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Article *in* Malacologia · January 2009

DOI: 10.4002/1543-8120-49.1.121

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SYSTEMATIC REVISION AND CLADISTIC ANALYSIS OF *EPIPHRAGMOPHORA* DOERING FROM ARGENTINA AND SOUTHERN BOLIVIA (GASTROPODA: STYLOMMATOPHORA: XANTHONYCHIDAE)

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ABSTRACT

As a first step towards a comprehensive revision of the South American genus *Epiphragmophora* Doering, 1874, taxa described from Argentina and Bolivia, inhabitants of the rainforest Yungas (Amazonian biogeographic subregion) Monte, Pre-Puna biogeographic provinces, and Chacoan biogeographic subregion are studied. Special attention has been paid to the morphology of the terminal genitalia with respect to its relevance for systematics. The revision is based on the examination of nearly all type material, plus extensive field work and examination of additional material deposited in several museums. Shell, pallial system and genitalia of each species have been described and illustrated, some of them for the first time. Detailed description on the structure and connections of the dart sac apparatus and associated mucous glands in the terminal genitalia in each species is provided. A total of 27 species, including three new taxa, are described from the region. From the total number of species, the anatomy of seven species is described for the first time. Six unambiguous synapomorphies support the monophyly of the genus: body whorl surface malleated with diagonal ribs (character 1 [2]), umbilicus overlapping but not fused to body whorl (character 2 [1]), peristome thick, widely reflexed (character 4[1]), mucous glands unequal in size and shape (character 15 [1]), insertion of mucous glands ducts in middle portion of dart sac (character 17 [1]), and penial retractor muscle inserting in medial epiphallus (character 23 [1]). Most of the synapomorphies of the generated phylogenetic hypothesis are characters from the genitalia, and shell characters proved to be less informative. The short duct of the bursa copulatrix, a character that traditionally had been used to define the genus is characteristic only of a small group of species. The distribution of the Argentinean species studied is illustrated on maps according to the biogeographic areas. An area cladogram based on the cladistic analysis is presented. According to this hypothesis, the species inhabitants of the Yungas biogeographic province are basal groups of the remaining species inhabitants of the Chacoan, Monte, and Pre-Puna regions. The Monte and Pre-Puna species conform a monophyletic clade. The biogeographic relationships are in agreement to former studies on Latin-American entomofauna (Morrone, 2006).

Key words: Helicoidea, Xanthonychidae, *Epiphragmophora*, South America, cladistics, taxonomy, dart sac complex, biogeography.

INTRODUCTION

The genus *Epiphragmophora* Doering, 1874, is a component of the land snail family Xanthonychidae and inhabits exclusively in South America. *Epiphragmophora* is distributed in Perú, Bolivia, Paraguay and Argentina. There are also isolated occurrences in southern Colombia (type locality of *E. pilsbry* Haas, 1934) and southern Brazil (*E. bernardius* Pilsbry & Ihering, 1900). This genus is known to be a typical component of the Andean fauna, although in Argentina and Bolivia it inhabits elevated cloud rainforest areas (Yungas biogeographic subregion) and also flatlands areas of Chacoan biogeographic subregion (Morrone, 2002, 2006).

The species included in *Epiphragmophora* Doering have been catalogued by Richardson (1982) and grouped into five subgenera

(*Epiphragmophora* Doering, 1874; *Angrandiella* Ancey, 1886; *Doeringiana* Ihering, 1929; *Karlchmidtia* Haas, 1955; and *Pilsbrya* Ancey, 1887) (Thiele, 1929–1935; Zilch, 1959–1960). The monophyly of these subgenera is not yet established or even discussed. Most of the species were located by Zilch (1959–1960) in the subgenus *Epiphragmophora s. s.,* whereas the rest of the subgenera are formed by one or two species. Most of the species of the genus are known from their shell morphology, with their anatomies unknown. The anatomical information is only available for certain species classified within the subgenera *E.* (*Epiphragmophora*) and *E.* (*Doeringia*) (Hesse, 1930; Hylton Scott, 1951, 1962, 1965; Parodiz, 1955; Fernández & Rumi, 1984b; Cuezzo, 1996, 1997, 1998).

The high conchological variability found within some of the species of *Epiphragmophora* and the convergence of certain shell characters, obscure their value for the diagnosis of the genus. Previous diagnoses of the *Epiphragmophora* (Fernández & Rumi, 1984b; Schileyko, 1979; Nordsieck, 1987) are not supported by a strict character evaluation and a system of autapomorphic characters. Only one apomorphy, the presence of a penial muscular band, was identified supporting the monophyly of *Epiphragmophora* in a cladistic analysis of Xanthonychidae (Cuezzo, 1998). In the published literature, the structure of the dart apparatus, as well as the connections between mucous glands and dart sac in the different species of the genus, are not clearly described and illustrated. Due to the lack of basic anatomical knowledge, the evolution of the dart sac complex, a relevant structure for the systematics of most Helicoidean families, can hardly be reconstructed unequivocally in *Epiphragmophora*.

The objective of this study is to provide information on the anatomy of species of *Epiphragmophora* inhabiting Argentina and part of Bolivia, many for the first time, and to review their taxonomic status. Finally, to provide a cladistic hypothesis of relationship among the species reviewed those are inhabitants of two South American biogeographic units, the Yungas province (Amazonian subregion) and the Chaco province (Chacoan subregion).

Extensive field work to collect live specimens in Peru, belonging to other biogeographic provinces, will have to be done before the approximately 20 remaining nominal species of the genus, known only by their shell descriptions, can be appropriately reviewed.

Previous Classifications and Delimitations of the Genus

Doering (1874) created *Epiphragmophora* as a group within the genus *Helix*, family Heliacea. He originally described two species within *Epiphragmophora*: *E. hieronymi* Doering and *E. cuyana* Strobel. Other species now classified within *Epiphragmophora* were originally included by Doering within the groups *Aglaja* Albers and *Eurycampta* Martens.

Pilsbry (1894) included *Epiphragmophora* in the Helicidae, tribe Belogona Euadenia, characterized by having mucous glands of typically glandular structure, in contrast to the tube-like glands of the Belogona Siphonadenia. The characters described for *Epiphragmophora* by Pilsbry were the typical for the whole family because he adopted the name *Epiphragmophora* for all the American dart-bearing helices, except *Lysinoe* (= Helmintoglyptidae). The distribution of the genus, according to him, ranged then from British Columbia, Canada, to Argentina, mainly confined to the Pacific drainage, but spreading to the Gulf slope in Central America. Pilsbry also divided the genus in South American, Central and North American forms. The South American forms included three Sections, *Epiphragmophora, Pilsbrya*, and *Angrandiella*. Later, in 1939, Pilsbry recognized the error of considering the Argentine and North American helices as congeneric and then assembled all the American dart-bearing helices in the family Helminthoglyptidae. He recognized 14 genera in eight subfamilies. *Epiphragmophora* was restricted to the South American Epiphragmophorinae and considered being an “aberrant genus by its very short spermathecal duct” (Pilsbry, 1939).

Thiele (1929–1935) classified *Epiphragmophora* in the family Fruticicolidae, subfamily Epiphragmophorinae. He maintained within this genus all the American groups, dividing it into two subgenera: *Micrarionta* and *Epiphragmophora s.s.* The diagnostic characters of *Epiphragmophora s.s.* were: “shell fairly low-spire; body whorl rounded or angulated; calcified operculum (epiphragm); dart sack long, weakly curved, two edged in the center, mucous glands unequal in size, sack-shaped, short stalked; aperture non denticulate (type species: *E.* (*E.*) *hieronymi* Doering)”. According to Thiele, *E.* (*Pilsbrya*) Ancey, 1887 (type species: *E. farrisi* (Pfeiffer), and *E.* (*Doeringia*) Ihering (type species: *E. trenquelleonis*

(Grateloup), were hardly separable, but he did not provide any diagnostic character of those two sections. The section *E.* (*Angrandiella*) Ancey (type species: *E.* (*A.*) *angrandi* (Morelet)) has an aperture with an unfolding below, which projects an inward tooth-like structure.

Zilch (1959–1960) adopted Pilsbry's criteria and classified *Epiphragmophora* in Helminthoglyptidae. Fernández & Rumi (1984b) reviewed the systematics of the Argentine species classifying the genus within the family Helminthoglyptidae.

Schileyko (1991) gave Epiphragmophorinae family rank defining *Epiphragmophora* with the following character combination: "There is no accessory sac. There are two mucous glands, sac-like; one of them opens directly into the stylophore or its base, another into the vagina. There is no diverticle of the spermatheca. The duct of the spermatheca is cylindrical or with a swelled base". He included in that family only the genus *Epiphragmophora* Doering with the subgenera previously established by Zilch (1959–1960).

Nordsieck (1987) maintained the subfamily Epiphragmophorinae Hoffman 1928, into Xanthonychidae, stating that its reproductive system resembles that of the Cepoliinae: diverticulum usually missing, one dart sac, dart glands unequal, one elongate and the other compact, inserting on the dart sac or on its base. Cuezzo (1998) confirmed the close phylogenetic relationships between Cepoliinae and *Epiphragmophora* through a cladistic analysis of the Xanthonychidae, in which both taxa are sister groups, whereas *Helminthoglypta* was sister group of the previously mentioned clade.

In the present study, I follow Nordsieck's (1987) suprageneric classification.

MATERIALS AND METHODS

The species examined in the present study were classified by Zilch (1959–1960) into the subgenera *E.* (*Epiphragmophora*) and *E.* (*Doeringia*). The material on which this study is based is deposited in the following institutional collections: IBNP = Inventario Biológico Nacional del Paraguay, Asunción, Paraguay; FML = Fundación Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina; FMNH = Field Museum of Natural History, Chicago, USA; MACN = Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MLP = Museo de Ciencias Naturales de La Plata, Buenos Aires, Argentina; NKC = Museo de Historia Natural "Noel Kempff Mercado", Santa Cruz de la Sierra, Bolivia; BMNH = The Natural History Museum, London, England; MNHN = National Museum of Natural History, Paris, France; SMF = Senckenberg Museum, Frankfurt am Main, Germany.

All dimensional parameters (shell diameter; shell height, etc.) were measured using calipers. The counting of the shell whorls follows Kerney & Cameron (1979). The terms proximal and distal refer to the position in relation to the gonad. Abbreviations used in the text: D ap: apertural shell diameter; D maj: major shell diameter; Dept.: state department; det: taxonomically identified by; D min: minimum diameter; H: shell height; H ap: shell aperture height; leg.: collected by; leg. & det.: collected and identified by; Prov.: Province. Both maximal and minimum size in each kind of measurement is reported followed by the median ($\tilde{x}$) within parenthesis. In each species treated, the terminal genitalia has been drawn in a dorsal and a ventral view to see the connections and insertion points of the mucous gland ducts and their relationship to the dart sac. Type locality is given as published by the author. In the list of material used following each species description, a collection number followed by an "*", means that specimens from the species type locality have been dissected for anatomical examination. In order to avoid repetition, species descriptions are based on characters of shell, external features of the animal, jaw, terminal genitalia, plus data on the distribution and habitat preferences. Only when any particular difference was noticed in other anatomical systems (e.g., pallial complex), or when the anatomy of the species is described for the first time, a complete description of the organ or system is added. When viewing the genitalia in dorsal view after dissecting it without changing its natural position in the animal, the penial complex is located to the right of the vagina and spermoviduct; in ventral view, it will be located to the left. When referring in the text to the right mucous gland, this will always be the gland located to the right when the genitalia is viewed dorsally in natural position. General scheme for the description of genitalia follows Cuezzo (1997). Divisions into biogeographic regions for South America used in this study follows Morrone (2002, 2006).

Cladistic Analysis

The ingroup taxa used in the analysis correspond to the species of *Epiphragmophora* taxonomically reviewed in the present study. The rest of the species were not included because alcohol-preserved material was not available; in this way, about 60% of the species described for the genus (Richardson, 1982) are represented in the present analysis. Two species, *Bradybaena similaris* (Férussac), representing the family Bradybaenidae, and *Helminthoglypta tudiculata* (Binney), the type species of one of the closest genera of *Epiphragmophora*, were selected as outgroups based on previous hypotheses of relationships (Cuezzo, 1998; Wu, 2004). Cepoliinae was not included in the analysis because of the existing problems on the determination of the homology of genitalic characters and the scarce information on the anatomy of most of these genera. A complete list of characters and character states is as follows:

1 Body whorl surface: (0) with thin growth lines; (1) with thick growth ridges; (2) malleated with diagonal ribs; (3) with axial ribs regularly distributed; (4) with pustules to wrinkles.
2 Umbilicus: (0) fused; (1) with basal lip of peristome overlapped but not fused to body whorl; (2) perforate, perspective wide not overlapped by peristomal lip; (3) perforate, perspective narrow, slightly overlapped.
3 Shape of the aperture: (0) subcircular; (1) oval-horizontal; (2) subquadrangular; (3) oval-vertical.
4 Peristome: (0) thin, expanded slightly reflexed; (1) thick, wide strongly reflexed; (2) thin, highly expanded.
5 Spire: (0) high, conic; (1) shallow; conic; (2) strongly depressed.
6 Basal callus in basal peristome: (0) absent; (1) present.
7 Number of peripheral bands: (0) absent; (1) one, well-defined; (2) two or three even, continuous; (3) more than three, usually thick and interrupted.
8 Body whorl periphery: (0) convex; (1) equatorially subcarinated; (2) supra-equatorially subcarinate.
9 Aperture respect to body whorl: (0) not descending; (1) descending.
10* Diameter: (0) less than 20 mm; (1) between 21 and 29 mm; (2) more than 30 mm.
11 Number of mucous glands: (0) multiple; (1) two.
12 Shape of dart sac: (0) long, finger-like usually with constriction; (1) short cylindrical no constriction; (2) roundish.
13 Dart sac insertion: (0) in vagina; (1) in atrium; (2) in atrial sac.
14 Dart sac papillae: (0) absent; (1) present.
15 Mucous glands: (0) equal in shape or size; (1) unequal in shape or size;
16 Relation between ducts of both mucous glands: (0) separated; (1) distally fused or contiguous.
17 Point of insertion of mucous glands ducts: (0) in distal portion of dart sac; (1) in middle portion of dart sac.
18 Position of left mucous gland duct: (0) distal respect to the body of the gland; (1) ecuatorial respect to the body of the gland.
19 Presence of a sac-like mucous glands in terminal genitalia: (0) absent; (1) present.
20 Right mucous gland: (0) not fused with atrium wall; (1) distally fused with atrium wall.
21* Penis length respect to epiphallus (0) half epiphallus length; (1) as long as epiphallus; (1) longer than epiphallus length.
22 Penial papillae (= verge): (0) absent; (1) present.
23* Penial retractor muscle: (0) inserts in distal epiphallus; (1) inserts in medial zone of epiphallus; (2) inserts in proximal epiphallus.
24* Duct of bursa copulatrix: (0) extremely short, not longer than sac; (2) medium; (3) long.
25 Bursa copulatrix's diverticulum: (0) absent; (1) present.
26* Length of vagina: (0) short; (1) medium to long; (2) extremely long.
27 Atrium: (0) short, not expanded; (1) medium to long, not expanded; (2) long, prolonged into an atrial sac.
28 Flagellum: (0) absent; (1) triangular, thick, curved, short; (2) finger-like short to medium; (3) thin, long.
29 Penial muscular band: (0) absent; (1) present.
30 Penial sheath (= penial-tucica): (0) simple; (1) double or multilayer.
31 Habitat: (0) in association to rocks; (1) in association with tree logs.
32 Vas deferens: (0) passing by the constriction of dart sac; (1) not.
33 Epiphallus proximal portion: (0) Not widen at point of entrance of vas deferens; (1)

widen at point of entrance of vas deferens.
34 Penial retractor: (0) not forming a loop around vas deferens before inserting in epiphallus; (1) forming a loop.
35 Secondary ureter: (0) open; (1) closed.

A total of 35 morphological and ecological characters from shell morphology (10), genital system (23), pallial system (1), and one corresponding to habitat preferences were selected from the 29 species examined. These selected characters for the taxa examined were coded in a matrix (Appendix). From the total number of characters, 18 were coded as multistate (characters 10, 21, 23, 24 and 26 are additive) and the remaining 17 as binary. The symbol "?", in the matrix means "character state unknown". For the cladistic analysis of the character matrix, the computer program PeeWee 2.9 (Goloboff, 1993) was used. PeeWee is a program for parsimony analysis under implied weights. The weighting method implemented in PeeWee is explained in detail by Goloboff (1993, 1995). The ingroup taxa were rooted in Bradybaenidae, representing the closest Helicoidean family of the Xanthonychidae (Cuezzo, 1998; Wu, 2004). Alternatively, *Helminthoglypta tudiculata* was also used to root the ingroup. With PeeWee parsimony program the characters are weighted in inverse relation to the amount of homoplasy (extra steps) they show on each examined tree. Trees with highest total fit or "optimal trees", are retained in the search. The command "mult*100", was used through which the order of the taxa were randomized, a Wagner tree was created and submitted to branch-swapping (TBR), and 1,000 trees each time were stored in memory. This process was repeated one hundred times. Bremer support, which evaluates the support for clades, was calculated with the command "bs", implemented in PeeWee (Command sequence: "suboptimal 300; hold 1000; max*; bsupport"). To facilitate character evaluation and tree illustration, the computer program WinClada 1.00.08 (Nixon, 2002) was used. Two different searches were done with the created matrix. In the first, all species included in the matrix were treated and analyzed as terminals. In a second step, species known only by shell characters were eliminated from the matrix and a new search for optimal trees was conducted. Species known only by shell characters are indicated with underlined letters in the matrix (Appendix).

RESULTS

Epiphragmophora Doering 1874

Helix group *Epiphragmophora* Doering, 1874
Helix group *Aglaja* Albers [partim] – Doering, 1874: 445.
Helix group *Eurycampta* Martens [partim] – Doering, 1874: 448.
Epiphragmophora – Pilsbry, 1894: 193; Parodiz, 1957: 29; Zilch, 1959–1960: 655; Fernández, 1973: 157; Fernández & Rumi, 1984b: 231.

Type Species: Epiphragmophora hieronymi Doering, 1874, by original designation.

Diagnosis: Shell with one to three dark distinctly peripheral bands around body whorl; protoconch smooth; aperture with medium to thick calcareous epiphragm; aperture without tooth in most species, only one species known to have a single basal tooth; terminal genitalia with dart sac complex (= stimulatory complex) having a single dart sac and two unequal mucous glands, some species with one sac-like mucous gland enveloping basal vagina and dart sac complex, in others both mucous glands cylindrical, oval to club-shaped; efferent ducts of mucous glands fused or separated, inserting in medial zone of dart sac; single dart sac cylindrical, usually with median constriction bellow with mucous glands insert; dart sac inserting in vagina before joining with penial complex or in atrium level with vagina and penial complex; single internal, long dart gland usually present in distal dart sac; bursa copulatrix without diverticulum, duct with variable lengths; penial papilla (= verge) generally short present in some species; penial muscular band present in some species; epiphallus generally shorter than penis, externally not well differentiated from it; penial retractor muscle inserting in middle zone of epiphallus; penial sheath usually present, sometimes double or multiple layered.

Distribution: The distribution of *Epiphragmophora* in Argentina ranges from northern Jujuy to central Cordoba and San Luis provinces. The western part of the country is the species richest area. The genus inhabits a variety of ecoregions from rainforest of the Yungas to the xerophilic environments of Monte, Pre-Puna and Chacoan regions. Ver-

tical distribution ranges from lowlands (200–400 m above sea level) to highlands of about 3,500 m above sea level. In Bolivia, *Epiphragmophora* is distributed from the Cordillera Oriental and Sierra Subandina in the western part of the country to the Serranias Chiquitanas in southeastern Bolivia. They inhabit very different environments, from Yungas (Tucumano-Boliviano forests) to xerophilic ecoregions such as Chaco and Chaco Serrano (Ibisch et al., 2003).

Remarks: According to previous phylogenetic hypothesis (Nordsieck, 1987; Cuezzo, 1998), *Epiphragmophora* is most closely related to Cepoliinae and *Helminthoglypta*. Zilch (1959–1960) arranged the genus into five subgenera, but their status as natural monophyletic groups has not been tested. Further comparative anatomical information among the different species is needed before the acceptance of the classification into subgenera.

Epiphragmophora argentina (Holmberg, 1909) (Figs. 1A, 8A, B, 20)

Helix argentina Holmberg, 1909b: 91.
Epiphragmophora tucumanensis (Doering) – Hesse, 1930: 137.
Epiphragmophora argentina – Parodiz, 1957: 30.
Epiphragmophora argentina – Fernández & Rumi, 1984b: 236.

Neotype: MACN 9913, Argentina, Tucumán, Cadillal, M. Doello Jurado, 22/III/1919.

Material Examined:
Neotype: MACN 9913, Argentina, Tucumán, Cadillal, M. Doello Jurado, 22/III/1919
Dissected Material: Argentina, Tucumán Prov.: FML 14415 A, Tafí Viejo Dept., Raco, 1/VII/1996, between *Bromelia* leaves, E. Dominguez leg. *FML 14406, Tafí Viejo Dept., El Cadillal, on road to Aguas Chiquitas, 26°36'48"S, 65°11'11"W, 560 m, 13/VIII/1990, M. G. Cuezzo leg. & det. FML 114 A, Yerba Buena Dept., San Javier, II/1990, M. G. Cuezzo leg. FML 14408 A, Burruyacu Dept., Rio Nio, 1/XII/1996, M. G. Cuezzo leg. & det. FML 14411 A, Tafi Viejo Dept., El Cadillal, Aguas Chiquitas, 7/III/1990, M. G. Cuezzo leg. FML 14412 A, Yerba Buena Dept., in a garden of "Las Lomitas", close to Horco Molle, 8/V/1995, Molineri, C. leg. FML 14409 A, Trancas Dept., Tapia, road branching from route 341 at km 13, between Raco and route 9, 6/IV/2003, M. G. Cuezzo leg. & det. FML 14416 A, Yerba Buena Dept., San Javier, University of Tucumán Ville, 9/III/2001, M. G. Cuezzo leg. FML 14417, Tafi Viejo Dept., San Javier, 7 km N from street 3, 1/I/1999, M. G. Cuezzo leg. & det.
Dry Material: Argentina, Tucumán Prov.: MACN 9913-1, Tapia Dept. FML 543, Yerba Buena Dept., San Javier, 600–650 m, 3/III/1962, W. Weyrauch leg. & det. FML 753, Yerba Buena Dept., San Javier mountains close to Tucumán city, 600–650 m, 1967, W. Weyrauch leg. & det. FML 75, El Saladillo, 8/IV/1947, Parodiz, J. det. FML 11049, Quebrada de La Hoyada, 1/IX/1936, Dionisio Ollea leg., W. Weyrauch det. FML 14284, Aconquija, W of city of Tucumán, 650–700 m, 1/VI/1970, leg. & det. by W. Weyrauch. FML 1392, Yerba Buena Dept., Horco Molle, 700 m, 4/II/1968, leg. & det. by W. Weyrauch. FML 765, Burruyacú Dept., Rio Nio, 900 m, 25/V/1967, leg. & det. by W. Weyrauch. FML 747, Trancas Dept., near Tapia, on road from Tucumán to Tapia, 700 m, 18/VI/1967, leg. & det. by W. Weyrauch. FML 14276, J. B. Alberdi Dept., Escaba, 1/VII/1998, F. Drahg leg. FML 14402, Trancas Dept., Ticucho, 15 km from El Cadillal and 19 km from route 9, 1/XII/1998, M. Maya leg. FML 14400, Tafi Viejo Dept., El Cadillal, Aguas Chiquitas, 30/VIII/1986, M. G. Cuezzo leg. FML 62, Tafí Viejo Dept., El Duraznito, 6/V/1947, W. Weyrauch det. FML 11052, Tafi Viejo Dept., San Javier, La Cascada, 1,400 m, 6/I/1964, Meyer, T. leg., Weyrauch det. FML 1449, Tafí Viejo Dept., El Cadillal, 600 m, 17/VIII/1968. leg. & det. W. Weyrauch. Argentina, Salta Prov.: FML 85, El Morenello, Rosario de La Frontera, 1/X/1936, R. Schreiter leg.

Description:
External Features: Animal light brown to pale yellow; homogeneous color over cephalopedal region; two lines of pustules separated by groove running dorsally from mantle collar to cephalic region ending between ommatophores; dorsal groove in pedal region well marked.
Shell (Fig. 1A): Dextral, helicoidal, globose, solid, elevated conical spire; small to medium size, 4½ to 5 convex whorls; color variable from light yellow to dark brown; single thick equatorial, dark brown even band in body whorl periphery; protoconch smooth; teleoconch with growth lines in spire and

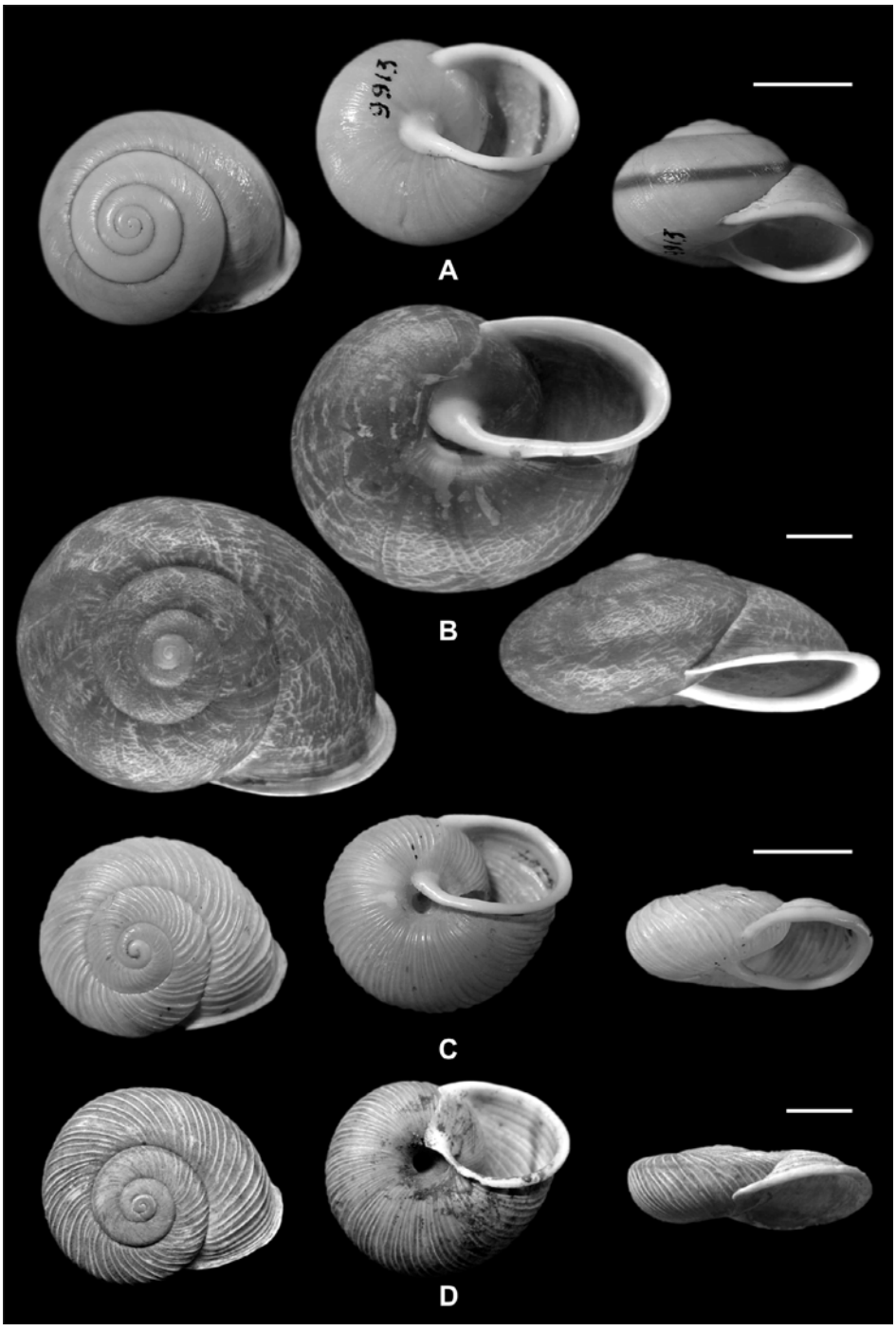

FIG. 1. Shells in dorsal, ventral and lateral view. A: *Epiphragmophora argentina* (MACN 913, neotype). Scale bar = 15 mm; B: *Epiphragmophora audouini* (MNHN, syntype). Scale bar = 10 mm; C: *Epiphragmophora birabeni* (MACN 23034, holotype). Scale bar = 15 mm; D: *Epiphragmophora costellata* (MLP 4291, holotype). Scale bar = 10 mm.

surface strongly malleated in body whorl; suture deep impressed; aperture subcircular; peristome whitish, thick, reflexed; body whorl distinctly descending towards aperture; generally imperforated, some specimens with umbilicus totally overlapped by basal lip but not fused with parietal wall.

Measurements: Neotype: D maj: 27.6 mm; D min: 23 mm; H: 18.4 mm.

Other Material (n = 20): D maj: 31.4–24.1 mm (28.5 mm); D min: 27.5–21.6 mm (24.4 mm); H: 19.5–15.3 mm (17.4 mm); D ap: 21.0–16.1 mm (18.5 mm); H ap: 17.0–13.8 mm (14.8 mm).

Jaw: Corneous, thin, orange-translucent; three vertical wide ribs on central jaw with two other wider plaques on each side of central ones; vertical plaques projecting at both jaw edges.

Pallial Complex: Kidney triangular not exceeding half pulmonary roof length; main pulmonary vein thick, splitting into two secondary branches before reaching mantle collar; pulmonary roof between main pulmonary vein and rectum furrowed by minor veins; some specimens with lung mottled with dark spots.

Genitalia (Fig. 8A, B): Terminal genitalia with dart sac complex having two mucous glands symmetrically located in either side of dart sac, both elongated to cylindrical in shape, with thin ducts inserting independently in middle zone of dart sac; duct of right mucous gland (dorsal view) distally located with respect to body of gland, while duct of left mucous gland equatorial with respect to body of gland; dart sac muscular, cylindrical, even in diameter, inserting in medial portion of vagina; internal wall of dart sac with uniform longitudinal bands, dart papillae thick and short in distal dart sac; bursa copulatrix elongate-oval, extending towards middle zone of spermoviduct; duct of bursa copulatrix long, convoluted, running parallel to distal portion of spermoviduct; penial complex with long, thin, convoluted flagellum, transition between epiphallus and penis not evident externally but internally through different wall sculpture; proximal portion of epiphallus thickening at point of insertion of vas deferens; internally wall sculpture of epiphallus consisting of straight longitudinal bands; epiphallus thin, slender, as long as penis; wall sculpture of proximal penis with thin zigzag longitudinal bands, distal penis with closer columns in a zigzag pattern; penial papillae absent; penial sheath simple, muscular, enveloping penis in its complete length, distally fused with atrium; penial muscular band long, located under penis sheath; penial retractor muscle thick, inserting in middle portion of epiphallus; penis and vagina entering side by side in atrium, distally to dart sac complex; atrium long.

Habitat: *Epiphragmophora argentina* is found under or inside tree trunks on the ground in both xerophilic and humid forests. Rarely found adhering to rocks.

Distribution (Fig. 20): *Epiphragmophora argentina* is distributed mainly in Tucumán Province, northwestern Argentina, where is very abundant. There are some other scarce records in Catamarca and Salta provinces. This species is found in subtropical rainforest (Yungas biogeographic province), xerophilic forests and also in the Chacoan biogeographic subregion (Morrone, 2006).

Remarks: *Epiphragmophora argentina* has often been confused with *E. tucumanensis* (Doering) probably because they are partly simpatric in their distribution. Hesse (1930) published an anatomical study on *E. tucumanensis* based on an erroneously identified material of *E. argentina.* The holotype of Holmberg from the locality of Tapia in Tucumán was lost, and J. J. Parodiz selected a neotype for *E. argentina* from El Cadillal, Tucumán (MACN 9913). This species is one of the most abundant of the genus and is easily collected during rainy days. *Epiphragmophora argentina* differs from *E. tucumanensis* in having a sealed shell umbilicus or narrower open one. *Epiphragmophora tucumanensis* is usually bigger in shell diameter than *E. argentina,* with darker shells and less globose body whorl. *Epiphragmophora argentina* has both the flagellum and epiphallus, thinner and longer than in *E. tucumanensis.* The epiphallus in *E. argentina* is as long as the penis, while in *E. tucumanensis* it is half the penis length. They also differ in the structure of the penial sheath, which is simple and thin in *E. argentina* and it is double and muscular in *E. tucumanensis.*

The original description of the present species indicates that the shell umbilicus is sealed to the wall of the body whorl; however, in the type locality of *E. argentina*, several specimens with umbilicus not fused but overlapped by peristomal lip were collected. Later examination of the anatomy confirmed those specimens as *E. argentina.*

The original locality of the type designated by Holmberg (1909b) was in Tapia, Tucumán, a region with xerophilic vegetation and dry substratum of the Chacoan biogeographical subregion. The locality of the neotype designated by Parodiz (1957) is from El Cadillal, Tucumán, a locality with subtropical rainforest in the Yungas biogeographical province. Yungas regions are typical areas inhabit by *E. argentina*, but some Chacoan localities of occurrence are also registered for this species.

Epiphragmophora audouini (d'Orbigny, 1835) (Fig. 1B)

Helix (*Lysinoe*) *audouini* d'Orbigny, 1835: 239, pl. 24, figs. 4–6.

Material Examined:
Syntypes: MNHN, Bolivia, Yungas. BMNH, Bolivia, Yungas, Carcuata.
Type Locality: Bolivia, La Paz Dept., Yungas and Inquisivi Prov., between the villages of Chirca and Chulumani, environments of Circuata, Carcuata and Suri (for a precise locality: Breure, 1973).

Description:
Shell (Fig. 1B): Dextral, helicoidal, globose, solid, subcarinated with conical spire; large size, 4¾ convex whorls, dark brown, no peripheral band evident in the body whorl; protoconch smooth; teleoconch surface malleated with diagonal ribs on body whorl; suture deep impressed; aperture elliptical, peristome white, strongly expanded, with strong callus in parietal wall; body whorl distinctly descending towards the aperture; umbilicus narrow, almost totally overlapped by ventral columelar fold of the peristome.
Measurements: Syntype: D maj: 58.8 mm; D min: 50.6 mm; H: 31.8 mm; D ap: 36.6 mm; H ap: 27.4 mm.

Remarks: Neither live specimens nor empty shells were found by the author in the type locality in Bolivia; one possible reason was that the type locality area has been greatly modified since d'Orbigny visited. Pilsbry (1890) considered that *H. audouini* d'Orbigny has a variety, *H. a. var. oresigena* d'Orbigny. Here *E. oresigena* (d'Orbigny) is considered a species different from *E. audouini* (d'Orbigny) on the base of shell characters of the type material. Materials corresponding to other syntypes of the species deposited at NHM were examined from photographs. *Epiphragmophora audouini* differs from *E. oresigena* in having larger shell diameter (D maj = 58.8 mm; *E. oresigena* D maj = 39.9 mm), shells of *E. audouini* usually don't have a peripheral band, whereas in *E. oresigena* three pigmented peripheral bands are present. The shell aperture in *E. audouini* is elliptical in shape, whereas in *E. oresigena* the shape of the shell aperture is subquadrate. Other marked differences between these two species are in the peristome; in *Epiphragmophora audouini* the peristome is strongly expanded, whereas in *E. oresigena* the peristome is reflected.

Epiphragmophora birabeni Parodiz, 1955 (Fig. 1C)

Epiphragmophora birabeni Parodiz, 1955: 93, fig. 1.
Epiphragmophora birabeni – Parodiz, 1957: 29
Epiphragmophora birabeni – Fernández & Rumi, 1984b: 238.

