Taxonomic Revision of the *Bostryx stelzneri* Species Complex, with Description of a New Species (Gastropoda: Orthalicoidea: Bulimulidae)

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Source: American Malacological Bulletin, 32(1):74-93. 2014.
Published By: American Malacological Society
DOI: http://dx.doi.org/10.4003/006.032.0107
URL: http://www.bioone.org/doi/full/10.4003/006.032.0107

Amer. Malac. Bull. **32**(1): 74–93 (2014) http://www.bioone.org/toc/malb/32/1

Taxonomic revision of the *Bostryx stelzneri* species complex, with description of a new species (Gastropoda: Orthalicoidea: Bulimulidae)

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Abstract: The *Bostryx stelzneri* species complex is taxonomically reviewed with the description of a new species. This complex is formed by *Bostryx stelzneri* (Dohrn, 1875), *B. peristomatus* (Doering, 1879), *B. scaber* (Parodiz, 1948) and *Bostryx roselleus* n. sp., all distributed in Argentina. *Bostryx peristomatus* and *B. scaber* are elevated to specific status on the basis of morphological characters. This complex has the spire less than half the total shell height and the aperture higher in relation to total shell height than in any other species of the genus. Traditional shell morphometry and a geometric morphometric analysis were used to document shell variation in size and shape among species. Radula, jaw and shell morphology were examined with SEM. All species in the complex are described or redescribed using new morphological information. In this species complex, pallial organs are very similar among species and vary only in the degree of opening of the secondary ureter. The genitalia differ in the relative proportion of organs, such as length of vagina relative to free oviduct and penis or epiphallus length relative to penis length. Sculpture of the inner wall of the flagellum and epiphallus is similar in all species studied, whereas sculpture of the inner wall of the penis is variable. Geometric morphometric analysis allows an objective interpretation of shell shape variation detecting differences in shape components irrespective of the differences in size between *Bostryx* Troschel, 1847 species of the *stelzneri* group.

Key words: morphology, Argentina, distribution, endemism, morphometric analysis

Bostryx was described by Troschel (1847) who originally designated *Bulimus* (*Bostryx*) *solutus* Troschel, 1847 as the type species. The taxonomic position and monophyly of this group is still a matter of discussion. Some authors considered *Bostryx* as a separate entity from *Bulimulus* Leach, 1814, the most similar group within Bulimulidae (Breure 1979, Parodiz 1946, Miquel 1993, 1995). Others, because of the absence of good diagnostic characters merged *Bostryx* into *Bulimulus* and classified *Bostryx* as a subgenus of the latter. *Bulimulus* (*Bostryx*) was described by Pilsbry (1896 [1895–1896]), by the smooth and frequently rather teat-like apex or less calcareous texture and unexpanded or but little expanded lip. Thiele 1931 and Zilch (1959–1960) maintained this classification. Breure (1979) reports 274 available names within *Bostryx*. Breure and Romero (2012) in a recent molecular work, using only 10 *Bostryx* species among other orthalicoids, introduced the possibility that *Bostryx* is probably polyphyletic and created the subfamily Bostrycinae. This subfamily was composed exclusively by *B. solutus,* the type species of the genus plus six other species of *Bostryx*. Later, Breure (2012) used two morphological characters (shell with smooth protoconch, genital organs with a relatively long penis sheath) to diagnose and justify the creation of this subfamily, characters that are not unique to the genus *Bostryx,* introducing new uncertainties in the taxonomy of *Bostryx*.

Bostryx is endemic to South America and is widely distributed in Argentina, Bolivia, Chile, Paraguay, Peru, Colombia, and Ecuador (Breure 1979, Breure *et al*. 2010). *Bostryx stelzneri* (Dohrn, 1875) species complex is found from Chuquisaca (Bolivia) to Coronel Pringles (San Luis, Argentina) (20°–32°S). In Argentina this species complex inhabits High Monte, Dry Chaco, Central Andean Puna, Southern Andean steppe, and Espinal, and in Bolivia, Montane Dry forest ecoregions.

Breure (1979) listed 23 species of *Bostryx* in Argentina, while Miquel (1993, 1995) recognized only 13 valid species using shell morphology similarities to justify his synonymic actions. Most of the species of the genus are still scarcely known and were originally described using only shell morphology and radular features. Intraspecific shell variability is marked in *Bostryx* even among specimens from the same locality (co-occurrence of forms) and also among specimens from geographically distant localities. Curiously, shell variability has not been analyzed in any species of the genus. Anatomical aspects of Argentinean species of *Bostryx* have been provided in different publications (Hylton Scott 1945, 1954, 1967, Breure 1978). Previous works on *B. stelzneri* (Doering 1875, 1879, Pfeiffer 1876, Pilsbry 1896 [1895–1896], Holmberg 1912, Parodiz 1946, 1948, Miquel 1993) are based mainly on shell and jaw descriptions, with scarce anatomical information (Hylton Scott 1945, Breure 1978). Because of the high shell intraspecific variation, many varieties and forms have been described: *Bostryx stelzneri stelzneri* (Dohrn, 1875) *B. stelzneri peristomatus* (Doering, 1879), *B. stelzneri conispirus*

(Doering, 1879), *B. stelzneri hector* (Holmberg, 1909), *B. stelzneri apertus* (Hylton Scott, 1948), *B. stelzneri hybrida* (Parodiz, 1948), *B. stelzneri nonogastanus* (Parodiz, 1948), *B. stelzneri tinogastanus* (Parodiz, 1948), and *B. stelzneri scaber* (Parodiz, 1948). The taxa *Bulimulus hector* Holmberg, 1909, *Bulimulus* (*Scutalus*) *peristomatus* Doering, 1879, and *Bulimulus* (*Scutalus*) *conispirus* Doering, 1879 were originally described as species but were later treated as varieties of *B. stelzneri* by Parodiz (1948). He considered that there was no clear distinction between these species and *B. stelzneri,* and as their distributional ranges were not sufficiently different, Parodiz reclassified *Bulimulus hector, Bulimulus* (*Scutalus*) *peristomatus,* and *Bulimulus* (*Scutalus*) *conispirus* as varieties of *B. stelzneri*. Parodiz (1948) following Pilsbry (1939), used the term "form" to designate ecological forms which are those whose peculiarities are presumably owing to the action of some special factors of their station on a genotypically unchanged stock. Miquel (1993) reviewed the genus *Bostryx* and synonymized all described forms and varieties into *B. stelzneri* because he considered that these variable forms corresponded to different populations of *B. stelzneri*.

In the course of the taxonomic revision of the species of *Bostryx* distributed in Argentina it became obvious that clarification of the status of the taxonomic entities composing the *B. stelzneri* group was necessary. We were interested in using morphology as a tool for species delimitation. Additional information on traditional morphometry and a geometric morphometric analysis was carried out to study shell variation and to confirm differences in shell size and shape among species.

MATERIALS AND METHODS

Adults and juvenile specimens of *Bostryx stelzneri* species complex were collected from northern (24°S) to central Argentina (32°S) during summer-autumn seasons from 1996 to 2011. The area included eight political provinces of Argentina and the whole distributional area of this species complex in the country. Extensive materials, including type materials, were also studied from malacological collections from the following institutions: Instituto Fundación Miguel Lillo (IFML), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-In), Museo de La Plata (MLP), and Natur-Museum Senckenberg, Frankfurt am Main(SMF).

Type locality for each species is given as it is stated in the original publications. Further detail was added, when possible, to clarify the geographic location of each type locality. This includes clarification on Province (Prov.) and Political Department Division (Dept.) of each locality. Live specimens were photographed prior to fixation to record body and shell coloration and possible color variability. Adult specimens were drowned in deoxygenated water and fixed in 96% ethanol and later preserved in 80% ethanol. Shell morphology was observed, measured, and described under a Leica MZ6 stereoscopic microscope. Shell protoconch was photographed with a Jeol Scanning Electron Microscope 35CF at the Integral Center of Electron Microscopy of the National University of Tucumán (CIME). Standard shell measurements were obtained using a caliper (0.01 mm of accuracy) under stereoscopic microscope with shell axis (columella) to Y axis of coordinates and the maximum shell breadth accurately in plane view. Shell height (H) was measured from the apex of the shell to basal portion of aperture (Fig. 1A); body whorl height (HBw) was measured from last suture to basal portion of aperture (Fig. 1A); spire height (Hs) was measured from the apex to the lower suture; shell apertural height (Hap) was measured from top of aperture to the outer lip of the peristome (Fig. 1A); shell apertural diameter (Dap) was measured including the peristome (Fig. 1A). Major diameter of the shell (DM) was measured including the peristome (Fig. 1A). Minor diameter (dm) is a measurement perpendicular to the major diameter (Fig. 1B). Maxima and minima for each measurement are reported with the median value. Pearson Correlation coefficient was calculated (InfoStat v.2009) (Di Rienzo *et al*. 2009)) among the shell measurements of specimens from different populations of *Bostryx stelzneri*, climate parameters (minima and maxima temperature, precipitation), altitude, latitude, and longitude, to test if there were

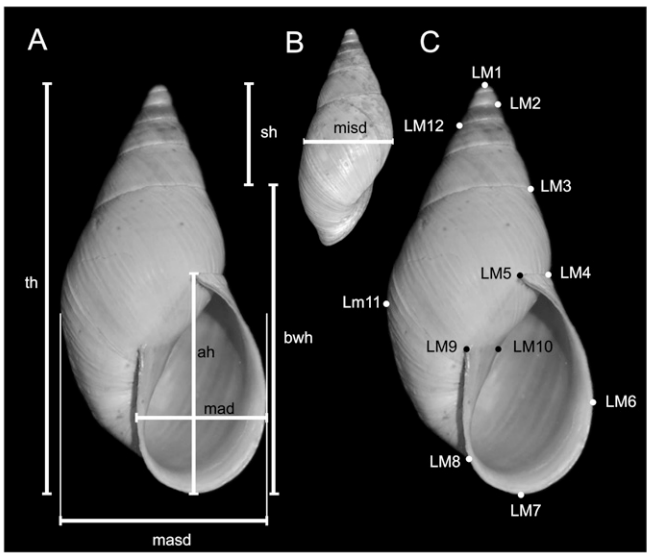

Figure 1. A, B, shell Measurements; **C,** ventral view of *Bostryx roselleus* n. sp. showing the landmarks used in the geometric morphometric analysis. Abbreviations: **ah,** apertural height; **bwh,** body whorl height; **LM 1–12,** landmarks; **mad,** major apertural diameter; **masd,** major shell diameter; **misd,** minor shell diameter; **sh,** spire height; **th,** total height.

any correlation between shell diversity and these parameters. Climate data for each locality were obtained from DivaGis Software v.7.3.0.1 (Hijmans *et al.* 2007) and altitude, latitude, and longitude were recorded in the field with a Garmin GPS.

Number of shell whorls was calculated following Kerney and Cameron (1979)'s methodology. Radula and jaw were extracted and prepared according to Ploeger and Breure (1977). Different anatomical systems were dissected out from alcohol-fixed specimens; organs were drawn with the aid of a camera lucida under microscope. Number of specimens dissected varied upon availability from four to 20 in each case. Terminology for the anatomical descriptions follows Tompa (1984). Terms proximal and distal refer to the position of an organ, or part of an organ, in relation to the direction of gamete flow, from ovotestis (proximal) towards genital atrium (distal). The distinction between epiphallus and penis is based on the internal sculpture differences of these organs (Cuezzo 1997, 2006). Holotype and paratypes of the new species are deposited at IFML collection with additional paratypes also deposited at MACN-In and MLP.

The geographic distribution map was done using Diva-Gis Software v.7.3.0.1 (Hijmans *et al.* 2007) with georeferenced data, altitudinal data layers, and political divisions of Argentinean provinces. Ecoregion definition and delimitations for Argentina are according to Olson *et al.* (1998, 2001).

