

Taxonomic notes on the *Phalotris bilineatus* group (Serpentes: Dipsadidae: Elapomorhini), with the description of a new species from northwestern Argentina

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ABSTRACT

The examination of 93 specimens of the *Phalotris bilineatus* group housed in the major Argentinian collections allowed us to recognize three additional species of this group. We propose the resurrection of two names, *Phalotris spegazzinii* and *Phalotris suspectus*, previously placed in the synonymy of *P. bilineatus*, and describe a new species from northwestern Argentina. The new species is recognized based on a unique combination of morphological characters. In addition, we redescribe the resurrected taxa (providing variation in color patterns, meristic and morphometric characters) and present new data on their geographic distributions.

Key Words: *Phalotris*; Species boundaries; Meristic characters; Morphological characters; Color patterns.

RESUMEN

El examen de 93 ejemplares del grupo de *Phalotris bilineatus* depositados en las principales colecciones de la Argentina permitió reconocer tres especies adicionales del complejo. Proponemos la revalidación de dos nombres, *Phalotris spegazzinii* y *Phalotris suspectus*, previamente ubicados en la sinonimia de *Phalotris bilineatus*, y se describe una nueva especie del noroeste de la Argentina. La nueva especie se reconoce con base en una combinación única de caracteres. Adicionalmente, redescrimos los taxones revalidados (brindando información sobre patrones de coloración, caracteres morfológicos y merísticos) y presentamos nuevos datos sobre su distribución geográfica.

Palabras clave: *Phalotris*; Límites de especie; Caracteres merísticos; Caracteres morfológicos; Patrones de coloración.

Introduction

The tribe Elapomorhini includes approximately 50 Neotropical species belonging to the genus *Apostolepis* Cope, 1861; *Coronelaps* Lema & Deiques, 2010; *Elapomorphus* Wiegmann, 1843; and *Phalotris* Cope, 1861 (Entiauspe-Neto *et al.*, 2020). Elapomorhini snakes are characterized by the following suite of characters: reduction of the number of supralabial scales to six; entire nasal plate; frontal bones dorsally included by the anterior-lateral processes of the parietal and almost excluded from the reduced optic

foramen; exoccipitals in contact on the dorsal surface of the condyle; second supralabial scale contacting the eye (Zaher *et al.*, 2009). The monophyly of the tribe Elapomorhini was corroborated by several recent studies based on molecular phylogenies (Zaher *et al.*, 2009; Grazziotin *et al.*, 2012; Pyron *et al.*, 2013). They are small to moderate-sized fossorial snakes that feed mostly on elongated fossorial vertebrates (e.g., amphisbaenians and snakes) (Lema, 1989; Braz *et al.*, 2014). The complex taxonomy of

this group is even more intricate due to the scarcity of specimens in herpetological collections of these hard to find fossorial snakes, which hampers morphological studies (Ferrarezzi, 1993a,b).

Ferrarezzi (1993a,b) resurrected the genus *Phalotris* to accommodate Elapomorphini species presenting only one prefrontal. The number of species of the genus is still debated. Uetz *et al.* (2022) mention 14 species, but their list does not include *Phalotris bilineatus*, a species that has been accepted for some time (i.a. Puerto and Ferrarezzi, 1993; Wallach *et al.*, 2014; Williams *et al.*, 2021), they also do not include *Phalotris punctatus*, a species revalidated by Martins and Lema (2017). The recently described *Phalotris shawnella* is also missing from the list (Smith *et al.*, 2022). Therefore, up to now the genus must be considered composed of 17 species, arranged in three species groups: *Phalotris tricolor*, *P. bilineatus*, and *P. nasutus*. The *P. bilineatus* group is characterized by vertebral and dorsal-lateral black longitudinal stripes laterally expanded and black venter (Ferrarezzi, 1993a; Cabral and Cacciali, 2015), comprising five recognized species (see below).

Brief taxonomic history

The taxonomic history of the species of the *Phalotris bilineatus* group is particularly convoluted, with many names with uncertain status demanding careful revision and was in part summarized by Ferrarezzi (1993a) and Puerto and Ferrarezzi (1993). The first species described in this group were *Phalotris bilineatus* (Duméril, Bibron and Duméril, 1854) and *P. lemniscatus* (Duméril, Bibron and Duméril, 1854), followed by *P. reticulatus* (Peters, 1860), *P. iheringi* (Strauch, 1884), *P. melanopleurus* Cope, 1885, *P. trilineatus* (Boulenger, 1889), *P. spegazzinii* (Boulenger 1913), *P. suspectus* (Amaral, 1924), and *P. bollei* (Mertens, 1954). Most of these latter species were described based on a single specimen, and the validity of several assignments generated controversy (Puerto and Ferrarezzi, 1993), until Amaral (1930) and posteriorly, Peters and Orejas-Miranda (1970) considered all these names as synonyms of *P. bilineatus*. Lema (1970, 1979, 1984) proposed the recognition of only one species with several subspecies and later considered two species as follows: (i) *P. lemniscatus* including four subspecies: *P. l. lemniscatus*, *P. l. iheringi*, *P. l. trilineatus*, and *P. l. divittatus* (Lema, 1984); and (ii) *P. spegazzinii*, containing two subspecies: *P. s. spegazzinii* and *P. s. suspectus*. Also, it suggested that the holotype of

Phalotris bilineatus would be a hybrid or an intergrade specimen between *P. spegazzinii* and *P. suspectus* (Lema, 1979, 1984). Ferrarezzi (1993a) reviewed the taxonomy of Elapomorphini snakes, recognizing three species belonging to the *P. bilineatus* group: *P. bilineatus*, *P. lemniscatus*, and *P. reticulatus*, and described a new species of the group from Brazil, *P. multipunctatus* (Puerto and Ferrarezzi, 1993). This last arrangement was followed by most of the posterior authors that studied the genus (Giraudó, 2001; Giraudó and Scrocchi, 2002). Recently, Cabral and Cacciali (2015) proposed a new species from Paraguay named *P. normanscottii*. In summary, five species are currently recognized in the group, as follows: *Phalotris bilineatus* distributed in central and northern Argentina; *P. lemniscatus* from Uruguay, eastern Argentina and southern Brazil; *P. multipunctatus* in central to southeastern Brazil and eastern Paraguay; *P. reticulatus* that dwells in eastern Argentina and southern Brazil; and *P. normanscottii* present in western Paraguay (Puerto and Ferrarezzi, 1993; Cabral and Cacciali, 2015).

The overlap in pholidosis and meristic characters and the complex variations in color patterns account for the difficulties in precisely identifying many forms of the *Phalotris bilineatus* group. Herein, we discuss the status and validity of the species of the *P. bilineatus* group based on a geographically representative sample. We propose a new taxonomic scheme in which eight species are recognized in the group, including the description of a new species and the recognition of taxa previously placed in the synonymy of *Phalotris bilineatus*.

Materials and methods

We examined 93 specimens from the species included in the *Phalotris bilineatus* group, housed in herpetological collections (Appendix I). Institutional abbreviations are those of Sabaj (2016), except for CZA (Centro de Zoología Aplicada, Universidad Nacional de Córdoba), PNP (Parque Nacional El Palmar, Entre Ríos) and EX-CENAI (CENAI snakes collection now accessed in MACN). The types of *Elapomorphus spegazzinii* (MSNG 30651) and *Elapomorphus suspectus* (USNM 48939) were studied through photographs. Data on the geographic distribution include coordinates, names of localities and respective provinces, and associations with their ecoregions, as defined by Olson *et al.* (2001).

Taxonomic characters. We examined traditional

meristic characters. Counts of ventral scales follow Dowling (1951), while for cephalic shields the terminology follows Ferrarezzi (1993a,b) and Puerto and Ferrarezzi (1993). Paired structures are presented as right/left. We took measurements, with the aid of a digital caliper to the nearest 0.1 mm, except for snout-vent length (SVL) and tail length (TL), for which we used a flexible ruler to the nearest 1.0 mm. The head length was measured from the tip of the retroarticular process on the mandible to the tip of the snout. The maximum head width has been taken at the widest point. Cephalic shields measurements follow Peters (1960). The eye was measured on the right side from its anterior to posterior end. We determined sex based on direct observation of the presence/absence of hemipenes. When necessary, we performed a small mesial incision on the base of the tail to verify the presence of hemipenes. We base the description of coloration features mostly on the specimens preserved in ethanol solution 70% after fixation of formalin, increased by examining some photographs of live specimens. Coloration traits follow Ferrarezzi (1993a,b), Puerto and Ferrarezzi (1993) and Harvey (1999). According to Harvey (1999), the nuchal collar length was typically recorded as a range of occupied dorsal scales (i.e., 2–3), and dorsal stripes are described using the dorsal number as a landmark and expressing the width of stripes. We follow Cabral and Cacciali (2015) in using “collar” for structures associated with the neck and “caudal ring” for the black transversal band on the cloacal region, typical of the *Phalotris bilineatus* group.

