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Not withering on the evolutionary vine: Systematic revision of the Brown Vine Snake (Reptilia: Squamata: Oxybelis) from its northern distribution

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1 **Not withering on the evolutionary vine: Systematic revision of the Brown Vine Snake**
2 **(Reptilia: Squamata: *Oxybelis*) from its northern distribution**

3

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25 **Running title** Systematic revision of the Brown Vine Snake

26 **Abstract**

27 The genus *Oxybelis* currently is composed of four taxa despite numerous studies suggesting and
28 describing multiple taxa within the *O. aeneus* complex. Here, we utilize a multilocus molecular
29 dataset (i.e. *cyt b*, ND4, 12S, 16S, *cmos*, PRLR, 3663 bp) to conduct phylogenetic analyses to
30 assess the evolutionary history of *Oxybelis*. Our molecular analyses find three major lineages of
31 *Oxybelis* (i.e. *O. aeneus* complex, *O. brevirostris*, *O. fulgidus* complex) with a sister relationship
32 between *O. brevirostris* and the *O. aeneus* complex to the exclusion of the *O. fulgidus* complex.
33 More specifically, *O. aeneus* appears to harbor at least five taxa currently unrecognized while *O.*
34 *fulgidus* was found to be paraphyletic with respect to *O. wilsoni*, suggesting cryptic diversity and
35 novel taxa in that clade as well. Additionally, we use morphological data in concert with our
36 molecular analyses and the literature to support removing *Oxybelis microphthalmus* Barbour and
37 Amaral, 1926, *Oxybelis potosiensis* Taylor, 1941, and *Dryophis vittatus* Girard, 1854 from the
38 synonymy of *O. aeneus*. Finally, we describe two new species from Central and northern South
39 America.

40

41 **Keywords** Bayesian analysis – biodiversity – cryptic species – Serpentes – species delineation –
42 taxonomy

43

44 **Introduction**

45 Arboreal lifestyles in snakes have evolved in numerous clades and some arboreal lineages have
46 exploded into radiations that exploit numerous niches in the forest canopies of Asia (e.g.
47 *Ahaetulla*), Africa (e.g. *Thelotornis*), and the New World (e.g. *Oxybelis*). Species with extremely
48 attenuated, slender bodies, an elongated head, large eyes capable of binocular vision, a long tail,
49 and diurnal behaviour collectively are often called “vine snakes”. This ecomorph exploits the
50 smallest branches in the canopy, their low mass-to-length ratio allowing them to cantilever, or
51 bridge, distances between branches that pass 50% of their body length to reach prey, often
52 lizards (Henderson 1980; Ray 2012). Additionally, the ability to move from tree to tree instead
53 of descending to the ground to climb again likely saves energy (Ray 2012).

54 The colubrid genus *Oxybelis* currently contains four species of vine snakes, all of which have
55 populations in Central America (Köhler 2008; Uetz et al. 2018). *Oxybelis brevirostris* (Cope
56 1861) and *O. fulgidus* (Daudin 1803) occur in Central and northern South America, while *O.*
57 *wilsoni* Villa and McCranie, 1995 is known only from Isla de Roatán, a Caribbean island located
58 48 km from Honduras mainland (McCranie et al. 2005). On the other hand, the Brown Vine
59 Snake, *O. aeneus* (Wagler, 1824), is found at low and high elevational ranges and throughout
60 contrasting habitats, from semi-desert to tropical rainforest (Keiser 1982; Van Devender et al.
61 1994). *Oxybelis aeneus* exhibits a vast distributional range, and it is one of the most widespread
62 species of terrestrial snakes worldwide, ranging from southern USA to southeastern Brazil. The
63 colonization capability of *O. aeneus* (*sensu* Keiser 1974) becomes apparent by its presence
64 throughout the mainland and on various islands. More specifically, the species occurs on both
65 coasts of Mexico and Central America; the island populations in Central America are known
66 from the Tres Márias Island (Nayarit, Mexico), Isla de la Blanca (Quintana Roo, Mexico), Islas

67 de la Bahía (Honduras), Los Blancos Islands (El Salvador), Corn Islands (Nicaragua), and the
68 Pearl islands and Coiba (Panama). In South America it occurs on both sides of the Andes,
69 extending to the Guiana shield and Atlantic coast southward to Central Bolivia and southeastern
70 Brazil, and most likely Paraguay (Keiser 1982), although Keiser (1991) mentioned the southern
71 limits of its range are still poorly known. Other island populations are present on both Trinidad
72 and Tobago (Murphy et al. 2018), as well as the Venezuelan islands of Margarita and Los
73 Testigos (Roze 1966). Keiser also reported *O. aeneus* from Aruba (Southern Antilles); however,
74 there is no specimen record to confirm it.

75 *Oxybelis aeneus* can be defined as having an elongate head and body with a low mass-to-
76 length ratio, a brown to gray dorsum, and a cream to gray to tan ventral surface, often with
77 narrow stripes or fine mottling. Dorsal scales are usually in 17–17–13 rows, keeled dorsal scales
78 are absent in most populations, and when present they are on the posterior portion of the body.
79 Ventrals can number 173 to 205, subcaudals 137 to 203, the anal plate is divided. The head
80 width/head length ratio is 0.22–0.47 and varies with the size of the specimen and population.
81 Despite these similarities, the large distribution and morphological variation in *O. aeneus* has
82 resulted in populations being described as “distinct” numerous times. Keiser's (1974, 1982) are
83 the most recent reviews of the species and, given that polytypic species were accepted widely as
84 the norm at the time, Keiser considered *O. aeneus* a single, extremely variable species.
85 Therefore, although numerous important geographic barriers (e.g. Isthmus of Tehuantepec,
86 Trans-Mexican Volcanic Belt, Isthmus of Panama, Andes Mountains) and biogeographic areas
87 (Atlantic forest, Chocó, Llanos, Cerrados) occur across its wide range and many morphological
88 distinctions exist for specific populations (see Fig. 1), the Brown Vine Snake currently is
89 considered a single species (Keiser 1974, 1982).

90 Jadin et al. (2019) assembled a multilocus molecular dataset of *Oxybelis* from populations in
91 the northern part of their range to examine its evolutionary history and test for evidence of
92 cryptic lineages using Bayesian and maximum likelihood criteria. This study showed evidence
93 that *O. aeneus* is likely a complex of species showing relatively deep species-level divergences
94 initiated during the Pliocene. Here we expand on that work incorporating an increased molecular
95 dataset and population sampling of the New World vine snakes throughout most of their northern
96 range. More specifically, we implement multiple phylogenetic analyses using multigene datasets,
97 including both mitochondrial (mtDNA) and nuclear (nDNA) DNA sequences, to assess the
98 evolutionary history within the genus *Oxybelis*. Our analyses recovered numerous distinct
99 species-level clades and we combined these results with morphological data to revise the
100 species-level taxonomy of *O. aeneus*. This study resurrects several synonyms as distinct species
101 while also describing two novel taxa.

102

103 **Materials and methods**

104 **Morphological data**

105 Museum specimens were examined from across the range of *Oxybelis aeneus* (Appendix I).
106 Specimen examination was conducted at the Field Museum, the University of Arizona's
107 herpetology collection in Tucson, University of Wisconsin – Eau Claire, University of Wisconsin
108 – Stevens Point Museum of Natural History, and Arizona State University's collection at Tempe.
109 Scale counting methodologies generally follow those of Peters (1964) with some minor
110 exceptions. Dorsal scales were counted on the neck at about the 10th ventral, at mid-body, and
111 about 10 ventral scales anterior to the vent, and they were counted on the diagonal. Dorsal scale
112 rows expressed here as 17–17–13 refers to the number of rows on the anterior body, at mid-body,

113 and at posterior body, respectively. Scale counts and scale measurements on most specimens
114 were done under a dissection microscope. Measurements were taken with a meter stick, metric
115 tape, and dial calipers. Scale counts separated by a dash (–) represent a range taken from
116 different individuals. Scale counts separated by a slash (/) represent scale counts taken from a
117 single individual; the number on the left is the number of scales on the snake’s left, and the
118 number to the right is the number of scales on the specimen’s right side. We also rely heavily on
119 Keiser (1974) for his excellent data and analysis of *Oxybelis aeneus*.

120 Photographs of scale arrangements were taken with Canon EOS cameras and macro lenses.
121 Sex was determined by probing, tail shape, dissection, and/or visual inspection of the hemipenes,
122 testes, and/or ovaries.

123 Ventral count data were obtained from museum specimens as well as published data (Taylor
124 1941; Bogart and Oliver 1945; Keiser 1974) and counting methods used for this study follow
125 Dowling (1951). Previous authors (Bogert and Oliver 1945; Keiser 1974) as well as this study
126 found no evidence of sexual dimorphism in the ventral scale counts so male and female data are
127 combined to compare populations. However, sexual dimorphism was found in the subcaudal
128 counts. Complete subcaudal counts are rarely available for these snakes because so many have
129 broken tails.

130 To determine whether geographic regions harbored distinct units within *Oxybelis aeneus*, we
131 conducted a discrimination analysis (DA) using the following sixteen morphological and
132 morphometric characters: (1) eye diameter/frontal length, (2) eye diameter/head length, (3) eye
133 diameter/internasal length, (4) eye diameter/prefrontal length, (5) eye diameter greater or lesser
134 than preocular length, (6) eye-nostril distance/eye diameter, (7) head width/head length, (8)
135 internasal length/prefrontal length, (9) prefrontal length/frontal length, (10) supraoculars longer

136 or shorter than prefrontal, (11) second pair of chin shields in contact or separated for most of
137 their length, (12) presence or absence of mid-ventral stripe, (13) number of upper labials, (14)
138 number of upper labials contacting orbit, (15) number of upper labials contacting post orbitals,
139 and (16) the snout shape varying among three types of tapering (Fig. 2).