Geometric morphometrics was performed to quantitatively analyze the relationship between shape and size of the different species, testing if these analyses gave complementary information to our morphological observations or differed from them. On these grounds, geometric morphometric analysis was performed on 15 specimens of *Bostryx roselleus* sp. nov., *B. peristomatus*, and *B. stelzneri* and ten specimens of *B. scaber*. Numbers were determined on the basis of adult shell specimen availability. Specimens were randomly selected and photographed with a Nikon D5000 digital camera. Shell landmarks, discrete anatomical loci that are homologous in all individuals in the analysis, expressed by coordinates, were chosen in each case. Landmarks were always selected from shells in ventral view and were defined as follows: Twelve landmarks (LM) representative of the shell were chosen on ventral view (Fig. 1C): LM1 = represents the apex of the shell; LM2 = is in the suture between the second and third whorls; LM3 = is in the upper suture of the penultimate whorl; LM4 = is in the lower suture; LM5 = is at the end of the lower suture; LM6 = is the most external position in the external part of the outer lip; LM7 = is the lowest point at the base; LM8 = is the most external point in the external border of the columellar edge of aperture; LM9 and LM10 = show the external and internal border, respectively, of the columella; LM11 = is the most external point in the last whorl at the left profile of the shell; LM12 = is in the suture between the third and fourth whorls. All specimens were digitalized with the software TPS dig2 (Rohlf 1996). Shape analysis begins by removing the information that is not about shape. Differences due to rotation, translation and scale were filtered by Procrustes Analysis (GPA) (Rohlf and Slice 1990). GPA is an iterative, least-squares procedure that scales specimens to a unit size, the centroid size, translates them to a common origin, and rotates them to minimize the sum of squared distances across all landmarks and specimens (Slice 2005). The centroid size was a variable used for size normalization, calculated as the square root of the sum of the squared deviations of landmarks from the centroid (Bookstein 1991). Differences in centroid size distributions among species were tested with one-way ANOVA using InfoStat software v.2009 (Di Rienzo *et al.* 2009). To display the differences in shape, the data are reduced to a comprehensible (low-dimensional) form. We computed a multivariate regression of shape (Procrustes coordinates used as dependent variables) on size (independent variable) to assess and control putative allometric effects. Then, we carried out a permutation test with 10,000 rounds to evaluate the independence between the shape and size variables. This methodology follows Signorelli *et al.* (2013). To describe the diversity of shapes in a sample, we used two methods: Principal Component Analysis (PCA) and Canonical Variate Analysis (CVA). The principal components of shape were calculated from a principal component analysis (PCA) of the variance–covariance matrix of the Procrustes coordinates. PCA was used to show the shell shape variation of specimens along the axes generating linear combinations of the original variables ordered sequentially (Slice *et al.* 1996, Slice 2005).

In order to simplify descriptions of differences between groups and maximize the separation of specified species we computed a CVA on the first PCs with software MorphoJ (Klingenberg 2008). CVA is a method in which the variation among groups is expressed relative to the pooled within-group covariance matrix. Canonical Variate Analysis finds linear transformations of the data which maximize the among group variation relative to the pooled within-group variation. The canonical variates are displayed as an ordination to show the group centroids and scatter within groups. This may be thought of as a "data reduction" method in the sense that one wants to describe among group differences in few dimensions (Slice *et al.* 1996).

Institutional Abbreviations

IFML: Instituto Fundación Miguel Lillo, Tucumán, Argentina, FS: Centro de Biología de Linz, MACN-In: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina, MLP: Museo de La Plata, La Plata, Argentina, MNCN: Museo Nacional de Ciencias Naturales de Madrid, Spain, SMF: Natur-Museum Senckenberg, Frankfurt am Main, Germany, ZMB: Museum für Naturkunde, Humboldt Universität, Berlin, Germany.

RESULTS

Taxonomy

Class Gastropoda Cuvier, 1798
Subclass Heterobranchia Haszprunar, 1985
Order Pulmonata Cuvier, 1817
Suborder Stylommatophora Schmidt, 1856
Superfamily Orthalicoidea Albers, 1860
Family Bulimulidae Tryon, 1867
Genus *Bostryx* Troschel, 1847

Type species

Bulimulus (*Bostryx*) *solutus* Troschel, 1847 [original designation by monotypy].

Remarks

This genus has a protoconch generally smooth or with axial costules or wrinkles, sometimes with numerous fine spiral grooves well marked and densely arranged. Penial retractor muscle inserted in terminal portion of phallic complex. Flagellum inner wall with diagonal folds converging at a central longitudinal fold. Epiphallus divided into proximal thin and wider distal portion. Penis divided by a thin area into proximal swollen portion 1/3 of total penis length and distal cylindrical portion, ¾ of total penis length. Penis proximal portion with inner penis gland. Penial sheath muscular overlapping more than half portion of penis with retractor muscle inserted in its proximal end.

Bostryx stelzneri species complex

Spire height less than half the total shell height. Shell aperture taller than in any other species of the genus in relation to total shell height. Peristome usually slightly expanded. Shell wall thick in relation to other species.

Bostryx roselleus new species (Figs. 2–5)

Type material

Holotype (IFML 15531 A), Paratypes (IFML 15490, 15490 A) (six dry shells and ten specimens in alcohol), MACN-In 39122 (seven specimens in alcohol), MLP 13740 (seven specimens in alcohol).

Type locality

Argentina, Salta Prov., Rosario de Lerma Dept., route to San Antonio de los Cobres, 5 km from Campo Quijano to El Alisal, 24°53′19″S, W65°41′05″W, 1700 m.

Material examined

Argentina, Prov. Salta, Rosario de Lerma Dept., route to San Antonio de los Cobres (IFML 15490 A, 15531 A), seven kilometers after Campo Quijano (IFML 15487 A, 15489 A), between Campo Quijano and El Alisal (IFML 928), Santa Rosa de Tastil (IFML 15488 A), Quebrada del Toro (MLP 11017), Chicoana Dept., Quebrada La Gotera (IFML 15491 A, 15534 A, 15535 A).

Diagnosis

Pale chestnut brownish shell, especially marked at first whorls. Shell aperture half of total shell length. Spire conic, tall. Length of vagina corresponding to ¼ of penis length. Bursa copulatrix duct inner wall sculpture with proximal longitudinal straight folds and distal zigzag folds.

Etymology

The species epithet *roselleus* is a reference to the pinkish coloration of the shell. The epithet is used as an adjective.

Shell

Dextral, fusiform, slender, thin, of 5½ to 6 ½ whorls, flat to slightly convex whorls (Figs. 2A–C). Shell pale, chestnut brownish, with first whorls darker. Protoconch with thick, axial, elevated costules slightly wavy, discontinuous, parallel to each other (Figs. 2D–E). Costules separated by regular narrow spaces. Spiral grooves, parallel, densely arranged, crossing them (Fig. 2E). Spire high conic, with whorls increasing regularly in diameter (Fig. 2A). Body whorl tall in relation to the total height of the shell, 70% of the total length (Fig. 2A). Teleoconch with axial oblique shallow ribs slightly pronounced (Figs. 2A–C), spaces between them progressively more separated towards body whorl. Suture simple, slightly deep (Figs. 2A–D). Aperture elongated-ovate, tall, half the total shell length (Fig. 2A). Parietal space narrow (Fig. 2A). Peristome slightly expanded, more developed in basal edge (Figs. 2A, C). Umbilicus narrow, partially overlapped by the peristome (Figs. 2A, C).

Measurements (averages in parenthesis)

Holotype: DM = 9.55 mm; dm = 8.70 mm; H = 19.47 mm; HBw = 13.97 mm; Hs = 6.37 mm; Hap = 9.82 mm; Dap = 6.39 mm. Paratypes (*N* = 10), DM = 9.10–9.90 mm (9.45 mm); dm = 7.40–8.90 mm (8.37 mm); H = 19.40–21.10 mm (20.23 mm); HBw = 12.10–14.30 mm (12.74 mm); Hs = 7.20–9.0 mm (8.27 mm); Hap = 9.30–11.10 mm (9.89 mm); Dap = 6.10–7.50 mm (6.95 mm). Additional measurements in Table 1.

External morphology

Animal body homogeneously yellowish to pale brown, with lateral groove from genital orifice towards mantle collar, well-marked. Foot elongate, basal sole homogeneous, not divided. Genital orifice located below right ommatophore (Fig. 2F).

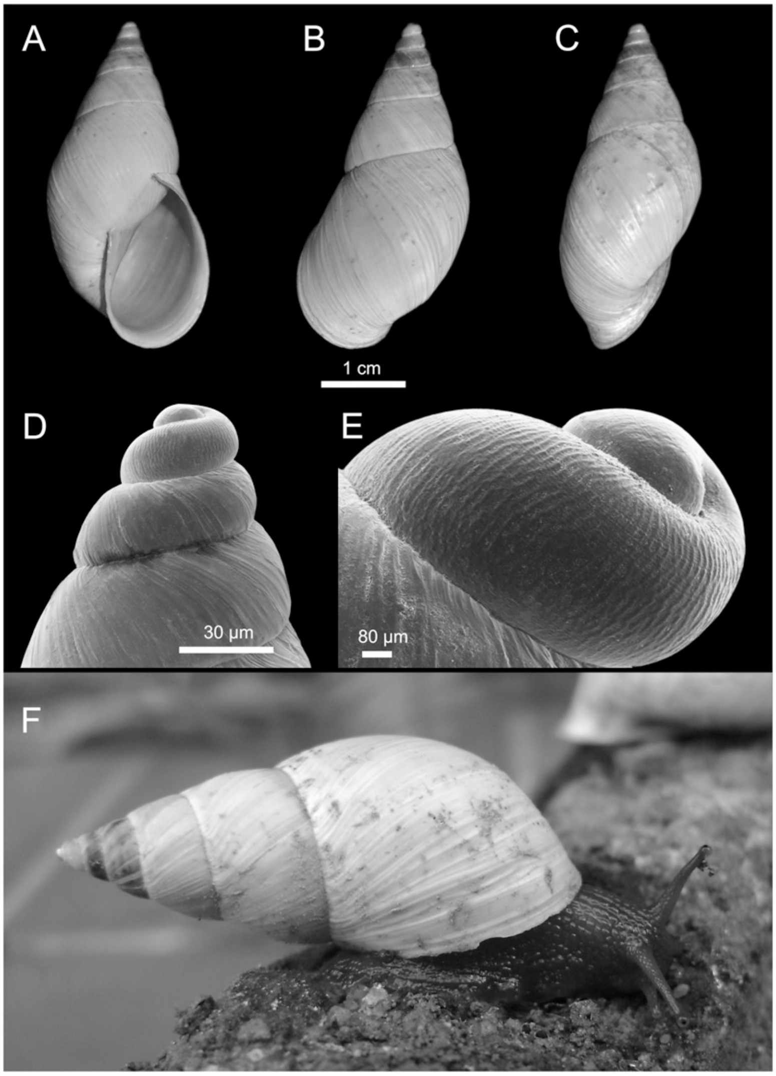

Figure 2. *Bostryx roselleus* n. sp. **A,** shell in ventral view; **B,** dorsal view; **C,** lateral view; **D,** view of the spire; **E,** scanning electron microscopy of the protoconch showing dense, spiral grooves crossing axial wavy costules; **F,** living specimen.

Digestive system

Jaw orange, arched with ten to eleven plates (two jaws observed with Scanning Electron Microscopy (SEM), twenty observed under light microscope) (Fig. 3A). Central plate triangular divided into three minor plates (Fig. 3A). Lateral plates rectangular in shape, more regular in size (Fig. 3A). Jaw with fine transverse striae (Fig. 3B). Radula narrow and long (Fig. 3C) (three radula observed with SEM). Central tooth triangular, unicuspid, with rounded tip (Fig. 3D). First lateral tooth unicuspid, similar in size and shape to central tooth, with triangular basal plate (Fig. 3D). Following lateral teeth bicuspid, ectocones progressively increasing size (Fig. 3E). Marginal teeth similar to lateral teeth, bicuspid with a sharply pointed ectocone (Fig. 3F). Buccal mass spherical-shaped. Esophagus opening dorsally from buccal mass. Initial and ending portions of esophagus thinner than middle portion. Esophagus inner wall with longitudinal, thin, parallel folds between two thicker folds. Salivary glands elongated, joined to each other by thin connective tissue, located on either side of posterior portion of esophagus. Salivary glands efferent ducts separated, very elongated, with main duct opening on each side of the esophageal opening. Esophageal crop absent. Gastric crop cylindrical. Stomach inner wall without sculpture. Intestine running along columellar side of visceral mass. Rectum following intestine running parallel to pulmonary roof and ending at mantle collar.

Pallial system (20 specimens dissected)

Kidney triangular, wider than long, slightly longer than pericardial cavity with inner longitudinal lamellae contacting one to each other (Fig. 4A). Primary ureter bordering kidney along its length towards lung roof proximal portion (Fig. 4A). Secondary ureter parallel to rectum, opening at half rectum length (Fig. 4A). Distally secondary ureter splitting into adrectal and abrectal branches close to mantle collar. Interramus zone, rectangular, excavated (Fig. 4A). Rectum opening at mantle collar. Pericardial cavity, left side of pulmonary roof, shorter than kidney (Fig. 4A). Main pulmonary vein, parallel to rectum, with distal portion thinner than proximal portion (Fig. 4A). Minor veins well marked, thin, splitting, becoming more abundant and marked towards distal portion, equally abundant on both sides of main pulmonary vein (Fig. 4A).

