Anatomy of *Solaropsis caperata* F. S. Silva, Mendes-Júnior, and Simone, 2022 from the Brazilian Amazon (Gastropoda: Solaropsidae)

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ABSTRACT

Solaropsis caperata is a species from the Brazilian Amazon known only by its shell. The present study describes the anatomy of *Solaropsis caperata* including shell micro-ornamentation and ultrastructure; digestive system including the radula and jaw; organs of the pallial cavity; nervous system; and reproductive system. The anatomy of *Solaropsis caperata* is compared with other *Solaropsis* species for which anatomical information is available. The species is characterized by a highly variable, globose to flattened shell with two deep depressions located half a whorl from aperture; nephridium half as long as pallial cavity; rachidian tooth monocuspid, mesocone blunt with serrated edges up to the apex; lateral teeth monocuspid, mesocone blunt with serrated edges up to the apex; marginal teeth bicuspid, mesocone blunt, not serrated; bursa copulatrix duct as long as spermoviduct, with small digitiform diverticulum as wide but considerably shorter than bursa copulatrix duct; penial complex shorter than spermoviduct; epiphallum absent; flagellum smaller than penis. *Solaropsis caperata* anatomy is very similar to that of *Solaropsis undata* ([Lightfoot], 1786), type species of *Solaropsis*.

Additional Keywords: Biodiversity, land snail, Stylommatophora

INTRODUCTION

Silva *et al*. (2022) described *Solaropsis caperata* F. S. Silva, Mendes-Júnior, and Simone, 2022, an unusual species from the Brazilian Amazon, using shell characters only, as only those were available at the time. The authors also described and resolved some taxonomical misperceptions regarding the validity of some species, highlighting the importance of more comprehensive anatomical studies for *Solaropsis* H. Beck, 1837 and the taxonomical misunderstandings surrounding this genus.

The history of the classification of *Solaropsis* and its allies has been complex and confusing (as described in detail by Calcutt *et al*., 2020) up until they were assigned to their own family, Solaropsidae H. Nordsieck, 1986 in Sagdoidea Pilsbry, 1895 (Sei *et al*., 2017). However, the taxonomy of *Solaropsis* is still somewhat unresolved. For example, the presently synonymized *Psadara* K. Miller, 1878 includes *Solaropsis* with small, depressed and fragile shells, closed secondary ureter, short bursa copulatrix duct, and a nephridium almost as long as the pallial cavity (Tillier, 1980), but the species assigned to *Psadara* based on these characters do not seem to define a monophyletic group (Cuezzo, 2002) and can even render *Solaropsis* paraphyletic (Calcutt *et al*., 2020). The taxonomical uncertainty in *Solaropsis* is probably due to the use of shell characters only for taxonomy and the lack of detailed anatomical data for most of its species (Cuezzo, 2002). Although it must be recognized that most studies that use only shell characters are limited to them by specimen availability, the characters that have been extensively used for the systematics of this group, such as shell ornamentation, general shape, size and presence of depressions, do not show as possible synapomorphies in phylogenies using either anatomical nor molecular data (Cuezzo *et al*., 2018; Calcutt *et al*., 2020). However, detailed anatomical data are available for only seven of the approximately 50 species of *Solaropsis* (Tillier, 1980; Cuezzo and Fernández, 2001; Cuezzo, 2002; Cuezzo, 2003; Simone, 2010; Cuezzo *et al*., 2018; MolluscaBase, 2025). Knowing the anatomy of *Solaropsis* species is fundamental for a better understanding of how these species relate to each other.

Hence, the goals of this study were to: (1) describe the anatomy of *Solaropsis caperata* including shell features such as micro-ornamentation and ultrastructure; digestive system including the radula and jaw; organs of the pallial cavity; nervous system; and reproductive system; (2) discuss the anatomical differences and similarities between *S. caperata* and other *Solaropsis* species for which anatomical data are available (Tillier, 1980; Cuezzo and Fernández, 2001; Cuezzo, 2002; Simone, 2010; Cuezzo *et al*., 2018).

MATERIALS AND METHODS

The study material is housed in the collection of Museu de Zoologia da Universidade de São Paulo, São Paulo,

Brazil (MZSP). Lots listed in bold indicate they include specimens that were dissected. Five adult specimens were dissected.

Dissections followed standard procedures, beginning with an incision along the mantle border to expose the pallial cavity, followed by a cut along the pallial cavity, alongside the lower digestive tract, then to the top of the spire. Specimens were dissected under 70% ethanol, using Zeiss Stemi SV 11 stereomicroscope with a *camera lucida*. The pallial structures and reproductive, digestive, circulatory, excretory, and nervous systems were isolated, examined, and described. Illustrations made using a *camera lucida* were digitized using a scanner and later vectorized and edited using Inkscape. Buccal masses were dissected, radulae and jaws were manually extracted without additional chemical digestion and rinsed in distilled water. Pieces of the shell were extracted from the body whorl and visualized axially to for determination of shell ultrastructure. Well-preserved shells were selected, the bodies extracted, and the shell cleaned with a fine-tipped paint brush. Scanning electron micrographs (SEM) of shell, radulae, and jaw were performed using a JEOL-JSM-6390-LV at the "Plataforma de Microscopia Eletrônica Rudolf Barth", Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil. The material was sputter-coated with gold before imaging with SEM.

For the descriptions of the nervous system, acronyms used for nerves were defined by their insertion (letters) and position from anterior to posterior axis (numbers).

