

Anatomy of an abundant and widespread but poorly known terrestrial snail from Brazil: *Angulata angulata* (G. B. Sowerby II, 1842) (Gastropoda: Helicinidae)

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ABSTRACT

***Angulata angulata* (G. B. Sowerby II, 1842) new combination**, originally and traditionally included in the genus *Helicina*, is a poorly known terrestrial gastropod endemic to Brazil, occurring in Bahia, Rio de Janeiro, São Paulo, and Santa Catarina states. The species is known only by details of its shell from the original description, although the species is very common and cited in many species surveys. The present study aims to describe the complete anatomy of *Angulata angulata* through detailed investigation of shell features, including microornamentation and ultrastructure, radula, and detailed anatomical data from its pallial cavity and associated organs, digestive, nervous and reproductive systems. The anatomical differences and similarities between *A. angulata* and other helicinids with available data occurring in Brazil are examined and the generic allocation of the species is discussed. The species is characterized by a globose, strongly keeled shell with a semielliptical aperture pointed ventrally; operculum slightly concave, semielliptical, brown to orange, muscle scar sinusoidal; radular formula (28–4–1–4–28); short accessory prostate cecum; large bursa copulatrix, small provaginal sac, long accessory sperm sac duct; large dorsal ganglia, markedly divided, statocyst dorsally inserted on pedal ganglia. A comparison with other helicinids from Brazil is provided. *Angulata* is here proposed as a genus level taxon, including at least three species, ***Angulata angulata* new combination**, ***Angulata variabilis* (J. A. Wagner, 1827) new combination**, and ***Angulata brasiliensis* (J. E. Gray, 1824) new combination**.

Additional Keywords: Biodiversity, Neritimorpha, land snail, new combination

INTRODUCTION

Gastropods have independently colonized terrestrial habitats at least 30 times (Vermeij and Watson-Zink, 2022), becoming widespread across a wide range of environments, ranging from subpolar to tropical and from deserts to rainforests, and even in urbanized areas (Barker, 2001; Kano *et al.*, 2002; Chapman, 2009; Bouchet *et al.*, 2017). Among these, only six clades contain more than 100 extant species (Vermeij and Watson-Zink, 2022; MolluscaBase

eds., 2025). One of these is Helicinoidea A. Férussac, 1822, which comprises more than 800 species, most of which, approximately 720 species, within the family Helicinidae A. Férussac, 1822 (Bouchet *et al.*, 2017; MolluscaBase eds., 2025). Helicinids occur mostly in the Neotropics, but also in parts of southeast Asia and Oceania (Barker, 2001; Kano *et al.*, 2002; Richling, 2014). In some parts of Central America they are a dominant group of terrestrial mollusks (Wagner, 1907–1911; Richling, 2004). The most diverse genus of the family is *Helicina* Lamarck, 1799, with approximately 170 extant species (Bouchet *et al.*, 2017; MolluscaBase eds., 2025).

Very little is known about the anatomy of most species of the genus *Helicina*. Baker (1926) described the anterior portion of the reproductive system of 12 species of *Helicina* and provided details about the pallial cavity for some of these. Richling (2004) provided a more complete description of the reproductive system and radula of *Helicina funcki* L. Pfeiffer, 1849. In Brazil, more than 30 species of *Helicina* are known (Salvador *et al.*, 2024), but most remain poorly understood beyond their original descriptions. Most of the anatomy of ***Angulata variabilis* (J. A. Wagner, 1827) new combination** has been described (Simone, 2018, as *Helicina variabilis*), while only the anterior portion of the reproductive system of *Helicina concentrica* L. Pfeiffer, 1849 is known (Baker, 1926), and only the radula described for *Helicina inaequistriata* Pilsbry, 1900 (Fernandes *et al.*, 2025). ***Angulata angulata* (G. B. Sowerby II, 1842) new combination** is a poorly known species occurring only in Brazil, specifically in Bahia, Rio de Janeiro, São Paulo, and Santa Catarina states (Figure 1) (Simone, 2006; Agudo-Padrón, 2011). Only details of its shell are known from the original description, although the species is very common and cited in many species surveys (Hidalgo, 1870; Hidalgo, 1872; Hidalgo, 1893; Agudo-Padrón, 2011; Agudo-Padrón, 2012; Agudo-Padrón, 2014; Agudo-Padrón, 2018; Agudo-Padrón, 2022; Rangel *et al.*, 2021; Agudo-Padrón, 2024). *Angulata angulata* is also the type species of *Angulata* J. A. Wagner, 1905. It was proposed by Richling (2004) that the South American *Helicina* do not necessarily belong to *Helicina*, but possibly

