



A revision and key for the tribe Diaphorolepidini (Serpentes: Dipsadidae) and checklist for the genus *Synophis*

R. ALEXANDER PYRON^{1,7}, ALEJANDRO ARTEAGA^{2,3}, LOURDES Y. ECHEVARRÍA^{4,5}
& OMAR TORRES-CARVAJAL⁶

¹Department of Biological Sciences, The George Washington University, 2023 G St. NW, Washington, D.C. 20052 USA

²Centro de Investigación en Biodiversidad y Cambio Climático (BioCamb), Ingeniería en Biodiversidad y Recursos Genéticos, Facultad de Ciencias de Medio Ambiente, Universidad Tecnológica Indoamérica, Calle Machala y Sabanilla, Quito, Ecuador

³Tropical Herping, Av. 6 de Diciembre N31-50 y Whymper, Torres Santa Fe, Quito 170517, Ecuador

⁴Laboratório de Sistemática de Vertebrados, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS, Brazil

⁵División de Herpetología-Centro de Ornitología y Biodiversidad (CORBIDI), Santa Rita N°105 Of. 202, Urb. Huertos de San Antonio, Surco, Lima, Perú

⁶Museo de Zoología, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Avenida 12 de Octubre y Roca, Apartado 17-01-2184, Quito, Ecuador

⁷Corresponding author. E-mail: rpyron@colubroid.org

Abstract

The genus *Synophis* contains a number of enigmatic species, distributed primarily in the Andean highlands of northern South America. Their extreme crypsis and rarity has precluded detailed study of most species. A recent flurry of collection activity resulted in the accession of many new specimens, and the description of 4 new species in 2015, doubling the number of described taxa. However, lingering questions remain regarding the assignment of many new and historical specimens, the morphological limits and geographical ranges of the species, and their phylogenetic relationships. We analyze new and existing morphological and molecular data to produce a new molecular phylogeny and revised morphological descriptions. We validate the previously unavailable tribe name Diaphorolepidini Jenner, Pyron, Arteaga, Echevarría, & Torres-Carvajal **tribe nov.**, describe a 9th species *Synophis niceforomariae* Pyron, Arteaga, Echevarría, & Torres-Carvajal **sp. nov.**, and offer new Standard Names in English and Spanish for the group: Andean Shadow Snakes and Culebras Andinas de la Sombra, respectively. A variety of features such as vertebrae and hemipenes show an interesting range of variation in the group, which should be evaluated in future studies, to refine species limits and diagnoses further. Cryptic and undiscovered diversity undoubtedly remains, and we hope this summary provides a robust basis for future work.

Key words: species delimitation, taxonomy, phylogeny, morphological, molecular, systematics, Diaphorolepidini, *Synophis*, *Synophis niceforomariae*, Andean Shadow Snakes

Introduction

Snakes of the tribe "Diaphorolepidini" (see Jenner 1981; Pyron *et al.* 2015) have long been considered enigmatic, with only a handful of individuals collected over 150 years (Jan 1863; Peracca 1896; Boulenger 1898; Nicéforo - María 1950; Bogert 1964; Fritts & Smith 1969; Hillis 1990; Sheil & Grant 2001). Remarkably, the last several field seasons have seen a drastic increase in the number of accessioned specimens, culminating in the description of four new species in 2015 (Pyron *et al.* 2015; Torres-Carvajal *et al.* 2015). However, confusion remains over species boundaries and the taxonomic assignment of referred material, resulting in uncertainty in geographic distributions and diagnostic characters for some species, such as *S. bicolor* and *S. lasallei*. Finally, the tribe name "Diaphorolepidini Jenner, 1981" is unavailable under Article 8 of the International Code of Zoological Nomenclature (ICZN 1999), as it originates from an unpublished PhD thesis (Jenner 1981).

Here, we take advantage of the combined molecular datasets of Pyron *et al.* (2015) and Torres-Carvajal *et al.* (2015), as well as new sequence data, to generate a new phylogeny of Dipsadidae including dense species-level

sampling in *Synophis*. Similarly, we combine the morphological and distributional datasets of those two studies, to generate new diagnoses and updated species limits within *Synophis*. We clarify lingering uncertainty regarding several taxa, describe a new species from the Colombian highlands, and provide more descriptive Standard English Names. Finally, we validate the tribe name "Diaphorolepidini" and provide a key to the species. Combined, these updates provide a synthesis of the recent developments in diaphorolepidine systematics, and a firm foundation for future studies investigating diversity in *Synophis*, which is undoubtedly much higher than known at present.

