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VANINIA, A NEW DEEPWATER GENUS OF CALLIOSTOMATIDAE (VETIGASTROPODA) FROM THE SOUTHWESTERN ATLANTIC, WITH DESCRIPTION OF A NEW SPECIES

Luiz Ricardo L. Simone^{1*} & Ana Paula Dornellas²

ABSTRACT

Additional material of previously described species attributed to *Margarites* J. E. Gray, 1847 and *Falsimargarita* A. W. B. Powell, 1951 from Brazil was examined using detailed anatomical data and constructing a morphological phylogeny. The new analysis revealed that these taxa are more closely related to the Calliostomatidae and should be placed in the new genus ***Vaninia***, with the type species *Margarites imperialis* Simone & Birman, 2006. The following new combinations and species are proposed: *Vaninia dnophera* (Watson, 1879) *comb. nov.*; *Vaninia mirabilis* (Simone & Birman, 2006) *comb. nov.*; and ***Vaninia vanini gen. nov. sp. nov.*** The placement of ***Vaninia gen. nov.*** as a calliostomatid is supported mainly by radular synapomorphies, including the presence of long, delicate, serrated rachidian teeth and an enlarged innermost pair of marginal teeth. ***Vaninia gen. nov.*** differs from other calliostomatid genera primarily by its thinner shell lacking strong color and pattern, a protoconch without a honeycomb pattern, the absence of a pseudoproboscis, no intestinal loop inside of the hemocoel, and the presence of a brood pouch in the right kidney.

Key words: Calliostomatidae, new genus, new species, morphology, phylogeny, southern Brazil.

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INTRODUCTION

Calliostomatidae is a species-rich family of trochoideans, divided into five extant subfamilies: Calliostomatinae Thiele, 1924; Thysanodontinae Marshall, 1988; Fautricinae Marshall, 1995; Xeniostomatinae McLean, 2012; and Margarellinae Williams, 2013 (Williams, 2012; McLean, 2012; Marshall, 2016). It is characterized primarily by a honeycomb-patterned protoconch, a radula with a long, delicate, finely serrate rachidian, and a greatly enlarged innermost marginal tooth. The calliostomatids also exhibit typical anatomical features, including the presence of a pseudoproboscis, an oral disk with projecting papillae, and a buccal cavity with a cuticularized lining (Hickman & McLean, 1990; Hickman, 1996; Dornellas & Simone, 2013). However, some studies have proposed new arrangements for the family, e.g., the inclusion of Margarellinae within Calliostomatidae (Williams, 2012) and the description of a new subfamily, Xeniostomatinae (McLean, 2012), suggesting that

this set of characters defining the family could need future re-evaluation.

The taxonomy of Calliostomatidae and Margaritidae, particularly the genera *Calliostoma* Swainson, 1840, *Margarella* Thiele, 1893, and *Margarites* J. E. Gray, 1847, has a convoluted history, because these groups were all once considered part of Trochidae (e.g., Rios, 2009). Even now, species boundaries and generic placements within these families remain poorly understood. For example, *Trochus (Margarita) dnopherus* Watson, 1879, was placed in *Calliostoma* by Quinn (1992) and in *Margarites* by Simone & Birman (2006). Additionally, recent molecular and phylogeographic studies reassigned five of the 24 species from *Margarella* to *Cantharidus* Montfort, 1810 (Trochidae: Cantharidinae) (González-Wevar et al., 2021). This highlights the ongoing taxonomic flux within the superfamily Trochoidea. Notably, the number of recognized families within Trochoidea has recently grown to 25 (MolluscaBase, 2024), with many still lacking clear morphological definitions.

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The southwestern Atlantic Calliostomatidae encompass ~35 species, including Antarctic and sub-Antarctic species (Powell, 1951; Dornellas, 2012; Cavallari & Simone, 2018; González-Wevar et al., 2021). The Margaritidae of the Atlantic coast of South America consists of 16 species distributed among three genera: *Margarites*, *Gaza* Watson, 1879, and *Callogaza* Dall, 1881 (Simone & Cunha, 2006; Simone & Birman, 2006; Rios, 2009).

Additional material collected over recent decades has provided new anatomical insights, particularly for Brazilian representatives of these genera. A morphological phylogeny was conducted to determine the placement of these taxa within Trochoidea. The results strongly suggest that they belong to a new genus within the Calliostomatidae family. Furthermore, a new species has been described from off of the coast of São Paulo and Santa Catarina. This paper formally introduces these discoveries.

MATERIAL AND METHODS

Samples and Taxonomy

The complete list of examined material is provided in the description for each species. Dry shells are reported as “shells,” whereas live-collected specimens preserved in 70% ethanol are referred to as “specimens” (spms). All material is deposited in the collection of the Museu de Zoologia da Universidade de São Paulo (MZSP). The other repository cited herein is The Natural History Museum, London (NHMUK).

The animals were removed from their shells and dissected using standard techniques (Simone, 2011), with the animal immersed in fixative and examined under a stereomicroscope. Composite drawings from multiple animals were made with a camera lucida. All steps of the dissections were photographed using a digital camera attached to the microscope. A more detailed description is provided for *Falsimargarita imperialis* (Simone & Birman, 2006); for the remaining species, the focus is on distinctive anatomical characters.

Abbreviations: af, afferent gill vessel; an, anus; ap, genital aperture; bp, brood pouch; br, subradular membrane; cc, cerebral commissure; ce, cerebral ganglia; cm, columellar muscle; cv, ctenidial vein; dd, duct to digestive gland; dg, digestive gland; ec, esophageal

crop; ef, esophageal folds; eg, esophageal gland inside crop; ep, epipodium; es, esophagus; et, epipodial tentacle; ey, eye; fs, foot sole; gd, gill right (dorsal) filament; gi, gill or left (ventral) gill filament; gl, glandular portion of brood pouch; ft, foot; go, gonad; he, head; hg, hypobranchial gland; ih, intestinal loop inside haemocoel; in, intestine; jw, jaws; ki, left kidney; lc, cephalic lobe; ln, neck lobe; m1–m11, odontophore muscles; mb, mantle edge; mj, jaw and peribuccal muscle; mo, mouth; ms, gill suspensory membrane; mt, mantle; ne, nephrostome; nr, nerve ring; oc, anterior odontophore cartilage; od, odontophore; om, ommatophore (eye stalk); on, osphradial nerve; os, osphradium; ov, ova; pc, pericardium; pd, pedal ganglia; pg, pedal gland anterior furrow; pl, pleural ganglia; po, posterior cartilage; ra, radula; rn, radular nucleus; rt, rectum; rs, radular sac; sa, anterior papillated surface of snout; sc, subradular cartilage; sg, salivary gland; sn, snout; st, stomach; su, suprabranchial chamber; sy, statocyst; tg, integument; to, tissue in anterior region of radular sac; te, cephalic tentacle; un, fusion of anterior odontophoral cartilages; vf, pair of ventral buccal folds.

Phylogenetic Analysis

The data from the morphological phylogeny of Tegulinae (Dornellas et al., 2020: see MorphoBank (<http://www.morphobank.org/>); Project 3392) was expanded with *Margarites* sp., *Margarites amabilis* Simone & Birman, 2006, and *Falsimargarita imperialis*, whereas 11 tegulids and four homoplastic characters (characters 5, 40, 53, and 77 of Dornellas et al., 2020) were removed. The new data matrix consists of 27 terminals with 128 morphological characters (MorphoBank: Project 4512).

A parsimony analysis was performed with TNT (Goloboff et al., 2008) with New Technology algorithms and the following parameters: sectorial search (Goloboff, 1999) in default mode, 20 interactions of ratchet (Nixon, 2002), 20 cycles of drift (Goloboff, 1999), and five rounds of tree fusing (Goloboff, 1999). Branch support was assessed using nonparametric bootstrap (Felsenstein, 1985) and Bremer decay index (Bremer, 1994). Character optimizations were examined using Winclada (Nixon, 2002). In case of ambiguity, both ACCTRAN and DELTRAN optimizations were applied.

RESULTS

Systematics

Superfamily Trochoidea Rafinesque, 1815
Family Calliostomatidae Thiele, 1924

Genus *Vaninia* gen. nov.

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4648-951A-CEC1E17824FC

Diagnosis: Shell slightly discoid, suture deep, rather iridescent; sculpture spiral, with dotted subsutural cord(s). Large brood pouch in females. Deep-water environment.

Description: Shell trochiform, slightly discoid. Iridescent. Protoconch simple, smooth, of one whorl, maximum width 0.6–0.7 mm. Sculpture predominantly spiral, with one or two crenelated subsutural cords. Umbilicus closed to slightly open. Snout with anterior wide projection, ventrally papillated. Epipodium tentacles not paired. Radula with long, serrate teeth; rachidian with flattened shaft; lateral teeth with square base and shaft without interlocking with adjacent marginals; innermost marginal tooth enlarged. Odontophore with posterior transverse muscle (m9). Esophagus wide, lacking chambers. Stomach simple, lacking appendices. Female with large brood pouch, opening through right kidney.

Etymology: The generic name is in honor of the late entomologist and shell collector Sergio Antonio Vanin, Instituto de Biociências, U.S.P., our mentor and source of inspiration. Gender feminine.

Included species: *Vaninia imperialis* (Simone & Birman, 2006), the type species; *Vaninia mirabilis* (Simone & Birman, 2006); *Vaninia dnophera* (Watson, 1879), all new combinations; *Vaninia vanini* sp. nov.

Vaninia imperialis (Simone & Birman, 2006)
comb. nov.
Figs. 1–23

Margarites imperialis Simone & Birman, 2006: 14 (figs. 6–10); Rios, 2009: 48 (fig. 104: as synonym of *M. dnopherus*); Dornellas & Simone, 2011: 19 (figs. 6–10); Dornellas et al., 2021: 61 (figs. A–C).

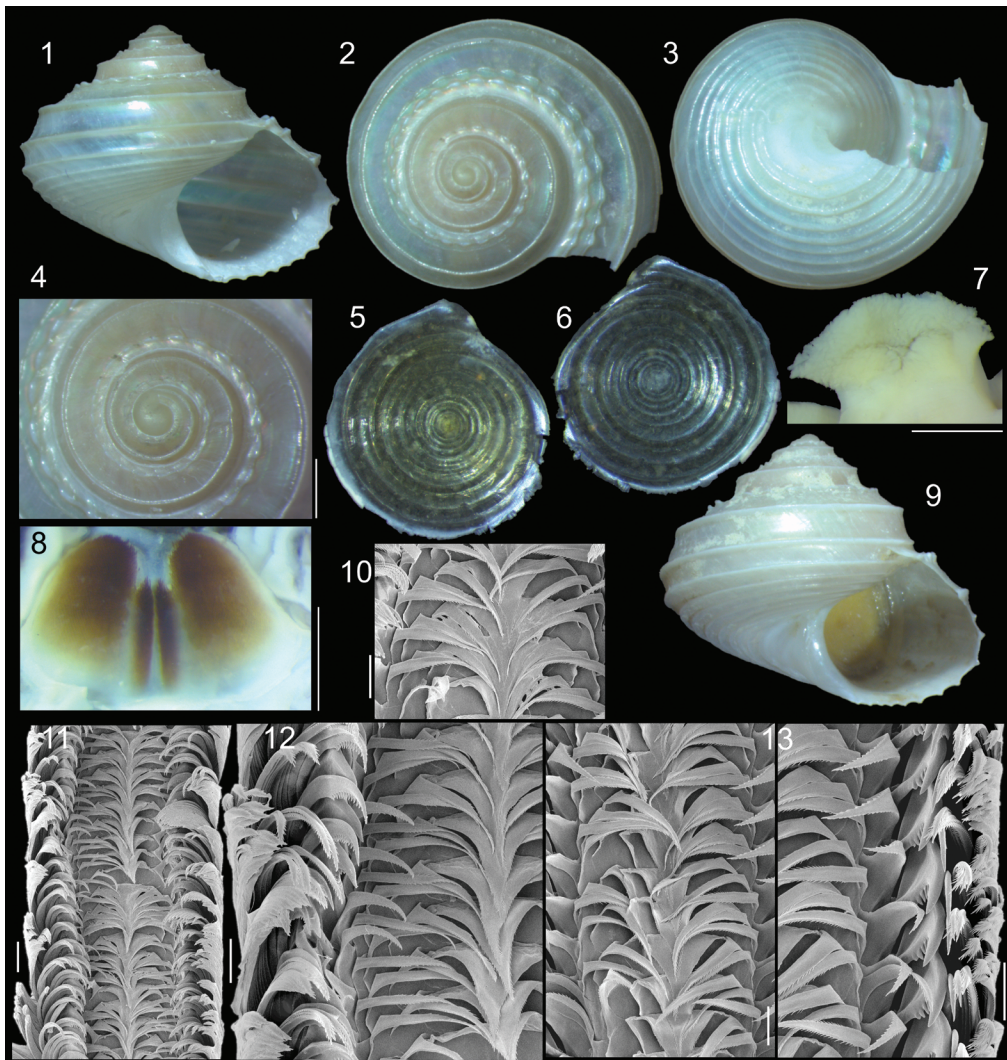
Falsimargarita imperialis: Marshall, 2016: 11, 16; MolluscaBase, 2024.