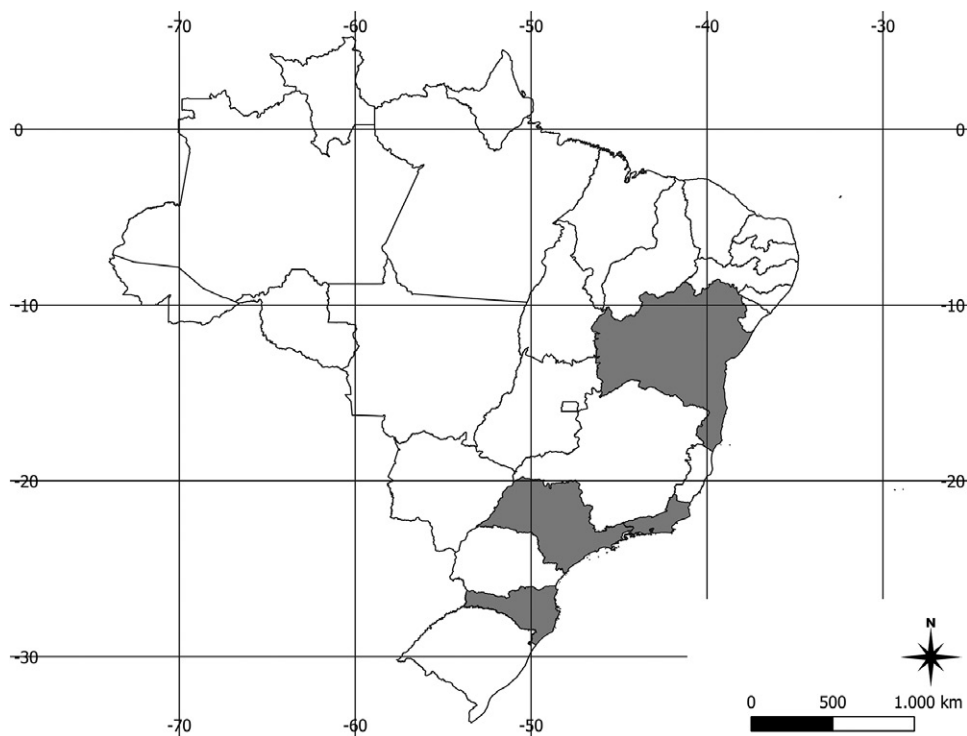


Figure 1. Documented distribution of *Angulata angulata*.

to *Angulata*, and in this case should warrant a new combination. (Richling [2004], however, did not analyze *A. angulata*.)

Hence, the goals of this study were to: (1) describe the anatomy of *Angulata angulata* including shell features like, shell microornamentation, and ultrastructure; digestive system including the radula; organs of the pallial cavity; nervous system; and reproductive system; (2) propose the allocation of *Helicina angulata* to the nominal genus *Angulata*; (3) discuss the anatomical differences and similarities between *Angulata angulata* and other Brazilian heliciniids for which data are available

MATERIALS AND METHODS

Analyzed material is housed in the collection of Laboratório de Malacologia da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (IBUFRJ). Lots listed in bold indicate specimens that were dissected. Five males and six females were dissected in detail.

Dissections followed standard procedures beginning with an incision along the mantle edge to expose the pallial cavity, followed by a cut along the pallial cavity, near the body's spiral axis, extending to the apex of the visceral mass. Specimens were dissected under 70% ethanol, using a Zeiss Stemi SV 11 stereomicroscope with *camera lucida*. The pallial, reproductive, digestive, circulatory, excretory, and nervous systems were isolated, examined, and described. Illustrations made using *camera lucida*

were digitized using a scanner, and later vectorized and edited using Inkscape. Buccal masses were dissected, radulae were manually extracted without digestion and rinsed in distilled water. Well preserved shells were selected, extracted, and cleaned with a fine tipped paint brush. Scanning electron micrographs (SEM) of radulae, protoconch and opercula were performed using a JEOL-JSM-6390-LV at the Rudolf Barth Electron Microscopy Platform at Instituto Oswaldo Cruz / FIOCRUZ, Rio de Janeiro, Brazil. The material was sputter-coated with gold before imaging with SEM.

For the descriptions of the nervous system, abbreviations used for nerves were defined by their insertion (letters) and position from anterior to posterior axis (numbers). No assumptions of homology were made in the identification of these nerves.

Material Examined: *Angulata angulata*: Type material: Not located (Breure and Araujo, 2017), but figures from original description included (Figures 2–3); Other material: Brazil, Rio de Janeiro State: Guapimirim: IBUFRJ 21248 (seven whole specimens in ethanol), IBUFRJ 21249 (five whole specimens in ethanol), IBUFRJ 21260 (two whole specimens in ethanol), IBUFRJ 21306 (two whole specimens in ethanol), IBUFRJ 21307 (two whole specimens in ethanol), IBUFRJ 21308 (two whole specimens in ethanol), IBUFRJ 21309 (two whole specimens in ethanol), IBUFRJ 21310 (one whole specimen in ethanol), IBUFRJ 21311 (four whole specimens in ethanol), IBUFRJ 21312 (five whole specimens in ethanol), IBUFRJ



Figures 2–3. *Angulata angulata*, original figures from G. B. Sowerby II, 1842. **2.** Pl. ii, fig. 61. **3.** Pl. iii, fig. 100.

21327 (one whole specimen in ethanol), IBUFRJ 21430 (one whole specimen in ethanol), IBUFRJ 21562 (two whole specimens in ethanol), IBUFRJ 21563 (four dry shells), IBUFRJ 21565 (two dry shells), IBUFRJ 21566 (two dry shells), IBUFRJ 21644 (three whole specimens in ethanol), IBUFRJ 22709 (one whole specimens in ethanol), IBUFRJ 22721 (two dry shells), IBUFRJ 22722 (one whole specimen in ethanol). Rio de Janeiro: IBUFRJ 21606 (four whole specimens in ethanol, 22°57'12" S, 43°17'29" W), IBUFRJ 21690 (five whole specimens in ethanol, 22°57'12" S, 43°17'29" W), IBUFRJ 21698 (one whole specimen in ethanol, 22°57'19" S, 43°17'8" W), IBUFRJ 21732 (five whole specimens in ethanol), **IBUFRJ 22012 (one whole specimen in ethanol, 22°57'22" S, 43°16'52" W)**, **IBUFRJ 22025 (one whole specimen in ethanol, 22°57'14" S, 43°17'9" W)**, IBUFRJ 22026 (one whole specimen in ethanol, 22°57'14" S, 43°17'9" W), IBUFRJ 22027 (two whole specimens in ethanol, 22°57'14" S, 43°17'9" W), IBUFRJ 22029 (one whole specimen in ethanol, 22°57'12" S, 43°17'29" W), IBUFRJ 22030 (one specimen, 22°57'12" S, 43°17'29" W), IBUFRJ 22031 (one specimen, 22°57'12" S,