140 We lumped our examined specimens into groups representing six geographically distinct
141 regions corresponding to potentially distinct species based on molecular data (e.g. Jadin et al.
142 2019). These regions include: Western Region (Southern Arizona through Western Mexico and
143 into Southern Mexico), Eastern Mexico, Central America, Panama, Northern South America
144 (Tobago, Trinidad, and Venezuela), and Central Brazil.

145 Statistical analyses were completed with Excel (2019 v16) and XLstats (v 2020.1), ($\alpha =$
146 0.05). Abbreviations are: n = number of specimens, \bar{x} = mean value, SD = standard deviation,
147 SVL = snout–vent length. ANOVA single factor tests were used to compare ventrals and
148 subcaudals between males and females.

149

150 **Molecular data**

151 Genomic DNA was extracted from tissues of specimens of *Oxybelis* (Table 1, Fig. 3) using a
152 Qiagen DNeasy extraction kit and protocol. Four mitochondrial [Cytochrome *b* (*cyt b*), NADH
153 dehydrogenase subunit 4 (ND4), ribosomal RNA (12S rRNA, 16S rRNA)] and two nuclear
154 [oocyte maturation factor *mos* (*cmos*) and prolactin receptor (PRLR)] gene fragments were
155 independently amplified using GoTaq Green master mix by Promega, (Madison, WI, USA) with
156 the primer pairs: L14910 + H16064 (*cyt b*), ND4 + LEU (ND4), L1091 + 12E (12S), L2510 +
157 H3059 (16S), S77 + S78 (*cmos*), PRLR_f1 + PRLR_r3 (PRLR) described in previous studies
158 (i.e. *cyt b*: Burbrink et al. 2000; ND4: Arévalo et al. 1994; 12S and 16S: Knight and Mindell

159 1993; cmos: Lawson et al. 2005; PRLR: Townsend et al. 2008). For PCR of five fragments
160 (excluding PRLR), we implemented thermocycler conditions of an initial denaturation of 3 min
161 at 95°C followed by 40 cycles 40s at 95°C, 40 s at 48°C, 1 min at 72°C, and a final elongation at
162 72°C for 5 min. Annealing temperature for PRLR was 50°C. Sequencing was performed in both
163 forward and reverse directions using the PCR primers and sequence chromatographs were edited
164 using Geneious R6 6.1.6. No internal stop codons were found in protein coding gene fragments
165 and indels were treated as missing data. Novel sequences generated were deposited in GenBank
166 (XXXXXX–XXXXXX) and combined with sequences of several other *Oxybelis* and other
167 colubrid taxa previously published on GenBank (Appendix II). We selected our outgroup taxa
168 based on recent studies that found *Oxybelis* in a clade of New World colubrids (Pyron et al.
169 2013; Jadin et al. 2014, 2019; Figueroa et al. 2016; Zaher et al. 2019). Sequence alignments for
170 each gene fragment were conducted separately, first automatically using the program MUSCLE
171 (Edgar 2004), and then manually rechecked using Se-AI v.2.0a11 (Rambaut 2002).

172

173 **Phylogenetic and species delimitation analyses**

174 We used IQ-TREE v.1.6.12 (Nguyen et al. 2015) to estimate maximum likelihood (ML)
175 phylogenies and determine the evolutionary history of *Oxybelis*. We used ModelFinder
176 (Kalyaanamoorthy et al. 2017) to perform substitution model selection (using BIC) and tree
177 inference in a single command. We implemented a partition model (Chernomor et al. 2016) for
178 the concatenated analysis using the MFP+MERGE command in IQ-TREE. We created a
179 partition file specifying different data partitions by gene and by codon position (for the protein
180 coding genes). This initial partitioning scheme was chosen because ModelFinder can only merge
181 partitions (there is no additional splitting). However, to quantify potential issues with data

182 partitioning we compared our results to an unpartitioned analysis. The results were virtually
183 identical with conflict only at poorly supported nodes, suggesting that the choice of partitioning
184 scheme had little influence on the analysis. Support for nodes was assessed using both 1,000 SH-
185 aLRT replicates (Guindon et al. 2010) and 10,000 ultrafast bootstrap (UFboot) replicates (Hoang
186 et al. 2017). Nodes with SH-aLRT > 80% and UFboot > 95% were indicative of strong support.
187 Unrooted trees were rooted with *Drymarchon corais* (Jadin et al. 2014, 2019).

188 Additionally, we conducted Bayesian Markov chain Monte Carlo [MCMC] mixed-model
189 analyses in MrBayes v.3.0b4 (Ronquist and Huelsenbeck 2003), partitioning by gene as well as
190 by codon (Table 2). Two simultaneous runs of four MCMC analyses, consisting of one cold and
191 three incrementally heated chains, were initiated with random trees for a total of 8×10^6
192 generations per run, sampling trees and parameters every 100 generations. We used potential
193 scale reduction factor values (output by MrBayes), together with plots of cold-chain likelihood
194 values and parameter estimates visualized in TRACER v.1.6 (Rambaut et al. 2014) to confirm
195 stationarity and convergence of MCMC runs. Based on this evaluation, the first 3×10^6
196 generations from each run were discarded as burn-in.

197 We also performed a coalescent-based species tree analysis using SVDquartets (Chifman
198 and Kubatko 2014, 2015) in PAUP*v.4.0b10 (Swofford 2002). SVDquartets uses site pattern
199 frequencies and algebraic statistics to estimate relationships among quartets. A subsequent
200 quartet assembly step is then used to estimate a species tree containing all taxa. We assigned
201 individuals to species based on a combination of current taxonomy and the results from the
202 concatenated ML and Bayesian analyses. All quartets were evaluated (i.e. exhaustive sampling)
203 and the full species tree was assembled using QFM (Reaz et al. 2014). The unrooted species tree

204 was rooted using *Drymarchon corais*, and support for nodes was determined using 100 non-
205 parametric bootstrap replicates.

206 To further estimate the number of species/populations among *Oxybelis* lineages we used
207 the program BPP v.4.1.3 (Yang 2015; Flouri et al. 2018). BPP uses the multispecies coalescent
208 model (MSC) in a Bayesian framework for the estimation of species limits, species trees, and
209 associated parameters (i.e. divergence times and population sizes). Given the recent concerns
210 that BPP may oversplit (Sukumaran and Knowles 2017; Leaché et al. 2018), we took a
211 conservative approach to our analysis. We initially defined 10 species based on the results of the
212 concatenated ML and Bayesian analyses. We also used the concatenated Bayesian topology as
213 the starting topology for all BPP runs. We implemented four joint species delimitation/species
214 tree (A11) analyses, testing the impact of species delimitation algorithm used (Alg 0, Alg 1) and
215 the theta prior on the results. For all analyses we specified an inverse gamma prior of (3, 0.04)
216 for tau. For theta, we tested the influence of a large (3, 0.04) and small (3, 0.004) prior on our
217 results. All analyses used a uniform rooted tree prior. To accommodate the combined
218 mitochondrial and nuclear data we turned on the locus rate option ($\alpha = 2.0$) and introduced
219 heredity multipliers (G 4,4]). Analyses used an initial burnin of 100,000 generations followed by
220 a total of 50,000 posterior samples taken every 10 generations. Convergence was assessed
221 through visual inspection of results from independent runs.

222

223 **Results**

224 **Morphology**

225 Our morphological analyses show distinction among lineages across geographically separated
226 populations of *Oxybelis aeneus*. The discrimination analysis results found Wilks' Lambda test,

227 Pillai's Test, Hotelling-Lawley Trace, and Roy's Greatest Root all had p values <0.0001 with
228 alpha set at <0.05) rejecting the null hypothesis of no discriminating ability. The Eigenvalue for
229 F1 accounted for 62.1% of the total variance (Table 3). The factor/correlations for the traits in
230 the analysis are shown in Table 3. Figure 4 shows the observations on the factor axes and
231 confirms that the species are discriminated on the basis on the morphometric and meristic
232 variables. The group means are designated by the centroids that allow for visualization of how
233 the functions discriminate between groups by plotting the individual scores for the discriminant
234 functions.

235

236 **Phylogeny and species diversity**

237 The BI, ML and SVDquartets analyses recovered nearly identical tree topologies with
238 mostly strong node support, especially towards the tree tips (Figs 3 and 5). ModelFinder in IQ-
239 TREE selected the following partition scheme and substitution models: (1) *cyt b*-1st + ND4-1st +
240 12S + 16S + PRLR-2nd + PRLR-3rd (TIM2 + F + I + G4); (2) *cyt b*-2nd + ND4-2nd + *cmos*-3rd
241 (HKY + F + R2); (3) *cyt b*-3rd + ND4-3rd (TIM3 + F + R2); (4) *cmos* 1st + *cmos* 2nd + PRLR 1st
242 (K2P + I). All our molecular phylogenetic analyses strongly support the presence of three major
243 lineages (i.e. the brown vine snakes, *O. brevirostris*, and the green vine snakes) (Figs 3 and 5).
244 Furthermore, we found strong support that *O. brevirostris* is sister to the *O. aeneus* complex,
245 which together were sister to the green vine snakes (i.e. *O. fulgidus*, *O. wilsoni*). Additionally,
246 our analyses show a paraphyletic *O. fulgidus* with respect to *O. wilsoni* (Figs 3 and 5). Within the
247 brown vine snakes, all our analyses strongly support a sister relationship between lineages in
248 Central America and those from Eastern Mexico. Incongruence among analyses occurs with the
249 position of the Western Region, which is found as sister to the Eastern Mexico-Central America

250 clade in the BI and both ML analyses (though with low support) whereas the SVDquartets
251 analysis strongly supports a sister relationship between the Western Region and the remaining
252 brown vine snake populations (Fig. 3). Finally, the unpartitioned ML analysis placed the South
253 American clade sister to the rest of the brown vine snakes and the Panama clade sister to a
254 Western Region-Eastern Mexico-Central America clade. However, these relationships had low
255 support (not shown).