Material Examined:
Holotype: MACN 23034, Argentina, Catamarca Prov., Quebrada de La Hoyada. R. Schreiter leg., 1936.

Description:
Shell (Fig. 1C): Dextral, helicoidal, globose, translucent, delicate, spire shallowly elevated, medium size, 3½ convex whorls, yellowish to golden; peripheral pigmented band in body whorl absent; protoconch smooth; sculpture of teleoconch with delicate axial whitish ribs regularly distributed, more spaced and thicken in body whorl, thin axial undulated or concentric lines between ribs giving the appearance of fingerprints; suture sinuous, well impressed; aperture transverse oval, peristome white, thick, reflexed; body whorl abruptly descending behind aperture; umbilicus deeply perforated and partially overlapped by columelar fold of peristome.
Measurements: Holotype: D maj: 25.6 mm; D min: 23.2 mm; H: 11.4 mm.

Distribution: This species is only known from the type locality.

Remarks: *Epiphragmophora birabeni* is very similar to *E. saltana* in shell morphology. Dif-

ferences between the two species are: the sculpture of the inter-rib spaces, absence of peripheral pigmented band in *E. birabeni* and shell size. *Epiphragmophora saltana* is bigger in shell diameter than *E. birabeni* and posseses a dark peripheral band in the body whorl. The type locality of *E. birabeni* is La Hoyada in Catamarca, located in higher mountains at more than 3,000 m altitude corresponding to the Pre-Puna biogeographic region. It is an almost desert place with scarce vegetation. It is possible that *E. birabeni* inhabit in narrow rock crevices, although no live specimens were found. Due to this situation *E. birabeni* is still known from a single specimen (the holotype) deposited at Museo Argentino de Ciencias Naturales (MACN).

Epiphragmophora costellata Fernández & Rumi, 1974
(Figs. 1D, 20)

Epiphragmophora costellata Fernández & Rumi, 1984a: 217; 1984b: 238.

Holotype: MLP 4291, Argentina, Salta Prov., "El Rey" National Park. Obregoso & Brown leg.

Other Material Examined:
Dry Material: MLP 4291 Holotype and Paratypes; MLP 4292 Paratypes, Argentina, Salta Prov., "El Rey", National Park. MPL 4310, Argentina, Salta Prov., Cerro EL Chañar, "El Rey", National Park, Brown, A. leg., 1981.

Description:
Shell (Fig. 1D): Dextral, planorboid to discoidal, solid, spire depressed, large, 4¾ whorls, with body whorl supraequatorally slightly angled at periphery; whitish to light brown; thin, supraequatorial pale brown peripheral band evident in last two whorls; protoconch smooth; body whorl with strong axial ribs regularly separated, less marked in upper whorls, spaces between ribs with irregularly arranged granules; suture sinuous, well impressed; aperture subcircular; peristome thin, white, reflexed; body whorl slightly descending behind aperture; umbilicus wide, deeply perforated, partially overlapped by basal lip.
Measurements: Holotype: D maj: 38.0 mm; D min: 30.0 mm; H: 13.3 mm.
Paratypes (n = 7): D maj: 35.0–40.0 mm (37.5 mm); D min: 30.6–34.6 mm (32.2 mm); H: 14.3–16.8 mm (15.7 mm).

Habitat: Between and below rocks in grassland (= pastizal) on top of mountains, this environment is classified as belonging to the Yungas biogeographic province, Amazonian subregion of the Neotropical region (Morrone, 2006).

Distribution (Fig. 20): *Epiphragmophora costellata* is only known from the type locality in Cerro Maldonado and in Cerro "El Chañar", both localities from the Argentinean National Park "El Rey", Salta Province.

Remarks: *Epiphragmophora costellata* is similar to *E. birabeni* and *E. saltana* in the presence of regular axial ribs on the shell. Major differences among the three mentioned species are found in shell microsculpture among the ribs, in the spire, in general shell shape and size.

Epiphragmophora cryptomphala Ancey, 1897
(Figs. 2A, 8C, D)

Epiphragmophora cryptomphala Ancey, 1897: 10.
Epiphragmophora trigrammephora cryptomphala – Parodiz, 1957: 31.
Epiphragmophora cryptomphala – Fernández & Rumi, 1984b: 239.

Material Examined:
Dissected Material: FML 14760 A, Argentina, Salta Prov., Ledesma Dept., on road to Valle Grande, 30/I/1990, E. Dominguez leg.
Dry Material: Argentina, Salta Prov.: FML 14382 (ex 195523), La Quena, Bermejo river, 6 km S of Embarcación, 270 m, 22/IX/1968, leg. & det. by W. Weyrauch. FML, Salta, 3/I/1990. E. Dominguez, leg. FML 852, Oran Dept., 6 km S of Embarcación, close to Bermejo river, 270 m 27/II/1964, leg. & det. by W. Weyrauch. FML 323, Oran Dept., VIII/1944, leg. A. Castellanos. MLP 4299, Orán. MLP 1667, Embarcación, Hylton Scott-Biraben leg., 27/II/1945. MLP unnumbered, Manuel Elordi, Birabén, M. leg. 22/V/1947, ex collection Hylton Scott. Argentina, Jujuy Prov.: MLP 4284, Viñalito.
Argentina, Formosa Prov.: MLP unnumbered, Santa Victoria, Prosen, A. X/1948, ex col. Hylton Scott.

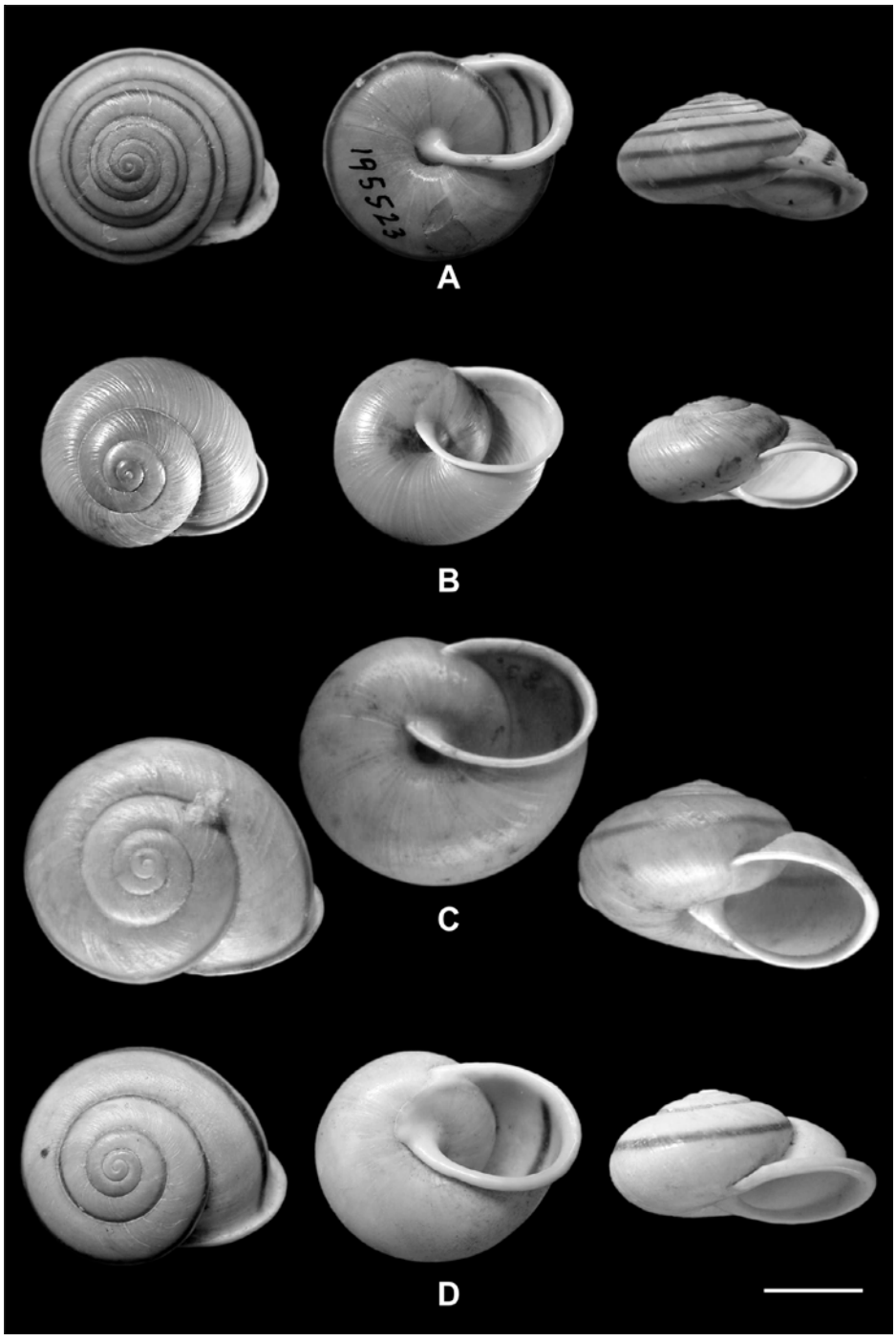

FIG. 2. Shells in dorsal, ventral and lateral view. A: *Epiphragmophora cryptomphala* (FML 14382); B: *Epiphragmophora escoipensis* (FML 14090, holotype); C: *Epiphragmophora estella* (MNHN, syntype); D: *Epiphragmophora hemiclausa* (MLP, holotype). Scale bar = 15 mm.

Description:

External Features: Body color homogeneous light gray to pale brown.

Shell (Fig. 2A): Dextral, helicoidal, subglobose, semisolid to solid, with conical spire, usually high; medium size, 4½ convex whorls; whitish, pale cream to yellowish; three peripheral thin, darker brown bands clearly visible on spire and body whorl, usually ventral band wider than others; protoconch smooth, first whorls with thin growth lines; teleoconch surface malleated with diagonal ribs on body whorl; suture deep impressed; aperture subquadrangular or subovoidal, peristome white, wide, expanded, slightly reflexed; body whorl abruptly descending towards aperture; umbilicus completely overlapped by ventral columelar fold of peristome; in some specimens peristome partially fused with umbilicus.

Measurements: Specimens from Salta (n = 15): D maj: 28.6–22.9 mm (25.9 mm); D min: 25.3–20.9 mm (23.3 mm); H: 15.3–11.9 mm (13.8 mm); D ap: 18.0–13.8 mm (16.10 mm); H ap: 13.6–10.9 mm (12.5 mm).

Jaw: Thin, translucent; three shallow central plaques with only concave border of central vertical plaque exceeding border of jaw.

Genitalia (Fig. 8C, D): Terminal genitalia with single dart sac and two mucous glands, left one cylindrical with thick duct ending at dart sac, right mucous gland sac-like, distally fused with upper portion of atrium, with thin duct ending in dart sac; both mucous gland ducts inserting independently below dart sac medial constriction; dart sac muscular, with thick walls, long, cylindrical with medial constriction, dart sac naturally folded by itself at level of constriction; dart papillae as long as distal portion of dart sac; dart sac ending at atrium level with vagina and penial complex; bursa copulatrix sac round with short to medium length duct; sac and duct of bursa copulatrix neatly delimited; vagina short; free oviduct short, enveloped by connective tissue together with bursa copulatrix; vas deferens surrounding dart sac at level of constriction before reaching peni-oviducal angle and inserting in penial complex; penial complex medium to short; flagellum thin, finger-like, ending level where vas deferens enters penial complex and epiphallus begin; proximal portion of epiphallus widening at point of entrance of vas deferens; epiphallus longer than penis externally differentiated from it; penial retractor muscle inserting in median portion of epiphallus; penis cylindrical, half-length of epiphallus, entering genital atrium level with dart sac and vagina; penial papillae short, triangular; internal wall of penis with three longitudinal pilasters; penial muscular band absent; thin, muscular sheath overlapping distal portion of penis; atrium long.

Distribution: *Epiphragmophora cryptomphala* is distributed in Chacoan biogeographic subregion in Salta and Jujuy provinces.

Remarks: *Epiphragmophora cryptomphala* is very similar in shell morphology to *E. trigrammephora*, their distributional ranges overlapping. Mostly based on shell morphologies, Parodiz (1957) and Fernández (1973) considered *E. cryptomphala* to be a subspecies of *E. trigrammephora.* However, the main differences between *E. cryptomphala* and *E. trigrammephora* are found in both the shell and genitalia. In *E. cryptomphala*, the shell umbilicus is completely overlapped or fused with the columelar side of the peristome. The shape of the aperture is not as constant as in *E. trigrammephora*, being subquadrangular to subovoidal, while in *E. trigrammephora*, all shells examined have a subquadrangular aperture. Terminal genitalia of both species are significantly different, main differences are: shape of mucous glands, length of penis and flagellum, length and thickness of bursa copulatrix duct, length of dart sac and proportion of epiphallus respect to penis. *Epiphragmophora cryptomphala* is similar to ***E. walshi*** n. sp. in that both have three peripheral bands in the shell. Also, both species live in Salta Province and are typical from xerophilic environments. *Epiphragmophora cryptomphala* differs from ***E. walshi*** n. sp. in the umbilicus that is narrower in ***E. walshi*** n. sp. and not overlapped by peristomal basal fold. ***Epiphragmophora walshi*** n. sp. is smaller in shell diameter than *E. cryptomphala.* Differences in the genitalia are mainly in the shape of mucous glands, insertion of their efferent ducts and shape and length of dart sac.

Epiphragmophora escoipensis Cuezzo, 1996
(Figs. 2B, 9A–C, 19)

Epiphragmophora escoipensis Cuezzo, 1996: 361; figs.1, 2.

Holotype: FML 14090, Argentina, Salta Prov., Chicoana Dept., Quebrada de Escoipe, 25°10'46"S, 65°45'01"W, 1,950 m, II/1993, E. Dominguez leg.

Other Material Examined:

Dissected Material: Argentina, Salta Prov.: FML 14426 A, Chicoana Dept., Quebrada de Escoipe, route 33, 25°09'26"S, 65°41'24"W, 1,650 m, 90 km from Salta city. I/1998, leg. & det. by M. G. Cuezzo. "*" FML 14091 A, PARATYPES. Chicoana Dept., Quebrada de Escoipe, 25°10'46"S, 65°45'01"W, 1,950 m, II/1993. E. Dominguez leg.

Dry Material: Argentina, Salta Prov.: FML 14427, Chicoana Dept., Quebrada de Escoipe, 1,520 m, 19/XII/2001, 25°10'03"S, 65°37'54"W, M. G. Cuezzo leg. & det.

Description:

External Features: Homogeneous light brown to yellowish body color, even color in cephalopedal region; double row of pustules in cephalic region from mantle collar to ommatophores.

Shell (Fig. 2B): Dextral, helicoidal, fragile, translucent, globose, shallow spire, small to median, 4¼ convex whorls; pale yellowish to golden; with one very thin peripheral supraequatorial band when present; holotype without peripheral band; shiny periostracum; protoconch smooth; body whorl with thin axial growth lines; suture deep impressed; aperture subovoidal; peristome whitish, thin, slightly reflexed; body whorl slightly descending towards aperture; umbilicus narrow partly overlapped by ventral columelar fold of the peristome; calcareous epiphragm.

Measurements: Holotype: D maj: 23.8 mm; D min: 21.4 mm; H: 13.8 mm; D ap: 14.1 mm; H ap: 12.5 mm.

Paratypes (n = 10): D maj: 25.2–21.0 mm (22.9 mm); D min: 20.9–18.9 mm (20.2 mm); H: 14.6–11.1 mm (13.5 mm); D. ap: 15.4–12.5 mm (13.7 mm); H ap: 12.8–10.5 mm (11.5 mm).

Jaw: Arcuate, thin, translucent; six central vertical ribs well marked with convex and concave borders projecting over jaw borders.

Pallial Complex (Fig. 9A): Pulmonary roof pale cream; kidney triangular of about 60% of pulmonary roof length; space between kidney and rectum with several thin shallow ramified veins; thick main pulmonary vein splits into two major branches close to mantle collar, with several further minor divisions forming net in distal portion of pulmonary roof.

Genitalia (Fig. 9B, C): Terminal genitalia with dart sac complex consisting of single dart sac and two mucous glands, right one globose sac-like, enveloping distal zone of vagina and dart sac, distally fused with atrial wall, left mucous gland oval ending in thin, short duct that joins with efferent duct of right gland, both inserting in medial zone of dart sac; dart sac long, muscular, cylindrical without medial constriction; dart gland thin, cylindrical located in interior of dart sac distal portion; dart sac ending at atrium level with vagina and penis; bursa copulatrix roundish with thin medial length duct; vagina shorter than penis; free oviduct short; penial complex long; flagellum thin, finger-like, ending level with where vas deferens enters penial complex and epiphallus begins; epiphallus longer, thinner than penis, externally clearly differentiated from penis; epiphallus widening in its proximal portion at point of insertion of vas deferens; penial retractor muscle inserting in medium zone of epiphallus; vas deferens surrounding dart sac; penis proximally thin, progressively widening toward distal portion; penial papillae absent; internal wall of penis with thin smooth, longitudinal folds; penis sheath, simple, muscular overlapping all penis length, distally attaching to atrium wall; atrium short.

Habitat: *Epiphragmophora escoipensis* inhabits xerophilic environments, usually adhering to cactus, under shrubs, inside crevices or below big rocks on the ground.

Distribution (Fig. 19): *Epiphragmophora escoipensis* is only known from Quebrada de Escoipe in Salta Province, northwestern Argentina. This locality is classified into the Yungas biogeographic province, although is a transition forest with some vegetational elements of the Monte biogeographic province.

Remarks: In the original species description, only one mucous gland (the left one) of the terminal genitalia was detected. The specimens used to describe the new taxon probably had the second gland collapsed, as a result of the fixative solution (formaldehyde) used. In the present study, the dissection of several other specimens showed that the two mucous glands are indeed present in *E. escoipensis* genitalia, one of them as a sac enveloping the basal portion of the genitalia.

Epiphragmophora estella (d'Orbigny, 1835) (Fig. 2C)

Helix estella d'Orbigny, 1835: 241.

Syntypes: MNHN, Bolivia, Valle Grande, close to the village of Tasajos. BMNH, Bolivia, Chuquisaca. BMNH, Bolivia, Valle Grande, BMNH, Bolivia, Sicasica.

Other Material Examined:
Dry Material: Bolivia: MNHN, Santa Cruz Dept., Valle Grande. FML, Cochabamba Dept., Punata Prov. Cerro Tuti, 4,000 m, 17/I/1950. R. Zischka leg. W. Weyrauch det. FML, Cochabamba Dept., Cozomi, 3,200 m, 30/XII/1949. R. Zischka leg. W. Weyrauch det. MLP unnumbered, Cochabamba Dept., Aguirre, 3,200 m, ex col. Hylton Scott.

Description:
Shell (Fig. 2C): Dextral, helicoidal, globose, fragile not translucent, with conical spire, medium size, 4¾ convex whorls; pale cream to yellowish; with peripheral equatorial thin, darker brown band; protoconch smooth; teleoconch surface malleated with diagonal ribs on body whorl; suture deep impressed; aperture elliptical to subcircular, peristome whitish, thin, slightly expanded; body whorl distinctly descending towards aperture; umbilicus narrow partly overlapped by ventral columelar fold of peristome.
Measurements: Syntypes (n = 2): D maj: 30.0 mm, 32.2 mm (31.1 mm); D min: 26.8 mm, 27.9 mm (27.3 mm); H: 17.9 mm, 19.9 mm (18.9 mm); D ap: 18.6 mm, 19.8 mm (19.2 mm); H ap: 15.2 mm, 17.2 mm (16.2 mm).

Distribution: The distribution of this species is restricted to the departments of La Paz, Santa Cruz, and Chuquisaca in Bolivia.

Remarks: When d'Orbigny described the present species, he mentioned the existence of three varieties, called by him "A, B and C", from three different localities in Bolivia. Variety "A", was called "reticulata, imperforata", which has the most globose shell, is smaller in diameter (13–24 mm) and was found in the localities of Inquisivi (16°58'S, 67°10'W) and Caranavi (17°13'S, 66°57'W), both from La Paz Dept. Variety "B", called "substriata, perforata, magna", is the largest in shell diameter (20–38 mm) and it was found in Chuquisaca Dept., Bolivia. Variety "C", called "laevignata, perforata, depressa", has the most depressed shell among the three varieties and an open umbilicus, found in the village of Tasajos (18°08'S, 64°15'W) in Valle Grande, Santa Cruz Dept., Bolivia. The major differences between them are shell diameter, shell sculpture and degree of closure of the umbilicus. The shell description provided here corresponds to the "varieté B, substriata, perforata, magna", of d'Orbigny species description, the biggest variety of *E. estella*. Photographs of the syntypes deposited at The Natural History Museum, London, corresponding to Varieties A and C were examined, corresponding also to this species. However, only the availability of anatomical information will clarified the status of d'Orbigny varieties.

Epiphragmophora guevarai Cuezzo, n. sp. (Figs. 7A, 18A–C, 21)

Holotype: FML 14420 A (alcohol-preserved specimen), Argentina, Santiago del Estero, 20 km S from Ojo de Agua, 29°19'32"S, 63°48'52"W, 570 m 30/XII/2002, M. G. Cuezzo leg.
Paratypes: FML 14420 (dry material, type locality); MLP unnumbered (type locality). FML 14766, near Ojo de Agua, km 922 on the highway from Tucumán to Córdoba, 24/XII/1967, leg. W. Weyrauch.

Other Material Examined:
Argentina, Cordoba Prov.: FML 14717, 5 km N from Villa María, 440 m, 25/XII/1967, W. Weyrauch leg. FML 10989, Dean Funes Dept., Cerro de La Cruz, Sierra de Orcosumi, 800 m, J. Durango leg.

Diagnosis: Shell with three thin, continuous peripheral bands, central one distinctly delimited, the others more tenuous; shell surface with thin, delicate axial growth-lines; two unequal mucous glands in terminal genitalia, both basally attached to atrium inserting through separated efferent ducts into distal dart sac; dart sac ending at atrium level with vagina and penial complex; bursa copulatrix duct extremely short but thin, basally wider; penis proximally globose abruptly becoming thinner towards distal portion; atrium globose, not enveloped by mucous gland.

Etymology: The present species is named after Dr. Ernesto Guevara de la Serna, for his life and ideals.

Description:

External Features: Animal color uniformly light gray with double dorsal line of pustules in cephalic region.

Shell (Fig. 7A): Dextral, subglobose, fragile, not translucent, spire medium elevated, conical, medium size with 4 convex whorls; pale brown; body whorl with three thin, continuous peripheral bands, central one darker and well marked close to aperture, dorsal and ventral bands wider at body whorl, both tenuous close to aperture, darker central band overlapping with suture; protoconch smooth; teleoconch surface with thin axial growth-lines; suture shallow; aperture subcircular with white, thin, slightly expanded peristome; space between terminal point of peristomal lips narrow with shallow callous present in some specimens; body whorl descending behind aperture; umbilicus wide, deep, partly overlapped with peristomal lip.

Measurements: Holotype: D maj: 24.6 mm; D min: 21.9 mm; H: 14.7 mm; D ap: 14.0 mm; H ap: 13.0 mm.

Paratypes (n = 12): D maj: 23.7–27.2 mm (25.1 mm); D min: 20.3–22.6 mm (21.7 mm); H: 13.3–15.3 mm (14.2 mm); D ap: 13.6–16.6 mm (14.9 mm); H ap: 12.3–14.6 mm (12.8 mm).

Jaw: Arcuate, orange, thin and translucent with three central wide ribs.

Pallial Complex: Pulmonary roof pale cream without darker spots; kidney length about 60% of pulmonary roof length; space between kidney + primary ureter and rectum + secondary ureter traversed by several thin ramified veins; thick main pulmonary vein splitting into two thinner main branches close to mantle collar.

Genitalia (Fig.18A–C): Terminal genitalia with single dart sac and two unequal mucous glands, right gland smaller, roundish, located between dart sac and vagina, distally fused with atrium wall, with thin, short duct; left mucous gland oval with wider short efferent duct, basally attached to atrium; both efferent ducts opening into dart sac contiguous, not fused; dart sac long, muscular, cylindrical, with medial constriction, mucous gland ducts inserting below constriction; dart papillae cylindrical, as long as distal portion of dart sac; dart sac inserting in atrium level with vagina and penial complex; bursa copulatrix sac oval, with thin, short duct distally slightly wider; sac and duct of bursa copulatrix neatly delimited; vagina shorter than penis; penial complex short; flagellum short, finger-like; epiphallus cylindrical to globose in proximal portion where vas deferens inserts, shorter than penis, externally differentiated from it; penial retractor muscle inserting in median portion of epiphallus, basally wider; penis proximal portion globose to cylindrical, abruptly getting thinner towards distal portion, penis twice epiphallus length, entering at genital atrium level with dart sac and vagina; penial papillae short, located in proximal penis; internal wall of penis with thin zigzag folds in all its length; penis sheath simple, muscular, overlapping distal portion of penis and proximally attaching to vas deferens by connective tissue and muscular strands; penial muscular band absent; atrium medium in length, globose, not enveloped by mucous gland.

Distribution (Fig. 21): Southern Santiago del Estero to Northern Cordoba provinces, Argentina. The present species is an habitant of the Chacoan biogeographic subregion.

Remarks: The present species is similar to *E. trifasciata* Fernández & Rumi. Some of the dry material in museum collections has been misidentified as *E. trifasciata* or as *E. trenquelleonis.* ***Epiphragmophora guevarai*** n. sp. differs from *E. trifasciata* mainly in shell characters: 1. Smaller shell size, 2. Peripheral bands thinner, median neatly delimited, 3. Shell sculpture consisting in thin stria instead of strong growth-ridges and both shell and animal color. Concerning the terminal genitalia, main differences are: (1) duct of bursa copulatrix is short but thinner and basally wider, bursa copulatrix is oval instead of round as in *E. trifasciata*, (2) flagellum shape and length, being finger-like instead of triangular, (3) left mucous gland oval in shape and smaller than in E*. trifasciata* inserting into dart sac separately from the thinner efferent duct of the other mucous gland, (4) penial morphology, especially penis shape with proximal portion globose abruptly diminishing in diameter towards atrium. Both species have contiguous distributions. ***Epiphragmophora guevarai*** differs from *E. trenquelleonis* in having a smaller shell size, different shell and body color, three peripheral bands, and a genital morphological pattern completely different. General shell shape is similar in both species.

Epiphragmophora hemiclausa Hylton Scott, 1951
(Figs. 2D, 10A–D, 19)

Epiphragmophora semiclausa Hylton Scott, 1951: 257, fig. 3.2, *non E. semiclausa* (Martens, 1869).
Epiphragmophora hemiclausa Parodiz, 1957: 30, *nom. nov*.
Epiphragmophora hemiclausa – Fernandez & Rumi, 1984 b: 239.

Holotype: MLP unnumbered, Argentina, Catamarca Prov., Cuestecilla de La Viña, 9/III/1950, Gladys Biraben leg.

Other Material Examined:
Dissected Material: Argentina, Catamarca Prov.: *FML 14410A, Paclin Dept., Route 38, 5 km to the S of provincial limit, La Viña, 28°02'20"S, 65°35'48"W, 600 m, 25/I/1997, M. G. Cuezzo & E. Dominguez leg. FML 14424, Andalgalá Dept., Alto de las Juntas, 15 km N of Rodeo, II/1997, P. Fidalgo, leg. *FML 14425, Paclin Dept., La Viña, 600 m, 12/XI/2001, M. G. Cuezzo leg. Argentina, Tucumán Prov.: FML 14403A, Lules Dept., margins of Lules river, 2,000 m E. Dominguez leg.
Dry Material: Argentina, Catamarca Prov.: FML 454, El Alto, 950 m, 13/XI/1958, Z. Ajmat leg., W. Weyrauch det. FML 744, Cuesta El Totoral, 950–1,200 m, 6/VIII/1967, W. Weyrauch leg & det. FML 775, El Totoral, 950–1,200 m, 16/XII/1963, W. Weyrauch leg.& det. FML 562, El Rodeo, I/1958, R. Golbach leg., W. Weyrauch det. FML 752, Near La Merced, subtropical rainforest, 6/VIII/1967, W. Weyrauch leg. & det. FML 11053, Between La Viña and the river Huacra, 550–600 m, 16/XII/1963, W. Weyrauch leg & det. FML 773, El Durazno, 850–900 m, W. Weyrauch leg. & det. FML 655, Ambato Dept., Sierra de La Puerta, 2/I/1939, Pierotti leg. FML 1245, Cuesta de La Viña, 700 m, 13/VIII/1967, W. Weyrauch leg. & det. MLP 4279, Cuesta de La Viña, Gladys Birabén leg., 9/III/1950. MACN 24251, Cuesta La Viña (Paratypes). MLP unnumbered, Sumampa, Biraben-Scott leg., 9/III/1950, ex collection Hylton Scott. Argentina, Tucumán Prov.: FML 801, on road from Tapia to Raco, 900 m, under rocks, 14/II/1964, W. Weyrauch leg. & det.

Description:
External Features: Uniform light yellowish, with double dorsal line of pustules in cephalic region.
Shell (Fig. 2D): Dextral, helicoidal, globose, semisolid to fragile, with conical spire; small to medium size, 4¼ convex whorls; light yellowish to pale brown, with single peripheral equatorial, dark brown even band more evident in body whorl periphery but running over suture of spire; protoconch smooth; teleoconch surface with thin axial growth lines and body whorl malleated, both dorsal and ventrally; suture deep impressed; aperture subcircular, peristome whitish, thin, slightly expanded, reflexed; body whorl distinctly descending towards aperture; umbilicus narrow, partly overlapped by ventral columelar fold of umbilicus; holotype with peristome totally overlapped by peristome, not fused.
Measurements: Holotype: D maj: 27.5 mm; D min: 23.2 mm; H: 14.6 mm.
Paratypes (n = 8): D maj: 21.9–24.0 mm (22.7 mm); D min: 18.921.2 mm (20.3 mm); H: 11.0–13.6 mm (12.8 mm).
Shell of the specimens dissected from Catamarca Province (n = 12): D maj: 24.6 mm; D min: 22.5 mm; H: 15.0 mm.
Jaw: Arcuate, thin, translucent, with three vertical, central ribs; concave and convex borders of ribs projecting at jaw edges.
Pallial Complex (Fig. 10D): Pulmonary roof with great number of minor transverse veins; kidney thin, triangular, with half pulmonary total roof length; thick main pulmonary vein splitting into two main branches close to mantle collar.
Genitalia (Fig. 10A–C): Terminal genitalia with dart sac complex consisting of single dart sac and two unequal mucous glands, right one round-shaped and left one elongate oval-shaped, both with ducts inserting independently in middle zone of dart sac; dart sac muscular, short, widening at base, inserting in distal portion of vagina; internal wall of dart sac with uniform longitudinal bands; dart papillae present, short, in distal portion of dart sac; bursa copulatrix elongate-oval, running towards middle zone of spermoviduct; duct of bursa copulatrix long, slightly swollen at base; vagina long (as long as penis); free oviduct short; penial complex with thin flagellum, finger-like; transition between epiphallus and penis not evident externally; epiphallus slightly longer to double penis length; proximal portion widening at vas deferens point of insertion; internal walls bearing series of slender longitudinal pleats; penis retractor muscle, thick, wide, inserting in middle epiphallus; wall sculpture of proximal penis with thin zigzag longitudinal

pleats, distal portion with thin straight longitudinal bands; small penial papillae present; penial sheath muscular, thin, proximally translucent, penis completely enveloped by penial sheath; vas deferens not surrounding dart sac; penis and vagina entering side by side atrium, distally to dart sac complex; penial muscular band present.

Habitat: *Epiphragmophora hemiclausa* is usually found under pieces of tree logs on the floor or among dead leaves.

Distribution (Fig. 19): Distributed in Argentina, its area of distribution corresponds to the Yungas biogeographic province that extends in Catamarca and in central and southern Tucumán Province.

Remarks: The present species was originally described by Hylton Scott (1951) as *Epiphragmophora semiclausa*, but later the name was changed to *E. hemiclausa* by Parodiz (1957) because *Lysinoe semiclausa* Martens, 1869, was classified into the genus *Epiphragmophora* and therefore the species name was preoccupied.
Epiphragmophora hemiclausa is similar to *E. argentina* in shell morphology, but it is usually smaller in diameter and presents a perspective umbilicus instead of being imperforated. It also differs in characters of the genitalia: shape of mucous glands and dart sac, length of bursa copulatrix duct.

Epiphragmophora hieronymi Doering, 1874
(Figs. 3A, 9D–F, 21)

Helix Epiphragmophora hieronymi Doering, 1874: 168.
Helix Aglaja Yocotulana – Doering, 1874: 446.
Helix Hieronymi – Kolbelt, 1878, 5: 146.
Epiphragmophora hieronymi – Parodiz, 1957: 29.
Epiphragmophora (*Epiphragmophora*) *hieronymi* – Zilch, 1959–1960: 655.
Epiphragmophora hieronymi – Fernández & Rumi, 1984b: 240.

Lectotype: SMF 7712, Catamarca, Quebrada del Tala, Hieronymus leg.
Paralectotypes: MACN 9127, Argentina, Catamarca, Sierra de Belén, close to Yocotula.