43°17'29" W), **IBUFRJ 22032 (one whole specimen in ethanol, 22°57'12" S, 43°17'29" W)**, IBUFRJ 22034 (one whole specimen in ethanol, 22°56'57" S, 43°17'6" W), **IBUFRJ 22041 (one whole specimen in ethanol, 22°57'19" S, 43°17'8" W)**, IBUFRJ 22456 (one whole specimen in ethanol, 22°57'19" S, 43°17'8" W), IBUFRJ 22536 (one whole specimen in ethanol, 22°57'19" S, 43°17'8" W), IBUFRJ 22537 (three dry shells, 22°57'19" S, 43°17'8" W), IBUFRJ 22612 (six whole specimens in ethanol, 22°57'12" S, 43°17'29" W), **IBUFRJ 22615 (six whole specimens in ethanol, 22°57'12" S, 43°17'29" W)**, IBUFRJ 22618 (one whole specimen in ethanol, 22°57'12" S, 43°17'29" W), IBUFRJ 22620 (one whole specimen in ethanol, 22°57'12" S, 43°17'29" W), IBUFRJ 22660 (four whole specimens in ethanol, 22°57'14" S, 43°17'29" W), IBUFRJ 23604 (one whole specimen in ethanol, 22°57'29" S, 43°16'40" W), IBUFRJ 23617 (one whole specimen in ethanol, 22°57'14" S, 43°17'29" W). Teresópolis: **IBUFRJ 22832 (one whole specimen in ethanol, 22°29'35" S, 43°4'24" W)**.

RESULTS

Helicinoidea A. Férussac, 1822

Helicimidæ A. Férussac, 1822

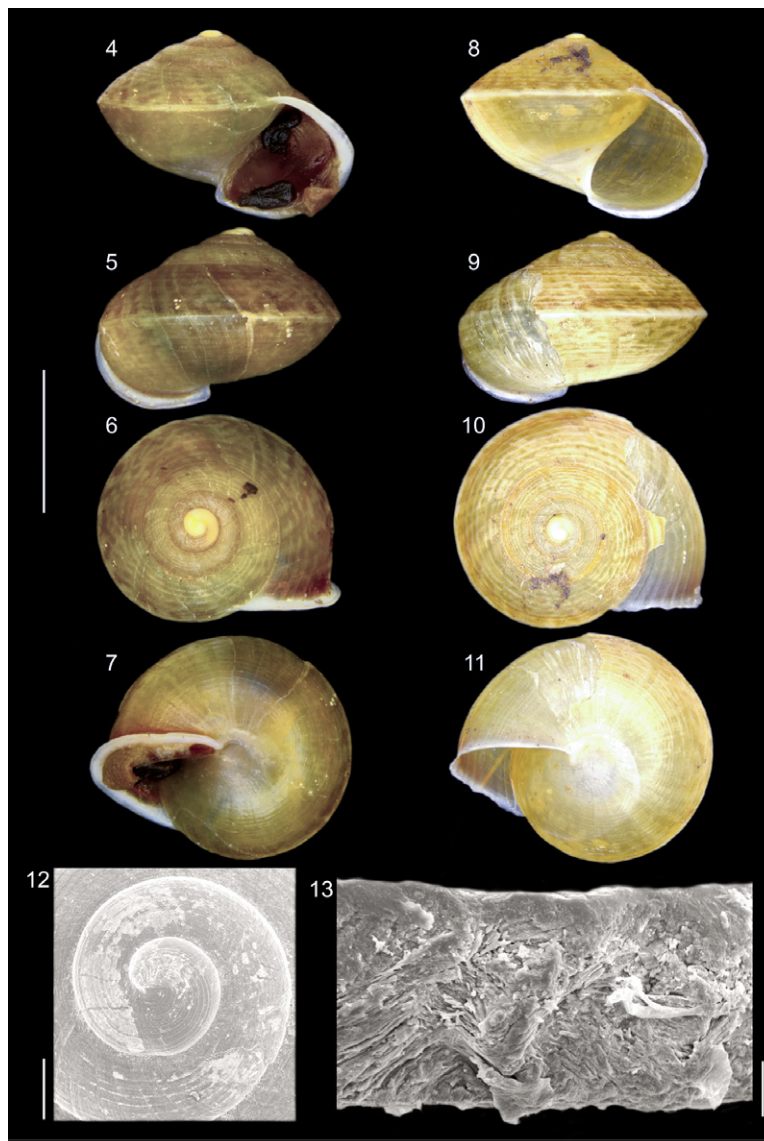
Angulata J. A. Wagner, 1905

Angulata angulata (G. B. Sowerby II, 1842) new combination

Helicina angulata G. B. Sowerby II (1842: 12, pl. 2, fig. 61, pl. 3, fig. 100).

Helicina angulata.—Pfeiffer (1850–1853: 60); Crosse and Fischer (1870: 69); Hidalgo (1870: 69); Hidalgo (1872: 152); Hidalgo (1893: 118); Wagner (1910: 185–186); Agudo-Padrón (2011: 6); Agudo-Padrón (2012: 36, fig. 2); Kotzian and Amaral (2013: 310, fig. 6a-c); Agudo-Padrón (2014: 10); Birckolz *et al.* (2016: 148); Sazima and Muscat (2016: 2, fig. 2); Breure and Araujo (2017: 9, fig. 9d-f); Salvador *et al.* (2017: 137); Agudo-Padrón (2018: 55); Agudo-Padrón (2022: 3103); Rangel *et al.* (2021: 4–5, 8, fig. 3g, fig. 7f); Agudo-Padrón (2024: 5); Salvador *et al.* (2024: 149).