SYSTEMATICS

Sagdoidea Pilsbry, 1895
Solaropsidae H. Nordsieck, 1986

Solaropsis H. Beck, 1837

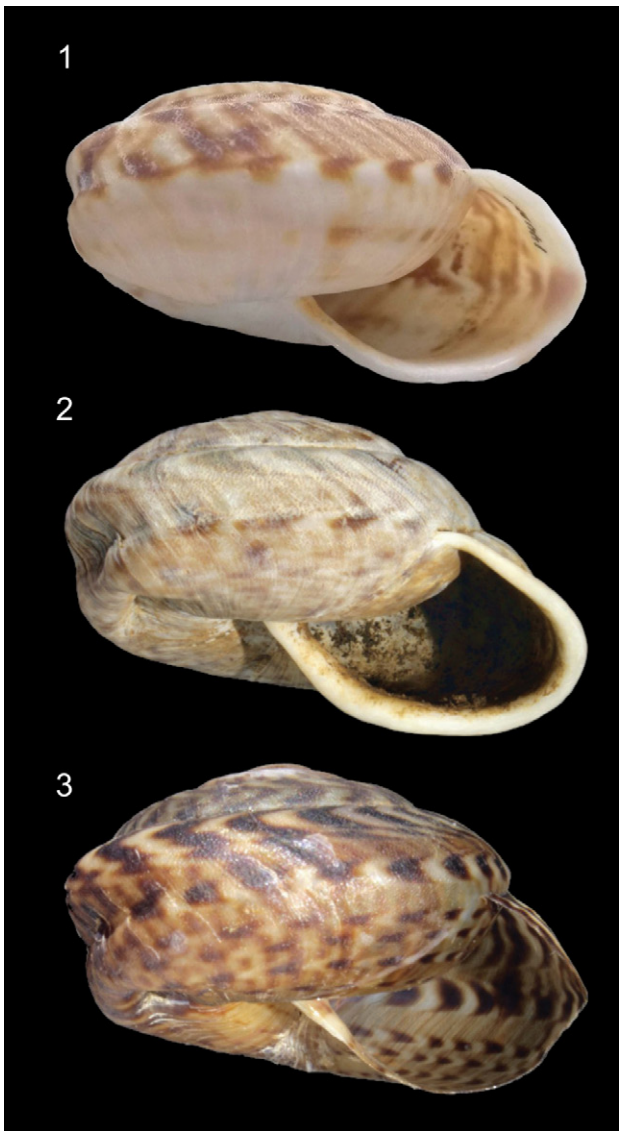
Solaropsis caperata F. S. Silva, Mendes-Júnior, and Simone, 2022

(Figures 1–38)

Solaropsis caperata Silva *et al*., 2022: 83–87, figs 2–16.
Solaropsis caperata.—Salvador *et al*., 2024: 162.

Type Locality: Brazil: Amapá; municipality of Laranjal do Jari, Rio Cajarí Extractive
Reserve, highway BR-156, 0.82093611°S, 52.03254722° W (Silva *et al*. 2022).

Description: Shell (Figures 5–26): Large (~30–40mm height; ~55–65mm width), ~6 whorls, body whorl ~4/5 shell height; globose to flattened, keeled, dextral, apex blunt, with two deep depressions located a half whorl from aperture; spire angle ~130–150°. Color brown, paler ventrally; dorsal surface with two narrow spiral bands formed by well-defined arrow-shaped chestnut or dark brown marks over a cream ground, one subsutural and other suprasutural only on body whorl; ventral surface with dotted chestnut spiral lines of different thicknesses or well-defined arrow-shaped dark brown marks over a cream ground. Periostracum thin. Suture well-marked, well-impressed, almost perpendicular to columellar axis. Teleoconch sculpture of strong axial lirae and regularly arranged, rounded to oval granules. Protoconch ~2.5 whorl, smooth. Aperture elongate-ovate, ~80% of shell height, ~50% of shell width; parietal callus absent; peristome expanded, reflected, white. Umbilicus wide, partially hidden by columellar end of aperture in adapical view. Shell ultrastructure composed of an external periostracum ~5µm in thickness followed by four calcified layers. First, and outermost, is amorphous ~90µm. Second is crossed-lamellar ~150µm. Third is amorphous ~50µm. Fourth, and innermost, is solid ~280µm.



Figures 1–3. *Solaropsis caperata*, types. **1.** Holotype, MZSP 144000, apertural view. **2.** Paratype, MZSP154136, apertural view. **3.** Paratype, MZSP154137, apertural view. Figures from Silva *et al*. (2022).

