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ARTICLE

Morphoanatomical, genetic, and distributional characterization of *Epiphragmophora semiclausa* (Martens, 1868), an Atlantic Forest snail endemic to Rio Grande do Sul (Gastropoda, Stylommatophora)

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Abstract. Family Epiphragmophoridae is endemic to South America, albeit known in Brazil from only three species: two belonging to the genus *Epiphragmophora* Doering, 1875 and the monotypic genus *Minaselates* Cuezzo & Pena, 2017. Here, we investigate material from natural history collections and newly collected specimens from Rio Grande do Sul state to revise the endemic and poorly known *Epiphragmophora semiclausa* (Martens, 1868). We provide a redescription of the species, including shell morphology, external soft-body morphology, jaw and radula, as well as the first detailed study of this species' reproductive anatomy and genetic data. Furthermore, we revise the species' historical and current distribution and provide observational behavioural data in the wild. *Epiphragmophora semiclausa* is endemic to the Atlantic Forest of Rio Grande do Sul state and historical data show that the species' range has contracted in the past decades. Field observations show that the species is arboreous, contrary to most congeners. Finally, we also provide an initial molecular phylogenetic framework for the family, showing that, so far, the Brazilian species form a monophyletic group and that the monotypic *Minaselates* renders *Epiphragmophora* non-monophyletic.

Keywords. Barrier snails; Brazil; Epiphragmophoridae; Helicoidea; Land snails.

INTRODUCTION

Barrier snails have only recently been shown to be a monophyletic lineage within the mega-diverse superfamily Helicoidea, being now considered a family on their own, Epiphragmophoridae (Cuezzo, 2006; Calcutt *et al.,* 2020), which takes its name from the chalky epiphragm the animals form during winter dormancy (Richardson, 1982). The family is endemic to South America and contains four genera, of which two are present in Brazil: *Epiphragmophora* Doering, 1875 and *Minaselates* Cuezzo & Pena, 2017. While *Minaselates* is monotypic (Cuezzo & Pena, 2017), *Epiphragmophora* is a very diverse group with over 50 species currently recognised and great variability in shell shape, size and teleoconch sculpture (Cuezzo, 2006). Still, the genus's presence in Brazil is very restricted, with only two known species, *E. bernardius* Ihering, 1900, from São Paulo state, and *E. semiclausa* (Martens, 1868), from Rio Grande do Sul state (Simone, 2006, 2008; Salvador *et al.,* 2024).

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Both Brazilian *Epiphragmophora* species have been seldom mentioned in the literature and remained somewhat enigmatic. In fact, *E. semiclausa* was absent from the first national checklists (Lange de Morretes, 1949, 1953) and was not assessed by either Wolfang K. Weyrauch or José W. Thomé and his team, whose studies formed the basis of the knowledge of the land snail fauna of Rio Grande do Sul. Therefore, in order to better define the identity of *E. semiclausa,* we investigate material from natural history collections worldwide (including types) and newly obtained specimens from collection efforts in Rio Grande do Sul. We provide a detailed redescription of the species, including the first anatomical account, as well as genetic data and ecological information. We also provide an initial molecular phylogenetic framework for the family Epiphragmophoridae.

MATERIAL & METHODS

For the present study, we analysed specimens in natural history collections and also conducted new collections in Rio Grande do Sul. Material from the following collections was used: FMNH, Field Museum of Natural History (Chicago, IL, USA); MCN, Museu de Ciências Naturais do Rio Grande do Sul (Porto Alegre, RS, Brazil); MCP-MOLUSCOS, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (Porto Alegre, RS, Brazil); MNHNM, Museo Nacional de Historia Natural (Montevideo, Uruguay); MZUSP, Museu de Zoologia da Universidade de São Paulo (São Paulo, SP, Brazil); RMNH, Naturalis Biodiversity Center (Leiden, The Netherlands); ZMB, Museum für Naturkunde (Berlin, Germany).

New material was obtained via collections that took place during 2022-2025, which are part of regular activities of the MCN group and thus, were not specifically targeting *Epiphragmophora semiclausa*. The specimens were deposited in the MCN collection, preserved either as dry (shells only) or in ethanol 70% (whole specimens).

Dissection and illustration of the reproductive system were performed under a ZEISS Stemi SV6 stereomicroscope equipped with a camera lucida. The confection of the final anatomical plate was carried out using the Affinity 3 software suite (v.3.1.0). Counting of shell whorls follows Parodiz (1951). For the orientation of the reproductive system, the terms proximal and distal refer to the position of structures relative to the gonad. The drawings of the reproductive system were based on the dissection of specimen lot MCN-42222 (of which genetic data was also obtained, see below), collected in January 2024. The configuration of the penial complex as observed after opening the pallial cavity, as well as the internal walls of the epiphallus and penis, were also illustrated.

Analysis of the radula and jaw under scanning electron microscopy (SEM) was performed using a Zeiss Evo MA10, at "Centro de Microscopia e Microanálise BR-Sul" (CMM-BRSul, UFRGS, Brazil).

A distribution map was created with QGIS v.3.30 (QGIS, 2026), using the map of Hasenack *et al.* (2023) as the base layer map for plotting the points. The map files provided by those authors also contain the division of Rio Grande do Sul into forest and grassland ecological systems.

Genetic data and phylogenetic analysis

Four specimens of "*Epiphragmophora* sp." (= *E. semiclausa*) from Rio Grande do Sul were sampled for genetic sequencing (Table 1). To build upon the work of Calcutt *et al.* (2020), we also sampled a representa-

Table 1. Specimens sequenced for the present study, alongside further genetic sequences used in the phylogenetic analysis. Information on GenBank accession numbers, locality where the specimens were collected, registration number of the voucher specimens in natural history collections, and references to the original publications are provided. Abbreviations of further collections: IBN, Instituto de Biodiversidad Neotropical, Universidad Nacional de Tucumán (Tucumán, Argentina); NHMUK, Natural History Museum (London, UK).

Species	C01	16S	ITS2+28S	Provenance	Voucher spm.	Reference
Epiphragmophora parodizi Fernández & Rumi, 1984	MT080605	MT080818	MT080831	Argentina: Tucumán, Trancas, Gonzalo close to Hualinchay	IBN 806	Calcutt *et al.* (2020)
Epiphragmophora semiclausa (Martens, 1868)	PZ840738	PZ840762	PZ840755	Brazil: Rio Grande do Sul, Itati	MCN 42041	this study
Epiphragmophora semiclausa (Martens, 1868)	PZ840739	PZ840763	PZ840756	Brazil: Rio Grande do Sul, São Francisco de Paula, Josafaz Canyon	MCN 42087	this study
Epiphragmophora semiclausa (Martens, 1868)	PZ840740	PZ840764	PZ840757	Brazil: Rio Grande do Sul, Maquiné, Barra do Ouro, Vale do Ligeiro	MCN 42148	this study
Epiphragmophora semiclausa (Martens, 1868)	PZ840741	PZ840765	PZ840758	Brazil: Rio Grande do Sul, Riozinho, Cascata da Gruta	MCN 42222	this study
Epiphragmophora estella (d'Orbigny, 1835)	—	PZ840766	PZ840759	Bolivia: Cordillera, Lagunillas	MZSP 101733	this study
Epiphragmophora cf. *multesima* Pilsbry, 1926	PZ840742	PZ840767	PZ840760	Bolivia: Potosí, Toro Toro	MZSP 122457	this study
Epiphragmophora sp.	PZ840743	PZ840768	PZ840761	Peru: Angaraes, Huancavelica, Cochacasa, Minas Julcani	RMNH.MOL.114305	this study
Epiphragmophora tomsici Fernández & Rumi, 1984	MT080606	MT080815	MT080832	Argentina: Tucumán, Trancas, Rearte River margin	IBN 807	Calcutt *et al.* (2020)
Epiphragmophora trenquelleonis (Grateloup, 1851)	MT080607	MT080817	—	Argentina: Córdoba, Punilla, La Falda	IBN 659	Calcutt *et al.* (2020)
Epiphragmophora trenquelleonis (Grateloup, 1851)	MT080608	MT080816	MT080833	Argentina: Córdoba, Cruz del Eje, Sierra San Marcos	IBN 894	Calcutt *et al.* (2020)
Epiphragmophora trigrammephora (d'Orbigny, 1835)	MT080609	MT080812	MT080834	Argentina: Córdoba, Totoral, 5 km S. Santa Catalina	IBN 340	Calcutt *et al.* (2020)
Epiphragmophora trigrammephora (d'Orbigny, 1835)	MT080610	MT080814	MT080835	Argentina: Jujuy, Ledesma, Calilegua National Park	IBN 844	Calcutt *et al.* (2020)
Minaselates cf. *paradoxa* Cuezzo & Pena, 2017	PZ840744	PZ840769	PZ840752	Brazil: Minas Gerais, Januária, Morro do Ipê	MZSP 162744	this study
Outgroup						
Labyrinthus bifurcatus (Deshayes, 1838)	MT080611	MT080820	MT080836	Ecuador: Nuevo Corrientes (River?)	NHMUK 20190592	Calcutt *et al.* (2020)
Monadenia fidelis (Gray, 1834)	MN022743	KF247021	AY014142	USA: Washington/Oregon	not informed	Saadi & Wade (2019), Wade & Mordan (2000)

tive of the monotypic genus *Minaselates* from Brazil and three other *Epiphragmophora* spp. from South America (Table 1) to provide an initial molecular phylogenetic framework for the family.

DNA extraction was conducted on a tissue clip from the specimen's foot using the QIAGEN DNeasy® Blood & Tissue Kit. The standard extraction protocol was followed, though we included a minor modification to the final step of the procedure to increase yield: we used only one-quarter (50 µL) of the suggested amount of buffer AE, and also included a repetition of the final step.