Description: SHELL (FIGURES 4–13): Globose, 45mm height, 65mm width, with ~4.5 whorls. Whorl margins strongly keeled at midpoint, dextral, apex blunt, spire angle ~120°, shell of male slightly rounder. Color light-to dark-beige, with blots of red close to aperture; aperture white. Periostracum thin. Suture well-marked, simple, almost perpendicular to columellar axis. Teleoconch sculptured with weak growth lines and spiral lirae. Protoconch with ~0.75 whorls, sculptured by fine lirae only. Aperture semielliptical, ~2/3 of shell height; peristome slightly reflected, pointed basally; parietal callus thin or absent. Shell imperforate. Shell ultrastructure



Figures 4–13. *Angulata angulata*, shell. **4–7.** IBUFRJ22012, Male, apertural, adapertural, apical, and adapical views, respectively. **8–11.** IBUFRJ22615, Female, apertural, adapertural, apical, and adapical views, respectively. **12.** IBUFRJ22615, Details of protoconch microsculpture. **13.** IBUFRJ22615, Details of shell ultrastructure. Scale bar for 4–11=5mm; 12=500µm; 13=20µm.

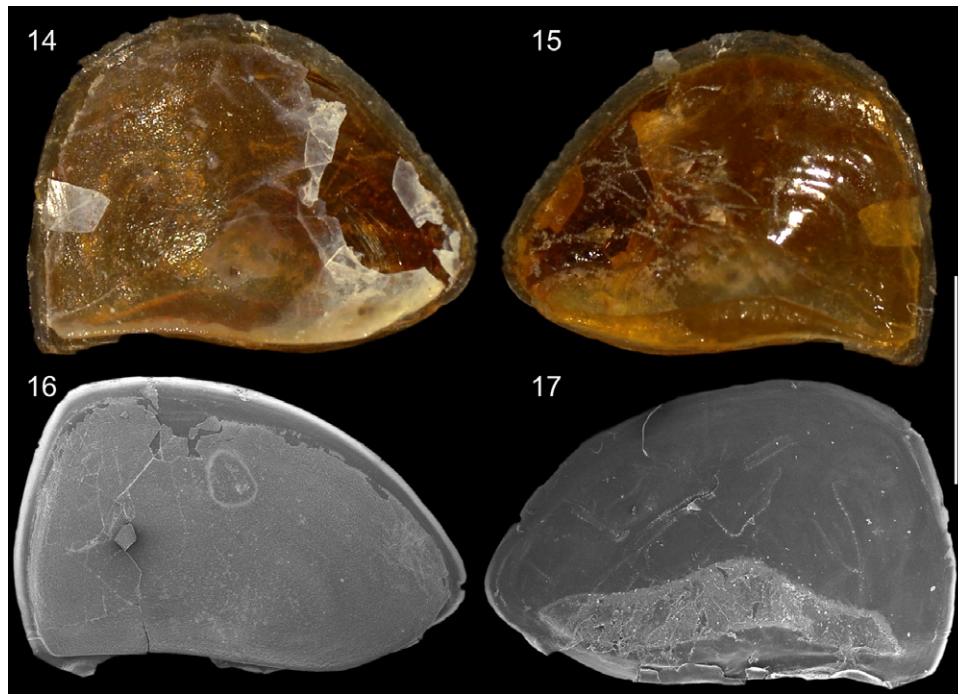
composed of an external periostracum of ~15µm thickness followed by two calcified layers. Outermost is crossed-lamellar of ~50µm. Innermost is ~10µm, solid, with no apparent lamellae.

OPERCULUM (FIGURES 14–17): Operculum slightly concave, semielliptical, hard, thin, brown to orange, slightly translucent, occupying entire aperture. Nucleus barely visible, located close to muscle scar. Edges thinner and less colored. Outer surface smooth, sculptured with weak concentric lines. Inner surface smooth, glossy; muscle scar sinusoidal, occupying ~30% of inner surface.

PALLIAL CAVITY AND ASSOCIATED ORGANS (FIGURES 18–19): Pallial cavity short, occupying ~1/2 whorl. Mantle

edge thin, white. Anterior reproductive system (primary, secondary, and accessory prostate in males; pallial oviduct in females) running parallel to rectum and nephridioduct. Veins weak, barely visible throughout pallial surface. Pulmonary vein ~1/3 caliber of rectum, running to a thick and opaque pericardium. Heart occupies ~1/2 of pericardium space; ventricle 2–3 times size of auricle. Heart and nephridium combined occupying ~1/9 of pallial cavity area. Nephridium elliptical, white, almost translucent, occupying ~1/6 of renopericardial volume. Nephridioduct thin, running parallel to rectum almost since origin. Nephridioduct opening next to anus.

DIGESTIVE SYSTEM (FIGURES 20–21): Mouth a horizontal slit in antero-ventral margin of snout. Buccal mass