256 Our BPP results indicated support for eight species level lineages within *Oxybelis*.
257 Species delimitation results were similar among algorithms, but differed based on the prior
258 specified for theta (Fig. 6). For example, when utilizing a smaller prior, there was > 95%
259 posterior support for seven species and relatively weak support for the distinction of *O. wilsoni*
260 and *O. fulgidus* from Central America. When using a larger prior, the best delimitation model
261 merged these three taxa with moderate posterior probability (0.87). In all BPP analyses each *O.*
262 *aeneus* lineage was supported as distinct with high posterior probability. These geographically
263 defined lineages correspond to our morphological analyses above, strongly supporting species
264 recognition and we therefore describe and diagnose the taxa below.

265

266 **Systematics**

267 ***Oxybelis aeneus* (Wagler, 1824)**

268 Amazonian Brown Vine Snake

269 *Dryinus aeneus* – Wagler 1824

270 *Oxybelis aeneus* – Duméril et al. 1854: 819

271 *Dryophis acuminata* – Günther 1858: 156

272 *Oxybelis aeneus aeneus* – Bogert and Oliver 1945: 391

273 *Oxybelis aeneus* – Keiser 1974: 7

274

275 **Lectotype** ZSM 2645/0 from the forest along the Solimões River, near Ega, now Tefé,
276 Amazonas, Brazil (~ 03°21'S 64°42'W). Keiser (1976) considered ZSM 2645/0 the
277 holotype but Hoogmoed and Gruber (1983) gave it lectotype status suggesting that
278 Wagler, 1824 had seen more than one specimen.

279

280 **Diagnosis** Using data from Keiser (1974) and our examination of specimens from Central Brazil
281 (Fig. 7) we constructed the following description for *Oxybelis aeneus*. A vine snake with (1)
282 three upper labials (4–5–6) bordering the orbit; (2) black bars or spots present on the anterior
283 body; (3) no stripes on the ventral surface, venter is mottled; (4) eye diameter greater than
284 preocular; (5) second pair of chin shields separated by smaller scales for most of its length; (6)
285 nine upper labials, three located behind the orbit; (7) snout from above narrow, tapered, and flat
286 at rostral (snout type B); (8) supraocular slightly longer than prefrontals; (9) last upper labial
287 longer than primary temporal; (10) lower surface of head uniform in colour; (11) second upper
288 labial does not contact the preocular.

289 Tail is 0.7 of the SVL; the eye diameter is 1.4 times the length of the preocular scale and
290 0.93 of the internasal length. Primary temporal contacts both postoculars, the parietal, and two
291 secondary temporals. Upper labials 6–7–8–9 contact the primary temporal. Ventral counts in
292 males 179–197 (n = 15, x = 188.8, SD = 9.00). In females, ventral counts ranged from 184–203
293 (n = 20, x = 192.1, SD = 9.54). Subcaudal counts 154–188 in males (n = 12, x = 169.5, SD =
294 17.16) in females 146–184 (n = 15, x = 168.2, SD = 19.08). It has 17–20 maxillary teeth.

295

296 **Variation** The rostral is visible from above and followed by nine plate-like scales on the crown:
297 a pair of internasals, a pair of prefrontals, the frontal and two larger supraoculars, and a pair of
298 parietals. The preoculars extend slightly on to the crown between the prefrontals and
299 supraoculars. In profile the nasal scale is elongate, extending from the edge of the rostral, beyond
300 the posterior edge of the internasal to the anterior border of the fused prefrontal-loreal. The
301 preocular scale is short and less than the length of the eye's diameter. The eye
302 diameter/internasal ratio for one specimen is 0.93. Scales bordering the orbit are the preocular,
303 the supraocular, two small post oculars and upper labials 4–5–6. The primary temporal contacts
304 both postoculars, the parietal, and two secondary temporals, upper labials 6–7–8–9 contact the
305 primary temporal. Upper labials are usually nine but range from 8–10. The eighth upper labial is
306 the shortest. The ninth upper labial is the longest. Upper labials 1–2 contact the nasal, 2–3
307 contact the prefrontal-loreal, 3–4 contact the preocular. The tallest upper labial can be the sixth
308 or seventh. Lower labials range from 8–10, (usually nine). The first four (rarely five) contact the
309 anterior chin shields, a total of six contact both pair of chin shields. The anterior pair of chin
310 shields are shorter (about 50%) of the length of the second pair of chin shields; the second pair
311 are completely separated by smaller scales. Ventral counts in males vary from 179–197 (n = 15,
312 x = 188.8, SD = 9.00). Ventral counts in females, vary from 184–203 (n = 20, x = 192.1, SD =
313 9.54). Subcaudal counts 154–188 in males (n = 12, x = 169.5, SD = 17.16) in females 146–184
314 (n = 15, x = 168.2, SD = 19.08). Maxillary teeth vary from 17–20.

315

316 **Colouration and pattern** The crown of the head and upper face are golden-brown to tan. The
317 upper labials and ventral surface of the head are a uniform cream. The transition in colour is
318 separated by a preocular dark brown stripe extending from the nasal scale, under the eye and

319 onto the anterior body. This stripe may continue as a series of spots onto the body. On the
320 anterior body the first two scale rows are the same yellow colour as the ventral surface and form
321 a ventrolateral stripe. A series of black marks occurs on some scales scattered on the sides of the
322 body. An indistinct mid-line stripe occurs on the ventral surface.

323

324 **Geographic distribution** This species appears restricted to the Amazon Basin.

325

326 **Comparison** A vine snake with the combinations of the second pair of chin shields mostly
327 separated by smaller scales, three upper labials bordering the orbit, four upper labials in contact
328 with the primary temporal, and the eye diameter is about equal to the length of the internasal.
329 Specimens from populations in Central America, Panama, and the Western Region have the
330 second pair of chin shields in contact and two or three upper labials in contact with the primary
331 temporal. Populations from Eastern Mexico have the second pair of chin shields in contact for
332 most of their length and an eye diameter that is about 0.8 the length of the internasal. Those from
333 Northern South America have only two upper labials bordering the orbit.

334

335 ***Oxybelis koehleri* sp. nov.**

336 Köhler's Brown Vine Snake

337 *Oxybelis aeneus* – Duméril et al. 1854: 819

338 *Dryophis acuminata* – Günther 1858: 156

339 *Oxybelis acuminata* – Boulenger 1896: 192

340 *Oxybelis aeneus aeneus* – Bogert and Oliver 1945: 381

341 *Oxybelis aeneus* – Keiser 1974: 7

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Holotype UTA R-46846 (ENS 9858), a female from Guatemala: El Arenal (circa 560 m, 14°53'1.788"N, 89°46'31.799"W) of the Municipio Cabañas in the Department of Zacapa. Collected by a local between Feb and May 1998, preserved 24 Aug 1998.

Paratypes UTA R-44838 Nicaragua: Jinotega, El Paraiso Km 152.5, carretera Jinotega-Matagalpa, 1490 m; UTA R-46865 Honduras: Comayagua, Playitos: Aldea "Lo de Reina", 785 m. UTA R-53176–77 Honduras: Gracias a Dios, Mocerón, 30–50 m.

Diagnosis Using data from our examination of specimens from Central America we constructed the following description for *Oxybelis koehleri*. A vine snake with (1) three upper labials (4–5–6) bordering the orbit; (2) black spots or bars on anterior body, brown uniform brown with little black pigment; (3) labials white and underside of head red-brown with a medial red brown stripe in females; (4) eye diameter greater than preocular length; (5) second pair of chin shields in contact for most of their length; (6) nine upper labials, three located behind the orbit; (7) snout from above is narrow, tapered, and rounded (snout type A); (8) supraocular is longer than the prefrontal; (9) last upper labial and primary temporal about the same length. (11) second upper labial does not contact the preocular.

Description of holotype (UTA R-46846, Fig. 8) A female, total length 905 mm, tail length 439 mm. Rostral broader than tall; barely visible from above; upper labials 8 (5 + 6 fused) / 9; internasals paired, extending past the posterior border of the first upper labial but not the nasal, which is longer than both; prefrontals paired, contact upper labials 2–3; triangular frontal and

365 supraoculars elongated and circa 8 mm long, paired parietals slightly longer circa 9 mm;
366 supraoculars and parietals, contact upper postocular; postoculars 2/2, upper larger; upper labials
367 3–4 contact the preocular; 4–5–6 are in the orbit (4 + 5 on left side because of fusing); 7–8–9
368 contact the primary temporal; 9 interriectals; one preocular less than the diameter of the eye;
369 lower labials 10 / 10, first four contact the first pair of chin shields; second pair of chin shields
370 longest; four paired gulars. Dorsal scales smooth in 17–17–13 rows. Ventrals 198, 119 divided
371 subcaudals, anal plate divided.