Morphological Analyses. We compared potential evolutionary lineages considering putative natural barriers (e.g., Paraná River, ecoregions, mountain systems) and geographical proximity of the available sample to define six operational groups (see Passos and Prudente, 2012 for a similar procedure). Based on the cumulative frequencies of character states, we investigated if each group have any geographical basis. Independently, we searched for correspondence between the above groups and the taxa previously described (see taxonomy history account). We performed a discrete analysis of qualitative characters based on the frequency of occurrence of each state throughout the sample. We followed Passos *et al.* (2009) in considering the presence of one or more exclusive, apparently fixed diagnostic characters to distinguish species among the populations of the *Phalotris bilineatus* complex. Our sample size did

not allow us to address statistical confidence in qualitative characters from some populations (*sensu* Wiens and Servedio, 2000); therefore, we looked for concordance between the discrete/continuous characters, and the distributional patterns of the analyzed taxa, as our main parameters in sorting out putative evolutionary units.

Results

All the species herein studied from the *Phalotris bilineatus* group shared a unique combination of the following features: prefrontal one; nasal entire; supralabials 6/6 (rarely 5/5), with 2–3rd entering the eye (rarely 3–4th); infralabials 7/7 (rarely 6 or 8), with 4–5 contacting the first chinshield; loreal absent, nasal contacting unique preocular; two postoculars; dorsal scales in 15 rows without reduction; cloacal plate and subcaudals divided.

Our evidence points out the recognition of six species of the *Phalotris bilineatus* group in Argentina. Comparisons with literature data and type specimens allowed us to associate five taxa to available names, whereas the sixth form represents a new species described in the following section.

Species account

Phalotris illustrator sp. nov.

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Figs. 1-2, Table 1

Phalotris bilineatus Scrocchi, Moreta & Kretzschmar, 2006

Holotype. Adult female (FML 23858) collected on October 03, 2010, by M. Paz, 3 km from the cemetery of Nío River (26.438312°S, 64.998233°W; 991 m above sea level, asl hereafter), Departamento Burruyacú, Tucumán, Argentina.

Paratypes. Four specimens, all from Argentina: juvenile of unknown sex (FML 29520) and adult female (FML 29521) collected between 23–28 August 1978 by E. Lavilla, G. Scrocchi and E. Terán at Balderrama (25.489520° S, 65.039234° W; 1337 m asl), Sierra de Metán, Departamento Metán, province of Salta; female (FML 23860, partially damaged with crushed head and cut body) collected on April 24, 2010 by M. Torres-Bugeau at Raco (26.665408° S, 65.420254° W; 1153 m asl), Departamento Tafí Viejo, province of Tucumán; female (FML 12388) collected on May 12, 2001 by G. Coronel at Finca El Milagro (24.858180°S, 65.538322° W; 1321 m asl),

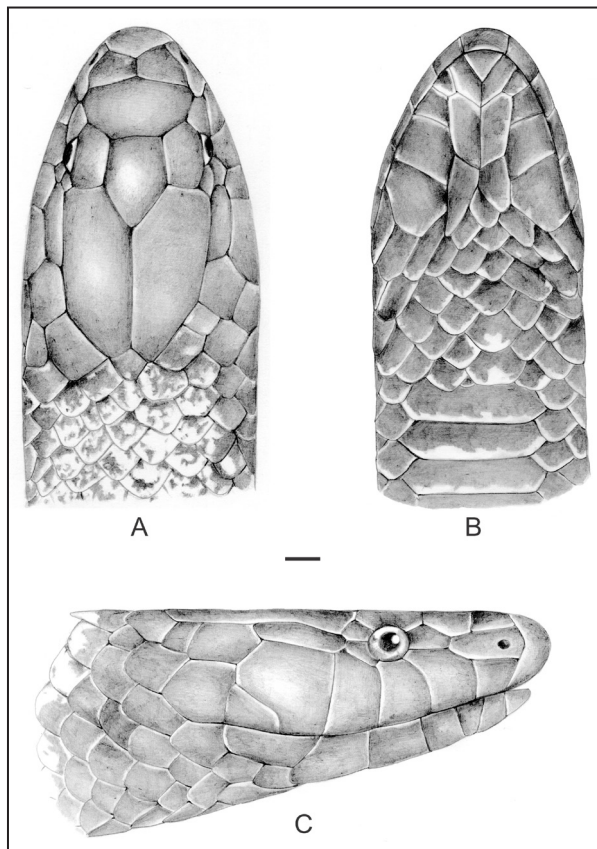


Figure 1. Dorsal (A), ventral (B) and lateral (C) view of the head of the holotype (FML 23858) of *Phalotris illustrator* sp. nov. Scale bar = 1 cm.

La Merced Chica, Departamento Rosario de Lerma, province of Salta.

Diagnosis. *Phalotris illustrator* is distinguished from all congeners in the *P. bilineatus* group (including the two revalidated taxa and *P. bilineatus* redefined in this paper) by a unique combination of the following characters: head entirely black (vs. head with light areas or blotches on rostral and supralabials and head venter almost uniformly white in all other species); nuchal collars absent (vs. present in other species of the group, except for *P. bilineatus* and *P. spegazzinii*); venter almost uniformly black (vs. venter white or with black blotches in all other species); flanks uniformly black to the level of lower half of fifth dorsal scale row (vs. flanks with a narrow black stripe between 4–5th dorsal scale row and 1–3rd dorsal rows white in *P. bilineatus*; white dot in each scale in *P. reticulatus*; or black stripe from 2nd or 3rd to 5th dorsal row, and the first dorsal row (or 1st and 2nd) white in *P. spegazzinii*); cloacal black ring present (vs. absent in *P. multipunctatus*); rostral well separated from the prefrontal (vs. rostral contacting the prefrontal or slightly separated in *P. bilineatus*).

Description of the holotype. Total length 554 mm, 512 mm SVL, 42 mm TL; head length 16 mm; maximum head width 8.6 mm; tail 8.2% SVL; head 3.1% SVL; head, not distinct from body; body subcylindrical; eye diameter smaller than one-third length of frontal; rostral protruded, visible from above one-third as long as its distance to frontal; internasals trapezoidal; prefrontal large, single, the wide a half of the long; frontal pentagonal; parietals longer than wide, almost twice as long as frontal; nasal entire; preocular single, contacting nasal; postoculars two, lower postocular contacting third and fourth supralabials; temporals 1+1; supralabials seven, second and third contacting orbit; infralabials seven, first to fourth contacting first pair of chinshields and fourth-fifth contacting second pair of chinshields; chinshields two pairs; dorsal scale rows smooth in 15/15/15; apical pits absent; ventrals 217; subcaudals 27; cloacal plate divided.

Head entirely black in dorsal, lateral and ventral views (Figs. 1-2); dorsum of body between 5–11th



Figure 2. Dorsal (A) and ventral (B) views of the holotype (FML 23858) of *Phalotris illustrator* sp. nov.

Table 1. Meristic and morphometric variation of *Phalotris illustrator* sp. nov. Data on the holotype is marked in boldface. Abbreviations are as follows: SVL= snout-vent length, TL=tail length.