Following the study of Calcutt *et al.* (2020), four genetic markers were targeted: the barcoding fragment of the mitochondrial COI gene (primers LCO/HCO of Folmer *et al.,* 1994); the mitochondrial 16S rRNA gene (primers 16SarL/16SbrH of Simon *et al.,* 1994), c. 450 bp; and a continuous fragment of nuclear DNA encompassing the 3′ end of the 5.8S rRNA gene, the ITS2 region, and the 5′ end of the 28S rRNA gene (amplified in 2 fragments using primer pairs LSU-1/LSU-3 and LSU-2/LSU-5 of Wade & Mordan, 2000, Wade *et al.,* 2007).

PCR amplification for COI and 16S consisted of initial denaturation at 96°C (3 min); 35 cycles of denaturation at 94°C (30 s), annealing at either 48°C (COI) or 50°C (16S) (1 min), and extension at 72°C (2 min); final extension at 72°C (5 min). PCR protocol for ITS2+28S consisted of initial denaturation at 96°C (3 min); 40 cycles of denaturation at 95°C (30 s), annealing at either 50°C (ITS2 section) or 45°C (28S section) (1 min) and extension at 72°C (2 min); final extension at 72°C (4 min). The success of PCR was visually assessed via agarose gel electrophoresis. PCR products were cleaned using ExoSAP-IT™ (Affymetrix Inc.), following the manufacturer's protocol, and samples were then prepared and sent to Macrogen Europe (Amsterdam, The Netherlands) for Sanger sequencing.

Resulting sequences were visually quality checked through Phred Quality Score of bases, and *de novo* assembled in Geneious Prime (v.2025, Biomatters Ltd.). The consensus sequences were extracted and uploaded to GenBank (Table 1).

Our sequences were combined with those of Calcutt *et al.* (2020) (Table 1) for phylogenetic analysis. Two species were selected as outgroup: *Monadenia fidelis* (Gray, 1834), which was recovered as sister to Epiphragmophoridae by Calcutt *et al.* (2020) and *Labyrinthus bifurcatus* (Deshayes, 1838), representing Labyrinthidae, the most "basal" family of Helicoidea. These additional sequences were obtained from GenBank (Table 1).

The sequences of each marker (CO1, 16S, and ITS2+28S) were aligned in Geneious Prime using the default settings of the MUSCLE plugin (Edgar, 2004) (*i.e.,* optimised for accuracy). Alignments were visually proofed for inconsistencies and then concatenated for analysis. A Bayesian inference phylogenetic analysis was performed using MrBayes (v.3.2.7; Ronquist *et al.,* 2012) through the CIPRES Science Gateway (v.3.3; Miller *et al.,* 2015). Two concurrent analyses were run, each with 4 Markov chains of 50 million generations, using a generalised time reversible model, nst = 6, rates = invgamma, default priors; substitution model parameters were unlinked across the 3 markers. The first 20% trees were discarded as 'burn-in'. MCMC convergence was assessed by examining the standard deviation of split frequencies (~0.002) and the potential scale reduction factor (PSRF = 1.0), as well as trace plots (Ronquist *et al.,* 2009).

RESULTS

The resulting phylogenetic tree (Fig. 1) has *Epiphragmophora* as a non-monophyletic group, as the representative of the monotypic genus *Minaselates* is placed inside it. *Minaselates* cf. *paradoxa* is the sister group of our species of interest, *E. semiclausa* (posterior probability, PP = 0.99). *Epiphragmophora semiclausa* is a well-supported monophyletic group (PP = 1), showing very little genetic distance between its four terminals (collected at four different localities), indicating it consists of a single species. The identity of the COI sequences among *E. semiclausa* specimens goes from 96.3% to 99.4%.

The clade composed of *E. semiclausa* and *Minaselates* is sister to a Bolivian species (PP = 0.92). All these together are sister (PP = 0.90) to a clade (PP = 0.99) containing another Bolivian species as sister to a group (PP = 1) of Argentinean *Epiphragmophora* spp. There is a single terminal (a Peruvian species) sister to all the other *Epiphragmophora* spp.

Systematics

Superfamily Helicoidea Rafinesque, 1815
Family Epiphragmophoridae Hoffmann, 1928
Genus *Epiphragmophora* Doering, 1875

Type species: *Helix* (*Epiphragmophora*) *hieronymi* Doering, 1875.

Epiphragmophora semiclausa (Martens, 1868)
Figs. 2-6

Helix semiclausa Martens, 1868: (in Pfeiffer, 1868) 381, pl. 88, figs. 10-12; Heynemann, 1868: 106, fig. 4; Martens, 1868: 175; Pfeiffer, 1876: 415.

Helix (*Epiphragmophora*) *semiclausa:* Tryon, 1888: 80, pl. 18, figs. 65-66.

Epiphragmophora semiclausa: Pilsbry, 1894: 198; Richardson, 1982: 34; Salgado & Coelho, 2003: 174; Simone, 2006: 248, fig. 952; Thomé *et al.,* 2007: 19; Salvador *et al.,* 2024: 163.

Epiphragmophora sp.: Thomé *et al.,* 2006: 84, fig. 68.

Type locality: "Prope Rödersberg (São Leopoldo) Brasiliae" (Pfeiffer, 1868); *"Im Urwald bei Rödersberg (Colonien von Sao Leopoldo), unter Baumrinde"* (Martens, 1868: 175). The locality referred to as Rödersberg (sometimes also spelt Reitersberg) by early German immi-

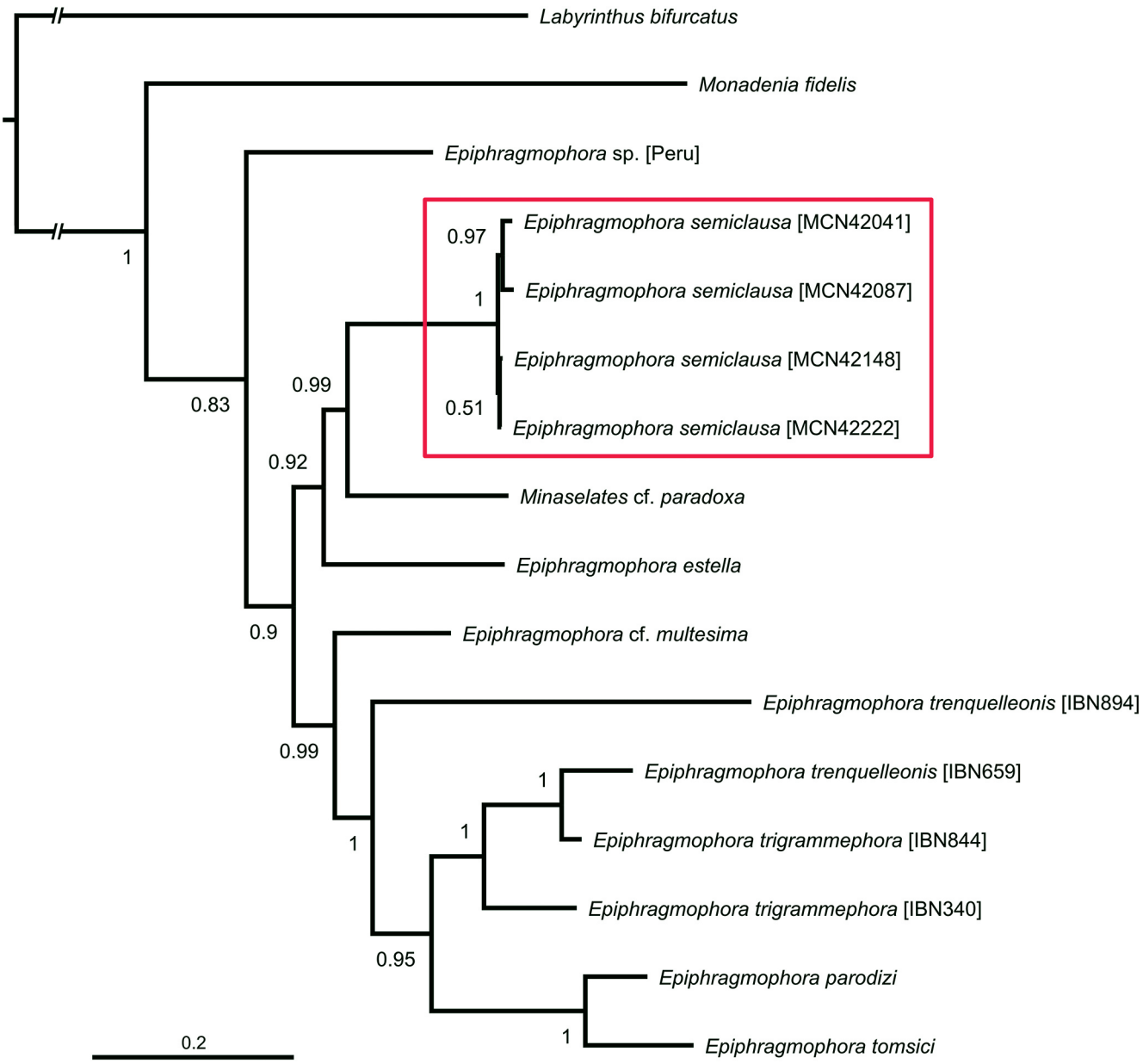


Figure 1. Bayesian inference phylogenetic tree (50% majority-rule consensus) based on the concatenated four markers. Nodes show posterior probabilities. The scale bar represents substitutions per site.

grants, and mentioned in Hensel's material, is presently known as Morro Reuter (Fig. 7), a municipality in Rio Grande do Sul (Pereira & Thomé, 1999).