372

373 **Variation** Rostral is not visible from above and followed by nine plate-like scales on the crown:
374 a pair of internasals, a pair of prefrontals, the frontal, two larger supraoculars, and a pair of
375 parietals. Preoculars extend slightly on to the crown between the prefrontals and supraoculars.
376 The internasals are 75% ($r = 0.63$ – 1.0) of the prefrontal length. Average eye diameter is 1.19 ($r =$
377 0.83 – 1.53) the preocular length. In profile the nasal scale is elongate extending from the edge of
378 the rostral, beyond the preocular scale is short and less than the diameter of the eye. Scales
379 bordering the orbit are the preocular, the supraocular, two small postoculars and upper labials 4–
380 5–6. Primary temporal contacts both postoculars, the parietal, and two secondary temporals, as
381 well as upper labials 6–7–8–9. Upper labials number nine (rarely eight or ten). The shortest
382 upper labial can be the first or the eighth. The last (usually the ninth) upper labial is the longest.
383 Upper labials 1–2 contact the nasal, 2–3 contact the prefrontal-loreal, 3–4 contact the preocular.
384 Lower labials vary from eight through 10, usually 9; the first four contact the anterior chin
385 shields, a total of six contact both pair of chin shields. The anterior pair of chin shields are
386 shorter (about 60%) than the length of the second pair; the second pair are in contact for most of
387 their length. Dorsal scales are in 17–17–13 rows.

388 In males total length ranges from 1135–1432 mm (n = 6, x = 1329.83, SD = 106.68),
389 SVL 673–835 mm (n = 7, x = 783.71, SD = 62.55) tail lengths 462–600 mm (n = 7, x = 554.0
390 SD = 47.75) tail/SVL ratios (n = 7, r = 0.67–0.79, x = 0.71, SD = 0.04). In females, total lengths
391 ranged from 1137–1300 mm (n = 8, x = 1221.43, SD = 63.72), tails ranged from 425–527 mm (n
392 = 7, x = 478.14, SD = 31.22). Tail/SVL ratios in females 0.53–0.73, x = 0.65, SD = 0.06.

393 Ventrals in males vary from 176–191 (n = 7, x = 183.83, SD = 4.88); ventrals in females
394 vary from 184–191 (n = 7, x = 187.57, SD = 2.26). Subcaudals in males vary from 164–186 (n =
395 5, x = 177, SD = 8.12); in females; subcaudals vary from 176–189 (n = 5, x = 184.8, SD = 5.91).

396

397 **Colouration and pattern** (Fig. 9) Head usually a uniform brown (it may have some darker
398 pigmented spots), body brown with light mottling and some dark spots anteriorly, posteriorly
399 indistinct transverse blotches that are wide on the vertebral line and narrow laterally; upper
400 labials cream to white and separated from the brown by a black stripe on the dorsal edge of the
401 second labial that extends past the eye to the last labial; lower labials have some red-brown
402 pigmentation; ventral surface of head tan laterally with a red-brown medial stripe that extends
403 from the mental onto the first 15 ventrals. Longitudinal ventral stripes absent. All adult females
404 we have examined (including sequenced material) have a red-orange stripe on the underside of
405 the head and onto the first 12 anterior ventrals and the colouration is present as spots on some
406 upper labial scales.

407 In alcohol, (FMNH 27050) the colouration and pattern are much reduced. The head is a
408 gray-brown, the labials are white and the marking on the lower labials, along with the reddish-
409 brown chin, are usually absent. The ventral side of the head is a uniform cream. The dorsum is

410 gray with black lateral spots where the transverse blotches were in life. The ventrals are pale
411 with dense mottling.

412

413 **Geographic distribution** This species occurs from Guatemala to Costa Rica in Central America.

414

415 **Etymology** The specific epithet is a patronym honoring Gunther Köhler, who has contributed
416 greatly to our knowledge on the systematics and natural history of amphibians and reptiles with
417 particularly impressive contributions in Central America. Dr. Köhler has published more than
418 200 scientific articles and numerous books in English, Spanish, and German, greatly increasing
419 scientific and public access to Central American herpetology.

420

421 **Comparison** A vine snake with nine upper labials, three of which border the orbit, an eye
422 diameter that is about equal to the length of the internasal, three upper labials in contact with the
423 primary temporal and the second pair of chin shields in contact for most of their length.

424 Specimens of *O. aeneus* and those from Northern South America have the second pair of chin
425 shields separated for most of their length. Specimens from the Western Region have an eye
426 diameter that is less than the length of the internasals while those from Panama usually have eight
427 upper labials.

428

429 ***Oxybelis microphthalmus* Barbour and Amaral, 1926**

430 Thronscrub Brown Vine Snake

431 *Dryinus aeneus* – Wagler, 1824

432 *Oxybelis aeneus* – Duméril et al. 1854: 819

433 *Dryophis acuminata* – Günther 1858: 156

434 *Oxybelis acuminata* – Boulenger 1896: 192

435 *Oxybelis microphthalmus* – Barbour and Amaral 1926

436 *Oxybelis aeneus auratus* – Bogert and Oliver 1945: 381

437 *Oxybelis aeneus auratus* – Zweifel and Norris 1955

438 *Oxybelis aeneus* – Keiser 1974: 7

439

440 **Holotype** MCZ 22417 from Calabasas Canyon, Arizona (circa 31°28'N, 110°58'W) designated
441 by Barbour and Amaral 1926: 80.

442

443 **Diagnosis** Using data from our examination of specimens from the Western Region we
444 constructed the following description for *Oxybelis microphthalmus*. A vine snake with (1) three
445 upper labials (4–5–6) bordering the orbit; (2) black spots or bars on anterior body, dorsum
446 mostly uniform brown with little black pigment; there are small scattered black spots on the
447 dorsum; (3) venter is finely mottled and it can have a dark lateral stripe on the outer edge of each
448 ventral, and a pale mid-ventral stripe; (4) eye diameter shorter than preocular; (5) second pair of
449 chin shields in contact for most of their length; (6) eight upper labials in most Arizona and
450 Sonora specimens, nine upper labials in other Mexican populations, but all tend to have three
451 labials behind orbit; (7) snout from above is narrow, tapered, and rounded at the tip (snout type
452 A); (8) supraoculars are longer than the prefrontals; (9) lower surface of the head is uniform
453 white or yellow in colour (not mottled); (10) last upper labial shorter than primary temporal; (11)
454 second upper labial does not contact the preocular.

455 The rostral is visible from above and followed by nine plate-like scales on the crown: a
456 pair of internasals, a pair of prefrontals, the frontal and two larger supraoculars, and a pair of
457 parietals. Preoculars extend slightly on to the crown between the prefrontals and supraoculars. In
458 profile the nasal scale is elongate extending from the edge of the rostral, beyond the posterior
459 edge of the internasal to the anterior border of the fused prefrontal-loreal. Eye
460 diameter/internasal ratio in this species averages 0.82 ($n = 34$, $r = 0.58-0.97$, $SD = 0.10$).
461 Preocular scale is long and greater in length than the diameter of the eye. Scales bordering the
462 orbit are the preocular, the supraocular, two small post oculars and upper labials 4-5-6 (rarely 5-
463 6-7). Primary temporal contacts both postoculars, the parietal, and two secondary temporals,
464 upper labials 7-8 or 7-8-9 or 6-7-8-9. Upper labials vary from 8-10. Of 66 sides of heads
465 examined 30 (45%) had 8 upper labials; 30 (45%) had 9 upper labials, and six (10%) had 10
466 upper labials. The shortest upper labial can be the first or the fifth. The longest upper labial is the
467 eighth or ninth. Upper labials 1-2 contact the nasal, 2-3 contact the prefrontal-loreal, 3-4 contact
468 the preocular. The tallest upper labial can be the sixth or seventh. Lower labials range from 8-10,
469 (usually 9). The first four labials (rarely five) contact the anterior chin shields, a total of six
470 contact both pair of chin shields. The anterior pair of chin shields are shorter (about 50%) of the
471 length of the second pair of chin shields; the second pair are in contact anteriorly and partially
472 separated by a pair of scales posteriorly. Dorsal scales are in 17-17-13 rows with the posterior
473 scales being weakly keeled.

474

475 **Variation** Geographic variation in the upper labial and ventral counts exists. Arizona (USA) and
476 Sonoran (Mexico) populations tend to have eight upper labials, while Oaxaca and Guerrero

477 (Mexico) populations have nine upper labials. Ventral counts in Arizona and Sonora tend to be at
478 the high end of the range, populations to the south have lower numbers.

479 In males total length varies from 1197–1337 mm ($n = 10$, $x = 1262.13$, $SD = 73.17$), SVL
480 varies from 713–834 mm ($n = 10$, $x = 766.68$, $SD = 46.37$) tail lengths vary from 484–538 mm
481 ($n = 8$, $x = 502.21$, $SD = 35.99$); tail/SVL ratios vary from 0.63–0.74 ($n = 8$, $x = 0.68$, $SD =$
482 0.03). Female total lengths vary from 667–1407 mm ($n = 14$, $x = 1238.0$, $SD = 195.99$), tails
483 vary from 250–544 mm ($n = 12$, $x = 475.83$, $SD = 107.19$). Tail/SVL ratios in females vary from
484 0.60–0.72 ($x = 0.64$, $SD = 0.04$).

485 Ventrals in males vary from 184–202 ($n = 14$, $x = 192.0$, $SD = 5.92$); ventrals in females
486 vary from 184–204 ($n = 12$, $x = 193.58$, $SD = 5.2$). Subcaudals in males vary from 163–175 ($n =$
487 5, $x = 168.4$, $SD = 4.18$); in females; subcaudals vary from 170–183 ($n = 7$, $x = 177.2$, $SD =$
488 4.22).

489

490 **Colouration and pattern** The crown of the head and upper face are brown to tan (Fig. 10). The
491 upper labials and ventral surface of the head are a uniform cream. The transition in colour is
492 separated by a preocular dark brown stripe extending from the nasal scale, under the eye and
493 onto the anterior body. This stripe may continue as a series of spots onto the body. The first two
494 scale rows on the anterior body are the same yellow colour as the ventral surface, and form a
495 ventrolateral stripe. At mid–body, the first four dorsal scale rows and the lower half of the fifth
496 scale row are mottled heavily with dark pigment, the upper half or row five and rows 6–8 lack
497 the dense mottling, giving the overall impression of a series of lateral stripes. On the ventral
498 surface is an indistinct mid–ventral stripe.

