of the Indo-West Pacific led to the description of several species and genera that deviate from this pattern (e.g. *Amiantofusus*, Fraussen et al. 2007; *Chryseofusus*, Hadorn et al. 2008; and *Angulofusus*, Fedosov and Kantor 2012). All aforementioned genera have the radula closer to Peristerniinae than to Fusininae. Table 1 lists relevant radular features of *P. ogum* and *H. beckyae*, as well as those of other members of Peristerniinae compiled from the literature.

According to Fraussen et al. (2007), the ducts of the salivary glands embedded in the esophagus wall is diagnostic for the family; this feature was reported for *Latirus polygonus*, but not for *Pustulatirus mediamericanus, Turrilatirus turritus, Peristernia nassatula, P. ustulata, Opeatostoma pseudodon* and *Tarantinae lignaria* studied by Kosyan et al. (2009), and therefore a reinvestigation is needed in these species. In the species

Table 2. – Comparison between major anatomical features among Peristerniinae species based on this study and literature. Data was extracted, when available, from [1] Couto and Pimenta (2012) and [2] Kosyan et al. (2009); shell characters were taken from various sources.

	Leucozonia nassa [1]	*Leucozonia ocellata* [1]	*Pustulatirus ogum*	*Hemipolygona beckyae*	*Latirus polygonus* [2]	*Turrilatirus turritus* [2]	*Peristernia nassatula* [2]	*Opeatostoma pseudodon* [2]	*Tarantinae lignaria* [2]
Protoconch	2 whorls	1,5 whorls	2 whorls	2 whorls	-	-	-	-	-
Labral tooth	present or absent	absent	absent	absent	absent	absent	absent	present	absent
Outer lip - margin	smooth	smooth	crenulated	crenulated	crenulated	crenulated	-	-	-
Outer lip - inner side	discontinuous lirae	discontinuous lirae	continuous or discontinuous lirae	continuous or discontinuous lirae	discontinuous lirae	continuous lirae	-	-	-
Siphonal fasciole	present or absent	present or absent	absent	absent	absent	absent	-	-	-
Pseudoumbilicus	usually present	usually absent	present	present	present	absent	-	-	-
Head	prominent, 1/2 width of foot	prominent, 1/2 width of foot	medium-sized, 1/3 width of foot	small, 1/4 width of foot	-	-	-	-	-
Cephalic tentacles	large, length 1/2 the width of head	small, length 1/5 the width of head	large, length 1/2 the width of head	very large, same length of width of head	-	-	-	-	-
Columellar muscle	1.5 whorls	1.5 whorls	1.25 whorls	1 whorl	-	-	-	-	-
Pallial cavity	1 whorl	3/4 whorl	1 whorl	3/4 whorl	-	-	-	-	-
Osphradium	symmetrical	non-symmetrical	symmetrical	-	non-symmetrical	-	non-symmetrical	non-symmetrical	non-symmetrical
Osphradium leaflets	sharp, 2/3 height of ctenidium filaments	rounded, same height of ctenidium filaments	sharp, 1/2 the height of ctenidium filaments	-	-	-	-	-	-
Ctenidium filaments	triangular, 1.5 times width of osphradium	triangular, twice the width of osphradium	triangular, same width of osphradium	-	-	-	-	-	-
Rhynchostome	transversal, central, smooth	transversal, central, smooth	longitudinal, central, rimmed by longitudinal folds	transversal, non-central, rimmed by longitudinal folds	-	-	-	-	-
Odontophore	40% fused	30% fused	25% fused	-	-	-	-	-	-
Buccal mass	same length as proboscis	same length as proboscis	2/3 length of proboscis	1/2 length of proboscis	same length as proboscis	1/2 length of proboscis	1/2 length of proboscis	same length as proboscis	same length as proboscis
Proboscis muscles	single	single	1 pair	single	1 pair	single	single	1 pair	single
Salivary ducts	embedded	embedded	embedded	embedded	embedded	free	free	free	free
Valve of Leiblein	1.5 width of esophagus	same width of esophagus	1.5 width of esophagus	2 times width of esophagus	-	-	-	-	-
Penis tapering	1/2 total penis length	1/3 total penis length	diminute	1/3 total penis length	-	-	-	-	-
Nephridial gland	indistinct	indistinct	distinct	-	-	-	-	-	-
Pericardium	1/3 renal cavity area	1/3 renal cavity area	1/5 renal cavity area	-	-	-	-	-	-
Buccal ganglia	1/2 the length of buccal ganglia	internal commissure	internal commissure	1/3 the length of buccal ganglia	-	-	-	-	-
Posterior statocyst	ventral to pedal ganglia	ventral to pedal ganglia	ventral to pedal ganglia	left of pedal ganglia	-	-	-	-	-