Number	Sex	Supra-labials	Ventrals	Sub-caudals	Head length	Head width	SVL	TL	% TL/SVL	Ros-tral length (mm)	Interna-sal length (mm)	Prefron-tal length (mm)	Fron-tal length (mm)	Pa-rietal length (mm)
23858	F	7 (2-3)	217	27+1	16	8.6	512	42	8.2	1.2	0.8	2	3.4	4.4
23860	F	6 (2-3)	-	32+1	8	-	-	23	-	0.4	0.3	1	2	2.9
29521	F	6 (2-3)	202	31+1	10	-	340	31	9.1	0.6	0.5	1.5	2.6	2.9
29520	juv	6-5 (2-3)	215	27+1	8.5	4	172	15	8.7	0.5	0.3	1.2	1.8	2.6
12388	F	6 (2-3)	203	31+1	8	4.4	213	25	11.7	0.5	0.3	1.3	1.7	2.7

scale rows brown, with small black dots irregularly disposed; dots denser on the vertebral row forming an inconspicuous vertebral line; flanks and ventral surface of body black (from the first to lower half of fifth dorsal scale rows), with a thin white border on each dorsal and ventral scales; white border of ventral scales gradually increases toward posterior region of body (Fig. 2B); black caudal ring occupying 5–11th dorsal scale rows; subcaudal predominantly white irregularly marked with black (Fig. 2B).

Variation. The paratypes agree with the holotype in coloration except for the following features: FML 12388, 29520–21 the vertebral line is very faded or absent (coloration in preservative from well-conserved specimens); dorsal color of smaller specimens FML 12388 and 29520 reddish-brown. Table 1 synthesizes the variation of *Phalotris illustrator*.

Etymology. The specific epithet *illustrator* is a noun referring to the secular philosophical movement of the XVII Century, known as "enlightenment" in English and "illustration" in Latin. This philosophy gave rise to both science and Latin American independence movements. Because Argentina celebrates in 2016 the bicentennial of its independence, and several major battles against the Spanish colonizers were fought in northwestern Argentina (Tucumán and Salta), where inhabit the new species; we decided to honor the Argentinian heroes of the independence in Latin America belonging to the "enlightenment" philosophical movement.

Distribution. This species is known from the northern portion of the provinces of Tucumán and Salta. The distribution range of the type-series lies mainly in the Yungas phytogeographic province or southern Andean Yungas and transitional areas between Yungas and the Dry Chaco ecoregion (*sensu* Cabrera, 1976; Olson *et al.*, 2001) (Fig. 3). This region is characterized by several types of forests, ranging from dry to humid rainforests, including

some open areas such as high altitude grasslands of the Sub-Andean mountains.

***Phalotris bilineatus* (Duméril, Bibron & Duméril, 1854)**

Fig. 4A

Elapomorphus bilineatus Duméril, Bibron & Duméril, 1854:839.

Holotype MNHN-RA-0.3667. Type Locality "provincia de Los Corrientes"

Elapomorphus bilineatus, Jan, 1862

Phalotris bilineatus, Cope, 1861.

Elapomorphus bilineatus, Jan & Sordelli, 1865.

P.[halotris] bilineatus, Cope, 1885.

Elapomorphus bilineatus, Serié, 1936 (in part).

Elapomorphus bollei Mertens, 1954.

Elapomorphus bilineatus, Peters & Orejas-Miranda 1970 (in part).

Elapomorphus bilineatus bilineatus, Lema 1970.

Elapomorphus bilineatus, Abalos & Mischis, 1975 (in part).

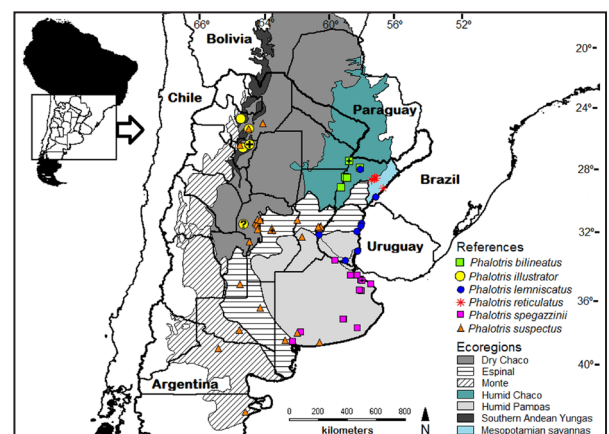


Figure 3. Distribution of the species of *Phalotris bilineatus* group in Argentina. + type localities of *Phalotris illustrator* sp. nov., *P. suspectus*, *P. bilineatus*, *P. bilineatus* and *P. spegazzinii*. The symbol "?" represents doubtful locality based on the confused collection data available.



Figure 4. General view in life of Argentinian members from *Phalotris bilineatus* group, *P. bilineatus* from Estancia La Adelita, Departamento Capital, Corrientes (A), *P. lemniscatus* from Gualeguaychú, Entre Ríos (B), *P. reticulatus* from Colonia Carlos Pellegrini, Corrientes (C), *P. spegazzinii* from City Bell, Partido de La Plata, Buenos Aires (D), and *P. suspectus* from Santa Fe (E). Photos by E. Etchepare (A), S. Nenda (C), L. Giambelluca (D), A. Giraudo (B, E).

Elapomorphus bollei, Ábalos & Mischis, 1975.
Elapomorphus bilineatus bilineatus, Lema 1978b.
Phalotris bilineatus, Ferrarezzi, 1993b (in part).
Phalotris bilineatus, Scrocchi *et al.*, 2000.
Phalotris bilineatus, Giraudo & Scrocchi, 2002.
Phalotris bilineatus, Giraudo, 2004.

Phalotris bilineatus, Giraudo *et al.*, 2012 (in part).
Phalotris spegazzinii, Cabral and Cacciali, 2015 (in part).
Phalotris lemniscatus, Cacciali *et al.* 2016 (in part).
Diagnosis. *Phalotris bilineatus* can be distinguished from all other congeners in the *P. bilineatus* group by a unique combination of the following characters:

head dorsally black with rostral and first supralabials lighter; and ventrally almost white (vs. head entirely black in *P. illustrator*); nuchal collars absent (vs. present in other species of the group, with exception of *P. illustrator* and *P. spegazzinii*); belly with ventral scales white, with a half-moon shaped black dot in the anterior portion of each ventral scale; the dots enlarge toward posterior region of body, occupying almost all surface of ventral scales, being white only on the borders in contact with dorsal scale rows (vs. almost entirely black in *P. illustrator*, and *P. spegazzinii*); sides of the body with a narrow black stripe on 4–5th dorsal scale rows and 1–3rd dorsal scales rows white (vs. wider black lateral stripe 3–4 scales wide in *P. illustrator*, *P. reticulatus* and *P. spegazzinii*); cloacal shield with black ring present (vs. absent in *P. multipunctatus*); rostral scales projected backward, reaching or slightly separated from the prefrontal (vs. rostral well separated from the prefrontal in other species of the group).

Coloration (Fig. 4A). Dorsum of head with black cephalic-cap reaching first or second postparietal scales; rostral and three first supralabials lighter, nearly grey; head ventrally black with lighter areas on border of infralabials and chinshields; dorsum of body brown with or without black dots; black dots vary in density and size but never defining a pattern; sometimes dorsal dots arrangement constitute a barely noticeable vertebral stripe on the cloacal region and tail; dorsum often darker on the vertebral area and lightens at upper margins of dorsal-lateral stripes; dorsum of cloacal region with black area, covering 4–7 scales wide; body flanks exhibit dorsal-lateral black stripe (one scale wide) anteriorly connected to cephalic-cap and reaching the tip of tail posteriorly, over lower half of 5th and upper half of 4th dorsal scale rows; dorsal scales below the stripes immaculate white; dorsum of tail similar to body color pattern; belly with ventral scales white, with a half-moon shaped black dot on the anterior portion of each ventral scale; dots enlarges posteriorly, occupying almost all surface of ventral scales, being white only on the borders; ventral surface of tail white with black dots covering the suture region between subcaudals.

Variation. The largest specimen was a female 695 mm SVL, TL 50 mm; TL 9.5% SVL in a single male, 6.1–10.3% in females; ventrals 205 in male, 206–210 in females (mean= 207.5, SD= 1.76, $n= 6$); subcaudals 30 in male, 20–28 in females (mean= 23.8, SD= 3.43, $n= 6$); from ten specimens studied, four have

the typical head scales of the genus; four specimens have 5/5 (2nd and 3rd in contact with orbit) supralabials; one has 8/8 infralabials, and one has 1+2+1 temporals in one side of the head.