Materials and methods

Molecular dataset. We combined the molecular datasets of Pyron *et al.* (2015) and Torres-Carvajal *et al.* (2015), which resulted in sampling 30 individuals of at least 8 diaphorolepidine species, and ~245 other dipsadid species. To this, we added other existing data from GenBank and gracious donations from our colleagues. In total, we sampled nine genes, four mitochondrial (12S, 16S, CYTB, and ND4), and five nuclear (BDNF, CMOS, DNAH3, HOXA13, and NT3). These genes have been used in numerous previous studies of snake systematics (Vidal *et al.* 2007; Pyron *et al.* 2011; Grazziotin *et al.* 2012). Overall, the matrix was 59% complete. Within the sampled diaphorolepidines, all 30 specimens were sampled for a ~2,000bp mitochondrial segment consisting of 16S, CYTB, and ND4 with 88% completeness, in addition to the various other genes sampled for some of the specimens.

Data were aligned using MAFFT (Katoh & Standley 2013) under the default parameters in Geneious 7.1.9 (Biomatters Ltd.). One sequence for CYTB from MZUTI3694 (*Synophis calamitus*; KR814772) used in Pyron *et al.* (2015) was found not to group within *Synophis* on preliminary examination of the individual alignments. Raw chromatograms of MZUTI3694 showed doubled peaks at some variable sites, possibly indicating PCR contamination. Thus, we omitted this sequence from our analyses. This did not occur for the other genes sequenced for that sample, which grouped with other *S. calamitus* in preliminary analyses.

We determined the optimal partitioning strategy using PartitionFinder (Lanfear *et al.* 2012). We estimated the phylogeny using MrBayes 3.2.5 (Ronquist *et al.* 2012), with 4 runs of 4 chains each, run for 20 million generations with the first 25% discarded as burnin. Convergence was assumed as the average standard deviation of split frequencies went to zero and the potential scale reduction factors went to one (Ronquist *et al.* 2012). The GenBank accession numbers for the new and existing data are given in Appendix I.

Morphological & distributional datasets. Both Pyron *et al.* (2015) and Torres-Carvajal *et al.* (2015) presented new, revised, or updated diagnoses for *Synophis* species, along with associated distributional data of referred specimens. As both made taxonomic changes that affected the diagnoses of numerous species, these data needed to be cross-referenced to produce coherent summaries for individual species. Thus, we compared the data given in each manuscript, re-assigned specimens as necessary, and generated revised estimates of morphological species limits. We focus here primarily on the external, objective, and unambiguous characters presented by both studies, such as scale counts, with occasional reference to subjective features such as the degree of keeling.

Specifically, we report counts of infralabials (IL); supralabials (SL); postoculars (PO); ventrals (V); subcaudals (SC); nuchal (D1), midbody (D2), and anal (D3) dorsal scale-rows; measurements of SVL and TL in millimeters; contact of intranasals; presence of loreal; and sex of each specimen when known, along with comments on sexual dimorphism. We also report evidence of light-colored nuchal collars; relief of nuchal and dorsal scales; and condition of the hemipenes in male specimens when observed. These are tabulated across species to provide updated estimates of species limits. These will be useful for identifying cryptic species and diagnosing new taxa in future studies. For *Synophis bogerti* and *S. calamitus*, which had multiple samples positively identified as male and female, we tested for sexual dimorphism using a *t*-test. If reported as a single range, there was no significant difference. If significant ($P < 0.05$), we report the ranges for the sexes.

Results and discussion

The molecular phylogeny (Fig. 1) is very similar to most previous results (Zaher *et al.* 2009; Pyron *et al.* 2011; Grazziotin *et al.* 2012; Pyron *et al.* 2013; Pyron *et al.* 2015; Torres-Carvajal *et al.* 2015). "Diaphorolepidini" is

strongly supported (Pp=100%) as the sister lineage of the primarily Central American clade of dipsadines. The genus *Synopsis* is strongly supported (95%) as monophyletic, as are each of the included species for which more than one individual was sampled: *S. bicolor*, *S. zaheri*, *S. calamitus*, *S. insulomontanus*, *S. zamora*, and *S. bogerti*. The sampling reveals that several specimens were mis-classified by Pyron *et al.* (2015) and Torres-Carvajal *et al.* (2015) by implication, as well as high cryptic diversity in *S. calamitus*, and the genetic distinctiveness of a new species in the *S. bicolor* group (Table 1; Figs. 1–3).

Articles 8 and 9 of the ICZN provide the criteria for what is and is not a published work. Many products, such as PhD theses, are considered unpublished, as per the Example of Article 9.12. Thus, "Diaphorolepidini Jenner, 1981" is not an available nomen. We rectify this here by formally introducing the name. By her consent, it is to be considered authored by Janann V. Jenner and the present authors, as published "*in*" this manuscript.

Diaphorolepidini tribe nov.