Studied material: Syntypes: ZMB.Moll.13701, 4 shells ("Südl. Brasilien, Rödersberg"; Hensel leg.) (Fig. 2). **Further specimens:** Brazil, Rio Grande do Sul: FMNH 39728, 1 shell (Porto Alegre, ex Prosch & Wissel coll., ex ZMB coll., ex Walter F. Webb coll.); MCN-5548, 1 shell (Porto Alegre, Morro Santana, -30.051805 -51.121825, 06/05/1978, T. de Lema leg.); MCN-2037, 2 specimens (Viamão, Morro do Côco, -30.270112 -51.063165, 22/05/1966, J.W. Thomé and students leg.); MCN-1499, 1 specimen (Viamão, Morro do Côco, -30.270112 -51.063165, 18/11/1963, A. Lise leg.); MCN-42041, 1 specimen (Itati, -29.383889 -50.188056, 18/10/2022, P. Colombo leg.); MCN-42307, 1 specimen (Itati, -29.42498 -50.197312, 23/09/2025, P. Colombo leg.); MCN-42087, 1 specimen (São Francisco de Paula, -29.395577 -50.044613, 09/11/2022, J.O. Arruda leg.); MCN-42141, 1 shell (São Francisco de Paula, -29.350262 -50.033738, 28/02/2023, J.O. Arruda leg.); MCN-42148, 1 specimen (Maquiné, -29566710 -50.229970, 05/12/2023, P. Colombo leg.); MCN-42210, 1 shell (Três Cachoeiras, -29.4408 -50.0422, 25/01/2024, L. Teixeira leg.); MCN-42222, 1 specimen (Riozinho, -29.657085 -50.380914, 18/01/2024, L. Teixeira leg.); MCP-MOLUSCOS 6556, 1 specimen (São Francisco de Paula, -29.4480556 -50.5833333, 14/04/1997, Lab. Malaco leg.); MCP-MOLUSCOS 9751, 1 shell (São Francisco de Paula, -29.4480556 -50.5833333, 08/09/2002, Equipe Labmalac leg.); MCP-MOLUSCOS 6555, 1 specimen (São Francisco de Paula, -29.4480556 -50.5833333, 14/04/1997, Lab. Malaco leg.); MCP-MOLUSCOS 6553, 1 specimen (São Francisco de Paula, -29.4480556 -50.5833333, 22/10/1998, Lab. Malaco leg.); MNHNM 5485, 1 shell, (Serra Geral, Aratinga, 15/02/1964, M.A. Monné leg.);

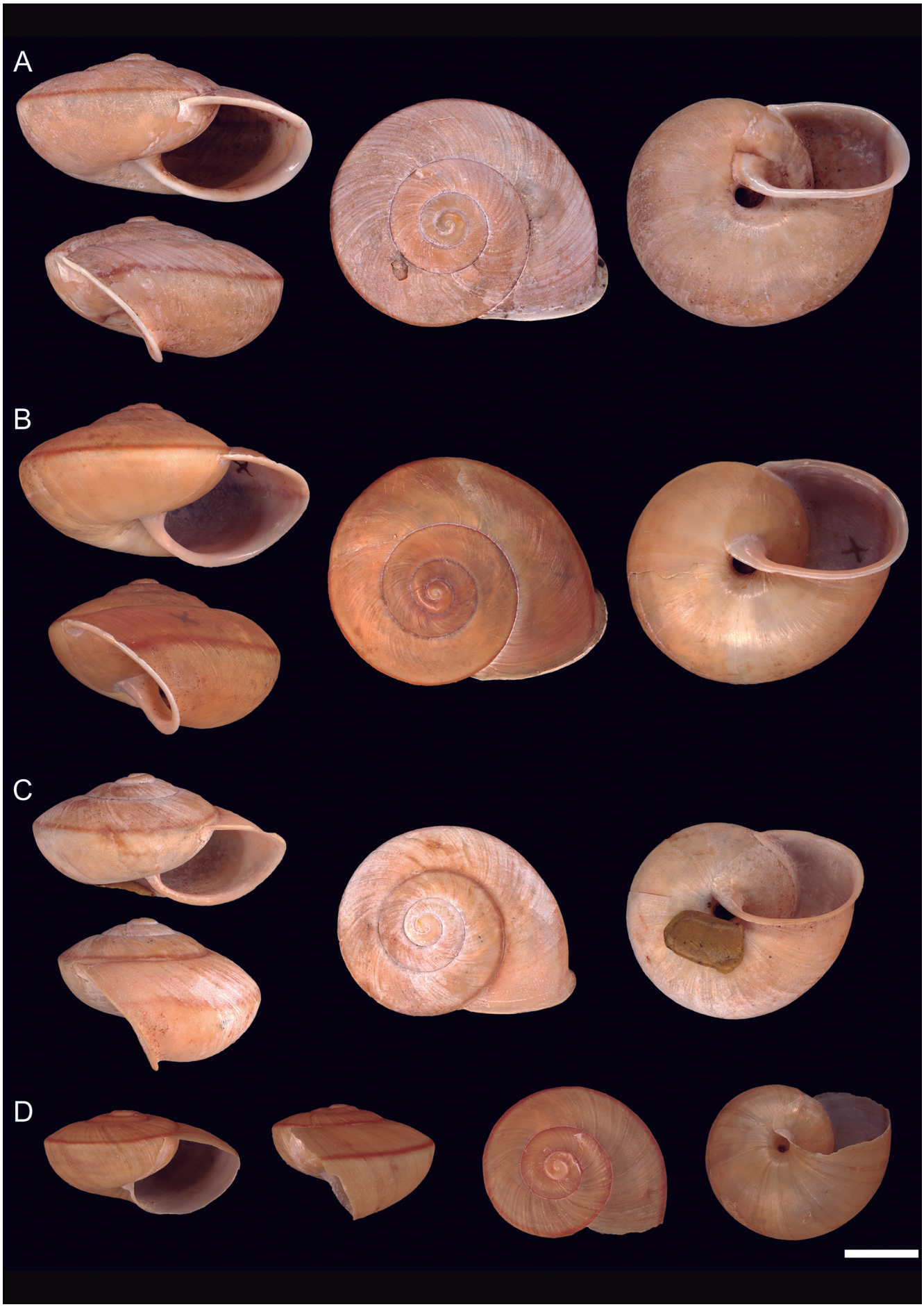


Figure 2. The four syntypes of *Epiphragmophora semiclausa* (von Martens, 1868), ZMB.Moll.13701. Scale bar = 10 mm.

MNHNM 14883, 3 shells (Guaíba, Fazenda São Maximiano, km 307 of BR-116 highway, in humid forest, -30.175850 -51.393701, 27/01/1993, F. Scarabino leg.); MCN-34659, 2 specimens (Guaíba, Fazenda São Maximiano, km 307 of BR-116 highway, -30.175850 -51.393701, 08/11/1994, M. Picoral leg.); MCN-34660, 1 specimen (Guaíba, Fazenda São Maximiano, km 307 of BR-116 highway, -30.175850 -51.393701, 13/12/1994, A.P. Lopes leg.); MCN-34662, 1 specimen (Guaíba, Fazenda São Maximiano, km 307 of BR-116 highway, -30.175850 -51.393701, 24/08/1996, M. Chaparro & F. Negri leg.); MCN-34663, 3 specimens (Guaíba, Fazenda São Maximiano, km 307 of BR-116 highway, -30.175850 -51.393701, 14/09/1996, M. Chaparro & F. Negri leg.).

Diagnosis: A combination of unique characters can be used to identify *E. semiclausa,* namely: a medium-large (typically circa 3.5 to 4.0 cm in width) keeled shell, with