Distribution. Species known only from Argentina (Ferrarezzi, 1993a, Giraudo and Scrocchi, 2002), our data restricted the distribution of *Phalotris bilineatus* to the northwestern province of Corrientes, eastern from the Paraná River, in the Humid Chaco ecoregion (*sensu* Olson *et al.*, 2001) (Fig. 3). There is only one specimen westwards to the Parana River, from Resistencia, Chaco. This species does not overlap its known distribution with any congeners and probably has a parapatric distribution with *P. lemniscatus*, with the nearest records between these two species separated by a 10 km airline (Manantiales and Mburucuyá National Park).

***Phalotris lemniscatus* (Duméril, Bibron & Duméril, 1854)**

Fig. 4 B

Elapomorphus lemniscatus Duméril, Bibron & Duméril, 1854. Erp. Gen., 7:840.

Holotype. Adult, MNHN-RA-0.3668, from “Amérique du Sud” (= South America).

Elapomorphus lemniscatus, Jan, 1862.

Elapomorphus lemniscatus, Jan & Sordelli, 1865.

Phalotris lemniscatus, Cope, 1861.

P.[halotris] lemniscatus, Cope, 1885.

Elapomorphus trilineatus, Boulenger, 1889.

Elapomorphus lemniscatus, Koslowsky, 1898.

Elapomorphus bilineatus, Bertoni, 1914.

Elapomorphus lemniscatus, Bertoni, 1914.

Elapomorphus bilineatus, Schouten, 1931.

Elapomorphus lemniscatus, Schouten, 1931.

Elapomorphus bilineatus, Schouten, 1937.

Elapomorphus lemniscatus, Schouten, 1937.

Elapomorphus bilineatus, Bertoni, 1939.

Elapomorphus bilineatus, Gatti, 1955.

Elapomorphus bilineatus, Peters and Orejas-Miranda 1970. In part.

Elapomorphus bilineatus lemniscatus, Lema, 1970

Elapomorphus bilineatus lemniscatus, Lema, 1978b

Elapomorphus lemniscatus lemniscatus, Lema, 1979

Elapomorphus bilineatus, Talbot, 1979.

Elapomorphus (P) lemniscatus lemniscatus, Lema, 1984

Elapomorphus (P) lemniscatus trilineatus, Lema, 1984

Elapomorphus lemniscatus lemniscatus, Williams and Francini, 1991.

Elapomorphus (Phalotris) lemniscatus lemniscatus, Ceï 1993.

Phalotris lemniscatus, Ferrarezzi, 1993.

Elapomorphus spegazzinii, Aquino, Scott, and Motte, 1996.

Phalotris lemniscatus, Scrocchi *et al.*, 2000.

Phalotris lemniscatus, Giraudo and Scrocchi, 2002.

Phalotris lemniscatus, Giraudo, 2004.

Phalotris lemniscatus, Carreira, Meneghel, and Achával, 2005.

Phalotris bilineatus, Cacciali, 2009.

Phalotris lemniscatus, Giraudo *et al.*, 2012.

Phalotris lemniscatus, Costa and Bernils, 2014.

Phalotris lemniscatus, Costa and Bernils, 2015.

Phalotris lemniscatus, Cacciali *et al.* 2016 (in part).

Phalotris lemniscatus, Costa and Bernils, 2018.

Diagnosis. *Phalotris lemniscatus* can be distinguished from all congeners in the *P. bilineatus* group by a unique combination of the following characters: head dorsally black, with rostral and first supralabials lighter, and ventrally almost white (vs. head totally black in *P. illustrator* and *P. spegazzinii*); white nuchal collar present, 2–3 dorsal scales width, followed by a narrow black ring, one scale width (vs. nuchal collar absent in *P. bilineatus*, *P. illustrator* and *P. spegazzinii*); ventral scales almost black with the lateral and posterior edge white (vs. venter almost uniformly black in *P. illustrator*); flanks of the body with a black stripe on 3–5th dorsal rows, 1–2nd dorsal rows, white (vs. wider black lateral stripe 3–4 scales wide in *P. illustrator*, *P. reticulatus* and *P. spegazzinii*); cloacal black ring present (absent in *P. multipunctatus*); rostral well separated from the prefrontal (vs. rostral contacting the prefrontal or slightly separated in *P. bilineatus*). Additionally, *P. lemniscatus* have a well-defined vertebral stripe (vs. vertebral stripe absent or faded in other species, except *P. illustrator*, *P. spegazzini* and *P. reticulatus*).

Coloration (Fig. 4B). Dorsum of head dark (black to light brown); snout lighter than other cephalic portion in dorsal view; light area occupies the rostral, internasals and anterior prefrontal; head laterally black with first four supralabials mostly whitish or cream, and last supralabials dark; head ventrally almost white, usually with black to brown spots that run from the mental over the suture between chinshields and all infralabials. Behind the head, there is an immaculate white ring of variable width in the dorsum, occupying from one to three dorsal scales and being commonly two scales wide. In all specimens, the white ring occupies the sides of the body. The white ring is bordered by front and rear by a thin black line. The dorsum of the body, behind the white

ring, is reddish-brown. All specimens have three black stripes, one vertebral occupying the vertebral and half of paravertebral scales, and two lateral stripes on the sides of the body that run over the lower half of the fifth to the upper half of the third row of dorsal scales. The dorsal scales below the lateral black stripes to the venter are whitish. The tail coloration continues the pattern of the body. Dorsally, over the cloaca, there is a black ring of 5–7 dorsal scales wide, which extends to the differentiated white anal plates. The ventral scales are almost black, with the lateral and posterior edge white. Ventrally the tail is black, with mostly black subcaudals that have sutures and lateral edges white. The tip of the tail is black. **Variation.** The largest specimen was a female 658 mm SVL and 51 mm tail. Tail short, corresponding to 8.5–11.8% of SVL in males and 7.8–9.4% in females. Males with 188–199 (\bar{X} = 193.70, SD = 5.51, n = 3) ventral scales (180–200 reported for Brazilian and Uruguayan populations by Ferrarezzi, 1993a), females 202–217 (\bar{X} = 209.33, SD = 10.60, n = 3; 195–217 reported for Brazilian and Uruguayan populations by Ferrarezzi 1993a). Subcaudal scales 29–31 (\bar{X} = 30.30, SD = 0.58, n = 3) in males (21–36 reported by Ferrarezzi 1993a), and 25–31 in females (\bar{X} = 28.00, SD = 2.65, n = 3; 19–28 reported by Ferrarezzi, 1993a). The specimens studied have the typical head scales of the genus. The rostral is not projected backwards and is separated from the prefrontal.

Distribution (Fig. 3). Species known to occur in Argentina from Corrientes and Entre Ríos provinces, inhabiting mainly the ecoregion called Southern Cone Mesopotamian Savannas by Olson *et al.* (2001), and marginally in the Espinal and Humid Pampas, mostly associated with the high banks of the Uruguay and Paraná Rivers. All reliable records of *P. lemniscatus* are restricted to the east of Paraná River in the Argentine Mesopotamia. Two specimens labeled as coming from Buenos Aires and Córdoba probably correspond to wrong locations, because the characteristics of the localities are different from all the others known, and they are several hundred km from the closest localities. Our data showed that *P. lemniscatus* has a parapatric distribution with respect to other Mesopotamian species, *P. bilineatus* and *P. reticulatus* (Fig. 3).

Phalotris reticulatus (Peters, 1860)

Fig. 4 C

Elapomorphus reticulatus Peters, 1860

Holotype. Adult ZMB 3811, collected at "Brasilien"

(= Brazil)

Phalotris reticulatus Cope, 1861.

Elapomorphus iheringi Strauch, 1884.

Phalotris melanopleurus Cope, 1885.

Elapomorphus bilineatus, Peters and Orejas-Miranda 1970. In part.

Elapomorphus bilineatus reticulatus, Lema, 1970.

Elapomorphus bilineatus reticulatus, Lema, 1978b.

Elapomorphus lemniscatus reticulatus, Lema, 1979.

Elapomorphus (P) lemniscatus iheringi, Lema, 1984.

Elapomorphus (Phalotris) lemniscatus divittatus Lema, 1984.

Elapomorphus lemniscatus iheringi, Williams and Francini, 1991.

Elapomorphus (Phalotris) lemniscatus iheringi, Cei 1993.

Phalotris reticulatus Ferrarezzi, 1993.