Reproductive System (20 specimens dissected)

Ovotestis embedded in digestive gland, two lobes fan-shaped with acini homogeneous yellowish to clear brown. Albumen gland bean-shaped (Figs. 4B–C). Hermaphroditic duct divided into three parts with central, convoluted seminal vesicle (Figs. 4B–C). Distal hermaphroditic duct portion inserting into half portion of albumen gland (Figs. 4B–C). Fertilization pouch-spermathecal complex long, finger-shaped (Figs. 4B–C). Spermoviduct oviducal portion transversely sacculated (Fig. 4B). Distally, spermoviduct splitting into free oviduct and vas deferens (Fig. 4B). Free oviduct long, same length of vagina (Fig. 4B). Bursa copulatrix duct long, reaching middle portion of albumen gland, with broader distal portion (Figs. 4B–C). Bursa copulatrix duct with two different inner wall sculpture, proximal longitudinal straight folds, distal zigzag folds. Bursa

Table 1. Morphometric data of the *Bostryx stelzneri* species complex (Min.: minimum, Max.: maximum, SD: standard deviation, *N*: number of specimens).

Character/Index	Statistical parameter	*B. roselleus* n. sp.	*B. peristomatus* (Doering, 1879)	*B. scaber* (Parodiz, 1948)	*B. stelzneri* (Dorhn, 1875)
N		56	64	11	357
H	Mean	22.07	28.10	28.30	27.03
	SD	2.74	1.54	1.65	2.90
	Min.	17.0	25.20	25.46	19.31
	Max	30.30	32.50	31.50	34.0
DM	Mean	10.47	13.42	22.25	15.49
	SD	1.25	1.15	1.37	1.96
	Min.	8.80	11.51	19.45	10.69
	Max	13.60	15.70	23.80	22.52
dm	Mean	9.21	10.51	17.49	12.65
	SD	0.98	0.65	1.26	1.31
	Min.	7.40	9.13	15.52	9.21
	Max	11.40	11.80	19.40	17.10
Hap	Mean	11.29	15.74	20.02	16.08
	SD	1.45	1.08	1.55	2.16
	Min.	9.20	13.77	17.86	10.80
	Max	14.70	20.59	22.30	22.10
Dap	Mean	7.60	10.20	14.37	10.83
	SD	0.91	0.87	0.87	1.54
	Min.	6.0	8.18	13.05	7.90
	Max	9.70	12.16	15.80	15.0
HBw	Mean	14.72	20.95	25.34	21.14
	SD	1.91	1.17	2.07	2.52
	Min.	10.90	18.30	22.07	14.70
	Max	19.40	24.0	28.30	27.90
Hs	Mean	8.14	8.26	6.06	7.33
	SD	1.02	1.02	0.70	1.08
	Min.	6.30	6.29	5.20	3.76
	Max	10.0	10.80	7.10	10.60

copulatrix sac rounded, small (Figs. 4B–C), usually pressed against albumen glad wall. Vagina cylindrical, ¼ of penis length (Fig. 4B), inner wall with longitudinal parallel folds. Penial retractor muscle short, inserted terminally in flagellum (Figs. 4B, D–E). Flagellum thin, short and cylindrical (Figs. 4B, D) with inner folds diagonal with respect to central fold, longitudinal, thin fold extending towards epiphallus (Fig. 4E). Epiphallus longer than flagellum, progressively increasing its width towards penis (Figs. 4B, D–E). Inner epiphallus wall with straight, parallel folds in proximal portion, zigzag folds in distal portion (Fig. 4E). Epiphallus length 2/3 of penis length (Figs. 4B, D–E). Penis divided in two regions by a thinner middle section (Figs. 4B, D–E). Proximal penis swollen, with inner zigzag folds followed by smooth area, distal portion cylindrical with inner relaxed zigzag folds, followed by straight longitudinal folds area (Fig. 4E). Inner penial papilla in proximal penis portion, elongated, triangular with terminal pore (Fig. 4E). Penis sheath muscular, folded upon itself in its proximal portion, overlapping the distal portion of penis (Figs. 4B, D–E). Retractor muscle, not divided, inserting on upper end of penis sheath (Fig. 4B). Vas deferens thin, running towards distal genitalia, then turning upward parallel to penial complex, inserting at basal penis sheath (Figs. 4B, D). Inside, under muscular penis sheath vas deferens making a loop before emerging at proximal portion, then running stick to penis and epiphallus and inserting in epiphallus (Fig. 4D). Atrium short (Fig. 4B), inner wall with zigzag folds.

Distribution

Salta province (Fig. 5), in the Dry Chaco and Central Andean Puna ecoregions of Argentina. *Bostryx roselleus* n. sp. is usually found on rocks or inside crevices between rocks. Common at high altitudes (1550–3200 m).

Remarks

Bostryx roselleus n. sp. was originally identified as a new subspecies of *B. stelzneri* by W. Weyrauch. He wrote lot labels using the name *altispira* to identify this new taxon, but he

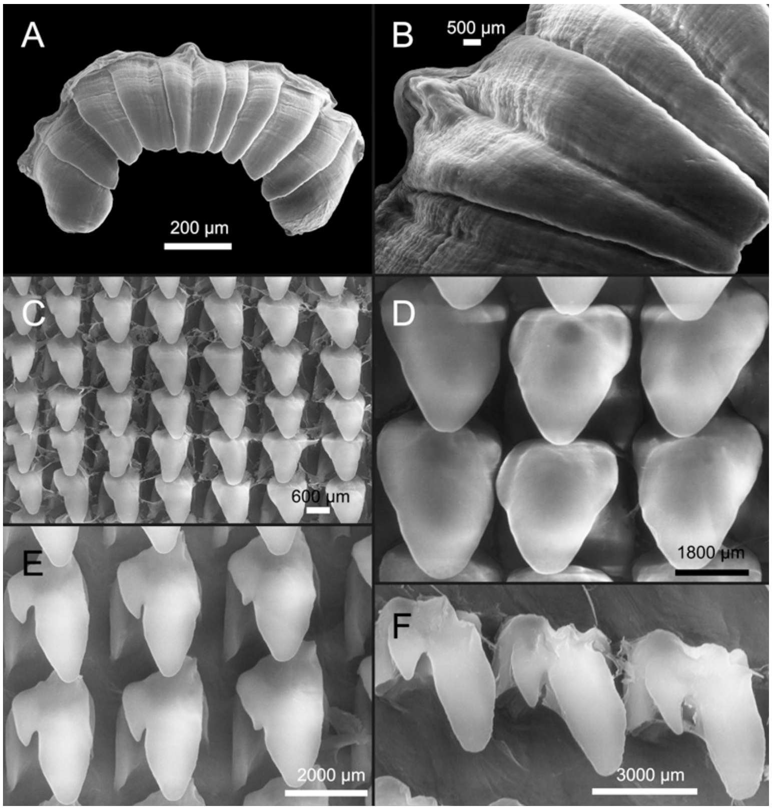

Figure 3. *Bostryx roselleus* n. sp. Digestive system. **A,** jaw; **B,** detail of jaw sculpture; **C,** radula, general view; **D,** detail of the central tooth plus the first lateral teeth; **E,** transition from lateral to marginal teeth; **F,** detail of marginal teeth.

never published it so the name was unavailable at that time according to International Code of Zoological Nomenclature (ICZN). Moreover, Weyrauch distributed material bearing the unpublished name to different malacological collections worldwide (MNCN 15.05/40698, Museo Nacional de Ciencias Naturales de Madrid, Spain; FS 3492, Centro de Biología de Linz, Austria and MLP 928, Museo de La Plata, Argentina).

Bostryx roselleus n. sp. differs from *B. peristomatus* (Doering, 1879), *B. scaber* (Parodiz, 1948) and *B. stelzneri* mainly by shell characters. Total shell height is shorter than other species of the *B. stelzneri* group and its shell is more slender, with a darker coloration distinctly marked in the first whorls. *Bostryx roselleus* n. sp. shell aperture is shorter and thinner than any other species of the *B. stelzneri* group. It has a high spire in relation to its total shell height. Also, *B. roselleus* n. sp. differs from *B. stelzneri* in its protoconch, which has axial costules slightly wavy, its radula with first lateral tooth more similar in size to central tooth, and a jaw more arched with fine transverse striae. *Bostryx stelzneri* has a protoconch with axial straight costules and jaw with grooves transverse. *Bostryx roselleus* n. sp. is comparable to *B. stelzneri, B. scaber*, and *B. peristomatus* in pallial system characters where only the degree of secondary ureter seems to vary. Two diagnostic anatomical characters that distinguish *B. roselleus* n. sp. from the other species of the complex are the length of vagina, shorter than the penis length and the inner wall morphology of the bursa copulatrix duct showing two sectors according to their different sculpture. In the other species of the *B. stelzneri* group, there is only one kind of sculpture within the bursa copulatrix duct.

In *Bostryx roselleus* n. sp. the length of the free oviduct is the same to the length of the vagina as well as in *B. stelzneri*. In comparison the length of the free oviduct respect to the vagina is longer in both, *B. peristomatus* and *B. scaber*. In *B. roselleus* n. sp. and *B. peristomatus,* the epiphallus is shorter than the penis, whereas in *B. scaber* and *B. stelzneri* is the same length.

Bostryx roselleus n. sp. has a restricted distribution in Salta Province, coincident in part with the area of distribution of *B. stelzneri.*

***Bostryx peristomatus* (Doering, 1879) [New status]**
(Figs. 5–7)
Bulimulus (*Scutalus*) *peristomatus* Doering, 1879: 66; Pilsbry, 1897–1898: 29.
Neopetraeus stelzneri var. *peristomatus*—Parodiz, 1948: 14.
Neopetraeus stelzneri peristomatus—Parodiz, 1957: 135; Hylton Scott, 1965: 25; Fernández 1973: 112.
Bostryx stelzneri peristomatus—Breure, 1978: 130; Breure, 1979: 57.
Bostryx stelzneri—Miquel, 1993: 163; Breure, 2012: 38 [*partim*]

Type material

Syntype (ZMB 34723).

Type locality

"Sierra de Pocho (Quebr. de Yatán, de Mermela, etc.)." Sierra de Pocho is located in western Córdoba into de Pocho Dept. Quebrada de Mermela is a place close to los Tuneles on the road from Las Palmas to Chancani in Sierra de Pocho. However, Quebrada de Yatán is located to the southern of Córdoba in Pampa de Achala between San Alberto and Santa Maria Depts., Córdoba Prov.

Material examined

Córdoba Prov., Pocho Dept. (IFML 15471 A), between Las Palmas and El Cadillo (MACN-In 25869, 36934 A, IFML 31619), Chancani (MACN-In 37032 A, MLP 9512, 9530), Sierra de Pocho (IFML 10881, 15595,).

