



A new vine snake (Reptilia, Colubridae, *Oxybelis*) from Peru and redescription of *O. acuminatus*

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Abstract

The Brown Vine Snake, *Oxybelis aeneus*, was until recently considered a single species, distributed from southern Arizona through the Neotropics into southeastern Brazil. However, newly conducted research restructured the species with a substantial taxonomic revision, recognizing five additional taxa (i.e. *O. koehleri*, *O. microphthalmus*, *O. potosiensis*, *O. rutherfordi*, *O. vittatus*) in this species complex. This revision focused on populations in North America, Central America, and northern South America while neglecting the southern portion of its distribution. Here, we examine the taxonomic history of the complex and use it along with specimen data to resurrect *O. acuminatus* from southeastern Brazil. Finally, we describe a new species from the Peruvian Amazon based on morphological characters. This work increases the species diversity of the *O. aeneus* complex to eight, and we expect further increases in biodiversity discoveries with continued exploration of the New World vine snakes.

Key Words

Amazon, conservation, Inkaterra, morphology, new species, Serpentes, Squamata, South America, systematics, taxonomy

Introduction

Widespread Neotropical snakes with distributions extending from North America to South America, occupy a variety of habitats and often contain unrecognized species diversity. Species such as the *Boa constrictor* (Reynolds and Henderson 2018), *Chironius exoletus* (Hamdan et al. 2017), and the *Oxybelis aeneus* complex (Jadin et al. 2019, 2020) occur in many important biogeographical areas such as the Chacoan, Paraná, Boreal

Brazil, southern Brazil, southeastern Amazonia, Middle America, the Mexican Transition Zone, the Antilles, and the Pacific Coast. These distributions have populations on both sides of many extant biogeographic barriers that impede gene flow in the present day but may not have been isolating populations in the past (e.g. Daza et al. 2009, 2010; Jadin et al. 2012; Bagley and Johnson 2014). Additionally, some of these widespread taxa have complex nomenclatural histories, further challenging any attempts at revision.

The Brown Vine Snake, *Dryinus aeneus* Wagler, 1824, was described from a specimen collected at Ega, Brazil, (now Tefé, Brazil) on the south bank of the Amazon River at its junction with the Rio Tefé (Holotype ZSM 2645/0). Wagler was unaware that the generic name was preoccupied by *Dryinus* Latreille (1804), a Hymenopteran. Fitzinger (1826) used the combination *Dryophis aeneus*. Still, the generic name had been proposed previously by Dalman (1823) for the arboreal Asian snakes now in the genus *Ahaetulla*, but later rejected as invalid by ICZN Opinion 524. Subsequently, Wagler (1830) proposed the generic name *Oxybelis* but it did not gain common usage until the early 20th century.

Bell's (1825) description of *Dryinus auratus* (Fig. 1) on the basis of a specimen said to be from Mexico is likely in error. Günther (1858) reported 14 specimens of *Dryiophis acuminata* in the British Museum. Specimen b in Günther's (1858:156) list is described as "Adult. Brazil? Presented by T. Bell Esq." Keiser (1974) considered this specimen as the holotype of Bell's *D. auratus* and comments that A.G.C. Grandison and L.C. Stuart concurred with him. However, Grandison reported the specimen was no longer in the BMNH collection (Keiser 1974), and the

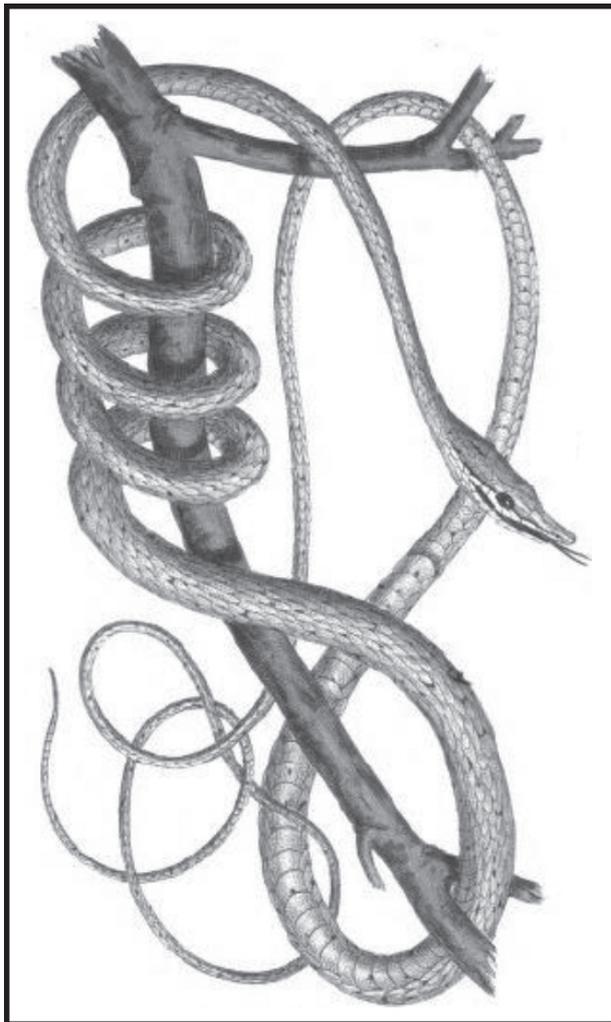


Figure 1. Illustration reproduced from Bell 1825 of *Dryinus auratus* from "Mexico".

lost holotype is supported by Boulenger (1896) who listed all of the BMNH specimens with ventral and subcaudal counts. None of the counts come close to those in the specimen described by Bell. Keiser (1974) raised the issue of collectors not being active in Mexico until later in the 19th century. Smith and Smith (1973) and Flores-Villega et al. (2004) discussed the history of herpetological collections in Mexico. The timing of Bell's publication suggests that if the specimen was from Mexico it most likely would have been collected by the Sessé and Moctino expedition (1788–1803). If the type specimen were indeed from "Mexico" it would share traits with populations described as being either from Western Mexico (*O. microphthalmus*) or Eastern Mexico (*O. potosiensis*). Bell's original description suggests the snout was truncated, ventrals numbered 196, and subcaudals were 160. Jadin et al. (2020) found that populations from Eastern Mexico have a truncated snout but fewer than 190 ventrals and more than 160 subcaudals, though the tail tips of Bell's specimen may have been broken as is often the case in vine snakes. The ventral and subcaudal counts fall within the range of those of *O. microphthalmus*, but those individuals do not have a truncated snout. Therefore, given the missing holotype, the lack of a detailed original description, and a questionable type locality, we are unable to allocate specimens to this name and consequently, we consider this name a *nomen nudum*.