Other Material Examined:
Dissected Material: Argentina, Tucumán Prov.: FML 14414 A, Tafi del Valle Dept., between Amaicha and El Infiernillo close to Ampimpa, 26°38’06"S, 65°50’05"W, 2,610 m, 20/V/2003, M. G. Cuezzo leg. & det. Argentina, Catamarca Prov.: FML 14421 A Andalgalá Dept., Las Estancias, El Pucará, 2,040 m, 19/IV/2003, 27°42’21"S, 66°00’12"W, M. G. Cuezzo leg. & det. FML 14444 A, Tinogasta Dept., Cuesta de Zapata, between Belén and Tinogasta, 27°53’53"S, 67°22’23"W, 1,710 m, 28/XI/2003, Ituarte, C. leg.
Dry Material: Argentina, Tucumán Prov.: FML 212, Tafi del Valle Dept., Tafi, 26/IX/1946, Haywart, R. leg., W. Weyrauch det. FML14422, Tafi del Valle Dept., Route 307, close to Amaicha, 26°40’49"S, 65°48’46"W, 2,850 m, XII/2001, M. G. Cuezzo leg. & det. FML 14441, Tafí del Valle Dept., Amaicha, close to Castillo de las Brujas, 26°38’04"S, 65°52’10"W, 2,245 m, 15/IX/2003, D. Garcia Lopez leg. FML 14720, Tafi del Valle Dept., Route 307, between Amaicha and El Infiernillo, 26°38’18"S, 65°49’30"W, 2,650 m, M. G. Cuezzo leg. FML 14731, Tafi del Valle Dept., Quilmes, ruins of Quilmes, 26°27’41"S, 66°02’19"W, 2,000 m, 24/III/2005, M. G. Cuezzo leg. & det. Argentina, Catamarca Prov.: FML 135, Andalgalá Dept., La Mina, 13/VIII/1929, W. Weyrauch det. FML 14370, Dique las Pirquitas, 21/I/1968, W. Weyrauch leg. & det. FML 14423, Route 60, Quebrada de La Cébila, between Chumbicha and Mazán, IV/1998, M. G. Cuezzo leg. & det. FML 972, Cuesta de Las Chilcas, 24/X/1933, Schreiter, R. leg., W. Weyrauch det. FML 10897, Cuesta de Zapata, 1,500–1,850 m, 28/XI/1967, W. Weyrauch leg. & det. FML 14726, Andalgalá Dept., Cuesta Mina Capillitas, 27°29’54"S, 66°22’53"W, 1,630 m, 29/XI/2003, M. G. Cuezzo & C. Ituarte leg. FML 14727, Belén Dept., Farallón Negro, 27°17’37"S, 66°40’36"W, 2,500 m, 26/XI/2003, M. G. Cuezzo leg. & det. FML 14728, Belén Dept., Cuesta de Belén, 5 km N of Belén, 27/I/2003, 27°37’07"S, 67°01’19"W, 1,310 m, M. G. Cuezzo leg. & det. MACN 9127. MACN 19618, Fiambalá Mountains, E. Kittl col., 1930. MACN 9127, Sierra de Belén, close to Yocotula. MLP 3663, Mutquib, O. Ferraris leg. V/1953. MLP 1293, Los Angeles, 1,800 m MLP 4237, El Rodeo. MLP 4238, Las Trancas. MLP unnumbered, Las Pirquitas, ex collection Hylton Scott, Palma, A. leg., X/1950. Argentina, La Rioja Prov.: MLP 4235: Peñas. Biraben, M. Ex Hylton Scott collec-

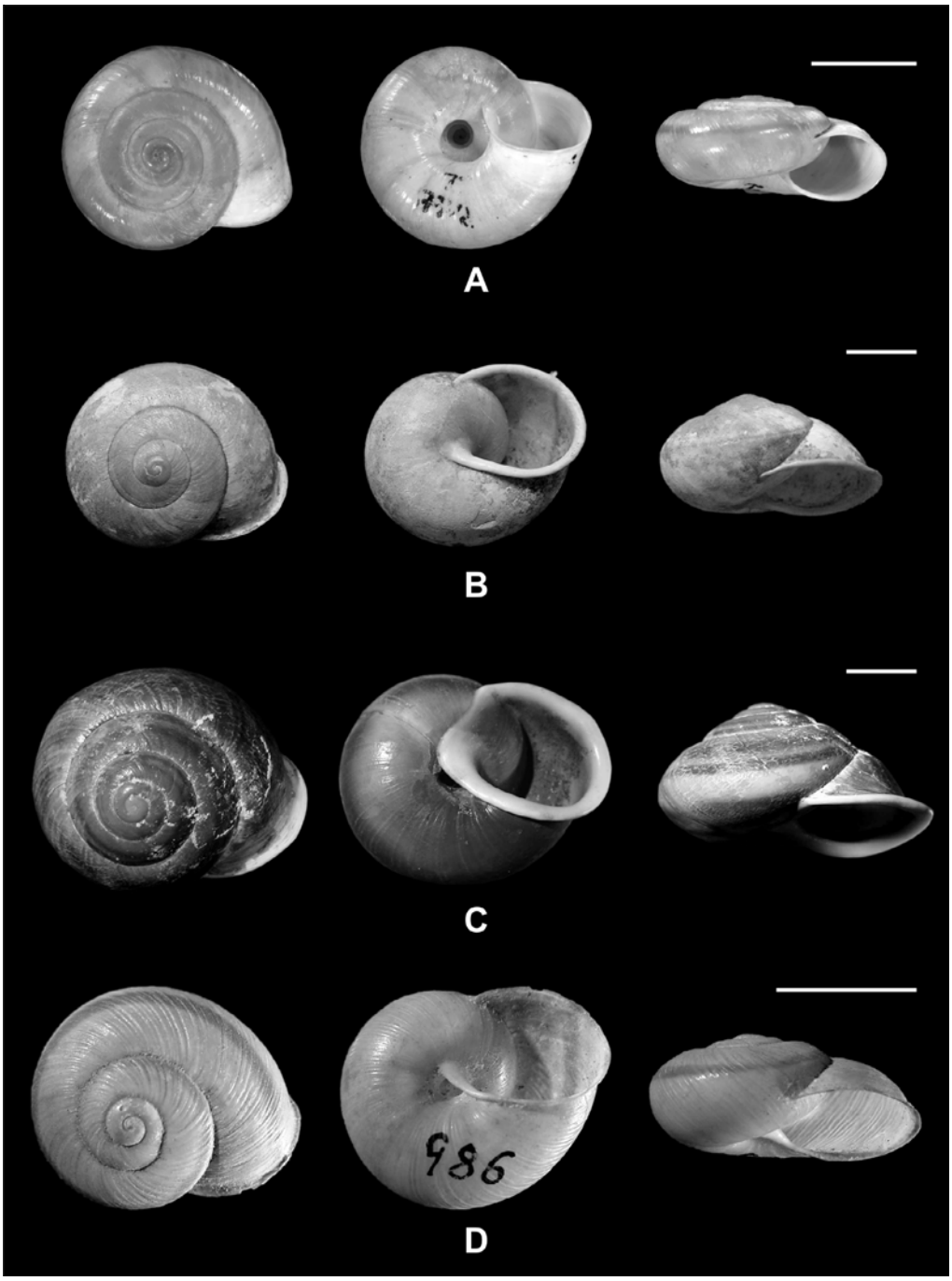

FIG. 3. Shells in dorsal, ventral and lateral view. A: *Epiphragmophora hieronymi* (SMF 7712, lectotype). Scale bar = 15 mm; B: *Epiphragmophora jujuyensis* (MLP, holotype). Scale bar = 10 mm; C: *Epiphragmophora oresigena* (MNHN, syntype). Scale bar = 10 mm; D: *Epiphragmophora parodizi* (FML 986 a, holotype). Scale bar = 20 mm.

TABLE 1. Main characters differencing the species: *E. hieronymi,* ***E. quirogai****, E. puella*, and *E. villavilensis.*

Characters	*E. hieronymi* (Doering)	*E. puella* Hylton Scott	***E. quirogai*** New Species	*E. villavilensis* Parodiz
Animal body color	Pale cream to pale grey	Not known	Black	Pale cream
Sculpture of body whorl	Axial growth lines	Granules and wrinkles	Axial growth lines and peripheral lines to malleated	Axial growth lines and peripheral thin lines
Suture	Shallow	Deeply marked	Deeply marked	Deeply marked
Shell Shape	Flat, low spire	Flat, low spire	Subglobose, low spire	Subglobose, depressed
Number of peripheral bands	One	None	None	None
Body whorl periphery	Convex	Equatorially subcarinated	Convex	Supraequatorially subcarinated
Peristomal lip	Thin, slightly expanded	Expanded	Thick, slightly reflexed	Thick, slightly reflexed
Aperture	Subcircular to oval	Subcircular to oval	Subcircular	Subquadrate
Internal sculpture of aperture and wall	With pustules	With pustules	With pustules	With pustules
Proximal portion of dart sac (until constriction)	Usually longer than distal portion	Not known	Usually longer than distal portion	-
Mucous gland	Incompletely surrounding basal dart sac and vagina	Not known	Incompletely surrounding basal dart sac and vagina	Completely surrounding basal dart sac plus vagina
Flagellum	Thin, finger-like, as long as epiphallus lenght	Not known	Thin, finger-like, less than half epiphallus lenght	Thin, finger-like, as long as epiphallus lenght
Epiphallus lenght	As long as penis	Not known	Double lenght of penis	Half penis lenght

tion. 13/XII/1951. FML 11044, La Torre, on road to Patquia, km 75, 1,000 m, 1/IV/1966, R. Herbst leg. W. Weyrauch det. Argentina, Formosa Prov.: MLP unnumbered, Estero Bellaco. Pierotti leg. (ex coll. Hylton Scott). Argentina, San Luis Prov.: MLP 4309, Carolina, 1,600 m 25/X/1970. Viana leg. (ex collection Hylton Scott). Argentina, Salta Prov.: FML 14730, Metán Dept., 6 km from national route 9 on margins of road to Cabra Corral, 25°07'33"S, 65°04'16"W, 837 m, 9/II/2005, M. G. Cuezzo leg. & det.

Description:

External Features: Body color varies from grayish to pale cream.

Shell (Fig. 3A): Dextral, helicoidal, semisolid to fragile, with low conical to flat spire; small to medium size, 4¼ convex whorls; pale yellowish to whitish; single peripheral supraequatorial, brownish, thin, even band running in body whorl periphery and on suture between third and fourth whorl; protoconch smooth; teleoconch surface with thin axial growth lines; suture shallowly impressed; aperture subcircular, peristome usually whitish, thin, slightly expanded; wall sculpture inside aperture with small irregularly distributed pustules; body whorl not descending towards aperture or scarcely descending; umbilicus wide, perspective not overlapped by ventral columelar fold of the peristome.

Measurements: Lectotype: DM: 18.4 mm; H: 8.6 mm.

Specimens from Argentina, Tucumán, Tafi del Valle Dept. (n = 25): DM: 24.6–10.4 mm (22.4 mm); D min: 21.4–18.5 mm (19.7 mm); H: 11.0–9.1 mm (9.5 mm); D ap: 12.3–10.0 mm (11.0 mm); H ap: 10.6–8.8 mm (9.7 mm).

Jaw: Small, translucent; four to five vertical ribs in center of jaw; borders of ribs projecting at convex and concave edges of jaw.

Pallial Complex: As described in Cuezzo (1997).

Genitalia (Fig. 9D–F): Terminal genitalia with dart sac complex consisting of single dart sac and two unequal mucous glands; right mucous gland sac-like enveloping distal zone of vagina and dart sac, distally fused with atrial wall; left mucous gland oval-elongate, ending in efferent duct that joins and fuses with thinner duct of right gland, both forming single efferent duct inserting in medial zone of dart sac below its constriction; dart sac muscular, long, cylindrical, with a constriction dividing the organ in two portions; dart sac proximal portion longer than distal portion; thin, internal dart gland located in distal portion of dart sac; dart sac ending in atrium level with vagina and penis; bursa copulatrix round, with thick, short duct; vagina very short almost completely covered by mucous gland; flagellum thin, finger-like, short, ending level where vas deferens enters penial complex and epiphallus begins; flagellum as long as epiphallus length; internally, proximal epiphallus with thick pilaster beginning at point of insertion of vas deferens and progressively tapering towards distal epiphallus; epiphallus as long as penis, proximally broad and progressively becoming thinner; penial retractor inserting close to vas deferens entering at proximal epiphallus; vas deferens forming a loop around penial retractor before inserting in epiphallus; penis cylindrical entering at genital atrium level with dart sac and vagina; penial papillae short, triangular; internal wall of penis with thin delicate longitudinal pleats; penis sheath muscular, thick, overlapping terminal portion of penis, distally fused to atrium wall; atrium long.

Habitat: Snails of this species are found under rocks in contact with the soil or inside rock crevices. Usually not found adhering to rocks, generally grounded in soil under rocks. Alive specimens are difficult to find, probably living most of their life inside deep crevices to avoid water loss.

Distribution (Fig. 21): *Epiphragmophora hieronymi* is found in Tucumán, Salta, Catamarca, Formosa, San Luis and La Rioja provinces, Argentina. It inhabits the Monte biogeographic province, and in Pre-Puna generally in places of high altitude (above 1,000 m). In Salta and Formosa, Chacoan biogeographic subregion at lowers altitudes.

Remarks: The epiphragm in this species is calcareous-like, white and thick, never transparent. It is very conspicuous compared to the epiphragm of the rest of the species examined. Some differences in epiphallus lengths were registered in specimens of different localities and could be assumed as individual variations. In specimens dissected that were previously fixed in formaldehyde or that have several years of being collected and preserved in malacological collections, the mucous glands were collapsed and the tissues were hardened, especially the mucous gland surrounding the distal genitalia. Because of this artificial modification, the mucous gland seems to be a thick sheath that surrounds terminal genitalia similar to the one present in some Cepoliinae instead of a soft glandular tissue of a mucous gland with similar position. Main shell and genitalia differences among *E. hieronymi, E. puella,* ***E. quirogai*** n. sp. and *E. villavilensis* are detailed in Table 1.

Epiphragmophora jujuyensis Hylton Scott, 1962
(Figs. 3B, 11A–C, 19)

Epiphragmophora jujuyensis Hylton Scott, 1962: 107.

Epiphragmophora jujuyensis – Fernández & Rumi, 1984b: 241.

Holotype: MLP unnumbered, Argentina, Jujuy, Las Capillas, 4/XII/1951.

Paratypes: MACN 16234, Argentina, Jujuy.

Other Material Examined:

Dissected Material: Argentina, Salta Prov.: FML 14513 A, Anta Dept., National Park “El Rey”, Aguas Negras, 25°15’36"S, 64°55’15W, 645 m, 23/III/1999, M. G. Cuezzo leg. & det. FML 14514 A, Anta Dept., National Park “El Rey”, Cerro Maldonado, 1,400 m, 24°43’27"S, 64°38’46"W, 24/III/1999, M. G. Cuezzo leg. & det., FML 14515 A, Orán Dept., San Andrés, 23°05’50"S, 64°46’10"W,

1,090 m, 16/XII/1999, E. Dominguez leg. FML 14512 A Orán Dept., on road to San Andrés, junction between San Andrés river with Seco river, 23°05'50"S, 64°46'01"W, 1,000 m, E. Dominguez leg. FML 14516 A, Anta Dept., National Park "El Rey", margins of La Sala river, 24/III/1999, M. G. Cuezzo leg.

Dry Material: MLP unnumbered, Top of the mountains Maldonado, National Park "El Rey", Brown, A. 15/VII/1979. MLP unnumbered, Burela, Birabén, M. Argentina, Jujuy Prov.: FML 960, La Caldera Dept., on road between Salta and Jujuy, km 1650, 1,400 m, 29/II/1964, W. Weyaruch leg. & det. FML 806, Manuel Belgrano Dept., Las Capillas, 36 km NE from San Salvador de Jujuy, 1,400 m, 25/II/1964, W. Weyrauch leg. & det. FML 893, Manuel Belgrano Dept., Los Perales, 1,300 m, 25/II/1964. FML 14517, Ledesma Dept., National Park Calilegua, margins of the river "tres cruces", 23°41'36"S, 64°52'08"W, 1,100 m, 2/IV/2004, M. G. Cuezzo leg. FML 14729, Santa Bárbara Dept., Villa Monte, Finca Portal del Cerro, 24°05'S, 64°23'W, 1,068 m, 1/III/2005, F. C. Cuezzo leg.

Description:

External Features: Body dark brown, with tentacles usually darker; well-marked dorsal row of pustules in cephalic region passing between ommatophores; lung spots visible through shell by transparency, appearing as shell spots in live specimens.

Shell (Fig. 3B): Dextral, helicoidal, globose, solid, with elevated conical spire; medium to large size, 4½ convex whorls; dark to light brown, with thin, peripheral supraequatorial dark brown band more evident in body whorl; protoconch smooth; teleoconch surface malleated with diagonal ribs on body whorl; suture deeply impressed; aperture elliptical, peristome whitish slightly reflected, with callous lower margin; body whorl distinctly descending towards aperture; umbilicus narrow, overlapped by ventral columelar fold of peristome in holotype; some specimens with umbilicus not totally overlapped by peristome.

Measurements: Holotype: Argentina, Jujuy, Las Capillas, D maj: 32.4 mm; D min: 29.7 mm; H: 19.1 mm.

Specimens from Argentina, Salta, Parque Nacional "El Rey" (n = 10): D maj: 30.7–35.0 mm (32.6 mm); D min: 27.4–31.2 mm (29.2 mm); H: 18.3–21.6 mm (19.5 mm).

Specimens from Argentina, Jujuy, Parque Nacional "Calilegua" (n = 8): D maj: 38.3–44.1 mm (42.0 mm); D min: 33.0–39.0 mm (36.0 mm); H: 21.3–27.7 mm (23.9 mm).

Jaw: Corneous, strong; two strong vertical ribs in central portion.

Pallial Complex: Lung roof densely mottled with black spots when viewing externally; kidney triangular, as long as half of pulmonary roof length; main pulmonary vein splitting into three major veins and several minor longitudinal veins.

Genitalia (Fig. 11A–C): Terminal genitalia with dart sac complex consisting of single dart sac and two mucous glands on opposite sides; mucous glands oval, pear-shaped; right mucous gland (dorsal view) slightly shorter than left; both mucous glands opening above medial constriction of dart sac via individual efferent ducts independent from each other; dart sac cylindrical, muscular, with medial constriction, slightly longer than bursa copulatrix; vas deferens surrounding dart sac at level of dart sac constriction; proximal dart sac internal wall with longitudinal folds, distal internal dart sac with cylindrical dart papilla; dart sac opening into atrium; vagina cylindrical, short; free oviduct cylindrical thinner than vagina; bursa copulatrix with short, thick duct; bursa sac not sharply differentiated from duct; penial complex consisting of flagellum, epiphallus and penis; flagellum finger-like, short, curved, ending where vas deferens enters penial complex and epiphallus begins; epiphallus long, with internal longitudinal pleats; proximal portion of epiphallus broadening at point of insertion of vas deferens; penial retractor muscle inserting in middle zone of epiphallus; vas deferens forming loop around penial retractor; penis longer than epiphallus, entering at genital atrium level with respect to vagina and dart sac openings; penial papilla short, triangular, located in proximal portion of penis; proximal penis wall with convoluted zigzag glandular bands close to penial papillae; distal penis wall with longitudinal straight bands; penis sheath thin, translucent, overlapping distal portion of penis; genital atrium large, with inner wall smooth.

Habitat: Usually found under leaf litter and fallen tree trunks in humid forests.

Distribution (Fig. 19): *Epiphragmophora jujuyensis* is known from Jujuy and Salta

provinces, northwestern Argentina. This species is a typical habitant of the cloud rainforest or Yungas biogeographic province although it is not easily found.

Remarks: Holotype measurements in the original description of the species (Hylton Scott, 1962) are not coincident with the real measurements of the holotype deposited at La Plata Museum, Argentina. There is a great variability in shell diameter among populations of Jujuy and Salta localities, the specimens from Calilegua National Park, Jujuy Province, being bigger.

Epiphragmophora oresigena (d'Orbigny, 1835)
(Fig. 3C)

Helix oresigena d'Orbigny, 1835: 239: pl. 24.

Syntypes: MNHN, Bolivia, Yungas.
Type Locality: Provincia Yungasensi, republica Boliviana, prés du confluent du Rio Meguilla et du Rio de La Paz.

Other Material Examined:
Dry Material: FML 399, BOLIVIA, La Paz Dept., Yungas Prov. Coroico, 1,700 m, in a coffee plantation. 25/I/1966, E. de la Sota leg.

Description:
Shell (Fig. 3C): Dextral, helicoidal, globose, very solid with conical, obtuse spire; large size, 5 $^1/_3$ convex whorls; dark to light brown; three peripheral dark brown bands more evident in body whorl, ventral pigmented band usually wider, central and dorsal supraequatorial, only central and dorsal bands in spire; protoconch smooth; teleoconch surface malleated with diagonal ribs on body whorl; suture deep impressed; aperture subquadrangular, peristome thick, white, reflected; narrow, shallow fold in parietal wall between margins of peristome; body whorl abruptly descending behind aperture; umbilicus narrow partly overlapped by ventral columelar fold of peristome.
Measurements: Syntypes (n = 2): D maj: 37.9 mm, 41.9 mm (39.9 mm); D min: 32.7 mm, 35.3 mm (34.0 mm); H: 23.3 mm, 26.7 mm (25.0 mm); D ap: 21.4 mm, 25.7 mm (23.5 mm); H ap: 18.0 mm, 21.1 mm (19.5 mm).

Distribution: Known from few localities in La Paz Dept., Yungas Province, Bolivia (Breure, 1973).

Epiphragmophora parodizi Fernández & Rumi, 1984
(Figs. 3D, 11D, E, 19C, 20)

Epiphragmophora parodizi Fernández & Rumi, 1984b: 242; pl. 5, figs. 7–9.

Holotype: FML 986a, Argentina, Tucumán Prov., Tafi del Valle Dept., Infiernillo. W. Weyrauch leg., 5/IV/1965.

Other Material Examined:
Dissected Material: Argentina, Tucumán Prov.: FML 14395A, Trancas Dept., on road to Gonzalo. 26°19'35"S, 65°32'21"W, 1,360 m, 7/V/2002, M. G. Cuezzo leg. & det. FML 14396A, Trancas Dept., on road from San Pedro de Colalao to Gonzalo, close to Rearte, 26°19'35"S, 65°32'21"W, 13/XI/2000, 1,460 m, M. G. Cuezzo leg. & det. FML 14389A, Trancas Dept., close to San Pedro de Colalao, 15/X/1996, M. G. Cuezzo & F. Romero leg. FML 14397A, Trancas Dept., close to the bifurcation to Hualinchay, 26°21'05"S, 65°32'25"W, 1,450 m, 13/XI/2000. M. G. Cuezzo leg. & det.
Dry Material: Argentina, Tucumán Prov.: FML 889, Tafi del Valle Dept., El Infiernillo, 3,100 m, 10/III/1964. A. Willink leg. FML 14388, Tafí del Valle Dept., road between Tafí and El Rincón behind Loma Pelada, 26°56'20"S, 65°46'31"W, 26/XI/2002, M. G. Cuezzo & E. Dominguez leg. FML 14394, Trancas Dept. on road to Gonzalo before Los Rearte, km 31. 15/X/1996. M. G. Cuezzo & F. Romero leg. FML 14398, Trancas Dept., South of San Pedro de Colalao, I/1986, M. G. Cuezzo det. FML 230, Tafi del Valle Dept., Tafi del Valle, 2,000 m, 27/X/1947, R. Golbach leg. FML 14739, Tafi del Valle Dept., El Mollar, 2,000 m, XI/1998, M. G. Cuezzo & E. Dominguez leg. FML 14740, Trancas Dept., on road to Gonzalo, 7/V/2002, 1,400 m, M. G. Cuezzo leg. & det.

Description:
External Features: Body light brown with suprapedal dark brown longitudinal band extending from head to tail; suprapedal dark band thicker close to tail.
Shell (Fig. 3D): Dextral, helicoidal, semisolid to fragile, with conical shallow spire; small size, 4 $^1/_4$ convex whorls; light yellowish to golden brown, with peripheral supraequatorial, dark brown band progressively becoming thicker towards body whorl, band running above suture in spire; protoconch

smooth; teleoconch with regularly distributed axial ribs separated at regular intervals; suture deep impressed; aperture subcircular to transverse oval; peristome whitish, thick, reflexed; body whorl distinctly descending towards the aperture; umbilicus narrow, partly overlapped by ventral columelar fold of peristome.

Measurements: Holotype: D maj: 19.7 mm; D min: 17.0 mm; H: 9.6 mm; D ap: 12.2 mm; H ap: 9.4 mm.

Specimens from Trancas Dept. (n = 18): Dmaj: 23.9–18.7 mm (20.5 mm); D min: 20.9–16.4 mm (16.8 mm); H: 13.1–9.6 mm (11.2 mm); D ap: 14.5–11.2 mm (12.3 mm); H ap: 11.6–9.0 mm (10.2 mm).

Specimens from Tafí del Valle Dept. (n = 7): D maj: 23.3–19.4 mm (20.8 mm); D min: 20.4–17.5 mm (18.2 mm); H: 11.8–9.5 mm (10.3 mm); D ap: 14.3–11.9 mm (12.8 mm); H ap: 11.2–9.6 mm (10.3 mm).

Jaw: Thin, translucent; specimens with either wide, shallow plaques or four ribs in center of jaw.

Genitalia (Fig. 11D, E): Terminal genitalia with dart sac complex consisting of single dart sac and two mucous glands; right mucous gland sac-like, enveloping distal zone of vagina and dart sac, distally fused with atrial wall; left mucous gland oval-elongated, basally wider opening into broad duct that joins with thinner duct of right gland, both ducts inserting below constriction of dart sac adjacent to each other; dart sac muscular, long, cylindrical, with medial constriction; presence of thin, short dart gland located inside distal portion of dart sac; dart sac ending at atrium level with vagina and penis; vas deferens surrounding dart sac medial constriction before entering penial complex; bursa copulatrix oval, with thin medium duct; free oviduct as long as bursa copulatrix duct; vagina shorter than penis; penial complex long, slender; flagellum thin, finger-like, ending level where vas deferens enters penial complex and epiphallus begins; epiphallus thin, widening at point of insertion of vas deferens; internally epiphallus with longitudinal, slender, undulating pleats; penis long, slender, twice or three times longer than epiphallus, entering at genital atrium level with dart sac and vagina; penial papillae absent; internal wall of penis with thin delicate longitudinal pleats, becoming taller with zigzag pattern in proximal penis zone; penial muscular band absent; penis sheath muscular, thick, overlapping all penis length, distally fused with atrium wall; atrium extremely short.

Habitat and Distribution (Fig. 20): *Epiphragmophora parodizi* is found in both Yungas and Pre-Puna biogeographic provinces, although live specimens have only been found in Yungas rainforest, mostly under trunks on the ground in contact with soil. It is distributed in Tucumán Province, northwestern Argentina.

Remarks: Specimens from northwestern Tucumán, in the locality of Gonzalo, have thin axial irregular, undulating lines on the shell surface of the first whorls and regular axial ribs separated by regular spaces on the the body whorl. These irregular thin lines are not present in the holotype and paratypes, but are constant in the specimens from Gonzalo, Tucumán.

Epiphragmophora proseni Hylton Scott, 1951 (Fig. 4A)

Epiphragmophora proseni Hylton Scott, 1951: 258, fig. 3.3.

Epiphragmophora proseni – Parodiz, 1957: 30.

Epiphragmophora proseni – Fernández & Rumi, 1984b: 243.

Holotype: MLP unnumbered, Argentina, Jujuy, Tumbaya Dept., Quebrada de Humahuaca, Tumbaya, II/1950, A. F. Prosen leg. ex Hylton Scott Collection.

Description:

Shell (Fig. 4A): Dextral, globose, solid; conic spire fairly elevated; medium size; with 4¼ convex whorls; dark brown to chestnut homogeneous color; peripheral band on body whorl absent; protoconch smooth; first spire whorls with axial ribs, body whorl malleated with axial to diagonal ribs, ventrally fine spiral lines well marked around umbilicus; suture well impressed; oval transversal aperture with peristome white, fine narrowly reflexed, interior of aperture chestnut brown; wall space between lips narrow without callus; body whorl descending abruptly behind aperture; umbilicus perspective, narrow, partly overlapped by peristomal lip.

Measurements: Holotype: D maj: 30.1 mm; D min: 24.4 mm; H: 15.3 mm; D ap: 17.7 mm; H ap: 15.0 mm.

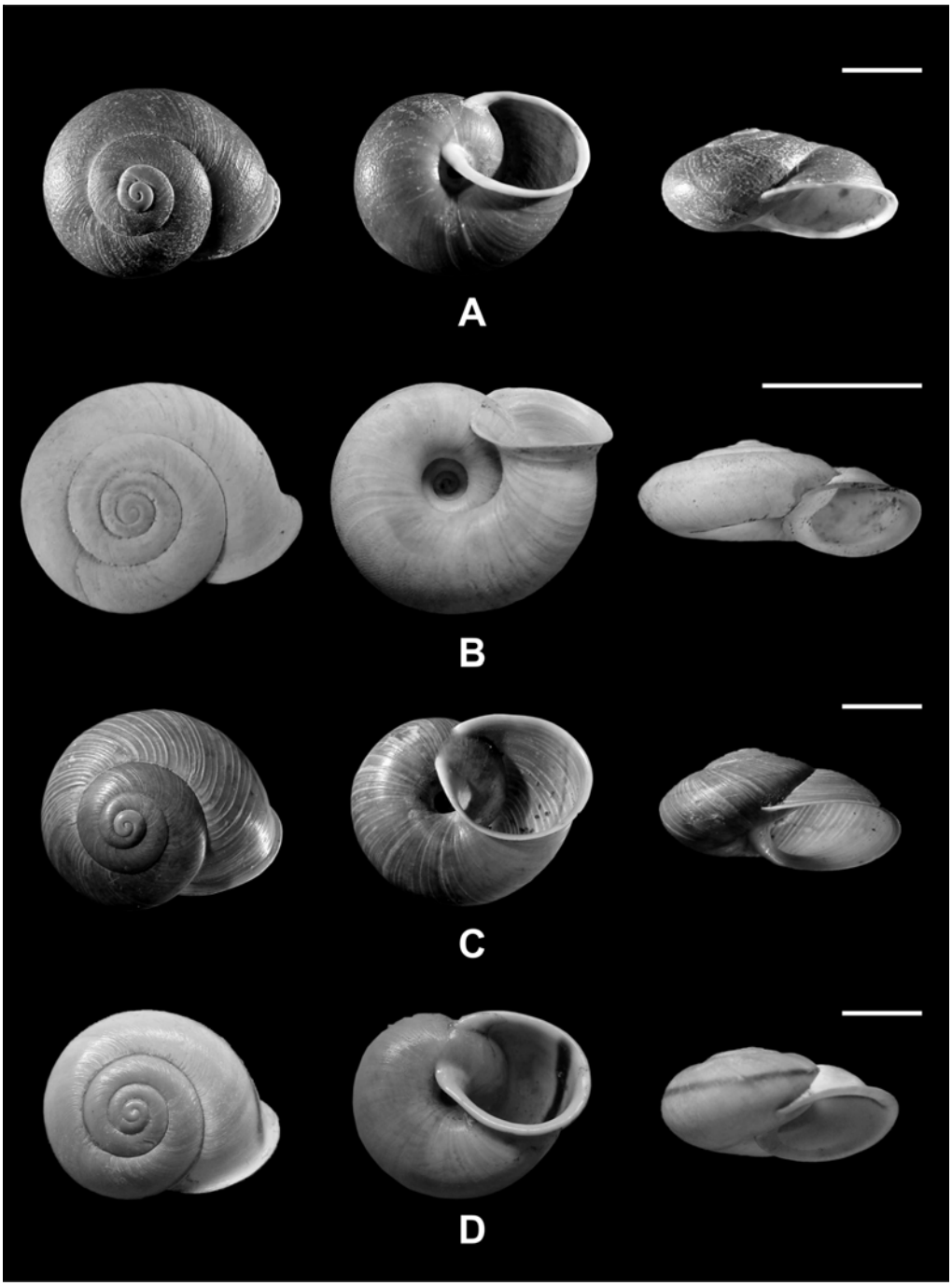

FIG. 4. Shells in dorsal, ventral and lateral view. A: *Epiphragmophora proseni* (MLP, holotype). Scale bar = 10 mm; B: *Epiphragmophora puella* (MLP, holotype). Scale bar = 20 mm; C: *Epiphragmophora puntana* (MACN 1284, lectotype). Scale bar = 10 mm; D: *Epiphragmophora rhathymos* (FML 14520). Scale bar = 10 mm.

Distribution: Single known locality of occurrence in Tumbaya, Jujuy Prov., Argentina.

Remarks: The original description of *E. proseni* was based on a single dry shell, the holotype, collected by A. Prosen. This shell is similar to *E. jujuyensis*, in most of its characters, except in the spire shape, which is shallower in *E. proseni* than in *E. jujuyensis* and the umbilicus, which is narrower in *E. proseni*. Hylton Scott stated that the shell color, the interior of the aperture chestnut brown and the absence of the peripheral band were the characters that allow the recognition of the present species. Nevertheless, all those mentioned characters are also present in some specimens of E*. jujuyensis*. The validity of the present species will remain dubious due to the unavailability of other specimens for comparison and the lack of anatomical studies. Neither dry shells nor live specimens of *E. proseni* were found in a field trip to the type locality.

Epiphragmophora puella Hylton Scott, 1951
(Figs. 4B, 21)

Epiphragmophora puella Hylton Scott, 1951: 253, fig. 3.1.
Epiphragmophora puella – Parodiz, 1957: 30.
Epiphragmophora puella – Fernández & Rumi, 1984b: 242.

Holotype: MLP unnumbered: Argentina, Catamarca, Capayán Dept., Quebrada de La Cébila.
Paratypes: MACN 16701, *Paratype*, Capayán Dept., Quebrada de La Cébila, 1950. MLP unnumbered, Paratypes, Capayán Dept., Quebrada de La Cébila.

Other Material Examined:
Argentina, Catamarca Prov.: FML 14378, Capayán Dept., Quebrada de La Cébila, 1,100 m, 15/IX/1968, leg. & det. by W. Weyrauch. MLP unnumbered, Capayán Dept., Quebrada de La Cébila, 13/III/1950. MLP unnumbered, Las Totoritas, Hylton Scott det., Martinez, A. leg.

Description:
Shell (Fig. 4B): Dextral, helicoidal, fragile; low to flat spire; small; 4¾ whorls equatorially subcarinated; pale yellowish to pale brownish; peripheral band absent; protoconch smooth; first whorl with axial growth lines, rest of teleoconch surface with tiny, oval pustules giving appearance of wrinkled surface; suture deeply impressed; aperture subcircular to subovoid; peristome whitish, thin, well expanded; body whorl not descending towards aperture or scarcely descending; umbilicus wide, perspective not overlapped by ventral columelar fold of peristome.
Measurements: Holotype: D maj: 18.0 mm; D min: 15.5 mm; H: 6.6 mm.
Paratypes (n = 5): D maj: 17.6–18.0 mm (17.6 mm); D min: 14.7–16.0 mm (15.3 mm); H: 6.4–8.6 mm (7.1 mm).

Distribution (Fig. 21): Southern Catamarca Prov., Argentina. Monte biogeographic province.

Remarks: This is a conspicuous species due to its small shell diameter, periphery of the body whorl and shell sculpture. The sculpture consisting of small regularly distributed pustules is unique among the species described in this paper. Fernandez & Rumi (1984b) described and illustrated the genitalia of *E. puella,* but unfortunately it was not possible to find the material on which the description was based. The published anatomical description is poor, and the connections and point of insertions of the different organs and their ducts are not clear in their figures.
Epiphragmophora puella is very difficult to find, usually deeply inside crevices of rocks, and it is only known from its type locality in Catamarca. It shares with *E. hieronymi* and *E. rhathymos* the same dry environment of the Monte biogeographic region.

Epiphragmophora puntana (Holmberg, 1909)
(Figs. 4C, 12A–C)

Helix puntana Holmberg 1909a: 9.
Epiphragmophora puntana – Paródiz, 1957: 29.
Epiphragmophora puntana – Fernández, 1973: 159.
Epiphragmophora puntana – Fernández & Rumi, 1984b: 243.

Lectotype: MACN 1284, Argentina, and San Luis, Cerro del Volcán.

Other Material Examined:

Material Dissected: Argentina, San Luis Prov.: FML 14518 A, Capital Dept., El Volcán, 22/I/2003, 33°12'26"S, 66°12'44"W, 1,200 m, M. G. Cuezzo & E. Dominguez leg.

Dry Material: Argentina, San Luis Prov.: FML 14393, Capital Dept., El Volcán, Mountain El Volcán, 33°15'02"S, 66°11'13"W, 910 m, 17/XI/2001. M. G. Cuezzo leg. & det. FML 14433, Potrero de Funes, 30 km from El Volcán, 33°12'02"S, 66°12'20"W, 1,000 m, 21/I/2003, M. G. Cuezzo & E. Dominguez leg. MLP 1665, Coronel Pringles Dept., Paso del Rey, Vigniatti leg. Argentina, Córdoba Prov.: FML 14519 (ex WW 1056), San Javier Dept., Las Cañadas. E. Palavecino leg., 1939, det. by J. J. Parodiz. MLP unnumbered, Punilla Dept., Pampa de Olain. Cicheros, J. leg., I/1967, ex collection Hylton Scott. MLP unnumbered, Candelaria de la Sierra, Cichero-Martinez leg. XII/1966, ex collection Hylton Scott.

Description:

External Features: Body color reddish to dark orange, ommatophores with darker red to brown color; double row of pustules regularly located on middle dorsal cephalic region running from mantle to space between ommatophores well marked.

Shell (Fig. 4C): Dextral. helicoidal, globose, semisolid; medium size; spire conic, elevated; medium to large; 4½ convex whorls; yellowish to golden brown; single, thin dark brown supraperipheral band present in body whorl; protoconch smooth; axial whitish to light yellow ribs regularly distributed in all whorls except in protoconch, ribs more evident in body whorl; space between ribs with fine line growth crossed by other fine transversal lines slightly marked; suture well impressed; aperture transverse oval, internal wall of aperture light chestnut; peristome thin, slightly expanded, whitish; thin parietal callus usually raised; body whorl strongly descending behind aperture; umbilicus perspective, partly overlapped by peristomal lip.