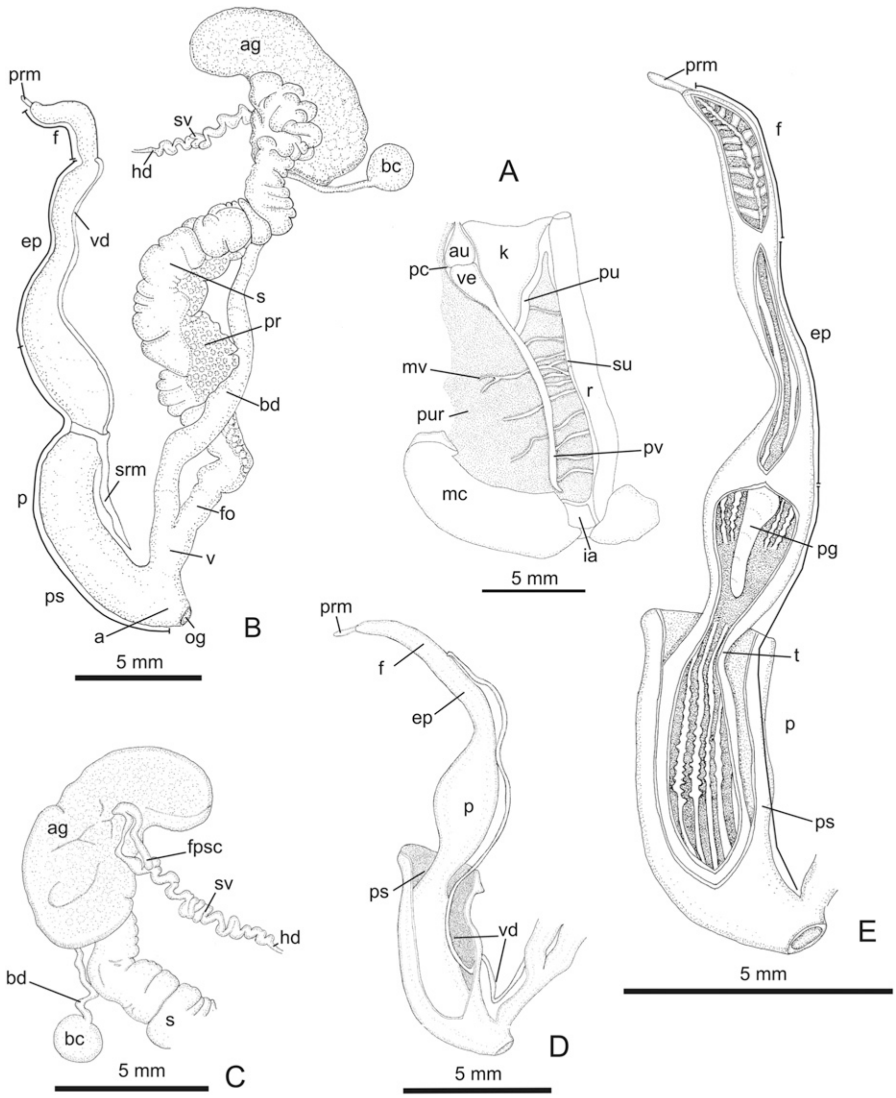

Figure 4. *Bostryx roselleus* n. sp. **A,** view of pallial system dissected out; B, general view of reproductive system dissected out; C, detail of fertilization pouch-spermathecal complex; **D,** course of vas deferens, detail of penis without sheath; **E,** phallic complex inner wall. Abbreviations: **a,** atrium; **ag,** albumen gland; **au,** auricle; **bc,** bursa copulatrix; **bd,** bursa copulatrix duct; **ep,** epiphallus; **f,** flagellum; **fo,** free oviduct; **fpsc,** fertilization pouch-spermathecal complex; **hd,** hermaphroditic duct; **ia,** interramus area; **k,** kidney; **mc,** mantle collar; **mv,** minor veins; **og,** opening genital; **p,** penis; **pc,** pericardic cavity; **pg,** penis gland; **pr,** prostate; **prm,** penial retractor muscle; **ps,** penial sheath; **pu,** primary ureter; **pur,** pulmonary roof; **pv,** pulmonary vein; **r,** rectum; **s,** spermoviduct; **srm,** sheath retractor muscle; **su,** secondary ureter; **sv,** seminal vesicle; **t,** thinning; **v,** vagina; **vd,** vas deferens; **ve,** ventricle.

Shell

Dextral, ovate-oblong, thin, of 6 to 6 ½ whorls, flat to slightly convex whorls (Figs. 6A–B). Shell brown pale to whitish. Protoconch with thick axial, elevated costules separated by regular narrow spaces, slightly wavy, discontinuous, and parallel to each other. Fine spiral grooves parallel to each other, crossing them (Figs. 6D–E). Spire conic, tall, with whorls increasing regularly in diameter (Fig. 6A). Body whorl tall in relation to the total height of the shell, 70% of the total shell length (Fig. 6A). Spire with axial oblique shallow ribs replaced in body whorl by axial thicker ribs, irregular, wavy, discontinuous (Figs. 6A–C). Intersection of ribs with spiral lines give a densely and finely granulate appearance to the last whorls. Suture simple, slightly deep, more marked in last whorls (Figs. 6A–C). Subsutural line present in some specimens. Aperture elongated-ovate, wide, 60% of total shell length (Fig. 6A), with delicate peristome highly expanded (Figs. 6A, C). Parietal space narrow (Fig. 6A). Umbilicus wide, surrounded by carina (Fig. 6C). Shell measurements in Table 1.

External morphology

Animal body homogeneously brownish, with lateral groove from genital orifice towards mantle collar, well-marked and suprapedal groove from cephalic portion to caudal portion on foot. Foot elongate, basal sole homogeneous, not divided. Genital orifice below right ommatophore.

Digestive system

Jaw orange, arched with 15 imbricate plates (seven jaws observed in light microscopy). Central plate triangular divided into two minor plates. Lateral plates rectangular in shape, regular in size. Outer plates bigger and rounded. Digestive system idem to previously described species.

Pallial system (four specimens dissected)

Idem to *B. roselleus* n. sp. Secondary ureter opening at distal portion of lung roof.

Reproductive System (four specimens dissected)

Free oviduct longer and thinner than vagina (Fig. 7A). Bursa copulatrix sac rounded to slightly elongated (Fig. 7A). Bursa copulatrix duct reaching middle portion of albumen

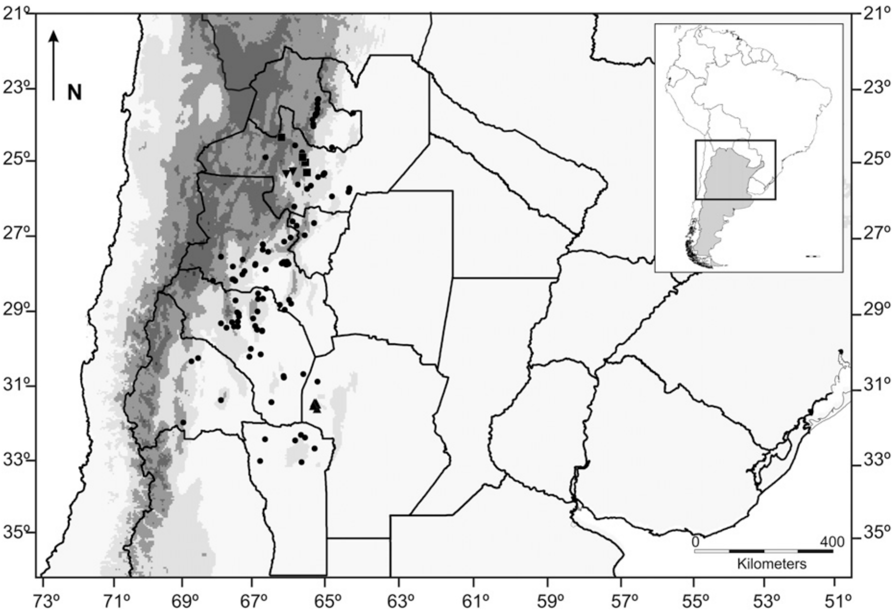

Figure 5. Geographic distribution map of *Bostryx stelzneri* species complex. Detail showing position of Argentina in South America. References: **square (■),** *B. roselleus* n. sp., **triangle (▲),** *B. peristomatus*, **inverted triangle (▼),** *B. scaber*, circle: *B. stelzneri*.

gland, with distal portion broader than the proximal portion (Fig. 7A), inner wall sculpture only with longitudinal zigzag folds. Vagina, 1/3 of penis length (Fig. 7A), inner wall with longitudinal parallel straight folds. Penial retractor muscle short and thin, inserted terminally in flagellum (Figs. 7A–B). Flagellum inner wall with diagonal folds ending in a central, longitudinal, thin fold reaching epiphallus (Fig. 7B). Epiphallus length 2/3 of penis length (Fig. 7A). Proximal penis swollen, with inner straight folds followed by smooth area, distal portion cylindrical with inner straight folds to relaxed zigzag folds area (Fig. 7B). Rest of reproductive system idem to previously described species.

Distribution

Bostryx peristomatus is an endemic species from Córdoba province, known from Chancani in Sierra de Pocho (Fig. 5). The known area of distribution of this species is located within the Dry Chaco ecoregion of Argentina. According to Hylton Scott (1965), Chancani is a place with special physiographic and climatic conditions, with some species of land snails strictly adapted to their environment (*Spixia chancanina* (Doering, 1875), *Spixia aconjigastana* (Doering, 1875), *Plagiodontes weyenberghi* (Doering, 1875), etc.).

Fernández (1973) reported that the distribution of *Bostryx peristomatus* includes Catamarca and San Luis Prov., based on specimens deposited at MACN collection (MACN-In 9229 and MACN-In 15711). However, these lots were reexamined and are re classified into *B. stelzneri* not *B. peristomatus*. This species is difficult to collect and live specimens are usually found on rocks. Altitudinal distribution ranges from 921 to 1300 m above sea level.

Remarks

Bostryx peristomatus was originally described by Doering (1879) in *Bulimulus* (*Scutalus*) Albers, 1850, on the basis of shell morphology and jaw. Doering (1879) indicated that this species has shell morphological characters related to *Neopetraeus stelzneri* Dohrn, 1875, although both species were clearly distinguishable. In 1948, Parodiz considered *B. peristomatus* as a variety of *Neopetraeus stelzneri* because of their conchological affinities. He also described a new “ecological form” called *Neopetraeus stelzneri peristomatus* form *paraconispirus* Parodiz, 1948 from Sierra Gigante (Belgrano Dept., San Luis Prov.), with a tooth in the supracolumelar portion of its aperture, an intermediate form between the varieties *N. stelzneri peristomatus* and *Neopetraeus stelzneri conispirus* (Doering, 1879). Later, *B. peristomatus* was considered as a valid subspecies of *Neopetraeus stelzneri* by Parodiz (1957), Hylton Scott (1965) and Fernández (1973). Hylton Scott (1965) considered that *N. peristomatus* was a local variety of *N. stelzneri* resulting from geographical isolation. Breure (1978, 1979) maintained *B. peristomatus* as subspecies of *B. stelzneri.* Finally, in 1993 Miquel synonymized *B. s. peristomatus* and *B. s. peristomatus* f. *paraconispirus* with *B. stelzneri* for considering them too similar in shell morphology.

Bostryx peristomatus differs from the other species of the *B. stelzneri* complex by it shell characters, especially by its wider umbilicus surrounded by a carina and a shell showing a more expanded peristome. The presence of a marked granulate teleoconch is also a notable difference that allows its unequivocal taxonomic identification. All these morphological characters justify raising this taxon to species level.

Bostryx peristomatus has a very restricted distribution being endemic of Sierra de Pocho in Córdoba province with a narrow altitudinal range. Although *B. stelzneri* is also found in Córdoba province it is absent from Sierra de Pocho.

***Bostryx scaber* (Parodiz, 1948) [New status]** (Figs. 5, 8–9)
Neopetraeus stelzneri form *scaber* Parodiz, 1948: 14; Parodiz, 1957: 134; Fernández, 1973: 108.
Bostryx stelzneri scaber—Breure, 1979: 58.
Bostryx stelzneri—Miquel, 1993: 163. [*partim*]

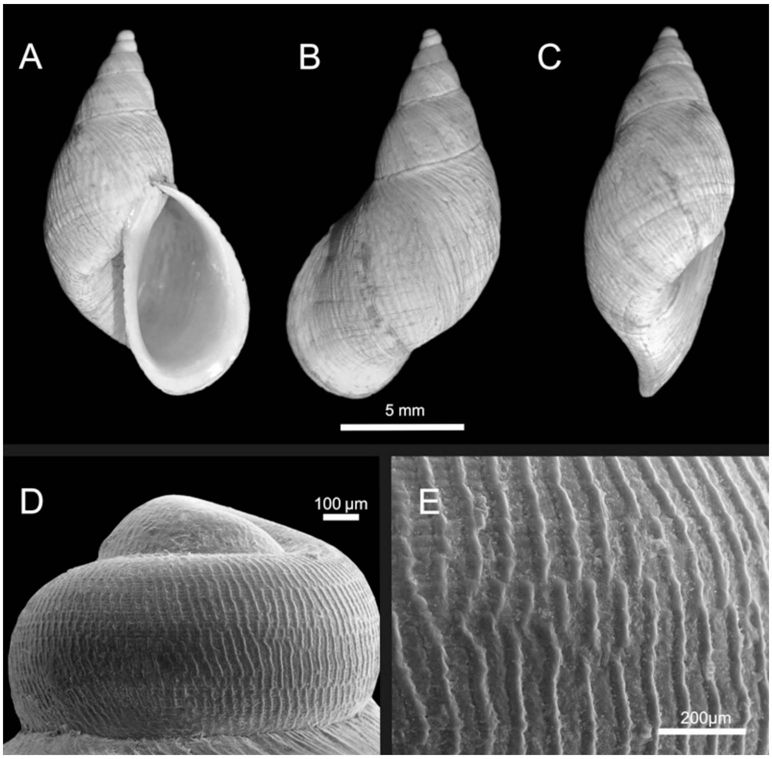

Figure 6. *Bostryx peristomatus* (Doering, 1879). **A,** shell in ventral view; **B,** dorsal view; **C,** lateral view; **D,** protoconch showing axial costules interrupted by spiral grooves; **E,** detail of microsculpture of protoconch.

Type material

Holotype (MACN-In 3217); Paratypes (MACN-In 3217-1, 4221-3).

Type locality

"Cachi, Provincia de Salta."

Additional material examined

Salta Prov., Cachi Dept. (MACN-In 3217, 3217-1, 4221-3, IFML 15472 A, 15517,).