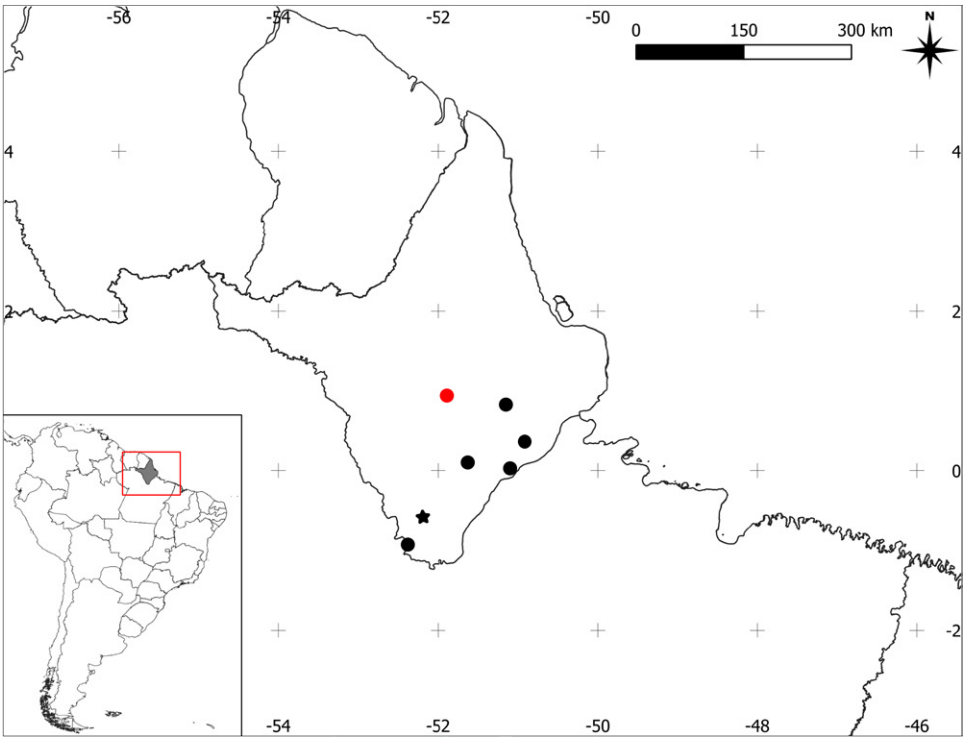


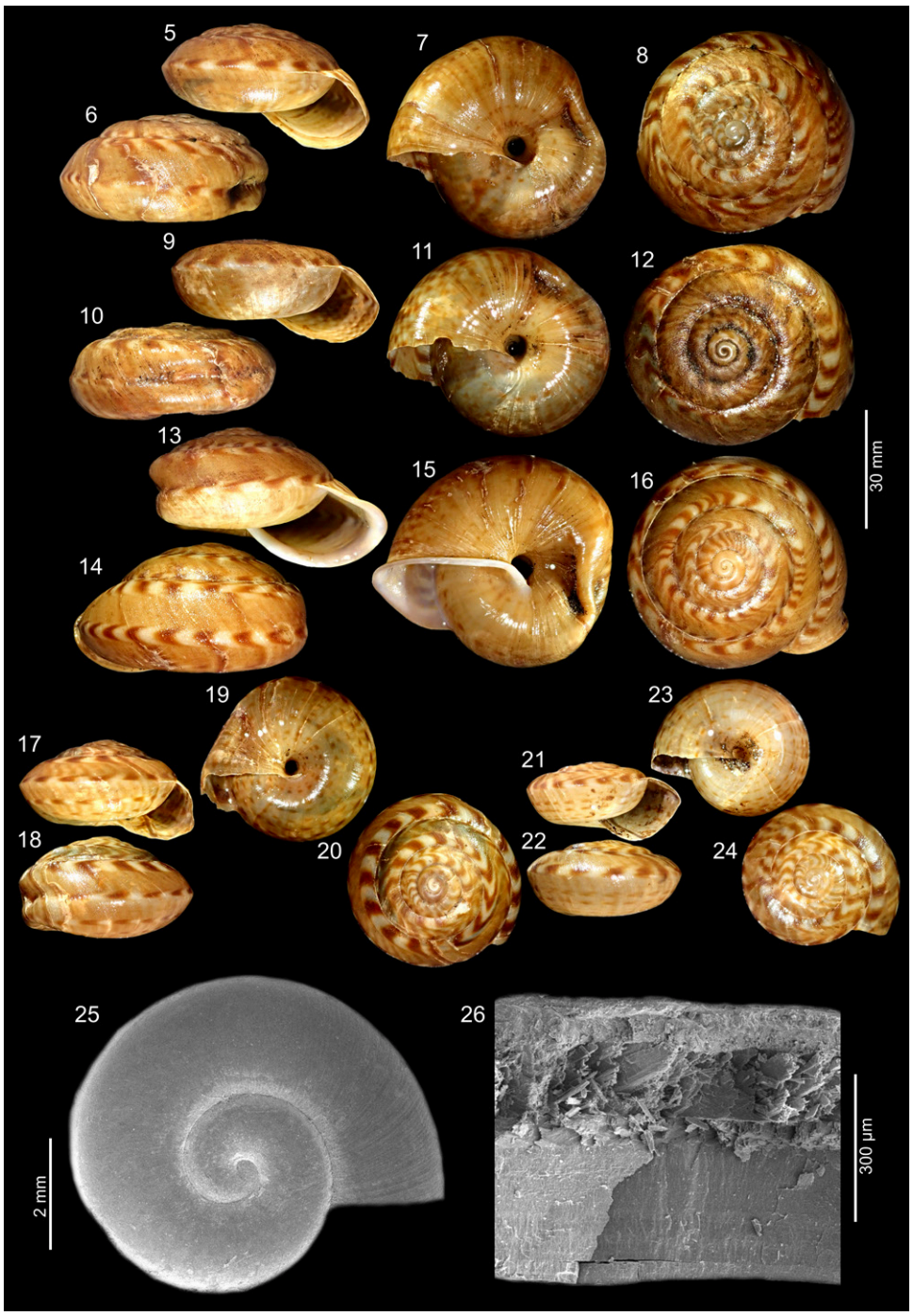
Figure 4. *Solaropsis caperata*, known occurrences. Label: **star:** type locality; **circles:** new records; **red circle:** locality from which came the dissected specimens.