Phalotris reticulatus, Scrocchi *et al.*, 2000.

Phalotris reticulatus, Giraud, 2001.

Phalotris reticulatus, Giraud and Scrocchi, 2002.

Phalotris reticulatus, Giraud *et al.*, 2012.

Phalotris reticulatus, Costa and Bernils, 2014.

Phalotris reticulatus, Costa and Bernils, 2015.

Phalotris reticulatus, Costa and Bernils, 2018.

Diagnosis. *Phalotris reticulatus* can be distinguished from other species of the group by unique combination of the following characters: head dorsally almost totally black, with lighter snout, and a notable white dot on 3rd–4th supralabials (this last character is unique within the *P. bilineatus* group), and ventrally almost white (vs. black in *P. illustrator* and *P. spagazzinii*); white nuchal collar present and reaching ventral scales (2–3 dorsal scales width), followed by a black ring (1–3 scale width) (vs. nuchal collar absent in *P. bilineatus*, *P. illustrator* and *P. spagazzinii*); venter almost totally black, each ventral scale black with thin whitish free posterior border (vs. venter white or with black blotches in all other species); vertebral black stripe can be from very noticeable to almost faded and runs over the vertebral and the inner half of paravertebral dorsal scales. The stripe is formed by irregular dots over each scale and could fade after fixation. On both sides of the vertebral stripe, there is a reddish stripe two dorsal scales wide. The sides of the body, from the reddish stripes to the venter, almost black, where each scale is black with a thin whitish posterior border resulting in a reticulated lateral pattern in general view; black in *P. spagazzinii* and *P. illustrator* and a narrow lateral black stripe in others species); cloacal black ring present (vs. absent in *P. multipunctatus*); rostral well separated from the

prefrontal (vs. rostral contacting the prefrontal or slightly separated in *P. bilineatus*).

Coloration (Fig. 4C). The head is black, and the coloration extends until to an almost straight line behind the parietals. There is a clear area, with irregular black dots, from the snout to the anterior half of frontal, supraoculars, and first supralabials. There is a noticeable big white spot on the third and fourth supralabials. Ventrally the head is white and presents a sub-triangular to sub-rhombic black spot over the gulars, that extends forward as a line over the chinshields suture. Behind the head, in the dorsum, there is a white nuchal collar of two to three dorsal scales wide; the white collar is posteriorly bordered by a black collar of one to two dorsal scales width, which is formed by the union of the enlarged end of the vertebral stripe, and the color of sides of the body. A vertebral black stripe can be from very noticeable to almost faded and runs over the vertebral and the inner half of paravertebral dorsal scales. The stripe is formed by irregular dots over each scale and could fade after fixation. On both sides of the vertebral stripe, there is a reddish stripe two dorsal scales wide. The sides of the body, from the reddish stripes to the ventral shields, are black, and only the free border of the scales can be clear, forming a reticulated pattern. There is a white line between the first dorsal scale rows and the ventral shields. Ventrally almost black, only a thin whitish border can exist in each ventral shield. Tail ventrally with the same pattern as the belly. Dorsally, in correspondence to the cloacal region, there is a black area of 8–9 dorsal scales wide that extends in a triangular shape over vertebral and paravertebral scales.

Variation. The largest specimen was a female 453 mm SVL and 42 mm tail. Tail short, corresponding to 10.9–12.4% of SVL in males, and 8–9.3 % in females. Males with 188–197 (\bar{X} = 192.00, SD = 4.69, n = 4) ventral scales (188–198 reported for Brazilian populations by Ferrarezzi, 1993a), females 201–207 (\bar{X} = 205.00, SD = 3.46, n = 3; 202–211 reported by Ferrarezzi, 1993a). Subcaudal scales 30–33 (\bar{X} = 31.30, SD = 1.26, n = 4) in males (27–33 reported by Ferrarezzi, 1993a), and 23–27 in females (\bar{X} = 24.67, SD = 2.08, n = 4; 23–27 reported by Ferrarezzi, 1993a). The specimens studied have the typical head scales of the genus. **Distribution** (Fig. 3). In Argentina, only corroborated by voucher specimens from eastern Corrientes Province, inhabiting the Southern Cone Mesopotamian Savannas ecoregion, and cited from the pro-

vince of Misiones by Lema (1984) without mention of any voucher specimen.

***Phalotris spegazzinii* (Boulenger, 1913) Status revalidated**

Figs. 4 D – 5 A-B

Elapomorphus spegazzinii Boulenger, 1913.

Holotype. Adult, MSNG 30651, collected at “La Plata”.

Elapomorphus bilineatus spegazzinii, Lema, 1978b.

Elapomorphus lemniscatus spegazzinii, Lema, 1979.

Elapomorphus (P.) spegazzinii spegazzinii, Lema, 1984.

Elapomorphus spegazzinii spegazzinii, Williams and Francini, 1991.

Elapomorphus spegazzinii Aquino, Scott, and Motte, 1996.

Elapomorphus (Phalotris) spegazzinii spegazzinii, Cei, 1993.

Phalotris bilineatus, Cabrera, 2004. In part.

Phalotris bilineatus, Giraudo *et al.*, 2012. In part.

Phalotris spegazzinii, Cabral and Cacciali, 2015 (in part).

Phalotris lemniscatus, Cacciali *et al.*, 2016 (in part).

Diagnosis. *Phalotris spegazzinii* can be distinguished from the other species of the group by a unique combination of the following characters: head dorsally black, some specimens with rostral and first supralabials lighter and ventrally almost black (vs. light areas, blotches, or both, present on rostral and supralabials of other species of the group, completely black in *P. illustrator* and ventrally mostly white in other species of the group, but completely black in *P. illustrator*); nuchal collars absent (vs. present in other species of the group, except for *P. bilineatus* and *P. illustrator*) but with two light dots behind parietals (vs. absent in all others species); ventral shields are almost completely black except for the posterior border lighter (vs. venter almost uniformly black in *P. illustrator*, and white or with black blotches in all other species); sides of the body with a black stripe 3–4 scales width in 3–5th or 2–5th dorsal rows (vs. narrow lateral black stripe in others species, except for *P. reticulatus* and *P. illustrator*); cloacal black ring present (vs. absent in *P. multipunctatus*); rostral well separated from the prefrontal (vs. rostral contacting the prefrontal or slightly separated in *P. bilineatus*).

Coloration (Figs. 4D, 5 A–B). Based on photographs of the holotype (MSNG 30651) and live and preserved specimens. Head dorsal, lateral, and ventrally almost black. In a few specimens, the rostral area is somewhat clearer. The body is dorsally light brown with a dark vertebral stripe that continues

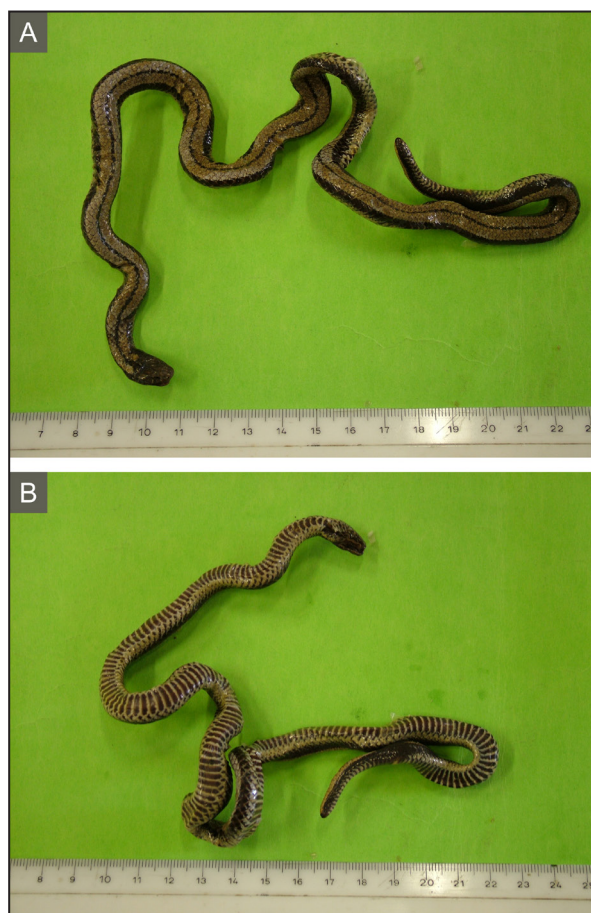


Figure 5. Dorsal (A) and ventral (B) views of the holotype of *Phalotris spegazzinii* (MSNG 30651) from La Plata, Argentina. Photo by G. Doria.