Shell

Dextral, globose, thick, of 5 ½ to 6 whorls, convexity progressively increasing from first to last whorls (Figs. 8A–C). Shell whitish, opaque. Protoconch with elevated axial costules crossed by dense number of spiral grooves giving the appearance of granules (Figs. 8D–E). Spire very short, less than ¼ of shell total length (Fig. 8A). Growing of whorls is even and regular in first two whorls with slowly incrementing diameter. Abrupt change in diameter in the last whorls in relation to spire (Figs. 8A, B). Body whorl strongly convex, globose (Figs. 8A, B). Teleoconch with axial oblique ribs well pronounced, irregularly arranged with spiral lines crossing them in spire (Figs. 8A–C). Suture deep and crenulated with marked suprasutural line. Aperture ovate, tall, 60% the total shell length, wide (Fig. 8A). Parietal space narrow (Fig. 8A). Peristome simple, not expanded (Figs. 8A, C). Umbilicus narrow (Fig. 8C).

Measurements (averages in parenthesis)

Holotype: DM = 23.28 mm; dm = 18.91 mm; H = 31.47 mm; HBw = 27.34 mm; Hs = 6.99 mm; Hab = 21.22 mm; Dab = 14.91 mm. Paratypes (MACN 4221(N = 5)): DM = 19.45–22.75 mm (21.28 mm); dm = 15.52–16.71 mm (16.35 mm); H = 25.46–28.44 mm (27.25 mm); HBw = 22.07–25.34 mm (23.83 mm); Hs = 5.92–7.02 mm (6.21 mm); Hab = 17.86–19.91 mm (18.92 mm); Dab = 13.05–14.24 mm (13.68 mm). Additional measurements in Table 1.

External morphology

Lateral groove from genital orifice towards mantle collar, well-marked. Foot elongate, basal sole homogeneous, not divided. Genital orifice located below right ommatophore.

Digestive system

Jaw orange, arched with 9–15 plates (ten jaws observed in light microscopy). Central plate rectangular, bigger than the rest, divided into three minor plates. Lateral plates rectangular in shape, more regular in size. Outer plates wider and rounded. Digestive system idem to previously described species.

Pallial system (five specimens dissected)

Idem to *Bostryx roselleus* n. sp. Secondary ureter opening to distal portion of lung roof.

Reproductive System (five specimens dissected)

Free oviduct longer and thinner than vagina (Fig. 9A). Bursa copulatrix sac rounded (Fig. 9A). Bursa copulatrix duct extends to middle portion of albumen gland, with its distal portion broader than the proximal portion (Fig. 9A) and inner wall sculpture with only longitudinal zigzag folds. Vagina, 1/3 of penis length (Fig. 9A), inner wall with longitudinal parallel straight folds. Penial retractor muscle short, inserted terminally in flagellum (Figs. 9A–B). Flagellum inner wall with diagonal folds ending in a central, longitudinal, thin fold, reaching epiphallus (Fig. 9B). Epiphallus wider and longer than flagellum, progressively increasing its width towards penis (Figs. 9A–B). Penis equals in length to epiphallus (Figs. 9A–B). Proximal penis swollen, with inner zigzag or straight folds followed by smooth area, distal portion cylindrical with

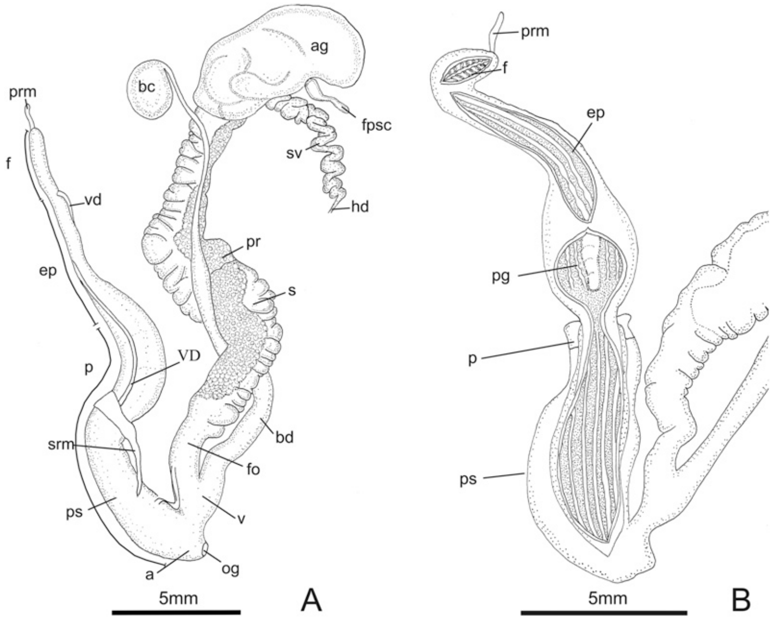

Figure 7. *Bostryx peristomatus.* View of reproductive system dissected out. **A,** general view; **B,** morphology of phallic complex showing inner wall. Abbreviations: **a,** atrium; **ag,** albumen gland; **au,** auricle; **bc,** bursa copulatrix; **bd,** bursa copulatrix duct; **ep,** epiphallus; **f,** flagellum; **fo,** free oviduct; **fpsc,** fertilization pouch-spermathecal complex; **hd,** hermaphroditic duct; **ia,** interramus area; **k,** kidney; **mc,** mantle collar; **mv,** minor veins; **og,** opening genital; **p,** penis; **pc,** pericardic cavity; **pg,** penis gland; **pr,** prostate; **prm,** penial retractor muscle; **ps,** penial sheath; **pu,** primary ureter; **pur,** pulmonary roof; **pv,** pulmonary vein; **ro,** rectum opening; **s,** spermoviduct; **srm,** sheath retractor muscle; **su,** secondary ureter; **sv,** seminal vesicle; **t,** thinning; **v,** vagina; **vd,** vas deferens; **ve,** ventricle.

only inner straight folds or zigzag folds followed by straight longitudinal folds area (Fig. 9B). Rest of reproductive system idem to previously described species.

Distribution

Bostryx scaber is an endemic species known only from Cachi department in Salta province (Fig. 5), northwestern Argentina. This species occurs exclusively in High Monte ecoregion of Argentina. *Bostryx scaber* is usually found in open environments with short shrubbery, cacti and bromeliads. Common at high altitudes between 2160–3200 m.

Remarks

Bostryx scaber was originally described by Parodiz (1948) as a form of *Neopetraeus stelzneri* Dohrn, 1875. Breure (1979) recognized this group as a valid subspecies of *N. stelzneri*. Miquel (1993) synonymized *B. s. scaber* with *B. stelzneri* on the basis of shell characters, with the justification that *B. s. scaber* is only a local variation of *B. stelzneri*. However, *B. scaber* can be clearly differentiated from *B. stelzneri* by its shell shape and size. The shell of *B. scaber* is clearly more globose and bigger as well as its shell aperture (in height and diameter), the spire is shorter bearing spiral lines and the protoconch has granules. *Bostryx scaber* has a free oviduct longer than the vagina while in *B. stelzneri* both organs have the same length. All these differences justified that this taxon is raised to species level.

Bostryx scaber has a very restricted distribution in Cachi, Salta where *B. roselleus* n. sp., *B. peristomatus* and *B. stelzneri* were not found.

***Bostryx stelzneri* (Dohrn, 1875)** (Figs. 5, 10–12)

Bulimulus (*Scutalus*) *stelzneri* Dohrn, 1875: 202; Dohrn, 1877: 157; Doering, 1879: 66; Holmberg, 1912: 23.

Bulimus (*Scutalus*) *Stelzneri*—Doering, 1875: 339.

Bulimulus stelzneri—Pfeiffer, 1876: 58; Kobelt, 1878: 149.

Bulimulus (*Scutalus*) *conispirus* Doering, 1879: 67.

Bulimulus (*Scutalus*) *conispirus fasciata* Doering, 1879: 67.

Bulimulus (*Bostryx-Lissoacme*) *conospirus*—Pilsbry, 1896 [1895–1896]: 189 [incorrect subsequent spelling].

Bulimulus (*Bostryx-Lissoacme*) *stelzneri*—Pilsbry, 1896 [1895–1896]: 190.

Bulimulus (*Thaumastus*) *hector* Holmberg, 1909: 11; 1912: 149.

Bulimulus hector var. *cora* Holmberg, 1909: 12.

Bulimulus hector var. *helena* Holmberg, 1909: 12.

Bulimulus hector var. *giovanni* Holmberg, 1909: 12.

Bulimulus hector var. *montana* Holmberg, 1909: 12.

Bulimulus hector var. *cactorum* Holmberg, 1909: 12.

Bulimulus stelzneri hector—Hylton Scott, 1945: 204.

Neopetraeus stelzneri—Parodiz, 1946: 315; Parodiz, 1948: 7; Parodiz, 1957: 134; Zilch, 1971: 198; Fernández, 1973: 106.

Neopetraeus stelzneri apertus Hylton Scott, 1948: 238; Parodiz, 1957: 135; Fernández, 1973: 109.

Neopetraeus stelzneri f. *hybrida* Parodiz, 1948: 12; Fernández, 1973: 107.

Neopetraeus stelzneri f. *nonogastanus* Parodiz, 1948: 13; Fernández, 1973: 107.

Neopetraeus stelzneri f. *tinogastanus* Parodiz, 1948: 13; Fernández, 1973: 108.

Neopetraeus stelzneri peristomatus f. *paraconispirus* Parodiz, 1948: 16; Fernández, 1973:112.

Neopetraeus stelzneri var. *conispirus*—Parodiz, 1948: 16.

Neopetraeus stelzneri var. *hector*—Parodiz, 1948: 18.

Neopetraeus stelzneri conispirus f. *minuta* Parodiz, 1948: 18; Fernández, 1973: 110.

Neopetraeus stelzneri hector—Parodiz, 1957: 135; Fernández, 1973: 110.

Neopetraeus stelzneri conispirus—Parodiz, 1957: 134; Fernández, 1973: 109.

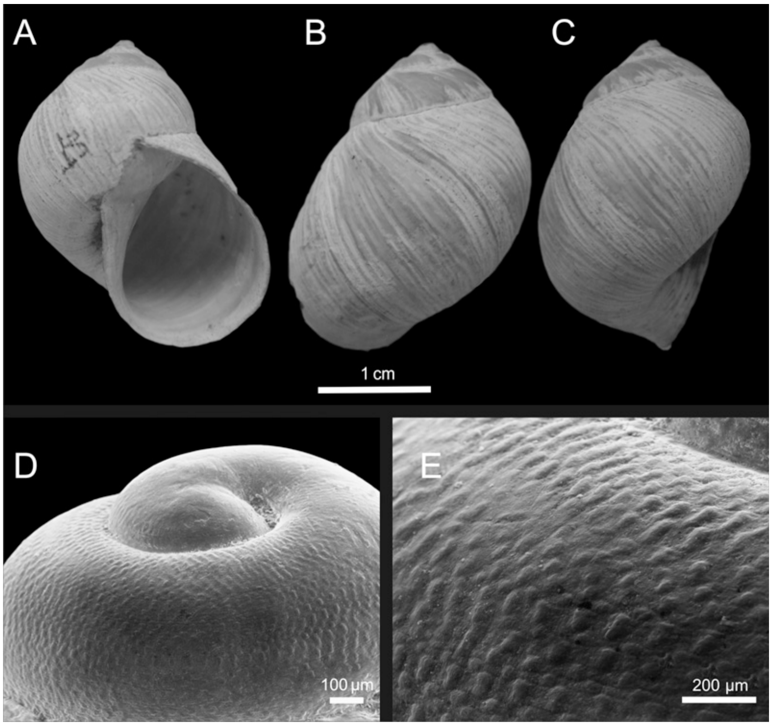

Figure 8. *Bostryx scaber* (Parodiz, 1948). **A,** shell in ventral view; **B,** dorsal view; **C,** lateral view; **D,** general view from protoconch showing elevated axial costules interrupted by dense number of spiral grooves; **E,** detail at higher magnification of the protoconch showing its granule-like morphology.

Neopetraeus stelzneri hector f. *multicincta*—Parodiz, 1948: 20; Fernández, 1973: 110.
Neopetraeus stelzneri hector f. *tricincta*—Fernández, 1973: 111.
Bostryx stelzneri apertus—Breure, 1979: 51.
Bostryx conospirus—Breure, 1979: 52.
Bostryx hector—Breure, 1979: 54.
Bostryx stelzneri nonogastanus—Breure, 1979: 56.
Bostryx stelzneri tinogastanus—Breure, 1979: 59.
Bostryx stelzneri—Breure, 1978: 127; Breure, 1979: 58; Miquel, 1993: 163; Breure, 2013: 47 [*partim*].