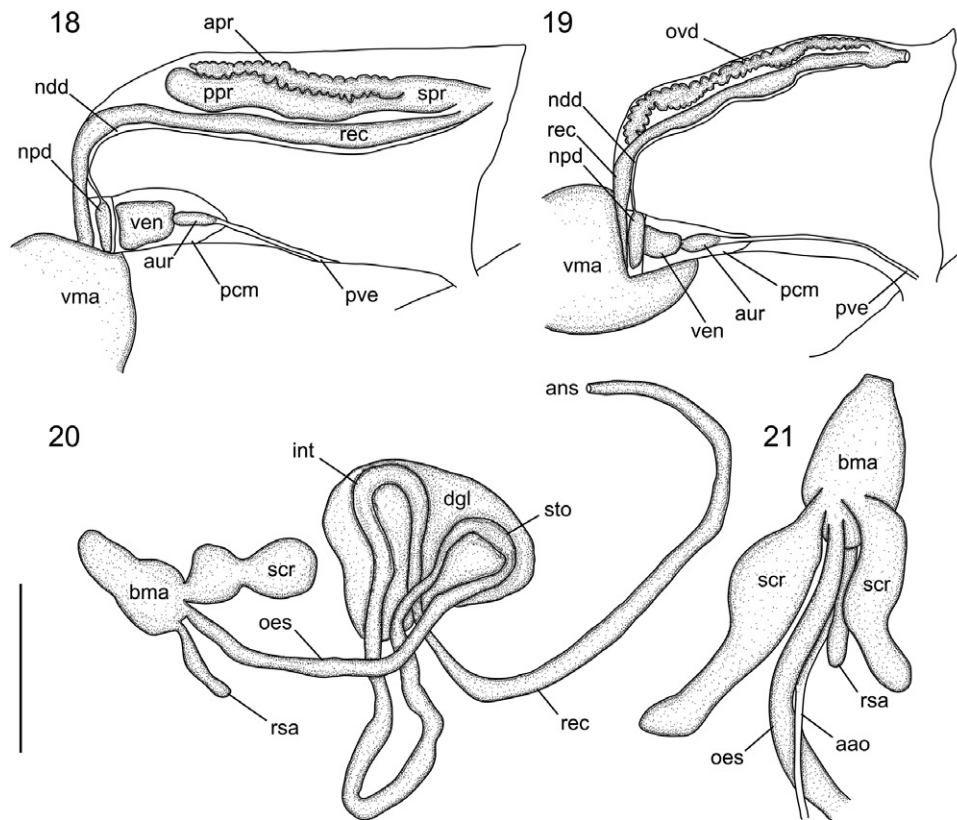
Figures 14–17. *Angulata angulata*, operculum. **14–15.** IBUFRJ22615, Optical microscopy, outer, and inner surfaces, respectively. **16–17.** IBUFRJ22012, Scanning electron microscopy (SEM), outer, and inner surfaces, respectively. Scale bar=2mm.

subcircular, with long elongation on snout. Odontophore ~3/4 of buccal mass volume. Radular sac slender, posterior, ~1/4 of volume of buccal mass. Two large, peanut shaped, secretory crypts, opening in buccal mass on each side of esophagus insertion. Esophagus postero-dorsally inserted on buccal mass; esophageal walls thick. Crop absent. Stomach large, mostly embedded in digestive gland. Intestine very long, approximately same diameter as esophagus, with thin and almost translucent walls. Intestine loops twice, once after stomach and before inserting in digestive gland, and again after inserting in digestive gland. Digestive gland small, brown, granulose, with thin walls. Rectum thin-walled, almost same caliber as esophagus. Anus opening in small atrium close to genital opening.

RADULA (FIGURES 22–25): Radula measuring about 400 μ m width, with 65 teeth per row (formula 28–4–1–4–28); each row trapezoid: straight in rachidian and lateral teeth, and oblique in marginal teeth. Rachidian tooth symmetrical, slightly elliptical, monocuspid, mesocone blunt, strongly curved downward. Lateral teeth asymmetrical, with different shapes; L1 flat, monocuspid, mesocone blunt, strongly curved downward and outward; L2 flat, five similar acute cuspids, all strongly curved downwards and outwards; L3 flat, narrow-ended with five similar small acute cuspids, all strongly curved downward and outward; L4 flat, wider than L1 to L3 combined, with ten similar acute cuspids, all slightly curved downward and inward. Marginal teeth asymmetrical, slender, with three similar lanceolate cuspids, all strongly curved downward and outward.

MALE REPRODUCTIVE SYSTEM (FIGURE 26): Male gonad beige, fragile, partially embedded in digestive gland; composed of large bean-shaped ramifications, forming one compact structure of almost same size as digestive gland. Spermoduct beige, longer than gonad, large, slightly convoluted. Primary prostate white, as long as pallial cavity, digitiform; with small digitiform orange projections on posterior end. Accessory prostate beige, shorter than primary prostate, with many lobes; small triangular cecum present right before insertion on secondary prostate. Secondary prostate white, almost translucent. Genital opening round, simple, in small atrium close to anus.

FEMALE REPRODUCTIVE SYSTEM (FIGURES 27–28): Female gonad beige, fragile, partially embedded in digestive gland; composed of several small oval ramifications, forming one compact structure larger than digestive gland. Gonad discharges into a small, oval, light brown egg sac. Primary oviduct white, very thin and fragile, short, originating on egg sac and running to V-organ. V-organ white, drop-shaped, larger portion as large as pallial oviduct. Seminal receptacle black, oval, small, inserted on V-organ, near pedicel. V-organ connected to reception chamber by a white, short, cylindrical pedicel. Small, white, oval slender accessory sperm sac connected to pedicel by a slender duct. Reception chamber white, oval, smaller than V-organ, inserted on posterior end of pallial oviduct. Reception chamber connected to a ventral bursa copulatrix and a provaginal sac. Bursa copulatrix white, with many lobes, smaller than V-organ. Provaginal sac white, slightly lobed, almost same size as



Figures 18–21. *Angulata angulata*, anatomy. **18.** IBUFRJ22041, Pallial cavity, male. **19.** IBUFRJ22615, Pallial cavity, female. **20.** IBUFRJ22032, Digestive system. **21.** IBUFRJ22615, Details of buccal mass, dorsal view. Abbreviations: **aa**: anterior aorta; **ans**: anus; **apr**: accessory prostate; **aur**: auricle; **bma**: buccal mass; **dgl**: digestive gland; **int**: intestine; **ndd**: nephridioduct; **npd**: nephridium; **oes**: esophagus; **ovd**: pallial oviduct; **pcm**: pericardium; **ppr**: primary prostate; **pve**: pulmonary vein; **rec**: rectum; **rsa**: radular sac; **scr**: secretory crypts; **spr**: secondary prostate; **sto**: stomach; **ven**: ventricle; **vma**: visceral mass. Scale bar for 18–20=3mm; 21=2mm.