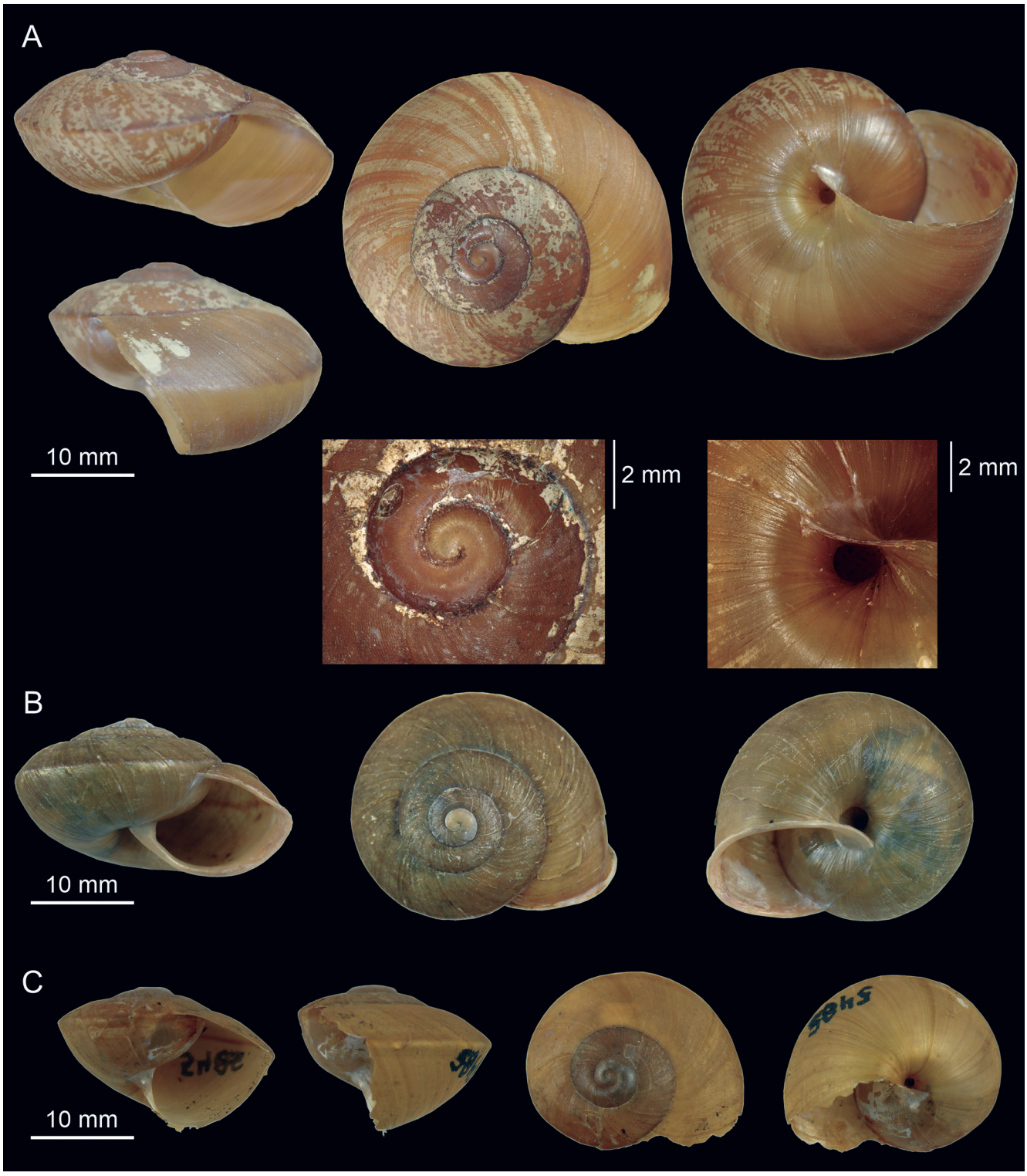


Figure 3. Shell morphology of specimens *Epiphragmophora semiclausa* in different growth stages. (A) MCN-42222, sub-adult; (B) MNHNM 14883, adult; (C) MNHNM 5485, juvenile.



Figure 4. Live specimen of *Epiphragmophora semiclausa* (MCN-42087) in situ. Photos: Mariano Pairet.

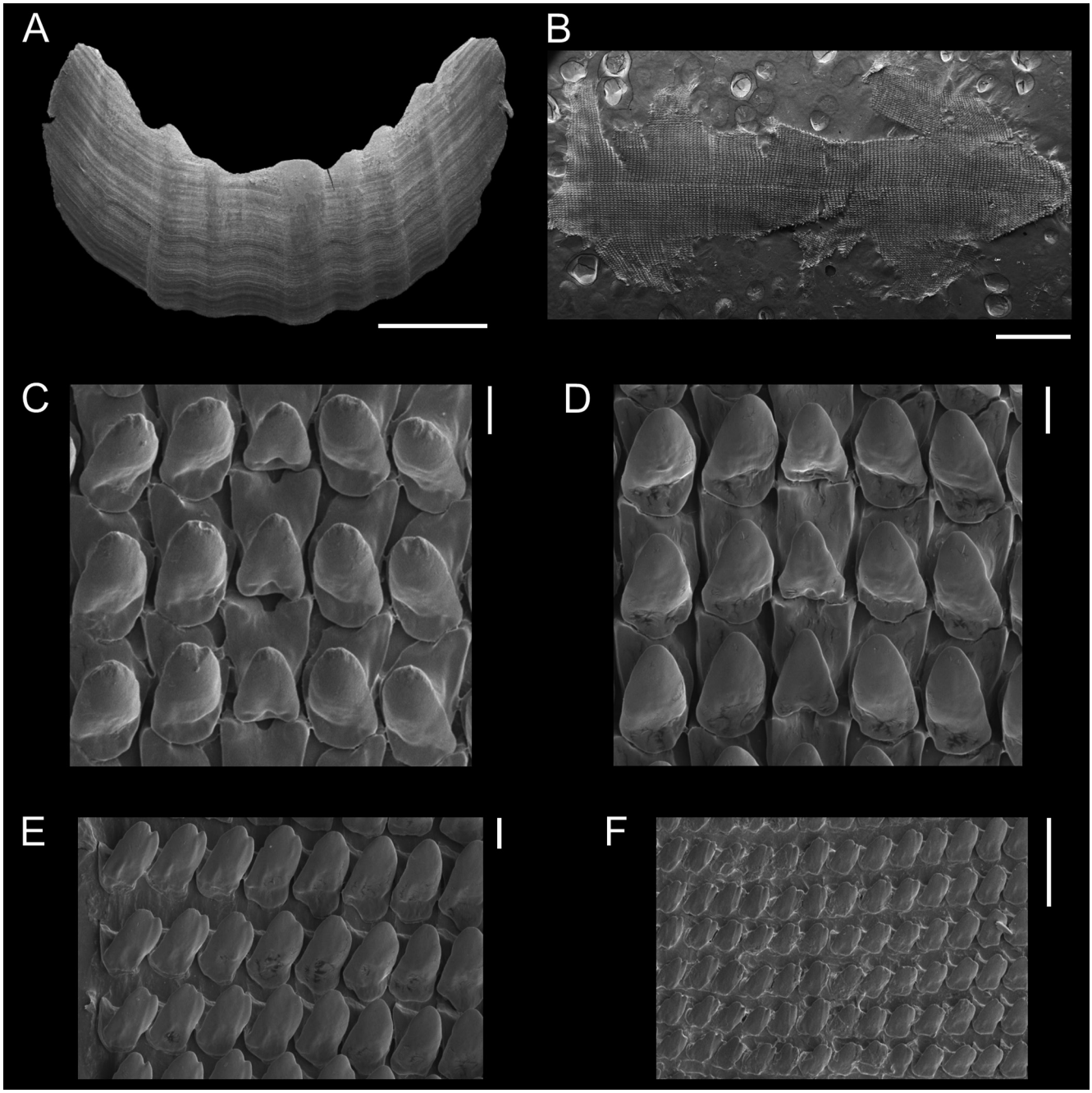


Figure 5. Jaw and radula of *Epiphragmophora semiclausa* (MCN-42222) under scanning electron microscopy (×40-×1010 magnification). (A) entire view of the jaw; (B) wide-range view of the radula; (C, D) detail of the central region, showing rachidian tooth in the middle, in two areas of the radula; (E) detail of the lateral teeth; (F) detail of the marginal area. Scale bars: A = 500 µm; B = 1 mm; C-E = 20 µm; F = 100 µm.

a spire typically more elevated than most congeners, a large and laterally elongated aperture, teleoconch periostracum with granulose aspect; a single dark brown spiral band running throughout the shell, located immediately above the keel (though faint in live specimens).

Description: Shell (Figs. 2-4): Shell dextral, medium to large (typically circa 3.5 to 4.0 cm in width), depressed helicoid, 4 to 4¼ whorls, keeled. Periostracum brown, with tone varying from lighter to darker shades; a single dark brown spiral band runs throughout the shell, located immediately above the keel. In live animals (Fig. 4), the shell has a flecked pattern, with lighter brownish golden flecks on a darker brown-black background, due to the soft body of the animal underneath; the spiral band of the shell is only faintly visible. Spire slightly elevated, of wide conical shape. Whorl profile lightly convex. Suture well marked. Protoconch 1¼ to 1½ whorl, with delicate thin axial growth lines; transition to teleoconch clear. Teleoconch sculptured by axial growth lines that become more pronounced and rib-like (particularly closer to the suture) as the shell grows; teleoconch periostracum with granulose aspect, both dorsally and ventrally. Aperture large, laterally elongated. Peristome reflected, lightly thickened; light brown to whitish in colour. Umbilicus narrow (circa 10% of shell diameter), deep; partially to half covered by peristome.

Syntypes measures: syntype #1: 4¼ whorls, shell height = 2.1 cm, shell width = 4.1 cm; syntype #2: 4¼ whorls, shell height = 2.3 cm, shell width = 4.0 cm; syntype #3: 4¼ whorls, shell height = 1.8 cm, shell width = 3.5 cm.

Head-foot (Fig. 4): Soft body brown, of granulose aspect (more prominent towards the "tail" end of the foot). Edge of foot more lightly coloured; tail end of the foot often also more lightly coloured. A narrow light-coloured line runs straight along the animal's back, from between the eyestalks to the shell. Both tentacle pairs are darker, going from dark brown to black. Eyestalks have small white flecks. "Eyeballs" greyish white.