Description: Shell (Figs. 1–4, 9): Height/width ratio ~0.8 (Figs. 1, 9). Protoconch maximum width 0.7 mm (Fig. 4). Subsutural dotted line beginning on first teleoconch whorl, flanked externally by smooth area (Fig. 4). For details see Simone & Birman (2006).

Operculum (Figs. 5, 6): Rounded, corneous, thin, translucent, beige, occupying entire shell aperture (Fig. 9). Exterior surface multispiral; nucleus central; growth terminal edge expanding operculum width ~8% beyond previous margin. Flexiclaudent, fragile, edges usually damaged. Interior surface simple, glossy; scar inconspicuous, occupying approximately one-half of interior surface.

Pallial cavity (Figs. 16, 17): Almost one whorl in length. Mantle edge (mb) simple, relatively thick. Gill (gi) with approximately one-quarter of pallial cavity width, ~80% of its length; anterior end bluntly pointed; posterior end rounded. Gill suspensory membrane (ms) thick, occupying almost one-half of gill length. Gill ventral leaflet triangular (Fig. 16, gi), approximately as tall as wide; tip sharp pointed; left edge weakly concave and longer than almost straight right edge; dorsal leaflet (Fig. 16, gd) approximately five times shorter than ventral leaflet, rounded, simple. Ctenidial vein (cv) simple, uniform; tapered anteriorly, flanking posterior end of gill toward right. Osphradium (os) approximately one-tenth of gill length, spherical; located slightly posterior of suspensory membrane base; osphradial nerve (on) in middle of its left surface. Hypobranchial gland (hg) white, relatively thick in posterior half of pallial cavity only, compressed between gill and right pallial structures, disappearing in middle pallial level. Rectum (rt) relatively broad, sigmoid along right side, contouring kidneys. Anus (an) siphoned, located approximately one-fifth of pallial cavity length posterior to mantle edge.

Visceral mass (Fig. 19): Occupying entire shell spire, to its apex. Color uniform yellowish beige. Digestive gland (dg) lying along ventral half and genital structures on dorsal half of all whorls. In male, testis thicker in median whorl, tapering both toward shell apex and pallial cavity. In female, genital structures narrow in shell apex, gradually increasing to pallial cavity (see genital descriptions below). Stomach (st) as wide curve (concavity ventral), ½ whorl in length, located just posterior to pallial cavity posterior end; width approximately one-quarter of local visceral width (more details below). Renopericardial structures at anteriormost limit, occupying approximately one-quarter whorl, encroaching on pallial roof.

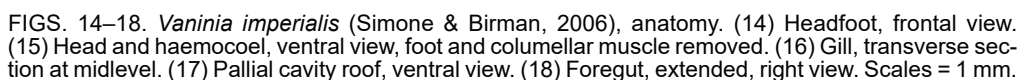


FIGS. 1–13. *Vaninia imperialis* (Simone & Birman, 2006). (1–8) MZSP 36783#1: (1) shell, apertural view (width 10.0 mm); (2) same, apical view; (3) same, basal view; (4) same, detail of apex; (5) operculum, interior view (width 5.2 mm); (6) same, exterior view; (7) snout, ventral view; (8) jaws, inner ventral view. (9) MZSP 36783#2, shell, apertural view (width 11.4 mm). (10–13) Radulae (SEM): (10) detail of central region; (11) panoramic view; (12) detail of lateral and central regions; (13) detail of central (left) and lateral (right) regions. Scale bars = 50 μ m (10, 12, 13), 100 μ m (11), 1 mm (4, 7, 8).

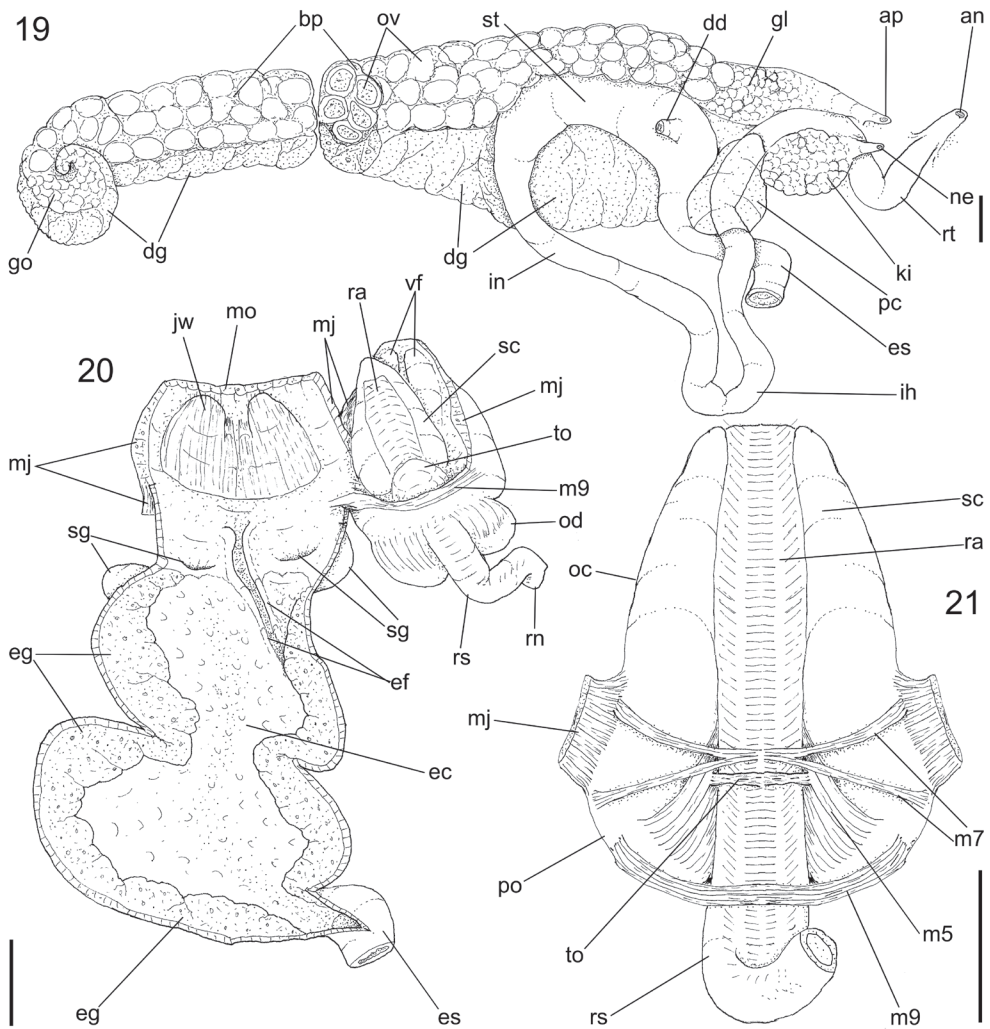
Renopericardial structures (Figs. 17, 19): Left kidney (ki) apparently the only functional one, balloon-like, internally almost solid, yellow; nephrostome (ne) as simple pore preceded by relatively long peduncle. Right kidney mixed with genital structures, but apparently still having some glandular function (Fig. 19, gl) of similar configuration as left kidney. Pericardium

(pc) and heart features similar to those of other trochoideans.

Digestive system (Figs. 15, 18–23): Snout and mouth described above (headfoot). Buccal mass from mouth to anterior third level of haemocoel (Fig. 15, od); oral tube and peribuccal muscles (mj) relatively thick, occupying approximately one-half of buccal



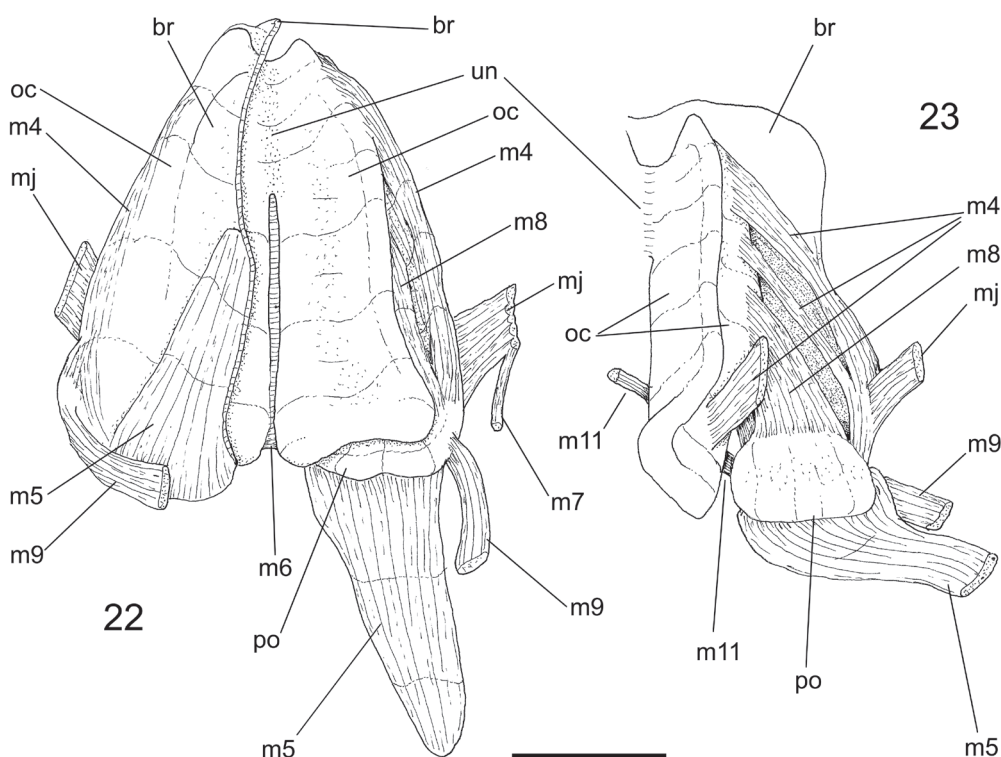
od) of approximately one-half of buccal mass volume. Odontophore muscles (Figs. 21–23): mj: pair of jaw peribuccal muscles, originating from mouth walls (Fig. 18), with most fibers running laterally, inserting in laterodorsal edge of both anterior cartilages (Fig. 21); m4: pair of main dorsal tensor muscles of radula, thick, with three layers (Fig. 23), origin along outer surface of anterior cartilages, inserting along



FIGS. 19–21. *Vaninia imperialis* (Simone & Birman, 2006), anatomy. (19) Uncoiled visceral mass and posterior region of pallial hoof, ventral view; transverse section at center artificially done. (20) Foregut opened longitudinally, ventral view; buccal mass deflected to right. (21) Odontophore, dorsal view; superficial layer of muscles and membranes removed; radular sac only partially shown. Scales = 1 mm.

subradular membrane (br) in its region in oral cavity; m5: pair of auxiliary dorsal tensor muscles of radula, thin with same width as cartilages, origin in posterior surface or posterior cartilages, running medially and anteriorly, inserting in subradular membrane medially to m4 insertion (Fig. 22); m6: horizontal muscle, thin and narrow, connecting nonfused ventral edges of both anterior cartilages (Fig. 22); m7: small, narrow pair of muscles, X-shaped,

located in dorsal-posterior region of odontophore (Fig. 21), anterior branch originating in mj, posterior branch originating in cartilage outer dorsal surface, running toward medial, inserting in base of radular sac in its region opening to oral cavity; m8: pair of cartilage approximator muscles, short, thick, connecting anterior surface of posterior cartilages with outer dorsal surface of anterior cartilages (Fig. 23), covered by m4; m9: transverse muscle



FIGS. 22–23. *Vaninia imperialis* (Simone & Birman, 2006), anatomy. (22) Odontophore, dorsal view; both anterior cartilages deflected; left muscles as in situ; right muscles expanded; m5 deflected downward; (23) detail of right side with anterior cartilage deflected upward, separated from posterior cartilage to show intrinsic muscle origins and insertions. Scale = 1 mm.

located in posterodorsal region of odontophore, originating from both sides of posterior cartilages (Figs. 20–22); m10: pair of ventral protractor muscles of buccal mass, originating in anteroventral region of snout, running toward posterior, close to median line, inserting in posteroventral surface of odontophore (Fig. 18); m11: pair of ventral tensor muscles of radula, narrow, long, originating in midventral surface of posterior cartilages (Fig. 23), running toward anterior, inserting in subradular membrane in its terminal edge. Nonmuscular odontophore structures: to, ligament connecting anterior end of radular sac with surrounding structures of posterior end of buccal cavity (Fig. 21); oc, pair of anterior odontophore cartilages, flattened, relatively thick, anterior end bluntly pointed, posterior end flat, approximately three times longer than wide, ventral edge with anterior third fused with its pair (Figs. 22, 23, un); po, pair of posterior cartilages, elliptical, ap-

proximately one and one-half times wider than long, located in posterior outer side of anterior cartilages.