Pallial Cavity and Associated Organs (Figures 27–28): Pallial cavity very long and narrow, occupying ~2.5 whorls. Mantle border thick, beige. Pneumostome present, a nephridiopore and anus as separated apertures. Rectum large, running parallel to nephridioduct. Imbricated veins present on pallial surface, greater in abundance in anterior third of pallial cavity. Pulmonary vein ~1/2 width of rectum, running to and inserting on pericardium. Collar vessel inconspicuous. Auricle occupies ~1/2 of pericardium volume; ventricle almost same size as auricle. Heart and nephridium combined occupy ~1/8 of pallial cavity. Nephridium elongate-ovate, dark beige, about four times as wide as heart; primary nephridioduct ~1/2 width of rectum, originating close to heart and running near nephridium; secondary nephridioduct as wide as primary, running parallel to rectum. Nephridiopore opening next to pneumostome.

Digestive System (Figure 29): Buccal mass subrectangular. Odontophore retractor muscle large, running parallel to and from columellar muscle to ventral surface of odontophore, attaching buccal mass postero-ventrally after branching two times, first in two almost symmetrical muscles, and second in six closely attached pack of fibers. Radular sac posterior, ~1/16 volume of buccal mass. One fused pair of white, salivary glands, overlaying partially around esophagus in its medial third; salivary ducts opening in buccal mass close to esophagus insertion. Esophagus postero-dorsally inserted in buccal mass. Esophageal walls thin. Stomach muscularized, partially embedded in digestive gland. Intestine very long, ~1/2 width of esophagus, with thick walls. Intestinal loop present mostly outside digestive gland, partially inserted on pallial cavity; anterior portion of intestinal loop is partially overlaid by a projection of digestive gland, while posterior portion of intestinal loop is partially associated with anterior lobe of digestive gland, going through it. Digestive gland brown, granulose, with thin walls, occupying ~3 whorls. Rectum thick walled, ~1/2 width of esophagus. Anus opening close to pneumostome.

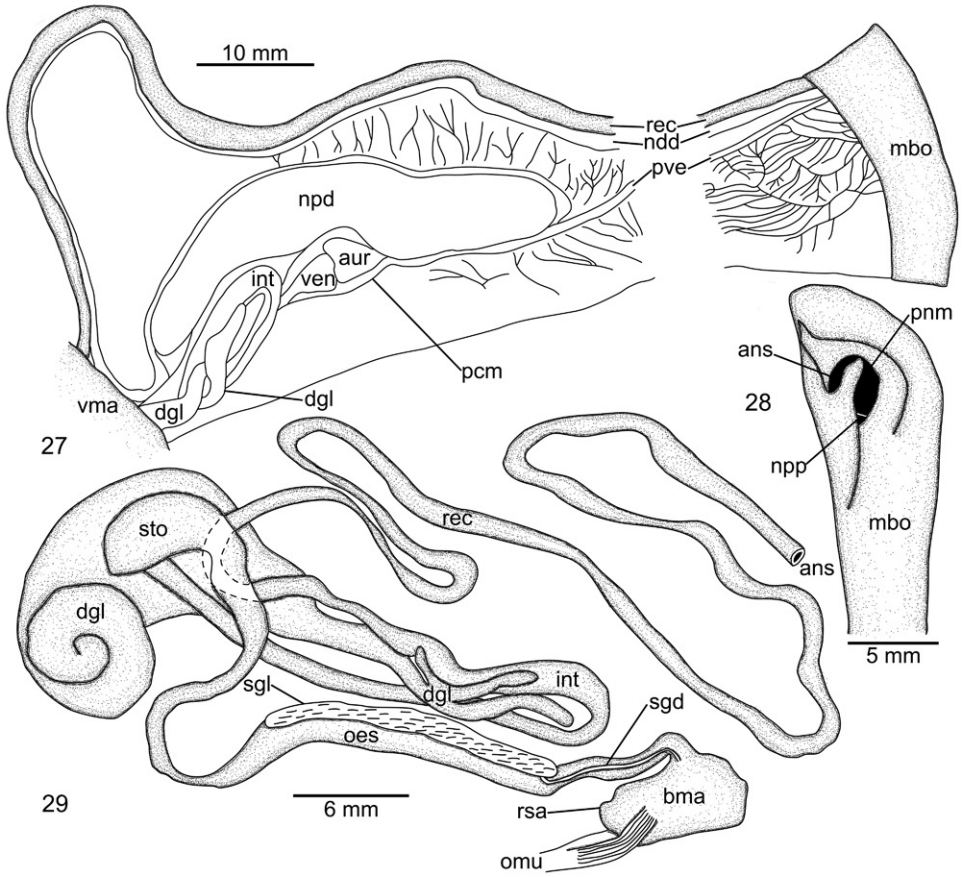
Radula and Jaw (Figures 30–35): Radula ~3mm in width, with 119 teeth per row (23–36–1–36–23). Rachidian tooth symmetrical, monocuspid, mesocone blunt, elongate, with serrated edges. Lateral teeth symmetrical, monocuspid, mesocone weakly arched towards rachidian tooth, blunt, elongate, with serrated edges. Marginal teeth asymmetrical, biscupid, mesocone weakly arched towards rachidian tooth, mesocone larger, blunt, elongate, without serrated edges, ectocone ~1/2 width of mesocone, blunt, deltoid. Jaw thin, smooth, dark orange, crescentic shaped, with 16 asymmetrical partially fused plates, middle plate with same length as adjacent plates, rectangular.