Radula and jaw (Fig. 5): Rachidian tooth (Fig. 5C, D) trigonal in shape, ranging from 25-30 µm high, unicuspid, not very acute. Lateral teeth vary from ovoid (Fig. 5C) to trigonal shape (Fig. 5D), tip more rounded. Teeth in marginal (Fig. 5E) area slightly inclined towards the centre, more rectangular in shape; teeth close to the edge (Fig. 5E, F) with incipient bicuspid tips and a lateral in-

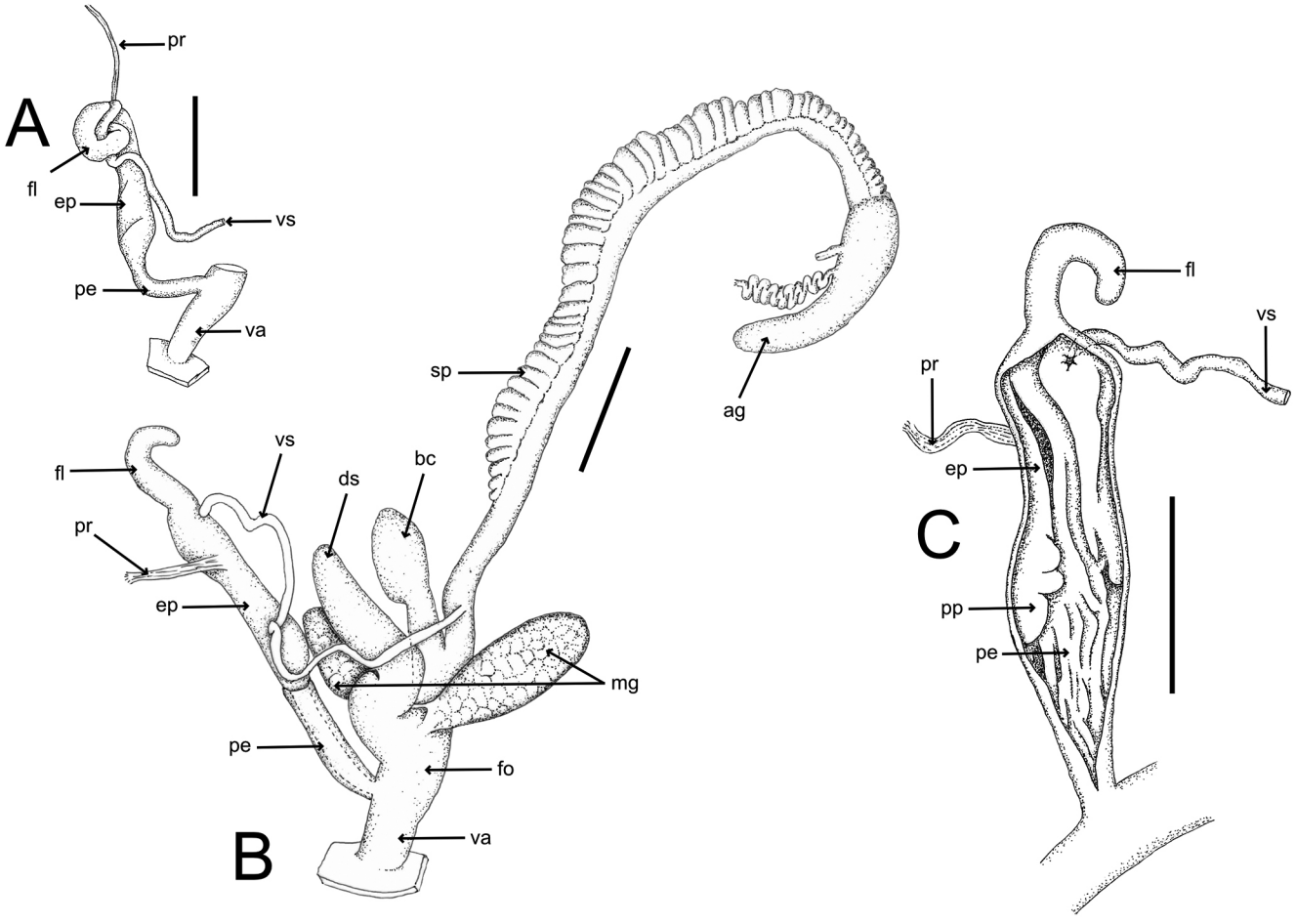


Figure 6. Schematic illustration of the reproductive tract of *Epiphragmophora semiclausa* (MCN-42222). Scale bars = 5 mm. (A) Overview of epiphallus and penis. (B) Detailed structure of the reproductive tract. (C) View of the internal walls of the epiphallus and penis. Abbreviations: ag = albumen gland, bc = bursa copulatrix, ds = dart sac, ep = epiphalus, fl = flagellum, fo = oviduct, mg = mucous gland, pe = penis, pp = papillae, pr = penis retractor muscle, sp = spermoviduct, va = vagina, vs = vas deferens.

dentation on the left. Jaw (Fig. 5A) horseshoe-shaped, moderately arched, translucent; surface wavy and with thin, transverse grooves visible with high magnification.

Reproductive system (Fig. 6): Terminal genitalia with dart sac complex consisting of single dart sac and two mucous glands with similar size and shape, both elongate oval-shaped, both with ducts inserting independently close to the middle of dart sac; dart sac muscular, long, with a "s" curve close to its base, inserting in distal portion of vagina; internal wall of dart sac with poorly defined folds resembling glandular tissue; dart papillae present, short, in distal portion of dart sac; bursa copulatrix discoid or elongate-oval, running towards middle zone of spermoviduct; duct of bursa copulatrix short, slightly swollen at base; vagina short, about ⅔ of penis length, with strong longitudinal folds at its internal wall; free oviduct medium (as long as penis) and straight; penial complex with finger-like flagellum; transition between epiphallus and penis not evident externally; epiphallus slightly longer to 1½ penis length, median portion slightly narrower than the proximal and distal portion, internal walls bearing high longitudinal folds; penis retractor muscle, thick, wide, inserting in middle epiphallus; penis inner wall with longitudinal folds; penial papillae present; penial sheath muscular, thin, proximally translucent, penis completely enveloped by penial sheath.

Distribution: Restricted to northeastern Rio Grande do Sul state, Brazil (Fig. 7), in the Atlantic Forest biome (altitude ranging approximately from 100 to 900 m). Importantly, this species is presently not known to occur in Santa Catarina state; its record from that state was a typo in Simone (2006), which the author later corrected (Simone, 2008), though the error can sometimes be found in contemporary literature (*e.g.,* Thomé *et al.,* 2007).

Habitat and ecology: The species is arboreal, typically observed on trees at approximately 1.8 m above ground level. Expectedly, individuals were observed active during the nocturnal phase. No further information is known about this species.

Remarks: There are two junior homonyms of *Epiphragmophora semiclausa:* (1) *Epiphragmophora semiclausa* Hylton Scott, 1951 from the Yungas in Argentina (Cuezzo, 2006), for which a rather confusing new name was later coined: *Epiphragmophora hemiclausa* Hylton Scott, 1957 (in Parodiz, 1957); and (2) *Epiphragmophora diluta semiclausa* Weyrauch, 1960 from Peru, for which Weyrauch (1964) later provided the new name *Epiphragmophora diluta semiaperta* Weyrauch, 1964.

Ihering (1910) described one subspecies of *E. semiclausa* from Catamarca, Argentina, namely *Helicigona semiclausa deflexa* Ihering, 1910. Analysis of the syntypes (MZSP 7473) shows that the shells are clearly typical discoid Argentinean *Epiphragmophora* spp. and completely distinct from the expanded keeled shell of the actual *E. semiclausa*. Judging by shell morphology, Ihering's taxon is potentially related to (and perhaps a se-

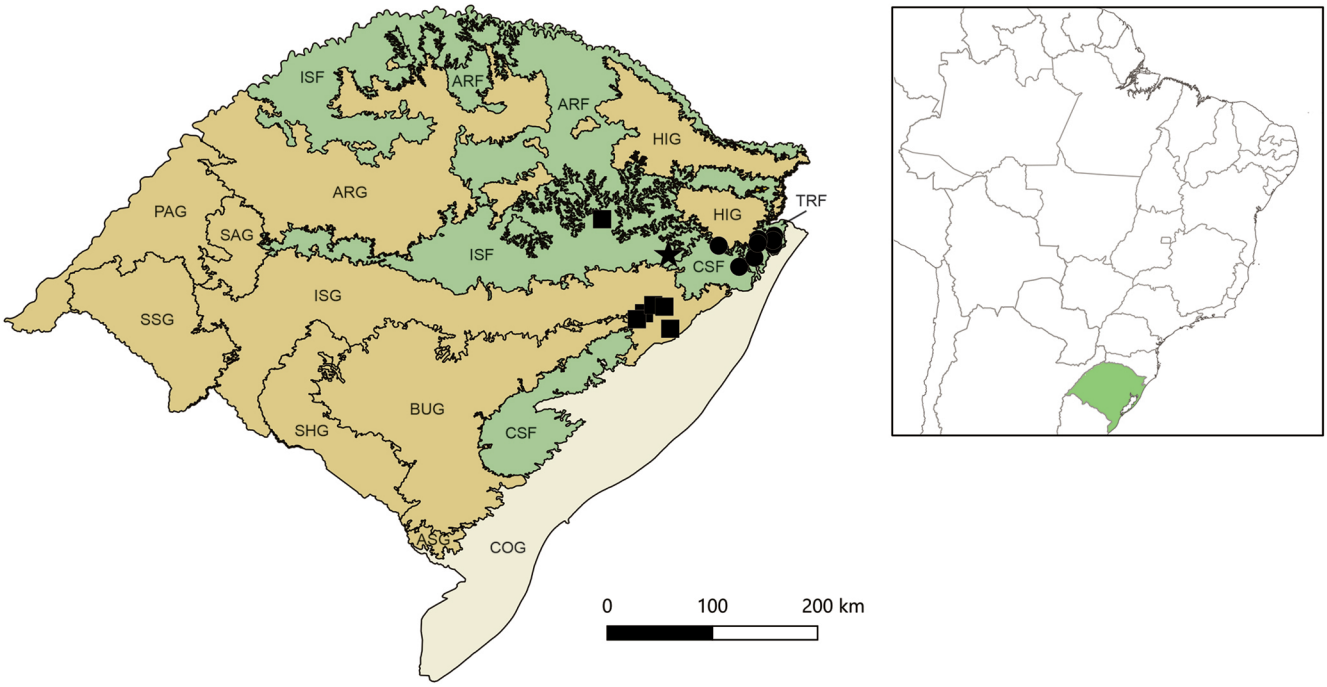


Figure 7. Map showing the known occurrences of *Epiphragmophora semiclausa,* so far endemic to Rio Grande do Sul state, indicating the forest (shown in green) and grassland (shown in brown) ecological systems *sensu* Hasenack *et al.* (2023). Historical records (of more than 30 years ago) are indicated by squares; newer records (less than 30 years ago) are indicated by circles; the type locality (Morro Reuter) is indicated by a star. The inset map shows the location of Rio Grande do Sul state in Brazil. Abbreviations: ARF, *Araucaria* forest; ARG, *Aristida* grassland; ASG, Atlantic submontane grassland; BUG, bush grassland; COG, coastal grassland; CSF, coastal subtropical forest; HIG, highland grassland; ISF, inland subtropical forest; ISG, inland submontane grassland; PAG, park grassland; SAG, sandy grassland; SHG, short-grass grassland; SSG, shallow soil grassland; TRF, tropical forest.

nior synonym of) *E. puella* Hylton Scott, 1951, but a more in-depth study is required to assess this matter.