the coloration of the head and is one dorsal scale wide, occupying the vertebral row of dorsals and the border of paravertebral rows. The scales in the paravertebral rows have black dots, and the posterior border is lighter. Behind the head and between the vertebral stripe and the lateral bands, some specimens (including the holotype) have two spots of two dorsal scales wide, somewhat lighter than the rest of the back and inconspicuous. Dorsally, over the cloaca, there is a black area of 4–9 dorsal scales wide that extends in a triangular shape over vertebral and paravertebral scales. The sides of the body have a black stripe 2–3 dorsal scales wide that runs over the second to fifth dorsal scales rows, from the head to the tip of the tail. In the dorsum, in some specimens appears, between the lateral and vertebral stripes, little black dots not regularly disposed and very inconspicuous. The anterior half of the dorsal scales of the first and second rows are normally black, but in some specimens are immaculate or with a few little dots. In the tail the pattern continues that of the

body. The infralabials and chinshields are normally black, but in some specimens can be lighter. Other scales in the ventral side of the head are black with lighter borders. The ventral shields are almost completely black except for the lighter posterior border. The anal and subcaudals have the same pattern, but the subcaudals can be light with a black suture between them in some specimens.

Variation. The largest specimen was a female 544 mm SVL and 40 mm tail. The tail is short, corresponding to 10.3–11.2% of SVL in males, and 7.1–8.9 % in females. Males with 191–200 (\bar{X} = 195.00, SD = 1.15, n = 4) ventral scales, females 201–218 (\bar{X} = 210.09, SD = 5.01, n = 11). Subcaudal scales 29–35 in males (\bar{X} = 31.00, SD = 2.71, n = 4), and 21–25 in females (\bar{X} = 23.09, SD = 1.58, n = 11). Almost all the specimens studied (24 of 30) have the typical head scales of the genus, with the follow variation recorded: one specimen with 6(2–3)/7(3–4) supralabials, one with 8/8 infralabials and two with 1+1+1 temporals. The rostral is slightly projected backwards and is separated from the prefrontal.

Distribution (Fig. 3). Known only from eastern and southern Buenos Aires province, Argentina, in the Humid Pampas ecoregion (*sensu* Olson *et al.*, 2001).

Phalotris suspectus (Amaral, 1924) Status revalidated

Figs. 4 E – 6 A-B

Elapomorphus suspectus Amaral, 1924.

Holotype. Adult male, USNM 48939, collected at "Pilar", near Córdoba, Argentina.

Elapomorphus bilineatus, Serié, 1936. In part.

Elapomorphus bilineatus, Peters and Orejas-Miranda, 1970. In part.

Elapomorphus bilineatus, Ábalos and Mischis, 1975. In part.

Elapomorphus bilineatus suspectus, Lema, 1978a

Elapomorphus lemniscatus suspectus, Lema, 1979

Elapomorphus (P) spegazzinii suspectus, Lema, 1984

Phalotris bilineatus, Ferrarezzi, 1993a. In part.

Elapomorphus (Phalotris) spegazzinii suspectus, Cei, 1993

Elapomorphus spegazzinii (sic) suspectus, Reati, 1996.

Phalotris bilineatus, Giraudo and Scrocchi, 2002.

In part.

Phalotris bilineatus Cabrera, 2004. In part.

Phalotris bilineatus, Scrocchi *et al.*, 2010.

Phalotris bilineatus, Giraudo *et al.*, 2012. In part.

Phalotris spegazzinii, Cabral and Cacciali, 2015 (in part).

Phalotris lemniscatus, Cacciali *et al.*, 2016 (in part).

Diagnosis. *Phalotris suspectus* can be distinguished from all congeners in the *P. bilineatus* group by a unique combination of the following characters: head dorsally black, with rostral and first supralabials lighter; and ventrally almost white (vs. head totally black in *P. illustrator* and *P. spegazzinii*); white nuchal collar present, followed by a narrow black collar (vs. nuchal collar absent in *P. bilineatus*, *P. illustrator* and *P. spegazzinii*); venter whitish with dark, almost black, dots in the anterior portion of the ventral shields, being white at the posterior border (vs. venter almost uniformly black in *P. illustrator*); flanks with a narrow black stripe on 4–5th dorsal scale rows, 1–3rd dorsal scale rows white (vs. wider black lateral stripe 3–4 scales wide in *P. illustrator*, *P. reticulatus* and *P. spegazzinii*); cloacal black ring present (vs. absent in *P. multipunctatus*); rostral well separated from the prefrontal (vs. rostral contacting the prefrontal or slightly separated in *P. bilineatus*).

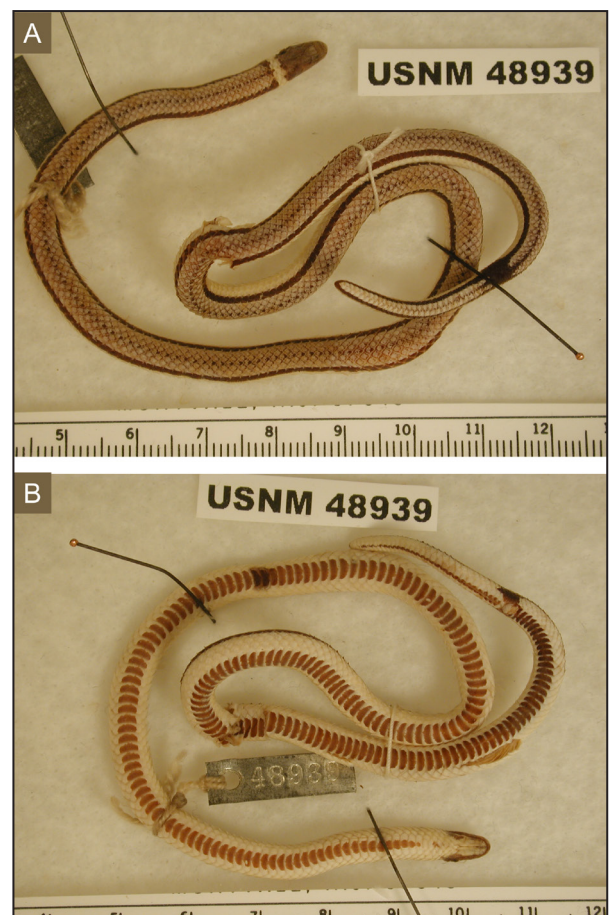


Figure 6. Dorsal (A) and ventral (B) views of the holotype of *Phalotris suspectus* (USNM 48939) from Pilar, Córdoba, Argentina. Photo J.A. Poindexter II.

Coloration (Figs. 4 E, 6 A–B). Based on photographs of the holotype: National Museum of Natural History; Smithsonian Institution, USA. USNM 48939; (additional detailed photographs of the holotype are available at https://www.si.edu/object/nmnhvz_6556633); and live and preserved specimens. The rostral area of the head is clear; the rest of the head dorsally darker (light brown to black). Depending on the specimen, the light area in the head occupies the rostral, internasals, and a big area of prefrontals and supraoculars (MACN 38881, CZA 150); or is extended to parietals (JW 943) or all the head is light brown (MACN 32886, 20629, 11236, 12897). Laterally the pattern is the same of the dorsum, and the last supra and infralabials are dark. Almost all the supralabials are whitish or white, except the last ones that are dark because the black ring of the neck projects over them. Ventrally, the head is almost white or light brown, and almost all the specimens have a dark spot that runs from the mental over the suture between chinshields. Behind the head, there is an immaculate white ring in the dorsum, of variable width, occupying from one to two and a half dorsal scales, being commonly of two scales wide. In almost all specimens, the white ring occupies the sides of the body, but sometimes it is interrupted by the lateral stripes. The white ring is bordered by front and rear by a thin black line. The dorsum of the body posteriorly the white ring is light brown. In most specimens, a diffuse vertebral stripe is formed by the union of small spots on vertebral scales, but it is absent or almost indistinguishable in others. There are black dots irregularly disposed in the paravertebral scales. Dorsally, over the cloaca, there is a black area of 3–7 dorsal scales wide, which extends in a triangular shape over vertebral and paravertebral scales. The body sides have a black stripe that runs over the lower half of the fifth and the upper half of the fourth row of dorsal scales. The dorsal scales below the stripes are whitish, like the venter. In the tail, the coloration continues the pattern of the body, but the vertebral stripe is less conspicuous. The venter is whitish, with dark (almost black) dots in the anterior portion of the ventral shields that are white on their posterior border. The dots progressively increase in size being reduced only to the center of the gular and first ventral shields, while in the rest of the belly occupy almost the entire width of the ventral shield leaving only the lateral ends immaculate. The tail is immaculate white ventrally. Some specimens had little spots or a diffuse black line in

the suture of subcaudals. The tip of the tail is black.