499 In alcohol (UAZ 39545) the colouration has often faded but the elements of the pattern
500 and the colours are still detectable.

501

502 **Geographic distribution** Southeastern Arizona southward to Oaxaca, Mexico.

503

504 **Comparison** A vine snake with eight (Arizona and Sonora) or nine (remainder of distribution in
505 Mexico) upper labials with three behind the orbit, an eye diameter that is about 0.8 of the
506 internasal (no other species of *Oxybelis* has an eye diameter this small). It also has two or three
507 upper labials in contact with the primary temporal and the second pair of chin shields are in
508 contact for most of their length. *Oxybelis aeneus* and those from Northern South America have
509 the second pair of chin shields separated for most of their length. *Oxybelis koehleri* and those
510 from Panama usually have two upper labials behind the orbit.

511

512 ***Oxybelis potosiensis* Taylor, 1941**

513 Gulf Coast Brown Vine Snake

514 *Dryinus aeneus* – Wagler 1824: 12

515 *Oxybelis aeneus* – Duméril et al. 1854: 819

516 *Dryophis acuminata* – Günther 1858: 156

517 *Oxybelis acuminata* – Boulenger 1896: 192

518 *Oxybelis potosiensis* – Taylor 1941

519 *Oxybelis aeneus auratus* – Bogert and Oliver 1945: 381

520 *Oxybelis aeneus* – Keiser, 1974: 7

521

522 **Holotype** UIMNH 25069 (Fig. 11), a female from 36 km northwest of Ciudad Maíz (circa
523 22°30'N, 99°56'W), San Luis Potosí, Mexico designated by Taylor, 1941: 128.

524

525 **Diagnosis** Using data from our examination of specimens from Eastern Mexico we constructed
526 the following description for *Oxybelis potosiensis*. A vine snake with (1) two or three upper
527 labials (4–5 or 4–5–6) bordering the orbit; (2) transverse black bars on the anterior body; (3)
528 venter finely mottled, a stripe or stripes are not apparent (4) eye diameter longer than preocular;
529 (5) second pair of chin shields are in contact for most of their length; (6) nine upper labials, two
530 or three upper labials behind the orbit. (7) snout from above is very broad, slightly tapered, and
531 rostral is very rounded (snout type C); (8) supraocular and prefrontals about the same length. (9)
532 last upper labial equal or greater in length than the primary temporal; (10) underside of head
533 uniform white or cream; (11) second upper labial does not contact the preocular.

534

535 **Description of holotype** (Fig. 11) Rostral is visible from above; preoculars extend slightly on to
536 the crown between the prefrontals and supraoculars and the postoculars can be seen from above.
537 Preocular scale is shorter than eye diameter. Scales bordering the orbit: preocular, the
538 supraocular, two small post oculars, and upper labials 5–6 on the left and 4–5 on the right. The
539 primary temporal is in contact with both postoculars, the parietal, two secondary temporals, and
540 upper labials 6–7–8–9. Eight upper labials on the right and nine on the left; the shortest upper
541 labial can be the first or the eighth; the longest upper labial is the last (eighth or ninth). Upper
542 labials 1–2 contact the nasal, 2–3 contact the prefrontal-loreal, 3–4 contact the preocular. The
543 tallest upper labial can be the fifth or sixth. Lower labials 9–10; the first four contact the anterior
544 chin shields, a total of six contact both pair of chin shields. The anterior pair of chin shields are

545 shorter (about 60%) that the length of the second pair of chin shields; the second pair are in
546 contact anteriorly and partially separated by a pair of scales posteriorly. Dorsal scales are in 17–
547 17–13 rows. Ventrals 196, subcaudals 160.

548
549 **Variation** In males, total lengths vary from 1175–1535 mm ($n = 4$, $x = 1371.75$, $SD = 164.08$),
550 tails vary from 500–628 mm ($n = 4$, $x = 564.75$, $SD = 58.09$). Tail/SVL ratios in males vary from
551 0.67–0.69 ($x = 0.68$, $SD = 0.01$). In females total lengths vary from 804–1272 mm ($n = 3$, $x =$
552 1083.33, $SD = 201.53$), SVL vary from 734–804 mm ($n = 3$, $x = 761.67$, $SD = 30.40$); tail
553 lengths vary from 440–525 mm ($n = 2$, $x = 482.5$, $SD = 42.50$); One female had a tail/SVL ratio
554 that was 0.70.

555 Ventrals in males vary from 174–190 ($n = 6$, $x = 185.67$, $SD = 5.73$); ventrals in females
556 vary from 186–195 ($n = 3$, $x = 191.67$, $SD = 4.03$). No subcaudal counts were take because of
557 broken or questionable tail tips.

558 *Size*: To at least 1290 mm total length.

559
560 **Colouration and pattern** In alcohol (UIMNH 25069), head and body gray-brown, upper labials
561 cream and separated from the gray-brown by a black stripe; ventral surface of head cream
562 transitioning to yellow posteriorly. Transverse black bars on the anterior body. No ventral stripes
563 (Fig. 11).

564
565 **Geographic distribution** This species occurs in San Luis Postosí and northern Veracruz,
566 southward to Yucatan, Mexico, and Belize.

567

568 **Comparison** A vine snake with nine upper labials, two bordering the orbit, eye diameter greater
569 than the length of the preocular, and second pair of chin shields in contact for most of their
570 length. Specimens of *Oxybelis aeneus* and those from Northern South America have the second
571 pair of chin shields separated by smaller scales. Specimens of *O. aeneus*, *O. koehleri*, *O.*
572 *microphthalmus*, and those from Panama have three upper labials bordering the orbit.

573

574 ***Oxybelis rutherfordi* sp. nov.**

575 Rutherford's Brown Vine Snake

576 *Dendrophis auratus* – Court 1858: 411

577 *Dryiophis aeneus* – Garman 1887: 284

578 *Oxybelis acuminatus* – Mole and Urich 1894: 86

579 *Oxybelis aeneus aeneus* – Bogert and Oliver 1945: 381

580 *Oxybelis aeneus* – Beebe 1952: 175

581 *Oxybelis a. aeneus* – Wehekind 1960: 75

582 *Oxybelis ae. aeneus* – Mertens 1972: 18

583

584 **Holotype** UTA R-64851 (Figs 12 and 13), from Trinidad, Arima Valley, William Beebe

585 Tropical Research Centre, circa 6 km N Arima, 247 m, 10°41'32" N, 61°17'22" W. Collected by

586 Mike G. Rutherford 20:00h, 31 March 2018. Measurement: SVL 745 mm, total length 1245 mm.

587

588 **Paratypes** FMNH 215839, Trinidad, circa 2 miles South of Simla-Quarry Rd, on Arima-

589 Blanchisseuse Rd. (10°39'21.73"N, 61°17'22.77"W), JCM, M. Dloogatch, and Reznick; FMNH

590 49978 and 49982 Trinidad, San Rafael (10°33'59"N, 61°15'59"W); FMNH 215838, circa 3 mi.

591 South of Simla-Quarry Rd, on Arima-Blanchisseuse Rd, egg farm (10°39'38"N, 61°17'22"W),
592 collected by JCM, M. Dloogatch, and R. Humbert; MBLUZ 1268, between San Francisco de
593 Macanao and Cerro Los Cedros, Isla de Margarita, Nueva Esparta, Venezuela (11°01'34"N,
594 64°17'30"W) by Gilson Rivas, Eusebio Millán, Ángel Fernández and Reina Gonto on 10
595 October 2013. FMNH 17839–40, Puerto Viejo, Península de Paria in the state of Sucre,
596 Venezuela.

597
598 **Diagnosis** Using data from our examination of specimens from Northern South America we
599 constructed the following description for *Oxybelis rutherfordi*. A vine snake with (1) two upper
600 labials (4–5) bordering the orbit; (2) black spots or bars on anterior body, dorsum mostly uniform
601 brown with little black pigment; there are small scattered black spots on the dorsum; (3) venter
602 finely mottled with a pale mid ventral stripe; (4) preocular longer than the diameter of the eye;
603 (5) second pair of chin shields in contact for most of their length; (6) eight upper labials with
604 three labials behind orbit; (7) snout from above narrow, tapered, and rounded at the rostrum
605 (snout type B); (8) supraoculars longer than the prefrontals; (9) last upper labial longer than the
606 primary temporal; (10) lower surface of head uniform in colour; (11) second upper labial does
607 not contact the preocular.