DISCUSSION

So far, there is just one species of *Epiphragmophora* living in Rio Grande do Sul state, *E. semiclausa,* endemic to the state. It is one of the most easily diagnosable *Epiphragmophora,* being large and having a keeled shell; the keel is particularly developed in juveniles (Figs. 2, 3). A keeled shell is a very rare character among the species of this genus and only a handful of Argentinean species are merely subcarinated (Haas, 1955; Fernández & Rumi, 1984; Cuezzo, 2006). Indeed, Haas (1955) defined his new then-monotypic genus *Karlschmidtia* Haas, 1955 (type species *K. lentiformis* Haas, 1955, from Peru), based on a keeled shell and strong axial sculpture (he also indicated that the also-Peruvian *E. huanucensis,* a poorly known species, is keeled). Weyrauch (1960) considered *Karlschmidtia* a subgenus of *Epiphragmophora* and added a second Peruvian species to it, *E. cerrateae,* complementing the taxon's diagnosis with a flat-lenticular shell. Presently, *Karlschmidtia* is considered synonymous with *Epiphragmophora* (Zilch, 1960). Still, despite the keel and strong axial sculpture being also present in *E. semiclausa,* it differs from *Karlschmidtia* in numerous other features (*e.g.,* shell shape, aperture shape, banding pattern, size). Finally, *E. malkini,* from the Bolivian lowlands, has a similar shell shape, banding pattern, and keel (Haas, 1962), which could indicate a phylogenetic proximity to *E. semiclausa,* particularly considering the latter's relationship to other Bolivian lowland species in the phylogenetic tree (Fig. 1).

The comparatively high spire of the shell in relation to most congeners and large aperture (Figs. 2, 3) are also useful additional characters in identifying this species, though these features (particularly aperture size) tend to be more variable within the genus (Fernández & Rumi, 1984; Cuezzo, 2006). In relation to other Brazilian Epiphragmophoridae, it is quite straightforward to diagnose *E. semiclausa: Epiphragmophora bernardius* has a more compact shell, with three dark spiral bands and a small aperture; *Minaselates paradoxa* is small (less than 3 cm), with a rounded shell and covered umbilicus. Notably, the granulose aspect of the periostracum seen in *E. semiclausa* (Figs. 3, 4) is also observed to some extent in *M. paradoxa;* thus, this feature could have some phylogenetic meaning, as our preliminary results put these two as sister species (Fig. 1), though it is still too soon to say for certain. For a more detailed conchological comparison with all congeners, please refer to the Appendix.

Regarding the radula and jaw, a previous description of these features for *E. semiclausa* was done by Heynemann (1868: 106, fig. 4). The jaw is very similar in shape and sculpture to the present characterization. The rachidian tooth and lateral teeth are also very similar, but the teeth from the marginal area are slightly different. Heynemann (1868: fig. 4) illustrated the teeth from the longitudinal row 20 to the outermost rows as tricuspid. From the fragment we observed, we could only assess two cusps and a small indentation on the left side of the teeth, not so acute as Heynemann's drawing represented. Besides that, the transition to the teeth with a bicuspid tip is closer to the edge in the specimen we studied (> 30 longitudinal rows *vs.* > 20 rows in Heynemann's drawing).

Cuezzo (2006) provided anatomical information on several species of *Epiphragmophora* from Argentina and southern Bolivia. Considering the reproductive tract, the species that is anatomically most similar to *Epiphragmophora semiclausa* is *E. hemiclausa.* However, there are multiple characters that distinguish them. In *E. semiclausa,* the mucous glands are similar in size and shape to one another, whereas in *E. hemiclausa* they are unequal. In the latter species, the dart sac is straight, while in the former it shows an S-shaped curvature. The vagina is longer in *E. semiclausa* than in *E. hemiclausa.* The internal wall of the dart sac presents poorly defined folds resembling glandular tissue in *E. semiclausa* and uniform longitudinal bands in *E. hemiclausa.* The duct of the bursa copulatrix is short in *E. semiclausa* and long in *E. hemiclausa.* Finally, in *E. semiclausa* the inner wall sculpture of the proximal penis bears longitudinal folds, whereas in *E. hemiclausa* it shows thin zigzag longitudinal folds. For a more detailed anatomical comparison of the reproductive tract with all congeners for which data is available, please see Table A1 in the Appendix.

Epiphragmophora semiclausa is distributed across northern Rio Grande do Sul state (Fig. 7), inhabiting the Atlantic Forest biome. Its historical records, however, reveal a slightly larger distribution to the west and south until the early 1990s (Fig. 7). The records to the south are of particular interest, as they occur in the Pampas biome (grasslands). Those areas, however, were once Atlantic Forest and *E. semiclausa* cannot be found there anymore. This indicates a reduction in range in the past three decades and thus, makes this species a good contender for a more thorough conservation assessment, as it is currently not present in Rio Grande do Sul's Red List. The animal's unique dark and golden appearance could also make it suitable as a flagship invertebrate species for the region. Notably, specimens from the southern edge of the species' distribution are generally smaller in size (between 2.5 and 3.0 cm wide), which could represent a latitudinal pattern or, most likely reflect environmental conditions (*e.g.,* habitat quality) in the periphery of the species' range (*e.g.,* Wardhaugh *et al.,* 2013; Tytar & Baidashnikov, 2021). In addition, historical collections typically include two to three specimens per lot, whereas more recent collections typically contain only single specimens found each time. It is impossible to say whether this represents a reduction in density as well, though we consider it worthwhile to highlight this here for future investigations.

The species of *Epiphragmophora* in Argentina and Paraguay mostly live among crevices and under rocks and logs (Fernández & Rumi, 1984; Cuezzo, 2006). However, our observations in the field show that this is not the case for *E. semiclausa.* Field observations of

these nocturnal animals during their active phase have shown them to be arboreal. Thus, the arboreal habitat could be a unique trait of *E. semiclausa* among the family and deserves future attention. Habits of the other Brazilian Epiphragmophoridae should also be more closely scrutinized.

While it was not the immediate goal of this study, there is further information that can be gleaned from the phylogenetic tree (Fig. 1). As expected, Brazilian Epiphragmophoridae so far form a monophyletic clade, which means that *Minaselates* renders *Epiphragmophora* non-monophyletic. A phylogenetic study with a wider sampling, including the type species of *Epiphragmophora* (*E. hieronymi*), should elucidate this matter and clarify whether *Minaselates* should be treated as a junior synonym or whether *Epiphragmophora* should be split into more than one genus. For now, we opt for the most nomenclatural stable choice and retain *Minaselates* as a valid genus. Notably, there are three mostly monotypic (sub) genera currently synonymised with *Epiphragmophora* (Zilch, 1960) that could be reinstated, if needed, and potentially redefined to include more species: *Angrandiella* Ancey, 1886, *Doeringina* Ihering, 1929, *Karlschmidtia* Haas, 1955. The type species of each of these (sub)genera will likewise be necessary in a future phylogenetic study.

The phylogenetic relationships of the Brazilian species to other Epiphragmophoridae in our initial tree (Fig. 1) are also interesting to discuss. *Epiphragmophora estella* from the Bolivian lowlands is the sister taxon to the clade formed by all Brazilian terminals, while *E.* cf. *multesima* from the Bolivian Andes clusters with Argentinian terminals. *Epiphragmophora* is considered to be primarily an Andean clade, with fewer species living in the lowlands (Cuezzo, 2006). While the support of this lowland/upland split in the tree is weak (PP = 0.90), this is an interesting venue for further investigation. Finally, as already noted by Calcutt *et al.* (2020), some species in Argentina seem to be species complexes, as visible by the distances between terminals of *E. trenquelleonis* and *E. trigrammephora* on the tree and their non-monophyly. These species should be revised in the future, especially as the former is the type species of the synonymised subgenus *Doeringina*.