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studied here and those reported by other authors (e.g. Marcus and Marcus 1962, Couto and Pimenta 2012, Fedosov and Kantor 2012), this feature also occurs.

Hemipolygona beckyae has a single powerful proboscis retractor muscle, which emerges posteriorly and ventrally from the proboscis (Fig. 8A). *Pustulatirus ogum* has a pair of muscles (Fig. 3B). In the species studied by Kosyan et al. (2009), all fasciolariids but *Latirus polygonus* and *Fusinus tenerifensis* have a single muscle, while in the buccinids multiple fibres occur posteriorly to the proboscis. Golding et al. (2009a) distinguished different proboscis types among caenogastropods, although they studied only one species of Buccinoidea, the columbellid *Euplica scripta*, which possesses two ventro-lateral proboscis retractors, resembling those of *H. beckyae*. Both fasciolariids have the proboscis retractor passing outside the nerve ring and originating in the posterior hemocoel floor, near the diaphragm septum.

Kantor (2003) distinguished species of Fasciolariidae from other buccinoideans by the low relief of the folds on the inner stomach wall; presence of transverse striations on the low longitudinal fold; absence of clear differentiation of the gastric chamber into dorsal and ventral parts; absence of a posterior mixing area; and a shallow lateral sulcus. Despite this thorough examination of representatives of the three subfamilies (Fasciolariinae: *Fasciolaria lilium, F. filamentosa*; Fusininae: *Fusinus nicobaricus* and Peristerniinae: *Leucozonia nassa*), Kantor (2003) noted the difficulties of examination and the necessity of specially preserved specimens for stomach analysis, although the differences observed are likely due to phylogenetic relationships. While both *P. ogum* and *H. beckyae* have stomach morphology similar to the fasciolariids cited by Kantor (2003), species-level differentiation is unlikely.

Both species, as well as *Leucozonia* (Marcus and Marcus 1962, Couto and Pimenta 2012), have penises with terminal tapering. In *Leucozonia* (Couto and Pimenta 2012: Figs 4E and 8F) and *H. beckyae* (Fig. 9D) the terminal extension extends for more than half of the total penis length, while in *P. ogum* it extends less than half of its length (Fig. 4F).

Several morphological characters occur in both species and also occur diffused among other fasciolariids (Fraussen et al. 2007, Kosyan et al. 2009, Couto and Pimenta 2012). These include the outline of the gill lamellae, the length and anterior fusion of the odontophore cartilages, and the extension of the anus to the edge of the pallial cavity. For this reason, the soft-part traits of *Latirus* and related species studied so far do not allow a precise anatomical diagnosis. Table 2 lists the main differentiating characteristics.

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REFERENCES

Bandel K. 1984. The Radulae of Caribbean and other Mesogastropoda and Neogastropoda. Riiksmuseum van Natuurlijke Historie, 346 pp. 22 pls.

Bouchet P., Rocroi J.P. 2005. Classification and nomenclator of gastropod families. Malacologia 47(1-2): 397 pp.

Bullock R.C. 1974. A contribution to the systematics of some West Indian *Latirus* (Gastropoda: Fasciolariidae). Nautilus 88(3): 69-79.

Couto D.R., Pimenta A.D. 2012. Comparative morphology of *Leucozonia* from Brazil (Neogastropoda: Buccinoidea: Fasciolariidae). Am. Malacol. Bull. 30(1): 103-116. http://dx.doi.org/10.4003/006.030.0108

Fedosov A.E., Kantor Y.I. 2012. A new species and genus of enigmatic turriform Fasciolariidae from the Central Indo-Pacific (Gastropoda: Neogastropoda). Arch. Molluskenkunde 141(2): 137-144.