Reproductive System (Figure 36): Ovotestis pale orange, embedded in digestive gland along second whorl; numerous spherical granules leading to a granulose



Figures 5–26. *Solaropsis caperata*, shell, MZSP35571. **5–8.** Adult with globose shell, apertural, adapertural, adapical, and apical views, respectively. **9–12.** Adult with flattened shell, apertural, adapertural, adapical, and apical views, respectively. **13–16.** Adult with thickened lip, apertural, adapertural, adapical, and apical views, respectively. **17–20.** Juvenile with early shell depression, apertural, adapertural, adapical, and apical views, respectively. **21–24.** Juvenile before formation of shell depression, apertural, adapertural, adapical, and apical views, respectively. **25.** Details of protoconch micro-sculpture. **26.** Details of shell ultrastructure.

shape. Hermaphroditic duct beige, slightly convoluted anteriorly, with almost same length as spermoviduct; hermaphroditic duct connected to talon by a short elongation thinner than talon. Talon wide and folded on itself, without projection. Spermoviduct connected to talon by a short elongation thinner than talon, completely embedded in albumen gland. Albumen gland white, slender, ~1/3 length of spermoviduct. Spermoviduct ~3 whorls long. Prostate compressed, white, running alongside uterus, occupying ~1/2 volume of spermoviduct. Uterus

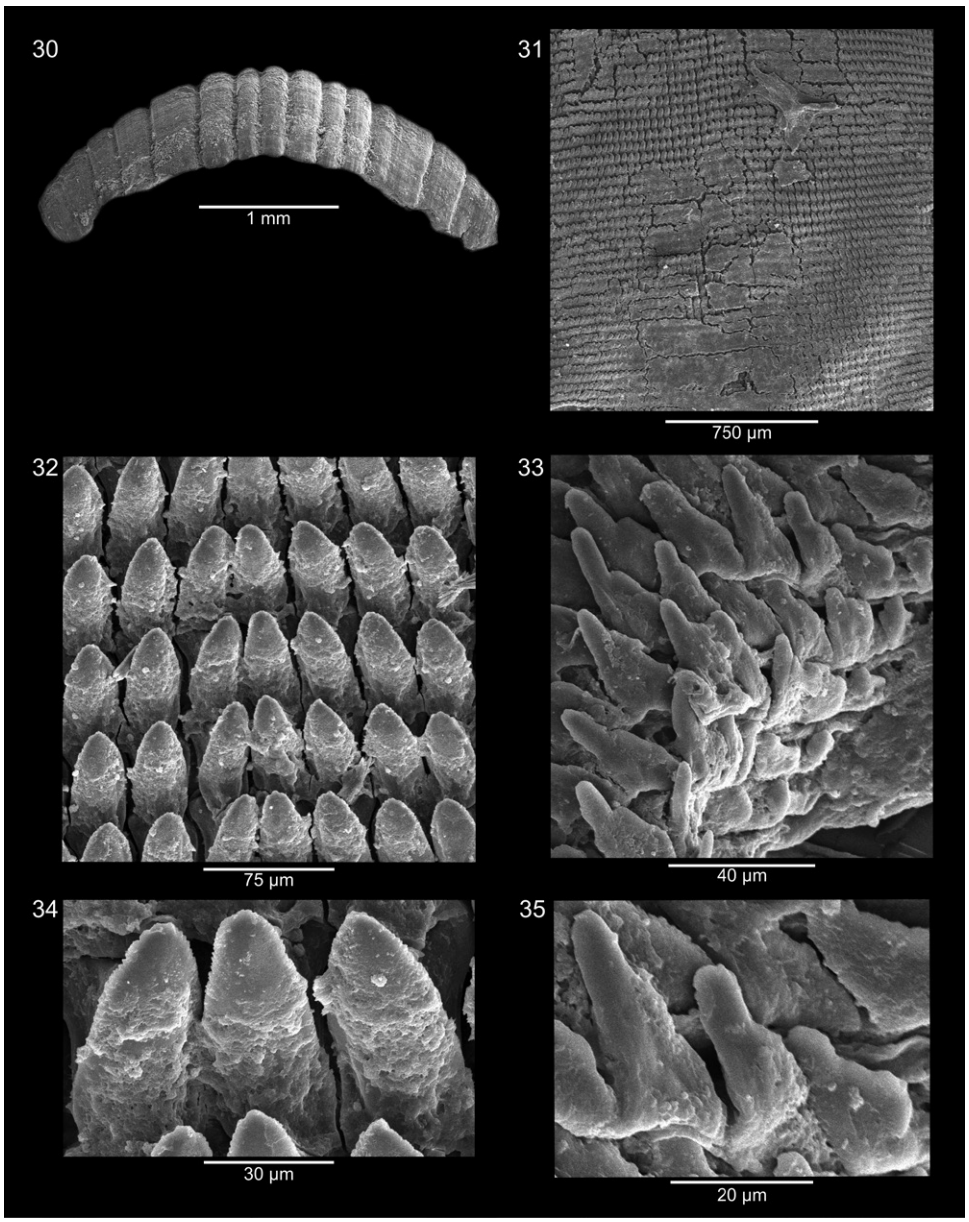


Figures 27–29. *Solaropsis caperata*, anatomy, MZSP35571. **27.** Pallial cavity. **28.** Details of pneumostome. **29.** Digestive system. Abbreviations: **ans:** anus; **aur:** auricle; **bma:** buccal mass; **dgl:** digestive gland; **int:** intestine; **mbo:** mantle border; **ndd:** nephridioduct; **npd:** nephridium; **npp:** nephridiopore; **oes:** esophagus; **omu:** odontophore muscles; **pcm:** pericardium; **pnm:** pneumostome; **pve:** pulmonary vein; **rec:** rectum; **rsa:** radular sac; **sgd:** salivary gland duct; **sgl:** salivary gland; **sto:** stomach; **ven:** ventricle; **vma:** visceral mass.

translucent, with small lobes, external walls thin. Bursa copulatrix duct slender slightly longer than spermoviduct. Bursa copulatrix white, large, twice width of albumen gland, elongate-ovate. Vagina short. Vas deferens wide and long. Penis wide and short, cylindrical, and muscular, oval in transverse section. Epiphallus absent. Flagellum ~1/4 length of penis. Penial retractor muscle short and wide, subapically attached to penis. Penis and vagina inserted alongside in a wide genital atrium. Genital pore lemniscate, simple.