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APPENDIX

Differential diagnosis (shell): *Epiphragmophora semiclausa* differs from the other species of the genus by the following combination of characters:

(1) Shell of adult specimens medium-large, typically *ca.* 3.5 to 4.0 cm wide, *vs.* less than 3.5 cm in *E. alsophila* (Philippi, 1867), *E. anceyana* Preston, 1909, *E. andivaga* Ancey, 1899, *E. angrandi* (Morelet, 1863), *E. argentina* (Holmberg, 1909), *E. atahualpa* Pilsbry, 1944, *E. bernardius* Pilsbry, 1900, *E. birabeni* Parodiz, 1955, *E. cerrateae* Weyrauch, 1960, *E. connectens* Haas, 1959, *E. cryptomphala* Ancey, 1897, *E. diluta* (Pfeiffer, 1842), *E. dormeri* Gude, 1901, *E. escoipensis* Cuezzo, 1996, *E. estella* (d'Orbigny, 1837), *E. feruglioi* Parodiz, 1969, *E. granulosa* Weyrauch, 1960, *E. guevarai* Cuezzo, 2006, *E. gueinzii* (Pfeiffer, 1857), *E. haasi* Zilch, 1953, *E. hemiclausa* Hylton Scott, 1951, *E. hemiomphalos* Haas, 1951, *E. hieronymi* (Doering, 1875), *E. higginsi* (Miller, 1878), *E. huanucensis* (Philippi, 1867), *E. jaspidea* (Pfeiffer, 1859), *E. lentiformis* (Haas, 1955), *E. leucobasis* Haas, 1951, *E. malkini* Haas, 1962, *E. mirabilis* Weyrauch, 1960, *E. mollegrandensis* Morton, 2007, *E. multesima* Pilsbry, 1926, *E. olssoni* Pilsbry, 1926, *E. orophila* Ancey, 1903, *E. oroyensis* Pilsbry, 1926, *E. parodizi* Fernández & Rumi, 1984, *E. pilsbryi* Haas, 1934, *E. proseni* Hylton Scott, 1951, *E. puella* Hylton Scott, 1951, *E. puntana* (Holmberg, 1909), *E. quirogai* Cuezzo, 2006, *E. rhathymos* (Holmberg, 1912), *E. saltana* Ancey, 1897, *E. tomsici* Fernández & Rumi, 1984, *E. trenquelleonis* (Grateloup, 1851), *E. trifasciata* Fernández & Rumi, 1984, *E. trigrammephora* (d'Orbigny, 1835), *E. turneri* Morton, 2007, *E. turtoni* Ancey, 1899, *E. variegata* Hylton Scott, 1962, *E. villavilensis* Parodiz, 1955, *E. walshi* Cuezzo, 2006, and *E. zilchi* Weyrauch, 1960; *vs.* over 4 cm in *E. audouini* (d'Orbigny, 1835) and *E. llaguenica* Zilch, 1953).

(2) Shell keeled, *vs.* non-keeled *E. anceyana, E. angrandi, E. argentina, E. atahualpa, E. basiplanata* Weyrauch, 1960, *E. claromphalos* (Deville & Hupé, 1850), *E. clausomphalos* (Deville & Hupé, 1850), *E. cryptomphala, E. diluta, E. dormeri, E. escoipensis, E. estella, E. guevarai, E. granulosa, E. haasi, E. hemiclausa, E. hieronymi, E. higginsi, E. huancabambensis* Pilsbry, 1926, *E. jujuyensis* Hylton Scott, 1962, *E. leucobasis, E. llaguenica, E. macasi* (Higgins, 1872), *E. mirabilis,* 1960, *E. oresigena* (d'Orbigny, 1835), *E. ormeai* Weyrauch, 1956, *E. oroyensis, E. parodizi, E. patasensis* (Pfeiffer, 1859), *E. pelliscolubri* (Philippi, 1867), *E. proseni, E. puntana, E. quirogai, E. rhathymos, E. saltana, E. tomsici, E. trenquelleonis, E. trifasciata, E. trigrammephora, E. tucumanensis* (Doering, 1874), *E. variegata, E. walshi, E. webbi* Pilsbry, 1932, and *E. zilchi.*

(3) Teleoconch perisotracum with granulose aspect, *vs.* with strong axial ribs in *E. birabeni* and *E. costellata* Fernández & Rumi, 1984.

(4) Presence of a single dark brown spiral band running throughout the shell, located immediately above the keel (faint in live specimens), *vs.* spiral band absent in in *E. audouini, E. birabeni, E. ormeai, E. proseni, E. puella, E. quirogai, E. tomsici* and *E. villavilensis; vs.* two spiral bands in *E. malkini, E. dormeri* and *E. lentiformis; vs.* three spiral bands in *E. anceyana, E. atahualpa, E. bernardius, E. cerrateae, E. claromphalos, E. cryptomphala, E. granulosa, E. guevarai, E. leucobasis, E. macasi, E. oresigena, E. pilsbryi, E. pollonerae* (Paravicini, 1894), *E. trifasciata* and *E. walshi; vs.,* three or four spiral bands in *E. diluta; vs.* four spiral bands in *E. basiplanata.*

Differential diagnosis (reproductive tract): Given the complexity and number of structures involved, a comparison between *Epiphragmophora semiclausa* and its congeners is presented as Table A1.

Table A1. Comparative table of anatomical features of *Epiphragmophora semiclausa* and other congeners. Anatomical data of the latter was extracted from the studies of Fernández & Rumi (1984) and Cuezzo (2006); note that (1) some information in missing for some species (indicated by a '-'), and (2) some specimens lack anatomical data altogether (being absent from the table).

Species	Dart sac complex	Mucous glands	Dart sac	Dart sac, internal wall	Dart papillae	Bursa copulatrix	Bursa duct
***E. semiclausa* (Martens, 1868)**	Single dart sac; two mucous glands, similar in size and shape.	Both elongated to oval.	Muscular, elongated, S-shaped near base.	Poorly defined folds, glandular-like.	Present; thick; short; in distal dart sac.	Discoid to elongate-oval.	Short; slightly swollen basally.
***E. argentina* (Holmberg, 1909)**	Single dart sac; two mucous glands, similar in size and shape.	Both elongated to cylindrical.	Muscular, cylindrical, even in diameter.	Uniform longitudinal bands.	Present, thick; short; in distal dart sac.	Elongate-oval	Long; convoluted.
***E. cryptomphala* Ancey, 1897**	Single dart sac; two mucous glands, with different size and shape.	Right one sac-like; left one cylindrical.	Muscular, with thick walls, long, cylindrical with medial constriction; it naturally folded by itself at level of constriction.	—	Present; dart papillae as long as distal portion of dart sac.	—	Short to medium length duct.
***E. escoipensis* Cuezzo, 1996**	Single dart sac; two mucous glands, with different size and shape.	Right one globose sac-like; left one oval.	Long, muscular, cylindrical, without medial constriction.	—	—	Roundish.	Thin; medial length duct.
***E. guevarai* Cuezzo, 2006**	Single dart sac; two unequal mucous glands.	Right one smaller, roundish; left one oval.	Long, muscular, cylindrical, with medial constriction.	—	Present; cylindrical; as long as distal portion of dart sac.	Oval.	Thin; short duct distally slightly wider.
***E. hemiclausa* Hylton Scott, 1951**	Single dart sac; two unequal mucous glands.	Right one round-shaped; left one elongate oval-shaped.	Short, muscular, widening at its base.	Uniform longitudinal bands.	Present; short; in distal portion of dart sac.	Elongate-oval.	Long; slightly swollen at base.
***E. hieronymi* Doering, 1874**	Single dart sac; two unequal mucous glands.	Right one sac-like; left one oval-elongate.	Long, muscular, cylindrical, with a constriction dividing the organ in two portions; its proximal portion longer than distal one.	Thin, internal dart gland located in distal portion of dart sac.	—	Round.	Thick; short duct.
***E. jujuyensis* Hylton Scott, 1962**	Single dart sac; two mucous glands on opposite sides.	Mucous glands oval, pear-shaped; right one (dorsal view) slightly shorter than left.	Cylindrical, muscular, with medial constriction.	Proximal dart sac internal wall with longitudinal folds; distal one with cylindrical dart papilla.	Present, cylindrical.	Bursa sac not sharply differentiated from duct.	Thick; short duct.
***E. parodizi* Fernández & Rumi, 1984**	Single dart sac; two mucous glands.	Right one sac-like; left one oval-elongated.	Long, muscular, cylindrical, with medial constriction.	Presence of thin, short dart gland located inside distal portion of dart sac.	—	Oval.	Thin; medium duct.
***E. puntana* (Holmberg, 1909)**	Single dart sac; two mucous glands.	Both glands round shaped; left one slightly bigger than right.	Long, muscular, cylindrical, with medial constriction.	—	Present, thick; cylindrical; as long as distal portion of dart sac.	Round.	Thin; medium length duct basally wider.
***E. quirogai* Cuezzo, 2006**	Single dart sac; two unequal mucous glands.	Right one sac-like; left one oval-elongate.	Long, muscular, cylindrical, with medial constriction.	Thin, internal dart gland located in distal portion of dart sac.	—	Round.	Thick; short duct.

Table A1 (continued). Comparative table of anatomical features of *Epiphragmophora semiclausa* and other congeners. Anatomical data of the latter was extracted from the studies of Fernández & Rumi (1984) and Cuezzo (2006); note that (1) some information in missing for some species (indicated by a '-'), and (2) some specimens lack anatomical data altogether (being absent from the table).