Fraussen K., Kantor Y.I., Hadorn R. 2007. *Amiantofusus* gen. nov. for *Fusus amiantus* Dall, 1889 (Mollusca: Gastropoda: Fasciolariidae) with description of a new and extensive Indo-West Pacific radiation. Novapex 8(3-4): 79-101.

Gofas S. 2014. Fasciolariidae Gray, 1853. Accessed through: World Register of Marine Species on 2014-07-15, at http://www.marinespecies.org/aphia.php?p=taxdetails&id=23038

Golding R.E., Ponder W.F., Byrne M. 2009a. The evolutionary and biomechanical implications of snout and proboscis morphology in Caenogastropoda (Mollusca: Gastropoda). J. Nat Hist. 43(43-44): 2723-2763. http://dx.doi.org/10.1080/00222930903219954

Golding R.E., Ponder W.F., Byrne M. 2009b. Three-Dimensional Reconstruction of the Odontophoral Cartilages of Caenogastropoda (Mollusca: Gastropoda) Using Micro-CT: Morphology and Phylogenetic Significance. J. Morphol. 270: 558-587.

Habe T. 1958. On the radulae of Japanese marine gastropods. Venus 20: 43-60.

Hadorn R., Snyder M.A., Fraussen K. 2008. A new *Chryseofusus* (Gastropoda: Fasciolariidae: Fusinus) from South and Western Australia. Novapex 9(2-3): 95-99.

Harasewych M.G. 1998. Family Fasciolariidae. In: Beesley P.L., Ross G.J.B., Wells A. (eds), Mollusca: The Southern Synthesis. Fauna of Australia. CSIRO publishing, Melbourne, pp 832-833.

Kantor Y.I. 1996. Phylogeny and relationships of Neogastropoda. In: Taylor J.D. Origin and evolutionary radiation of the Mollusca. Oxford Univ. Press, pp 221-230.

Kantor Y.I. 2003. Comparative anatomy of the stomach of Buccinoidea (Neogastropoda). J. Moll. Stud. 69(3): 203-220. http://dx.doi.org/10.1093/mollus/69.3.203

Kantor Y.I., Fedosov A. 2009. Morphology and development of the valve of Leiblein: possible evidence for paraphyly of the Neogastropoda. Nautilus 123(3): 1-73.

Kosyan A.R., Kantor Y.I. 2009. Phylogenetic analysis of the subfamily Colinae (Neogastropoda, Buccinidae) based on morphological characters. Nautilus 123: 83-94.

Kosyan A.R., Kantor Y.I. 2013. Revision of the genus *Aulacofusus* Dall, 1918 (Gastropoda: Buccinidae). Ruthenica 23(1): 1-33.

Kosyan A.R., Modica M.V., Oliverio M. 2009. The anatomy and relationships of *Troschelia* (Neogastropoda, Buccinidae): New evidence for a closer fasciolariid-buccinid relationship? Nautilus 123: 95-105.

Landau B., Vermeij G.J. 2012. The Peristerniinae (Mollusca: Gastropoda, Buccinoidea, Fasciolariidae) from the Neogene of Venezuela. Cainozoic Res. 9(1): 87-99.

Lyons W.G., Snyder M.A. 2013. The genus *Pustulatirus* Vermeij and Snyder, 2006 (Gastropoda: Fasciolariidae: Peristerniinae) in the western Atlantic, with descriptions of three new species. Zootaxa 3636(1): 35-58. http://dx.doi.org/10.11646/zootaxa.3636.1.2

Mallard D., Robin A. 2005. Fasciolariidae. La Mothe Achard, Les Sables-d'Olonne, France, 27 pp. 70 pls.

Marcus E., Marcus E. 1962. On *Leucozonia nassa*. Bol. Fac. Fil Cienc. Letr. Univ. São Paulo, Zool. 24: 11-30.

Petuch E.J. 1979. New Gastropods from the Abrolhos reef archipelago and reef complex, Brazil. Proc. Biol. Soc. Wash. 92(3): 520-526.