Nervous System (Figures 37–38): One pair of buccal ganglia **(bgl)** connected to each other through a long lateral connective **(bgc)**; three paired nerves emerge from each buccal ganglion, running to posterior region of buccal mass **(bcn1–3)**. Nervous ring almost symmetrical. Cerebral ganglia **(cgl)** partially fused, connected to buccal ganglia by a pair of long cerebro-buccal connectives **(cbc)**. Cerebral ganglia also connected to pleural and pedal ganglia respectively by cerebro-pleural **(cpl)** and cerebro-pedal **(cpc)** connectives. Six paired nerves run from each cerebral ganglion: two pairs connecting to ocular tentacles **(ten1–2),** connected to tip and base, respectively); three pairs connecting to buccal mass **(bcn4–6)**; one pair connecting to odontophore muscles **(omn)**. Left parietal **(pag)** and unpaired visceral **(vig)** ganglia completely fused, forming a homogeneous mass, partially fused with right parietal and both pleural **(plg)** ganglia. Two nerves run from right parietal ganglion running to visceral mass **(vin1–2)**. Two nerves emerge from left parietal ganglion running to columellar muscle **(cmn1–2)**. Three nerves emerge from visceral ganglion running to visceral mass **(vin3–5)**. Pedal ganglia **(pdg)** partially fused. Twelve paired nerves emerge from each pedal ganglion: eleven pairs running to pedal sole posteriorly **(ppn1–11)**; one pair emerging close to statocyst running to pedal sole medially **(syn)**. Two unpaired nerves emerge from left pedal ganglion running medially to pedal sole **(mpn1–2)**. One paired, small, oval statocyst **(syt)** inserted ventro-posteriorly inside each pedal ganglion.

Type Material (Figures 1–3): Brazil: Amapá: Laranjal do Jari: Holotype MZSP144000 (dry shell) 1°33'39"



Figures 30–35. *Solaropsis caperata*, jaw and radula, MZSP35571. **30.** Jaw. **31.** Radula, general view. **32.** Radula, details of rachidian and lateral teeth. **33.** Radula, details of marginal teeth. **34.** Radula, details of rachidian and lateral teeth showing the serrated edges. **35.** Radula, details of marginal teeth showing the edges not serrated.

S, 52°1'57" W col. Mendes Jr., R., October 8, 2015; Paratype: MZSP154136 (one dry shell) 1°37'11" S, 53°28'13" W col. Vicente, N., December 12, 2020; Paratype: MZSP154137 (one dry shell) 1°40'24" N, 53°27'43" W col. Vicente, N., December 1, 2020.

Other Material Examined: Brazil: Amapá: MZSP91212 (three whole specimens in ethanol) col. Diversitar Neotropical. Camaipi: MZSP116518 (one dry shell) col. Rodrigues, M.T.U., May 15, 2001. Ferreira Gomes: MZSP133557 (one whole specimen in ethanol) 00°52'14.3" N, 51°11'42.1" W col. Silva, R.S. Macapá: MZSP43096 (two dry shells); MZSP56437 (seven dry shells) col. Coltro Jr., J. Peixe Boi: MZSP43095 (two dry shells). Serra do Navio: **MZSP35571 (13 whole specimens in ethanol)** col. Bianchi, A., May 1, 2002; MZSP36851 (three dry shells) col. Coltro Jr., J. 2002; MZSP47646 (one whole specimens in ethanol) col. Skunk, G. and Daly, J., May 15, 1992; MZSP101558 (one dry shell) col. Gonçalves, E.P. 28/IV/1994; MZSP121028 (two dry shells) 00°53' N, 51°59' W, col. June 2002; MZSP169246 (six dry shells) col. Femorale, 2003. Vitória do Jari: MZSP66601 (one dry shell) col. local residents, January 2003.

Distribution (Figure 4): Brazil: Amapá State (Silva *et al*. 2022).