Variation. The largest specimen was a female 695 mm SVL and 50 mm tail. The tail is short, corresponding to 9.9–12.3% of SVL in males and 6.8–10.5% in females. Males with 195–206 ventral scales, females 200–226. Subcaudal scales 28–39 in males and 22–32 in females. Almost all the specimens (22 of 28) studied have the typical head scales of the genus. Two specimens have five supralabials on the left side of head, and in one of them the 3rd and 4th entering the eye; two with 6/6 infralabials; in one specimen the 1–5 infralabials contacting the first chinshield.

Distribution (Fig. 3). It is the species with the largest distribution in Argentina within the *Phalotris bilineatus* group, known from Buenos Aires, Chubut, Córdoba, La Pampa, Río Negro, Salta, San Luis, Santa Fe, and Tucumán Provinces, over at least four ecoregions, the Dry Chaco, Espinal, Monte, Humid Pampas (where it is marginally distributed and partially sympatric with *P. spegazzinii*), and Yungas (where it is sympatric with *P. illustrator*).

Discussion and Conclusion

The taxonomic history of the *Phalotris bilineatus* group is very complex, probably because of the small sample sizes used in previous studies (Ferrarezzi, 1993a,b; Lema, 1970, 1978a,b, 1979, 1984). As a rule, the lack of information regarding geographical variation in the group precluded a more robust assessment of the taxonomic status of most species. Lema (1979, 1984) suggests that the holotype of *Phalotris bilineatus* represents a hybrid specimen or an intergraded phenotype between *Phalotris spegazzinii* and *P. suspectus*. The examined specimens of *P. bilineatus* (including three topotypes) let us conclude that this species can be unambiguously distinguished from *P. spegazzinii* and *P. suspectus* (see species account). On the other hand, the distribution patterns of each of the three species do not support Lema's (1979, 1984) hypothesis because *P. bilineatus* is restricted to the northwest of the Corrientes Province, eastwards from the Paraná River, while *P. suspectus* and *P. spegazzinii* occur to the southwest of this river, with the closest records 300 and 600 km, respectively, from the nearest locality of the first. Moreover, we found no putative hybrids or intergrade phenotypes (i.e., presenting a mosaic of characteristic of different parental taxa) along the sympatric area of *P. suspectus* and *P. spegazzinii* in the south of Buenos Aires Province (Fig. 3). These

arguments support our taxonomic decision for the resurrections of *P. suspectus* and *P. spegazzinii*, independently of their parapatric distributions. We agree partly with Ferrarezzi (1993a,b) about the priority of the name *P. bilineatus*, but restricting it to northwestern Corrientes populations, defined by several unique characters that allow its distinction from the other Mesopotamian species, *P. lemniscatus* and *P. reticulatus*.

The *Phalotris bilineatus* group now included eight species; a resume of their principal color characteristics is presented in Table 2. The species of *Phalotris bilineatus* group in Argentina may be characterized by their distribution and principal characters:

Phalotris illustrator occurs in northwestern Argentina (Tucumán and Salta provinces), where it is sympatric with *P. suspectus* (Fig. 3). It is characterized by a head (dorsal and ventral) entirely black, nuchal collar absent, venter and flanks of the body almost black with only a thin white border on the scales.

Phalotris bilineatus is restricted to the northwestern of the province of Corrientes, eastwards from the Paraná River in the Argentine Mesopotamia (Fig. 3), without overlap with any other species analyzed here. It is characterized by rostral scales projected backwards, reaching or slightly separated from the prefrontal (a feature found exclusive of this taxon along with the *P. bilineatus* group), nuchal collars absent, flanks of the body with a narrow black stripe on 4–5th dorsal scale rows and white 1–3rd dorsal scale rows.

Phalotris lemniscatus showed a parapatric distribution with respect to *P. bilineatus* and *P. reticulatus* in the central and southern Argentine Mesopotamia, eastwards from the Paraná River (Fig. 3). It is diagnosed by a white and black nuchal collars, three longitudinal black stripes (one vertebral and two dorsal-lateral) with one scale width, and flanks of the body with 1–2nd dorsal scale rows white pigmented. All Argentinian specimens have similar coloration patterns, but Lema (1984) interpreted some variations of coloration pattern of Brazilian and Uruguayan populations as subspecies (see synonymy); nevertheless, Ferrarezzi (1993a) and Puerto and Ferrarezzi (1993) rejected this posture.

Phalotris reticulatus, as previously mentioned, shows a parapatric distribution with respect to *P. bilineatus* and *P. lemniscatus* in northeastern Argentine Mesopotamia (Fig. 3). It is distinguished by head

dorsally almost totally black, with lighter snout, a notable white dot on 3–4th supralabials, white and black nuchal collars and flanks of the body almost black.

Phalotris spegazzinii is distributed in Buenos Aires Province (Pampas ecoregion), with a narrow contact area with *P. suspectus* (Fig. 3). It is diagnosed by the lack of nuchal collars, two light and very inconspicuous dots behind the parietals, flanks of the body with a broad black stripe covering three or four scale rows width (3–5th or 2–5th).

Phalotris suspectus distribution extends from northwestern (where it is sympatric with *P. illustrator*) throughout central Argentina (where it marginally overlaps with *P. spegazzinii*), and up to the south (northern Patagonia), always westwards from the Paraná River (Fig. 3). It is characterized by a head dorsally black, with lighter rostral and first supralabials, a white nuchal collar (three scales width) followed by a narrow black one, and two dorsal-lateral narrow longitudinal black stripes on the flanks.

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Table 2. Principal color characteristics of the species of *Phalotris bilineatus* group.

	Dorsal Head coloration	Ventral Head coloration	Nuchal collars	Vertebral stripe	Sides of the body	Cloacal black ring	Ventral tail coloration
<i>P. illustrator</i> sp. nov. (n = 5)	Totally black (100%).	Totally black (100%).	Absent (100%).	Present (40%), faded (20%) or absent (40%)	Almost black (100%).	Present (100%)	Subcaudals are mostly white with black dots irregularly disposed (100%).
<i>P. bilineatus</i> (n = 10)	Black with rostral and first supralabials lighter (100%).	Almost black (100%).	Absent (100%).	Mostly absent (80%), some exemplars have a faded one (20%)	With a narrow black stripe on 4th–5th dorsal rows, 1st to 3rd dorsal rows white (100%).	Present (100%)	Almost white with the medial suture with black dots (100%).
<i>P. lemniscatus</i> (n = 9)	Black with rostral and first supralabials lighter (100%).	Almost White (100%).	A white collar, reaching the ventral scales, and 2–3 dorsal scales width, followed by a narrow black collar, 1 scale width (100%).	Present (100%)	With a black stripe on 3th–5th dorsal rows, 1st to 2nd dorsal rows white (100%).	Present (100%)	Mostly black (90%) or almost white with the medial suture with black dots (10%).
<i>P. multipunctatus</i> (n = 2)	Black with white contrastant dots and bigger dots in the supralabials (100%).	Almost white, with some scales with black borders (100%).	A white collar reaching the ventral scales, and 3–4 dorsal scales width, followed by a narrow black collar, 1 scale width (100%).	Absent (100%)	The first row and decreases to the fifth (100%). With a narrow black stripe on 4th–5th dorsal rows, 1st to 3rd dorsal rows white (100%).	Absent (100%)	Reticulate in black, with a white dot in each subcaudal (100%).
<i>P. normanscotii</i> (n = 3)	Completely black (100%).	Almost white (100%).	A white nuchal collar on tip of parietals 4–6 dorsal scales width, followed by a black collar 4–6 dorsal scales width (100%).	Absent (100%)	Almost black (100%).	Present (100%)	White (100%)
<i>P. reticulatus</i> (n = 8)	Almost totally black, with lighter snout (100%). A white notable dot on 3rd–4th supralabials (100%).	Almost white (100%).	A white collar, reaching the ventral scales, and 2–3 dorsal scales width, followed by a black collar, 1–3 scale width (100%)	Present (80%) to faded (20%)	Almost black (100%).	Present (100%)	Almost black (100%).
<i>P. spegazzinii</i> (n = 17)	Almost black, with rostral and first supralabials lighter (96%). Almost black (4%).	Almost black (100%).	Absent (100%). In most exemplars (95%) there are two light dots posterior to parietals.	Present (100%)	A black stripe 3 or 4 scales width (3–5 or 2–5 dorsal rows). The first dorsal rows (or 1st and 2nd) are white with or without black dots (100%).	Present (100%)	Black with white posterior border (90%). Mostly White (10%).
<i>P. suspectus</i> (n = 26)	Black with rostral and first supralabials lighter (96%). Almost black (4%).	Almost white (88%). Almost black (12%).	A white collar, reaching the ventral scales, 3 dorsal scales width (100%), usually followed by a narrow black collar, 1 scale width (62%).	Mostly absent (52%), some exemplars have a faded one (48%).	With a narrow black stripe on 4th–5th dorsal rows, 1st to 3rd dorsal rows white (100%).	Present (100%)	Almost white with the medial suture with black dots or line (56%). Mostly white (44%).