Wied (1824) described *Coluber acuminatus* (Holotype, AMNH 3886, Fig. 2) without reporting a type locality in the original description, though a second paper, Wied (1825:326), reported the specimen collected along the Río Espírito Santo in southeastern Brazil. He also remarks (rough translation) "Some differences notwithstanding it seems to me this snake is identical with Spix's (1824) *Dryinus aeneus*..." Confusion over the publication date of Wied's (1824) paper extended though most of the 19th century (see Keiser, 1974 for a discussion). Schlegel (1837) recognized *D. auratus* and placed Wagler's *D. aeneus* and Wied's *D. acuminatus* as synonyms in error. Duméril et al. (1854) gave Wagler's *D. aeneus* priority over *D. acuminatus* and *D. auratus*. That same year, Girard, 1854, described *Dryophis vittatus* based on USNM 7315 (Fig. 3) with a type locality of Taboga Island, Bay of Panama, Panama. By 1858 Günther had placed *O. aeneus* (Wagler, 1824), *D. auratus* Bell, 1825, and *O. vittatus* (Girard, 1854) in the synonymy of *Dryiophis acuminata*. And, Boulenger (1896), following Cope (1862) used the combination *Oxybelis acuminatus* because of continuing confusion over the publication date of Wied's (1824) paper. Given that the type localities of *O. acuminatus* and *O. aeneus* are separated by 3200 km, it would seem likely that they are separate species.

Barbour and Amaral (1926) described *Oxybelis microphthalmus* based on S. H. Beattie's specimen (MCZ 22417) from Calabasas Canyon, in Santa Cruz County's Pajaritos Mountains of Arizona; writing, "A large *Oxybelis*, similar in habit and coloration to *O. acuminatus* but differing from that species in having a much smaller eye

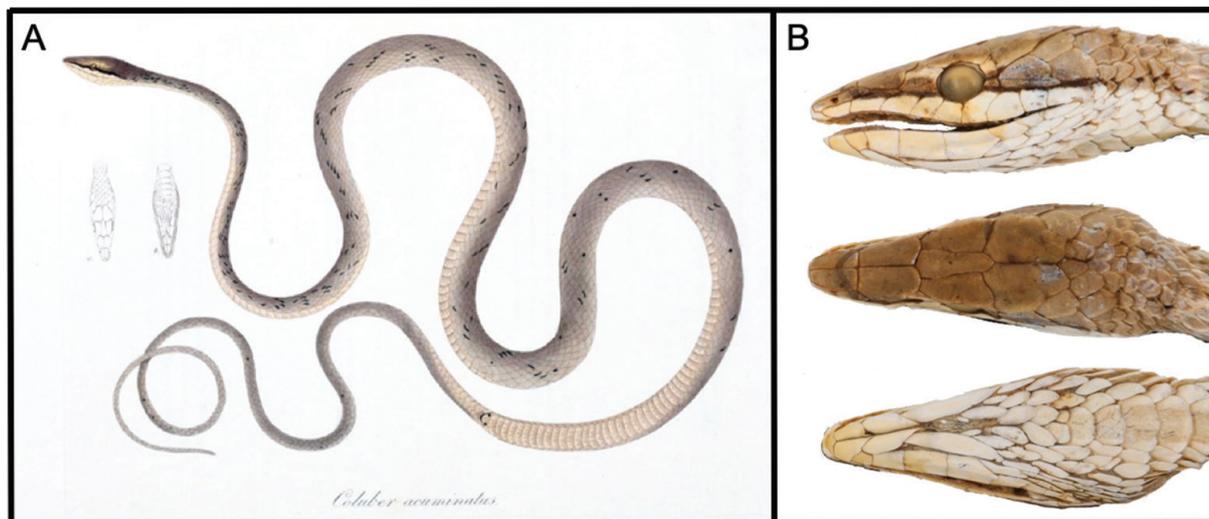


Figure 2. A, Illustration of *Coluber acuminatus* reproduced from Wied 1824. B, Holotype of *O. acuminatus* AMNH 3886.