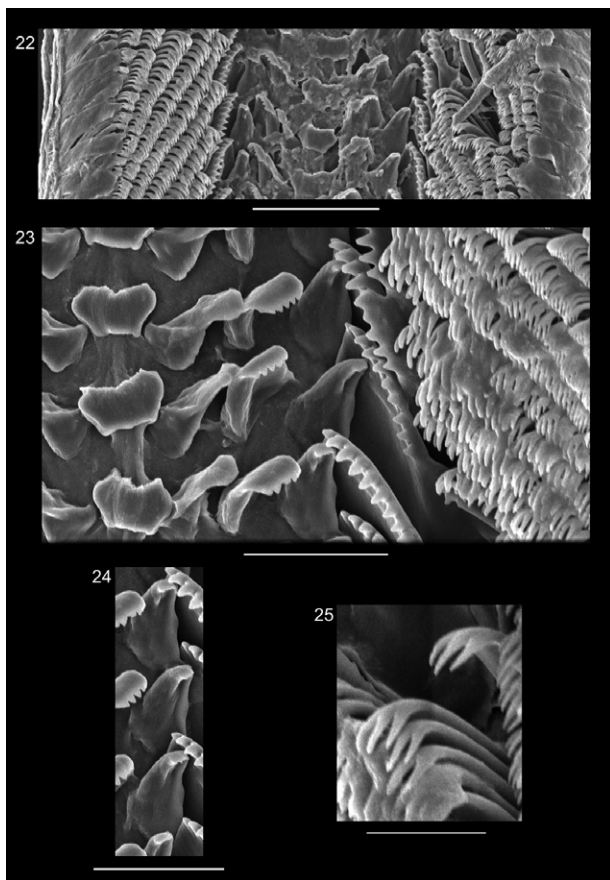
bursa copulatrix; from provaginal sac emerges a thin and fragile duct, almost as long as primary oviduct, ending in a round and simple vagina. Pallial oviduct white, longer than pallial cavity, with many large lobes; most anterior portion dark brown. Genital opening round, simple, in a small atrium close to anus.

NERVOUS SYSTEM (FIGURES 29–31): One pair of buccal ganglia (**bg**) partially fused; two paired nerves emerge laterally from each buccal ganglia (**bcn1–2**), running to posterior region of buccal mass. Nervous ring almost symmetrical. Cerebral ganglia (**cg**) connected to each other through a lateral connective (**cgc**), and to buccal ganglia by a pair of long cerebro-buccal connectives (**cbc**) that emerge ventrally. Cerebral ganglia also connected to pleural (**plg**) and pedal (**pdg**) ganglia by cerebro-pleural (**cpl**) and cerebro-pedal (**cpe**) connectives, respectively. Six paired nerves run from each cerebral ganglion: four pairs emerge laterally connecting to mouth and buccal mass (**bcn3–6**); one pair emerges laterally, connecting to tentacle (**ten**); one pair emerges laterally (**eyn**), connecting to eye (**eye**) at base of tentacle. Pleural (**plg**), parietal (**pag**) and visceral (**vig**) ganglia partially fused; right

pleural and parietal ganglia fused, forming an homogeneous mass. One paired nerve emerges dorsally from each pleural ganglion (**tmn**) connecting to tentacle retractor muscle nerve. Two paired nerves emerge dorsally from each parietal ganglion (**avn1–2**) enervating anterior portion of visceral mass. Three nerves run from visceral ganglion: one paired nerve emerges anteriorly (**odn**) attaching ventrally to odontophore; one unpaired nerve emerges postero-dorsally (**pvn**) enervating posterior portion of visceral mass. Pedal ganglia (**pdg**) partially fused. Four paired nerves emerge ventrally, running to pedal sole anteriorly (**apn1–2**), medially (**mpn**), and posteriorly (**ppn**). One pair of large, oval statocysts (**syt**) is present, inserted in a nervous mass dorsally on pedal ganglia; from each one, one nerve (**syn**) emerges, running posteriorly.

DISCUSSION

Generic Allocation: The separation of *Helicina* and *Angulata* is justified mainly by protoconch sculpture (Richling, 2004). The protoconch of *Helicina* is characterized



Figures 22–25. *Angulata angulata*, IBUFRJ22012, radula. **22.** General view. **23.** Details of central portion. **24.** Details of L3. **25.** Details of marginal teeth. Scale bar for 22=100 μ m; 23–24=50 μ m; 25=25 μ m.

by densely structured large pits arranged in concentric lines, while the protoconch of *Angulata* is characterized by regular, broad spiral lirae. Protoconch sculpture is considered a good character for defining genus level boundaries in other groups of terrestrial gastropods (Salvador and Cavallari, 2019) and is here used to confirm *Angulata* as a clade at the genus-level in agreement with Richling (2004, 2008). Simone (2018) and Richling (2004) described similar sculptures for the protoconch of *Helicina variabilis* and *Helicina brasiliensis* J. E. Gray, 1824, suggesting that these two species should also be included in the genus *Angulata*. Accordingly, they are herein treated as ***Angulata variabilis* new combination** and ***Angulata brasiliensis* new combination**.