Radular sac (rs) broad, as long as buccal mass, radular nucleus (rn) bifid. Radular teeth (Figs. 10–13): rachidian, occupying approximately one-half of radular width (Fig. 11), cutting edge triangular tall, highly curved inside, tip sharp pointed; edges covered by very small, uniform, spine-like cusps, serrated (Figs. 12, 13) except basal edge and tip; lateral teeth, five pairs with similar characters as rachidian, but much narrower, base relatively wide, approximately one-fifth of that of rachidian, abruptly tapering to long and slender shaft, gradually narrowing to sharp pointed tip; all lateral teeth relatively similar to each other; marginal teeth divided into two regions: (1) inner region with two pairs (Fig. 13), innermost tooth hook-like, broad, thick, as tall as lateral teeth, inner concave edge with 8–10 broad, strong cusps, outer

convex edge smooth; outermost tooth similar, of same height, but approximately one-half width; ~20 pairs of remaining marginal teeth more similar to rachidian-lateral model (Figs. 12, 13), each one curved rod-like, tall, with slightly expanded, spoon-like terminal region possessing edges with small, uniform, pointed cusps to tip, these marginal teeth gradually diminishing toward margin.

Pair of salivary glands as small hollow glandular diverticula (Figs. 18, 20, sg) located in dorsal region of posterior level of buccal mass. Buccal cavity with pair of dorsal narrow folds (Fig. 20, ef) running close to each other, separated by deep groove, initially to posterior, gradually curving to left in esophageal origin. Esophagus very wide, bearing three or four wide folds, but lacking clear distinctions of chambers or crops. Esophagus entirely covered by internal thick layer of glands (Fig. 20, eg) from salivary glands to short distance from gastric insertion, only free anterior portion of esophageal folds. Stomach (Fig. 19, st) as simple curve, relatively narrow; no internal structures or spiral caecum; esophageal insertion anterior left (es), intestinal origin (in) posterior left, each with no clear border; duct to digestive gland (dd) single, narrow, simple, turned posteriorly, located in anteroventral gastric region. Intestinal looping as in Fig. 19, including loop inside of haemocoel (Figs. 15, 19, ih); intestine of similar width along its length.

Genital system (Fig. 19): Female with ovary (go) restricted to last 1.5 visceral whorl. Brood pouch (bp) very large, lying along almost entire visceral mass anterior to ovary to pallial cavity. Brood pouch replete of encapsulated ova, apparently at same stage of development. In pallial cavity, brood pouch succeeded by glandular portion (gl), unclear whether vestige of right kidney or any female genital gland (or both); following this, short atrium and papillate female pore (ap) with similar aspect as nephrostome (ne) of left kidney, located posterior of anus. Male with equivalent structures as female, but much narrower, and lacking brood pouch; testis proportionally more elongated, reaching stomach.

Central nervous system: Similar to that of following described species.

Habitat: 270–900 m.

Distribution: Off Espírito Santo to Santa Catarina coasts.

Measurements (width and height in mm): MZSP 36783#1 (Fig. 1): 10 by 8.2; 36783#2 (Fig. 9): 11.4 by 9.7.

Material examined. All of the type material. BRAZIL. Rio de Janeiro; off Arraial do Cabo, 23°43.1'S, 42°00.7'W, 207 m, MZSP 157829, 4 spms (Deproas W Besnard sta. 6923, February 19, 2001); Bacia de Campos, off Campos dos Goytacazes, MZSP 116889, 1 shell. Paraná; off Paranaguá; 26°15'13"S 46°54'11"W, 684 m, MZSP 36695, 2 spms, MZSP 36783, 6 spms; MZSP 366787, 2 spms (PADCT2 PM1, R/V W Besnard col., May 26, 2001).

Vaninia mirabilis (Simone & Birman, 2006)
comb. nov.
Figs. 24–44

Margarites mirabilis Simone & Birman, 2006: 13, 14 (figs. 1–5, 11); Dornellas & Simone, 2011: 27, 28.

Calliostoma nudiusculum: Forcelli, 2000: 60 (fig.) (*non* Martens, 1881)

Description: Shell (Figs. 24, 26, 28–30): Shell description by Simone & Birman (2006: 13) particularly accurate. Height/width ratio ~0.8 (Figs. 24, 28). Protoconch maximum width 0.7 mm (Figs. 26, 29). Subsutural dotted line beginning gradually after first teleoconch 1.5 whorls, flanked externally by three or four similar-sized, but not dotted, lines (Fig. 26).

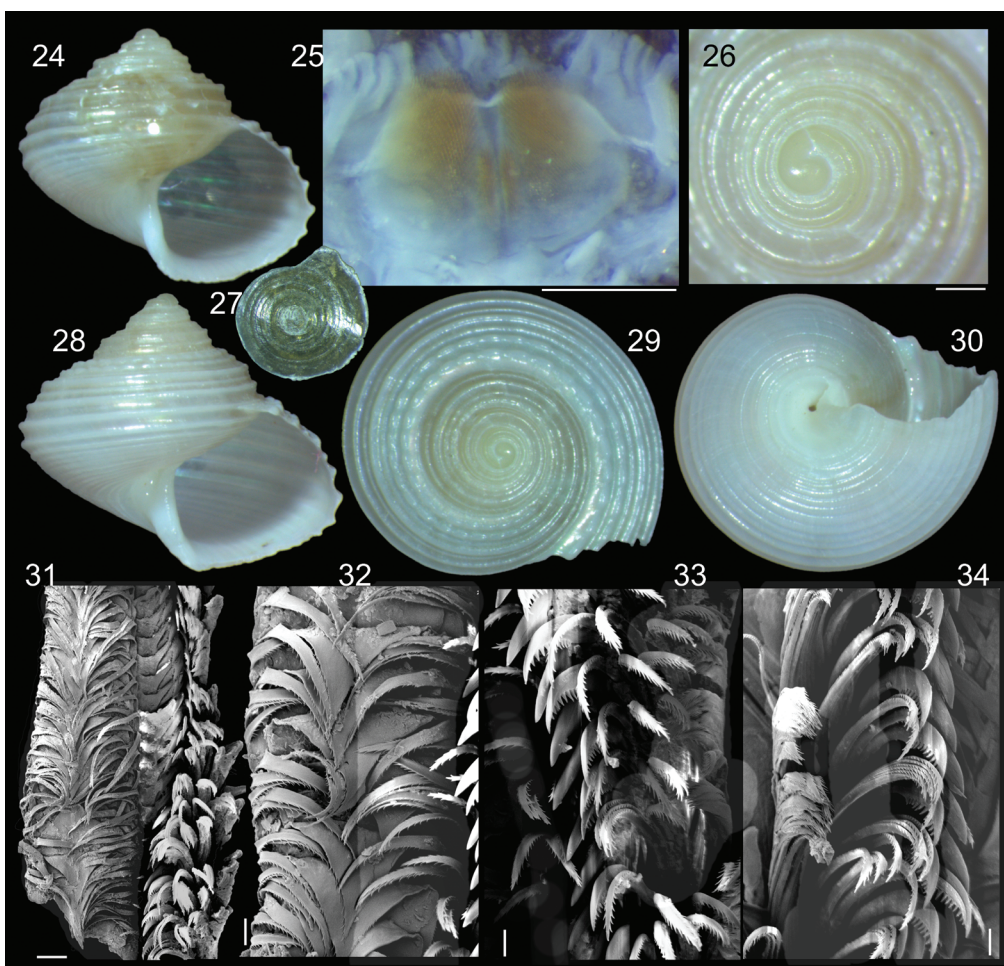
Operculum (Fig. 27): Similar to that of preceding species, except slightly less spiral, and with growth terminal edge expanding operculum width ~15% beyond previous margin.

Pallial cavity (Figs. 37, 38): Characters similar to preceding species, except for following. Mantle edge (mb) clearly bifolded; inner fold thicker, longer than outer fold; siphonal region bearing transverse folds. Gill ventral leaflet triangular (Fig. 37, gi), about as tall as wide; tip bluntly pointed; left and right edges similar to each other, almost straight; dorsal leaflet (Fig. 37, gd) approximately four times shorter than ventral leaflet. Hypobranchial gland not detected. Anus (an) long-siphoned, located approximately one-quarter of pallial cavity length posterior to mantle edge.

Visceral mass: Same as preceding species.

Renopericardial structures (Fig. 38): Similar features as in preceding species.

Digestive system (Figs. 36, 39–41, 44): Most characters as described for *Vaninia imperialis*, except for following. Pair of jaw plates (Figs. 25,



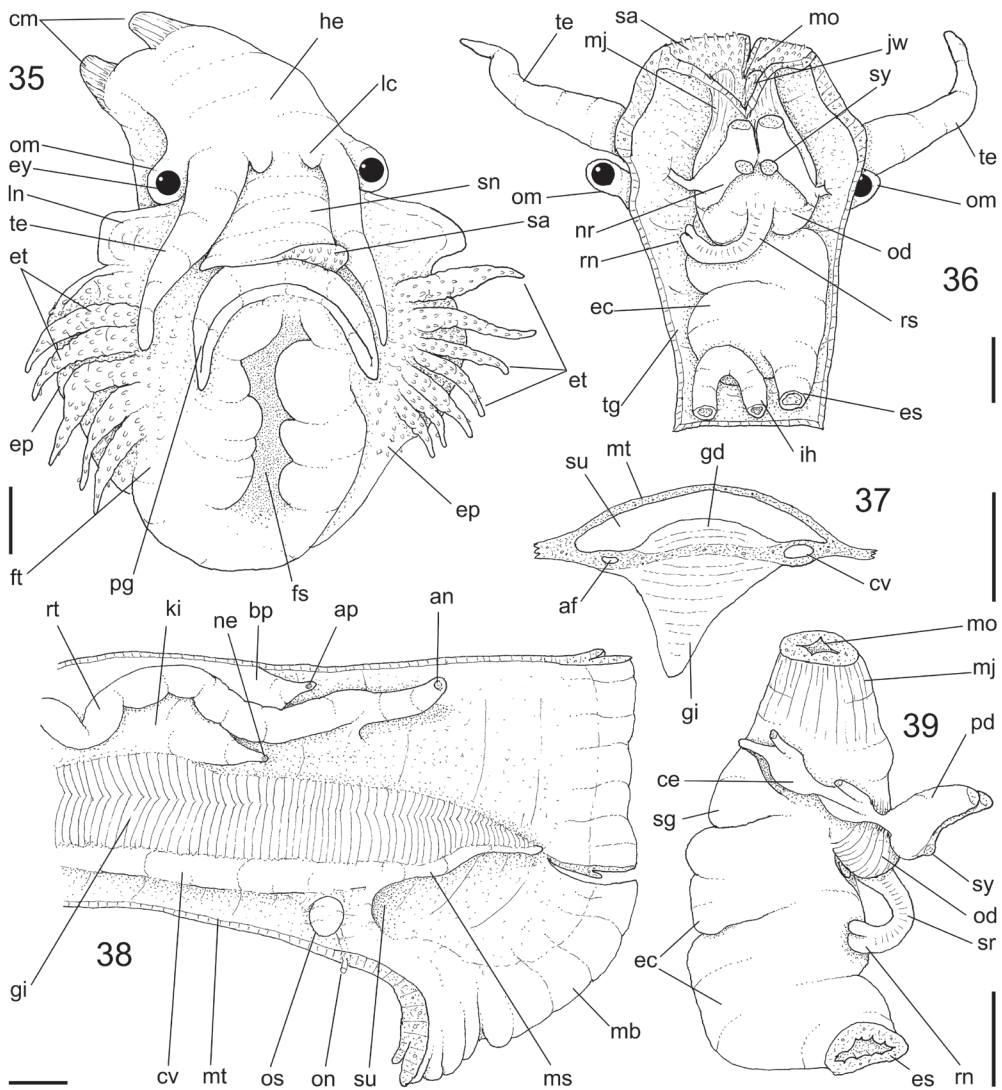
FIGS. 24–34: *Vaninia mirabilis* (Simone & Birman, 2006). (24) MZSP 63018#3, shell, apertural view (width 6.0 mm); (25) jaw plate. (26–30) MZSP 63018#5: (26) shell, detail of apex; (27) operculum, exterior view (width 3.2 mm); (28) shell, apertural view (width 8.7 mm); (29) same, apical view; (30) same, basal view. (31) Radula (SEM), panoramic view; (32) detail of central region; (33, 34) details of marginal region. Scale bars = 20 μ m (32–34), 50 μ m (31), 0.5 mm (25, 26).

40, jw) similar, but clearer and thinner, and with much shorter inner component; pair of inner components approximately one-third of outer components. Odontophore muscles (Figs. 41, 44) also similar, except: m4 pair not clearly separated into layers; m6 occupying entire ventral edge of both odontophore cartilages, which are not fused (Fig. 44); m9 narrower; m11 thicker. Radular teeth (Figs. 31–34) almost entirely similar, except for two pairs on inner marginal teeth, with more elongated, sharp-pointed cusps (Fig. 31, inferior-right side). Esophageal folds (Fig. 40, ef) much shorter,

weakly developed, restricted to perisalivary region only.

Genital system: Similar as preceding species.