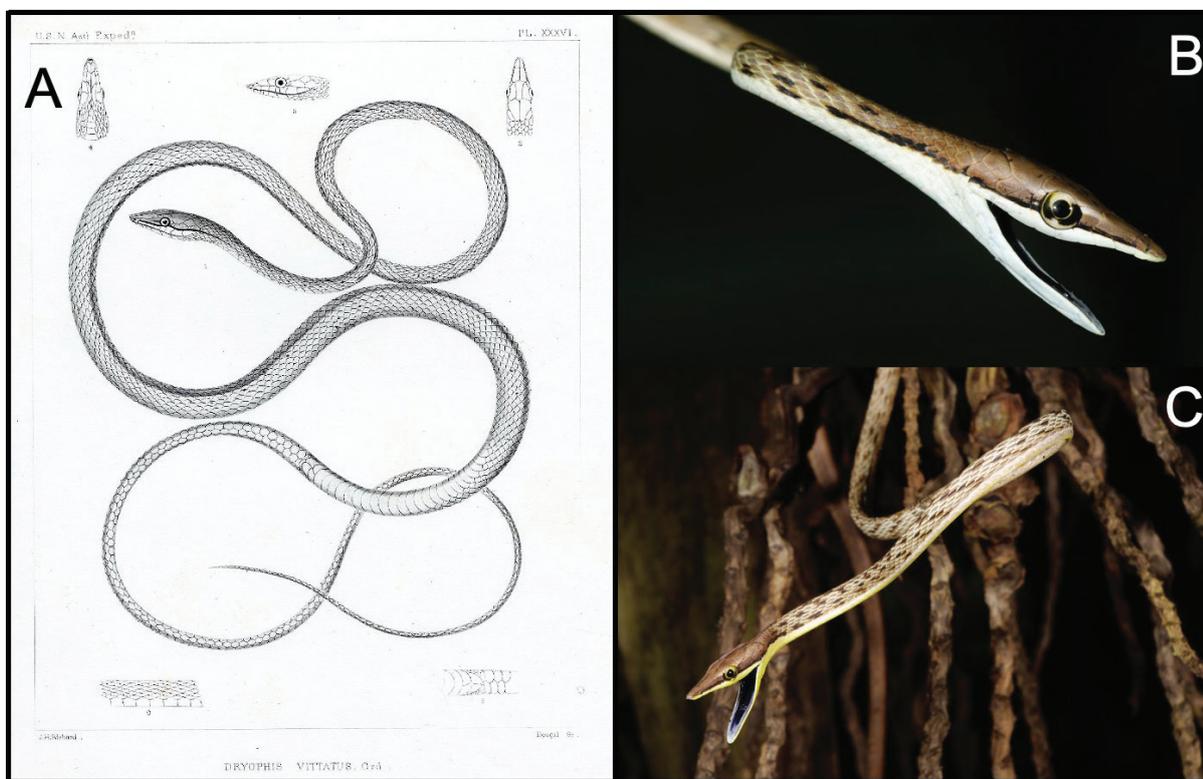


Figure 3. A, Illustration of *Dryophis vittatus* Girard 1854. B and C, in life photographs of *O. vittatus* from Panama (S. Lotzkat).

and a much longer and differently shaped snout.” More recently, *Oxybelis potosiensis* was described by Taylor (1941), which has a type locality near Ciudad Maíz, San Luis Potosí, México (Holotype UIMNH 25069). Bogert and Oliver (1945) examined several characters found in the *O. aeneus* complex. They concluded recognizing two populations of *O. aeneus*: *O. a. aeneus* with a range extending from Guatemala to southeastern Brazil, and *O. a. auratus* with a range from southern Arizona, in the northwest of its distribution, and from San Luis Potosi at the northeast, southward to the Isthmus of Tehuantepec and the Yucatan Peninsula, thus synonymizing *O. micro-*

phthalmus Barbour & Amaral, 1926 and *O. potosiensis* Taylor, 1941 into *O. a. auratus*.

Recently, Jadin et al. (2019) conducted the first significant phylogenetic study on *Oxybelis* and found strong support that *O. aeneus sensu lato* was a complex of species in drastic need of revision. Their work identified four novel taxa even as their dataset was restricted to populations in the northern part of the species’ distribution (i.e. Arizona, USA to Venezuela). However, they refrained from recognizing any additional species until morphological data could be included. Subsequently, Jadin et al. (2020) examined these populations to

include morphology and more molecular data and removed *O. microphthalmus*, *O. potosiensis*, and *O. vittatus* from the synonymy of *O. aeneus*. Furthermore, Jadin et al. (2020) described *O. koehleri* from populations in Central America and *O. rutherfordi* from northern South America. They suggested that many more species would likely result from further investigation. Here, we inspect the clade further and resurrect *O. acuminatus* as a valid taxon from the Atlantic Coastal Forest of southeastern Brazil and describe a new species of *Oxybelis* from the Peruvian Amazon.

Materials and methods

Morphological data

Alcohol-preserved specimens of *Oxybelis aeneus sensu lato* from throughout its range were examined at the Field Museum of Natural History and the University of Wisconsin – Stevens Point Museum of Natural History (Appendix 1). Scale counts generally follow Peters (1964) with minor exceptions. Dorsal scales were counted on the diagonal, approximately ten ventral scales from the head, at mid-body, and approximately ten ventral scales anterior to the vent. Scale counts and scale measurements were conducted using a Leica S8 APO dissection microscope. Larger body measurements were taken with a meter stick, metric tape, and/or dial calipers. Scale counts representing a range taken from different individuals are separated by a dash (–). Scale counts separated by a slash (/) are taken from a single individual, with the number on the left representing scale numbers on the snake’s left and the number on the right representing scale numbers on the snake’s right. Ventral counts follow Dowling (1951). Photographs of scale arrangements were taken with a Canon EOS cameras and macro lenses. Sex was determined by probing, tail shape, and/or visual inspection of the hemipenes, testes, and/or ovaries. Coloration in life of the holotype is based on field notes and photos taken by WED.

To determine the distinctiveness of our Peruvian specimens and *O. acuminatus* within the *Oxybelis aeneus* complex we conducted a principal component analysis (PCA). We lumped our examined specimens into groups representing these two groups and the distinct species identified in Jadin et al. (2020). Our principal components analysis was conducted using DataLab Version 3.911 (Epina GmbH, Pressbaum, Austria) software and the following twelve morphological characters: (1) second upper labial at preocular, (2) underside of head black pigmented, (3) orange pigment on labials, (3) eye diameter greater than preocular, (4) second pair of chin shields separated (5) supraocular longer than prefrontals (6) number of upper labials post orbit, (7) number of upper labials on one side, (8) head width/head length, (9) number of upper labials in orbit, (10) eye diameter/ prefrontal (11) eye diameter divided by internasal length, (12) eye-nostril distance/ head length.

Results

Our morphological analyses suggest distinctiveness among members of the *Oxybelis aeneus* complex, including *O. acuminatus* and specimens from Peru (Table 1). More specifically, our PCA produced five distinct groups: (1) *O. rutherfordi*, (2) *O. vittatus* and Peru, (3) *O. aeneus*, (4) *O. potosiensis*, and (5) *O. acuminatus*, *O. koehleri*, and *O. microphthalmus* (Fig. 4).

Oxybelis inkaterra sp. nov.

<http://zoobank.org/CC9C2A2E-8173-4F34-AC47-948543262969>

Figs 5–9

Suggested English Name: Inkaterra Vine Snake

Suggested Spanish Name: Inkaterra Serpiente de vid

Oxybelis aeneus – Keiser, 1974:7;

Duellman 2005: 363, pl 205 has a photograph of a live specimen

Jadin et al. 2020: Fig 1. has a photograph of a live specimen.