608
609 **Description of holotype** (UTA R-64851, Fig. 12) A female, SVL 735 mm, tail length 510 mm.
610 Rostral broader than tall, barely visible from above; upper labials 8/8; internasals paired,
611 extending to the anterior border of the second upper labial but not past the nasal, which is longer
612 than both and extends to the middle of the second upper labial; prefrontals paired, contact upper
613 labials 2–3 and nasal; frontal (circa 6.5 mm long) and supraoculars (circa 6 mm long) elongated;

614 paired parietals circa 7.5 mm; supraoculars and parietals, contact upper postocular; postoculars
615 2/2, upper larger; upper labials 3–4 contact the preocular, 4–5 are in the orbit; 6–7–8 contact the
616 primary temporal; 6 interrials; one preocular less than the diameter of the eye; lower labials
617 8/8, first four contact the first pair of chin shields; second pair of chin shields longest; three
618 paired gulars. Dorsal scales smooth in 17–17–13 rows. Ventrals in eight males vary from 183–
619 188 ($x = 185$, $SD = 1.87$); ventrals in eight females vary from 180–190 ($x = 184.63$, $SD = 3.42$).
620 *Variation:* Rostral visible from above and followed by nine plate-like scales on the crown: a pair
621 of internasals, a pair of prefrontals, the frontal and two larger supraoculars, and a pair of
622 parietals. The preoculars extend slightly on to the crown between the prefrontals and
623 supraoculars. Internasals are about 0.83 of the prefrontals. Preoculars are about 55% of the eye
624 diameter. In profile the nasal scale is elongate extending from the edge of the rostral, beyond the
625 posterior edge of the internasal to the anterior border of the fused prefrontal–loreal. The
626 preocular scale is short and less than the diameter of the eye. Scales bordering the orbit are the
627 preocular, supraocular, two small post oculars and upper labials 4–5 or 5–6. The primary
628 temporal contacts both postoculars, the parietal, and two secondary temporals, as well as upper
629 labials 6–7–8. Upper labials can be seven to nine, but most often eight. The shortest upper labial
630 can be the first or the eighth. The longest upper labial is the last (eighth or ninth). Upper labials
631 1–2 contact the nasal, 2–3 contact the prefrontal-loreal, 3–4 contact the preocular. The tallest
632 upper labial can be the fifth or sixth. Lower labials can number seven through 10, usually eight;
633 the first four contact the anterior chin shields, a total of six contact both pair of chin shields. The
634 anterior pair of chin shields are shorter (about 50%) than the length of the second pair of chin
635 shields; the second pair are in contact anteriorly and partially separated by a pair of scales
636 posteriorly. Dorsal scales are in 17–17–15 rows.

637 In males total lengths vary from 671–1475 mm ($n = 8$, $x = 1075.25$, $SD = 210.45$), SVL
638 varies from 391–860 mm ($n = 8$, $x = 658.75$, $SD = 128.1$) tail lengths vary from 280–449 mm (n
639 $= 7$, $x = 422.14$, $SD = 65.94$); tail/SVL ratios vary from 0.64–0.73 ($n = 7$, $x = 0.70$, $SD = 0.03$).
640 In females, total lengths vary from 831–1274 mm ($n = 8$, $x = 1090.63$, $SD = 166.01$), tails vary
641 from 382–521 mm ($n = 7$, $x = 464.0$, $SD = 56.15$). Tail/SVL ratios in females vary from 0.643–
642 0.715 ($x = 0.68$, $SD = 0.027$).

643 Ventrals in males vary from 183–188 ($n = 8$, $x = 185.0$, $SD = 4.88$); ventrals in females
644 vary from 180–190 ($n = 10$, $x = 184.63$, $SD = 3.42$). Subcaudals in males vary from 163–175 (n
645 $= 5$, $x = 168.4$, $SD = 4.18$). Ventrals in females vary from 180–190 ($n = 8$, $x = 184.63$, $SD =$
646 3.42); subcaudals in females, 162–171 ($n = 6$, mean = 166.33, $SD = 3.25$).

647 *Size:* To at least 1668 m in total length based on UWIZM.2012.27.49.

648

649 **Colouration and pattern** (Figs 12 and 14) Crown is brown sometimes with small black spots.
650 Overall head and body brown or gray-brown, upper and lower labials intense yellow and
651 separated from the brown by a black stripe on the dorsal edge of the second labial that extends
652 past the eye to the last labial; ventral surface of head yellow transitioning to cream posteriorly.
653 Small black dash-like marks on scale rows 1–7 on the upper edge of each scale, separated by two
654 scale rows. Ventral surface is yellow to cream with finely stippled pigment most restricted to the
655 outer edges of the ventrals leaving an indistinct mid-ventral stripe. Ventrals may have small
656 black marks with irregular borders. In preservative the brown pigment fades to gray.

657

658 **Geographic distribution** It occurs on both islands of Trinidad and Tobago and on the adjacent
659 mainland of Venezuela, including Margarita Island and Los Testigos Archipelago. The species

660 also is present in most of Northern Venezuela from eastern Andes to the Peninsula de Paria,
661 including the coastal ranges, and the lowland known as Llanos and the Orinoco Delta in the
662 Venezuelan Guayana.

663
664 **Remarks** Population from the Maracaibo-like basin and those from the Cordillera de Merida on
665 the Venezuelan Andes need to be evaluated to assess if these are conspecific with *O. rutherfordi*.
666 We believe it is likely that the population from southern and Amazonian Venezuela are *O.*
667 *aeneus*.

668
669 **Habitat** The holotype was resting coiled on a branch of *Miconia* sp. (Family Melastomataceae)
670 shrub at night, in a garden approx. five meters from a building. Top of the head and dorsum light
671 brown with occasional dark flecks, lateral stripe on head darker brown, venter yellow on head
672 and first few centimeters of body then fading to light tan. This species has been found in
673 relatively open habitats at Aripo Savanna in Trinidad as well as in secondary forests and in forest
674 edge situations. On Tobago it was found in roadside vegetation and in old cacao plantations. In
675 Venezuela, MBLUZ 1268 was collected active in a bush circa 1.5 m above the ground on a dry
676 creek.

677
678 **Etymology** This snake is named in honor of Mike G. Rutherford, collector of the holotype and
679 Curator of the Zoology Museum at the University of the West Indies, for his contributions to the
680 zoology and natural history of Trinidad and Tobago.

681

682 **Comparison** A vine snake with eight upper labials, two of them border the orbit, three are
683 behind the orbit and the shortest is the seventh. All other brown vine snake species have eight or
684 nine upper labials with three bordering the orbit and the shortest is the seventh. *Oxybelis aeneus*,
685 *O. koehleri*, *O. microphthalmus*, and those from Panama have eight or nine upper labials and the
686 fifth is the shortest.

687

688 ***Oxybelis vittatus* (Girard 1854)**

689 Striped Brown Vine Snake

690 *Dryinus aeneus* – Wagler 1824: 12

691 *Dryophis vittatus* – Girard 1854: 226.

692 *Oxybelis aeneus auratus* – Bogert and Oliver 1945: 381

693 *Oxybelis aeneus* – Keiser 1974: 7

694

695 **Holotype** USNM 7315 from Taboga Island, Bay of Panama, Panama. Girard (1854) reports the
696 holotype has 193 ventral scales and 165 plus subcaudal scales (the tail is broken).

697

698 **Diagnosis** Using data from our examination of specimens from Panam we constructed the
699 following description for *Oxybelis vittatus*. A vine snake with (1) three upper labials (4-5-6)
700 bordering the orbit; (2) transverse black bars or spots on the anterior body; (3) a pale, indistinct
701 stripe on the mid ventral, and black mottling; (4) eye diameter greater than length of preocular;
702 (5) second pair of chin shields in contact for most of their length; (6) eight upper labials, three
703 behind the orbit; (7) from above the snout is tapered and terminally rounded (snout type A); (8)
704 supraoculars longer than the prefrontals; (9) last upper labial longer than primary temporal; (10)

705 lower surface of head uniform and pale; (11) second upper labial does not contact the preocular
706 (Fig. 15).

707

708 **Variation** Rostral is barely visible from above and followed by nine plate-like scales on the
709 crown: a pair of internasals, a pair of prefrontals, the frontal and two larger supraoculars, and a
710 pair of parietals. Preoculars extend slightly on to the crown between the prefrontals and
711 supraoculars. In profile the nasal scale is elongate extending from the edge of the rostral, beyond
712 the posterior edge of the internasal to the anterior border of the fused prefrontal-loreal. Preocular
713 scale is long and greater in length than the diameter of the eye. The eye diameter/internasal ratio
714 in this species averages 1.16 ($n = 9$, $r = 1.05$ – 1.31 , $SD = 0.17$). Scales bordering the orbit are the
715 preocular, the supraocular, two post oculars (the upper one is usually the largest), and upper
716 labials 4–5–6. The primary temporal contacts both postoculars, the parietal, two secondary
717 temporals, and upper labials 5–6–7–8, 6–7–8 or 6–7–8–9 are common arrangements. Upper
718 labials range from 8–10. Of 20 sides examined 13 (65%) had 8 upper labials; six (30%) sides had
719 9 upper labials, and one side (0.05%) had 10 upper labials. The shortest upper labial can be the
720 fourth or the fifth. The longest upper labial is the last eight, nine, or ten. Upper labials 1–2
721 contact the nasal, 2–3 contact the prefrontal-loreal, 3–4 contact the preocular. The tallest upper
722 labial can be the sixth or seventh. Lower labials range from 7–9, (usually 8 or 9). The first four
723 (rarely five) contact the anterior chin shields, a total of six contact both pair of chin shields.

724 In males total lengths vary from 1149–1323 mm ($n = 2$, $x = 1236.0$ $SD = 87.00$), SVL
725 varies from 653–763 mm ($n = 2$, $x = 708$, $SD = 55.00$) tail lengths vary from 460–560 mm ($n =$
726 2 , $x = 505.33$, $SD = 41.35$); tail/SVL ratios vary from 0.73–0.76 ($n = 2$, $x = 0.74$, $SD = 0.01$). In
727 females, total lengths vary from 940–1345 mm ($n = 7$, $x = 1138.57$, $SD = 128.85$), SVL varies

728 from 510–832 (n = 7, x = 670 mm, SD = 95.53), tails vary from 410–518 mm (n = 7, x = 505.33,
729 SD = 41.35). Tail/SVL ratios in females vary from 0.62–0.84 (x = 0.74, SD = 0.01).