Central nervous system (Figs. 42, 43): Surrounding midlevel of buccal mass (Figs. 36, 39). Cerebral ganglia (ce) elliptical, approximately two times as long as wide, each one twice as wide as radular sac transverse section. Cerebral commissure (cc) thick, long, as wide as each ganglion length; no clear limit between ganglion and commissure. Each pedal ganglion (pd) approximately one and one-half times larger than cerebral ganglion, located



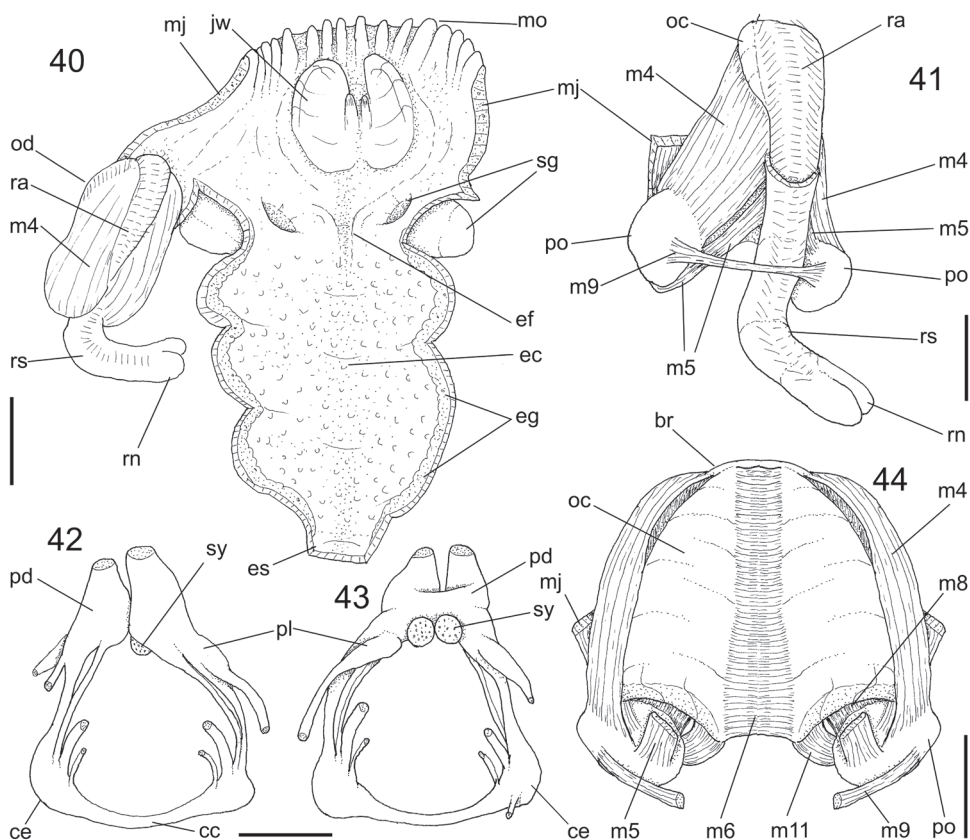
FIGS. 35–39: *Vaninia mirabilis* (Simone & Birman, 2006) anatomy. (35) Headfoot, frontal view. (36) Head and haemocoel, ventral view; foot and columellar muscle removed. (37) Gill, transverse section at midlevel. (38) Pallial cavity roof, ventral view. (39) Foregut, extended, right view. Scales = 0.5 mm.

inside ventral pedal musculature; slightly cuneiform, located very close to its counterpart; pedal commissure very short, restricted to ventral side (Fig. 43). Pair of pleural ganglia (pl) as lateroposterior appendices of pedal ganglia, approximately one-quarter of their size. Cerebropleural and cerebropedal connectives narrow, approximately as long as cerebral commissure; cerebro-pleural connective slightly broader. Pair of statocysts (sy) located very

close to each other, on ventral side between pedal ganglia (Fig. 43), of approximately one-quarter of pedal ganglion size; internally with several shining statoconia.

Habitat: 85–206 m.

Distribution: Off Rio Grande do Sul to Uruguay coasts.



FIGS. 40–44: *Vaninia mirabilis* (Simone & Birman, 2006) anatomy. (40) Foregut, opened longitudinally, ventral view; buccal mass deflected to left. (41) Odontophore; first layer of muscles and membranes removed; radular sac and cartilages deflected. (42) Nerve ring, dorsal view; (43) ventral view. (44) Odontophore, dorsal view; four cartilages deflected; radular sac removed. Scales = 0.5 mm.

Measurements (width and height in mm): MZSP 63018#3: 6.0 by 5.1; 63018#5: 8.7 by 7.5.

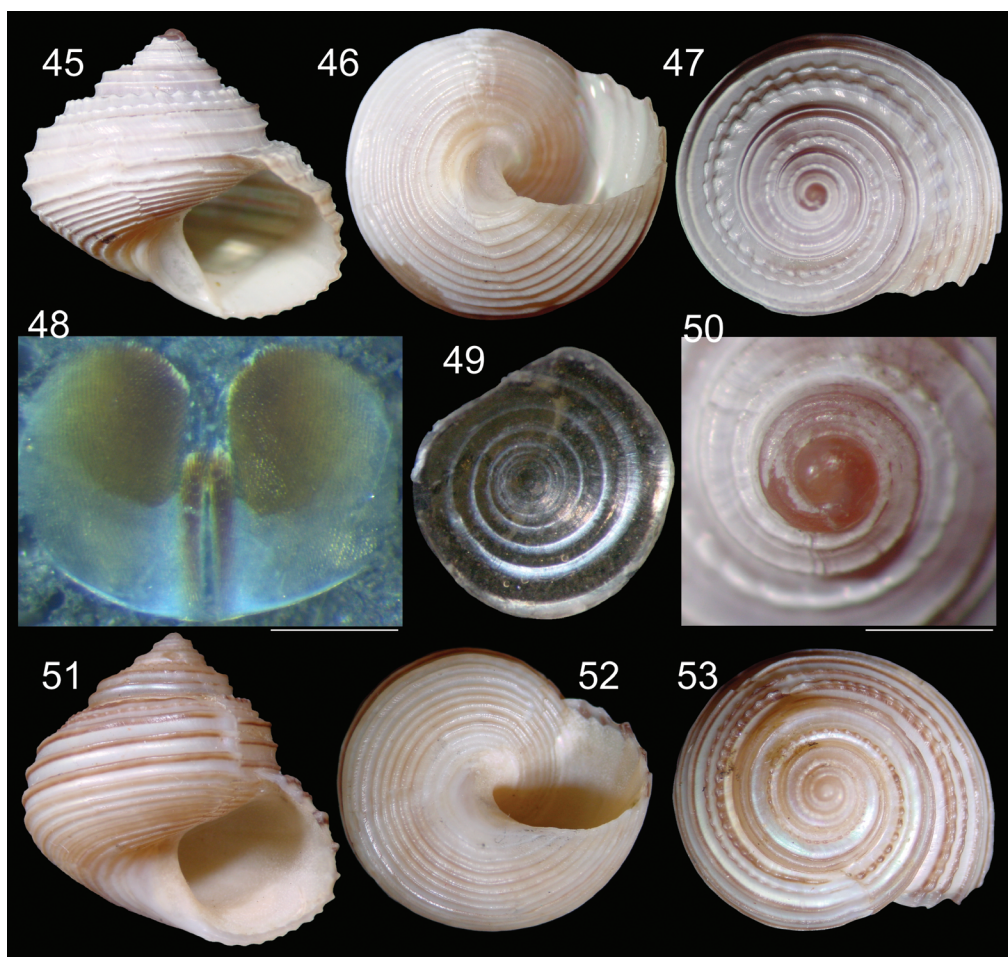
Material examined: All of the type material. BRASIL. Rio Grande do Sul; off Porto Alegre, 30°33'S, 44°05'W, 150 m, MZSP 40193, 3 shells (R/V Besnard col., 1978, ex collection Colella). URUGUAY. Maldonado; off Punta del Este, 35°51'S, 53°06'W, 206 m, MZSP 63018, 8 spms (Cruzeiro III sta. 7870, August 12, 1972). Montevideo; off Montevideo, 35°51'S, 53°06'W, 195 m, MZSP 139369, 2 shells (Besnard, August 18, 1972).

Vaninia vanini gen. nov. sp. nov.
Figs. 45–61, 65–67

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Types: Holotype, MZSP 157216, 1 spm. Paratypes: BRAZIL. São Paulo; off Ubatuba, 24°11'25"S, 43°27'49"W, 320 m, MZSP 157215, 1 shell (projeto integrado Besnard sta. 5365, December 7, 1988, ex collection Vanin); 24°16'S, 43°50'W, 250–260 m, MZSP 19422, 1 shell (Besnard sta. 1157, August 10, 1970). Santa Catarina, off Itajaí, ~400 m, MZSP 64659, 1 shell (otter trawl, January 2006).

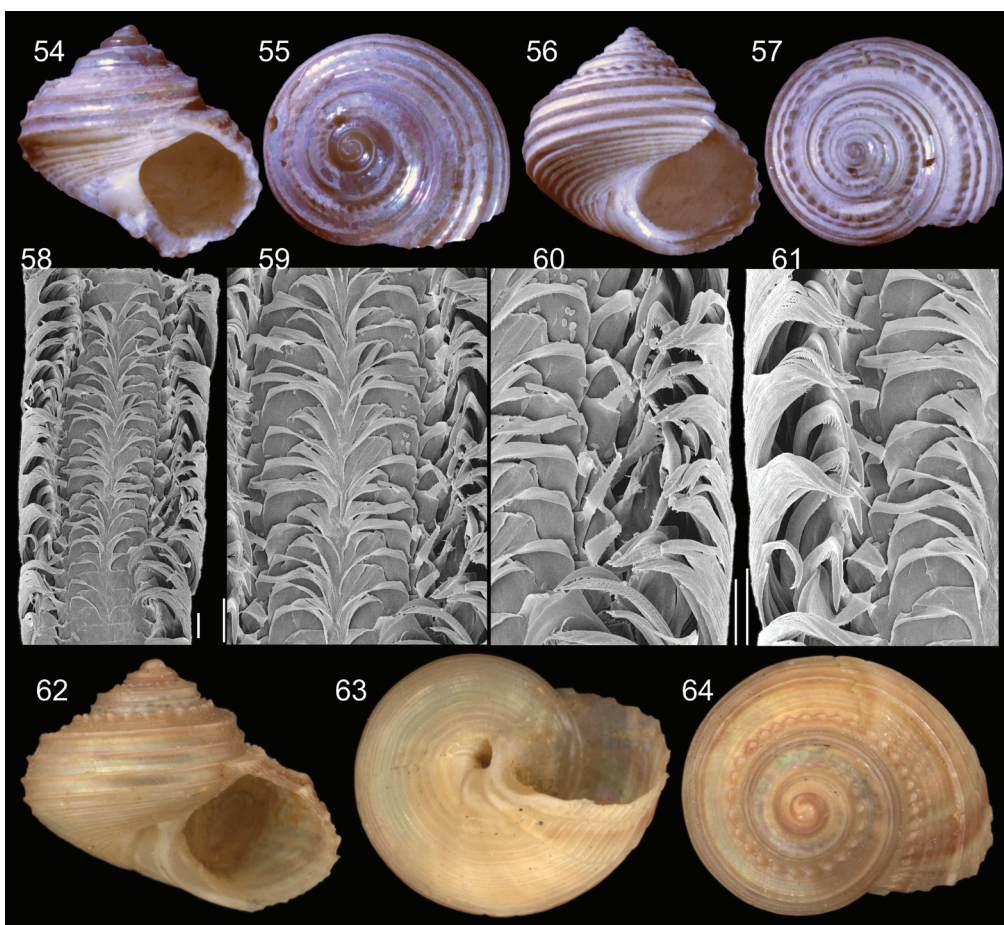
Type locality: BRAZIL, São Paulo, off Ubatuba, 24°11'25"S, 43°27'49"W, 320 m (projeto integrado Besnard sta. 5365).



FIGS. 45–53. *Vaninia vanini* gen. nov. sp. nov. (45–50) Holotype, MZSP 157216: (45) shell, apertural view (width 9.2 mm); (46) shell, basal view; (47) shell, apical view; (48) jaws in situ, ventral view; (49) operculum, exterior view (width 3.6 mm); (50) detail of shell apex. (51–53) Paratype, MZSP 157215, shell (width 9.8 mm): (51) apertural view; (52) basal view; (53) apical view. Scales = 200 μ m (48), 1 mm (50).

Diagnosis: Shell approximately as tall as wide; color beige with brown spiral cords; three undotted spiral cords on penultimate whorl; ten of them on inferior half of body whorl. Protoconch 0.6 mm. Inner lip of aperture with wide concavity. Umbilicus closed. Left epipodium with four small posterior tentacles, middle and anterior regions undulating only; lacking neck lobes. Mantle edge with tentacles in siphonal region. Jaw plates of intermediate thickness and rounded cutting edge. Radula with 12–14 pairs of marginal teeth.