Holotype. KU 220196 (Figs 5, 6), from Peru, Madre de Dios: Cusco Amazónico (now Reserva Amazónica), Río Madre de Dios, c. 15 km E Puerto Maldonado, 200 m, 12°34'59"S, 69°4'59"W; collected by William E. Duellman (WED 59561), 21 December 1991.

Paratypes. KU 214887, Peru, Madre de Dios: Cusco Amazónico, Río Madre de Dios, c. 15 km E Puerto Maldonado, 200 m, 12°34'59.88"S, 69°4'59.879"W; collected by Erik R. Wild (Field number WED 59004), 23 December 1989; ZMH R01702, Peru, Huánuco: Pachitea, Panguana Biological Fieldstation, Río Yuyapichis [= Río Llullapichis], 260 m, approx. 9°41'S, 74°57'W, collected by János Regös July 1980.

Other material examined. FMNH 56141, from Peru, Loreto, Río Ucayali: Yarinacocha (c. 13°51'S, 71°1'W), collected by J.M. Schunke, 05 Sep 1946. FMNH 40085 (female), from the Madre de Dios area of Peru (no specific locality). ZMH R01611, Peru, Huánuco: Pachitea, Panguana Biological Fieldstation, Río Yuyapichis [= Río Llullapichis], 260 m, approx. 9°35'S, 74°56'W, collected by Carlos Vasquez Modena 1980.

Like other members of the *Oxybelis aeneus* complex *O. inkaterra* has an elongated head and body, 8–9 upper labials, four lower labials contacting the first pair of chin shields, 173–205 ventrals and 158–203 subcaudals; a divided anal plate, dorsal scales in 17–17–13 rows, and undivided hemipenes.

Diagnosis. A vine snake with (1) three upper labials (4–5–6) bordering the orbit; (2) numerous bold black bars and spots present on the body; (3) ventral surface mottled with dense black spots; (4) preocular shorter than eye diameter; (5) second pair of chin shields separated by smaller scales posteriorly; (6) nine upper labials, three located behind the orbit; (7) snout from above relatively broad, tapered, and flat rostrum; (8) supraocular and prefrontal are about the same length; (9) last upper labi-

Table 1. A morphological comparison of the eight species in the *Oxybelis aeneus* complex.

	<i>Oxybelis acuminatus</i>	<i>O. aeneus</i>	<i>O. inkaterra</i> sp. nov.	<i>O. koehleri</i>	<i>O. microphthalmus</i>	<i>O. potosiensis</i>	<i>O. rutherfordi</i>	<i>O. vittatus</i>
Upper labials in orbit	3 (4-5-6)	3 (4-5-6)	3 (4-5-6)	3 (4-5-6)	3 (4-5-6)	2 (4-5) or (5-6)	2 (4-5)	3 (4-5-6)
Stripes on venter	Indistinct	No	No	Variable	Variable	Variable	Yes	Yes
Preocular shorter than eye diameter	Yes	Yes	Yes	Yes	no	Yes	Yes	Yes
Posterior border of internasals extends beyond posterior edge of first upper labial	Yes	Yes	No	Yes	Yes	Yes	No	No
Chin heavily mottled	No	No	Yes	Yes, in females	No	No	No	No
Supraocular longer than prefrontal	Yes	No, equal in length	No, equal in length	No, equal in length	Yes	Yes	Yes	Yes
Second upper labial contacts preocular	Yes	No	No	No	No	No	No	No
Second pair of chin shields contacting each other	No	No	No	Yes	Yes	Yes	Yes	Yes
Number of lower labials contacting first pair of chin shields	5	4	4	4	4	4	4	4

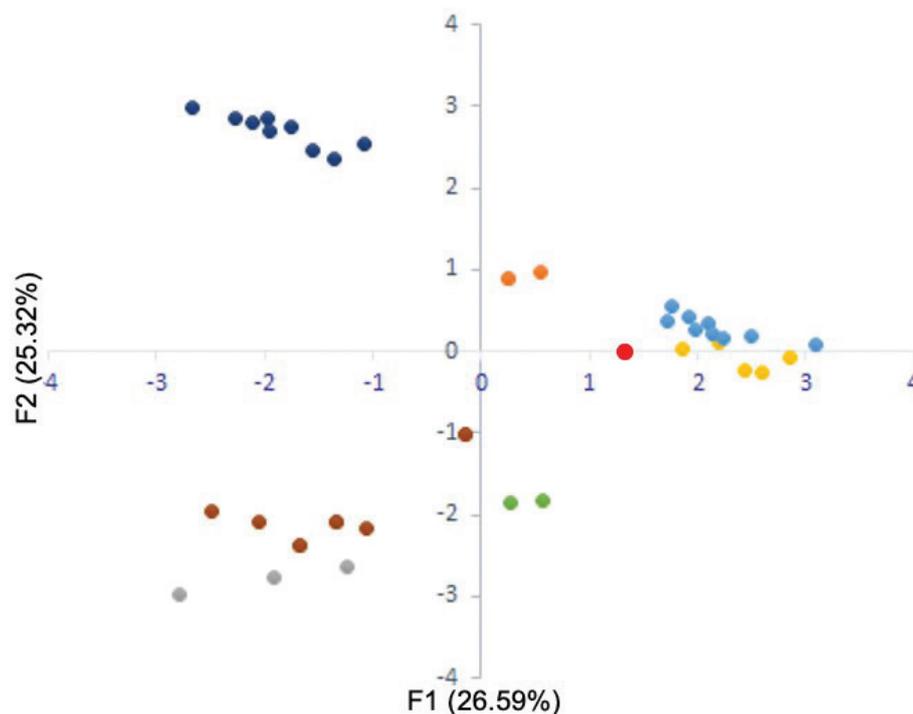


Figure 4. Plot of PC-1 and PC-2 scores extracted from a Principle Components Analysis of twelve morphological characters, showing distinct clustering among geographically defined groups. Circular symbols represent *Oxybelis acuminatus* (red), *O. aeneus* (orange), *O. koehleri* (yellow), *O. microphthalmus* (light blue), *O. potosiensis* (green), *O. rutherfordi* (dark blue), *O. vittatus* (brown), and Peruvian specimens (gray).

al about same length as primary temporal; (10) much of the lower surface of the head infused with black pigment; (11) second upper labial not in contact with preocular.