Species	Flagellum	Epiphallus	Penis-epiphallus transition	Penis' retractor muscle	Penis, internal wall	Penial papillae	Penial sheath
***E. semiclausa* (Martens, 1868)**	Finger-like.	Slightly longer than penis (up to 1.5×); median constriction.	Not externally distinct.	Thick; inserting at mid epiphallus.	With longitudinal folds.	Present.	Thin; muscular; proximally translucent; penis fully enclosed.
***E. argentina* (Holmberg, 1909)**	Long; thin; convoluted.	Thin; slender; epiphallus as long as the penis.	Not externally distinct.	Thick; inserting in middle portion of epiphallus.	Its proximal portion with thin zigzag longitudinal bands; distal portion with closer columns in a zigzag pattern.	Absent.	Simple; thin; muscular; enveloping penis in its complete length.
***E. cryptomphala* Ancey, 1897**	Thin; finger-like.	Its proximal portion widening at point of entrance of vas deferens; epiphallus 2x longer than penis.	—	—	With three longitudinal pilasters.	Present; short; triangular.	Thin; muscular; sheath overlapping distal portion of penis.
***E. escoipensis* Cuezzo, 1996**	Thin; finger-like.	Its proximal portion widening at point of insertion of vas deferens; longer; thinner than penis.	Externally differentiated.	Its inserting in medium zone of epiphallus.	With thin smooth, longitudinal folds.	Absent.	Simple; muscular; overlapping all penis length.
***E. guevarai* Cuezzo, 2006**	Short; finger-like.	Cylindrical to globose in proximal portion where vas deferens inserts; shorter than penis.	Externally differentiated.	Basally wider.	With thin zigzag folds in all its length.	Present; short.	Simple; muscular; overlapping distal portion of penis.
***E. hemiclausa* Hylton Scott, 1951**	Thin; finger-like.	—	Not externally distinct.	Thick; wide.	Its proximal portion with thin zigzag longitudinal pleats; distal portion with thin straight longitudinal bands.	Present; small.	Muscular; thin; proximally translucent; penis completely enveloped by penial sheath.
***E. hieronymi* Doering, 1874**	Thin; finger-like; short.	Proximally broad and progressively becoming thinner.	—	—	With thin delicate longitudinal pleats.	Present; short; triangular.	Thick; overlapping terminal portion of penis.
***E. jujuyensis* Hylton Scott, 1962**	Finger-like; short; curved.	Its proximal portion broadening at point of insertion of vas deferens; long.	—	—	Its proximal portion with convoluted zigzag glandular bands close to penial papillae; distal portion with longitudinal straight bands.	Present; short; triangular.	Thin; translucent; overlapping distal portion of penis.
***E. parodizi* Fernández & Rumi, 1984**	Thin; finger-like.	Its widening at point of insertion of vas deferens; thin; epiphallus ⅓ to ½ the penis length.	—	—	With thin delicate longitudinal pleats, becoming taller with zigzag pattern in proximal penis zone.	Absent.	Muscular; thick; overlapping all penis length.
***E. puntana* (Holmberg, 1909)**	Finger-like; distal portion thick.	Shorter than penis.	Externally differentiated.	Thin; long.	Its proximal portion with smooth strength pleats; distal portion with thick zigzag folds.	Present; short; rectangular; with surface sculpture consisting of vertical bands.	Muscular.
***E. quirogai* Cuezzo, 2006**	Thin; finger-like.	Its proximal portion thick, progressively becoming thinner; epiphallus double penis total length.	—	—	With thin delicate longitudinal pleats.	Present; short; triangular.	Short; muscular; overlapping terminal portion of penis.

Table A1 (continued). Comparative table of anatomical features of *Epiphragmophora semiclausa* and other congeners. Anatomical data of the latter was extracted from the studies of Fernández & Rumi (1984) and Cuezzo (2006); note that (1) some information in missing for some species (indicated by a '-'), and (2) some specimens lack anatomical data altogether (being absent from the table).

Species	Dart sac complex	Mucous glands	Dart sac	Dart sac, internal wall	Dart papillae	Bursa copulatrix	Bursa duct
E. rhathymos **(Holmberg, 1912)**	Single dart sac; two mucous glands.	Right one sac-like; left one oval-elongate, smaller than dart sac.	Muscular, thick wall, cylindrical, with medial constriction.	—	Present; cylindrical; half as long as distal portion of dart sac.	Oval.	Thick; short to medium duct.
E. saltana **Ancey, 1897**	Single dart sac; two mucous glands.	Right one sac-like; left one oval-elongate.	Muscular, cylindrical, with medial constriction.	Thin dart gland, located inside distal portion of dart sac.	—	Round to oval.	Thick; short to medium duct.
E. tomsici **Fernández & Rumi, 1984**	Single dart sac; two mucous glands.	Right one sac-like; left one cylindrical.	Muscular, cylindrical, with medial constriction.	Thin, cylindrical dart gland located inside distal portion of dart sac.	Present; as long as distal portion of dart sac.	Oval.	Thick; medium length duct.
E. trenquelleonis **(Grateloup, 1851)**	Single dart sac; two mucous glands.	Right one smaller than left, round or slightly elongated; left one oval elongated.	Very long, muscular, cylindrical, with distal portion thicker than proximal, both portions separated by medial constriction.	—	Present; thick, as long as distal portion of dart sac.	Round.	Very thick; short duct.
E. trifasciata **Fernández & Rumi, 1984**	Single dart sac; two unequal mucous glands.	Right one small, round; left one cylindrical to oval.	Long, muscular, cylindrical, with medial constriction.	—	Present; thick; cylindrical; as long as distal portion of dart sac.	Round.	Thick; very short duct.
E. trigrammephora **(d'Orbigny, 1835)**	Single dart sac; two unequal mucous glands.	Both sac-like, generally elongated, voluminous.	Long, muscular, with thick walls, cylindrical, with constriction located in basal ⅓ of total length, distal portion of dart sac longer than proximal.	—	Present; dart papillae half length of dart sac distal portion.	Round.	Extremely short; thick duct.
E. tucumanensis **(Doering, 1874)**	Single dart sac; two unequal mucous glands.	Right one oval to cylindrical; left one oval-elongated.	Short, muscular, cylindrical, with basal portion slightly wider in diameter, or short cylindrical and even in diameter.	Uniform longitudinal bands.	Present; short.	Elongate-oval.	Medium length duct.
E. variegata **Hylton Scott, 1962**	Single dart sac; two unequal mucous glands.	Right one oval, thinn; left one pea-shaped.	Cylindrical, muscular, smaller than mucous glands.	—	Present; small; located in basal portion of dart sac.	Oval.	—
E. villavilensis **Parodiz, 1955**	Single dart sac; two unequal mucous glands.	One of mucous glands sac-like, prominent, other gland oval-elongate.	Short, cylindrical, thick muscular walls, marked constriction in medial zone.	Thin, internal dart gland in distal portion of dart sac.	—	Round.	Thick; short duct.
E. walshi **Cuezzo, 2006**	Single dart sac; two unequal mucous glands.	One of mucous glands sac-like, prominent, other gland oval-elongate.	Muscular, with thick walls, cylindrical, with a median constriction; proximal portion of dart sac wider than distal portion.	—	Present; dart papillae half length of distal portion of dart sac.	Round to oval.	Very short duct.

Table A1 (continued). Comparative table of anatomical features of *Epiphragmophora semiclausa* and other congeners. Anatomical data of the latter was extracted from the studies of Fernández & Rumi (1984) and Cuezzo (2006); note that (1) some information in missing for some species (indicated by a '-'), and (2) some specimens lack anatomical data altogether (being absent from the table).

Species	Flagellum	Epiphallus	Penis-epiphallus transition	Penis' retractor muscle	Penis, internal wall	Penial papillae	Penial sheath
E. rhathymos **(Holmberg, 1912)**	Thin; cylindrical; thick distal portion.	Thin; as long as penis.	Externally differentiated.	—	With thin undulating pleats.	Absent.	Simple; muscular; overlapping distal portion of penis.
E. saltana **Ancey, 1897**	Thin; finger-like; short; gradually tapering towards end.	Long; thin.	Not externally distinct.	—	With thin undulating parallel pleats.	Absent.	Muscular, thick, distally multilayered; proximal penis sheath thin, single layer, overlapping all penis length.
E. tomsici **Fernández & Rumi, 1984**	Thin; long.	Its proximal portion widening at point of insertion of vas deferens; epiphallus as long as penis.	Not externally distinct.	—	With thin undulating folds in all its length.	Absent.	Muscular but thin; basally multilayer; overlapping half penis length.
E. trenquelleonis **(Grateloup, 1851)**	Thin; finger-like; medium in length.	Epiphallus ¼ the penis length.	Externally differentiated.	Thick.	Its proximal portion, close to penial papillae, with longitudinal thin pleats in zigzag pattern; distal portion with thin, smooth, straight folds.	Present; short; triangular.	Simple; very thick; muscular; penis sheath overlapping distal portion of penis.
E. trifasciata **Fernández & Rumi, 1984**	Triangular; with thick distal portion.	Cylindrical; thick; epiphallus ½ the penis length.	Externally differentiated.	—	With thin smooth strength pleats for all its length; some specimens with longitudinal pilaster.	Present; short.	Simple; muscular; overlapping distal portion of penis.
E. trigrammephora **(d'Orbigny, 1835)**	Thin; finger-like.	Epiphallus ½ the penis length.	Externally differentiated.	—	With thin smooth, straight folds.	Short, triangular.	Muscular; overlapping distal portion of penis.
E. tucumanensis **(Doering, 1874)**	Long; thin; convoluted.	Epiphallus ½ the penis length.	Externally differentiated.	Thick.	Its proximal portion with thin zigzag longitudinal bands; distal portion with closed columns in zigzag pattern ending in straight bands.	Absent.	Penial sheath double, internal one muscular and external transparent and thin.
E. variegata **Hylton Scott, 1962**	Short to medium; finger-like.	—	Externally differentiated.	—	With zigzag longitudinal pleats.	Absent.	Muscular; overlapping all penis length.
E. villavilensis **Parodiz, 1955**	Thin; finger-like; short.	Its proximally portion thick, progressively thinner towards penis; epiphallus about ½ the penis length.	—	Thick; short.	With thin delicate longitudinal folds.	Short, triangular.	Thin; overlapping terminal portion of penis.
E. walshi **Cuezzo, 2006**	Thin; finger-like; gradually tapering towards end.	Its proximal portion widens at point of entrance of vas deferens; epiphallus as long as penis or slightly longer.	—	—	With thin smooth zigzag pleats.	Short, triangular.	Muscular, gradually becoming thinner towards proximal penis.

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