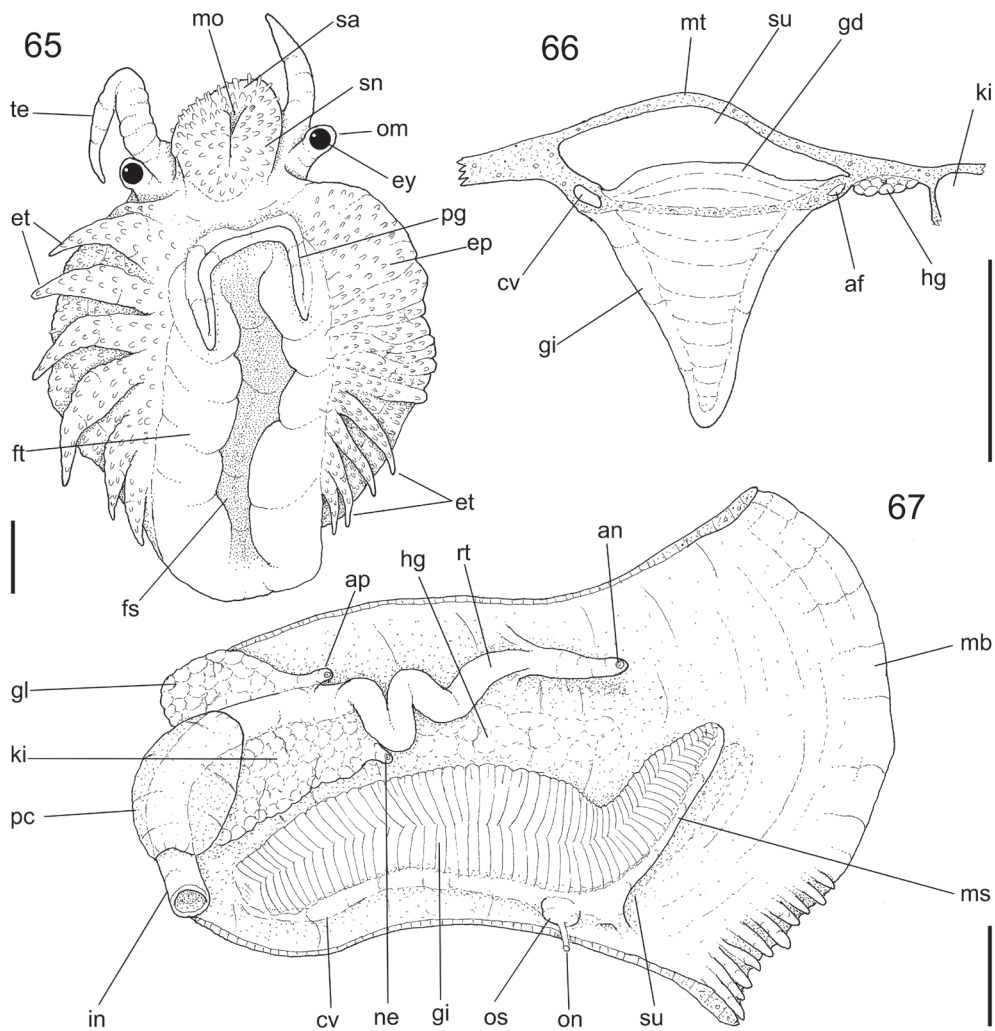
Description: Shell (Figs. 45–47, 50–57): Shell ~10 mm, turritiform, to 6.5 convex whorls; height/width ratio ~1.0. Color brownish, iridescent beige; spiral cords usually brown. Spire bluntly pointed, slightly shorter than body whorl; body whorl wide. Protoconch (Fig. 50) maximum width 0.6 mm, consisting of one smooth, convex whorl, border with teleoconch clear, orthocline. Remaining teleoconch spire whorls convex; sculptured by relatively tall, uniform spiral cords (Figs. 1, 3), with space between successive cords equivalent to twice their width. First teleoconch whorl with three



FIGS. 54–64. *Vaninia vanini* gen. nov. sp. nov.: (54, 55) paratype, MZSP 64659 (width 10.5 mm): (54) apertural view; (55) apical view; (56, 57) paratype, MZSP 19422 (width 10.5 mm): (56) apertural view; (57) apical view; (58–61) radula of holotype (MZSP 157216) (SEM): (58) panoramic view; (59) detail of central region; (60, 61) details of marginal region. (62–64) *Vaninia dnophera* (Watson, 1879), lectotype, NHMUK 1887.2.9.333–5 (width 8.7 mm; photos courtesy NHMUK): (62) apertural view; (63) basal view; (64) apical view. Scale bars = 50 μ m (58–61).

spiral cords (Figs. 47, 50, 53, 55, 57), two cords closer to superior suture dotted, one closer to inferior suture smooth and obsolete; cords gradually increasing in size to last spire whorl. Penultimate spire whorl with two subsutural dotted cords, located close to each other, the external cord narrower; another two (Figs. 45, 47, 54, 55) or three (Figs. 51, 53, 56, 57) smooth cords equidistantly distributed from dotted cords to inferior suture. Dotted subsutural spiral cords with successive elongated nodes, with height and width equivalent to those of remaining cords, running to outer lip.

Body whorl with peripheral cord as continuation of outer lip implantation similar to neighboring cords; approximately ten or 11 spiral cords on inferior half of body whorl, narrower and closer together than cords from dorsal region of body whorl; their interspaces equivalent to their width; higher cords dense in midregion of inferior surface, i.e., cords slightly more spaced toward exterior and interior (Figs. 46, 52). Aperture (Figs. 45, 51, 54, 56) rounded, slightly prosocline. Outer lip simple, bearing small outer projections relative to each spiral sculpture. Inner lip smooth, strongly truncated



FIGS. 65–67. *Vaninia vanini* gen. nov. sp. nov. anatomy: (65) head-foot, frontal view; (66) gill, transverse section at midlevel; (67) pallial cavity roof, ventral view. Scales = 1 mm.

at middle, with broad projection covering umbilicus; thin, transparent callus extending beyond, covering inferior surface of beginning of body whorl. Umbilicus (Figs. 46, 52, 54, 56) totally occluded by wide, concave, curved platform, originating from callus, ending inferiorly in small projection.

Operculum (Fig. 49): Similar to that of *Vaninia mirabilis*, slightly less spiral, and with growth terminal edge expanding operculum width ~15% beyond previous margin.

Pallial cavity (Figs. 66, 67): Characters similar to *Vaninia imperialis*, except for the following. Mantle edge (mb) not bifolded; siphonal region bearing well-delimited transverse folds, forming small tentacles. Gill ventral leaflet triangular (Fig. 66, gi), slightly taller than wide; tip bluntly pointed; left and right edges similar to each other, almost straight; dorsal leaflet (Fig. 37, gd) approximately four times shorter than ventral leaflet. Hypobranchial gland (hg) well-developed, thicker in anterior region of left

kidney. Rectum (rt) strongly zigzagging just anterior to kidney. Anus (an) long-siphoned, located approximately one-third of pallial cavity length posterior to mantle edge.

Visceral mass: Same as preceding species.

Renopericardial structures (Fig. 67): Similar to those of preceding species.

Digestive system (Figs. 36, 39–41, 44): Most characters as described for *Vaninia mirabilis*, except for the following. Pair of jaw plates (Fig. 48) outline slightly cordiform; terminal edges dark pigmented; inner components narrow, approximately one-eighth of total jaw width, approximately one-half of jaw length; outer cutting components rounded, slightly turned toward medial. Odontophore muscles and structures as in *Vaninia mirabilis*. Radular teeth (Figs. 58–61) almost entirely like those of *Vaninia imperialis*, including two pairs of inner marginal teeth with 8–10 long cusps on each side (Figs. 59, 61), but with fewer outer elongated, spoon-like marginal teeth, 12–14 pairs (Figs. 60, 61).

Genital system: Similar to those preceding species.

Central nervous system: As described for *Vaninia mirabilis*.

Habitat: 250–400 m.

Distribution: Off São Paulo and Santa Catarina coasts.

Measurements (width and height in mm): Holotype, MZSP 157216, 9.2 by 8.4. Paratypes: MZSP 157215, 9.8 by 10.3; MZSP 64659, 10.5 by 10.2; MZSP 19422, 10.5 by 10.2.

Material examined: Type material only.

Vaninia dnophera (Watson, 1879) *comb. nov.*
Figs. 62–64

Trochus (Margarita) dnopherus Watson, 1879: 711, 712; 1886: 90 (pl. 5, fig. 3).

Trochus (Margarita) dnophorus (err): Watson, 1886: pl. 6, fig. 6.

Margarites dnopherus: Morretes, 1949: 58; Rios, 1975: 20 (fig. 42); 1985: 19 (fig. 72); 1994: 30 (fig. 77); Simone & Birman, 2006: 13, 16; Dornellas et al., 2021: 61.

Calliostoma dnopherum: Quinn, 1992: 99, 100 (figs. 67–69); Amaral et al., 2003: 49; Rios, 2009: 48 (not the figs.).

Types: Lectotype (Figs. 62–64) and 1 paralectotype, NHMUK 1887.2.9.333–5 (examined).

Type locality: Challenger sta. 122, 9°5' to 9°10'S, 34°49' to 34°53'W, off Pernambuco, 350 fms (640 m).

Shell (Figs. 62–64): Description by Watson (1879: 711, 712; 1886: 90) particularly accurate and complete. Height/width ratio ~0.7. Protoconch maximum width ~0.7 mm.

Habitat: Red mud, 640 m.

Distribution: So far only known from the type locality.

Measurements (width and height in mm): Lectotype: 8.7 by 6.7; paralectotype: 3.3 by 1.6.

Material examined: Type material only.

PHYLOGENETIC ANALYSIS

The complete list of 128 characters, including the number of steps (L), consistency (CI), and retention (RI) indices for each character, can be found in MorphoBank (Project 4512) and Appendix 1. The phylogenetic analysis yielded two most-parsimonious trees with L 451 steps, CI 0.41, and RI 0.54 (Fig. 68). Based on the strict consensus, the *Vaninia* species anatomically studied here nested within the *Calliostoma* clade (Clade A), supported by a bootstrap value (bs = 75%) and Bremer support (Bs = 2). Our results show that Clade A is the sister group of Clade B, which includes the remaining trochoidean representatives, supported by six radular synapomorphies.

These three *Vaninia* species form a monophyletic group supported by five synapomorphies (bs = 68%; Bs = 4) (Fig. 68, red branch). However, the relationships among *Vaninia* species remain represented by a trichotomy. The species representing the genus *Margarites*, *Margarites pupillus* (Gould, 1849), was nested within Clade B (Fig. 68), closer to the trochid *Oxystele sinensis* (Gmelin, 1791). Clade B is supported by nine synapomorphies (Bs = 1), with the *Solariella* clade being the first split group. Our results indicate clear polyphyly of the trochids, but a branch uniting turbinids, phasianellids, and tegulids was supported by 12 synapomorphies (Bs = 2). The genera of these three families were, and still are, all con-

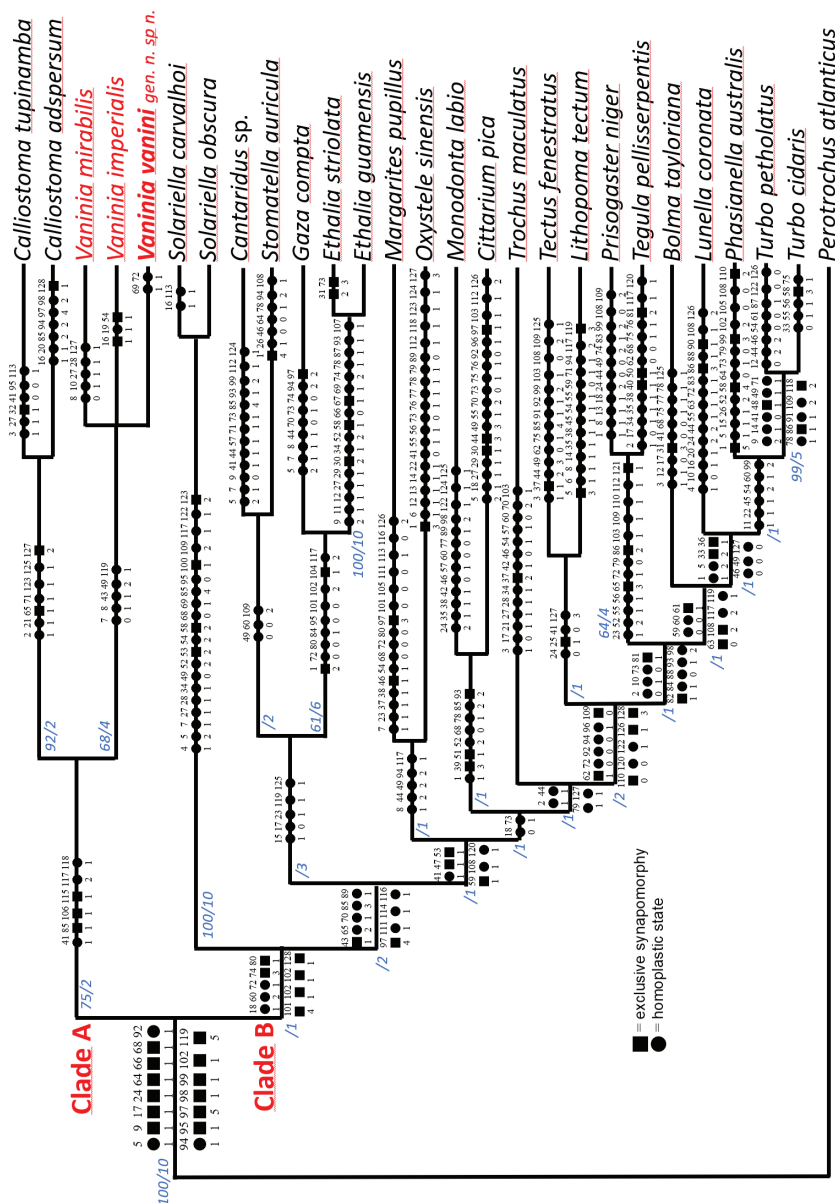


FIG. 68. Most parsimonious cladogram obtained using <http://www.morphobank.org>: Project 4512 database of Vetigastropoda; 450 steps; CI 41; RI 54. Synapomorphies of each node shown; character numbers above symbols; character state numbers below symbols. Blue numbers indicate bootstrap/Bremer support for each node. Clade A shows calliostomatids and presently studied *Vaninia* *gen. nov.* Species not discussed in text are: *Bolma tayloriana* (E. A. Smith, 1880); *Calliostoma adspersum* (R. A. Philippi, 1851); *Cittarium pica* (Linnaeus, 1758); *Ethalia guamensis* (Quoy & Gaimard, 1834); *Ethalia striolata* (A. Adams, 1855); *Gaza compta* Simone & C. Cunha, 2006; *Lithopoma tectum* (Lightfoot, 1786); *Lunella coronata* (Gmelin, 1791); *Monodonta labio* (Linnaeus, 1758); *Perotrochus atlanticus* Rios & Matthews, 1968; *Phasianella australis* (Gmelin, 1791); *Prisogaster niger* (W. Wood, 1828); *Solariella obscura* (Couthouy, 1838); *Stomatella auricula* Lamarck, 1816; *Tectus fenestratus* (Gmelin, 1791); *Tegula pellisserpentis* (W. Wood, 1828); *Trochus maculatus* Linnaeus, 1758; *Turbo cidaris* Gmelin, 1791; *Turbo petholatus* Linnaeus, 1758.

sidered in Turbinidae by some authors (e.g., Dornellas et al., 2020), a position supported by the present results.