Comparison. *Oxybelis inkaterra* can be distinguished from the seven other members of the *Oxybelis aeneus* complex by the presence of, upper labials three and four are in contact the preocular; a head with an irregular, darkly pigmented ventral surface with pale spots; and eyespot markings on the posterior ventral surface of the body and tail; the snout of *O. inkaterra* is also relatively short and broad compared to other species in the *Oxybelis aeneus* complex (Fig. 7); the lack the brown-gray dorsal coloration seen in the other members of the complex. The dorsum is instead a dirty cream with black flecking (Figs 6, 8).

Description of the holotype. A male with everted hemipenes (Fig. 6), SVL 732 mm, tail length 498 mm.

Rostral broader than high, barely visible from above; upper labials 9/9; internasals paired, not extending past the posterior border of the first upper labial; prefrontals paired, in contact with upper labials 2 and 3; frontal, paired parietals, and supraoculars elongated and about 6 mm long, and in contact with supraoculars and upper postocular; postoculars 2/2; upper labials in contact with the preocular; 4–5–6 enter the orbit; 7–8–9 contact the primary temporal; 9 interriectals; one preocular less than the diameter of the eye; lower labials 10/10, first four in contact with the first pair of chin shields; second pair of chin shields longest; five paired gulars. Dorsal scales smooth in 17–17–13 rows. Ventrals 182; 165 divided subcaudals; anal plate divided.

In alcohol. Top of the head is brown with dark brown to black mottling (Figs 7, 8); black spot on posterior

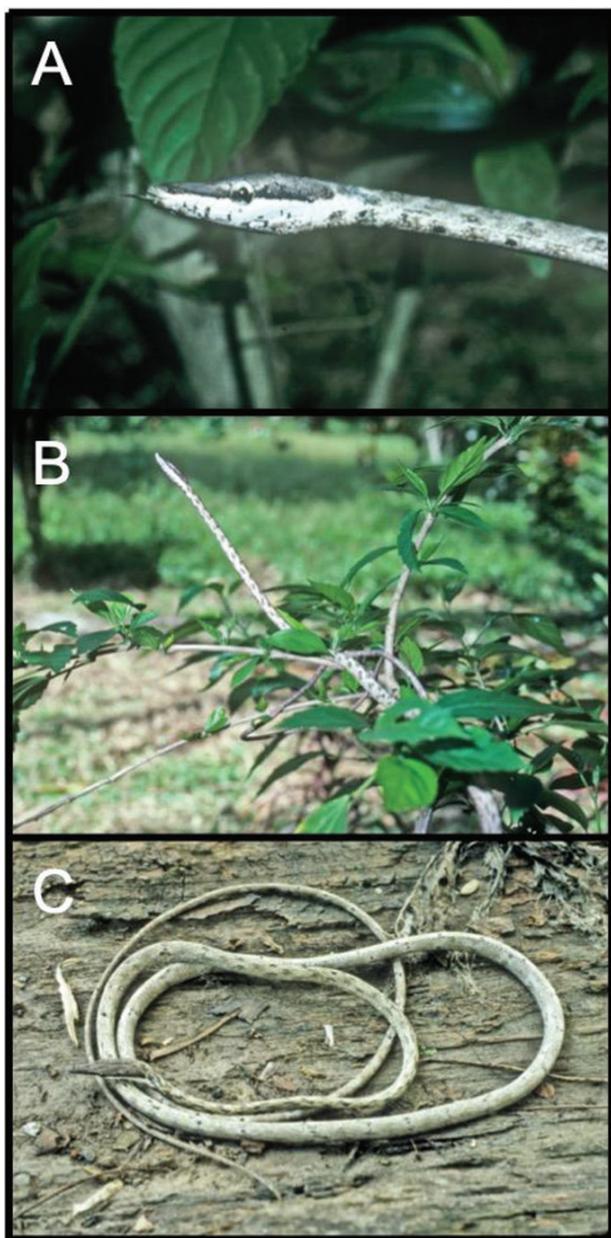


Figure 5. Holotype of *Oxybelis inkaterra* sp. nov., KU 220196 in life from Reserva Amazonica, formerly Cusco Amazonico, Peru (W.E. Duellman).

edge of nasal, and on preocular; black mottling on temporals forming an irregular postocular stripe that extends to second or third ventral; upper labials with mottling on borders, lower labials heavily mottled; mental, first pair of lower labials, and chin shields black with white spots; dorsal scales mottled with black and brown pigment in all rows; on anterior third of the body, some scales have heavy black pigment on their borders and form about 48 irregular transverse bands; anterior ventrals heavily mottled becoming fine stippling posteriorly; some ventrals mottled with scattered black spots anteriorly; posteriorly, these spots encircled with white pigment to form eye spot-like markings near the vent; some of these markings also occur on the ventral and lateral portions of the tail.

Coloration of the holotype in life (Fig. 5). Field notes by W.E. Duellman on 21 December 1991: Dorsum and venter grayish tan with dark brown flecks and streaks. Top of head brown; lateral stripe on head dark brown, bordered below by white. Iris cream with horizontal dark brown stripe. Lining of mouth and throat black.

Variation. Whereas surrounding the black spots was not as pronounced in smaller individuals, KU 220196 has the first 33 ventral scales almost completely black (in preservative), but the stripes are still visible (Fig. 6). The black pigment extends onto the chin shields in varying amounts. The largest female was 1075 mm in total length; the largest male was 1278 mm. Two females had SVLs of 484 and 660 mm ($\bar{x} = 572$ mm SD = 88.0) with tails that were 0.62 and 0.63 of the SVL ($\bar{x} = 358.5$, SD = 56.50). Two females (FMNH 40085, 56141) (had 184 and 191 ventrals ($\bar{x} = 187.5$, SD = 1.5). Eight upper labials, with 4–5–6 bordering the orbit. Usually 8–9 (nine on one side) lower labials, with four (usually) at first chin shield.