Richling (2004, 2008) also proposed that all species of heliciniids from South America, particularly from Brazil, could be allocated to *Angulata*; data on protoconch sculpture, however, is lacking for most species. This should also be evaluated in a comprehensive phylogenetic analysis along with other proposed *Helicina* subgenera discussed by Richling (2004) and Baker (1922), some of which share the concentric lines of pits, but which are

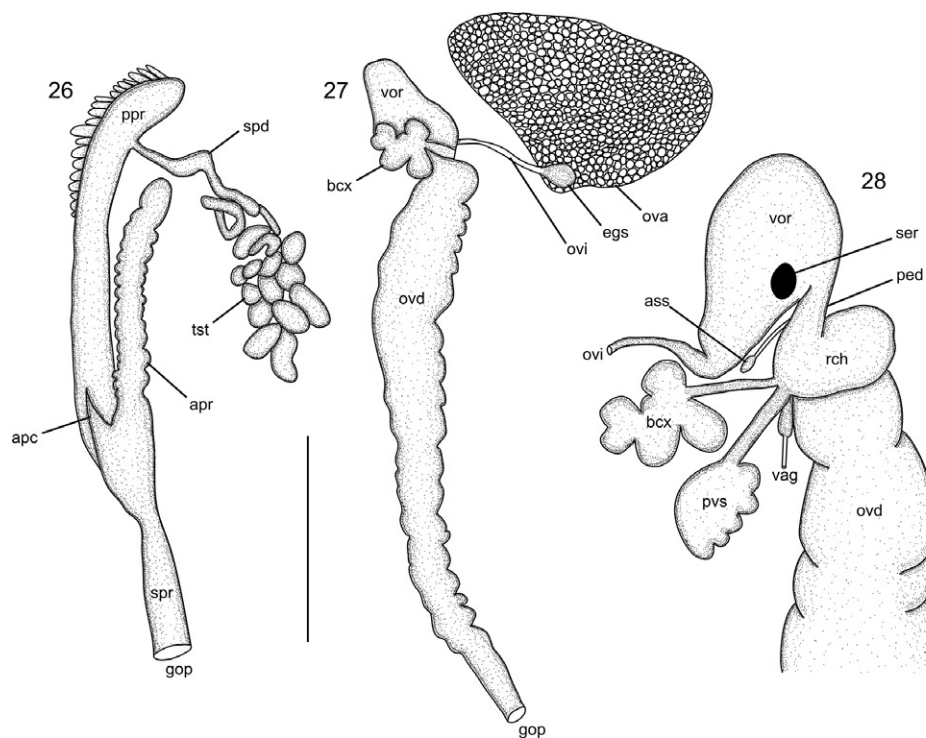
considerably smaller, such as in *Analcadia* J. A. Wagner, 1908. The relations of species of heliciniids should be evaluated along with protoconch sculpture variation to better define taxonomical boundaries, especially in cases in which the variation is subtle.

Comparative Anatomy: SHELL: The shell of *Angulata angulata* is distinguished from other globose and carinate heliciniids by the pointed basal projection near the inner edge of the shell lip. Neither *Helicina concentrica* nor *Angulata variabilis* have this pointed projection. *Helicina concentrica* also differs in having a taller spire, while *A. variabilis* lacks a keeled margin. Other species from Brazil that have a globose shell are *Helicina besckei* L. Pfeiffer, 1849, *Helicina leopoldinae* A. J. Wagner, 1905, *Helicina inaequistriata* and *Helicina leptotropis* A. J. Wagner, 1910, however these species also lack the pointed lip base and *H. inaequistriata* and *H. leptotropis* are also not keeled. The pointed aperture is also present in other strongly keeled species. *Helicina biangulata* L. Pfeiffer, 1851 differs from *A. angulata* by a rounder shape and a more reddish color. *Angulata brasiliensis* and *Helicina guajarana* F. Baker, 1914 have a considerably taller spire, while *Helicina carinata* A. d'Orbigny, 1835 and *Helicina wettsteini* A. J. Wagner, 1905 have a considerably shorter one.

OPERCULUM: The operculum of *A. angulata* is very similar to *A. variabilis*, but the muscle scar is smaller and sinusoidal rather than elliptical. In addition, the operculum of *A. angulata* usually has an orange coloration, differing from the brown operculum of *A. variabilis*.

PALLIAL CAVITY AND DIGESTIVE SYSTEM: *Angulata angulata* pallial cavity and digestive system are very similar to *H. concentrica*, but the stomach of *A. variabilis* is considerably larger and its secretory pouches (identified as esophageal pouches in Simone, 2018) are considerably smaller. The radular teeth of *Angulata angulata* do not differ in shape to *H. inaequistriata* and *A. variabilis*, but *A. angulata* has considerably fewer marginal teeth.

REPRODUCTIVE SYSTEM: The female reproductive system of *Angulata angulata* differs from that of *H. concentrica* in its wider V-organ, larger bursa copulatrix, smaller provaginal sac, and a longer accessory sperm sac duct. The uterus of *H. concentrica* is noticeably divided, which differs considerably from *A. angulata*. The male reproductive system differs by a smaller primary prostate and shorter accessory prostate cecum. There is no data about the gonads of *H. concentrica*. The female reproductive system of *Angulata angulata* differs from that of *A. variabilis* by having a slenderer uterus, and a larger bursa copulatrix. There is also no diverticulum of the V-organ (identified as albumen gland in Simone, 2018) as seen in *A. variabilis*. The reproductive system of *A. variabilis*, unlike *A. angulata*, has no provaginal sac, seminary receptacle, accessory sperm sac or vagina. There is no data about *A. variabilis* male reproductive system.



Figures 26–28. *Angulata angulata*, reproductive system. **26.** IBUFRJ22032, Male reproductive system. **27.** IBUFRJ22615, Female reproductive system. **28.** IBUFRJ22615, Details of V-organ. Abbreviations: **apc**: accessory prostate cecum; **apr**: accessory prostate; **ass**: accessory sperm sac; **bcx**: bursa copulatrix; **egs**: egg sac; **gop**: genital opening; **ova**: female gonad; **ovd**: pallial oviduct; **ovi**: primary oviduct; **ped**: pedicel; **ppr**: primary prostate; **pvs**: provaginal sac; **rch**: reception chamber; **ser**: seminal receptacle; **spd**: spermiduct; **spr**: secondary prostate; **tst**: male gonad; **vag**: vagina; **vor**: V-organ. Scale bar for 26–27=3mm; 28=1mm.