DISCUSSION

Generic and Family Discussion

The conchological similarity between *Vaninia* species and *Margarites* (Margaritidae) initially led to their attribution to the latter genus. However, our phylogenetic analysis clearly demonstrates their closer relationship to Calliostomatidae (Fig. 68, Clade A). The prior assignment to *Margarites* was likely based on factors such as their deep-water habitat, slightly discoid outline, and iridescent shells, even though *Margarites* typically lacks well-developed sculpture (Simone & Birman, 2006; Zhang & Zhang, 2017).

The placement of *Vaninia* gen. nov. within the Calliostomatidae is primarily supported by radular synapomorphies. These include a flattened shaft of rachidian tooth (#85, Fig. 11); a square base of the lateral teeth (#102, Fig. 13); the shaft of the lateral teeth without interaction in the row (#106, Fig. 12); the innermost marginal teeth modified (#115, Fig. 13); an apical cusp of the innermost marginal teeth twice the length of the outermost lateral teeth cusp (#117, Fig. 13); and the apical cusp of the innermost marginal teeth of approximately three times the length of the adjacent marginal tooth cusp (#118, Fig. 13).

Current diagnostic features for the Calliostomatidae do not fully capture the morphological variation seen across its subfamilies. For example, the typical reticulate protoconch and the enlarged innermost pair of marginal teeth are absent in Margarellinae and Xeniostomatidae (McLean, 2012; Williams, 2012).

Some anatomical characteristics previously proposed as diagnostic for *Calliostoma*, e.g., the presence of an ampulla in the female kidney, the reduction or absence of cephalic lappets, the presence of a pseudoproboscis, and the intestinal loop outside the hemocoel (Dornellas & Simone, 2013), were not observed in *Vaninia*, and appear to be absent in other calliostomatids as well. This suggests that they might be more relevant for distinguishing species within a genus than across the entire family. In terms of shell features, *Vaninia* gen. nov. exhibits greater resemblance to *Venustatrochus* Powell, 1951, compared to other calliostomatids. Both genera have nacre-

ous layers visible through the translucent outer shell, a teleoconch with median or submedian and peripheral angulations, and spiral cords that quickly become prominent, either smooth or finely beaded (Marshall, 2016). However, the shell of *Vaninia* gen. nov. differs from *Venustatrochus* in having a clear distinction between the subsutural dotted spiral cord and the remaining smooth cords, with the cords being much more pronounced. Additionally, *Vaninia* gen. nov. has a smooth protoconch. Furthermore, its radula has only five pairs of lateral teeth compared to the 11–40 pairs found in *Venustatrochus*.

Assigning *Vaninia* gen. nov. to a specific subfamily within Calliostomatidae presents significant challenges. Its shell morphology deviates from most calliostomatines in being thinner and lacking the typical color patterns (with the exception of *Akoya* Habe, 1961). The protoconch lacks the honeycomb pattern seen in xeniostomatines and margarellines, and some fauricines, e.g., *Falsimargarita* A. W. B. Powell, 1951 (Williams, 2012). Additionally, *Vaninia* gen. nov. does not possess a pseudoproboscis or an intestinal loop inside the hemocoel, characteristics of most calliostomatids. However, the absence of a pseudoproboscis is also reported in the monotypic subfamily Xeniostomatinae, which presents a peculiar morphology also lacking the enlarged marginal teeth and the jaws (McLean, 2012). On the other hand, *Vaninia* gen. nov. shares radular features, e.g., enlarged innermost marginal teeth and slender outer marginal teeth, with other calliostomatines. Thysanodontinae species have highly modified radulae, lacking the central field and featuring extremely slender teeth with backward-directed barbs, making these characters useful for subfamily assignment. The radular characteristics of the Fauricinae differ from those of *Vaninia* species, because they have thin, flexible, cusplless cutting areas of the central and lateral teeth. These radular features would be considered homologous and group the genera *Phenacomargarites* Marshall, 2016; *Falsimargarita*; *Selastele* Marshall, 1995; and *Faurix* Marshall, 1995 (Marshall, 2016). Although the radula can exhibit homoplasy among various molluscan taxa, it remains a valuable tool for classification in certain groups, e.g., Trochoidea. Although the classification of trochoideans proposed by Hickman & McLean (1990) has been partially revised by subsequent molecular studies, a consistent pattern of groups based on radu-

lar, external morphology, and shells should be recognized. Furthermore, a morphological phylogeny incorporating radular characters, as proposed by Hickman & McLean (1990), has been supported by both morphological and molecular systematics (Dornellas et al., 2020). *Vaninia gen. nov.* and margarellines share certain traits, e.g., the lack of a honeycomb pattern in the protoconch and lateral horn-like projections of the foot. However, there are noticeable morphological differences in the radula between them (discussed below).

Differentiating between trochiform shell patterns can be challenging, because they might not provide clear distinctions at the generic, subfamily, or even family levels. As mentioned earlier, both *Vaninia imperialis* and *Vaninia mirabilis* were previously referred to *Margarites* (Margaritidae) due to their discoid iridescent shells and deep-water habitats. The Margaritidae is comprised of five genera: *Margarites*, *Anomphalogaza* Hickman, 2012, *Antimargarita* Powell, 1951, *Callogaza*, and *Gaza*. Although this group is considered monophyletic, shell characters alone are insufficient for conclusive diagnosis (Williams, 2012). Margaritids share some anatomical traits that are absent in *Vaninia gen. nov.* For example, they have simple margins on the neck lobe and five or six epipodial tentacles. The cephalic lappets have undivided margins (Hickman & McLean, 1990). In the radula, the rachidian and lateral teeth have large oval bases, with simple overlaps along the row. A lateromarginal plate is usually present, but the development as an articulatory structure can vary (Hickman & McLean, 1990; Simone & Cunha, 2006). However, *Vaninia gen. nov.* shares with margaritids the presence of a brood pouch, indicating internal fertilization and oviposition (Williams, 2012).

The southwestern Atlantic and Antarctic species previously classified as *Margarites* are now recognized as *Margarella*. This change in generic rank was based on the study of radular and soft-part features (Zelaya, 2004), and molecular phylogenetic analysis, which revealed *Margarella* as nonmonophyletic. Among the Antarctic species, *Margarella antarctica* (Lamy, 1906) is closely related to calliostomatids, as is the type species, *Margarella expansa* (G. B. Sowerby I, 1838) (Williams, 2012). The southwestern Atlantic *Vaninia* species differ from *Margarella* species in several aspects. The rachidian tooth of *Vaninia gen. nov.* has a tubular shape, whereas *Margarella* has a larger base and a laterally expanded shaft.

The presence of a protolateromarginal plate between the outermost lateral tooth and the innermost marginal tooth is observed in margarelline species (Zelaya, 2004) but absent in *Vaninia gen. nov.* However, the occurrence of the lateromarginal plate is not exclusive to margaritids (Hickman & McLean, 1990), because it occurs independently in *Calliostoma tupinamba* Dornellas, 2012, *Solariella carvalhoi* Lopes & Cardoso, 1958, and *Margarites pupillus* (see Dornellas et al., 2020), with varying degrees of development (Hickman & McLean, 1990). *Vaninia gen. nov.* also has some resemblance to *Falsimargarita*, because both genera share a deep suture, iridescent surface, spiral sculpture, and deep-water habitat (Rios & Simone, 2005; Simone, 2008). However, *Vaninia gen. nov.* differs from *Falsimargarita* in having smaller shells (*Falsimargarita* species reach an average size of ~30 mm), with thicker walls (*Falsimargarita* has thin-walled, almost translucent shells) and dotted subsutural cord(s). Anatomically, *Vaninia gen. nov.* differs in having simpler epipodial tentacles (*Falsimargarita* has tentacles with papillae along their ventral surfaces); a more flattened snout; thinner and narrower jaw plates, with a narrower and shorter medial component; a radula with a much narrower rachidian and fewer marginals; and lack of brood pouch.

Given the uncertainties reported above, the attribution of *Vaninia gen. nov.* to a calliostomatid subfamily is considered premature and is postponed to a future study in which more representatives will be available. Similarly, the assignment of *Vaninia gen. nov.* to Margarellinae cannot be supported by our analysis, because there is no representative of that family with detailed anatomy known for comparison. Margarellinae is characterized by small shells with a glossy or dull external surface, lacking sculpture or with spiral sculpture; a thick columella that lacks denticles; shells that are typically not highly colored; a protoconch that does not display a reticulate honeycomb pattern; a radula with a protolateromarginal plate; and a foot with two horn-like projections (Williams, 2013). Margarellines are known to be endemic to the southern region of the globe, inhabiting Antarctica, the sub-Antarctic, and South America, particularly the Argentine province (González-Wevar et al., 2021).

Taxonomic Remarks at Species Level

The shells of the four *Vaninia* species occurring off the Brazilian coast exhibit distinct-

TABLE 1. Main conchological differences among the four known species of *Vaninia* gen. nov.

Character	<i>V. imperialis</i>	<i>V. mirabilis</i>	<i>V. vanini</i>	<i>V. dnophera</i>
Protoconch width (mm)	0.7	0.7	0.6	0.7
Height/width ratio	0.8	0.8	1.0	0.7
First teleoconch whorl, dotted spiral cord	present	absent	present	absent
First teleoconch whorl, smooth spiral cords	absent	present	present	weak
Number of dotted cords	2	2	2	1
Smooth spiral cords in penultimate whorl	2 or 3	4 or 5	2 or 3	3
Distance between these cords	wide	narrow	narrow	narrow
Average number of cords on inferior half of last whorl	9	12	10	12
Distance between these cords	wide	narrow	wide	narrow
Inner lip	narrow	narrow	broad	narrow
Umbilicus	closed	tightly open	closed	widely open
Periumbilical sculpture	longitudinal undulations	smooth	wide smooth concavity	strong curved riblets

tions (Table 1). The protoconch appears similar in all species, although that of *Vaninia vanini* gen. nov. sp. nov. is smaller, with a maximum width of 0.6 mm (Fig. 50), whereas the remaining species have a width of 0.7 mm (Figs. 4, 26, 64). In terms of shell profile, *Vaninia dnophera* has a more discoid shape with a height/width ratio of 0.7 (Fig. 62); whereas *Vaninia vanini* gen. nov. sp. nov. has a nearly spherical shape, with a ratio close to 1.0 (Figs. 51, 56), and the other two species have a ratio of 0.8 (Figs. 1, 9, 24, 28). All of the species are characterized by the conspicuous subsutural dotted cord running the entire length of the teleoconch, although this cord is absent in the first teleoconch whorl in *Vaninia mirabilis* (Fig. 26) and *Vaninia dnophera* (Fig. 64). The dotted cord is double in all species except *Vaninia dnophera* (Fig. 64), and in rare cases, it can even be triple (Fig. 53), possibly indicating an abnormality. The first teleoconch whorls lack additional cords besides the dotted cord in *Vaninia imperialis* (Figs. 4), have weakly developed smooth cords in *Vaninia dnophera* (Fig. 64), and well-developed cords in the other two species (Figs. 26, 50). The number of smooth spiral cords on

the penultimate whorl is four or five in *Vaninia mirabilis* (Figs. 24, 28) and two or three in the remaining species, particularly in *Vaninia imperialis*, which usually has two tall, well-spaced cords, unlike the other species (Figs. 1, 9). In the inferior half of the body whorl, an average of 12 spiral cords is observed in *Vaninia mirabilis* and *Vaninia dnophera* (Figs. 30, 63), whereas *Vaninia vanini* gen. nov. sp. nov. has ten cords (Figs. 46, 52) and *Vaninia imperialis* has nine (Fig. 3). In the same region, the distance between the spiral cords is wide, wider than the cord width itself, in *Vaninia imperialis* and *Vaninia vanini* gen. nov. sp. nov., whereas it is narrow in the other two species. The aperture of the four species is relatively similar, with the notable difference being the wide concavity of the inner lip in *Vaninia vanini* gen. nov. sp. nov. (Figs. 45, 51, 54). The umbilicus is completely closed in *Vaninia imperialis* (Fig. 3) and *Vaninia vanini* gen. nov. sp. nov. (Figs. 46, 52), tightly open in *Vaninia mirabilis* (Fig. 30), and more widely open in *Vaninia dnophera* (Fig. 63). Additionally, the umbilicus is flanked by a smooth area in *Vaninia mirabilis*, delicate longitudinal undulations in *Vaninia imperialis*,