Distribution. This species occurs in the Amazonian rainforest of Peru in the departments of Huánuco, Loreto, and Madre de Dios. It is likely the species also occurs in Ucayali between these departments and possibly adjacent Bolivia, Brazil, and Colombia.

Ecology. At Reserva Amazónica, *Oxybelis inkaterra* is found in the dense vegetation on the bank of the Río Madre de Dios and in an adjacent clearing. The steep riverbank has vegetation unlike that of the adjacent rainforest. There are shrubby plants and no canopy; adjacent to the river are stands of the cane-like *Gynerium sagittatum* (Ponaceae). *Oxybelis inkaterra* is a diurnal arboreal snake, which, if like other members of the genus, has a fondness for small lizards. In the scrub forest adjacent to the river two species, *Gonatodes humeralis* (Sphaerodactylidae) and *Anolis fuscoauratus* (Dactyloidae), inhabit the scrub and probably are primary prey of the vine snake.

Field notes. KU 220196, weight 30.5 g, caught on the ground in camp during the day. Dorsum and venter grayish tan with dark brown flecks and streaks. Top of head brown; lateral stripe on head dark brown, bordered below by white. Iris cream with horizontal dark brown stripe. Lining of mouth and throat black. KU 214887, caught in bush 1.5 m above ground by day edge of river in camp. Mass 15 g, 895 mm TL.

Etymology. The specific epithet honors the ecotourism company Inkaterra (<https://www.inkaterra.com/>) and its non-profit NGO counterpart Inkaterra Asociación. These two institutions started in 1975 and 1978, respectively, were founded by José E. Koechlin von Stein to promote education and conservation of Peruvian culture and ecosystems. Inkaterra and Mr. Koechlin have been recognized numerous times with awards and accolades for providing sustainable ecotourism and research opportunities for scientists. The type locality, Cusco Amazónico (now Reserva Amazónica), is owned and operated by Inkaterra and is the site of one of the most thoroughly studied areas in the Neotropics, particularly for amphib-



Figure 6. Holotype of *Oxybelis inkaterra* sp. nov., KU 220196 preserved. **A**, Dorsal whole specimen; **B**, ventral whole specimen views; **C**, top of the head; **D**, profile. Scale bar: 1 cm.



Figure 7. A comparison between the snout shapes of *Oxybelis aeneus* (FMNH 64417) (top) and *O. inkaterra* (FMNH 56141) (bottom) (JCM).

ian and reptile natural history (e.g. Duellman, 2005; Orlofske et al. 2012).

Notes on potential eyespots. Anti-predator adaptations in snakes are numerous and diurnal species can be expect-

ed to use visual coloration and behaviors to deter predators (Green, 1997). Eyespots are circular markings, often with concentric rings and conspicuous colors, that occur in many animals. They have been hypothesized to work as a

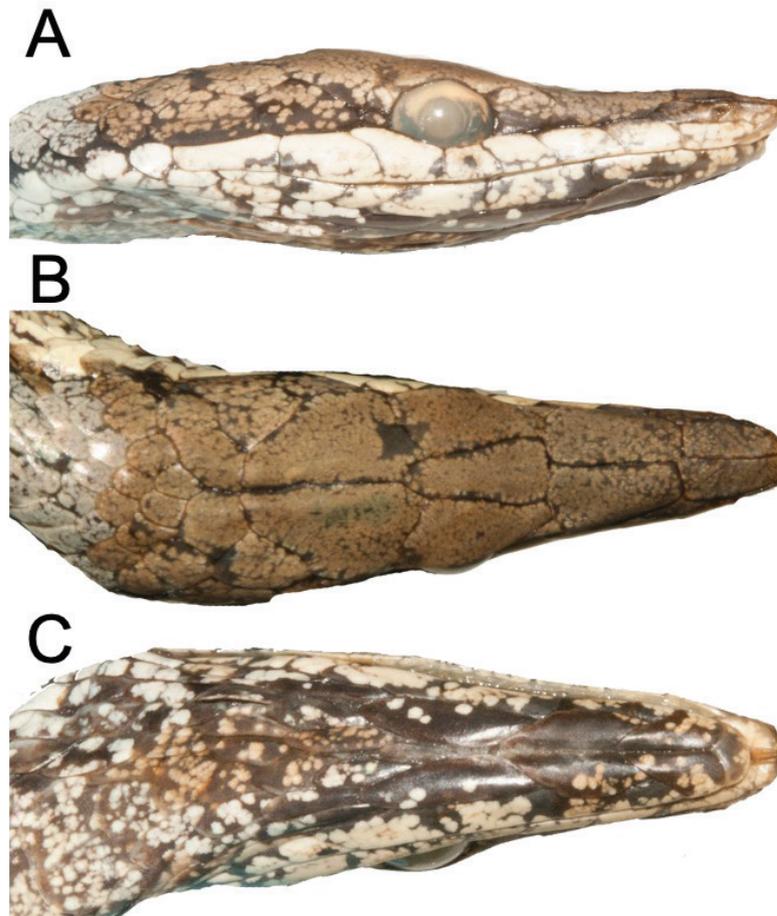


Figure 8. Referred specimen of *Oxybelis inkaterra* sp. nov., FMNH 56141 from Peru, Loreto, Rio Ucayali, Yarinacocha. **A**, profile; **B**, top of the head; **C**, bottom of the head.



Figure 9. Referred specimen of *Oxybelis inkaterra* sp. nov., FMNH 56141 displaying eyespots on posterior ventral scales (left) and on subcaudal scales (right).

way to startle or intimidate predators or they may work by being highly salient stimuli that promote sensory overload, biases, or neophobic reactions (Stevens and Ruxton 2014). Few snakes have been reported to have eyespots but *Oxybelis inkaterra* appears to be an exception and does exhibit ventral eyespots (Fig. 9). Although the markings are quite variable in size and definition, they are best developed in specimen FMNH 56141 from Yarinacocha, Peru. Given the absence of information in terms of how the snake uses these markings it is entirely possible that they simply make the snake more cryptic in its arboreal environment. However, the placement of the eyespots on the posterior ventral side of the body and on the tail suggests that they may be displayed in response to a predator.