Type material studied

Neopetraeus stelzneri apertus (Holotype, MLP 11292, Paratype, MACN-In 26645); *Neopetraeus stelzneri conispirus* f. *minuta* (Holotype, MACN-In 6243, Paratypes, MACN-In 6243-1, MLP 1298); *Neopetraeus stelzneri hybrida* (Holotype, MACN-In 433; Paratypes, MACN-In 433-1, MLP 1303); *Neopetraeus stelzneri* f. *nonogastanus* (Holotype, MACN-In 17591, Paratypes, MACN-In 17591-1, MACN-In 17613); *Neopetraeus stelzneri* f. *tinogastanus* (Holotype, MACN-In 19061, Paratypes, MACN-In 19061-1); *Neopetraeus stelzneri peristomatus* f. *paraconispirus* (Holotype, MACN-In 14086, Paratypes, MACN-In 14086-1).

Type material

Possible syntype (ZMB 34734) (Breure, 2013).

Type locality

"Cerro de Chepe." Cerro Chepe is located in Argentina, La Rioja Prov., Rosario Vera Peñaloza Dept.

Additional material examined

Catamarca Prov., Ambato Dept., Sierra de Ambato (MACN-In 9682, MLP 9538), Andalgalá Dept., Agua de Las Palomas (IFML 15591), Cuesta de Andalgalá (MLP 9529, 9533), Quebrada de Arenal (MACN-In 17850); Belén Dept., Cuesta de Belén (IFML 15526, MACN-In 21116 A, MLP 9531, 9536), Cuesta el Tambillo (IFML 11018), Hualfín (IFML 14925), Quebrada de Indalecio (IFML 15461 A), Villa Vil (MACN-In 382, MLP 9518); Capayán Dept., Chumbicha (MACN-In 9229 A), Concepción (MACN-In 9227, 17777 A); Esquiú Dept., Las Pirquitas dam (IFML 15459 A); Santa María Dept., El Desmonte (IFML 14447); Tinogasta Dept. (IFML 11002, 11020), Cuesta de La Chilca (IFML 78, 1616, 11019, 14443, 15473 A, 15474 A, 15475 A, 15592, 15593, 15594, IFML 15283,); Cuesta de Zapata (MLP 803, IFML 10896, 14446, 15460, 15515, 15527, A), La Coipita (MACN-In 19061, 19061-1), Santa Rosa (MLP 9515), Sierra de Fiambalá (MACN-In 19619, MLP 1298). Córdoba Prov., Cruz del Eje Dept., Aguas de Ramón (MACN-In 32849A). Jujuy Prov. (IFML 506), Dr. Manuel Belgrano Dept., before of Quebrada de Humahuaca (IFML 15481A), Humahuaca Dept., Coctaca (MACN-In 2466A, MLP 9527), Maimará (MACN-In 19590), Quebrada de Humahuaca (MACN-In 586 A, 19506 A, MACN-In 35642, IFML 15469 A, MLP 9523), Río Humahuaca (MACN-In 19460), Uquía (MACN-In 8838 A, 12335 A); Santa Bárbara Dept., Puesto Viejo (MACN-In 988); Tilcara Dept. (IFML 984, 15585, MLP 1299, 9519, 9522, MLP 9524, MACN-In 586 A, 1629), Cerro Negro (IFML 14878, 15468 A, 15516, 16467 A, MACN-In 1636 A), Cerro Pucará (MACN-In 13285 A, 19506 A, 19525 A, 30615, 30618 A,), Garganta del Diablo (IFML 560, 5584, 15466 A, 15518), Huacalera (IFML 10449, 15482 A, 15589), Sierra de Tilcara (IFML 410); Tumbaya Dept. (IFML 15470 A, 15583, 15587, MACN-In 30597 A), Quebrada de Purmamarca (MLP 9517), Volcán (MACN-In 24308 A). La Rioja Prov. (IFML 15590, MACN-In 19946), Arauco Dept., Aimogasta (MACN-In 7810 A, 24398 A); Castro Barros Dept., Chuquis (MLP 9534), Coronel Felipe Varela Dept., Cuesta de Miranda (MACN-In 434, 30441), Sierra de Velázquez (IFML 15456 A); Chilecito Dept. (IFML 11000, 11001, 15513, MLP 9539), Nonogasta (MACN-In 17591 A, 17613,), Sañogasta (IFML 467, 12764);

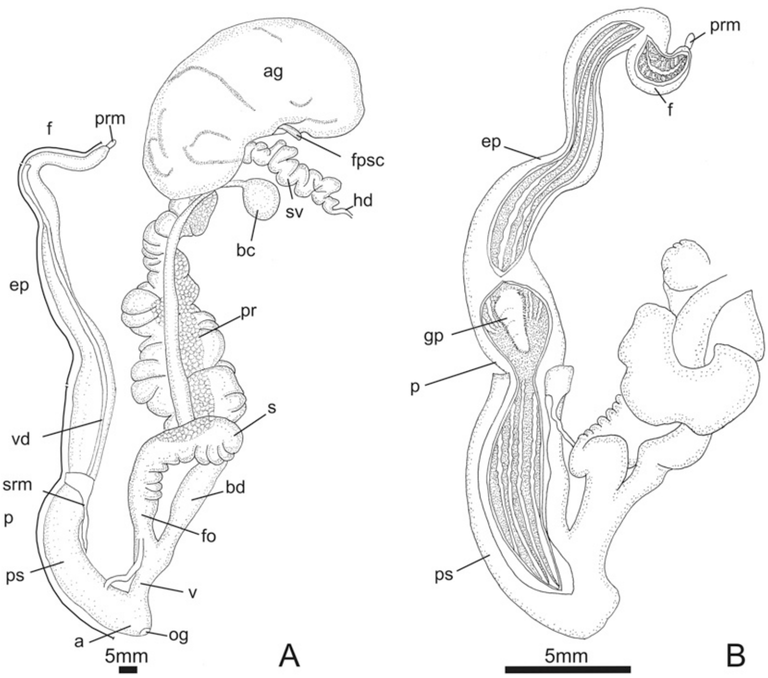

Figure 9. *Bostryx scaber*. View of reproductive system dissected out. **A,** general view; **B,** phallic complex inner wall. Abbreviations: **a,** atrium; **ag,** albumen gland; **au,** auricle; **bc,** bursa copulatrix; **bd,** bursa copulatrix duct; **ep,** epiphallus; **f,** flagellum; **fo,** free oviduct; **fpsc,** fertilization pouch-spermathecal complex; **hd,** hermaphroditic duct; **ia,** interramus area; **k,** kidney; **mc,** mantle collar; **mv,** minor veins; **og,** opening genital; **p,** penis; **pc,** pericardic cavity; **pg,** penis gland; **pr,** prostate; **prm,** penial retractor muscle; **ps,** penial sheath; **pu,** primary ureter; **pur,** pulmonary roof; **pv,** pulmonary vein; **ro,** rectum opening; **s,** spermoviduct; **srm,** sheath retractor muscle; **su,** secondary ureter; **sv,** seminal vesicle; **t,** thinning; **v,** vagina; **vd,** vas deferens; **ve,** ventricle.

Famatina Dept. (MACN-In 17849 A, IFML 15458 A, 15514); General Belgrano Dept., Iliar (MACN-In 18356 A), Olta (MACN-In 18325, MLP 1300); Independencia Dept., El Chiflón (MLP 9514), La Torre (IFML 11045, 15586), Patquia (MLP 9535); Sanagasta Dept. (MLP 9521), Quebrada de Los Sauces (MACN-In 15703 A, IFML 15457 A), Quebrada de Sanagasta (MACN-In 9852); San Blas de los Sauces Dept., Cerro de Velazco (MLP 1303, MACN-In 433, 433-1). Salta Prov. (MACN 17597 A), Chicoana Dept., Quebrada de Agua Negra (MLP 2393); Guachipas Dept. (MACN-In 17595), Alemanía (MACN-In 582 A, 17596, 17597, MLP 1535, 1545); La Viña Dept., Quebrada de Guachipas (MACN-In 3218); Metán Dept., Cerro Colorado (MACN-In 26522, 26229, 32861, 36890, MLP 9528), Cabra Corral dam (IFML 15543 A, 15544 A, 15545 A,), Pala Pala (IFML 15492 A); Rosario de la Frontera Dept. (MLP 1307); Rosario de Lerma Dept. (IFML 15463 A), between Alfarcio and Santa Rosa de Tastil (IFML 15464 A), El Golgata (IFML 14072, 15588,), Ruinas de Santa Rosa de Tastil (IFML 15455 A). San Juan Prov., Jáchal Dept., Cerro Agua Negra (MACN-In 24305), Ciénaga (MACN-In 10655); Zonda Dept., Cerro Negro (MACN-In 9920). San Luis Prov. (MACN-In 15711), Ayacucho Dept., Luján (MACN-In 9834), Santo Domingo (MLP 9516-1), Sierra de Quines (MACN-In 15122); Belgrano Dept., Sierra Gigante (MACN-In 14086, 14086-1); Coronel Pringles Dept., La Toma (MACN-In 1018 A), Las Cañas (MACN-In 2426); Libertador General San Martín Dept., between Quines and Libertador San Martín (IFML 15462 A). Tucuman Prov. (MACN-In 9159, IFML 10505), Tafí del Valle Dept. (IFML 71), Amaicha del Valle (MLP 1542), Ruinas de Quilmes (IFML 15465 A), Tafí Viejo Dept., Las Arquitas (MACN-In 10505). Bolivia, Chuquisaca Dept., Cerro Colorado near Tojo (IFML 15871), Villa Abecia (IFML 15872).

Shell

Dextral, fusiform to ovate, 5 to 6 ½ convex whorls (Figs. 10A–I). Spire large, shorter than body whorl (Figs. 10A–I). Body whorl tall, 60% of the total shell height (Figs. 10A–I). Shell whitish to pale brown, with darker spiral bands in some specimens, opaque or slightly glossy. Protoconch with thin, axial, elevated costules separated at regular narrow spaces, discontinuous, parallel to each other. Spiral grooves, densely arranged (Figs. 10J–K). Teleoconch with shallow ribs (Figs. 10A–I). Ribs traversed by spiral lines in some specimens. Type of suture variable, usually slightly deep (Figs. 10A–I), simple or crenulated with both sub and/or suprasutural lines present. Aperture elongate-ovate, narrow or slightly wide, tall, 60% of total shell length (Figs. 10A–I). Parietal space narrow (Figs. 10A–I). Peristome slightly expanded. Umbilicus variable narrow to wide. Shell measurements in Table 1.

External morphology

Animal body homogeneously brown. Lateral groove from genital orifice towards mantle collar, well-marked. Suprapedal groove running from cephalic to caudal portion. Foot short, basal sole homogeneous, not divided.

Digestive system

Jaw orange, arched with ten imbricate plates (Fig. 11A) (two jaws observed in SEM, thirty in light microscopy). Central plate triangular, bigger than the rest, divided into two plates (Fig. 11A). Lateral plates rectangular in shape, outer plates wider and rounded (Fig. 11A). Jaw with grooves transverse (Fig. 11B). Radula narrow and long, formed by central, lateral and marginal teeth (three radulae studied with SEM). Central tooth triangular, unicuspid (Fig. 11C). First lateral