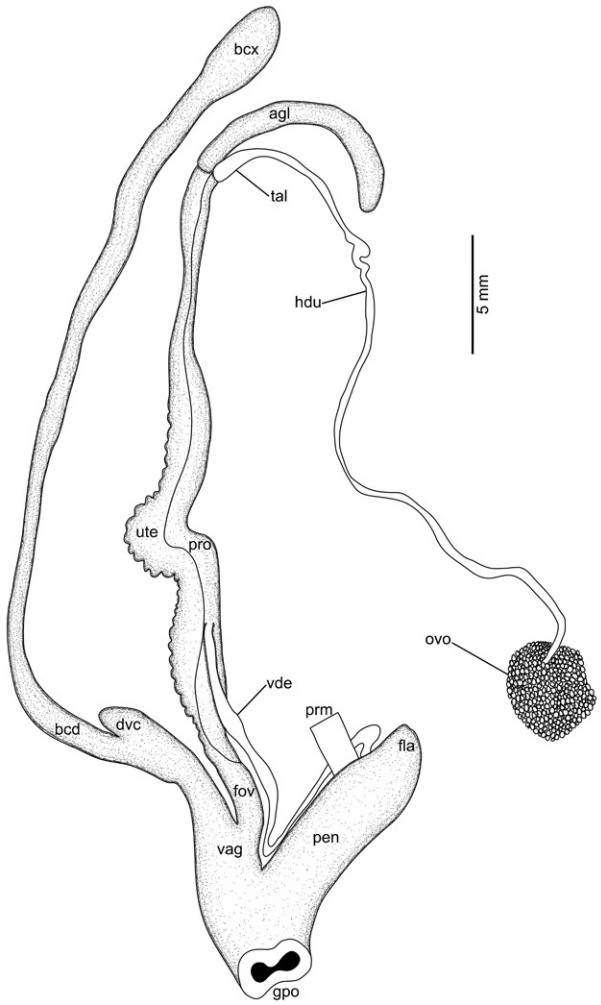


Figure 36. *Solaropsis caperata*, reproductive system, MZSP35571. Abbreviations: **agl:** albumen gland; **bcd:** bursa copulatrix duct; **bcx:** bursa copulatrix; **dvc:** diverticulum; **fla:** flagellum; **fov:** free oviduct; **gpo:** genital pore; **hdu:** hermaphrodite duct; **ovo:** ovotestis; **pen:** penis; **prm:** penis retractor muscle; **pro**: prostate; **psh:** penis sheath; **sde:** spermoviduct distal end; **tal:** talon; **ute:** uterus; **vag**: vagina; **vde:** vas deferens.

Remarks: Given that we do not have sampled individuals from different times of the year, we could not access seasonal variation of the reproductive system. Because of that, characters such as width of albumen gland, convolution of hermaphroditic duct, and relative size of prostate/uterus, among others that can vary with the reproductive season, although described, were not used in the anatomical comparisons with other congeners, some of which were also limited by sampling in the same manner.

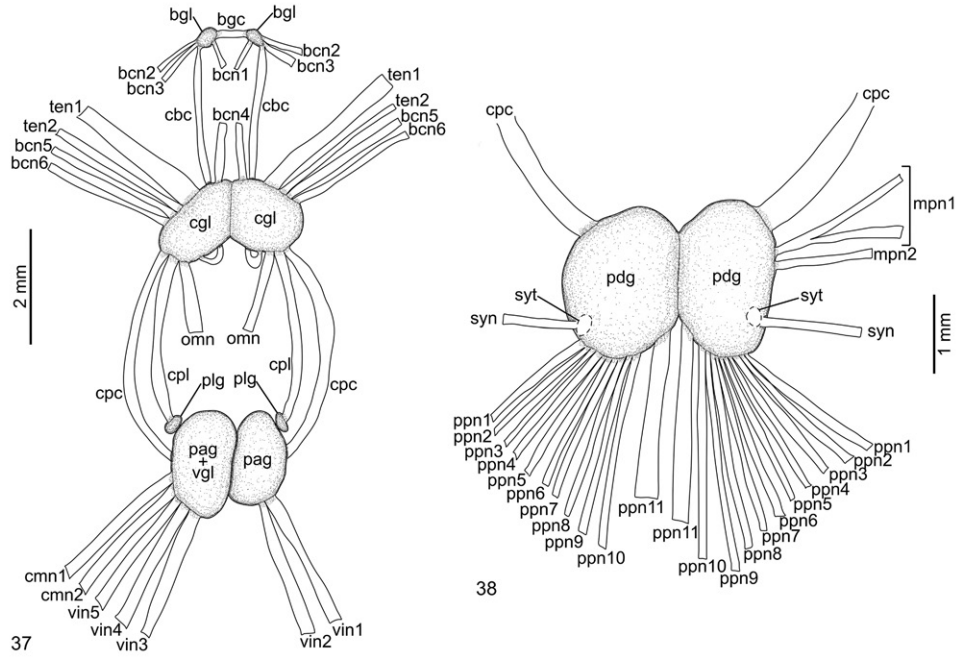
DISCUSSION

The anatomical comparisons include *Solaropsis undata* ([Lightfoot], 1786), type species of *Solaropsis*, whose anatomy is discussed by Tillier (1980). The other species of *Solaropsis* with available anatomical data are *Solaropsis nubeculata* (Deshayes, 1831), *Solaropsis marmatensis* (Reeve, 1854) (described in Tillier, 1980), *Solaropsis chicomendesi* Cuezzo and I. Fernández, 2001 (described in Cuezzo and I. Fernández, 2001), *Solaropsis angulifera* F. Haas, 1955, *Solaropsis heliaca* (A. d'Orbigny, 1835), *Solaropsis gibboni* (L. Pfeiffer, 1846) (described in Cuezzo, 2002), *Solaropsis nimbus* (Simone, 2010) (described in Simone, 2010), and *Solaropsis brasiliana* (Deshayes, 1832) (described in Tillier, 1980 and Cuezzo *et al*., 2017). Only species with detailed anatomical data were included in the discussion.

Shell: General shell shape in *Solaropsis* is subjected to great intraspecific variation (as seen in *Solaropsis caperata*). Spire angle, shell depression and aperture shape are highly variable even among a single species. However, some characters seem to be more conservative. *Solaropsis caperata* has a large, keeled shell sculptured with well-defined granules, similar to *Solaropsis undata*, *Solaropsis gibboni*, and *Solaropsis brasiliana*. *Solaropsis chicomendesi* and *Solaropsis heliaca* also have large shells, but they are not keeled and, although they share the granules, these are considerably weaker. *Solaropsis nubeculata*, *Solaropsis marmatensis*, *Solaropsis angulifera*, and *Solaropsis nimbus* differ even more, with small, fragile shells that are also not keeled and with very weak granules, which are sometimes inconspicuous in some parts of the shell.