Measurements: Lectotype: D maj: 30.7 mm; D min: 27.0 mm; H: 16.6 mm; D ap: 18.5 mm. Specimens from Type Locality (n = 11): D maj: 30.0–26.3 mm (28.7 mm); D min: 26.7–22.9 mm (25.6 mm); H: 17.8–15.0 mm (15.9 mm); D ap: 17.8–15.9 mm (17.1 mm); H ap: 15.7–13.6 mm (14.9 mm).

Jaw: corneous, arcuate, orange, thin; four central ribs, middle ones wider than both laterals.

Pallial Complex: Kidney extending about 60% of pulmonary roof length; pulmonary roof homogeneous pale gray, densely traversed by net of thin veins especially close to mantle collar.

Genitalia (Fig. 12A–C): Terminal genitalia with dart sac complex consisting of single dart sac and two mucous glands; both glands round shaped, left slightly bigger than right, both distally fused with atrium wall; each mucous gland with thin efferent duct distally fused with each other into single duct inserting below constriction of dart sac; dart sac long, muscular, cylindrical, with medial constriction; dart papillae thick, cylindrical, as long as distal portion of dart sac; distal portion of dart sac below constriction shorter than proximal; dart sac ending at atrium level with vagina and penial complex; bursa copulatrix sac round, with thin medium length duct basally wider; sac and duct of bursa copulatrix neatly delimited; free oviduct thin, longer than vagina; vagina shorter than penis; penial complex short to medium; flagellum finger-like with thick distal portion ending level where vas deferens enters penial complex and epiphallus begins; epiphallus shorter than penis, externally differentiated from it due to its smaller diameter; penial retractor muscle thin, long, inserting in median portion of epiphallus; penis cylindrical, broader at proximal portion, thinner at distal; penis longer than epiphallus, entering at genital atrium level with dart sac and vagina; internal sculpture of penis well differentiated into two regions, smooth strength pleats located in proximal portion of penis, externally overlapped by penis sheath and thick zigzag folds in distal portion of penis, externally free of penial sheath; penial papillae short, rectangular, with surface sculpture consisting of vertical bands; penis sheath muscular, distally fused with atrium wall.

Habitat: *Epiphragmophora puntana* inhabits mountains with xerophilic vegetation and is found always associated to rocks, usually inside narrow crevices formed between big rocks. This species inhabit the Monte biogeographic province.

Distribution: *Epiphragmophora puntana* is known to live in central and northeastern San Luis Province, Argentina, and occasionally have been found in southern Córdoba Province.

Epiphragmophora quirogai Cuezzo, n. sp.
(Figs. 7B, 18D–F, 21)

Holotype: FML 14721A, Argentina, La Rioja, Sierra de Velazco, Anillaco, 1/III/1998, G. Perotti leg.

Paratypes: FML 14719, Argentina, La Rioja, Sierra de Velazco, close to Anillaco, 2/III/1998, Perotti, M.G. leg. FML 14429 A, type locality, F. Cruz leg. MLP unnumbered, type locality.

Other Material Examined:

Dissected Material: Argentina, La Rioja Prov.: FML 14429A, Sierra de Velazco, close to Anillaco, II/1998, Cruz, F. leg.; FML 14428A , Sierra de Velazco, 1996, F. Cruz, leg.

Dry Material: Argentina, La Rioja: FML 14722, Castro Barros Dept., Santa Vera Cruz, 1/IV/1998, M. G. Cuezzo & E. Dominguez leg. Argentina, Catamarca: FML 447, Belén Dept. Belén, 25/I/1960, leg. Willink. FML 14369, Cuesta de La Puerta, 900 m, close to Pirquitas, W. Weyrauch leg. & det. FML 152, Andalgalá, 19/I/1934, Schreiter leg. FML 14724, Tinogasta Dept., Cuesta de Zapata, 27°49'00"S, 67°18'52"W, 1,710 m, 28/XI/2003, M. G. Cuezzo & C. Ituarte leg.

Diagnosis: Shell bright cream to bright pink, without peripheral pigmented band in body whorl; shell subglobose; spire and body whorl convex; spire shallow; suture deeply impressed; terminal genitalia with one mucous gland sac-like incompletely surrounding basal dart sac and vagina, the other oval-elongate; both mucous glands with efferent ducts that fuse together before inserting below constriction of dart sac; epiphallus double in length respect to penis.

Etymology: The species is named after Juan Facundo Quiroga, also known as “Tigre de Los Llanos”, who fighted for the independence of the Agentinean provinces towards a national organization and later was misjudged by history.

Description:

External Features: Animal with even black color of its body; single dorsal row of pustules in cephalic region running from mantle collar to ommatophores.

Shell (Fig. 7B): Dextral, helicoidal, depressed, semisolid; spire low, conical; small to medium size; 4¼ convex whorls; bright cream to bright pink; peripheral pigmented band absent; protoconch smooth; teleoconch surface with thin axial growth lines; body whorl surface with thin axial growth lines crossed by irregular peripheral lines, giving malleated appearance in some specimens; suture deeply impressed; aperture subcircular, with straight basal lip; peristome whitish, thin, slightly reflexed; parietal wall space between margins of upper and basal lip narrow; body whorl slightly descending towards aperture; umbilicus wide, not overlapped by ventral columelar fold of peristome.

Measurements: Holotype: DM: 20.4 mm; D min = 17.7 mm; H = 8.4 mm; D ap = 10.2 mm; H ap = 8.8 mm.

Paratypes FML 14719 (n = 10): DM: 19.4–21.6 mm (18.5 mm); D min: 15.8–18.8 mm (17.5 mm); H: 8.3–10.0 mm (9.0 mm); D ap: 10.0–12.0 mm (10.9 mm); H ap: 8.0–10.2 mm (9.2 mm).

Jaw: Arched, thin, orange, with five central thin ribs; ribs very pronounced and delimited; borders of ribs projecting at both upper and lower edges.

Pallial Complex: Lung roof without dark spots, homogeneously pale cream; kidney extending 50% of total pulmonary roof length; main pulmonary vein spliting proximally in two mayor veins that distally are divided into several minor veins before reaching mantle collar; portion of lung roof between rectum and kidney crossed by several minor transversal ramified veins.

Genitalia (Fig. 18D–F): Dart sac complex in terminal genitalia consisting of single dart sac and two unequal mucous glands; right mucous gland sac-like, incompletely surrounding distal zone of vagina and dart sac, distally fused with atrial wall; left mucous gland oval-elongate, opening into thick efferent duct; left gland duct fusing with right gland thinner duct into single efferent duct inserting in medial zone of dart sac below its constriction; dart sac muscular, long, cylindrical, with medial constriction; thin, internal dart gland located in distal portion of dart sac; dart sac ending at atrium level with vagina and penis; bursa copulatrix round, with thick short duct; vagina shorter than penis; penial complex long; flagellum thin, finger-like, less than half epiphallus length ending level where vas deferens enters penial complex and epiphallus begins; internal wall proximal epiphallus sculpture with thick pi-

laster beginning at point of insertion of vas deferens and progressively tapering towards distal epiphallus; epiphallus proximal portion thick, progressively becoming thinner, epiphallus double penis total length; penial retractor inserting in medial portion of epiphallus; vas deferens forming loop around penial retractor close to vas deferens point of insertion; penis cylindrical entering genital atrium level with dart sac and vagina; penial papillae short, triangular; internal wall of penis with thin delicate longitudinal pleats; penis sheath short, muscular, overlapping terminal portion of penis; atrium usually long.

Habitat and Distribution (Fig. 21): ***Epiphragmophora quirogai*** is found under rocks in dry environments of Monte biogeographic regions in Catamarca and La Rioja provinces, Argentina.

Remarks: ***Epiphragmophora quirogai*** is one of the smallest species of the genus. Some specimens in museums were originally identified as *E. hieronymi*, as its general shape is similar and their areas of distribution partially overlapped. However, identification of both species is possible by different shell and genitalia characters. A comparison of some characters among the closest species – *E. hieronymi, E. villavilensis, E. puella* and ***E. quirogai*** – is presented in Table 1.

Epiphragmophora rhathymos (Holmberg, 1912)
(Figs. 4D, 12D–E, 20)

Helix (*Eurycampta*) *rhathymos* Holmberg, 1912: 20.
Helix (*Eurycampta*) *monographa* – Doering, 1874: 450, *non Helix Eurycampta monographa,* Burmeister, 1861: 77.
Epiphragmophora trenquelleonis rhathymos – Parodiz, 1957: 29.
Epiphragmophora trenquelleonis rhathymos – Fernández, 1973: 161.
Epiphragmophora rhathymus – Fenández & Rumi, 1984b: 244.

Lectotype: SMF 20397, Argentina, Quebrada del Tola, Sierra de Catamarca, Hieronymus leg., Doering, det. (Zilch, 1971)
Paralectotype: MACN 1289, Argentina, Catamarca, El Desmonte. Holmberg Collection.

Other Material Examined:
Dissected Material: Argentina, Catamarca Prov.: FML 14520A, Esquiú Dept., Las Pirquitas, 28°16'07"S, 65°44'W, 760 m, 13/XI/2001, M. G. Cuezzo leg. & det. Argentina, Tucumán Prov.: FML 14404A, J. B. Alberdi Dept., Escaba. XI/1996, M. G. Cuezzo leg. Argentina, Córdoba Prov.: FML 14440 A, Cruz del Eje Dept., route 15 between Villa de Soto and La Higuera, 30°59'12"S, 65°04'45"W, 650 m, 14/XI/2001, M. G. Cuezzo leg. & det.
Dry Material: Argentina, Salta Prov.: FML 125, La Candelaria Mountain, 15/VII/1931, Schreiter, R. leg., W. Weyrauch det. FML 14526, Metán Dept., on road to Cabra Corral, 25°16'34"S, 65°18'45"W, M. G. Cuezzo leg. MLP unnumbered, La Viña Dept., Alemania, Birabén leg., ex Hylton Scott collection. FML 14734, Cafayate, Yacochuya del Norte, 26°02'14"S, 66°01'34"W, 2,000 m, 25/III/2005, M. G. Cuezzo leg. & det. Argentina, Catamarca Prov.: FML 14372, Esquiú Dept., Dique Las Pirquitas, 25 km N from Catamarca, 850 m, 21/I/1968, W. Weyrauch leg. & det. FML 563, El Rodeo, 1/I/1958, R. Golbach leg., J. J. Parodiz det. FML 14521, Capayán Dept., Quebrada La Cébila, 1,100 m, 15/XI/1968, W. Weyrauch leg. & det. FML 14525, El Desmonte, km 1331 on road from Catamarca to Pirquitas, 700 m, 15/XI/1968, W. Weyrauch leg. & det. FML 14523, Esquiú Dept., El Hueco, 7 km from Catamarca, on road to Pirquitas, 600 m, 15/IX/1968, leg. & det. by W. Weyrauch. FML 14522, Ambatos Dept., Cuesta de la Puerta, between Pirquitas and Ambato, 900 m, 15/IX/1968, leg. & det. by W. Weyrauch. FML 14450, Ambatos Dept., on road from Las Estancias to Singuil, 27°36'20"S, 65°58'36"W, 1,920 m, 29/XI/2003, M. G. Cuezzo leg. FML 14722, Ambatos Dept. Las Chacritas, on road to Singuil from Las Estancias, 27°41'42"S, 65°55'09"W, 1,780 m, 30/XI/2003, M. G. Cuezzo leg. FML 538, Close to El Alamito, km 80 on road from Andalgalá to Tucumán, 1,600 m, Weyrauch, Willink & Tomsic leg. J. J. Parodiz det.

Description:
External Features: Body dark red with dark brownish to blackish background.
Shell (Fig. 4D): Dextral, subglobose, semisolid; spire shallow conical; medium to large size; 4½ convex whorls; pale brown to pale chestnut; body whorl with one equatorial brown peripheral band that also lines the suture but is absent on spire; protoconch smooth; surface of body whorl with very thin growth-lines and peripheral lines, giving appearance of a malleated surface; suture shallow; aperture

circular with white to chestnut, thick, reflexed peristome; parietal wall space between margins of upper and basal lip narrow; body whorl abruptly descending behind aperture; umbilicus deep, narrow, partly overlapped by basal columelar peristomal lip.

Measurements: Paralectotype MACN 1289: D maj: 30.2 mm; D min: 25.4 mm; H: 15.6 mm; D ap: 18.1 mm.

Specimens from Quebrada de La Cébila, Catamarca (n = 10): DM: 30.8–27.7 mm (29.0 mm); D min: 26.8–23.6 mm (25.0 mm); H: 16.6–14.9 mm (15.5 mm); D ap: 18.8–17.3 mm (18.0 mm); H ap: 16.6–14.0 mm (15.3 mm).

Jaw: Arched, thin, orange, with three to six central wide ribs; ribs not very pronounced or delimited; borders of ribs projecting at both edges.

Pallial Complex: Lung roof without dark spots; kidney extending about 60% of pulmonary roof length; main pulmonary vein splitting into two mayor veins in distal portion of pulmonary roof.

Genitalia (Fig. 12D, E): Dart sac complex in terminal genitalia consisting of single dart sac with two mucous glands; right mucous gland sac-like, distally fused with atrium wall, opening into a thin duct; left mucous gland oval-elongate, smaller than dart sac, opening into thin distal duct; both mucous gland efferent ducts distally fused with each other before entering dart sac; dart sac muscular, thick, cylindrical, with medial constriction below which mucous glands duct inserts; dart papillae cylindrical, half as long as distal portion of dart sac; dart sac ending at atrium level with vagina and penial complex; vas deferens looping around dart sac constriction before running towards penial complex; bursa copulatrix sac oval with thick, short to medium duct; sac and duct of bursa copulatrix not neatly delimited; vagina short, as long as penis; penial complex medium in length; flagellum thin, cylindrical, with thick distal portion ending level where vas deferens enters penial complex and epiphallus begins; epiphallus thin, as long as penis; penial retractor muscle inserting in median portion of epiphallus; penis cylindrical, thicker than epiphallus, entering at genital atrium level with dart sac and vagina; penial papillae absent; internal wall of penis with thin undulating pleats; penis sheath simple, muscular, overlapping distal portion of penis and distally fused with atrium wall; penial muscular band absent; atrium very short.

Habitat: Usually found under rocks or adhered to walls in narrow rock crevices. In Catamarca, *E. rhathymos* inhabits xerophilic environments where also some bulimulids and odontostomids species are abundant. Its vertical habitat distribution ranges between 600 and 2,000 m above sea level.

Distribution (Fig. 20): *Epiphragmophora rhathymos* is more abundant in Catamarca Province, but it is also found in some localities of Salta, Tucumán and Córdoba provinces, northwestern and central Argentina. Although is distributed mainly in the Chaco biogeographic province, there are some localities in Salta and Tucumán, where the vegetation is a transition to Yungas rainforest.

Remarks: *Epiphragmophora rhathymos* is similar to *E. trenquelleonis* in general shell morphology except for the malleations sculpture on the body whorl. Shell color is also very different. Body color is similar but usually animals of *E. rhathymos* tend to be more reddish.

Epiphragmophora saltana Ancey, 1897
(Figs. 5A, 13A–C, 19)

Epiphragmophora saltana Ancey, 1897: 9.
Epiphragmophora saltana – Parodiz, 1957, 71: 30.
Epiphragmophora saltana – Fernández & Rumi, 1984b: 246.

Holotype: BMNH, Salta Prov., Argentina.

Other material Examined:
Dissected Material: Argentina, Salta Prov.: FML 14392A, Candelaria Dept., El Tala, X/1998, E. Dominguez leg. FML 14391A, Candelaria Dept., Route 6, 6 km from El Jardin, close to El Tala river, XI/1996, M. G. Cuezzo & C. Ituarte leg.
Dry Material: Argentina, Salta Prov.: FML14391, Candelaria Dept., Route 6, 6 km from El Jardin, close to El Tala river, XI/1996, M. G. Cuezzo & C. Ituarte leg. MACN 20369: Rosario de la frontera.

Description:
External Features: Animal body yellowish to light brown with double row of dorsal pustules in cephalic region from mantle collar to the ommatophores.

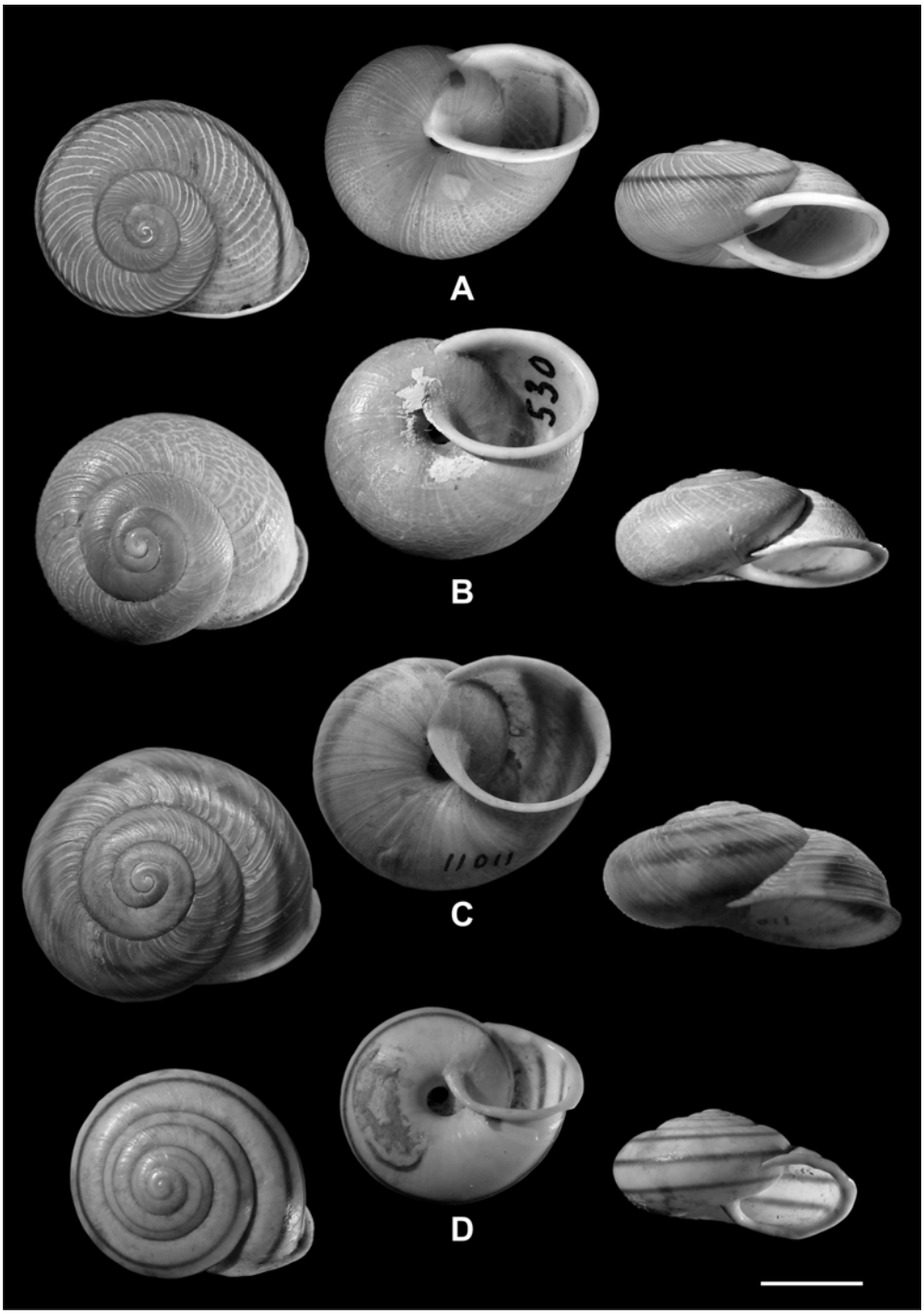

FIG. 5. Shells in dorsal, ventral and lateral view. A: *Epiphragmophora saltana* (NHM, holotype); B: *Epiphragmophora tomsici* (FML 530, holotype); C: *Epiphragmophora trifasciata* (MACN 24406, holotype); D: *Epiphragmophora trigrammephora* (MNHN, syntype). Scale bar = 15 mm.

Shell (Fig. 5A) Dextral, helicoidal, depressed-globose, solid; spire shallow conic; medium size; 4½ convex whorls; yellowish to golden; thin pigmented dark brown spiral band on body whorl; protoconch smooth; axial pale ribs regularly distributed in all whorls, surface between ribs strongly malleated; suture well impressed; aperture transverse, oval; peristome white, thick, reflexed; parietal callus usually raised, whitish, thin; body whorl abruptly descending towards aperture; umbilicus narrow partly to totally overlapped by peristomal lip.

Measurements: Ancey's original description (two shells): D maj: 32 mm, 29 mm; D min: 25½ mm, 25.0 mm; H: 17½ mm, 16½ mm.

Specimens from Type Locality Salta, El Tala (n = 16): D maj: 23.8–29.3 mm (27.2 mm); D min: 21.8–25.6 mm (23.6 mm); H: 13.4–16.4 mm (14.8 mm).

Specimens from Salta, El Jardín (n = 4): D maj: 26.6–29.1 mm (28.0 mm); D min: 22.0–24.6 mm (23.6 mm); H: 14.2–17.4 mm (15.2 mm).

Jaw: Arched, thin with five to seven thin ribs; margins of ribs projecting at both edges.

Pallial Complex: Lung roof without dark spots; kidney extending 60% of total pulmonary roof length; main pulmonary vein subdivided in two mayor veins proximally, distally they further divide into several minor veins before reaching mantle collar.

Genitalia (Fig. 13A–C): Dart sac complex in terminal genitalia consisting of single dart sac and two mucous glands; right gland sac-like, enveloping distal zone of vagina and dart sac, not fused to atrial wall; left mucous gland oval-elongate, opening into efferent duct that joins and fuses with thinner right gland efferent duct forming unique duct; dart sac muscular, cylindrical, with medial constriction, below which mucous glands duct inserts; thin dart gland, located inside distal portion of dart sac; dart sac gland half length of distal dart sac portion; dart sac ending at atrium level with vagina and penial complex; bursa copulatrix round to oval with thick, short to medium length duct; vagina shorter than penis; penial complex long; flagellum thin, finger-like, short, gradually tapering towards end; flagellum ending level where vas deferens enters penial complex and epiphallus begins; epiphallus long, thinner than penis, not externally differentiated from it; penis thin, slender, entering genital atrium level with dart sac and vagina; penial papillae absent; internal wall of penis with thin undulating parallel pleats; penis sheath muscular, thick, distally multilayered, fused with atrium wall, proximal penis sheath thin, single layer, overlapping all penis length; penial muscular band absent; atrium extremely short.

Habitat: Subtropical humid rainforest in Yungas biogeographic province, northwestern Argentina. Live specimens usually found below humid tree trunks on the floor in contact with soil.

Distribution (Fig. 19): *Epiphragmophora saltana* is known only from southern Salta Province, northwestern Argentina.

Remarks: *Epiphragmophora saltana* is similar in shell morphology to *E. birabeni*. It shares shell characters such as the presence of axial regular ribs with *E. birabeni* and *E. costellata*. The anatomy of these two species is unknown.

Epiphragmophora tomsici Fernández & Rumi, 1984
(Figs. 5B, 13D, E)

Epiphragmophora tomsici Fernández & Rumi, 1984b: 246, pl. 7, figs. 6–8.

Holotype: FML 530, Argentina, Catamarca, Dept. Andalgalá, 20 km from Andalgalá, road to Cafayate, 1,800 m, 26/II/1962, W. Weyrauch Col.

Other Material Examined:

Dissected Material: Argentina, Catamarca Prov.: FML 14529 A, Andalgalá Dept., junction of Blanco river with Candado river where Andalgalá river begins, 27°27'23"S, 66°16'15"W, 25/V/1997, Schrocchi, G. leg. FML 14445 A*, Andalgalá Dept., 20 km from Andalgalá on road to Mina Capillitas, 27°29'07"S, 66°22'57"W, 1,800 m, 29/XI/2003, Ituarte, C. leg. Argentina, Tucumán Prov.: FML 14390A, Trancas Dept., road 364 close to Rearte, 26°22'53"S, 65°31'35"W, 1,130 m, 15/X/1996, M. G. Cuezzo leg. & det. FML 14527A, Trancas Dept., road 364 close to Rearte, 26°22'53"S, 65°31'35"W, 1,130 m, 30/III/1997, M. G. Cuezzo leg. & det. FML 14528 A, Trancas Dept., on road 364, close to Rearte, 26°22'53"S, 65°31'35"W, 1,130 m, 7/5/2002, M. G. Cuezzo leg.

Dry Material: Argentina, Catamarca Prov.: FML 530, Paratypes, Andalgalá Dept., 20 km from Andalgalá on road to Santa María, 1,800 m, 8/XII/1968, W. Weyrauch leg. & det. FML 14725, Andalgalá Dept., Cuesta Mina Capillitas, 27°29'54"S, 66°22'53"W, 1,630 m, 29/XI/2003, M. G. Cuezzo & C. Ituarte leg. Argentina, Tucumán Prov.: FML 14390, Trancas Dept., road 364 close to Rearte, 26°22'53"S, 65°31'35"W, 1,130 m, 15/X/1996. M. G. Cuezzo leg. & det. FML 795, Trancas Dept., 3 km S of San Pedro de Colalao, 1,200 m, J. S. Guanuco leg., W. Weyrauch det. FML 1210, Trancas Dept., 6 km S of San Pedro de Colalao, 1/XI/1963, Guanuco, J. S. leg. FML 14288, Trancas Dept., San Pedro de Colalao, 1/II/1994, Dragh, F. leg. FML 11313, Trancas Dept., Vipos river, 10 km from Vipos gas station, 1/V/1964, R. Herbst leg.

Description:

External Features: Animal variable in body color, specimens from Tucumán Province usually homogeneously light brown; specimens from type locality in Catamarca Province bright red to bright orange; shell color similar in both localities.

Shell (Fig. 5B): Dextral, helicoidal, globose, solid; spire shallow conic, with thin axial growth lines; medium size with 4½ convex whorls; light brown to light chestnut; peripheral band absent; protoconch smooth; axial whitish ribs regularly distributed on body whorl; surface between ribs in body whorl strongly malleated, forming distinctive white reticulated pattern; suture well impressed; aperture transverse oval; peristome white, thick, reflexed; parietal callus usually raised, whitish, thin; parietal space between lips narrow; body whorl abruptly descending towards aperture; umbilicus open partly overlapped by peristomal lip.

Measurements: Holotype: D maj: 27.2 mm; D min 24.0 mm; H: 13.8 mm.
Paratypes (n = 4): D maj 24.0–26.3 mm (25.3 mm); D min: 21.6–24.9 mm (22.7 mm); H: 12.0–15.2 mm (13.7 mm).
Other Material: FML, Tucumán, Los Rearte (n = 10): D maj: 25.0–28.8 mm (27.3 mm); D min: 22.4–25.0 mm (23.6 mm); H: 14.0–15.3 mm (14.6 mm).

Jaw: Arched with five thin central ribs; margins projecting at both edges.

Pallial Complex: Lung roof homogeneously pale cream without pigmented dark spots, lung roof heavily traversed by minor thin venation, especially between kidney and rectum; kidney length 60% of total lung roof length; main pulmonary vein bifurcated into two thick veins in distal lung until mantle collar.

Genitalia (Fig. 13D, E): Dart sac complex in terminal genitalia consisting of single dart sac and two mucous glands; right gland sac-like, enveloping distal portion of vagina, dart sac and atrium in all its length, not fused with the atrial wall; left mucous gland cylindrical ending at thin efferent duct that joins with thinner duct of right gland closed to insertion point in dart sac; dart sac muscular, cylindrical, with medial constriction below which mucous glands duct inserts; thin, cylindrical dart gland located inside distal portion of dart sac; dart papillae as long as distal portion of dart sac; dart sac ending at atrium level with vagina; bursa copulatrix sac oval with thick medium length duct; limit between sac and duct not sharp; vagina medium length but shorter than penis; penial complex long; flagellum thin, long, ending level with where vas deferens enters penial complex and epiphallus begins; proximal epiphallus widening at point of insertion of vas deferens; epiphallus as long as penis, not differentiated from it externally; penial retractor muscle inserting in distal portion of epiphallus; penis simple entering at genital atrium level with dart sac and vagina; penial papillae absent; internal wall of penis with thin undulating folds in all its length; penis sheath muscular but thin, basally multilayer, overlapping half penis length, distally fused with atrium wall; penial muscular band absent; atrium short, totally overlapped by mucous gland.

Habitat: *Epiphragmophora tomsici* is found in xerophilic environments, usually hidden inside rock crevices or under fallen cactus.

Distribution: This species is found in Catamarca and Tucumán provinces, northwestern Argentina, in the Yungas and Chaco biogeographic provinces.

Remarks: Genitalia similar to *E. saltana* except for the length of the bursa copulatrix duct, shape of bursa copulatrix sac, length of atrium and length of flagellum. Shells of both species are very different in size, color and sculpture of the body whorl.

Epiphragmophora trenquelleonis (Grateloup, 1851)
(Figs. 6B, 14A–C, 21)

Helix trenquelleonis Grateloup, in Pfeiffer, 1851: 13, pl. 3, fig. 3–5.
Helix group *Eurycampta monographa* – Burmeister, 1861: 77, *non Helix Eurycampta monographa* Doering, 1874, = *E. rhathymus* (Holmberg).
Helix group *Eurycampta hidalgonis* Doering, 1875a: 315.
Helix group *Eurycampta Trenquelleonis* – Doering, 1875b: 156.
Helix hidalgonis – Kobelt, 1878: 144.
Helix doeringiana – Holmberg, 1909a: 9.
Epiphragmophora trenquelleonis – Parodiz, 1957: 29.
Epiphragmophora (*Doeringia*) *trenquelleonis* – Zilch, 1959–1960: 656.
Epiphragmophora trenquelleonis hidalgonis – Hylton Scott, 1965: 24.
Epiphragmophora trenquelleonis – Fernández & Rumi, 1984b: 247.

Lectotype SMF 7708, Argentinean: Vorberge der Sierra de Cordoba, namentlich die Sierra Chica und die Sierra de Pocho. A. Doering.

Other Material Examined:
Dissected Material: Argentina, Cordoba Prov.: FML 14434A, San Justo Dept., San Esteban, 5/XII/1986, leg. Z. Tomsic. FML 14435A Santa Maria Dept., 20 km S Alta Gracia, 28/I/1998, E. Dominguez leg. FML 14436A Calamuchita Dept., Rio Tercero, 28/I/1998, M. G. Cuezzo leg. FML 14437A, Punilla Dept., Valle Hermoso, La Falda, 28/I/1998, leg. M. G. Cuezzo FML 14438A, Cruz del Eje Dept., Route 15 between Villa de Soto and La Higuera, 30°59'12"S, 65°04'W, 650 m, 14/XI/2001, M. G. Cuezzo leg. & det. MLP unnumbered: Embalse Rio Tercero. Ringuelet leg., 1946. MLP unnumbered: Cabana.
Argentina, San Luis Prov.: FML 1314, Ayacucho Dept., 20 km from Santa Rosa, on road to Quines, 650 m, 23/II/1968, leg. W. Weyrauch. FML 14439 A, San Martín Dept., route 2 between Libertador General San Martín and Quines, 32°20'26"S, 65°41'W, 815 m, 15/XI/2001, leg. & det. Cuezzo, M. G.; FML 14768 A, San Martín Dept., close to Quines, 32°17'19"S, 65°41'21"W, 555 m, 16/XI/2001, leg. & det. M. G. Cuezzo.

Dry Material: Argentina, Córdoba Prov.: FML 14717, Rio Seco Dept., 5 km North of Villa María, 440 m, 25/XII/1967, W. Weyrauch leg. FML 10889, Rio Seco Dept., 5 km N of Villa María, 440 m, 25/XII/1967, Weyrauch leg & det. MLP 446, Rio Seco Dept., El Zapallar, Borello, A. leg. 24/V/1964, Hylton Scott det. FML 792, Ischilín Dept., 7–8 km from Charbonier, on road to Copacabana, 920 m, 26/III/1967, leg. & det. W. Weyrauch. MLP 1658-1, Ischilín Dept., Quilinos, Biraben, M., 5/III/1945. FML 705, Punilla Dept., close to Villa Carlos Paz, 700 m, 23/III/1967, leg. & det. W. Weyrauch. FML 929, Punilla Dept., Punilla Valley, San Esteban, leg. & det. W. Weyrauch. FML 14362, Punilla Dept., Villa Carlos Paz, 700 m, 23/III/1967, Weyrauch leg & det. FML 14361, Punilla Dept., 6 km from Capilla del Monte, 900 m, 25/XII/1967, Weyrauch leg. MLP 2164, Punilla Dept., Capilla del Monte. FML 910, Pocho Dept., Sierra de Pocho between Las Palmas and Chancani, 1,050 m, 12/XI/1967, leg. & det. W. Weyrauch. FML 14289, Pocho Dept., NW of Sierra de Pocho close to Chancani, 900 m FML 225, Colon Dept., Cabana, Sierra Chica, leg. & det. by Hylton Scott. FML 12766, Colón Dept., Sierra Chica, leg. & det. Hylton Scott. MLP 995, Colon Dept., Rumi Huasi, Cabana. MLP 4248-1, Colón Dept., Unquillo, Cabana, ex Hylton Scott collection. MLP 1640, Colón Dept., Rio Ceballos, 3/II/1939. FML 1319, Santa María Dept., Villa Anisacate, 40 km, SE of Córdoba, 21/III/1968, leg. & det. W. Weyrauch. MLP 4247, Santa María Dept, Alta Gracia, Hylton Scott leg. FML 716, Dean Funes Dept., San Vicente Mountain, 8 km E of Dean Funes, 300 m, 26/III/1967, Weyrauch leg. & det. FML 14375, Dean Funes Dept., San Vicente Mountain, 8 km E of Dean Funes, 800 m, 6/IV/1969, Weyrauch leg. FML 14363, San Alberto Dept., Los Pozos, on road from Mina Clavero to Villa Dolores, 21/II/1968, leg. & det. by Weyrauch. MLP 4249, Totoral Dept., Las Cortaderas, Hylton Scott-Biraben leg. 1949. MLP 4288, Calamuchita Dept., Las Bajadas, Ringuelet, R. leg. 06/I/1943. MLP unnumbered, Cuesta de Chancani, Cichero-Martinez leg., XI/1966. MLP 4306, Calamuchita Dept., San Agustín, X/1970. MLP 1674, La Calera, Pacheco, A. leg., 1934. Argentina, San Luis Prov.: FML 1314, Ayacucho Dept., on road to Quines, 20 km from Santa Rosa, 650 m, 23/II/1968, W. Weyrauch leg. MLP 4309, Piedra Blanca, II/1949. MLP 981, Ayacucho Dept., Quines, El

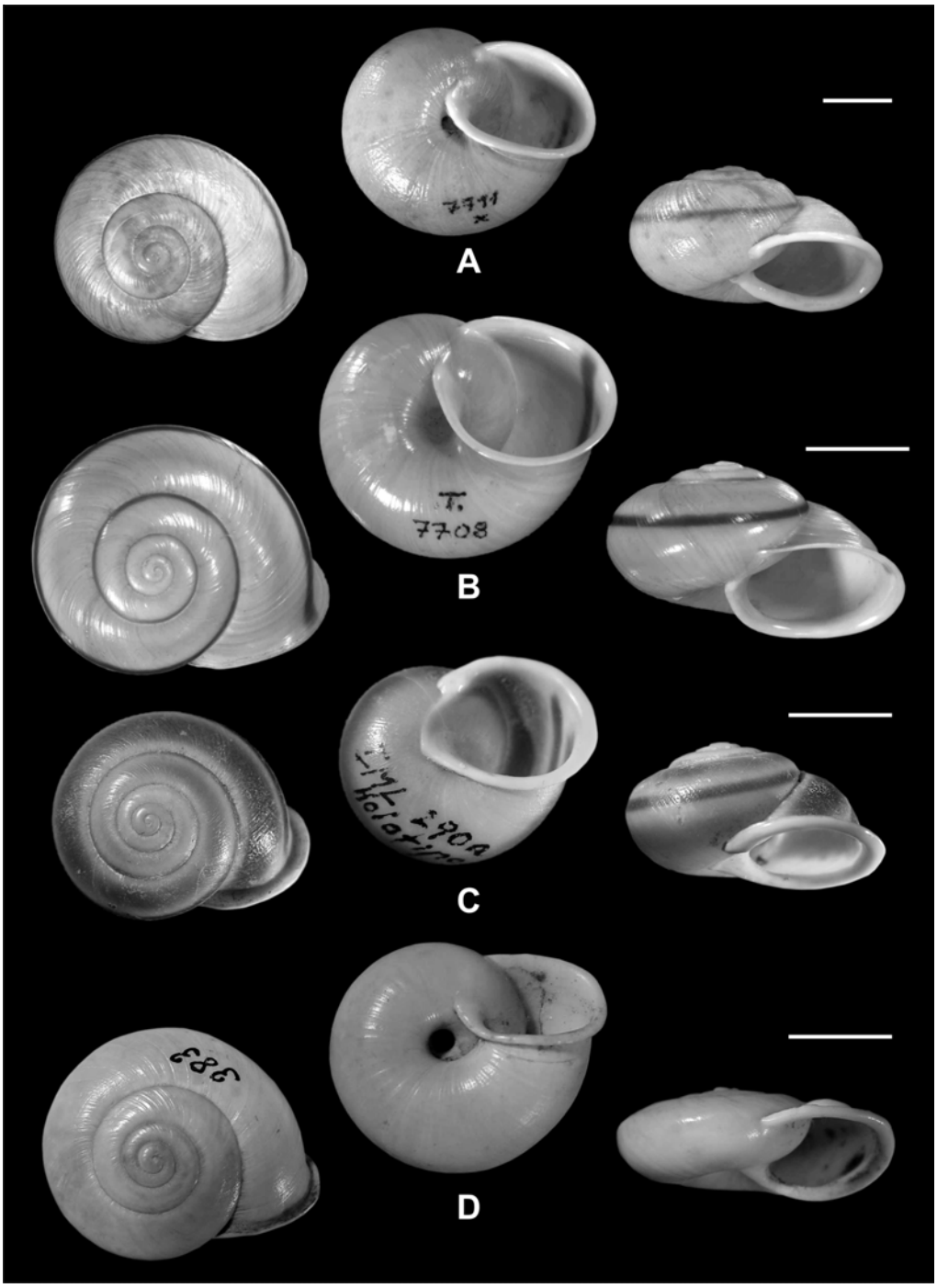

FIG. 6. Shells in dorsal, ventral and lateral view. A: *Epiphragmophora tucumanensis* (SKF 7711, lectotype). Scale bar = 10 mm; B: *Epiphragmophora trenquelleonis* (SMF 7708, lectotype). Scale bar = 10 mm; C: *Epiphragmophora variegata* (FML 290 a, holotype). Scale bar = 15 mm; D: *Epiphragmophora villavilensis* (MACN 383, holotype). Scale bar = 15 mm.