TABLE 2. Main anatomical differences among the three anatomically known species of *Vaninia* *gen. nov.*

Character	<i>V. imperialis</i>	<i>V. mirabilis</i>	<i>V. vanini</i> <i>gen. nov. sp. nov.</i>
Cephalic lobe	triangular	rounded	rounded
Pedal papillae coverage	rich	poor	poor
Left epipodial tentacles	7 widely distributed	7 concentrated at middle	4 posteriorly located
Neck lobe	evident, with papillae at edges	evident with smooth edges	inconspicuous
Pedal gland lateral expansions	absent	present	present
Operculum multispirality	high	medium	medium
Terminal edge	narrow (8%)	wide (15%)	wide (15%)
Cephalic tentacles	very long	intermediate length	short
Mantle edge	simple	double	simple
Siphonal region	smooth	clearly folded	with tentacles
Ventral gill leaflet	asymmetrical, tip pointed	symmetrical, tip blunt	symmetrical, tip blunt
Ventral gill leaflet	length = width	length = width	length > width
Hypobranchial gland	broader posteriorly	inconspicuous	broader anteriorly
Jaws	thick	thin	intermediate
Inner component length/ outer component	$\frac{3}{4}$	$\frac{1}{2}$	$\frac{1}{2}$
Jaw cutting edge	angled	angled	rounded
Esophageal inner folds	strong	weak	strong
Odontophore pair m4	in layers	not in layers	not in layers
m6	narrow	wide	wide
m9	wide	narrow	narrow
Odontophore anterior cartilages	partially fused anteriorly	not fused	not fused
Cusps of inner marginal teeth	short, rounded	long, pointed	long, pointed
Number of outer marginal teeth (pairs)	~20	~20	12–14

a wide smooth concavity in *Vaninia vanini* *gen. nov. sp. nov.*, and strong curved riblets in *Vaninia dnophora*.

Anatomical comparisons were conducted on three of the studied species (no living specimen of *Vaninia dnophora* has been collected) (Table 2). The three species are similar in most

aspects, differing by only minor details, as is typical in closely related species. Notable differences were not detected in systems such as genital, renocirculatory, and central nervous. It is important to note that these observations are based on multiple studied specimens, except for *Vaninia vanini* gen. nov. sp. nov. In the headfoot, the pair of cephalic lobes (lc), is small in all species, but they are triangular in *Vaninia imperialis* (Fig. 14), whereas the remaining species have rounded lobes. The dorsal foot surface is covered with papillae, which are more abundant in *Vaninia imperialis*, reaching almost to the sole (Fig. 14, fs), whereas the other two species lack detectable papillae on the dorsal region of the foot (Figs. 35, 65). The length of the pair of cephalic tentacles (te) differs among species. *Vaninia imperialis* has exceptionally long tentacles, almost as long as the foot (Fig. 14); *Vaninia vanini* gen. nov. sp. nov. has short tentacles, slightly longer than the snout (Fig. 62); and *Vaninia mirabilis* has tentacles of intermediate length (Fig. 35). Differences were also found in the epipodium, an important source of taxonomic information in vetigastropods. Whereas the right side of the epipodium is relatively similar in all species, the left side differs: *Vaninia imperialis* has seven evenly sized and distributed tentacles (Fig. 14, et); *Vaninia mirabilis* has seven narrow and diminishing tentacles concentrated in the midregion of the epipodium (Fig. 35); and *Vaninia vanini* gen. nov. sp. nov. has only four small tentacles located in the posterior region of the right epipodium, with undulating mid- and anterior regions (Fig. 65). Also related to the epipodium, *Vaninia imperialis* has evident neck lobes (ln) with well-developed papillae along their edges; *Vaninia mirabilis* also has evident neck lobes, but their edges are smooth without papillae (Fig. 35); however, *Vaninia vanini* gen. nov. sp. nov. lacks evident neck lobes, because they are part of the epipodial profile (Fig. 65, ep). *Vaninia imperialis* is the only species without small lateral expansions of the furrow of the pedal glands (Fig. 14, pg), which are present in the other two species (Figs. 35, 65). The operculum of *Vaninia imperialis* has greater spirality (Figs. 5, 6) compared to the other two species (Figs. 27, 49), resulting in a narrower superior terminal growth edge, ~8% of the opercular length; the other two species have a wider edge, ~15% of the opercular length. The mantle edge of *Vaninia mirabilis* is double-edged (Fig. 38, mb), whereas it is simple in the other two species. The siphonal region of the

mantle edge is smooth in *Vaninia imperialis* (Fig. 17, inferior-right corner), transversely folded in *Vaninia mirabilis* (Fig. 38); and has distinct, small tentacles in *Vaninia vanini* gen. nov. sp. nov. (Fig. 67). Like most trochoideans, the studied species exhibit high asymmetry of the bipectinate gill leaflets, with the ventral leaflet (Fig. 16, gi) larger than the dorsal leaflet (gd), which remains inside the confined supra-branchial chamber (su). However, the ventral leaflet of *Vaninia imperialis* has a pointed tip (Fig. 16), whereas in the other two species, it is symmetrical with a blunt tip (Figs. 37, 66), with *Vaninia vanini* gen. nov. sp. nov. having proportionally taller leaflets. The hypobranchial gland (hg) is concentrated posteriorly in *Vaninia imperialis* (Fig. 17), anteriorly in *Vaninia vanini* gen. nov. sp. nov. (Fig. 67), and is inconspicuous in *Vaninia mirabilis* (Fig. 38). The pair of jaw plates differs among the three species; *Vaninia imperialis* has thick, dark plates (Fig. 8); *Vaninia mirabilis* has thin, translucent plates (Fig. 25); and *Vaninia vanini* gen. nov. sp. nov. has intermediate plates (Fig. 48). The inner narrow components of the jaws are longer, occupying approximately three-quarters of the jaw length in *Vaninia imperialis*, whereas they are shorter, occupying approximately one-fifth in the other two species. The main components with the cutting edge are rounded in *Vaninia vanini* gen. nov. sp. nov., creating a slightly cordiform jaw set (Fig. 48), while they are angled in the other species. The esophagus of the studied species is wide, folded, and has thick glandular walls, but lacks detectable special chambers found in other vetigastropods (Dornellas et al., 2020). *Vaninia imperialis* and *Vaninia vanini* gen. nov. sp. nov. have well-developed inner longitudinal esophageal folds (Fig. 20, ef); whereas *Vaninia mirabilis* has less-developed folds (Fig. 40). In the odontophore, partial fusion of the anterior region of the anterior cartilages occurs in *Vaninia imperialis* (Fig. 22, un), which is absent in the other two species (Fig. 44). Consequently, the horizontal muscle (m6) is narrow in *Vaninia imperialis* and wide in the other species, connecting the two anterior cartilages. The main pair of radular tensor muscles (m4) has two layers in *Vaninia imperialis* (Fig. 23), whereas the other two species have a single layer. The posterior, transverse muscle (m9) is wider in *Vaninia imperialis* and narrower in the remaining two species. The radular features of the three species (Figs. 10–13, 31–34, 58–61) are relatively similar, with only two notable differences: the pair of

inner marginal teeth in *Vaninia imperialis* has short rounded cusps, whereas the other two species have long pointed cusps; also, the number of outer marginal teeth is greater in *Vaninia imperialis* and *Vaninia mirabilis* (~20 pairs), compared to *Vaninia vanini* *gen. nov. sp. nov.* (12–14 pairs).

Three additional species found on the south-eastern Atlantic coast of South America have been referred to as *Margarites*: (1) *Margarites kophameli* (Strebel, 1905), with type locality on the eastern coast of Patagonia; (2) *Margarites malouinus* (d'Orbigny, 1841), with type locality Falkland Islands; and (3) *Margarites sigaretinus* (G. B. Sowerby I, 1838), with type locality in Port Famine, Magellan Strait (Forcelli, 2000; Simone, in preparation). These three species are rare and very poorly understood. The four *Vaninia* species differ from *Margarites kophameli* by their larger size (former species < 9 mm), strong spiral sculpture, and lacking a peripheral blunt carina on the last whorl (Strebel, 1905: pl. 5, fig. 18). *Margarites malouinus* is known from a single, tiny specimen (3 mm), which could not be located in recent personal surveys (LRLS) in Paris and London institutions; its original description (d'Orbigny, 1841: 411, species #313) lacks illustrations and is relatively lacking in details. It is likely that this specimen is a young individual of what is now recognized as *Margarella wacei* (Melvill & Standen, 1819), also from the Falklands, and should be considered a *nomen oblitum* or *nomen dubium*. Nevertheless, d'Orbigny's (1841) description referred to axial striae as the sculpture instead of the spiral sculpture found in *Vaninia* species. *Margarites sigaretinus* has long been considered a *nomen dubium* (Strebel, 1905), and its description (G. B. Sowerby I, 1838: 24, species #4) displayed characteristics not found in any shells of *Vaninia* *gen. nov.*, e.g., fragile and thin walls, and a smooth surface. Another species worth comparing to *Vaninia* species in the region is *Calliostoma nodiustulum* (Martens, 1881). The original description is relatively poor and lacks illustrations, with more details and illustrations provided by Strebel (1905: 131, pl. 5, fig. 26). Some specimens of *Vaninia* *gen. nov.* have been identified as *Calliostoma nodiustulum* (e.g., Forcelli, 2000: 60) due to their predominantly spiral sculpture; however, the shell profile of *Calliostoma nodiustulum* is much straighter, with a taller shell and smaller spire compared to *Vaninia* species. Additionally, the presence of a dotted subsutural cord, which is typical of *Vaninia*, is not clear in *Calliostoma*

nodiustulum. Therefore, it is not likely that this species possibly is a young *Calliostoma*.

Regarding the geographic distribution, *Vaninia dnophera* has only been found at its type locality, off Pernambuco, northeastern Brazilian coast, which is influenced by the Caribbean fauna. The other species are found along the southeastern and southern coasts of Brazil. *Vaninia imperialis* is found from Espírito Santo to Santa Catarina coasts, overlapping with the distribution of *Vaninia vanini* *gen. nov. sp. nov.*, which is known from São Paulo to Santa Catarina coasts. *Vaninia mirabilis* is the southernmost species, with a known distribution from Rio Grande do Sul to the coast of Uruguay. In terms of bathymetry, *Vaninia mirabilis* occurs in shallower waters, with a known depth range of 85–206 m, whereas *Vaninia imperialis* is the deepest species, occurring between 270 and 900 m. *Vaninia dnophera* was found at a depth of 640 m, and *Vaninia vanini* *gen. nov. sp. nov.* is found between 250 and 400 m.

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APPENDIX 1. Character list for phylogenetic analysis. CI, consistency index; L, length (steps); RI, retention index; uninf, uninformative.

No.	Character	Character states	L	CI	RI
1	Shell shape	0 – trochiform; 1 – turbiniform; 2 – discoid; 3 – ventricose; 4 – auriform; 5 – bulimoid; 6 – globose	7	71	71
2	Shell whorl profile	0 – deeply convex; 1 – slightly convex	4	25	40
3	Shell, last whorl, keel	0 – absent; 1 – present	4	25	0
4	Shell spire, shoulder	0 – absent; 1 – present	2	50	50
5	Shell aperture, base	0 – oblique; 1 – slightly straight; 2 – rounded; 3 – straight; 4 – angulated	8	37	28
6	Shell aperture, growth of outer lip	0 – up to a quarter whorl; 1 – > half a whorl	2	50	0
7	Shell, external irides- cence	0 – absent; 1 – present	5	20	42
8	Shell, axial blotches	0 – present; 1 – absent	5	20	33
9	Shell, axial blotches, shape	0 – parallel lines; 1 – oblique patches; 2 – mosaic; 3 – striated	4	50	50
10	Shell, oblique blotches, arrangement	0 – irregular; 1 – regular	3	33	33
11	Shell, spiral blotches	0 – absent; 1 – present	2	50	75
12	Shell base, spiral blotch surrounding umbilical area	0 – absent; 1 – present	4	25	25
13	Shell, purplish-black color	0 – absent; 1 – present	2	50	0
14	Shell, spire, spiral cords	0 – present; 1 – absent	3	33	33
15	Shell, spire, spiral cords, shape	0 – nodulous; 1 – smooth	2	50	80
16	Shell, spire, differenti- ated and equidistant spiral cords	0 – absent; 1 – present	4	25	0
17	Shell, spiral cords, dis- tance between cords	0 – < cord width; 1 – ≥ cord width	5	20	42
18	Shell, spiral cords, nod- ules, shape	0 – conspicuous; 1 – inconspicuous	4	25	25
19	Shell, periphery, distinct beaded spiral cords	0 – absent; 1 – present	1	uninf	

(continues)

APPENDIX 1. Continued.