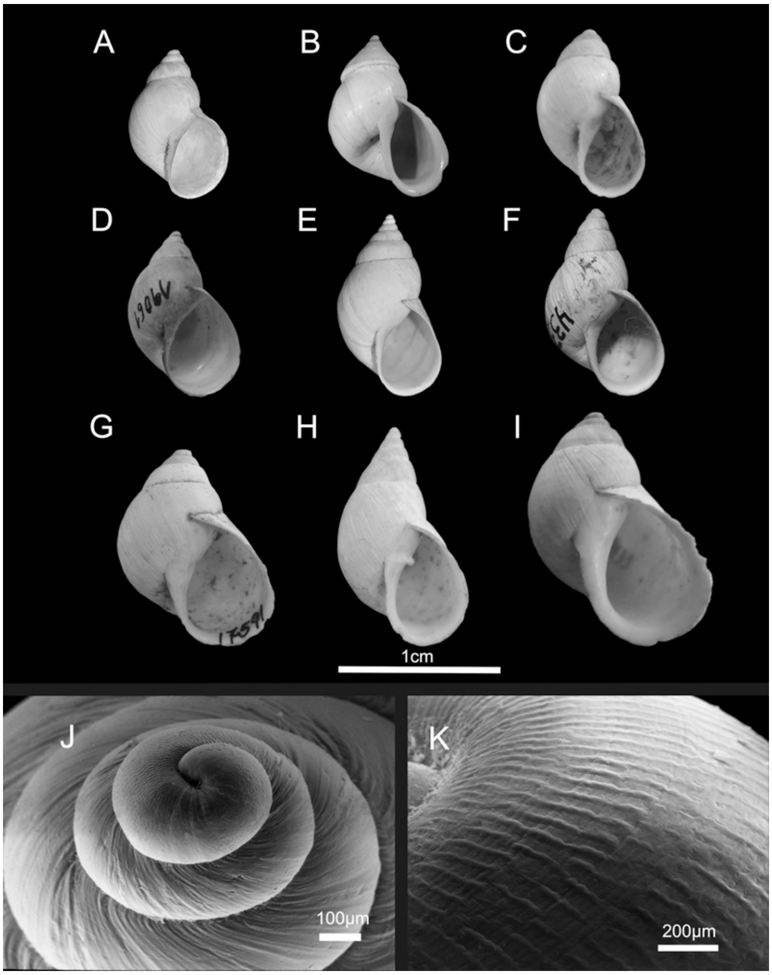

Figure 10. Morphological variability of *Bostryx stelzneri* (Dohrn, 1875). **A,** *Bostryx stelzneri conispirus* (Doering, 1879) (MACN-In 18356); **B,** *Bostryx stelzneri apertus* (Hylton Scott, 1948) holotype (MLP 11292); **C,** *Bostryx stelzneri conispirus minuta* (MACN-In 6243); **D,** *Bostryx stelzneri tinogastanus* (Parodiz, 1948) holotype (MACN-In 19061); **E,** *Bostryx stelzneri hector* (Holmberg, 1909) (IFML 15587); **F,** *Bostryx stelzneri hybrida* (Parodiz, 1948) holotype (MACN-In 433); **G,** *Bostryx stelzneri nonogastanus* (Parodiz, 1948) holotype (MACN-In 17591); **H,** *Bostryx stelzneri peristomatus paraconispirus* (Parodiz, 1948) holotype (MACN-In 14086); **I,** *Bostryx stelzneri stelzneri* (Dohrn, 1875) (MACN-In 17777); **J,** View of the protoconch showing axial costules crossed by spiral grooves; **K,** Detail of microsculpture of protoconch.

tooth unicuspid, similar in size and shape to central tooth, with broad basal plate (Fig. 11C). Lateral teeth bicuspid, ectocones increase in size after the twelfth tooth (Fig. 11D). Marginal teeth bicuspid to tricuspid (Fig. 11E). Digestive system idem to previously described species.

Pallial system (30 specimens dissected)

Idem to *B. roselleus* n. sp. Secondary ureter opening on proximal portion of lung roof.

Reproductive system (30 specimens dissected)

Free oviduct is the same length as the vagina (Fig. 12A). Bursa copulatrix sac is rounded (Fig. 12A) extending to middle portion of albumen gland, with distal portion broader than proximal portion (Fig. 12A). Inner wall sculpture in both portions consisting of longitudinal zigzag folds. Vagina cylindrical, 1/3 of penis length (Fig. 12A), inner wall with longitudinal parallel zigzag or straight folds. Penial retractor muscle variable, short or large, thick or thin, inserted terminally in flagellum (Figs. 12A–B). Flagellum inner wall with diagonal folds ending in a central, longitudinal, thin fold reaching epiphallus (Fig. 12B). Epiphallus wider, longer than flagellum, progressively increasing its width towards penis (Figs. 12A–B). Penis length equals epiphallus length (Figs. 12A–B). Proximal penis swollen, with different kinds of sculptures, consisting in zigzag or straight folds, or a combination of both sculptures, followed by smooth area (Fig. 12B). Distal portion cylindrical with inner straight or relaxed zigzag folds, followed by straight longitudinal folds area (Fig. 12B). Penis sheath retractor muscle can be divided or not (Fig. 12B). Rest of reproductive system idem to previously described species.

Distribution

It is found from Salta to San Luis provinces (24°–32°S) (Fig. 5). This species inhabits a variety of xerophilic environments of High Monte, Dry Chaco, Central Andean Puna, Southern Andean steppe and Espinal ecoregions. It is also recorded for southeast of Bolivia, in Chuquisaca Department, Cerro Colorado, near Tojo, 2700 m and in Villa Abecia (South of Camargo) in the same department. In Bolivia it is recorded in Montane Dry forest and Central Andean dry Puna ecoregions. According to Fernández (1973), *B. stelzneri* is distributed from Peru to Argentina but confirmation of its presence in Peru is still needed.

Bostryx stelzneri is usually found on or under rocks or in crevices between rocks usually exposed to direct sunlight. Common at altitudes between 555–4000 m.

Remarks

Bostryx stelzneri was originally described in the genus *Bulimulus* (*Scutalus*) Albers, 1850 by Dohrn (1875). Later the species was reclassified into different genera without further justification. It was moved to *Bulimulus* (*Bostryx-Lissoacme*) by Pilsbry (1895–1896) and to *Neopetraeus* Martens, 1885 by

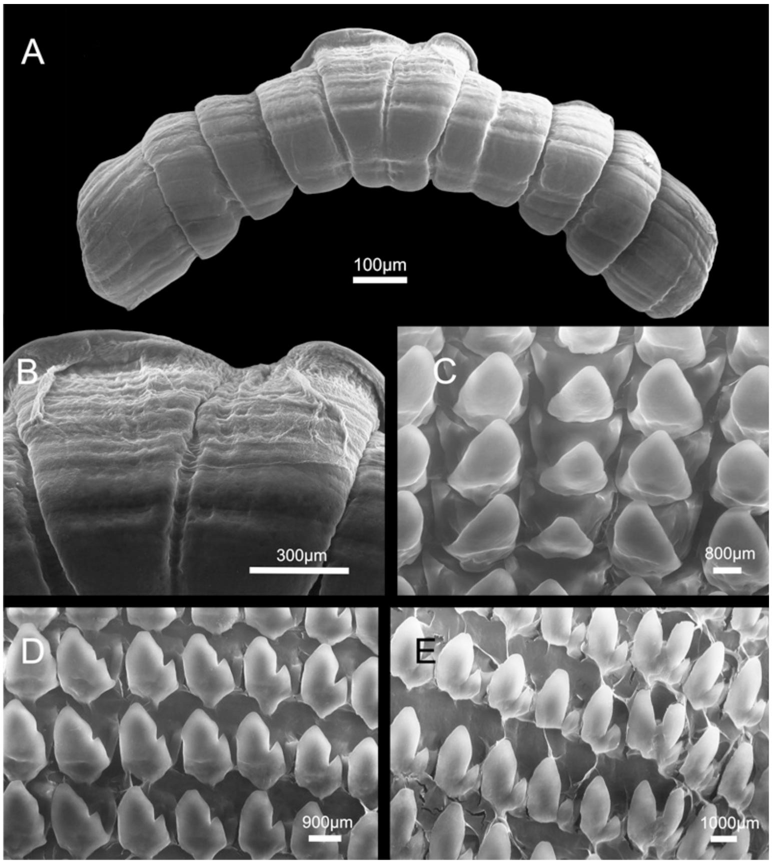

Figure 11. *Bostryx stelzneri.* Digestive system. **A,** jaw; **B,** detail of jaw sculpture; **C,** detail of the central tooth and first lateral teeth; **D,** transition from lateral to marginal teeth; **E,** detail of marginal teeth.

Parodiz (1946). Finally, Breure (1978, 1979) classified *B. stelzneri* in *Bostryx* Troschel, 1847. In 1945, Hylton Scott studied *Bulimulus hector* Holmberg, 1909, a species in which Holmberg (1909) described five varieties mainly on the basis of the number of spiral pigmented bands: *Bulimulus hector* var. *cora* (unicincta), *Bulimulus hector* var. *helena* (tricincta), *Bulimulus hector* var. *giovanni* (multicincta), *Bulimulus hector* var. *montana* (cingulis interruptis) and *Bulimulus hector* var. *cactorum* (cingulis inaequaliter ampliatis). Hylton Scott (1945) relocated *B. hector* as a subspecies of *Neopetraeus stelzneri* because of their similarities in anatomical characters. According to Parodiz (1948), the species *Bulimulus hector*, *B. peristomatus* Doering, 1879 and *B. conispirus* Doering, 1879 should be considered "varieties" of *Neopetraeus stelzneri* because they were not clearly distinct from the latter and also did not have significantly distinct distributional ranges. Additionally, Parodiz (1948) described new different "forms" such as *hybrida*, *nonogastanus*, *tinogastanus*, *scaber*, *peristomatus paraconispirus* and *conispirus minuta.* This confusing classification is resumed in Parodiz´s (1957) species catalogue where he listed *Neopetraeus stelzneri* with four subspecies, *N. s. conispirus, N. s. peristomatus, N. s. hector* and *N. s. apertus,* also indicating that the forms previously described in 1948 corresponded to other subspecies, without listing them.

Fernández (1973) classified *Neopetraeus stelzneri* and gave the category of subspecies to *peristomatus, hector, conispirus* and *apertus* while kept the different "forms" described by Holmberg (1909) and Parodiz (1948).

The first study on anatomy and histology of *Bostryx stelzneri stelzneri* (Dohrn, 1875) was done by Breure (1978). In 1979, Breure listed *B. stelzneri apertus*, *B. s. hybrida*, *B. s. conispirus minuta*, *B. s. nonogastanus*, *B. s. peristomatus, B. s. peristomatus paraconispirus*, *B. s. scaber* and *B. s. tinogastanus* for Argentina. Finally, Miquel (1993) synonymized all varieties and forms previously described by Holmberg (1909) and by Parodiz (1948) under *B. stelzneri.*

The present study examined specimens of *Bostryx stelzneri* from all the species distributional range. High intraspecific shell variation in shape, size, coloration, body whorl sculpture, umbilicus width and peristome expansion was recorded among different populations and among individuals within populations. However, the sculpture of the protoconch, body whorl height with respect to total shell length and aperture height with respect to total shell length, are constant characters in all specimens studied. Irrespective of shell differences, anatomical morphology, especially genital morphology was very similar, showing minimal variations only on the penis inner wall sculpture. Pearson Correlation coefficient did not indicate any significant correlation among shell measurements and minimum and maximum temperature, precipitation, latitude/longitude recorded for the different populations within the species area of distribution.

For the reasons mentioned above, entities previously described into *Bostryx stelzneri* are here considered as morphological or population variations of the species and their synonymy with *B. stelzneri* is maintained.

Morphometric analysis

Allometric growth was observed. The multivariate regression of shape on centroid size was highly statistically significant (permutation test with 10,000 random permutations, $p = 0.0032$), and accounted for 11.41% of the total amount of shape variation.

Geometric morphometrics analysis revealed a clear size distinction between the *Bostryx* species. The species showed significant differences in centroid size distribution (ANOVA, $F = 59.30$, $p < 0.0001$). *Bostryx roselleus* n. sp. was shorter than

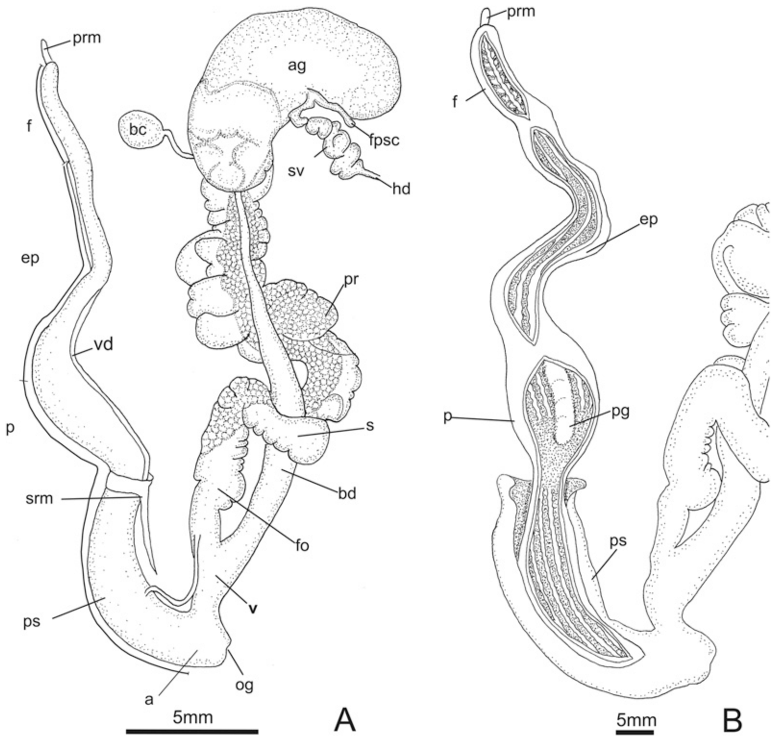

Figure 12. *Bostryx stelzneri.* View of reproductive system dissected out. **A,** general view; **B,** phallic complex inner wall. Abbreviations: **a,** atrium; **ag,** albumen gland; **au,** auricle; **bc,** bursa copulatrix; **bd,** bursa copulatrix duct; **ep,** epiphallus; **f,** flagellum; **fo,** free oviduct; **fpsc,** fertilization pouch-spermathecal complex; **hd,** hermaphroditic duct; **ia,** interramus area; **k,** kidney; **mc,** mantle collar; **mv,** minor veins; **og,** opening genital; **p,** penis; **pc,** pericardic cavity; **pg,** penis gland; **pr,** prostate; **prm,** penial retractor muscle; **ps,** penial sheath; **pu,** primary ureter; **pur,** pulmonary roof; **pv,** pulmonary vein; **ro,** rectum opening; **s,** spermoviduct; **srm,** sheath retractor muscle; **su,** secondary ureter; **sv,** seminal vesicle; **t,** thinning; **v,** vagina; **vd,** vas deferens; **ve,** ventricle.