Zapallar, Hylton Scott leg. 17/II/1940. MLP 1281, Piedra Blanca, Ringuelet, R. leg., II/1949. MLP 1664, Pringles Dept., Paso del Rey, Vignatti leg. MLP unnumbered, Pringles Dept., La Toma.

Argentina, Catamarca Prov.: FML 592, El Alto, 950 m, 2/XII/1958, Hayward, K. leg. W. Weyrauch det. FML 11050, Capayan Dept., Los Angeles, 1/XI/1944, Weyrauch det.

Description:

External Features: Body dark orange, with ocular tentacle brownish towards the tip.

Shell (Fig. 6B): Dextral, helicoidal, subglobose, semisolid; spire shallow conical; medium size; 4½ convex whorls; yellowish to dark brown or chestnut; body whorl usually with one equatorial brown periphery band that also lines suture, absent on spire; shells from some localities can has a maximum of three peripheral bands, medial one more neatly delimited; protoconch smooth; teleoconch surface with very thin growth-lines or with thick regularly separated growth-ridges; fine transversal lines located between them cutting transversally axial ridges; aperture circular with white, thin, slightly reflexed peristome; parietal space between lips narrow; body whorl abruptly descending behind aperture; umbilicus deep partly overlapped by basal columelar peristomal lip; suture shallow.

Measurements: (n = 15) Dm: 25.4–34.5 mm (29.3 mm); D min: 23.1–30.0 mm (25.4 mm); H: 12.9–20.4 mm (16.3 mm); D ap: 16.1–20.9 mm (17.7 mm); H ap: 14.0–18.3 mm (15.3 mm).

Jaw: Strong, arched; four vertical ribs with regular spaces between them, margins projecting at both concave and convex jaw edges.

Genitalia (Fig. 14A–C): Terminal genitalia with dart sac complex consisting of single dart sac and two mucous glands; right gland smaller than left, round or slightly elongated, located between dart sac and vagina, distally fused with atrium wall; with thin duct located distally respect to body of gland, duct inserting below constriction of dart sac; left mucous gland oval elongated, longer than right, opening into thin duct, distally located respect to body of gland; both mucous gland ducts fused together before entering dart sac; dart sac muscular, very long, cylindrical, with distal portion thicker than proximal, both portions separated by medial constriction; dart sac naturally pleated at level of constriction; dart papillae thick, as long as distal portion of dart sac; dart sac ending at atrium level with vagina and penial complex; bursa copulatrix sac round, with very thick, short duct; sac and duct of bursa copulatrix neatly delimited; vagina long, shorter than penis; free oviduct thin, long, folded by itself, enveloped by connective tissue attaching it to bursa copulatrix; vas deferens surrounding dart sac before reaching penioviducal angle and inserting in penial complex; penial complex very long; flagellum thin, medium in length, finger-like, ending level where vas deferens enters penial complex and epiphallus begins; epiphallus shorter than penis, externally differentiated from it by abrupt change in diameter; penial retractor muscle thick, inserting in median portion of epiphallus; penis very long, cylindrical, usually four times longer than epiphallus, entering at genital atrium level with dart sac and vagina; penis usually folded by itself, with a constriction where penial sheath ends; some specimens constriction not evident, but penis notably thinner at the same point; penis sheath simple, very thick, muscular; penis sheath overlapping distal portion of penis; distal portion of penis notably thinner but together with penis sheath considerably thicker than proximal one; penial papillae short, triangular; internal distal wall of penis with thin, smooth, straight folds; proximally, close to penial papillae, penial wall with longitudinal thin pleats in zigzag pattern; vas deferens attaching to proximal penial sheath; penial muscular band absent; atrium long, with thick walls.

Habitat and Distribution: This species is widely distributed, in contrast to the majority of the *Epiphragmophora* species. *Epiphragmophora trenquelleonis* is found in Cordoba, Santiago del Estero, San Luis, Catamarca, La Rioja, Chaco and Formosa provinces, Argentina. It is also recorded for southeastern Bolivia and Paraguay. In northwestern Córdoba, *E. trenquelleonis* is more abundant than in other provinces, Argentina. Its area of distribution is included into the Chacoan biogeographic subregion.

Remarks: *Epiphragmophora trenquelleonis* is very variable in shell size and morphology. Specimens from San Luis Province, central-western Argentina, have a characteristic thinner shell and have axial ridges in the body whorl instead of the characteristic fine shell

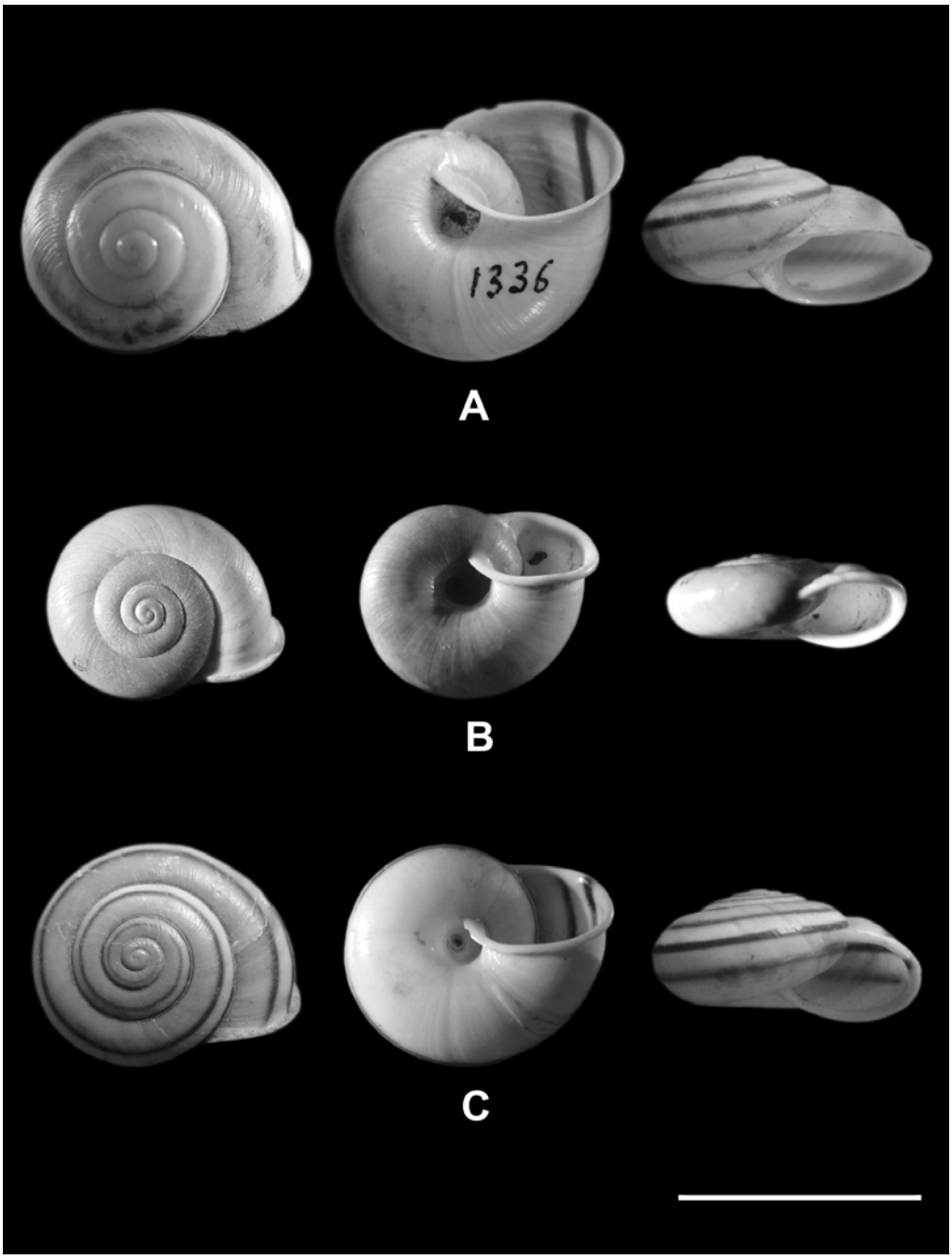

FIG. 7. Shells in dorsal, ventral and lateral view. A: ***Epiphragmophora guevarai*** (FML 14766, paratype); B: ***Epiphragmophora quirogai*** (FML 14719, paratype); C: ***Epiphragmophora walshi*** (FML 14764, paratype). Scale bar = 20 mm.

growth lines of specimens from Córdoba Province. Nevertheless, the genitalia show the same morphological pattern. Shell color is also very variable. Most noteworthy characteristics of the present species are the thick, short duct of the bursa copulatrix, a very long vagina, and the length of the penial complex, the longest of the species of *Epiphragmophora* studied. The presence of a penial constriction or a medial thinner portion is also a character not seen in other species studied. Some of the morphological variations in the genitalia are differences in vagina lengths and penial complex lengths, but the proportion between the length of the epiphallus and the penial length is constant in all specimens studied. Genitalia of *E. trenquelleonis* are similar to *E. trifasciata* Fernandez & Rumi but differ from it mainly in length of vagina, length and shape of penial complex and mucous glands. Both mentioned species, together with ***E. guevarai*** n. sp., have the shortest bursa copulatrix ducts of the genus.

Epiphragmophora trifasciata Fernández & Rumi, 1984
(Figs. 5C, 15A, B)

Epiphragmophora trifasciata – Fernández & Rumi, 1984b: 249. pl. 3, figs. 6–8, *non Helix Eurycampta trenquelleonis var. c. trifasciata* Doering, 1875a: 315.

Holotype and Paratypes: MACN 24406, Argentina, Córdoba, Agua de Oro, East Side of Sierra chica mountain, 1940, leg. José A. de Carlo.

Other Material Examined:
Dissected Material: Argentina, Córdoba Prov.: FML 14716A*, Argentina, Córdoba, Punilla Dept., Cruz Chica, 28/I/1998, Domínguez, E. leg.
Dry Material: Argentina, Córdoba Prov.: MACN 24406. FML 11011, Argentina, Córdoba, Colón Dept., between Ascochinga and El Chorrito on road from Jesús María to La Cumbre, 800 m., 25/II/1966. leg. W. Weyrauch. FML 11012, Argentina, Córdoba, El Chorrito, 1,100 m, 26/II/1966. W. Weyrauch Col. FML 942, Córdoba, Totoral Dept., Ascochinga, La Cumbre, 1,300 m, 24/XII/1967, leg. W. Weyrauch.

Description:
External Features: Body color homogeneous orange to dark red; facial groove well impressed.
Shell (Fig. 5C): Dextral, helicoidal, subglobose, solid; spire conical; medium size; 4½ convex whorls; yellowish to dark brown; body whorl with three brown peripheral bands, usually central band darker and wider than ventral and dorsal bands; protoconch smooth; surface with strong growth-ridges; suture shallow; aperture circular, with white, thin, slightly reflexed peristome; body whorl descending behind aperture; umbilicus deep, partly overlapped by peristomal lip.
Measurements: Paratypes (n = 2): D maj: 31.5 mm, 29.6 mm; D min: 26.7 mm, 28.2 mm; H: 16.8 mm, 15.4 mm; D ap: 19.5 mm, 16.6 mm.
Other Material: FML 14716 (n = 13): D maj: 28.3–32.5 mm (27.9 mm); D min: 25.0–28.3 mm (24.9 mm); H: 14.4–17.9 mm (14.7 mm).
Jaw: Arched, thin, orange; five vertical narrow ribs in central portion of the jaw.
Genitalia (Fig. 15A, B): Terminal genitalia with dart sac complex consisting of single dart sac and two unequal mucous glands; right gland small, round, located between dart sac and vagina, distally fused with atrium wall, opening into thin duct; left mucous gland cylindrical to oval with thin efferent duct running parallel to right mucous gland duct; both efferent ducts from glands distally fused with each other before entering dart sac; left mucous gland distally fused with atrial wall; dart sac long, muscular, cylindrical, with medial constriction below which mucous gland ducts inserts; dart papillae thick, cylindrical, as long as distal portion of dart sac, cylindrical papilla wrapped by connective tissue to dart sac wall ending at thin duct opening into atrium, love dart found within papilla; dart sac ending at atrium level with vagina and penial complex; bursa copulatrix sac round, with thick, very short duct; sac and duct of bursa copulatrix neatly delimited; vagina shorter than penis; penial complex short; flagellum triangular, with thick distal portion, ending level where vas deferens enters penial complex and epiphallus begins; epiphallus cylindrical, thick, shorter than penis, externally differentiated from it; penial retractor muscle inserting in median portion of epiphallus; penis cylindrical, thicker in proximal portion, gradually getting thinner

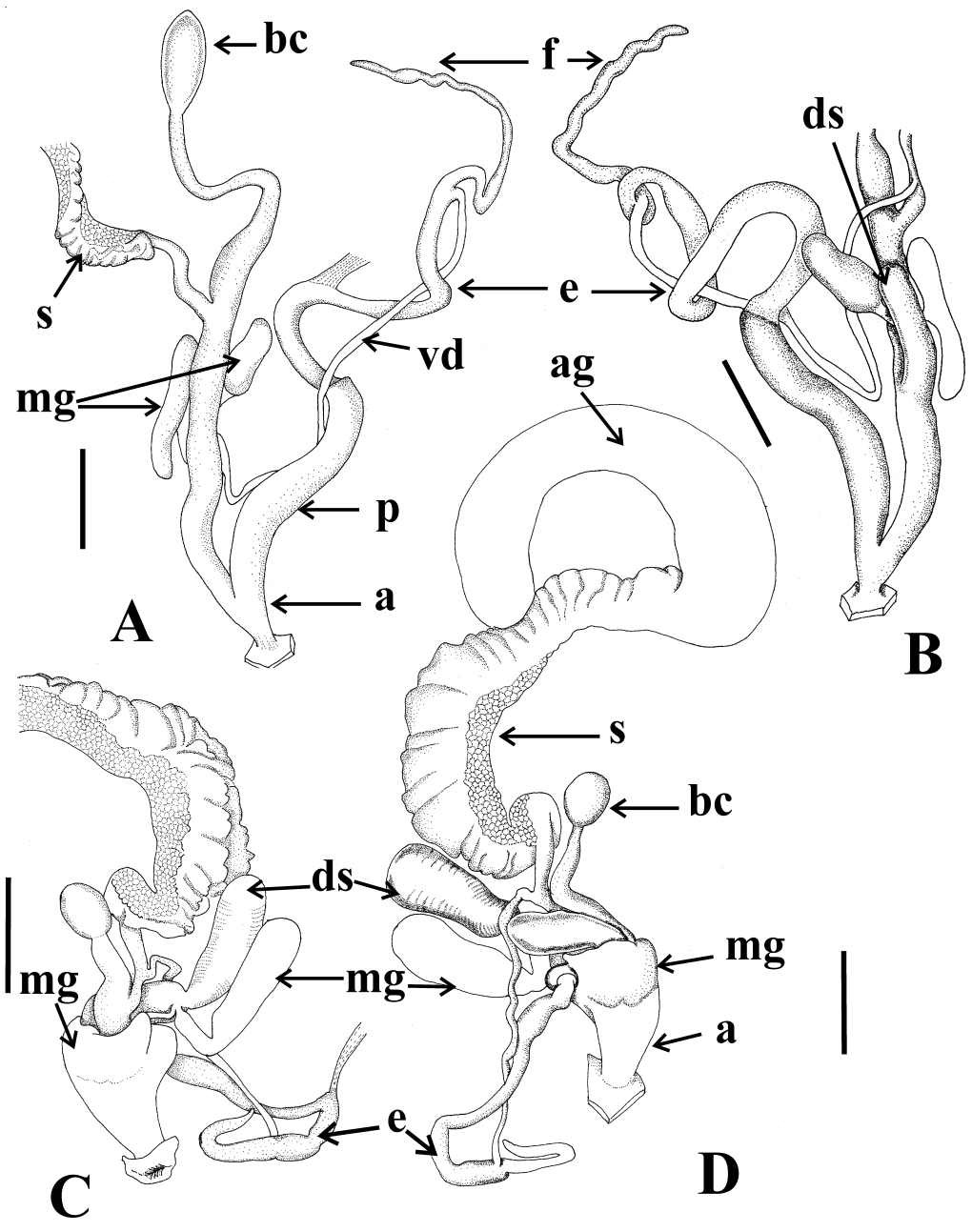

FIG. 8. *Epiphragmophora argentina and E. cryptomphala*. A: *E. argentina*, dorsal view of terminal genitalia; B: *E. argentina*, ventral view; C: *E. cryptomphala*, dorsal view of terminal genitalia, note mucous gland duct insertion; D: *E. cryptomphala*, ventral view of genitalia. Scale bars = 5 mm. Abbreviations: a, atrium; ag, albumen gland; bc, bursa copulatrix; ds, dart sac; e, epiphallus; f, flagellum; mg, mucous gland; p, penis; s, spermoviduct; vd, vas deferens.

towards distal portion, twice epiphallus length, entering at genital atrium level with dart sac and vagina; penial papillae short, located inside proximal penis; internal wall of penis with thin smooth strength pleats for all its length, some specimens with longitudinal pilaster; penis sheath simple, muscular, overlapping distal portion of penis, distally fused with atrium wall; penial muscular band absent; atrium medium in length not enveloped by mucous gland.

Habitat: *Epiphragmophora trifasciata* is found in close association to rocks or inside thin crevices between rocks.

Distribution: *Epiphragmophora trifasciata* is only known from northwestern and central Cordoba Province, Argentina, with a restricted area of distribution. Its area of distribution corresponds to the Chacoan biogeographic subregion (Morrone, 2006).

Remarks: Fernandez & Rumi (1984b) mentioned *E. trifasciata* as present in southwestern Santiago del Estero Province; nevertheless, no specimens has been found in that region nor in museum collections. For this reason, the distribution of *E. trifasciata* is now restricted to northwestern and central Córdoba Province, Argentina, based on the available data. *Epiphragmophora trifasciata* differs from *E. trenquelleonis* in shell characters such as body whorl sculpture, presence of three peripheral bands, size, and general shell shape. Differences in genitalia have been discussed in *E. trenquelleonis* and ***E. guevarai*** n. sp. descriptions.

Epiphragmophora trigrammephora
(d'Orbigny, 1835)
(Figs. 5D, 15C, D, 19, 21)

Helix trigrammephora d'Orbigny, 1835: 22.
Epiphragmophora trigrammephora – Ancey, 1897: 10.
Epiphragmophora trigrammephora – Parodiz, 1957: 30.
Epiphragmophora trigrammephora – Fernández & Rumi, 1984b: 250.

Syntypes: MNHN, Bolivia, Santa Cruz Dept., Valle Grande, 1835. BMNH, Bolivia, Santa Cruz, Pampa Grande.

Other Material Examined:
Dissected Material: Bolivia: NKC6, Santa Cruz Dept., Angel Sandoval Prov., Santo Corazón. 17°58'24"S; 58°48'28"E, NKC unnumbered, Santa Cruz Dept., Cordillera Prov., Parque Nacional Koá-Iya, 57 km O. from San José oil campament. 18°27'31"S, 61°22'53"W, 230 m, 13/VI/1998. Alfredo Fuentes leg. *FML 14784 A, Santa Cruz Dept., Valle Grande, margins of Ñancahuasu river, 19°04'41"S, 63°40'47"W, 538 m, 22/XII/2005. E. Dominguez leg. Paraguay: IBNP unnumbered, Chaco Dept., Parque Nacional Defensores del Chaco, Cerro León. 19/XI/1984. R. T. Bonace leg. IBNP unnumbered, Chaco Dept., Parque Nacional Defensores del Chaco, Cerro León, Sitio 5 hasta 8. Between 3er campament and sierra del Tigre, 16/XI/1984. J. A. Kochalka leg. Argentina, Jujuy Prov.: FML 14748 A, Santa Bárbara Dept., Sierra de Santa Bárbara, Octubre 1998. E. Dominguez leg. FML 108 A, Valle Grande Dept., on road to Valle Grande, 10/III/1989. E. Dominguez leg. FML 14749 A, Ledesma Dept., town of Yuto, margins of the river of the same name, 23°40'18"S, 64°29'44"W, 470 m, 3/IV/2004, M. G. Cuezzo leg. FML 14750 A, Valle Grande Dept., Route 83 on road to Valle Grande, 23°31'46"S, 64°57'47"W, 1,290 m, 3/IV/2004, M. G. Cuezzo leg. FML 14751 A, Ledesma Dept., Calilegua National Park, 23°45'36"S, 64°51'02"W, 700 m, 2/IV/2004, C. Nieto leg. MLP unnumbered, Jujuy Prov., Santa Bárbara Dept., El Palmar, 15/II/1947, Birabén leg. Argentina, Salta Prov.: FML 14752 A, Route 9, on road to El Carmen from Salta to Jujuy, 24°26'43"S, 65°17'59"W, 1,230 m, 18/XII/2001, M. G. Cuezzo leg. & det. MLP unnumbered, Gral. José de San Martín Dept., 27/XI/1954.
Dry Material: Argentina, Jujuy Prov.: FML 14737, Ledesma Dept., 6 km from Valle Grande, 23°30'39"S, 64°57'12"W, 1,570 m, 3/IV/2004, M. G. Cuezzo leg. & det. FML 14738, Ledesma Dept. town of Yuto, margins of Yuto river, 23°40'18"S, 64°29'44"W, 500 m, 3/IV/2004, M. G. Cuezzo leg. & det. FML 544, km 54 on road from Jujuy to San Pedro, 720 m, 24/II/1962. leg. & det. W. Weyrauch. FML 1385, San Pedro Dept., San Pedro, leg. P. Wygodzinsky, det. W. Weyrauch. FML 10, between Chalican and Quemado, 27/VII/1948. leg. A. Castellanos, det. Hylton Scott. FML 11055, Las Capillas, 36 km NW from Jujuy, 1,200 m, 25/II/1964.

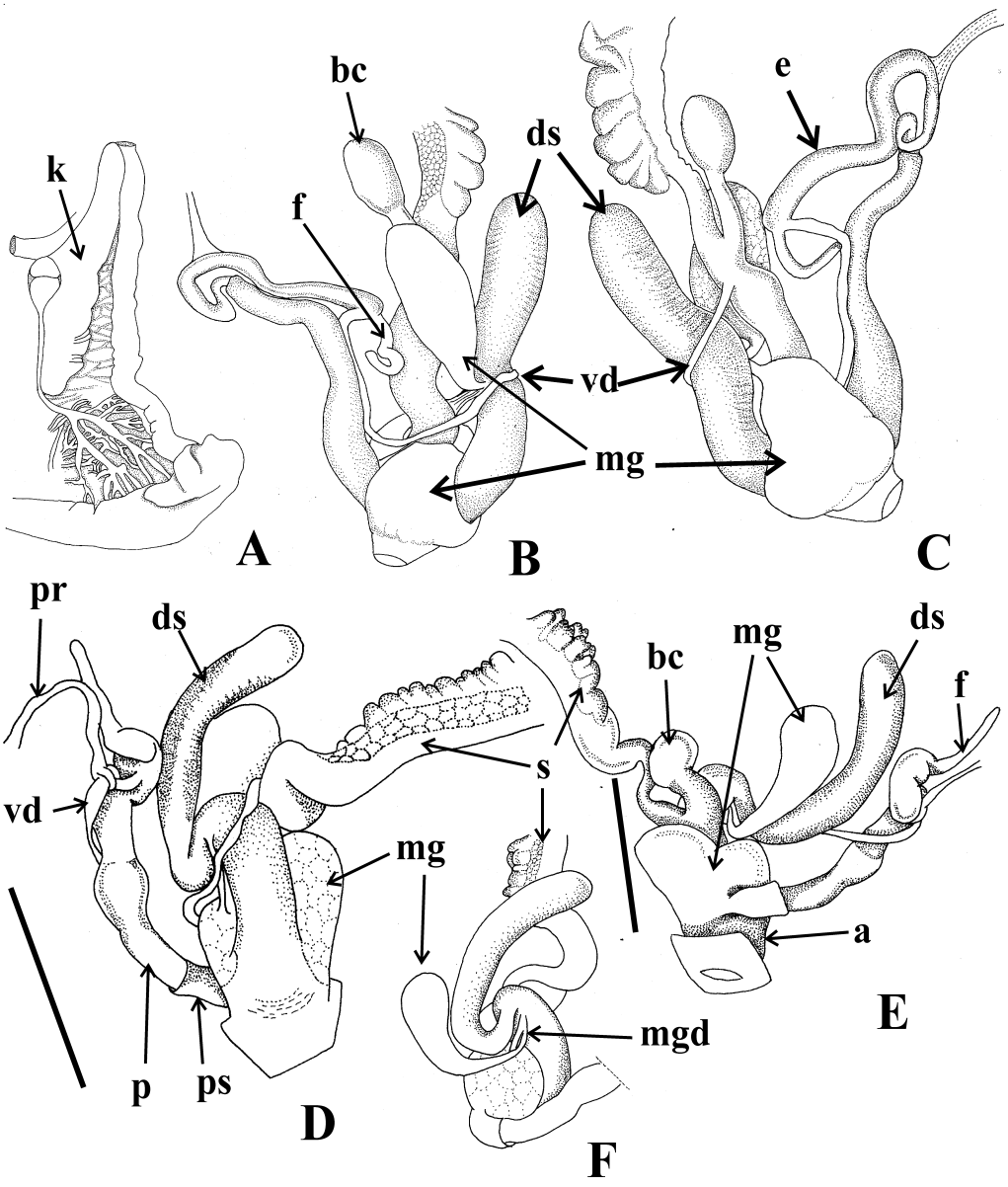

FIG. 9. *Epiphragmophora escoipensis* and *E. hieronymi*. A: *E. escoipensis*, pallial system; B: *E. escoipensis*, ventral view of terminal genitalia, note the point of insertion of both mucous glands ducts; C: *E. escoipensis*, dorsal view of terminal genitalia; D: *E. hieronymi*, ventral view of terminal genitalia; E: *E. hieronymi*, dorsal view of terminal genitalia, mucous gland is partially folded to see the fusion of both mucous glands ducts into one inserting in dart sac; F: *E. hieronymi*, lateral view of terminal genitalia shows point of insertion of mucous glands. Scale bars = 5 mm. Abbreviations: a, atrium; bc, bursa copulatrix; ds, dart sac; e, epiphallus; f, flagellum; k, kidney; mg, mucous gland; mgd, mucous gland duct; p, penis; ps, penis sheath; pr, penial retractor; s, spermoviduct; vd, vas deferens.

leg. & det. by W. Weyrauch. FML 926, La Cienaga, San Pedro, 3/III/1955, J. Foester leg. MLP 4258, El Aibal, Prosen, A. leg. I/1948. MLP 4266, Las Capillas, Biraben, M. 26/XI/1950. MLP unnumbered, San Pedro Dept., Las Quinas, La Mendieta, Birabén, M. 2/VI/1947. MLP unnumbered, El Palmar, Santa Bárbara, V/1947, ex Hylton Scott collection. MLP unnumbered, San Pedro Dept., La Mendieta, Birabén, M., V/1947, ex Hylton Scott collection. FML 901, 20 km South of Urundel, 400 m, 26/II/1964 leg. & det. by W. Weyrauch. FML 14736, Ledesma Dept. between Calilegua and Valle Grande, E. Dominguez leg. Argentina, Salta Prov.: FML 14365, Capital Dept., 13 km from Salta on road to Güemes, 1,300 m, 20/X/1968. leg. & det. by W. Weyrauch. FML 849, Orán Dept., 8 km N of Urundel, 350 m, 26/II/1964. leg. & det. W. Weyrauch. FML 827, Cerro Colorado, Puesto Pala-pala, 650 m, 21/II/1964, W. Weyrauch leg. & det. FML 633, Orán Dept., Urundel, 27/II/1949, Huek leg., W. Weyrauch det. FML 14735, Los Colorados, X/1993, F. Cruz & G. Scrocchi leg. FML 981, Gral. José de San Martín Dept., 10 km S of Embarcación, 300 m, leg. & det. by W. Weyrauch. FML 389, Güemes Dept., Cerro Pelado, 1,500 m, 4/I/1956. E. de la Sota leg. MLP unnumbered, Gral. Jose de San Martín Dept., Vespucio, ex Hylton Scott col. MLP unnumbered, Orán Dept., Urundel, ex Hylton Scott collection. MLP unnumbered, Carapacú, Bridarolli leg. 1945, ex Hylton Scott collection. MLP unnumbered, Anta Dept., Luis Burela, Birabén, M. leg. 20/XI/1954, ex Hylton Scott collection. MLP unnumbered, Termas del Palmar, Ramos de Martines leg. 10/I/1950, ex Hylton Scott collection. MLP unnumbered, Santa Victoria Dept., Cerro Colorado, Apostol, I. leg., I/1962. MLP 2152, Quebrada del Carapato, Birabén, M. leg., 22/XI/1951. MLP 1644, Gral. José de San Martín Dept., General Ballivian. MLP 4267, San Pedro, Birabén, M. 29/XI/1957. Argentina, Santiago del Estero Prov.: MACN 23037, Cerro del Remate, 1936, R. Schreiter leg. Argentina, Formosa Prov.: MLP 4264, Laguna Yema, Birabén, M. leg. 19/V/1947. MLP 4261, Ing. G. Juarez, M. Birabén, leg., XII/1954. Bolivia: FML 2241, 4–5 km W of Villa Montes, 400–500 m 6/VII/1969. leg. & det. by W. Weyrauch. FML 768, mountains W of Santa Cruz. leg. & det. by W. Weyrauch. MLP unnumbered, Santa Cruz, Rio Seco. 25/I/1964, Birabén, M. ex Hylton Scott collection. FML 240, Santa Cruz, 16/II/1947, Pierotti leg., W. Weyrauch det.

Description:

External Features: Uniform pale yellow to light gray; dorsal row of pustules between ommatophores well delimited.

Shell (Fig. 5D): Dextral, helicoidal, subglobose, semisolid; usually with high conical spire; medium size; 4¾ to 5¾ convex whorls; pale cream to yellow; three peripheral thin, darker brown bands clearly delimited on body whorl, upper band running centrally in each anfractum of spire, usually central band slightly wider, more darkely pigmented than others, always with well defined limits; protoconch smooth, first whorls with thin growth lines; teleoconch surface generally malleated, with diagonal ribs and transverse growth lines interrupted by axial ribs on body whorl, in some specimens body whorl with thick axial growth lines instead of malleated surface; suture deep impressed; aperture subquadrangular or subovoidal; peristome white, thin, delicate, expanded, slightly reflexed; body whorl abruptly descending towards aperture; umbilicus deep, wide.

Measurements: Syntypes (n = 2): D maj: 23.6 mm, 24.9 mm (24.2 mm); D min: 20.6 mm, 21.2 mm (20.9 mm); H: 12.6 mm, 13.5 mm (13.0 mm); D ap: 13.4 mm, 13.6 mm (13.5 mm); H ap: 11.9 mm, 12.3 mm (12.1 mm).

Jaw: Arched, thin, orange; four vertical narrow ribs in central portion of jaw with margins projecting at convex jaw edge.

Pallial Complex: Lung roof without dark spots, homogeneously pale cream; externally two to three shell peripheral bands conspicuously marked on distal portion of lung roof and mantle collar; kidney extending 50% of total pulmonary roof length; main pulmonary vein splitting proximally into two mayor veins that continue without further divisions until reaching mantle collar; portion of lung roof between rectum and kidney crossed by several minor transversal ramified veins, shallowly marked.