Oxybelis acuminatus (Wied, 1824)

Atlantic Forest Vine Snake

Coluber acuminatus – Wied, in Anonymous, 1824: 667. Holotype AMNH 3886. The type locality Rio Espirito Santo, in southeastern Brazil (~19°2'S, 40°43'W). Note that the name *Coluber acuminatus* was published in June of 1824, and it was long given priority over Wagler's *Dryinus aeneus* 1824, which was published in March of 1824, see Keiser (1974:4).

Oxybelis aeneus aeneus – Bogert & Oliver, 1945: 391. Bogert and Oliver (1945) reported on the type specimen, a female that is 1255 mm in total length with a 444 mm incomplete tail; the dorsal scales are in 17–17–15 rows; it has 197 ventral scales and 144 subcaudal scales but the tail tip is missing; the upper labials are 8/9, the fourth and fifth border the orbit on the right side, and upper labials 4–5–6 border the orbit on the left side; lower labials are 8/8; the preocular is single on both sides and two postoculars occur on each side; head width is 9.4 mm and the length is 23.8 (hl/w ratio is 2.53); eye diameter is 4.4 mm and the internasal is 4.6 mm (0.95 eye diameter/internasal ratio).

Diagnosis. A vine snake with (1) three upper labials (4–5–6) bordering the orbit on the left; (2) black bars or spots present on the anterior body; (3) indistinct stripe on the outer edges of ventral scales, venter finely mottled; (4) eye diameter greater than preocular length; (5) second pair of chin shields separated by smaller scales for most of their length; (6) nine upper labials, three located behind the orbit; (7) snout from above relatively broad, slightly tapered, and flat at rostrum; (8) supraocular longer than prefrontals; (9) last upper labial longer than primary temporal; (10) lower surface of head uniform in color; (11) second upper labial in contact with preocular (this character state appears to occur only in this taxa).

Comparison. *Oxybelis acuminatus* can be distinguished from all other members in the *O. aeneus* complex by having their second upper labial contacting their preocular (Fig. 2B); all other species have the third upper labial contacting the preocular (Table 1). Five lower labials are contacting the chin shields, a character state occasionally seen in *O. rutherfordi* from northern South America and *O. vittatus* from Panama. Posteriorly the

lower dorsum and ventral surface of the body and the tail have scattered small black spots. Keiser (1974) reported 17–20 maxillary teeth in specimens from southeastern Brazil. These traits and its presence in Brazil's Atlantic Forest, a center for endemism, revalidate this species.

Distribution. This species is likely restricted to the Atlantic Forest of southeastern Brazil.

Discussion

Biodiversity

Although our PCA analysis did not distinguish *O. acuminatus* or *O. inkaterra* from all other species of the *O. aeneus* complex, this not surprising given the large number of species in the analysis and the depauperate morphologically distinguishing characters available due to the cryptic nature of this species complex. Furthermore, the analysis placed these two species near Middle American taxa not likely to be the most closely related species based on geography. Therefore, we consider this analysis valuable in distinguishing them from other South American taxa and utilize additional morphological features to clearly distinguish all taxa from each other (see taxonomic descriptions above and Table 1).

Molecular techniques combined with morphological analyses are increasing the number of recognized squamate species. Uetz et al. (2020) reported 3,149 species of snakes in 2008 and 3,848 species in 2020: a difference of 699 species (>22%) in a span of 12 years. With the addition of these two South American species, we increase the known species diversity of the *Oxybelis aeneus* complex to eight. This is likely a continued underestimate of species diversity within *Oxybelis*. For example, we have seen members of the *O. aeneus* complex from the west side of the Andes with a pair of well-defined stripes on the venter that are lacking in specimens from the east side of the Andes. In addition, recent work on the phylogeography of *Oxybelis* (Jadin et al. 2020) recovered *O. fulgidus* from French Guiana and Venezuela paraphyletic to the Honduras and Mexico populations. Novel sampling and examination of present museum material of *Oxybelis* populations, especially in South America, is needed and further work with this genus should yield additional improvements to our understanding of the diversity and evolutionary history of *Oxybelis*.

Biogeography

Peru is a biodiversity hotspot (Myers et al. 2000) with a staggering 506 reptiles, of which 231 are snakes (Uetz et al. 2020). Its notable richness is further evidenced by ongoing discoveries of new reptile genera (Moravec et al. 2018; Lehr et al. 2019, 2020), which raises questions about the number of still undescribed species in the country. For example, Moravec et al.'s (2018) work on

the systematics of microteiid lizards found 19 unnamed lineages at the level of species in the *Cercosaurinae*, a reminder of how little is known about some reptile groups in the region. A total of 38 species of snakes representing 13 genera are endemic to Peru and the new description of *Oxybelis inkaterra* places it as a new Peruvian endemic, at least temporarily, raising the total number of endemic snake species to 39 and 14 genera in the country.

The presence of an endemic *Oxybelis* in Peru is noteworthy and may help elucidate how diverse ecological factors may drive regional patterns of species divergence and speciation (Card et al. 2016). Jadin et al. (2019) found a Mid-Miocene (14.5 Ma) divergence between the green colored clade composed by *O. fulgidus* (from Mexico and Guatemala) and *O. wilsoni* from (Roatán Island, Honduras) and the brown colored clade with all other remaining *Oxybelis* included in their analyses. Their divergence time and ancestral area estimates suggest a Central American origin of the *O. aeneus* clade and its invasion of South America when the Panamanian isthmus closed, approximately 2.8 Ma. The presence of *Oxybelis* in cis-Andean regions suggests that the Central and Eastern Cordillera of Colombia already uplifted after the timing of the Panamanian isthmus (Gregory-Wodzicki, 2000; Javadi et al. 2011; Murphy et al. 2017), and were not a deterrent to dispersal from west to east. In congruence, *Oxybelis* species are widespread and found at high elevations in mountainous regions, suggesting that mountain topography should not impose geographical barriers. In addition, the presence of trans-Andean *Oxybelis* is intriguing, which again indicates that *Oxybelis* species are efficient at crossing high altitude barriers. In favor of this scenario, Rojas-Morales (2012) has provided the example of a forest-dwelling dipsadid snake in the genus *Rhinobothryum* that crossed the Andes from west to east and speciated in the Amazon basin.