NERVOUS SYSTEM: *Angulata angulata* has a similar number of nerves of similar calibers as *A. variabilis*. The cerebral and pedal ganglia are also similar in size, shape and position, however the dorsal ganglia of *A. variabilis* are considerably smaller (identified only as pleural ganglia in Simone, 2018). The statocyst position also differs, being dorsal in *A. angulata*, while ventral in *A. variabilis*. There is no data about *A. variabilis* buccal ganglia.

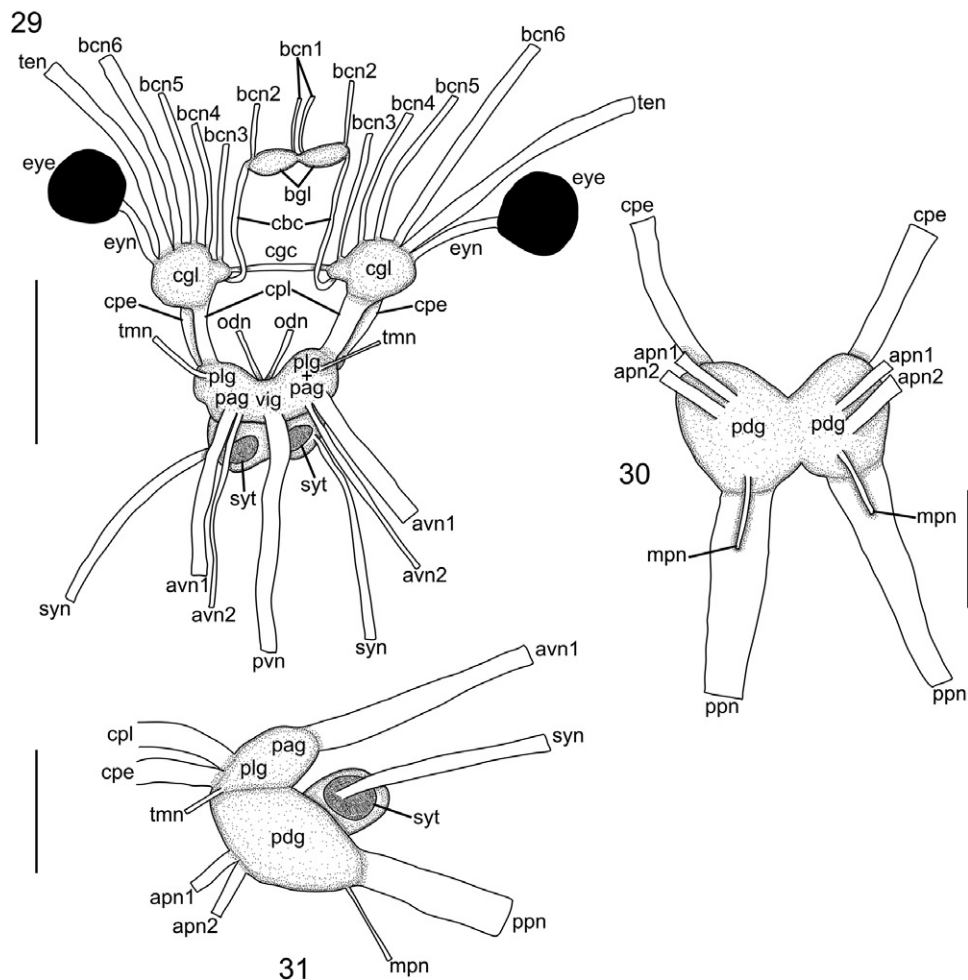
CONCLUSIONS

Angulata angulata differs from other species of helicids from Brazil by its strongly keeled globose shell, with a semielliptical aperture bearing a pointed projection on the inside edge of the expanded lip and also by having a reproductive system with a shorter accessory prostate cecum, smaller provaginal sac, longer accessory sperm sac duct, and a statocyst dorsally inserted on pedal ganglia. The South American terrestrial malacofauna is still widely unknown. This is especially true for groups such as helicids. More comprehensive anatomical surveys are essential, especially for widespread and common species, as internal morphological features often reveal

distinctions not apparent from shell morphology alone, which can even be misleading at times. These features can be important to help clarify species boundaries, support taxonomic revisions, and prevent the oversimplification of species-level diversity. We hope this work contributes to the knowledge about this poorly studied group and highlights how little we know about the anatomy of these snails and how we need a revision of South American helicids to properly define genera boundaries, encouraging future revisions to include anatomical data along with shells and radulae.

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Figures 29–31. *Angulata angulata*, IBUFRJ22615, nervous system. **29.** Dorsal view; ventral nerves removed for clarity. **30.** Pedal ganglia, ventral view; dorsal nerves removed for clarity. **31.** Posterior ganglia, left view; middle and right nerves removed for clarity. Abbreviations: **apn1–2:** anterior pedal nerve; **avn1–2:** anterior visceral nerve; **bcn1–6:** bucal nerve; **bgl:** buccal ganglion; **cbc:** cerebro-buccal connective; **cgc:** cerebral ganglia connective; **cgl:** cerebral ganglion; **cpe:** cerebro-pedal connective; **cpl:** cerebro-pleural connective; **eye:** eye; **eyn:** eye nerve; **mpn:** medial pedal nerve; **odn:** odontophore nerve; **pag:** parietal ganglion; **pdg:** pedal ganglion; **plg:** pleural ganglion; **ppn:** posterior pedal nerve; **pvn:** posterior visceral nerve; **syn:** statocyst nerve; **syt:** statocyst; **ten:** tentacle nerve; **tmn:** tentacle retractor muscle nerve; **vig:** visceral ganglion. Scale bar for 29=1mm; 30–31=500µm.

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