Genitalia (Fig. 15C, D): Terminal genitalia tight packed by connective tissue; presence of single dart sac and two mucous unequal glands, both sac-like, generally elongated, voluminous, enveloping distal vagina and dart sac, distally fused with atrium wall; each mucous gland opening into individual, thin, efferent duct that fuse together before inserting at same point below constriction of dart sac;

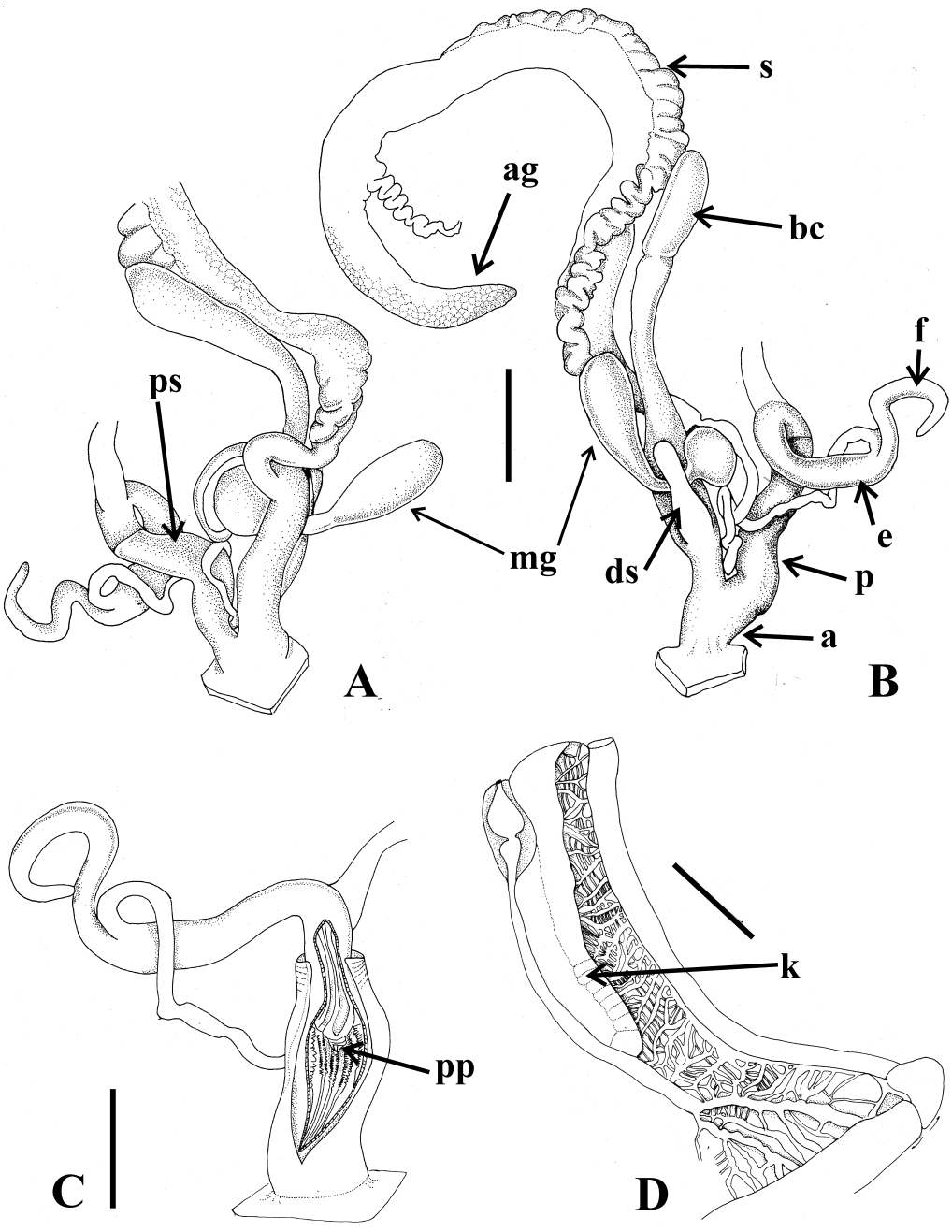

FIG. 10. *Epiphragmophora hemiclausa.* A: Ventral view of terminal genitalia; B: Dorsal view of genital system; C: Detail of penial complex; D: Pallial system. Scale bars = 5 mm. Abbreviations: a, atrium; ag, albumen gland; bc, bursa copulatrix; ds, dart sac; e, epiphallus; f, flagellum; k, kidney; mg, mucous gland; p, penis; pp, penial papilla; ps, penis sheath; s, spermoviduct.

dart sac muscular, with thick walls, long, cylindrical, with constriction located in basal $^1/_3$ of total length, distal portion of dart sac longer than proximal; dart sac naturally pleated by itself at level of constriction; vas deferens surrounding dart sac level with constriction before inserting in penial complex; dart papillae half length of dart sac distal portion; dart sac ending at atrium level with vagina and penial complex; bursa copulatrix sac round, with extremely short, thick duct; sac and duct of bursa copulatrix neatly delimited; vagina shorter than penis; free oviduct short, enveloped by connective tissue together with bursa copulatrix; penial complex medium to short in total length; flagellum thin, finger-like, ending level where vas deferens enters penial complex and epiphallus begins; proximal portion of epiphallus widening at point of entrance of vas deferens; epiphallus shorter than penis, externally differentiated from it; penial retractor muscle inserting in median portion of epiphallus; penis cylindrical, double length of epiphallus, entering at genital atrium level with dart sac and vagina; penial papillae short, triangular in proximal penis; internal wall of penis with thin, smooth, straight folds; penis sheath muscular overlapping distal portion of penis, distally fused with atrium wall; atrium long.

Habitat: Under or below tree logs or under rocks, from 200 to 1,600 m above sea level.

Distribution (Figs. 19, 21): In Argentina, *E. trigrammephora* inhabits the Yungas and Chaco biogeographic provinces. Its distribution ranges the provinces of Jujuy, Salta, Formosa, Chaco, and Santiago del Estero. In Bolivia and Paraguay, it lives in dryer habitats in the Chacoan biogeographic subregion and within transition habitats from dry forest to more humid rainforest of Yungas.

Remarks: *Epiphragmophora trigrammephora* shows high variability in spire height; although always conic, it is shallow in populations of some localities of Salta and Santiago del Estero provinces, Argentina. However, the spire is generally taller and conic in specimens from Bolivia and other localities in northern Argentina. The umbilicus is always perspective, deep, but the diameter is variable. The three peripheral bands are not always present, with some specimens having two or even only one band. In general, most of the specimens have thicker shell peripheral bands than in ***E. walshi*** sp. nov.

Epiphragmophora tucumanensis (Doering, 1874)
(Figs. 6A, 14D, E, 19)

Helix Group *Aglaja estella tucumanensis* Doering, 1874: 445.
Helix tucumanensis – Kobelt, 1878: 148.
Helix tucumanensis – Tryon, 1888: 77.
Epiphragmophora tucumanensis – Pilsbry, 1894: 198.
Helicigona catamarcana Ihering, 1910: 423.
Epiphragmophora tucumanensis – Parodiz, 1957: 30.
Epiphragmophora tucumanensis – Fernández & Rumi, 1984b: 251.

Lectotype: SKF 7711, Argentina, Tucumán [en la pendiente del Oeste de la Sierra de Tucumán, en bosques exuberantes, a 500–900 mts. de altura]. Stelzner leg. Doering det.

Other Material Examined:
Dissected Material: Argentina, Tucumán Prov.: FML 14413, Tafí del Valle Dept., route 307 between El Mastil and Tafi del Valle, 26°58'06"S, 65°39'24"W, 1,741 m, 21/XII/2001, M. G. Cuezzo leg. FML 123, Chicligasta Dept., Cochuna, 1,130 m, M. G. Cuezzo leg. FML 124, Tafi del Valle Dept., route 307 before reaching El Mastil, 6/V/1995, E. Dominguez leg. *FML 102, Tafi del Valle Dept. "El Indio", 963 m, 15/IV/1989, M. G. Cuezzo leg.
Dry Material: Argentina, Tucumán Prov.: *FML 755, Tafí del Valle Dept., Valley of river Los Sosa, 650–900 m, W. Weyrauch leg. & det. *FML 762, Tafi del Valle Dept., Los Sosa river, 700–900 m, 16/XI/1963, W. Weyrauch leg. FML 527, Burruyacú Dept., Alto de Medina, 1,400 m, 18/II/1962, W. Weyrauch leg. & det. FML 200, Quebrada de La Hoyada, det. W. Weyrauch. FML 164, Quebrada del Saladillo, 15/X/1933, R. Schreiter leg. FML 756, Burruyacú Dept., Alto de Medina, 1,400 m, 7/II/1967, W. Weyrauch leg. & det. FML 758, Tafí Viejo Dept. San Javier Mountains, 1,000 m 12/VIII/1967, W. Weyrauch leg. & det. FML 1383, Aconquija, 6/VI/1948, Wygodzinsky leg., W. Weyrauch det. FML 1393, Tafi Viejo Dept., Horco Molle near Tucumán city, 700 m,

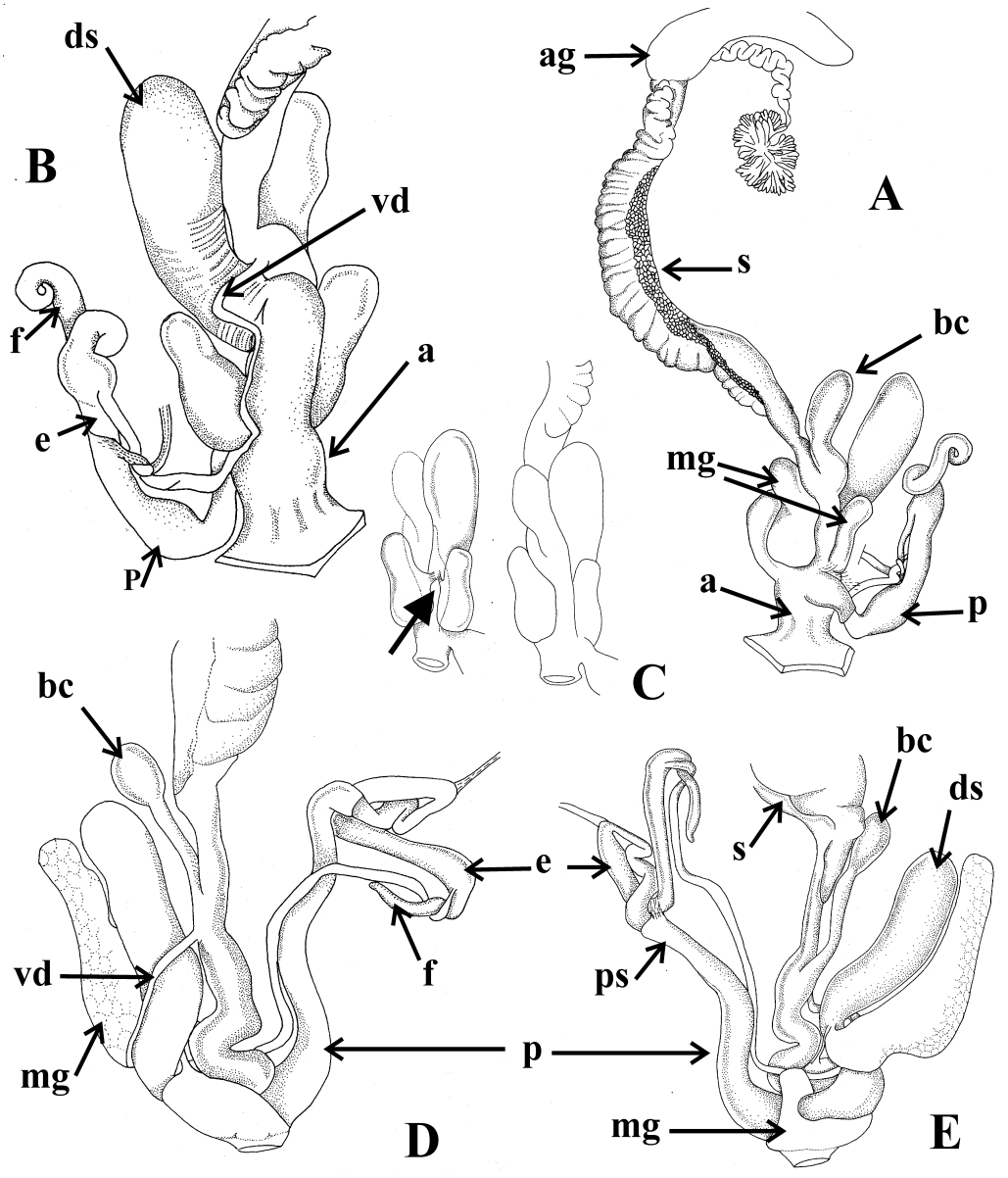

FIG. 11. *Epiphragmophora jujuyensis* and *E. parodizi*. A: *E. jujuyensis*, dorsal view of genitalia; B: *E. jujuyensis*, detail of dart sac complex in dorsal view of terminal genitalia; C: *E. jujuyensis*, detail of mucous gland ducts insertion with and without drawn of bursa copulatrix, arrow indicates point of insertion; D: *E. parodizi*, dorsal view of terminal genitalia; E: *E. parodizi*, ventral view of terminal genitalia. Scale bars = 5 mm. Abbreviations: a, atrium; ag, albumen gland; bc, bursa copulatrix; ds, dart sac; e, epiphallus; f, flagellum; mg, mucous gland; p, penis; ps, penis sheath; s, spermoviduct; vd, vas deferens.

4/II/1968, W. Weyrauch leg. & det. FML 11310, Tafi Viejo Dept., Taficillo, 18/VIII/1966, W. Weyrauch det. MACN 9009, Aconquija. MACN 608, Aconquija. MLP 4273, Tafi Viejo Dept. Horco Molle. MLP 4274, Cuesta del Clavillo, Aconquija.

Description:

External Features: Animal light to dark brown; homogeneous color over cephalopedal region; two lines of pustules separated by groove running dorsally from mantle collar to cephalic region, ending between ommatophores; dorsal groove in pedal region conspicuously marked.

Shell (Fig. 6A): Dextral, helicoidal, globose, solid; elevated conical spire; medium to large size; 4¾ to 5 convex whorls; color variable from yellowish to dark brown; presence of single thick supraequatorial, dark brown, even, band most notable in body whorl periphery; protoconch smooth; teleoconch with axial ridges, surface of body whorl strongly malleated to reticulated; suture deep impressed; aperture subcircular to ovoid; peristome whitish, thick, reflexed; some specimens with basal lip thickened; body whorl distinctly descending towards aperture; umbilicus narrow, partly overlapped by margins of peristomal lips.

Measurements: Specimens from Argentina, Tucumán, Burruyacú Dept., Alto de Medina (n = 10): DM: 33.7–29.6 mm (31.9 mm); D min: 28.9–25.0 mm (27.3 mm); H: 18.6–15.5 mm (17.2 mm); D ap: 19.9–17.3 mm (19.0 mm); H ap: 16.0–14.3 mm (15.2 mm).

Specimens from Argentina, Tucumán, Yerba Buena Dept., San Javier, (n = 8): DM: 30.0–28.0 mm (28.4 mm); D min: 25.8–23.2 mm (24.5 mm); H: 16.5–14.2 mm (15.8 mm); D ap: 18.5–16.2 mm (17.3 mm); H ap: 15.0–13.5 mm (14.3 mm).

Specimens from Argentina, Tucumán, Tafi del Valle Dept., margins of Los Sosa river (n = 6): DM: 41.9–32.8 mm (37.3 mm); D min: 36.4–27.6 mm (32.1 mm); H: 29.3–17.7 mm (23.9 mm); D ap: 24.9–19.4 mm (22.1 mm); H ap: 19.8–15.6 mm (17.8 mm).

Pallial Complex: Lung roof heavily mottled with black spots lining most of the veins; several minor veins located between rectum and kidney; kidney extending half of pulmonary roof length; main pulmonary vein splitting into two major veins in distal lung roof below kidney and several minor longitudinal veins.

Jaw: Arched, generally narrow, orange, with four thin central ribs, margins projecting at both edges.

Genitalia (Fig. 14D, E): Terminal genitalia with dart sac complex consisting of single dart sac and two unequal mucous glands symmetrically located on either side of dart sac; left mucous gland oval-elongated; right gland oval to cylindrical; both glands with thin efferent ducts inserting independently in middle zone of dart sac; duct of left mucous gland departing from middle portion of body gland; duct of right mucous gland distal respect to body of gland; dart sac muscular, short, cylindrical, with basal portion slightly wider in diameter, or short cylindrical and even in diameter, inserting in middle portion of vagina; dart sac without medial constriction; internal wall of dart sac with uniform longitudinal bands, dart papillae short, located in distal dart sac; bursa copulatrix elongate-oval; duct of bursa copulatrix medium length, running parallel to distal portion of spermoviduct; penial complex long; flagellum long, thin, convoluted; transition between epiphallus and penis marked by abrupt increase in diameter of penis; internal wall sculpture of epiphallus consisting on straight longitudinal bands; penis half length of epiphallus; internal wall sculpture of proximal penis with thin zigzag longitudinal bands, distal penis with closed columns in zigzag pattern ending in straight bands; penial papillae absent; penial sheath double, internal one muscular fused with atrium, running to middle penis; external penis sheath transparent, thin, enveloping penis in its complete length; penial muscular band long, located under penial muscular sheath; penial retractor muscle thick, inserting in middle portion of epiphallus; penis and vagina entering side by side at atrium, distally to dart sac complex; atrium long.

Habitat: *Epiphragmophora tucumanensis* inhabits subtropical rainforests of Yungas Province from 500 m to 1,800 m above sea level, where the snails are found under tree logs or actively crawling on dead leaves on the ground.

Distribution (Fig. 19): *Epiphragmophora tucumanensis* is distributed mainly in Tucumán Province, northwestern Argentina. Some scattered records exist in Catamarca Province.

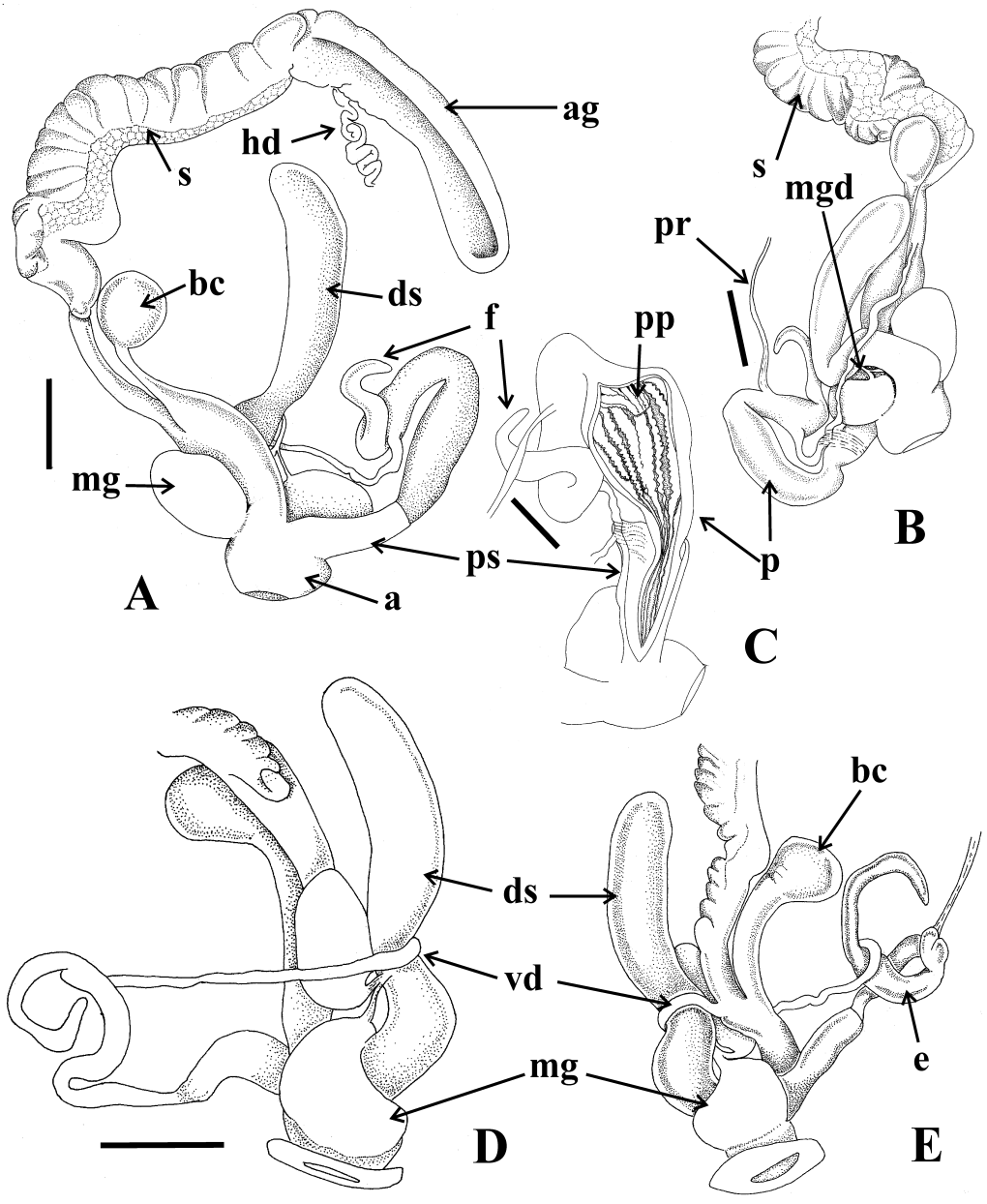

FIG. 12. *Epiphragmophora puntana* and *E. rhathymos.* A: *E. puntana*, ventral view of genitalia; B: *E. puntana*, detail of dorsal view of terminal genitalia; C: *E. puntana*, detail of penial complex showing internal sculpture of penis; D: *E. rhathymos*, ventral view of terminal genitalia; E: *E. rhathymos*, dorsal view of terminal genitalia. Scale bars = 5 mm. Abbreviations: a, atrium; ag, albumen gland; bc, bursa copulatrix; ds, dart sac; e, epiphallus; f, flagellum; hd, hermaphroditic duct; mg, mucous gland; mgd, mucous gland ducts; p, penis; pp, penial papillae; ps, penis sheath; s, spermoviduct; vd, vas deferens.

Remarks: *Epiphragmophora tucumanensis* (Doering) was originally described as a variety of *Helix estella* d'Orbigny, 1835. *Epiphragmophora estella* differs from *E. tucumanensis* in its smaller shell size, shell sculpture, less convex whorls and color. Unfortunately, the anatomy of *E. estella* is still unknown.

The type locality of the present species is confusing because the locality "Sierra de Tucumán", is imprecise, no other detail of the type locality has been recorded. Indeed, Tucumán Province has pre-Andean mountains often called as "sierras", running about 200 km in its western part from north to south. Because of this vague information on the type locality, some authors had considered San Javier, in the central to northern portion of the western mountains in Tucumán, as the type locality of *E. tucumanensis*, whereas others mentioned both San Javier and Tafi del Valle as the type locality. Considering *E. tucumanensis* distribution and the abundance of specimens between 500–900 m, I interpreted that Doering's type locality would be the mountains on the road to Tafi del Valle, from 500 to 900 m, on the western side of the mountains where the species is found in humid cloud forest of the Yungas biogeographic region. Specimens of Tafi del Valle are usually darker with shell size remarkably bigger than specimens of other localities. This is the only species of the genus for which the morphology of the spermatozoon has been investigated (Cuezzo, 1994).

Epiphragmophora variegata Hylton Scott, 1962
(Figs. 6C, 16A–D, 20)

Epiphragmophora variegata Hylton Scott, 1962: 105

Epiphragmophora variegata – Fernández & Rumi, 1984b: 252.

Holotype: FML (ex IML) 290a, Argentina, Catamarca, Dept. Belén, Agua de Dionisio, Farallón Negro, 1953.

Other Material Examined:

Dissected Material: Argentina, Tucumán Prov.: FML 14710 A, J. B. Alberdi Dept., Dique Escaba, Escaba Abajo, 27°38'17"S, 65°47'43"W, 1,640 m, 10/XI/1999, Dominguez leg. FML 14713 A, J. B. Alberdi Dept., Dique Escaba, 700 m, 27°40'03"S, 65°45'00"W, 24/IV/2003, M. G. Cuezzo leg. & det. FML 14712 A, J. B. Alberdi Dept., on road to Dique Escaba, 5 km from Alberdi, 1/XI/1996, M. G. Cuezzo leg. & det. Argentina, Catamarca Prov.: FML 14714 A, Andalgalá Dept., Las Estancias, El Lindero, 1 km from the Hostal Aconquija, 27°28'07"S, 66°00'37"W, 1,530 m, 19/IV/2003, M. G. Cuezzo leg. & det.

Dry Material: Argentina, Tucumán Prov.: FML 14366, Dique San Ignacio, 600 m, 17/V/1964, leg. & det. by W. Weyrauch. FML 14367, FML 709, San Ignacio river, 420 m, 4/XII/1966, leg. W. Weyrauch. FML 702, Dique Escaba, 5/XII/1966, leg. W. Weyrauch. FML 153, Santa Ana Mountain, 1/VII/1946, leg. R. Schreiter, det. W. Weyrauch. FML 973, Huasa-Pampa, 500 m, 9/V/1964, Arevalo leg. FML 400, Dique Escaba, 4/VI/1956, leg. Tomsic, det. W. Weyrauch. FML 289, Rio Chico Dept., close to river Marapa, 8/VI/1953, S. A. Pierotti leg.

Argentina, Catamarca Prov.: FML 290*, Hualfin Dept., Aguas de Dionisio, Farallón Negro, 16/X/1953, S. A. Pierotti leg., J. J. Parodiz det. FML 862, Las Viñas, 23/II/1964, Frias and Rodriguez leg. FML 5219, FML 10939, Las Estancias, 1,500 m, leg. & det. by W. Weyrauch

Description:

External Features: Specimens with several different body colors, from pale cream, yellow, orange, reddish to dark brown; there is no relationship between body and shell color, both of which are highly variable; dorsal row of pustules between ommatophores well delimited.

Shell (Fig. 6C): Dextral, helicoidal, globose, solid; medium to small; with high conical spire; 4½ convex whorls delimited by a well-impressed suture; shell color highly variable, from uniform pale yellow to dark brown; generally with three pigmented peripheral bands, dorsal and ventral bands wider than equatorial, about 2 mm in thickness, dark brown, neatly delimited, bands evident in body whorl persisting only dorsal band in spire; dorsal and ventral bands in some specimens with different color than central band, usually lighter; few specimens with one equatorial band; protoconch smooth; teleoconch with fine growth lines; surface of body whorl malleated; aperture subcircular with a thick, white, strongly reflexed peristome; callus between margins of dorsal and ventral lip usually raised; body whorl abruptly descend-

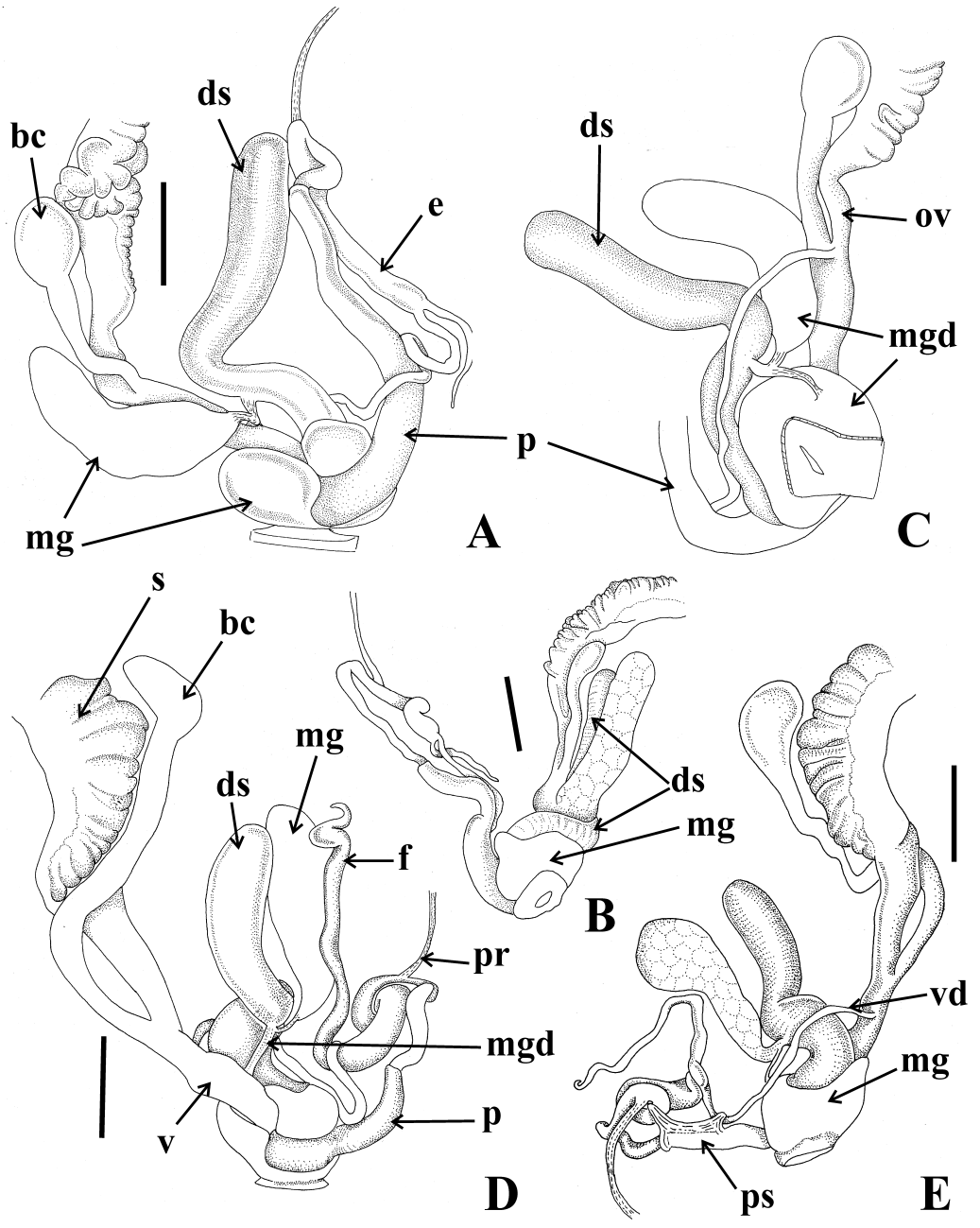

FIG. 13. *Epiphragmophora saltana* and *E. tomsici.* A: *E. saltana*, dorsal view of terminal genitalia; B: *E. saltana*, ventral view of terminal genitalia showing union of both mucous glands ducts; C: *E. saltana*, general view of terminal genitalia inverse side; D: *E. tomsici*, dorsal view of terminal genitalia; E: *E. tomsici*, idem, ventral view. Scale bars = 5 mm. Abbreviations: bc, bursa copulatrix; ds, dart sac; e, epiphallus; f, flagellum; mg, mucous gland; mgd, mucous gland ducts; ov, free oviduct; p, penis; ps, penis sheath; s, spermoviduct; v, vagina; vd vas deferens.

ing behind aperture; umbilicus completely overlapped by columelar portion of peristome but not fused with shell wall in most specimens, only in some specimens basal lip partially sealed to shell wall with umbilicus still visible.

Measurements: Holotype: D maj: 25.5 mm; D min: 22.1 mm; H: 15.7 mm.
Specimens from Escaba, Tucumán (n = 20): D maj: 21.8–32.2 mm (26.3 mm); D min: 20.0–27.3 mm (23.1 mm); H: 13.5–23.3 mm (17.6 mm).

Jaw: Arched, orange; number and width of vertical ribs in central portion of jaw highly variable, between two to five.

Pallial Complex: Lung roof dark, heavily mottled with small black spots between major and minor veins, dark pattern of color attenuated in some specimens; main pulmonary vein splitting into two main branches before reaching mantle collar; several minor branches departing from main veins; portion of lung roof between rectum and kidney crossed by several transverse minor veins; kidney as long as half pulmonary roof length.

Genitalia (Fig. 16A–D): Terminal genitalia with dart sac complex consisting of single dart sac and two mucous glands unequal in size; right mucous gland oval, thinn; left mucous gland pea-shaped, both gland efferent ducts ending independently at middle zone of dart sac; dart sac cylindrical, muscular, smaller than mucous glands; dart papilla small, located in basal portion of dart sac; dart sac complex ending at distal portion of vagina; penial complex and vagina ending level at atrium and distal with respect to dart sac; bursa copulatrix as long as half spermoviduct length; sac of bursa copulatrix oval, sharply differentiated from duct; vagina long, slightly less longer than penis, with internal longitudinal bands; penial complex long; flagellum short to medium, finger-like, $^1/_4$ length of epiphallus + penis; epiphallus slightly thinner than penis; penis sheath muscular, overlapping all penis length, distally fused to atrium wall; penial papilla absent; penial internal wall sculpture consisting of zigzag longitudinal pleats; atrium short to medium, internal wall with longitudinal bands wider than those in vaginal internal wall.

Habitat: On rocks walls in mountains or among grass in the southern portions of the cloud rainforest region, Yungas biogeographic province (Fig. 24).

Distribution (Fig. 20): *Epiphragmophora variegata* occurs from southern Tucumán to southern Catamarca provinces, northwestern Argentina. Specimens are very abundant in La Cocha and J. B. Alberdi departments, Tucumán Province.

Remarks: The present species is highly variable in shell color with eight different patterns of banding and color at the same locality, Escaba, in southern Tucumán Province. The same is observed in the animal body color, with variations ranging from black to brilliant orange. Holotype measurements in the original description of Hylton Scott (1962) are not coincident with the real measurements of the holotype shell deposited in FML. In the original description of the present species, Hylton Scott (1962) states that only one mucous gland is present in the dart sac complex, although she remarked that this must be reconfirmed. Based on the dissections of several specimens of *E. variegata*, I have shown the presence of two mucous glands inserting in the dart sac complex. The genitalia of *E. variegata* is similar to *E. hemiclausa* Parodiz, the main differences being the shape of the dart sac and the mucous glands.

Epiphragmophora villavilensis Parodiz, 1955
(Figs. 6D, 17A, B, 21)

Epiphragmophora villavilensis Parodiz, 1955: 94, fig. 1.

Epiphragmophora villavilensis – Fernández & Rumi, 1984b: 253.

Holotype and Paratypes: MACN 383, Argentina, Catamarca, Dept. Andalgalá, Villavil 1933, M. Gomez leg.

Other Material Examined:

Dissected Material: Argentina, Catamarca Prov.: FML 14442 A, Belén Dept., Villavil, Quebrada de Indalecio, 27°05'19"S, 66°49'28"W, 2,220 m, C. Ituarte leg.

Dry Material: Argentina, Catamarca Prov.: MLP unnumbered, Termas de Hualfin. Ex Hylton Scott Collection. MLP unnumbered, Termas de Villavil, Cisneros leg. V/1950. MLP 4276, Termas de Villavil. MACN 383, Baños de Villavil. FML 14718, Belén Dept., Villavil, Quebrada de Indalecio, 27°05'19"S, 66°49'28"W, 2,220 m, 25/XI/2003, M. G. Cuezzo leg.

Description:

Shell (Fig. 6D): Dextral, helicoidal, depressed, semisolid; spire highly depressed; with 4½ whorls; body whorl periphery with supra-equatorial angle delimiting dorsal and ventral regions; periostracum pale yellow brilliant; peripheral pigmented band absent; protoconch smooth; teleochonch with fine axial growth lines, in body whorl more spaced with spiral stria; aperture subquadrate with reflexed thin, peristome; body whorl not descending behind aperture; umbilicus deep, wide.