Petuch E.J. 1987. New Caribbean Molluscan Faunas. The Coastal education and Research foundation [CERF], Charlottesville, Virginia. 154 pp. A1-A4.
Ponder W.F. 1973. The Origin and Evolution of the Neogastropoda. Malacologia 12(2): 295-338.
Ponder W.F., Lindberg D.R. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. Zool. J. Linn. Soc. 119: 83-265. http://dx.doi.org/10.1111/j.1096-3642.1997.tb00137.x
Rios E.C. 1985. Seashells of Brazil. Museu Oceanográfico, Fundação Univesidade do Rio Grande, Rio Grande, 328 pp.
Rios E.C. 1994. Seashells of Brazil. Museu Oceanográfico Prof. E. C. Rios, Fundação Universidade do Rio Grande, Rio Grande, 368 pp. 113 pls.
Rios E.C. 2009. Compendium of Brazilian Sea Shells. Museu Oceanográfico Prof. E. C. Rios, Fundação Universidade do Rio Grande, Rio Grande, 668 pp.
Rosenberg G. 2009. Malacolog 4.1.0: A Database of Western Atlantic Marine Mollusca http://www.malacolog.org/
Simone L.R.L. 1996. Anatomy and systematics of *Buccinanops gradatus* (Deshayes, 1844) and *Buccinanops moniliferus* (Kiener, 1834) (Neogastropoda, Muricoidea) from the Southeastern coast of Brazil. Malacologia 38(1-2): 87-102.
Simone L.R.L. 2011. Phylogeny of the Caenogastropoda (Mollusca), based on comparative morphology. Arq. Zool. Mus. Zoo. Univ. São Paulo 42(2-4): 83-323.
Simone L.R.L., Cavallari D.C., Abbate D. 2013. Revision of the genus *Teralatirus* Coomans 1965 in the Western Atlantic, with an anatomical description of *T. roboreus* (Reeve 1845) (Gastropoda: Neogastropoda: Fasciolariidae). Arch. Molluskenkunde 142(2): 215-226.
Snyder M.A. 2000. *Latirus beckyae*, a new species of Fasciolariidae (Gastropoda: Neogastropoda) from Brazil. Nautilus 114(4): 161-163.
Snyder M.A. 2003. Catalogue of the marine gastropod family Fasciolariidae. Acad. Nat. Sci. Phila. Spec. Publ. 21. Philadelphia, iv + 431 pp.
Snyder M.A., Bouchet P. 2006. New species and new records of deep-water *Fusolatirus* (Neogastropoda: Fasciolariidae) from the West Pacific. J. Conchology 39: 1-12.
Strong E.E. 2003. Refining molluscan characters: morphology, character coding and a phylogeny of the Caenogastropod. Zool. J. Linn. Soc. 137: 447–554. http://dx.doi.org/10.1046/j.1096-3642.2003.00058.x
Taylor J.D., Lewis A. 1995. Diet and radular morphology of *Peristernia* and *Latirolagena* (Gastropoda: Fasciolariidae) from Indo-Pacific coral reefs. J. Nat. Hist. 29(5): 1143-1154. http://dx.doi.org/10.1080/00222939500770481
Thiele J. 1929-1935. Handbuch der Systematischen Weichtierkunde. Gustav Fischer, Jena vol 1: vi + 778 pp. vol. 2: v + 779-1134 pp.
Tryon G.W. 1880. Manual of Conchology, Structural and Systematic, with Illustrations of the Species. Philiadelphia. 310 pp. 87 pls.
Vermeij G.J., Snyder M.A. 1998. *Leucozonia ponderosa*, a new fasciolariid gastropod from Brazil. Nautilus 112: 117-119.
Vermeij G.J., Snyder M.A. 2002. *Leucozonia* and related genera of Fasciolariid Gastropods: shell-based taxonomy and relationships. Proc. Acad. Nat. Sci. Phila. 152: 23-44. http://dx.doi.org/10.1635/0097-3157(2002)152[0023:LARGOF]2.0.CO;2
Vermeij G.J., Snyder M.A. 2003. The fasciolariid gastropod genus *Benimakia*: new species and a discussion of Indo-Pacific genera in Brazil. Proc. Acad. Nat. Sci. Phila. 153: 15-22. http://dx.doi.org/10.1635/0097-3157(2003)153[0015:TFGGBN]2.0.CO;2
Vermeij G.J., Snyder M.A. 2006. Shell characters and taxonomy of *Latirus* and related fasciolariid groups. J. Moll. Stud. 72(4): 413-424. http://dx.doi.org/10.1093/mollus/eyl020