No.	Character	Character states	L	CI	RI
20	Shell, spire, prominent subsutural beaded spiral cord	0 – absent; 1 – present	2	50	0
21	Shell, secondary cords	0 – absent; 1 – present	2	50	50
22	Shell, base, spiral cords	0 – present; 1 – absent	2	50	66
23	Shell, base, width of spiral cords relative to width of spiral cords on spire	0 – thinner; 1 – equal; 2 – wider	3	33	71
24	Shell, base, shape	0 – straight; 1 – slight convex; 2 – convex	5	40	25
25	Shell, spire, axial ribs	0 – absent; 1 – present	1	100	100
26	Umbilicus	0 – present; 1 – absent	2	50	0
27	Umbilicus, shape	0 – closed; 1 – open	7	14	25
28	Umbilicus, columellar callus	0 – present; 1 – absent	4	25	25
29	Umbilicus, columellar callus, position	0 – at shell level; 1 – protruding	2	50	50
30	Umbilicus, occlusion from columellar callus in open umbilicus	0 – unoccluded; 1 – occluded by one-third of total umbilical area; 2 – occluded by > half of total umbilical area	2	uninf	
31	Umbilicus, columellar callus, color	0 – whitish; 1 – green; 2 – red; 3 – orange	2	uninf	
32	Umbilicus, columellar callus, width relative to diameter of umbilicus	0 – wider; 1 – thinner	2	uninf	
33	Umbilical area, color	0 – whitish; 1 – orange; 2 – greenish brown; 3 – dark brown	2	50	0
34	Umbilical area, spiral cords	0 – absent; 1 – present	4	25	40
35	Umbilical area, outer edge varix ending in a tooth	0 – absent; 1 – present	3	33	0
36	Umbilical area, crenated edge	0 – absent; 1 – present	1	100	100
37	Columella, posterior area, shape	0 – arched; 1 – twisted; 2 – serrated	2	uninf	
38	Columella, base, tooth	0 – absent; 1 – present	3	33	0
39	Columella, base, tooth, number	0 – one; 1 – two; 2 – three; 3 – multiple	1	uninf	
40	Columella, base, length of anterior tooth relative to others	0 – more than two times length; 1 – two times length	1	uninf	
41	Shell aperture, internal lirae	0 – absent; 1 – present	8	12	36
42	Shell aperture, internal lirae, shape	0 – smooth; 1 – nodulous	2	50	0

(continues)

APPENDIX 1. Continued.

No.	Character	Character states	L	CI	RI
43	Head, cephalic lappets	0 – absent; 1 – present	2	50	75
44	Head, cephalic lappets, width relative to ommatophore width	0 – narrower; 1 – two times as wide; 2 – three times as wide; 3 – same width	9	33	45
45	Head, cephalic lappets, longitudinal inner flap	0 – absent; 1 – present	2	50	66
46	Head, cephalic lappets, edge	0 – papillated; 1 – fringed; 2 – smooth	6	33	20
47	Head, cephalic tentacles, dorsal coloration	0 – uniform; 1 – longitudinal line(s); 2 – transverse lines	2	100	100
48	Epipodium, posterior region	0 – surrounding the posterior region of the opercular pad; 1 – surrounding the anterior region of the opercular pad	1	100	100
49	Epipodium, tentacle, number of pairs (Fig. 11)	0 – three; 1 – four; 2 – six; 3 – ten or more; 4 – non-paired	9	44	44
50	Epipodium, pair of anterior tentacles, position relative to each other	0 – symmetrical; 1 – asymmetrical	1	uninf	
51	Epipodium, neck lobe	0 – distinguishable from epipodium; 1 – indistinguishable from epipodium	1	100	100
52	Epipodium, left neck lobe, shape	0 – smooth; 1 – slightly fringed; 2 – bearing tentacles	9	22	46
53	Epipodium, left neck lobe, tentacles, number	0 – two to seven; 1 – more than 10; 2 – one	2	100	100
54	Epipodium, right neck lobe, shape	0 – smooth; 1 – slightly fringed; 2 – tentacled	7	28	16
55	Epipodium, right neck lobe, layers	0 – single; 1 – multiple	6	16	16
56	Epipodium, right neck lobe, layers, length	0 – same length; 1 – outer layer two times as long as inner layer	3	33	0
57	Epipodium, tentacles, base, sense organs, shape	0 – papilliform; 1 – fringed	3	33	0
58	Foot, anterior end, shape	0 – not extended, simple; 1 – bifid; 2 – laterally expanded, “horned”; 3 – medially expanded, in a longitudinal line; 4 – anteriorly expanded	4	100	100
59	Foot, coloration	0 – reddish to light brown; 1 – blackish to dark brown; 2 – intense red	3	33	71
60	Foot, dorsal papillae	0 – present; 1 – absent	6	16	54
61	Foot, opercular pad, shape	0 – reniform; 1 – round	2	50	66
62	Operculum	0 – corneous; 1 – calcareous	3	33	66
63	Operculum, calcareous surface	0 – smooth; 1 – rough	2	50	50

(continues)

APPENDIX 1. Continued.

No.	Character	Character states	L	CI	RI
64	Pallial cavity, mantle border, exhalant siphon	0 – absent; 1 – present	3	33	0
65	Pallial cavity, right female nephrostome, shape	0 – tubular; 1 – ampoule; 2 – rosette; 3 – undifferentiated	3	100	100
66	Pallial cavity, transverse pallial vein	0 – absent; 1 – present	2	50	50
67	Pallial cavity, ctenidium, ctenidial filaments	0 – bipectinate; 1 – monopectinate	1	100	100
68	Pallial cavity, ctenidium, suspensory membrane	0 – absent; 1 – present	6	16	28
69	Snout, dorsal surface	0 – smooth; 1 – papillate	3	33	50
70	Snout, anteroventral surface	0 – papillate; 1 – bearing longitudinal folds; 2 – bearing rounded folds	4	50	77
71	Snout, medial ventral line, shape	0 – single; 1 – everted in a pseudoproboscis	4	25	40
72	Jaws	0 – thick; 1 – thin	7	14	45
73	Odontophore muscle, m7a, width relative to width of m7	0 – ten times as thick; 1 – three times as thick; 2 – two times as thick; 3 – same thickness	9	33	40
74	Odontophore muscle m7a, point of intersection with m7 (Fig. 16)	0 – posterior end; 1 – posterior end of medial region; 2 – anterior end of medial region	4	50	50
75	Odontophore muscle m1d	0 – absent; 1 – present	6	16	0
76	Odontophore muscle m1d, length relative to cerebral ganglion length	0 – to one-half; 1 – > one-half	2	50	0
77	Odontophore muscle, posterior buccal retractor muscle	0 – absent; 1 – present	3	33	0
78	Odontophore muscle m9	0 – absent; 1 – present	6	16	37
79	Odontophore muscle m10d	0 – absent; 1 – present	4	25	50
80	Radula, rachidian tooth, base, interaction with the innermost lateral tooth	0 – overlapping; 1 – interlocking	3	33	77
81	Radula, rachidian tooth, base, interlocking position	0 – anterior; 1 – median; 2 – posterior	2	100	100
82	Radula, rachidian tooth, base, inner edge	0 – absent; 1 – present	2	100	100
83	Radula, rachidian tooth, base, inner edge length relative to rachidian	0 – one-third; 1 – one-half; 2 – > one-half	2	50	0

(continues)

APPENDIX 1. Continued.

No.	Character	Character states	L	CI	RI
84	Radula, rachidian tooth, shaft	0 – present; 1 – absent	2	50	87
85	Radula, rachidian tooth, shaft, shape	0 – lanceolate; 1 – flattened; 2 – triangular; 3 – rectangular; 4 – dorsally expanded, “hooded”	7	57	62
86	Radula, rachidian tooth, shape of shaftless tooth	0 – triangular; 1 – rhomboidal; 2 – hexagonal; 3 – trapezoid; 4 – hippocrepiiform	3	100	100
87	Radula, rachidian tooth, apical cusp	0 – present; 1 – absent	2	50	50
88	Radula, rachidian tooth, apical cusp	0 – undeveloped; 1 – well developed (protracted)	3	33	50
89	Radula, rachidian tooth, protracted apical cusp, serration	0 – present; 1 – absent	3	33	71
90	Radula, rachidian tooth, undeveloped apical cusp, length relative to inner edge	0 – one-third of length; 1 – one-half of length	1	uninf	
91	Radula, rachidian tooth, extra attachment membrane	0 – absent; 1 – present	2	50	50
92	Radula, rachidian tooth, row, teeth interaction	0 – absent; 1 – present	4	25	57
93	Radula, rachidian tooth, ratio	0 – longer than wide; 1 – wider than long; 2 – as wide as long	4	50	77
94	Radula, rachidian tooth, length relative to innermost laterals	0 – reduced; 1 – equal; 2 – longer	7	28	50
95	Radula, rachidian tooth, width relative to innermost lateral tooth	0 – equal; 1 – wider	4	25	50
96	Radula, rachidian tooth, distance between teeth in column	0 – no distance (interacting with each other); 1 – < tooth length; 2 – > tooth length	3	66	86
97	Radula, pairs of lateral teeth	0 – multiple; 1 – nine; 2 – seven; 3 – six; 4 – five; 5 – four	6	83	75
98	Radula, lateral tooth, shape relative to rachidian	0 – irregular; 1 – similar; 2 – different	4	50	71
99	Radula, lateral tooth, height within row	0 – decreases and increases; 1 – equal height; 2 – increasing gradually; 3 – decreasing gradually	6	50	25
100	Radula, outermost lateral tooth, shape relative to inner teeth	0 – similar; 1 – different	1	100	100
101	Radula, lateral tooth, base, interaction in row	0 – overlapping; 1 – interlocking	3	33	77

(continues)

APPENDIX 1. Continued.

No.	Character	Character states	L	CI	RI
102	Radula, lateral tooth, base, shape	0 – stalk-shaped; 1 – square; 2 – rounded; 3 – ball and socket	4	75	85
103	Radula, lateral tooth, ball-and-socket base, interaction with adjacent tooth	0 – ventral; 1 – dorsal	4	25	25
104	Radula, lateral tooth, shaft	0 – present; 1 – absent	1	100	100
105	Radula, lateral tooth, shaft, hood	0 – absent; 1 – present	3	33	71
106	Radula, lateral tooth, shaft, interaction in row	0 – present; 1 – absent	1	100	100
107	Radula, lateral tooth, apical cusp	0 – present; 1 – absent	1	100	100
108	Radula, lateral tooth, apical cusp, shape	0 – pointed; 1 – rounded; 2 – keel-shaped	7	28	50
109	Radula, outermost lateral tooth, apical cusp, length relative to cusps of inner teeth	0 – shorter; 1 – of equal length; 2 – longer	7	28	44
110	Radula, lateral tooth, apical cusp, lateral edge	0 – smooth; 1 – serrated; 2 – bicuspid	3	66	75
111	Radula, lateral tooth, secondary cusps, position	0 – laterally on apical cusp; 1 – medially and posteriorly on apical cusp	2	50	85
112	Radula, lateral tooth, dorsal side, keel	0 – absent; 1 – present	4	25	25
113	Radula, lateromarginal plate	0 – absent; 1 – present	3	33	0
114	Radula, marginal teeth, shape	0 – different shapes along row; 1 – feather-shaped; 2 – sickle-shaped	1	100	100
115	Radula, innermost marginal teeth	0 – unmodified; 1 – modified	1	100	100
116	Radula, innermost marginal tooth, shaft, interaction with outermost lateral teeth	0 – absent; 1 – present	3	33	81
117	Radula, innermost marginal tooth, apical cusp, length relative to outermost apical cusp of lateral tooth	0 – approximately one-half of length; 1 – same length; 2 – > two times length	7	28	54
118	Radula, innermost marginal tooth, apical cusp, length relative to cusp of adjacent marginal tooth	0 – same length; 1 – two times length; 2 – three times length	6	66	83

(continues)

APPENDIX 1. Continued.

No.	Character	Character states	L	CI	RI
119	Radula, innermost marginal tooth, apical cusp, shape	0 – tricuspid; 1 – bicuspid; 2 – serrated; 3 – smooth	5	50	80
120	Radula, innermost marginal teeth #1–5, apical cusps, shape	0 – pointed; 1 – rounded	3	33	60
121	Haemocoel	0 – esophagus covering < half of odontophore length; 1 – esophagus covering > two-thirds of odontophore length	1	100	100
122	Salivary gland, shape	0 – branched (indistinguishable); 1 – rounded (distinguishable)	4	25	57
123	Esophagus, esophageal folds, number	0 – four; 1 – three; 2 – > three	3	66	66
124	Esophagus, esophageal folds, shape	0 – free; 1 – fused	3	33	0
125	Esophagus, left dorsal esophageal fold, position	0 – curved left; 1 – straight	5	20	50
126	Esophagus, left dorsal curved esophageal fold, position	0 – extending to ventral right fold; 1 – extending to diverticulum; 2 – extending to posterior end of midgut	5	40	40
127	Esophagus, dorsal folds, width relative to ventral folds	0 – same width; 1 – one-half of width; 1 – < one-half of width; 2 – > one-half of width	7	42	55
128	Stomach, spiral caecum, number of whorls	0 – four; 1 – one and one-half; 2 – one-half; 3 – three and one-half; 4 – two	3	100	100