730 Ventrals in males vary from 179–187 (n = 5, x = 183.4, SD = 3.38); ventrals in females
731 vary from 182–193 (n = 7, x = 186.83, SD = 4.02. Subcaudals not counted because of damaged
732 tails.

733
734 **Colouration and pattern** The crown of the head and upper face are brown to tan, they may be
735 uniform or slightly mottled. Upper labials and ventral surface of the head are a uniform cream.
736 The transition in colour is separated by a preocular dark brown stripe extending from the nasal
737 scale, under the eye and onto the anterior body. This stripe may continue as a series of spots onto
738 the body. On the anterior body the first two scale rows are the same yellow colour as the ventral
739 surface, and form a ventrolateral stripe. At mid–body, the first four dorsal scale rows and the
740 lower half of the fifth scale row have a dark pigment streak in the middle of the scale giving the
741 impression of a faint stripe on each scale row, scale rows 6–8 lack the dark pigmentation. The
742 ventral surface is often flecked with dark pigment and indistinct lateral stripes on the edges of the
743 ventrals.

744
745 **Geographic distribution** Panama likely southward into the Chocoan region of Colombia.

746
747 **Comparison** A brown vine snake with eight upper labials, two behind the orbit, and the fifth is
748 the shortest; the second pair of chin shields are in contact for most of their length, and the
749 primary temporal is shorter than the last upper labial. *Oxybelis aeneus* and *O. rutherfordi* have
750 the second pair of chin shields separated, *O. koehleri* and *O. microphthalmus* usually have three

751 upper labials behind the orbit and the last upper labial is equal to the length of the primary
752 temporal.

753

754 **Discussion**

755 Biologists traditionally have relied on morphological traits to sort species, resulting in an
756 underestimation of diversity and incomplete understanding of the lineages' evolutionary history
757 (Beheregaray and Caccone 2007). Many cryptic taxa have remained unrecognized because
758 morphological variation may be subtle and overlooked, interpreted as individual variation, or
759 variation associated with a cline (Oliver et al. 2009; Padial et al. 2010). With the increase in
760 molecular phylogeographic studies, numerous wide-ranging “species” are found to be complexes
761 harboring cryptic species-level lineages (e.g. Bickford et al. 2006; Jadin et al. 2012; Murphy et
762 al. 2016; Ruane et al. 2018).

763 Vine Snakes in the *Oxybelis aeneus* complex appear incredibly diverse (Fig. 1) yet are
764 conservative in much of their external morphology, making diagnoses difficult. Like other vine
765 snakes they are attenuated with an elongated head distinct from the forebody with a stereotypical
766 nine plate-like scales on the crown: a pair of internasals, a pair of prefrontals that fuse with the
767 loreal, the frontal, two supraoculars, and a pair of parietals. In populations of the *O. aeneus*
768 complex, scales bordering the orbit include the preocular, the supraocular, two small postoculars
769 and upper labials 4–5–6 in most taxa, but 4–5 or 5–6 in others. Most taxa have upper labials 1–2
770 contacting the nasal, 2–3 contacting the prefrontal-loreal, 3–4 contact the preocular. The crown
771 of the head and upper face are usually golden–brown to tan with upper labials and ventral surface
772 of the head usually a uniform cream. The colour change is separated by a dark brown or black
773 preocular stripe extending from the nasal scale, under the eye and onto the anterior body.

774 Despite the similarities listed above, our morphological examination of specimens from
775 across the range suggests the *O. aeneus* complex is composed of numerous species that do
776 possess some distinguishing features (Table 4). Subsequently, our phylogenetic analyses of
777 *Oxybelis* lineages (Figs 3 and 5) support the presence of at least eight distinct species under the
778 general lineage concept of species (de Queiroz 1998), a considerably greater number than the
779 four taxa previously recognized. Finding diagnostic characters for each species is challenging but
780 possible, such as specimens of *O. rutherfordi* consistently showing the fourth and fifth upper
781 labial bordering the orbit. Likewise, some species are defined by having combinations of
782 characters not found in their congeners such as *O. microphthalmus* having a preocular longer
783 than diameter of the eye and a narrow, tapered snout with a barely rounded rostrum, while *O.*
784 *potosiensis* has a preocular less than the diameter of the eye and a broad, only slightly tapered
785 snout with a very rounded rostrum. These features, and others, are described for distinguishing
786 among the taxa we recognize above.

787

788 **Future prospects**

789 Recently, Hillis (2019) reviewed the importance of proximate sampling in taxonomy and
790 the need for proper interpretation of multispecies coalescent models. Similarly, Chamber and
791 Hillis (2020) argue that new species designations for widely distributed taxa should address
792 multiple evidences of geographic variation (i.e., behavior, genes, morphology) as well as data on
793 reproductive isolation and gene flow. In concert with these recommendations, this work
794 advances our understanding of the species diversity and evolutionary history of New World vine
795 snakes beyond the publication of Jadin et al. (2019), which strictly focused on molecular
796 analyses suggesting multiple taxa. In this study, we followed, where possible, such observations

797 by limiting our systematic analyses to the northern distribution of the genus, as southern
798 population sampling remains deficient. Our increased molecular sampling has added described
799 taxa (e.g. *O. brevirostris* and *O. potosiensis*) and new populations to our phylogenetic analyses,
800 while novel morphological data have allowed us to justify several lineages of Brown Vine
801 Snakes as distinct. Additional molecular and morphological sampling of populations within the
802 range of what was formerly considered *O. aeneus*, especially throughout South America, surely
803 will recover novel taxa not identified in this study.

804 Beyond the addition of species, the broad geographic distribution of these taxa,
805 particularly those populations formerly identified as *O. aeneus*, indicates that greater sampling of
806 these taxa will allow for a more in depth understanding of not only the species diversity and
807 evolutionary history of this complex, but provide a more complete understanding of the
808 geological and biological processes driving diversification across the Neotropics. In line with
809 this, molecular dating and genetic analyses of *O. vittatus* in South America may further explain
810 the role of the Panamanian isthmus closing and the colonization of South America by New
811 World vine snakes. Genetic assessment of Trans- and Cis-Andean populations will elucidate
812 vicariant speciation events and the timing of such. Furthermore, establishing more accurate
813 species distribution ranges will aid in the understanding of habitat boundaries and habitat
814 selection pressures between populations and species contact zones (e.g., *O. koehleri* and *O.*
815 *brevirostris*). For example, sampling in Costa Rica will clarify the southern range of *O.*
816 *koehleri* and likely northern range of *O. vittatus*.

817 Finally, our findings include strong support for a paraphyletic *O. fulgidus* with respect to
818 *O. wilsoni* and that the Isthmus of Panama is the likely dividing point between two divergent
819 sister clades. Although our analyses support the splitting of *O. fulgidus* North and South of the

820 Isthmus of Panama, we recommend maintaining the current taxonomy until a more thorough
821 taxonomic revision of the Green Vine Snakes is complete.

822

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853 are available from the corresponding author on reasonable request.

854

855 **Compliance with ethical standards**

856 **Conflict of interest** The authors declare that they have no conflict of interest.

857

858

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1038

1039 **Fig. 1** In life photographs of *Oxybelis aeneus* (*sensu* Keiser, 1974) from throughout its
1040 distribution showing tremendous morphological variation. A, Reserva Amazonica, Peru (W. E.
1041 Duellman); B, Santa Rosa, Costa Rica (L. Porras); C, Venezuela (D. A. Briceño C.); D, Jalapão,
1042 Tocantins, Brazil (LJV). Photos a and d show a gaping mouth that is a typical defense behaviour
1043 for members of the *Oxybelis aeneus* complex.

1044

1045 **Fig. 2** Image showing the variability in snout shape among populations of *Oxybelis aeneus*. A, a
1046 slender taper from occipital region to rostral scale (UAZ 16787, Arizona, USA); B, tapered, but
1047 snout in front of eyes is slightly constricted (FMNH 64417, Brazil); C, a taper from occipital
1048 region but the area in front of the eyes is broad and the rostral is rounded (UIMNH 25069, San
1049 Luis Potosí, Mexico).

1050

1051 **Fig. 3** Localities from which we obtained tissues for molecular work, other than the type locality
1052 represented by a black circle. Colors represent tissues of Brown Vine Snakes from Central
1053 America (orange), Eastern Mexico (light blue), Panama (yellow), Northern South America
1054 (purple), and the Western Region (light green), Other taxa with molecular data represented are
1055 *O. brevirostris* (dark green), *O. fulgidus* (gray and dark yellow), and *O. wilsoni* (dark blue).

1056 Inserts are a Brown Vine Snake from Pima Co. AZ, USA taken by JCM (left) and SVD quartets
1057 species tree (right). Node values on species tree represent support values from 100 non-
1058 parametric bootstrap replicates.

1059

1060 **Fig. 4** Plot of discrimination analysis of sixteen morphological characters, showing clustering
1061 among geographically defined groups. Colors represent specimens from: Central America (CA,

1062 orange), Central Brazil (CB, black stars), Eastern Mexico (EM, blue), Northern South America
1063 (NSA, purple), Panama (P, yellow), and Western Region (WR, green). Colors correspond to
1064 those in Figure 3.

1065
1066 **Fig 5** Phylogenetic estimate of relationships within *Oxybelis* estimated from a Bayesian 50%
1067 majority-rule consensus phylogram using a multilocus dataset (cyt *b*, ND4, 12S, 16S, cmos and
1068 PRLR; total of 3663 bp) with posterior probabilities (≥ 95) represented at the node (red circles).
1069 Values adjacent to nodes represent additional support values (SH-aLRT > 80% and UFboot >
1070 95%) from maximum likelihood (ML) analyses of the partitioned dataset obtained from IQ-
1071 TREE. Inserts are *O. fulgidus* (MBLUZ 1480; above) from the Sierra de Imataca, Bolivar,
1072 Venezuela and *O. aeneus* (below) photographed at Quebrada Chacaito, El Avila National Park,
1073 north of Caracas in Venezuela. Photographs were taken by D. A. Briceño C. and L. A. Rodríguez
1074 J., respectively. Colors correspond to those in Figures 3 and 4.