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Appendix

Phalotris illustrator (n=1, not included in the type series).

ARGENTINA: **CÓRDOBA: Departamento Pocho:** Pocho river (-31.4166 -65.3666), near Las Palmas: MACN 33132.

Phalotris bilineatus (n=10). ARGENTINA: **CHACO:**

Departamento San Fernando: Resistencia (-27.45° -58.9833°): FML 07501; **CORRIENTES: Departamento Capital:** Corrientes Capital (-27.482780° -58.851772°): UNNEC 068, 10667; Estancia La Adelita (-27.4808° -58.7416°): UNNEC 13063; Laguna Pampín, Corrientes (-27.483675° -58.745306°): MACN 49165; **Departamento Bella Vista:** Estación Hidrobiológica Bella Vista (-28.453526° -58.984808°): JW 04, 0525; **Departamento Goya:** Goya (-29.133333° -59.25°): MACN 44593-94 (former CENAI 1478 a-b); **Departamento Mburucuyá:** Manantiales (-27.921341° -58.098208°): MACN 14692.

Phalotris lemniscatus (n=11). ARGENTINA: **CÓRDOBA:**

Departamento Calamuchita: Río de los Sauces (-32.53° -64.58°): CZA 112; **CORRIENTES: Departamento Mburucuyá:** Mburucuyá (-28.046251297° -58.2251396179°): UNNEC 05776; **Departamento Paso de los Libres:** Paso

de los Libres (-29.716666° -57.083333°): CENAI 3184; **ENTRE RÍOS: Departamento Colón:** Parque Nacional El Palmar, Jardín de la Portada (-31.853055° -58.3225°): PNP 26; **Departamento Concordia:** INTA El Alambrado, near Concordia (-31.381408° -58.115306°): INALI 1116; Puerto Yerúa (-31.5314° -58.0153°): MACN 44597 (former CENAI 3739); **Departamento Diamante:** Diamante (-32.066666° -60.65°): INALI 4042, 5508; **Departamento Gualeguaychú:** Ñandubaysal beach (-33.066229° -58.389108°): INALI 3986; **Departamento Islas del Ibicuy:** Villa Paranacito (-33.7° -58.683333°): MACN 44590 (former CENAI 2145); **Departamento Paraná:** Paraná (-31.744444° -60.5175°): MACN 7822.

Phalotris reticulatus (n=8). ARGENTINA: **CORRIENTES: Departamento Mercedes:** Rincón del Socorro (-28.55° -57.2166°): UNNEC 10553; **Departamento San Martín:** Colonia Carlos Pellegrini (-28.5333° -57.1666°): UNNEC 10487-88, MLP.R. 5757, MACN 36085, 37824, 38882; La Cruz (-29.1666° -56.6333°): UNNEC 10164.

Phalotris spagazzinii (n=30). ARGENTINA: **BUENOS AIRES:** without specific locality: JW 683, 937; **Ciudad Autónoma de Buenos Aires:** Palermo (-34.575789° -58.424704): MACN 18; **Partido de Bahía Blanca:** Bahía Blanca (-38.7166° -62.2833°): MACN 24794; **Partido de Balcarce:** Sierra La Barrosa (-37.8833° -58.2666°): MACN 30820; **Partido de Chascomús:** Chascomús F.C.S. (-35.570706° -58.015807°): MACN 7063-64, Laguna Vitel (-35.529546° -58.115744°): MACN 5924-25; **Partido de La Plata:** City Bell (-34.8666° -58.05°): JW.0539; La Plata (-34.9313° -57.9488°): MLP 58A, 1886, 3106, JW 938, 953, 1682; **Partido de Magdalena:** 15 km E from Magdalena (-35.145742° -57.414751°): MACN 24795; **Partido de San Miguel:** Bella Vista (-34.576207° -58.698456°): MACN 9485, 10998; **Partido de San Pedro:** San Pedro (-33.674218° -59.661570°): MACN 4560; **Partido de Tandil:** Sierras de Tandil: MACN 11092, 11357-59; **Partido de Tornquist:** Sierra de la Ventana (-38.134288° -61.792563°): MACN 44592 (former CENAI 2935); Tandil

(-37.318889° -59.134722°): MACN 12193-96, 24838.

Phalotris suspectus (n=28). ARGENTINA: without specific locality: JW 943; **BUENOS AIRES: Partido de Coronel Dorrego:** Oriente (-38.7333° -60.6166°): MACN 38881; **Partido de Tornquist:** Parque Provincial Tornquist, Sierra de la Ventana (-38.15° -61.9833°): MACN 32886; **Partido de Villarino:** Salinas "Las Barrancas" Salinas Chicas (-38.604115° -62.769800°): MACN 12897; **CHUBUT: Departamento Rawson:** Ruta Nacional 3, 17 Km N from Trelew (-43.093326° -65.233343°): FML 9324; **CÓRDOBA: Departamento Alta Gracia:** (-31.6666° -64.4333°): MACN 20629; **Departamento Colón:** Salsipuedes (-31.15° -64.3166°): CZA not catalogued; Unquillo (-31.23° -64.32°): CZA 31; **Departamento Punilla:** La Falda (-31.083333° -64.5°): INALI 4021; Tanti (-31.3333° -64.6°): CZA 150-51; **Departamento Santa María:** La Serranita (-31.754125° -64.462009°): MACN 36279; Ave María: CZA not catalogued; Villa Carlos Paz (-31.4357° -64.4991°): CZA 163; **LA PAMPA:** without specific locality: FML 2093 (1-2); **Departamento Capital:** Santa Rosa (-36.620277° -64.290555°): FML 26170; **Departamento Lihué Calel:** Santa María Lihué Calel (-37.995219° -65.610087°): MACN 11236; **RÍO NEGRO: Departamento El Cuy:** 15 Km SE from Chichinales, Valle Azul (-39.162009° -66.772884°): FML 09382; **SALTA: Departamento Metán:** Balderrama, Sierra de Metán (-25.489520° -65.039234°): FML 1044-1,3,5; **SAN LUIS: Departamento Chacabuco:** Villa Elena, in front of Cortaderas, western slope of Comechingones (-32.507075° -64.968790°): MACN 43034; **Departamento Gobernador Dupuy:** Bagual (F.C.N.S.), Escuela N°51 (-35.139145° -65.568143°): MACN 15261; **SANTA FE: Departamento La Capital:** Leyes Stream: INALI 5444; S from Colastiné (-31.698294° -60.606804°): MACN 28781; **Departamento San Martín:** El Trébol (-32.1892° -61.7261°): MACN 44596 (former CENAI 2902); **TUCUMÁN: Departamento Trancas:** Rodeo Grande (-26.484170° -65.549086°): FML 1523.