Pallial Cavity and Associated Organs: *Solaropsis caperata* shares the pallial cavity surface extending more posteriorly than the nephridium with all *Solaropsis* species with available anatomical data, which is a probable synapomorphy of the genus. The nephridium of *Solaropsis caperata* is very long, measuring about half the length of the pallial cavity, a very similar condition to the one found in *Solaropsis undata*, but considerably longer than *Solaropsis brasiliana* and *Solaropsis gibbon,* and shorter than *Solaropsis nimbus*, *Solaropsis heliaca*, *Solaropsis angulifera*, and *Solaropsis nubeculata* whose nephridium extends almost as long as the pallial cavity.

Radula: *Solaropsis caperata* radular teeth are very similar to *Solaropsis undata* and *Solaropsis nimbus*. The number of cusps on the teeth of *Solaropsis caperata* is shared with *Solaropsis brasiliana*, but the apex of the rachidian and lateral teeth of do not have serrated edges, and the marginal teeth ectocones are serrated into several small cusps. The teeth of *Solaropsis heliaca*, *Solaropsis angulifera*, *Solaropsis chicomendesi*, *Solaropsis nubeculata*, and *Solaropsis marmatensis* have different number of cusps: the rachidian tooth is tricuspid and the lateral teeth are bicuspid, and they do not share the serrated edges. The marginal teeth are also bicuspid, but they also differ by serrated ectocones that are different from those of *Solaropsis brasiliana* by having less and larger cusps.



Figures 37–38. *Solaropsis caperata*, nervous system, MZSP35571. **37.** Dorsal view; ventral nerves removed for clarity. **38.** Pedal ganglia, ventral view; dorsal nerves removed for clarity. Abbreviations: **bcn1–6:** bucal nerve; **bgc:** buccal ganglia connective; **bgl:** buccal ganglion; **cbc:** cerebro-buccal connective; **cgl:** cerebral ganglion; **cmn1–2:** columellar muscle nerve; **cpc:** cerebro-pedal connective; **cpl:** cerebro-pleural connective; **mpn1–2:** medial pedal nerve; **omn:** odontophore muscle nerve; **pag:** parietal ganglion; **pdg:** pedal ganglion; **plg:** pleural ganglion; **ppn1–11:** posterior pedal nerve; **syn:** statocyst nerve; **syt:** statocyst; **ten1–2:** tentacle nerve; **vgl:** visceral ganglion; **vin1–5:** visceral nerve.

Reproductive System: *Solaropsis caperata* ovotestis, albumen gland and spermoviduct are very similar to every other *Solaropsis* with available data. Only *Solaropsis nimbus* does not share the presence of a diverticulum in the bursa copulatrix duct present in every *Solaropsis* with available data and considered as a possible synapomorphy of the genus (Cuezzo, 2002). Despite being widespread within *Solaropsis*, the diverticulum is highly variable. *Solaropsis caperata* and *Solaropsis undata* have only short, digitiform diverticula as wide as the bursa copulatrix duct, while the diverticula of *Solaropsis brasiliana* and *Solaropsis gibboni* are as long as the bursa copulatrix duct and in *Solaropsis heliaca*, *Solaropsis angulifera*, *Solaropsis chicomendesi*, *Solaropsis nubeculata*, and *Solaropsis marmatensis* the diverticula lengths relative to the bursa copulatrix duct vary, but are always considerably narrower than the bursa copulatrix duct. *Solaropsis caperata* has a penial complex shorter than the spermoviduct, which is similar to the condition in *Solaropsis undata*, *Solaropsis nimbus*, *Solaropsis heliaca*, *Solaropsis angulifera*, *Solaropsis chicomendesi*, *Solaropsis nubeculata*, and *Solaropsis marmatensis* but differs in *Solaropsis brasiliana* and *Solaropsis gibboni* whose penial complex is as long as the spermoviduct. However, *Solaropsis caperata* and *Solaropsis undata* differ from the above-mentioned species by the lack of an epiphallus. *Solaropsis caperata* differs by a penial retractor muscle shorter than the flagellum, a thick vas deferens, almost as thick as the prostate, and an hermaphrodite duct almost as long as the spermoviduct.

Nervous System: *Solaropsis caperata*, *Solaropsis nimbus*, *Solaropsis angulifera*, *Solaropsis heliaca* and *Solaropsis chicomendesi* share a completely fused left parietal ganglia and visceral ganglia, however *Solaropsis angulifera*, *Solaropsis heliaca* and *Solaropsis chicomendesi* have less numerous pedal nerves than *Solaropsis caperata* and *Solaropsis nimbus*.

CONCLUSION

Solaropsis caperata anatomy is very similar to *Solaropsis undata*, the type species of *Solaropsis*, however it differs from the latter by presence of two deep depressions on the shell located half a whorl from aperture, a penial retractor muscle shorter than the flagellum, a thick vas deferens, almost as thick as the prostate and an hermaphrodite duct almost as long as the spermoviduct. More comprehensive anatomical studies combined with extensive molecular phylogenies are essential to help clarify the relations among *Solaropsis* species. I hope this work contributes to the knowledge about this poorly known group and highlights the need for a further revision of *Solaropsis*.

ACKNOWLEDGMENTS

I am grateful to Rudolf Barth Electron Microscopy Platform of the Oswaldo Cruz Institute/FIOCRUZ, Rio de Janeiro, for support with the scanning electron micrographs; to Laboratório de Carcinologia of UFRJ and to Setor de Malacologia of Museu Nacional/UFRJ for the support; to Laboratório de Malacologia of MZSP for the support and access to the lots, without which this work would not be possible; to Jorge Aboud and Tarcilla de Lima for suggestions; and to Rodrigo Salvador and one anonymous reviewer for critical readings of the manuscript.

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