1075
1076 **Fig. 6** Bayesian posterior probability support for species/populations within *Oxybelis* from BPP
1077 analyses of the combined mtDNA and nDNA data. Four joint species delimitation/species tree
1078 analyses (A11) were performed to test the impact of species delimitation algorithm used (Alg 0,
1079 Alg 1) and the theta prior ((Large = IG [3, 0.04]); (Small = IG [3, 0.004])) on the results.
1080 Abbreviations after *O. fulgidus* refer to populations from South America (SA), Upper Central
1081 America (UCA = Guatemala and Yucatan), Lower Central America (LCA = Honduras and
1082 Mexico), and Central America (CA = UCA, LCA, and *O. wilsoni*) while those after *O. aeneus*
1083 refer to populations from Panama (P), Northern South America (NSA), Eastern Mexico (EM),
1084 Western Region (WR), and Central America (CA).

1085

1086 **Fig. 7** Specimen of *O. aeneus* (FMNH 64417) from Manaus, Amazonas, Brazil. This specimen
1087 was collected c. 518 km from the type locality.

1088

1089 **Fig. 8** Holotype of *Oxybelis koehleri* sp. nov., UTA R-46846 preserved; a, Dorsal; b, top of the
1090 head; c, profile; d, ventral views. Scale bar = 1 cm.

1091

1092 **Fig. 9** *Oxybelis koehleri* sp. nov. in life. a, Mocorón, Gracias a Dios, Honduras (C. J. Franklin);
1093 b, Santa Rosa, Costa Rica (L. Porras).

1094

1095 **Fig. 10** *Oxybelis microphthalmus* in-life. a and b show the profiles while C shows the gaping
1096 mouth defensive behaviour. Photograph A by JCM and b and c by J. Reyes-Velasco.

1097

1098 **Fig. 11** a–d, Holotype of *Oxybelis potosiensis* Taylor 1941 (UIMNH 25069) from San Luis
1099 Potosí, Mexico; B, Whole specimen; C, the crown, note the lack of a constriction anterior to the
1100 eyes, rostral not visible from above, and the relatively broad snout; D, the profile; E,
1101 arrangement of the chin shields.

1102

1103 **Fig. 12** Holotype (UTA R-64851) of *Oxybelis rutherfordi* sp. nov. in life prior to preservation
1104 collected in the Arima Valley, Trinidad (M.G. Rutherford).

1105

1106 **Fig. 13** Holotype *Oxybelis rutherfordi* sp. nov., UTA R-64851, preserved; A, Dorsal; B, top of
1107 the head; C, profile; D, ventral views. Scale bar = 1 cm.

1108

1109 **Fig. 14.** *Oxybelis rutherfordi* sp. nov. in life. A and B, Tobago specimens. JCM; C. Aripo
1110 Savanna, Trinidad. JCM; D, An exceptionally large specimen (2.1 m) from Tobago (M.
1111 Patrikeev).

1112

1113 **Fig. 15** *Oxybelis vittatus*. FMNH 170133, from the Canal Zone of Panama. A, Profile; B, Crown;
1114 C, Underside of head.

1115

1116

1117 Appendix I. Specimens examined

1118 Museum acronyms follow McDiarmid et al. (1999).

1119 *Oxybelis aeneus* – (n = 8) **Brazil:** FMNH 64417 Amazonas; FMNH 19203 Pará; KU R-124605,
 1120 124606, 140173, MCZ R-2582, 2778, and 53211 Pará.

1121

1122 *Oxybelis brevirostris* – (n = 2) **Ecuador:** UTA R-55952–53 Canton San Lorenzo: Parroquia
 1123 Santa Rita, Esmeraldas.

1124

1125 *O. koehleri* – (n = 34) **Costa Rica:** FMNH 179061 Cartago, Turrialba; **El Salvador:** FMNH
 1126 10997 Chalatenango; San Jose del Sacare, 3600'; FMNH 10998 Morazán, Divisadero; FMNH
 1127 64955, La Libertad, Volcan San Salvador, 1917 Lava, 500 m; FMNH 64956 La Paz, Los
 1128 Blancos; KU 289907 Usulután: Isla San Sebastian; **Guatemala:** FMNH 20088 Izabal: Bobos
 1129 Plantation, near Playitas; FMNH 20171 and 20418 Sololá: Olas de Moca; UTA R-46795
 1130 Chiguimula; UTA R-45880 Huehuetenango; UTA R-22182–83, 33040, 33042, 37256, 39236,
 1131 42433 Izabal; UTA R-37258 Peten; UTA R-46846 Zacapa, El Arenal; **Honduras:** FMNH 22231
 1132 Tela; FMNH 27050 San Pedro Sula; FMNH 34565, 34571, 34574, 34576, Bay Islands: Roatan,
 1133 near Coxen Hole; UTA R-55231 Bay Islands: Roatan; FMNH 34770 Yoro, Portillo Grande;
 1134 FMNH 40872 Gracias; UTA R-46865 Comayagua, Playitos: Aldea "Lo de Reina", 785 m; UTA
 1135 R-53176–78 Honduras: Gracias a Dios, Mocerón, 30–50 m. **Nicaragua:** UTA R-44838 Jinotega,
 1136 El Paraíso Km 152.5, carretera Jinotega-Matagalpa, 1490 m.

1137

1138 *O. microphthalmus* – (n = 36) **United States:** Arizona: UAZ 47314 2.8 mi west of Sycamore
 1139 Canyon; UAZ 519225 miles east Sycamore Canyon, Ruby Rd.; UAZ 39544 Patagonia Mts.;

1140 Santa Cruz County: ASU 33314, ASU 33364, ASU 35069, ASU 35563, UAZ 16787, UAZ
1141 39545; No specific locality: UMMZ 75779. **Mexico:** Colima: UTA R-57658; Guerrero UAZ
1142 106056, 106058, 38448, 38451, 38455, 38461, 38467, 106051, 106057, 106059, 106054;
1143 Oaxaca: UAZ 106055, 117841–43, 178707, 178708; Sonora: UAZ 26972 0.5 miles West
1144 Alamos; UAZ 28279 8.8 miles east Alamos; Alamos UAZ 16797, UAZ 26973, ASU 06735,
1145 ASU 68990, ASU 88990; 35 miles east of Cannansa junction w/ Aqua Prieta Rd. UAZ 16796.
1146
1147 *O. potosiensis* – (n = 6) **Mexico:** UIMNH 25069 San Luis Potosí; UTA R-6107–10, 8752, and
1148 12368 S of Zapotitl, Puebla; UTA R-9014 6.0 mi E San Rafael, road to Rancho Nuevo,
1149 Tamaulipas.
1150
1151 *O. rutherfordi* – (n = 20) **Tobago:** FMNH 251213 Bloody Bay Rd, between Roxborough and
1152 Bloody Bay; **Trinidad:** FMNH 49973 no specific locality; FMNH 49974–75 Brickfield; FMNH
1153 49976 Mount Harris, FMNH 49977–85 San Rafael; FMNH 215838 circa 3 miles S Simla-Quarry
1154 Rd, on Arima-Blanchisseuse Rd, egg farm; FMNH 215839 circa 2 miles S Simla-Quarry Rd, on
1155 Arima-Blanchisseuse Rd.; UTA R-64851 Arima Valley, William Beebe Tropical Research
1156 Centre, c. 6 km N Arima, 247 m; **Venezuela:** FMNH 17839–40 Puerto Viejo, Península de
1157 Paria, Sucre; MBLUZ 1268 between San Francisco de Macanao and Cerro Los Cedros, Isla de
1158 Margarita, Nueva Esparta.
1159
1160 *O. vittatus* – (n = 16) **Panama:** FMNH 152067 Almirante; FMNH 83552, 130674, 131314 Canal
1161 Zone: Summit; FMNH 161478 Canal Zone: Barro Colorado Island; FMNH 153665 Coiba
1162 Island; FMNH 170132 San Blas Territory: Soskantupu, 8°57'N, 77°44'W, 1 m; FMNH 154043

- 1163 Bocas del Toro, 11 km NW Almirante 600 ft.; FMNH 154478, 154517 no locality data; MCZ R-
1164 22274, 22231, and 25118 Canal Zone; UF 65037, 65038, and 170469 Canal Zone.
1165

1166 Appendix II. Genbank numbers for DNA sequences of New World colubrids analyzed in this
 1167 study.

<i>Species</i>	cyt <i>b</i>	ND4	12S	16S	cmos
<i>Coluber constrictor</i>	AY486914	AY487041	AY122819	L01770	AY486938
<i>Drymarchon corais</i>	AF471064	DQ902314	HM565758	HM582218	AF471137
<i>Leptophis depressirostris</i>	KR814686	KR814724	KR814617	KR814643	KR814682
<i>Oxybelis aeneus Arizona</i>	AF471056	————	————	————	AF471148
<i>Oxybelis aeneus French Guiana</i>	————	————	AF158416	AF158498	————
<i>Oxybelis aeneus</i>	————	————	HM565765	HM582225	HQ157829
<i>Oxybelis fulgidus</i>	MK209278	————	MK209203	MK209316	————
<i>Oxybelis fulgidus French Guiana</i>	————	————	AF158432	AF158497	————
<i>Oxybelis wilsoni</i>	KR814689	KR814710	KR814626	KR814647	KR814669

1168