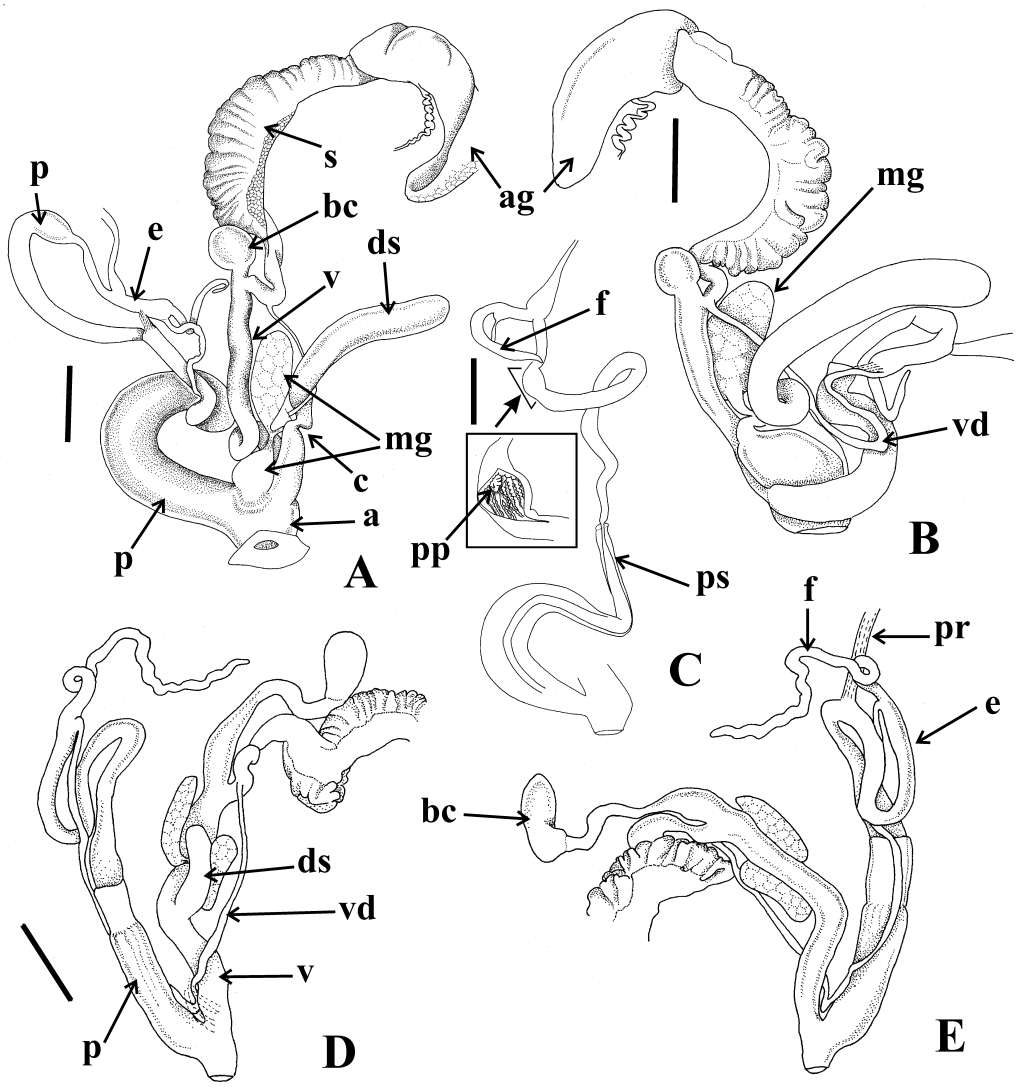

FIG. 14. *Epiphragmophora trenquelleonis* and *E. tucumanensis.* A: *E. trenquelleonis*, genital system in ventral view; B: *E. trenquelleonis*, genital system in dorsal view, different specimen; C: *E. trenquelleonis*, penial complex in stretched position, inset: detail of dissected proximal portion of penis showing penial papilla and pilasters of penial wall; D: *E. tucumanensis*, ventral view of terminal genitalia; E: *E. tucumanensis*, dorsal view of genitalia, same specimen. Abbreviations: a, atrium; ag, albumen gland; bc, bursa copulatrix; c, constriction; ds, dart sac; e, epiphallus; f, flagellum; mg, mucous gland; p, penis; pp, penial papilla; pr, penial retractor muscle; ps, penis sheath; s, spermoviduct; v, vagina; vd, vas deferens.

Measurements: Holotype: D maj: 27.2 mm; D min: 23.0 mm; H: 11.5 mm; D ap: 14.9 mm. Paratypes (n = 3): D maj: 21.1–28.9 mm (24.9 mm); D min: 18.3–24.7 mm (21.4 mm); H: 8.6–11.0 mm (9.5 mm).

Specimens from Type Locality (n = 8): D maj: 25.0–22.3 mm (23.5 mm); D min: 21.0–18.6 mm (19.5 mm); H: 10.0–8.6 mm (9.5 mm); D ap: 13.4–12.0 mm (12.4 mm); H ap: 11.3–9.5 mm (10.1 mm).

Genitalia (Fig. 17A, B): Terminal genitalia with dart sac complex consisting of single dart sac and two unequal dart glands; one of mucous glands sac-like, prominent, enveloping basal vagina and dart sac complex, other gland oval-elongate; efferent ducts of both mucous glands fused together before entering dart sac at constriction point; dart sac short, cylindrical, with thick muscular walls and marked constriction in medial zone; thin, internal dart gland in distal portion of dart sac; dart sac ending at atrium level with vagina and penis; bursa copulatrix round, with thick, short duct; vagina short, thick, almost completely covered by mucous gland; penial complex short; flagellum thin, finger-like short, ending level where vas deferens enters penial complex and epiphallus begins; epiphallus proximally thick, progressively thinner towards penis; epiphallus shorter than penis, about half its length; penial retractor thick, short, inserting in middle zone of epiphallus; penis cylindrical gradually becoming thinner until entering at genital atrium; penial papillae short, triangular in proximal penis; internal wall of penis with thin delicate longitudinal folds; penis sheath thin, overlapping terminal portion of penis, less than half length of penis; atrium very long.

Habitat and Distribution (Fig. 21): *Epiphragmophora villavilensis* inhabits the Pre-Puna biogeographical province of southern Catamarca Province, Argentina. Specimens are found in xerophilic habitats under rocks or in deep rock crevices. Although empty shells are easy to find on rocks or on the soil close to crevices, live specimens are very difficult to find. They live most of the day deep inside narrow crevices and are probably active only during part of the night or during rainy days.

Remarks: *Epiphragmophora villavilensis* differs from *E. hieronymi* in shell sculpture, absence of a peripheral band and the contour of body whorl (Table 1). The genitalia of *E. villavilensis* are similar to *E. hieronymi*, differing mainly in characters of penial complex, which is shorter in *E. villavilensis* than in the other species. The epiphallus is considerably shorter and the flagellum is longer in *E. villavilensis*. The point of insertion of the fused efferent ducts of the mucous glands is in the constriction of the dart sac, whereas in *E. hieronymi* the insertion point is below the constriction in the distal zone of the dart sac.

The description of the terminal genitalia is based on a single specimen collected by C. Ituarte at the type locality.

Epiphragmophora walshi Cuezzo, n. sp.
(Figs. 7C, 17C, D)

Holotype: FML 14765 A, Argentina, Salta, Metán Dept., route 5 road from Lumbrera to Las Víboras, 750 m, 29/XII/1996. M. G. Cuezzo leg.

Paratypes: FML 14764, Argentina, Salta, Metán Dept., Route 5 from Lumbrera to Las Víboras, 25°11'38"S, 64°53'07"W, 760 m, 27/IV/2005, leg. by E. Dominguez & M. G. Cuezzo. FML 14753 A, Metán Dept., Rout 5, Lumbrera. 29/XII/1996. M. G. Cuezzo leg.

Other Material Examined:

Dissected Material: Argentina, Salta Prov.: MLP unnumbered, Gral. José de San Martín Dept., Gral. Ballivián, 3/XII/1943. Maldonado leg. MLP unnumbered, Rivadavia Dept., La Curva, 1951, VII/1951, Boero leg.

Dry Material: Argentina, Salta: FML 809, Metán Dept., Estancia Lumbrera, 750 m leg. & det. W. Weyrauch. FML 577, Metán Dept., between Lumbreras and Juramento, km 1362, 750 m 23/II/1962. leg. & det. by W. Weyrauch. FML 14747, Metán Dept., route 5 to Lumbrera, XI/1996, M. G. Cuezzo leg. FML 389, Güemes Dept., Cerro Pelado, 1,500 m, 4/I/1956, E. de La Sota leg. FML 14763, Metán Dept., Route 9, 40 km N from Route 5, 24°53'40"S, 64°59'10"W, 900 m, 29/IV/2005, leg. M. G. Cuezzo.

Diagnosis: Shell medium to small; three thin continuous peripheral bands well marked in body whorl; aperture subcircular to oval; dart sac ending at atrium level with vagina and penial complex; proximal portion of dart sac wider than distal; two unequal mucous glands, one oval elongated in shape with a basal expansion; both mucous glands effer-

ent ducts joining and fusing together before inserting in dart sac; epiphallus as long as penis.

Etymology: This new species is dedicated to Rodolfo Walsh, an Argentinean writer and journalist, with admiration for his work and ideas.

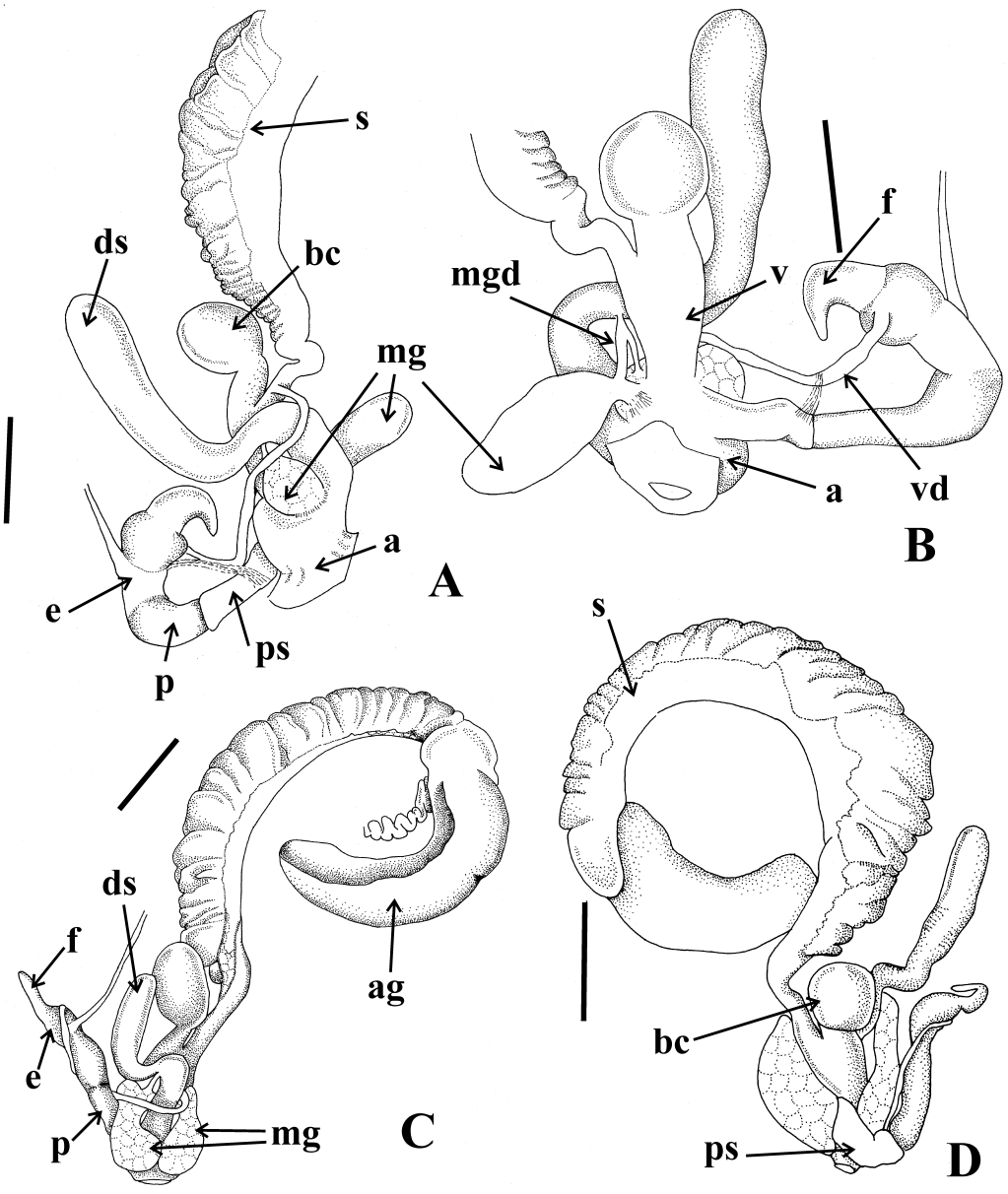

FIG. 15. *Epiphragmophora trifasciata* and *E. trigrammephora.* A: *E. trifasciata*, ventral view of terminal genitalia; B: *E. trifasciata*, dorsal view of terminal genitalia; C: *E. trigrammephora*, ventral view of genitalia; D: *E. trigrammephora*, other specimen showing genitalia in dorsal view. Scale bars = 5 mm. Abbreviations: a, atrium; ag, albumen gland; bc, bursa copulatrix; ds, dart sac; e, epiphallus; f, flagellum; mg, mucous gland; mgd, mucous gland ducts; p, penis; ps, penis sheath; s, spermoviduct; v, vagina; vd vas deferens.

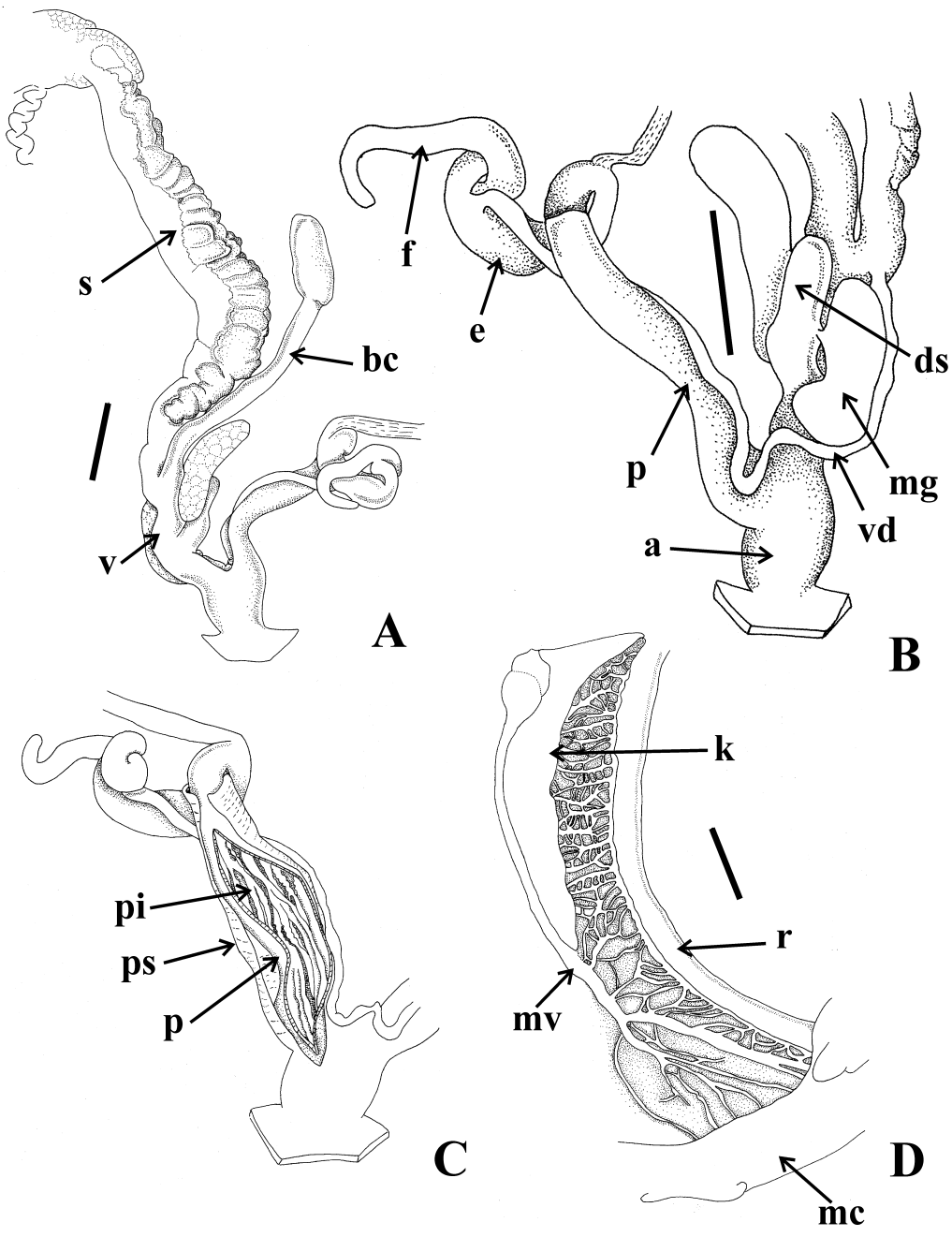

FIG. 16. *Epiphragmophora variegata*. A: Dorsal genitalia; B: Genitalia in ventral view; C: Detail of penial complex with penis dissected; D: Pallial system. Scale bars = 5 mm. Abbreviations: a, atrium; bc: bursa copulatrix, ds, dart sac; e, epiphallus; f, flagellum; k, kidney; mg, mucous gland; mv, main pulmonary vein; p, penis; pi, penial pilasters; ps, penis sheath; r, rectum; s, spermoviduct; vd, vas deferens.

Description:

External Features: Body color homogeneous light gray; some specimens with dorsal portion of cephalic region darker than foot color; single dorsal row of pustules from mantle collar to ommatophores well delimited.

Shell (Fig. 7C): Dextral, helicoidal, subglobose, semisolid; usually with low conical spire; medium to small size; 4¾ to 5¾ convex whorls; pale cream to yellow; three peripheral thin, darker brown bands clearly delimited on body whorl; upper band running

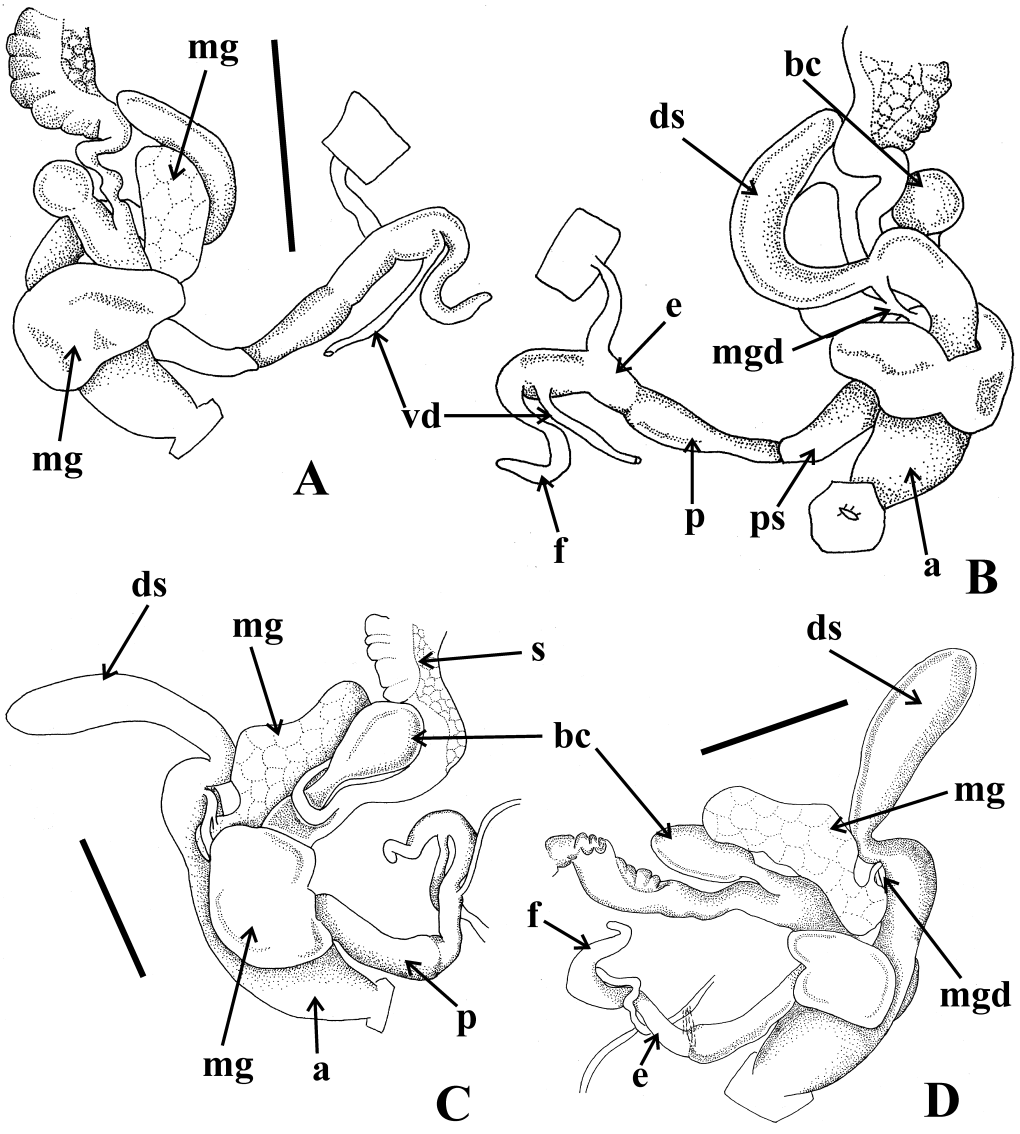

FIG. 17. *Epiphragmophora villavilensis* and ***E. walshi***. A: *E. villavilensis*, dorsal view of terminal genitalia; B: *E. villavilensis*, ventral view of terminal genitalia; C: ***E. walshi***, dorsal view of terminal genitalia; D: ***E. walshi***, ventral view of terminal genitalia. Scale bars = 5 mm. Abbreviations: a, atrium; bc, bursa copulatrix; ds, dart sac; e, epiphallus; f, flagellum; mg, mucous gland; mgd, mucous gland ducts; p, penis; ps, penis sheath; s, spermoviduct; vd vas deferens.

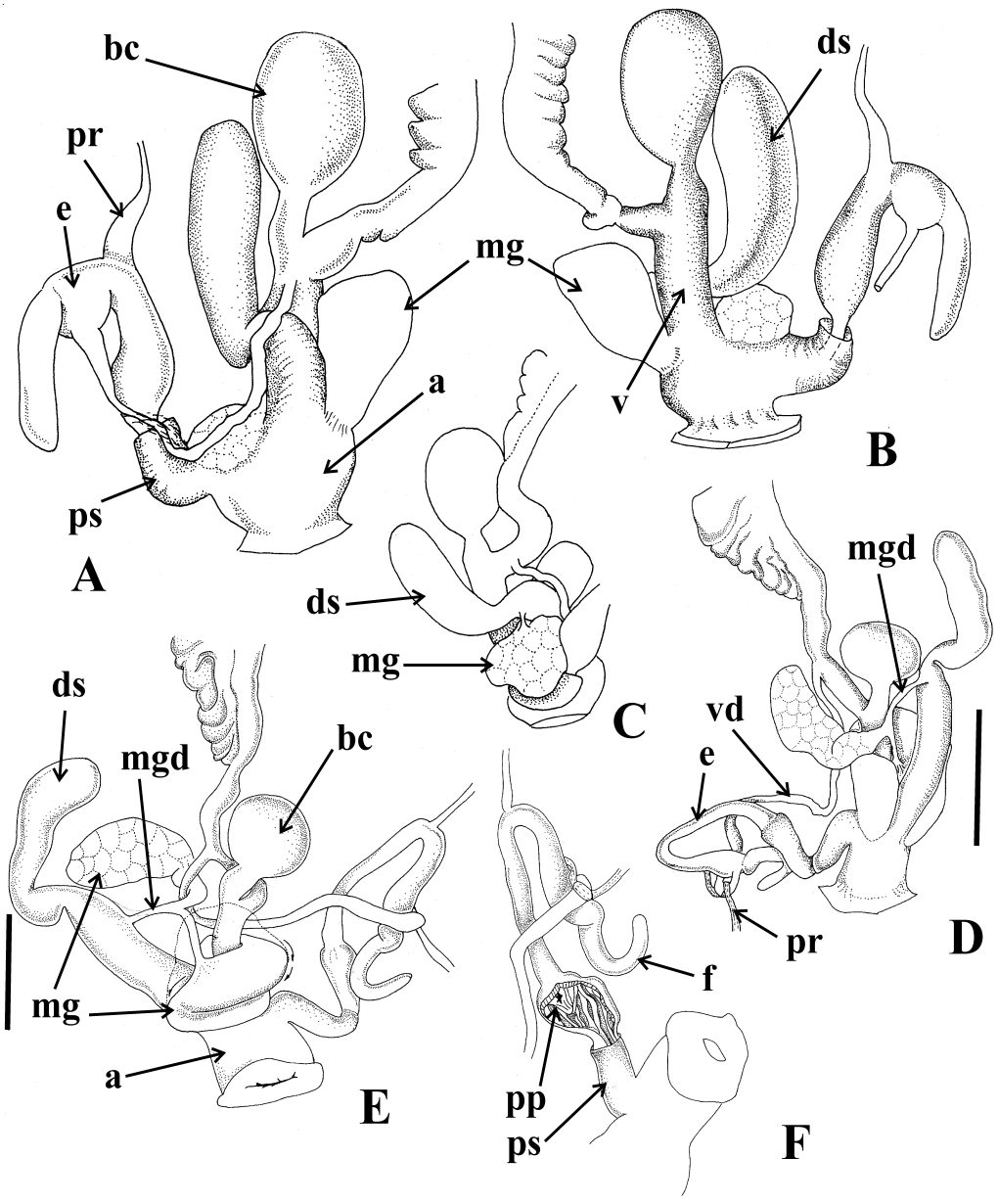

FIG. 18. ***Epiphragmophora guevarai*** and ***E. quirogai***. A: ***E. guevarai***, ventral view of terminal genitalia; B: ***E. guevarai***, dorsal view of terminal genitalia; C: ***E. guevarai***, lateral view of terminal genitalia showing point of insertion of mucous gland; D: ***E. quirogai***, dorsal view of terminal genitalia; E: ***E. quirogai***, ventral view of terminal genitalia; F: ***E. quirogai***, detail of penial complex with penis dissected. Scale bars = 5 mm. Abbreviations: a, atrium; bc: bursa copulatrix, ds, dart sac; e, epiphallus; f, flagellum; mg, mucous gland; mgd, mucous gland duct; p, penis; pp, penial papillae; ps, penis sheath; v, vagina; vd, vas deferens.

above suture in each anfractum of spire; bands always thin, with well-defined limits, sometimes central band darker; protoconch smooth, first whorls with thin growth lines; teleoconch surface generally malleated, with diagonal ribs and transverse growth lines interrupted by axial ribs on body whorl; suture deep impressed; aperture subcircular to oval, some specimens with basal lip straight, not curved; peristome white, thin, delicate, expanded, slightly reflexed; body whorl slightly descending towards aperture; umbilicus narrow, deep.

Measurements: Paratypes (n = 17): D maj: 20.0–25.5 mm (22.7 mm); D min: 16.8–22.4 mm (19.7 mm); H: 10.0–12.4 mm (11.4 mm); D ap: 10.6–14.3 mm (12.4 mm) H ap: 9.8–12.4 mm (11.1 mm).

Specimens from Type Locality (n = 10): D maj: 20.6–23.4 mm (22.7 mm); D min: 19.2–20.5 mm (19.4 mm); H: 11.4–13.3 mm (12.2 mm); D ap: 11.2–12.9 mm (12.3 mm); H ap: 9.9–12.5 mm (11.2 mm).

Jaw: Arched, thin, translucent; orange, with six vertical narrow ribs in central portion; upper and lower margins of ribs projecting at convex jaw edge.

Pallial Complex: Lung roof homogeneously pale cream; shell peripheral bands not marked on lung roof or mantle collar; kidney extending 60% of total pulmonary roof length; main pulmonary vein splitting proximally in two mayor veins that further divide into minor veins before reaching mantle collar; portion of lung roof between rectum and kidney crossed by several minor transversal ramified veins giving appearance of complex net.

Genitalia (Fig. 17C, D): Dart sac complex in terminal genitalia consisting of single dart sac and two unequal mucous glands; one mucous gland sac-like, partially enveloping distal vagina and dart sac, distally fused with atrium wall, with single thin efferent duct; other mucous gland elongate-oval, with basal globose expansion from which efferent duct departs; both efferent ducts joining and fusing together before inserting in dart sac; dart sac muscular, with thick walls, cylindrical, with a median constriction; proximal portion of dart sac wider than distal portion; vas deferens surrounding dart sac level with constriction before inserting in penial complex; dart papillae half length of distal portion of dart sac; dart sac ending at atrium level with vagina and penial complex; bursa copulatrix sac round to oval, with very short duct; sac and duct of bursa copulatrix neatly delimited; vagina shorter than penis; free oviduct short, enveloped by connective tissue together with bursa copulatrix; penial complex medium to short in total length; flagellum thin, finger-like, gradually tapering towards tip, ending level where vas deferens enters penial complex and epiphallus begins; proximal portion of epiphallus widens at point of entrance of vas deferens; epiphallus as long as penis or slightly longer; penial retractor muscle inserting in median portion of epiphallus; penis cylindrical, with proximal portion slightly wider, entering at genital atrium level with dart sac and vagina; penial papillae short, triangular in proximal penis; internal wall of penis with thin smooth zigzag pleats; penial sheath muscular, gradually becoming thinner towards proximal penis, distally fused to atrium wall; atrium long, thin.

Habitat and Distribution: In xerophilic environments where species of *Naesiotus* and *Bulimulus* (Bulimulidae) are also abundant. Live specimens are found inside shallow holes in the ground or attached to basal portions of shrubs. ***Epiphragmophora walshi*** is distributed in the Chacoan biogeographic subregion in Salta Province, northwestern Argentina.

Remarks: ***Epiphragmophora walshi*** n. sp. is similar to *E. trigrammephora* in shell shape and in having three peripheral pigmented bands on the body whorl. It differs from *E. trigrammephora* in its smaller shell diameter, and in the apertural shape, which is subcircular or oval instead of subquadrangular. The peripheral bands on the body whorl in ***E. walshi*** are always very thin and well delimited. Main differences in the genitalia between both mentioned species are: (1) the shape and position of one of the mucous glands, which in ***E. walshi*** is oval-elongate, with a basal expansion, whereas in *E. trigrammephora* both mucous glands are sac-like enveloping basal vagina and dart sac; (2) the length of the epiphallus, which is longer in ***E. walshi*** than in *E. trigrammephora.* Differences in the number of vertical ribs in the jaw of both species are also found, with ***E. walshi*** having six ribs while *E. trigrammephora* has only four vertical central ribs. ***Epiphragmophora walshi*** has been found exclusively in xerophilic environments of Salta Province, whereas *E. trigrammephora* also inhabits humid forests from Bolivia to Salta.

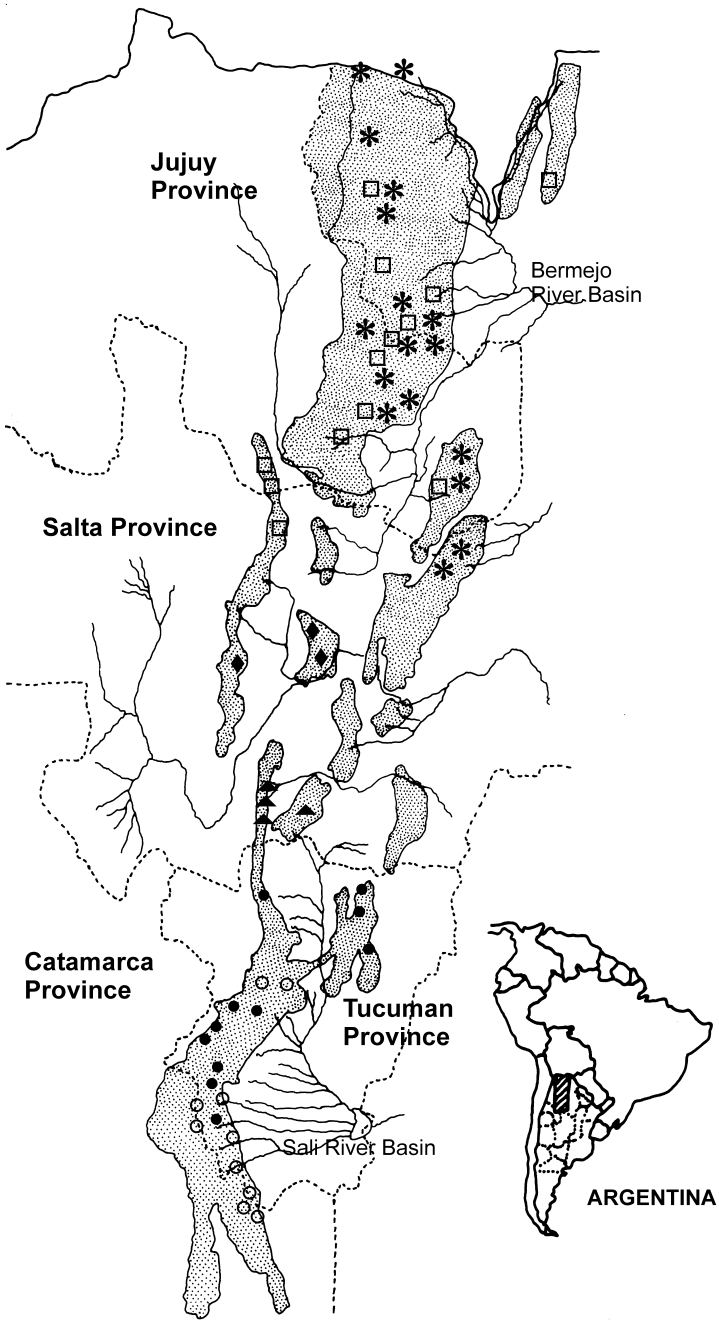

FIG. 19. Species distributed in the cloud rainforest biogeographic province of the Yungas: ● = *E. tucumanensis*; ▲ = *E. saltana*; ✻ = *E. jujuyensis*; O = *E. hemiclausa*; □ = *E. trigrammephora*; ♦ = *E. escoipensis*. Spotted areas correspond to the Yungas biogeographic province. Dot lines indicate the political limits of the argentinean provinces.