B. peristomatus, B. scaber, and *B. stelzneri*. The first six axes of the principal component (PC) of the residuals from the regression of shape on centroid size (allometric correction) explained 89.557% of the total variation. The PC1 (52.6% of total shape variance) was associated with a LM 2, 5 and 12 (spire, shape of aperture) (Figs. 13A–B). The second principal component (16.1%) was related to LM 1 and 12 (spire, shape of the last whorl) and a third PC (8.7%) with LM 5, 6, 8–9 (shape of aperture) (Figs. 13A–B). In the first principal component there are clear differences between specimens of *B. roselleus* and specimens of *B. scaber*. However, there was no grouping differentiated in relation to the second and third principal components, consequently specimens of *B. peristomatus* and *B. stelzneri* overlapped. Visualization of shape variation along the first principal component axis indicates that specimens with more negatives scores possess a thinner spire, whereas specimens with more positives scores present a wider spire. In the second principal component, negative scores indicate specimens with a shorter spire, and more positive scores indicate taller spires. The third principal component summarizes variation in shape aperture, and, respectively, negative and positive scores show specimens with smaller or bigger apertures. The shell shape variation among the four species, were effectively discriminated through CVA of the residuals from the regression of shape on centroid size. The first three PCs explained the 100% of total variance. Landmarks 1–3 associated to CV1 (71%) showed two highly differentiated groups, one with wider spire formed by *B. scaber* and *B. stelzneri* and other with thinner spire formed by *B. roselleus* n. sp. and *B. peristomatus*. The second CV (23.1%) was related to LM 4, 6–7 and differences were mostly associated with aperture shape variation. *Bostryx roselleus* n. sp. and *B. stelzneri* showed more negative scores having shorter apertures while *B. peristomatus* and *B. scaber* showed more positive scores having taller apertures. The third CV (5.9%) related to LM 2–4 (Figs. 14A–B) showed differences, as well as CV1, on the development of the spire. In summary, according to the geometric morphometric analysis, *B. roselleus* n. sp. has a more slender shell shape, and a thinner and shorter aperture than *B. peristomatus, B. scaber*, and *B. stelzneri.*

DISCUSSION

Bostryx is defined by a combination of shell characters, none of which is diagnostic in a strict sense (Troschel 1847, Albers 1850, Zilch 1959–1960, Breure 1979, 2012). Breure (1979) was the first author to attempt to define *Bostryx* using characters from the pallial, digestive and reproductive systems. However, he did not describe the inner penial anatomy which is unknown in all *Bostryx* species. Published information on genital anatomy of *Bostryx* showed that the reproductive system is very simple in comparison to other genera of Bulimulidae.

Shell characters are used in land snails as a primary tool for species identification, however quantifying the boundaries between species is difficult and geometric morphometric methods are a good tool to reduce these difficulties (Madec *et al.* 2003, Teso and Pastorino 2011). The geometric morphometric method was previously used in land snails to discriminate morphotypes (Haase and Misof 2008), species (Pfenninger *et al.* 2003, Perez 2011, Greve *et al.* 2012), to explore cryptic diversity (Pall-Gegerly *et al.* 2012), variation intraspecific (Perez and Strenth 2003), and shape differences between dextral and sinistral shells (Schilthuizen and Haase

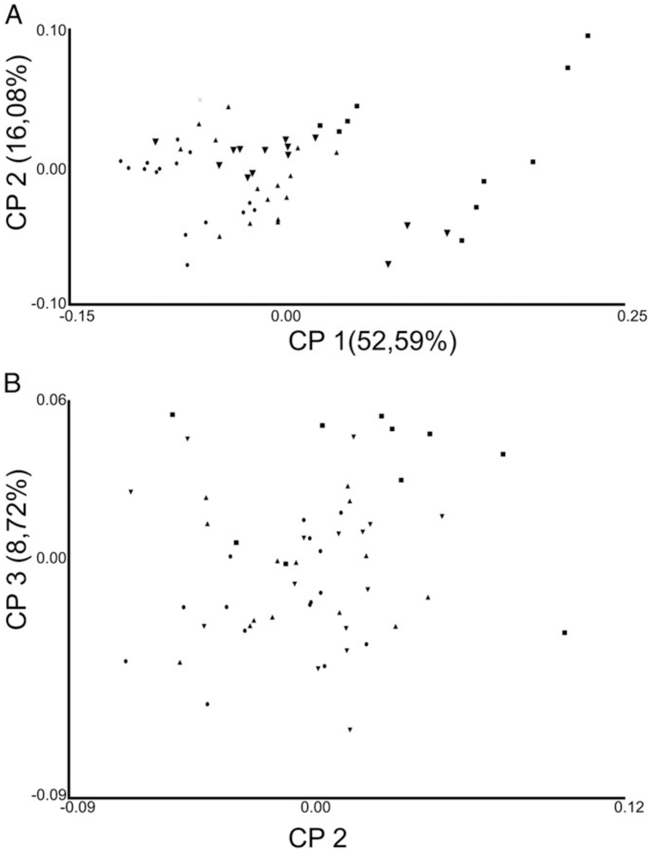

Figure 13. Principal components (PC) based on Procrustes distances. **A,** plots of the scores on PC1 and PC2; **B,** plots of the scores on PC2 and PC3. **Circle (●),** *Bostryx roselleus* n. sp; **inverted triangle (▼),** *B. peristomatus;* **square (■),** *B. scaber;* **triangle (▲),** *B. stelzneri.*

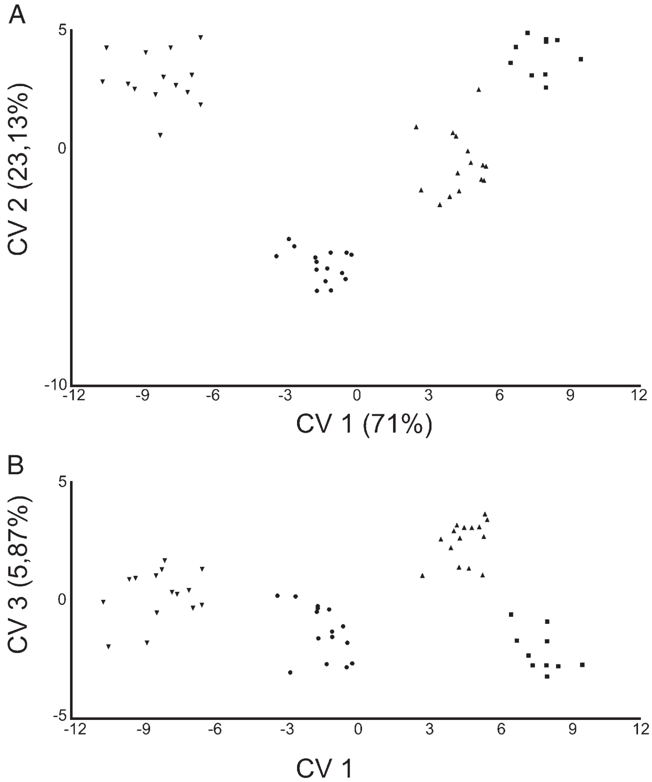

Figure 14. Canonical variates analysis. **A,** plots of the scores on CV1 and CV2; **B,** plots of the scores on CV1 and CV3. **Circle (●),** *Bostryx roselleus* n. sp; **inverted triangle (▼),** *B. peristomatus;* **square (■),** *B. scaber;* **triangle (▲),** *B. stelzneri.*

2010). Conde-Padin *et al.* (2007) used the geometric morphometric method to differentiate the species of the *Littorina saxatilis* (Olivi, 1792) complex and this method was efficient for discriminating among species.

The study of shell morphology in *B. stelzneri* species complex was important because it provided the main differences between the species of the complex. Interspecific differences were found in the total shell diameter, spire length, and length and diameter of the aperture.

The geometric morphometrics allowed an objective interpretation of shell shape variation and detection of differences in shape components irrespective of the differences in size between *Bostryx* species of the *stelzneri* group. This is very convenient as differences in size can depend considerably on specimens available in the sample. The existence of allometry (relation between size and shape) indicated that the shape variation were dependent of the size variation. The geometric morphometric study on shell size and shape showed that there are overall shell shape variations and considerable differentiation among the four species included into the *B. stelzneri* complex. Size was an important factor discriminating *B. roselleus* n. sp. from the other species of the complex. The analysis of principal components alone was overall less informative (regarding species relationships) than CVA, because the PCA constructs variables that can be used to examine variation among individuals within a sample, whereas CVA constructs variables to describe the relative positions of groups in the sample. The purpose of CVA is to simplify the description of differences among groups and the direction in which group means are most different is not necessarily the direction in which individuals are most different (Zelditch *et al.* 2012). PCA has revealed the overall shell shape intraspecific variation, which is more evident in *B. scaber* (specimens with variation in spire and shape of the last whorl) and *B. peristomatus* (specimens with variation in a development of spire and shape of aperture). Also, CVA revealed significant differences between species of the complex, based on differences in the development of the spire and a aperture shape variation. Geometric morphometric analyses support the results on qualitative observations and taxonomic studies previous carried out. Therefore, they are complementary results for taxonomic studies.

Pallial organs are very similar among species of the *Bostryx stelzneri* complex studied and only the degree of opening of the secondary ureter seems to vary. In the same way, the genitalia showed differences in relation to organ proportions such as length of vagina in relation to free oviduct and epiphallus length in relation to penis length. Sculpture of the inner wall of the flagellum and epiphallus are similar in all species studied, whereas sculpture of the inner wall of the penis is variable.

Bostryx roselleus n. sp., *B. peristomatus*, and *B. scaber* have narrow geographic ranges and narrow vertical distribution and can be easily distinguished by their shell morphology. In contrast, *B. stelzneri* has colonized a wide area ranging from northern to central Argentina with broadest altitudinal range and the geographically distant populations began to differentiate especially with regard to coloration and the degree of apertural expansion, but hardly in genital anatomy. We suggest that this intraspecific diversification may not be associated with habitat preferences since all populations are ecologically similar, in general associated with rocks in rather dry to semiarid environments. Radiations usually accompanied by morphological diversification in land snails have been frequently described and have been associated to habitat use (Cameron *et al.* 1980, Chiba 1996, 2004). We suggest that in the case of the *B. stelzneri* species group, divergence of shell morphology occurs independently of genital morphology and that shell shape diversity is not dependent on habitat preferences. To test this hypothesis molecular research with geographically distant populations of *B. stelzneri* will be conducted.

From a conservation perspective, areas inhabited by *Bostryx* species in Argentina such as the High Monte and Dry Chaco ecoregions are impacted by severe modification and transformation processes by human activities (deforestation, overgrazing, and fires). Only 9.7 % of High Monte and 1.6 % of Dry Chaco are under protection (Brown and Pacheco 2006). The loss and degradation of *Bostryx* species natural habitat raises an urgent need to study and protect these groups of land snails mostly composed of endemic species.

ACKNOWLEDGMENTS

We thank A. Andrada for help in obtaining SEM micrographs at the Integral Center of Electron Microscopy of the National University of Tucumán (CIME) and to curators of the Malacological collections consulted, A. Tablado (MACN-In) and G. Darrigran (MLP) for their assistance and loan of material. We also would like to thank X. Ovando for her help with the geometric morphometric analyses. We are also grateful to the two anonymous reviewers and to the Editor-in-Chief, C. Winters for their constructive criticisms. This research was financially supported by PIP 0055 (CONICET) awarded to MGC. The first author is a fellow and the senior author is a researcher of the Argentine National Council of Scientific Research (CONICET).

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Submitted: 14 November 2012**; accepted:** 29 July 2013;
final revisions received: 1 November 2013