Conservation

Approximately 12% of snakes are estimated to be threatened with extinction (Böhm et al. 2013). However, this is likely a considerable underestimate as it is well known that detecting snakes for scientific study is incredibly difficult due to their secretive habits and crypticity, resulting in many, if not most, as Data Deficient. When we initiated this project (see Jadin et al. 2019, 2020), the accepted hypothesis was that *Oxybelis aeneus* was a single, widespread species that was “well known” in museum collections and also understood from a few scattered field studies (i.e. Henderson 1974; Van Devender et al. 1994; Mesquita et al. 2012). With our addition of molecular and morphological analyses we revealed that this “species” is at least eight distinct species and while we recognize their existence, they likely are all Data Deficient. Thus, the number of Data Deficient species grows faster than the number of species that can be classified as a species of Least Concern or Vulnerable.

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Appendix 1

Specimens examined

Museum acronyms follow Sabaj (2019).

- Oxybelis aeneus* – (n = 8) Brazil: FMNH 64417 Amazonas; FMNH 19203 Pará; KU R-124605, 124606, 140173, MCZ R-2582, 2778, and 53211 Pará.
- O. brevirostris* – (n = 2) Ecuador: UTA R-55952-53 Canton San Lorenzo: Parroquia Santa Rita, Esmeraldas.
- O. inkaterra* – (n = 6) Peru: FMNH 40085, Madre de Dios; FMNH 56141, Loreto, Rio Ucayali: Yarinacocha; KU R-214887 & R-220196 Madre de Dios, Cuzco Amazonico, 15 km E Puerto Maldonado; ZMH R01702 & R01611, Huánuco, Panguana Biological Station, Rio Yuyapichis [= Rio Lullapichis], Pachitea.
- O. koehleri* – (n = 34) Costa Rica: FMNH 179061 Cartago, Turrialba; El Salvador: FMNH 10997 Chalatenango; San Jose del Sacare, 3600'; FMNH 10998 Morazán, Divisadero; FMNH 64955, La Libertad, Volcan San Salvador, 1917 Lava, 500 m; FMNH 64956 La Paz, Los Blancos; KU 289907 Usulután: Isla San Sebastian; Guatemala: FMNH 20088 Izabal: Bobos Plantation, near Playitas; FMNH 20171 and 20418 Sololá: Olas de Moca; UTA R-46795 Chiguimula; UTA R-45880 Huehuetenango; UTA R-22182–83, 33,040, 33,042, 37,256, 39,236, 42,433 Izabal; UTA R-37258 Peten; UTA R-46846 Zapaca, El Arenal; Honduras: FMNH 22231 Tela; FMNH 27050 San Pedro Sula; FMNH 34565, 34571, 34574, 34576, Bay Islands: Roatan, near Coxen Hole; UTA R-55231 Bay Islands: Roatan; FMNH 34770 Yoro, Portillo Grande; FMNH 40872 Gracias; UTA R-46865 Comayagua, Playitos: Aldea “Lo de Reina,” 785 m; UTA R-53176–78 Honduras: Gracias a Dios, Mocorón, 30–50 m. Nicaragua: UTA R-44838 Jinotega, El Paraíso Km 152.5, carretera Jinotega-Matagalpa, 1490 m.
- O. microphthalmus* – (n = 36) USA: Arizona: UAZ 47314 2.8 mi west of Sycamore Canyon; UAZ 519,225 miles east Sycamore Canyon, Ruby Rd.; UAZ 39544 Patagonia Mts.; Santa Cruz County: ASU 33314, ASU 33364, ASU 35069, ASU 35563, UAZ 16787, UAZ 39545; no specific locality: UMMZ 75779. Mexico: Colima: UTA R-57658; Guerrero UAZ 106056, 106058, 38448, 38451, 38455, 38461, 38467, 106051, 106057, 106059, 106054; Oaxaca: UAZ 106055, 117841–43, 178707, 178708; Sonora: UAZ 26972 0.5 miles West Alamos; UAZ 28279 8.8 miles east Alamos; Alamos UAZ 16797, UAZ 26973, ASU 06735, ASU 68990, ASU 88990; 35 miles east of Cannansa junction w/ Aqua Prieta Rd. UAZ 16796.
- O. potosiensis* – (n = 6) Mexico: UIMNH 25069 San Luis Potosí; UTA R-6107–10, 8752, and 12,368 S of Zapotitl, Puebla; UTA R-9014 6.0 mi E San Rafael, road to Rancho Nuevo, Tamaulipas.
- O. rutherfordi* – (n = 20) Tobago: FMNH 251213 Bloody Bay Rd., between Roxborough and Bloody Bay; Trinidad: FMNH 49973 no specific locality; FMNH 49974–75 Brickfield; FMNH 49976 Mount Harris, FMNH 49977–85 San Rafael; FMNH 215838 circa 3 miles S Simla-Quarry Rd., on Arima-Blanchisseuse Rd., egg farm; FMNH 215839 circa 2 miles S Simla-Quarry Rd., on Arima-Blanchisseuse Rd.; UTA R-64851 Arima Valley, William Beebe Tropical Research Centre, c. 6 km N Arima, 247 m; Venezuela: FMNH 17839–40 Puerto Viejo, Península de Paria, Sucre; MBLUZ 1268 between San Francisco de Macanao and Cerro Los Cedros, Isla de Margarita, Nueva Esparta.
- O. vittatus* – (n = 16) Panama: FMNH 152067 Almirante; FMNH 83552, 130674, 131314 Canal Zone: Summit; FMNH 161478 Canal Zone: Barro Colorado Island; FMNH 153665 Coiba Island; FMNH 170132 San Blas Territory: Soskantupu, 8°57'N, 77°44'W, 1 m; FMNH 154043 Bocas del Toro, 11 km NW Almirante 600 ft.; FMNH 154478, 154517 no locality data; MCZ R-22274, 22231, and 25118 Canal Zone; UF 65037, 65038, and 170469 Canal Zone.