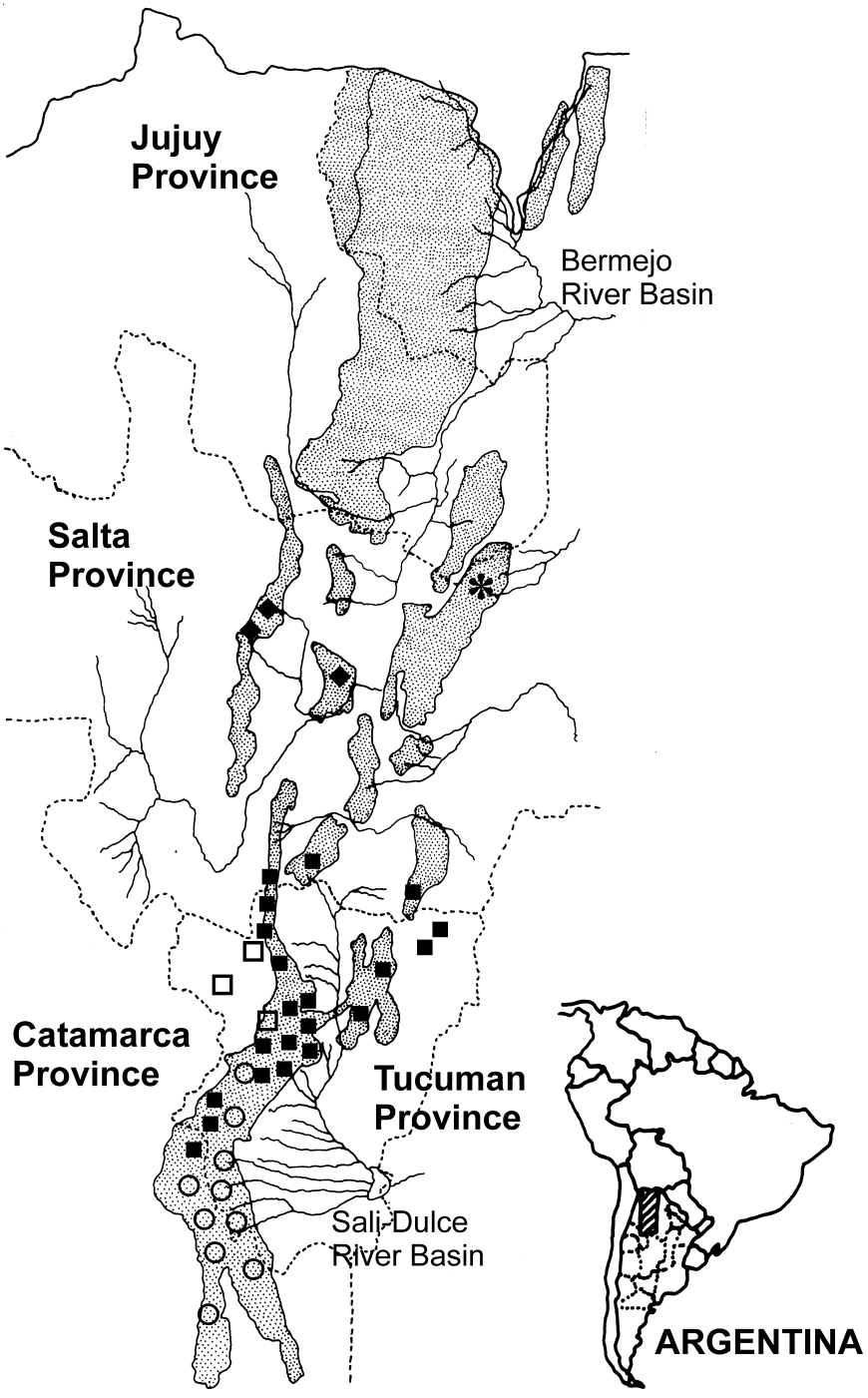

FIG. 20. Species ditributed in the cloud rainforest biogeographic province of the Yungas: O = *E. variegata*; ■ = *E. argentina*; ✻ = *E. costellata*; □ = *E. parodizi*; ♦ = *E. rhathymos.*

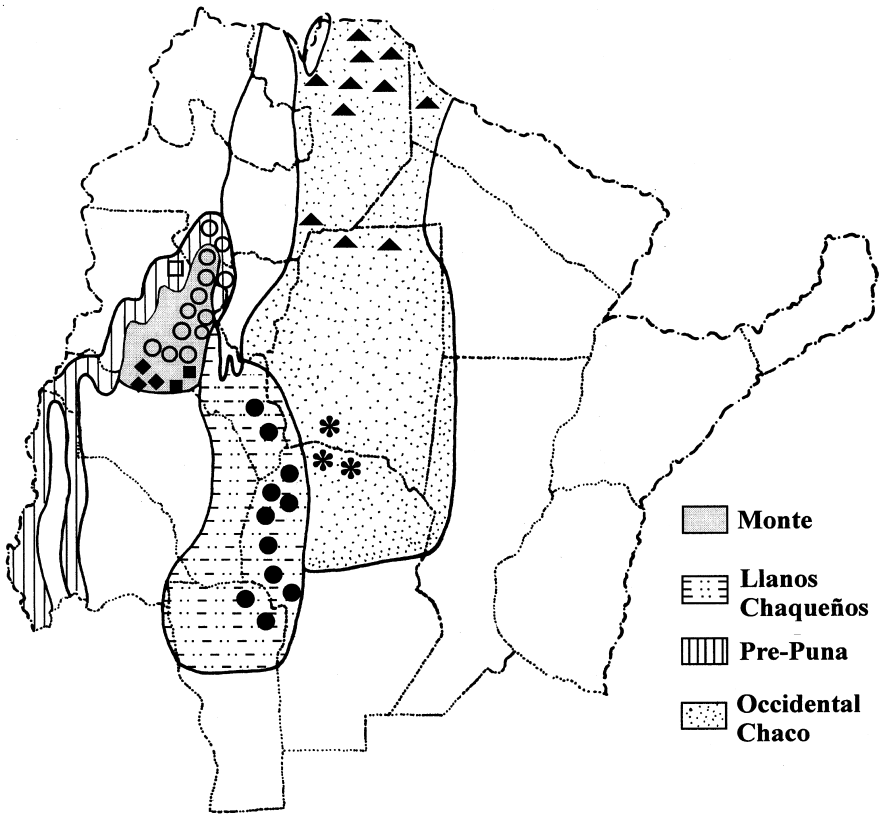

FIG. 21. Species distributed in the Chaco (Llanos Chaqueños and Chaco Occidental areas of endemism), Monte and Pre-Puna biogeographic provinces. Dot lines indicate the political limits of the argentinean provinces. Scale bar = 100 km. ▲ = *E. trigrammephora*; ■ = *E. puella*; ♦ = ***E. quirogai***; o = *E. hieronymi*; ✻ = ***E. guevarai***; ● = *E. trenquelleonis* and □ = *E. villavilensis.*

Parsimony Analysis

All the species treated were considered terminals and analyzed using *Bradybaena* to root the trees. In this first analysis, nine optimal trees with a fit of 190.7 were found. The strict consensus tree of these fundamental trees is illustrated in Fig. 22. Six unambiguous synapomorphies support the monophyly of the genus, with a good Bremer score of 6.0: body whorl surface malleated with diagonal ribs (character 1 [2]), umbilicus overlapping but not fused to body whorl (character 2 [1]), peristome thick, widely reflexed (character 4[1]), mucous glands unequal in size and shape (character 15 [1]), insertion of mucous glands ducts in middle portion of dart sac (character 17 [1]), penial retractor muscle inserting in medial epiphallus (character 23 [1]).

Epiphragmophora argentina, E. hemiclausa, E. tucumanensis, E. variegata form a clade in the majority of the nine optimal trees obtained; *E. jujuyensis* and *E. oresigena* were a sister group. However, three taxa, *E. audouini, E. oresigena* and *E. estella*, were unstable, being located in different trees as sister group of *E. jujuyensis* or alternatively forming part of the first-mentioned clade. Consequently, these clades collapsed in the strict consensus tree (Fig. 22). A major subgroup supported in the strict consensus tree is formed by ten *Epiphragmophora* species. The supporting synapomorphies of this main clade are: peristome slightly reflexed (character 4 [0], spire shallow conic (character 5 [1]), right mucous gland distally fused with atrial wall (character 20 [1]), penial papillae present (character 22 [1]), duct of bursa copulatrix extremelly short

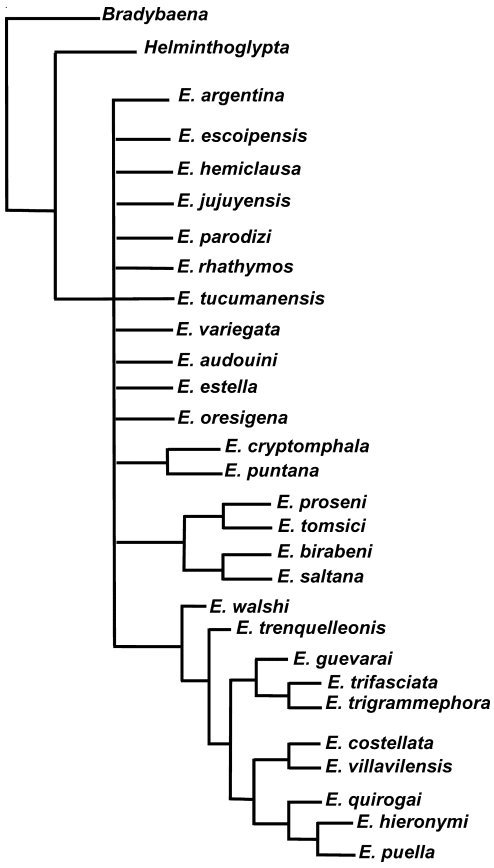

FIG. 22. Strict consensus tree of nine optimal trees obtained with PeeWee and illustrated with Winclada (first cladistic analysis).

(character 24 [0]), atrium medium to long, not expanded into an atrial sac (character 27 [1]), habitat preferences associated with rocks (character 31 [0]), and epiphallus proximal portion widening at point of entrance of vas deferens (character 33 [1]).

This main clade is subdivided into two main groups in the strict consensus tree with good resolution of the relationships and some unambiguous synapomorphies, but each has a low Bremer support (0.4). Within the second subgroup, character 23 [2] supports the monophyly of the following group: ((*E. hieronymi, E. puella*) ***E. quirogai*** n. sp.). Another clade with good support is formed by *E. costellata* and *E. villavilensis*, sustained by the unambiguous synapomorphies of characters 5 [2] spire height strongly depressed and character 8 [2] body-whorl periphery supraequatorally subcarinated. ((*E. trifasciata, E. trigrammephora*) *E. guevarai*)) conform a basal sister clade of the above-mentioned species. Two smaller clades are also mantained in the strict consensus tree, the sister species *E. cryptomphala* and *E. puntana* and ((*E. proseni*, *E. tomsici*) (*E. birabeni, E. saltana*)). These two clades show no resolution on their relationships respect to the other previously mentioned clades.

In the second analysis, all species known only by their shell characters were eliminated from the matrix for two reasons: (1) because some of them showed to be highly unstable, jumping from a clade to another in the different hypothesis obtained, as was explained in the case of *E. audouini* and *E. oresigena*; (2) to see if the relationships of the species with more characters improved with the elimination of those species known only by a part of their bodies. Consequently, *E. birabeni, E. costellata, E. proseni, E. audouini, E. estella* and *E. oresigena* were deleted from the original matrix.

This second analysis produced only one tree with a fit of 187.5 illustrated in Figure 23. In this tree, the genus is well supported by the following unambiguous synapomorphies, characters 1 [2], 2 (1), 4(1), 15 (1), 17 (1), 23 (1), which are also present in the first analysis. Two main clades are delimited, the first one (node 25) with a Bremer support score of 2.0 is: ((*E. argentina, E. tucumanensis*) *E. hemiclausa*) *E. variegata*) supported by character 26 (1). The second clade (node 41), with a good Bremer support score (3.0) is formed by the rest of the *Epiphragmophora* species, the monophyly of which is supported by the following synapomorphies: dart sac long, finger-like with a constriction (character 12 [0]), dart sac inserted in atrium (character 13 [1]), and duct of bursa copulatrix of medium length (character 24 [1]). Within this second main clade (node 41), E. *jujuyensis* is sister group of the rest of the species components that form a big sister clade (node 40). The monophyly of the clade in node 40 is supported by the following synapomorphies: 5 [1], 16[1], 19[1], 21[1] and 32[0]. Within the present clade (node 29), *E. villavilensis* is sister group of ((*E. hieronymi* (*E. puella, **E. quirogai*** n. sp.)) and together are sister groups of (node 32) *E. trifasciata, **E. guevarai*** n. sp. and *E. trigrammephora*.

Shell characters showed a better fit in the tree obtained in the second analysis with only

characters 1, 3 and 7, with fit below 5.0, while in the first analysis 6 out of 10 characters showed a fit below 5.0. Their extra steps are also notably lower. Anatomical characters mostly maintained their good fit in comparison to the consensus tree of the first analysis (Table 2). If we consider the stability of the taxa, the better Bremer support scores obtained for the clades and the better resolution of the relationships, the tree obtained in the second analysis is preferred as the phylogenetic hypothesis over the consensus tree obtained in the first analysis.

DISCUSSION

The comparative anatomy of the treated species revealed that the morphology of the dart sac complex (= stimulator by other authors) is unique and informative in assesing the phylogenetic relationships among the different species of the genus. In *Epiphragmophora,* the insertion of the dart sac is either in the atrium or in the vagina, and the insertion of the two unequal mucous glands is in the medial zone of a single dart sac. The position, as well as the shape of the mucous glands inserting in

TABLE 2. Character steps (ES), extra steps (ESi), minimun and maximun steps (Min/max) and weight implemented by PeeWee consensus tree of the first analysis (left collumn) (Fig. 22) and optimal tree of the second analysis (right collumn) (Fig. 23).

Character	ES	ESi	Min/max	Weight	Character	ES	ESi	Min/max	Weight
1	9	5	4/15	3.7	1	8	4	4/13	4.2
2	6	4	2/13	4.2	2	4	2	2/11	6.0
3	7	5	2/14	3.7	3	6	3	2/9	4.2
4	6	4	2/14	4.2	4	5	3	2/11	5.0
5	4	2	2/15	6.0	5	4	2	2/11	6.0
6	-	-	1/1	-	6	-	-	1/1	
7	11	9	2/14	2.5	7	7	5	2/10	3.7
8	2	0	2/3	10.0	8	-	-	2/2	-
9	3	2	1/4	6.0	9	3	2	1/4	6.0
10	9	7	2/11	3.0	10	5	3	2/6	5.0
11	-	-	1/1	-	11	-	-	1/1	-
12	2	0	2/6	10.0	12	2	0	2/6	10.0
13	2	0	2/6	10.0	13	2	0	2/6	10.0
14	-	-	1/1	-	14	-	-	1/1	-
15	1	0	1/2	10.0	15	1	0	1/2	10.0
16	2	1	1/6	7.5	16	2	1	1/6	7.5
17	1	0	1/2	10.0	17	1	0	1/2	10.0
18	4	3	1/6	5.0	18	4	3	1/6	5.0
19	2	1	1/10	7.5	19	2	1	1/10	7.5
20	1	0	1/9	10.0	20	1	0	1/9	10.0
21	11	9	2/16	2.5	21	11	9	2/16	2.5
22	3	2	1/10	6.0	22	3	2	1/10	6.0
23	4	2	2/6	6.0	23	4	2	2/6	6.0
24	4	2	2/15	6.0	24	4	2	2/15	6.0
25	-	-	1/1	-	25	-	-	1/1	
26	3	1	2/6	7.5	26	3	1	2/6	7.5
27	6	4	2/11	4.2	27	6	4	2/11	4.2
28	5	3	2/6	5.0	28	5	3	2/6	5.0
29	2	1	1/4	7.5	29	2	1	1/4	7.5
30	2	1	1/3	7.5	30	2	1	1/3	7.5
31	2	1	1/3	7.5	31	2	1	1/10	7.5
32	3	2	1/7	6.0	32	3	2	1/7	6.0
33	5	4	1/10	4.2	33	5	4	1/10	4.2
34	2	1	1/3	7.5	34	2	1	1/3	7.5
35	-	-	1/1	-	35	-	-	1/1	-

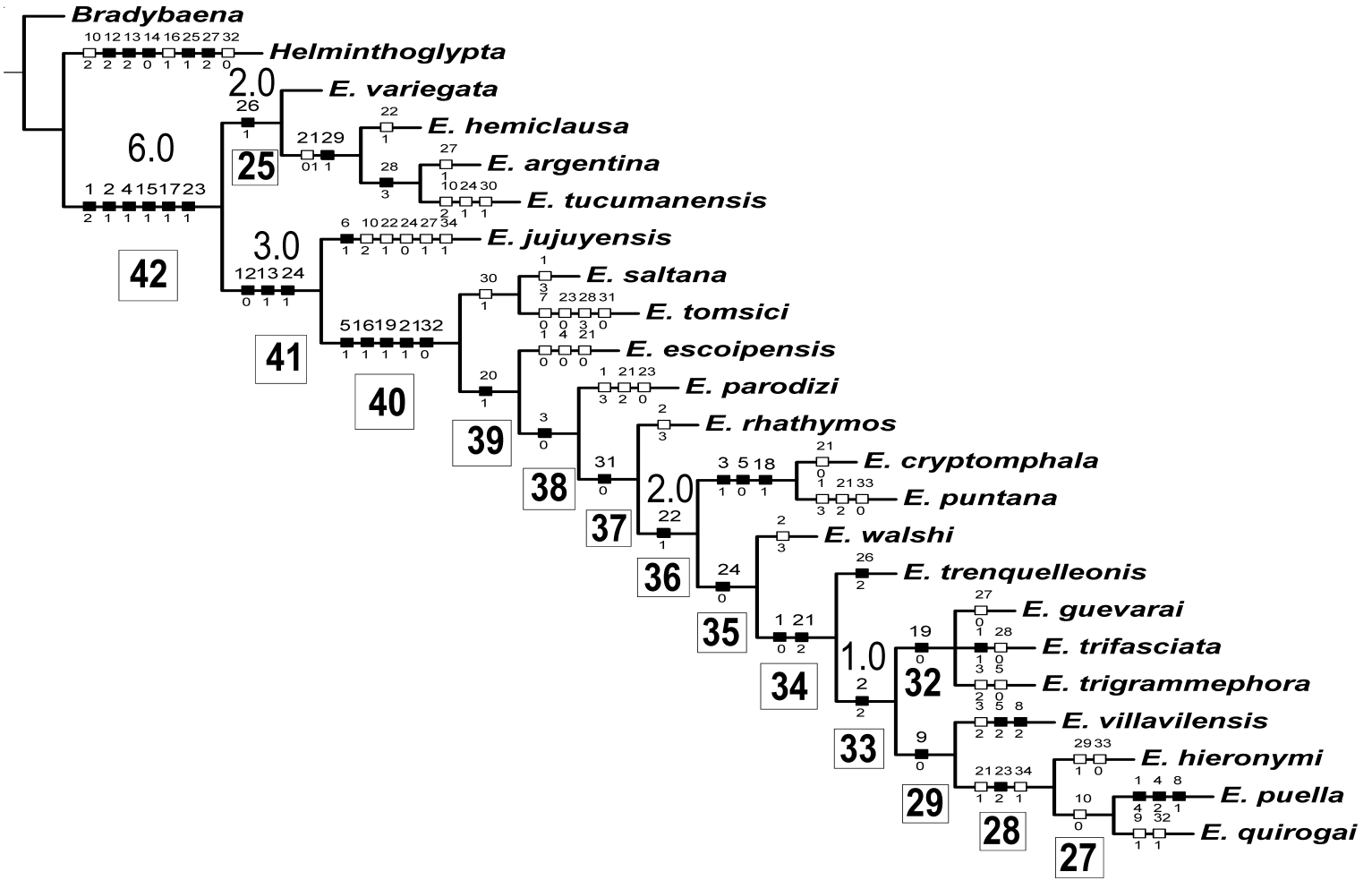

FIG. 23. Optimal tree obtained eliminating all taxa defined only by shell characters with no anatomical information from the matrix (second analysis). Black squares illustrating unambiguous synapomorphies according to PeeWee. Numbers below squares are state characters, Numbers above squares are characters detailed in Table 2. Bremer support scores are the numbers in bold above nodes. Big numbers within empty squares are node numbers.

the dart sac, are constant characters in all and each species studied. For this reason, the morphology of the terminal genitalia, especially referring to the dart sac complex, has been used to characterize each of the species treated.

Traditionally, some species such as *E. trenquelleonis, E. hieronymi* and *E. trigrammephora,* those with the widest areas of distribution that were mostly known only by their shells, have been suspected to be groups of species instead of single taxonomic units. In the present study, intensive fieldwork and collections of live specimens of *E. trenquelleonis* in different localities made possible the study on the variability of shell and anatomy, confirming its validity as a single species. *Epiphragmophora hieronymi* had been split into ***E. quirogai*** n. sp. and *E. hieronymi* species. Both species showed differences in shell morphology and were simpatric in some regions of Catamarca Province, northwestern Argentina. The analysis of the genitalia allows us to recognize the existence of two groups with a constant pattern of their genitalia. *Epiphragmophora trigrammephora* has also been exhaustively collected in localities from different ecoregions, including its type locality. Small specimens from Salta Province, usually identified as *E. trigrammephora* by shell characters, showed conspicuous differences also in the terminal genitalia so that a new species, ***E. walshi*** n. sp., has been erected.

The reconstructed phylogeny based on morphological data clearly supports the monophyly of *Epiphragmophora* on the base of six unambiguous synapomorphies and a good Bremer support score of 6.0. The cladistic hypothesis obtained is basally split into two main monophyletic sister clades, that also present a good Bremer support score (Fig. 23, node 42). Characters of the distal portion of the reproductive tract, such as the length of the vagina, shape and point of insertion of the dart sac complex, number and shape of mucous glands, are among the most informative characters. Shell characters proved to be less informative than anatomical characters (compare behavior of shell characters respect anatomical characters in Table 2). The species known only by shell characters, especially *E. audouini, E. estella* and *E. oresigena,* were unstable in their position in the cladograms, proposing relationships not well supported. The short duct of the bursa copulatrix, traditionally treated as an important character to diagnose the genus/subfamily by Pilsbry (1939), is not characteristic of all studied species but only from a small group of them (node 35, Fig. 23). The diverticulum of the bursa copulatrix, another character traditionally considered as a synapomorphy of Helicoidea, is absent in all studied species of *Epiphragmophora.* The diverticulum of the bursa copulatrix is present, however, in genera close to *Epiphragmophora* such as *Helminthoglypta.*

According to the preferred phylogenetic hypothesis of *Epiphragmophora* presented here (Fig. 23), the insertion of the dart sac (character 13) occurred in the vagina in one of the main monophyletic groups of species (*E. variegata, E. hemiclausa, E. argentina* and *E. tucumanensis*) whereas in its sister group (rest of the treated species, node 41) the insertion of the dart sac is in the atrium. In the first-mentioned clade, the dart sac does not have a medial constriction that is present in all the rest of the species. In the species of the second clade (node 41), one of the mucous glands is sac-like, surrounding the basal genitalia, usually being attached to the atrium wall. In the species of the first group (node 25), the mucous glands are usually oval to cylindrical, with efferent ducts not fused to each other.

Within the second clade, *E. villavilensis, E. hieronymi, E. puella* and ***E. quirogai*** n. sp., the smallest species of the genus in shell diameter are grouped into a derived monophyletic clade (node 29) with a high Bremer support score. This mentioned group of species is almost exclusively distributed in the Monte and Pre-Puna biogeographic provinces. *Epiphragmophora trifasciata, E. trigrammephora* and ***E. guevarai*** n. sp. also form a monophyletic clade (node 32), although the relationships among them are not well resolved.

Although the taxon sample used in the present hypothesis is not insignificant, as the genus is represented by more than the 50% of the known species, I do not propose subdivisions of *Epiphragmophora* until the anatomy of the northern species is known and a new cladistic analysis can be carried out. However, *E. hieronymi*, the type species of *Epiphragmophora* s.s., and *E. trenquelleonis*, the type species of *E.* (*Doeringina*), both belong to the second clade (node 41) delimited in the preferred tree (Fig. 23). Thus, the validity of these previously stablished subgenera as independent taxonomic identitites is dubious based on my preliminary phylogeny of the genus.

Among the Helicoidea, the dart sac complex (= stimulatory organ) generally inserts at the vagina except for the Sphincterochilidae, in which the insertion is at the atrium, and in some Helminthoglyptinae and Cepoliinae, in which the dart sac complex inserts at the atrial sac (= neophore). A "dart sheath" (Pilsbry, 1939), or a "basal genital sheath" (Cuezzo, 1998), present in Cepoliinae and Helminthoglyptinae, is absent in all *Epiphragmophora* species studied.

Nordsieck (1987) considered that the insertion of the dart sac complex at the atrium was an autapomorphy of the Helicoidea. Hausdorf (1998) stated that the insertion of the dart sac complex (= stimulator) on the atrium is not an autapomorphy but a symplesiomorphy shared with the Limacoidea *sensu lato.* He also supported the idea that in the ancestral state of the Cepoliidae + odontognath Helicoidea, the dart sac complex does not insert on the vagina but on the atrium, as in the Sphincterochilidae and in the Limacoidea *sensu lato.* Narrative hypotheses on the evolution of the dart sac complex established for the genus/subfamily until now (Ihering, 1929; Nordsieck, 1987; Schileyko, 1991) are not relevant, because they are not based on strict character analysis and testable methodologies. Further anatomical studies and new cladistic analyses in Helicoidea are necessary before a better understanding on the evolution of the dart sac complex is achieved.

Biogeographic Considerations

The species of *Epiphragmophora* that inhabit rainforest areas called Yungas – *E. tucumanensis, E. argentina, E. hemiclausa, E. variegata, E. jujuyensis,* and *E. saltana* – that are characteristics species living in relation to humids tree logs, occupy a basal position in the area cladogram (Fig. 24). Three species are widely distributed into the Yungas and Chacoan provinces – *E. trigrammephora, E. tomsici* and *E. rhathymos.* The rest of the *Epiphragmophora* species inhabit more arid environments of Chaco, Monte and Pre-Puna provinces and are found living in association to rocks, usually within narrow crevices. The Monte and Pre-Puna areas conform a monophyletic clade with a more derived position in the area cladogram (Fig. 24).

The Amazonian biogeographic subregion show closed relationships to the Chacoan biogeographic subregions. The development of the Chacoan subregion during the Tertiary splits the formerly continuous Amazonian forest into the Yungas (northwestern Argentina-southern Bolivia) and Paraná rainforest (northeastern Argentina-southern Brazil) representing an example of dynamic vicariance (Morrone, 2006). The Monte province comprises central Argentina between latitudes 24°S and 43°S, its fauna is basically of Chacoan origin, although some elements are Patagonian, Prepunean and Subantartic. It has been suggested that the Monte represents an "impoverished", Chaco (Morrone, 2006). A cladistic biogeographic analysis based on beetle and plant taxa showed that these provinces are closely related (Morrone, 1993). Roig Juñet & Flores (2001) divided the Monte province into three areas of endemism – the Boreal Monte, Central Monte, and Austral Monte. The Boreal Monte extends from Salta to northern La Rioja provinces through three longitudinal valleys limited by mountains higher than 3,000 m. ***Epiphragmophora quirogai*** sp. nov. and *E. puella* are endemic of the Boreal Monte area. No species of the genus have been collected or found in the other two areas of endemism of the Monte province. Within the Chacoan subregion two areas of endemism had been delimited (Roig Juñet & Flores, 2001), the Occidental Chaco and the "Llanos Chaqueños". The Occidental Chaco is an area that extends from southern Bolivia and western Paraguay to northern Córdoba Province in Argentina. *Epiphragmophora trigrammephora* and ***E. walshi*** inhabit this area of endemism. The "Llanos Chaqueños", ranges from southwestern Santiago del Estero Province through western part of Córdoba and eastern portion of Catamarca to northern San Luis Province. ***Epiphragmophora guevarai****, E. trenquelleonis, E. puntana, E. tomsici* and *E. trifasciata´*s areas of distribution are coincident with the "Llanos Chaqueños", area of endemism. Some of the *Epiphragmophora* species are habitants of the Pre-Puna, an area recently classified as a "South American Transition zone" (Morrone, 2006). This transitional zone extends along the highlands of the Andes between western Venezuela, northern Chile and west-central Argentina. The Pre-Puna and Monte provinces, previously assigned to the Neotropical region, are actually assigned to the transitional region because of the closed affinity existing between the Puna and the North Andean Paramo (Morrone, 2002, 2006). Although the species richness of such invertebrates as molluscs and insects in the Pre-Puna

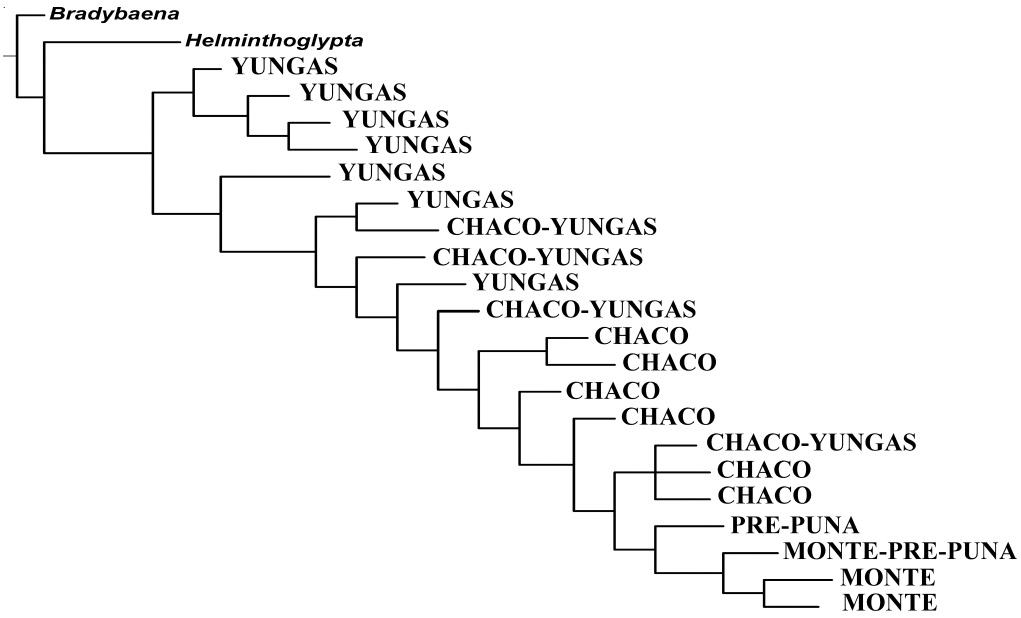

FIG. 24. Area cladogram of the *Epiphragmophora* species studied based on the preferred cladistic hypothesis obtained (Fig. 23).

area is very low, it has been postulated that this area presents a high degree of endemicity (Roig Juñet et al., 2002). *Epiphragmophora villavilensis* and *E. birabeni* are endemic species of the Pre-Puna in Argentina. *Epiphragmophora villavilensis* and *E. hieronymi* are sister groups of *E. puella* and ***E. quirogai*** that are habitants of the Monte province. *Epiphragmophora hieronymi*, usually an inhabitant of the Monte province, is also found in Pre-Puna locations of Catamarca Province. The relationships between Boreal Monte, the Chacoan areas of endemism and the Pre-Puna province remain unresolved in the present cladogram, although they are located in a derived position respect to the Yungas areas. In conclusion:

(1) *Epiphragmophora* is a monophyletic genus, the monophyly of which is supported in the present hypothesis (Fig. 23) by six unambiguous synapomorphies. There are two main monophyletic subclades within the genus that could potentially represent subgenera.

(2) Anatomical characters specially concerning the distal portion of the reproductive tract are more informative than shell characters to establish phylogenetic relationships. A new cladistic analysis is recommended only when the anatomy of the rest of the species presently known by shell descriptions or by single specimens is available.

(3) The insertion of the dart sac is either in the atrium or in the vagina and the two unequal mucous glands insert in the medial zone of a single dart sac.

(4) According to the area cladogram (Fig. 24) based on the phylogenetic hypothesis obtained, the rainforest areas or Yungas biogeographic province are paraphyletic. The xerophilic areas of Monte, Chacoan and Pre-Puna biogeographic provinces are located in a more derived position respect to the Yungas in the present hypothesis. The Monte and Pre-Puna conforms a monophyletic clade.

ACKNOWLEDGEMENTS

I would like to express my gratitude to several persons that over the years were my companion in many days of searching and collecting live land snails in the field, especially to E. Dominguez, C. Ituarte and F. Romero. Thanks are extended to both curators and museums that sent detailed photo-

graphs, type material for study, or allowed the revision of their malacological collections, facilitating in many ways the present work: C. Ituarte (MLP, La Plata, Argentina); A. Tablado (MACN, Buenos Aires, Argentina); I. Fernández (NKC, Bolivia); J. Kochalca (IBNP, Paraguay); P. Bouchet and V. Héros (MNHN, Paris, France); R. Janssen (SMF, Frankfurt am Main, Germany); R. Bieler (FMNH, Chicago, USA); and A. Mc Lellan (BMNH, London, England). Special gratitude is expressed to the Argentinean National Park Service Agency, especially to the northwestern regional office, which extended several working permits to carry on the research in national park areas. The support gave by many rangers during field work for the present study is also appreciated. Permission to work at the San Javier Park from the National University of Tucumán is also acknowledged. Thanks are extended to Manuel Quintana (MACN) who kindly provided special bibliography on some species of *Epiphragmophora* and to F. Cuezzo, who read the manuscript and made useful suggestions. I also thank the two anonymous reviewers who provided useful comments to improve the manuscript. The author is a researcher of the Argentine National Council of Scientific Research (CONICET). This study was financed by Grant PIP 0554/98 (CONICET) awarded to the author.

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Revised ms. accepted 2 June 2006

APPENDIX

Matrix of 29 taxa per 35 characters used in the cladistic analysis. Underlined taxa are those for which anatomical data are lacking and which are not considered in the second parsimony analysis.

	Character																																		
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Bradybaena	0	3	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	1	1	0	0	2
Helminthoglypta	[04]	[03]	1	0	0	0	1	0	1	2	1	2	2	0	0	1	0	0	0	0	2	0	0	2	1	0	2	3	0	0	1	0	0	0	1
E. argentina	2	[01]	0	1	0	0	1	0	1	1	1	1	0	1	1	0	1	1	0	0	1	0	1	2	0	1	1	3	1	0	1	1	0	0	1
E. birabeni	3	2	1	1	1	0	0	0	1	1	?	?	?	?	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	1	?	?	?	?
E. costellata	3	3	0	1	2	0	1	2	1	2	?	?	?	?	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	0	?	?	?	?
E. cryptomphala	2	[01]	[12]	1	0	0	2	0	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	2	0	0	0	0	1	0	1
E. escoipensis	0	1	1	0	1	0	[01]	0	1	1	1	0	1	1	1	1	1	0	1	1	0	0	1	1	0	0	0	2	0	0	1	0	0	0	1
E. hemiclausa	2	1	0	1	0	0	1	0	1	1	1	1	0	1	1	0	1	0	0	0	0	1	1	2	0	1	0	2	1	0	1	1	0	0	1
E. guevarai	0	2	0	0	1	0	2	0	1	1	1	0	1	1	1	1	1	0	0	1	2	1	1	0	0	0	0	2	0	0	0	0	1	0	1
E. hieronymi	0	2	0	0	1	0	1	0	0	1	1	0	1	1	1	1	1	0	1	1	1	1	2	0	0	0	1	2	1	0	0	0	0	1	1
E. jujuyensis	2	1	1	1	0	1	1	0	1	2	1	0	1	1	1	0	1	1	0	0	2	1	1	0	0	0	1	2	0	0	1	1	1	1	1
E. parodizi	3	1	0	1	1	0	1	0	1	1	1	0	1	1	1	1	1	0	1	1	2	0	0	1	0	0	0	2	0	0	1	0	1	0	1
E. proseni	2	1	1	1	1	0	0	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
E. puella	4	2	0	2	1	0	0	1	0	0	1	0	?	?	1	?	?	0	1	?	?	?	?	0	0	?	?	2	?	?	0	0	1	?	?
E. puntana	3	1	1	0	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	2	1	1	1	0	0	0	2	0	0	0	0	0	0	1
E. quirogai	0	2	0	0	1	0	0	0	1	0	1	0	1	1	1	1	1	0	1	1	0	1	2	0	0	0	1	2	0	0	0	1	1	1	1
E. rhathymos	2	3	0	1	1	0	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	0	0	0	2	0	0	0	0	1	0	1
E. saltana	3	1	1	1	1	0	1	0	1	1	1	0	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	2	0	1	1	0	0	0	1
E. tomsici	2	1	1	1	1	0	0	0	1	1	1	0	1	1	1	1	1	0	1	0	1	0	0	1	0	0	0	3	0	1	0	0	1	0	1
E. trenquelleonis	0	1	0	0	1	0	1	0	1	1	1	0	1	1	1	1	1	0	1	1	2	1	1	0	0	2	1	2	0	0	[01]	0	1	0	1
E. trifasciata	1	2	0	0	1	0	2	0	1	1	1	0	1	1	1	1	1	0	0	1	2	1	1	0	0	0	1	0	0	0	0	0	1	0	1
E. trigrammephora	[02]	2	2	0	0	0	2	0	1	1	1	0	1	1	1	1	1	0	0	1	2	1	1	0	0	0	1	2	0	0	[01]	0	1	0	1
E. tucumanensis	2	1	[01]	1	0	[01]	1	0	1	2	1	1	0	1	1	0	1	1	0	0	0	0	1	1	0	1	0	3	1	1	1	1	0	0	1
E. variegata	2	[01]	0	1	0	0	[012]	0	1	1	1	1	0	1	1	0	1	1	0	0	2	0	1	2	0	1	0	2	0	0	1	1	0	0	1
E. villavilensis	0	2	2	0	2	0	0	2	0	1	1	0	1	1	1	1	1	0	1	1	2	1	1	0	0	0	1	2	?	0	0	?	1	0	1
E. walshi	2	3	0	0	1	0	2	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	2	0	0	0	0	1	0	1
E. audouini	2	1	1	1	0	0	0	[01]	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?
E. estella	2	1	1	0	0	0	1	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
E. oresigena	2	1	2	1	0	0	2	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?