Content. *Diaphorolepis* Jan, 1863 (type genus), *Emmochliophis* Fritts & Smith, 1969, *Synopsis* Peracca, 1896.

Diagnosis. A group of relatively small-sized (<550mm SVL), slender, lizard-eating dipsadid snakes restricted to the Darien of Panama and northern Andes of South America, diagnosable from all other similar or related species by possessing fused prefrontals and either an expanded intervertebral scale row (*Diaphorolepis*) or expanded zygapophyses and neural spines in adults (*Emmochliophis* and *Synopsis*).

Notes. This is a greatly restricted definition of Diaphorolepidini over the original informal formulation, which included *Atractus*, *Chersodromus*, *Crisantophis*, *Elapomorphus*, *Enulius*, *Gomesophis*, *Pseudotomodon*, *Ptychophis*, and *Sordellina* (Jenner, 1981).

Additionally, we propose the following phylogenetic definition for Diaphorolepidini according to the rules of the draft of the International Code for Phylogenetic Nomenclature (ICPN, Cantino and de Queiroz, 2007).

Diaphorolepidini (*nomen cladi novum*)

Definition. The crown clade originating with the most recent common ancestor of *Diaphorolepis wagneri* Jan, 1863, *Emmochliophis* (*Synopsis*) *miops* (Boulenger, 1898), and *Synopsis bicolor* Peracca, 1896.

Reference phylogeny. Fig. 1 of this paper.

Hypothesized composition. *Diaphorolepis* Jan, 1863, *Emmochliophis* Fritts & Smith, 1969, and *Synopsis* Peracca, 1896.

Diagnostic apomorphies. Possession of fused prefrontals and either an expanded vertebral scale row (*Diaphorolepis*) or expanded zygapophyses and neural spines in adults (*Emmochliophis* and *Synopsis*).

Comments. The original definition of Diaphorolepidini by Jenner (1981) differs from the one presented here in that it also included *Atractus*, *Chersodromus*, *Crisantophis*, *Elapomorphus*, *Enulius*, *Gomesophis*, *Pseudotomodon*, *Ptychophis*, and *Sordellina*.

Pyron *et al.* (2015) also reported on a population of *Synopsis* cf. *bicolor* from the highlands of central Colombia (Fig. 4), which is morphologically distinct from the *S. bicolor sensu stricto* populations of the Chocó lowlands. Our molecular results here confirm the genetic distinctiveness of this population, which is weakly supported as the sister lineage of *S. bicolor sensu stricto*. Given the genetic, geographic, elevational, and morphological differences, we here name it

Synopsis niceforomariae sp. nov.

Holotype. MHUA14577 (Fig. 2), adult male collected 24 November 2007 at Finca La Esperanza, Valle de La Manguita, Municipio Amalfi, Departamento Antioquia, Colombia (N6.978611, W-75.044444; 1394m).

Paratypes. MHUA14413 (Fig. 3), adult collected at Municipio Anorí, Departamento Antioquia, Colombia (N6.987778, W-75.044444; 1320m); MLS2072, adult male collected at Municipio Campamento, Departamento Antioquia, Colombia (N6.979498, W-75.296602; 1656m).

TABLE 1. Morphological data for verified specimens of *Synophis*. Species assignments given here for vouchered specimens should supersede previous allocations, such as those given by Pyron *et al.* (2015) and Torres-Carvajal *et al.* (2015).

Species	Collection	IL	SL	PO	V	SC	D1	D2	D3	SVL	TL	Sex
<i>Synophis bicolor</i>	MECN 6732	9	8	2	174	138	19	17	17	361	236	M
<i>Synophis bicolor</i>	MECN 6733	9	8	2	174	132	19	19	17	406	245	M
<i>Synophis bicolor</i>	MECN 8076	9	8	2	183	135	19	17	17	376	233	M
<i>Synophis bicolor</i>	MZUT 257	9	8	2	180	136	-	19	17	-	-	-
<i>Synophis bicolor</i>	MZUTI 4175	11	8	2	174	143	19	19	17	365	245	M
<i>Synophis bicolor</i>	UTA R-55956	9	8	2	176	129	-	19	17	-	-	-
<i>Synophis bogerti</i>	FHGO 9186	11	9	2	164	105	19	17	17	379	184	M
<i>Synophis bogerti</i>	MECN 2220	10	8	2	165	117	19	19	17	294	146	M
<i>Synophis bogerti</i>	MZUTI 3529	11	8	2	163	106	19	19	17	407	202	M
<i>Synophis bogerti</i>	QCAZ 11070	11	8	2	168	111	19	19	17	419	184	-
<i>Synophis bogerti</i>	QCAZ 12791	10	8	2	163	115	19	19	17	367	184	M
<i>Synophis bogerti</i>	QCAZ 3511	11	8	2	161	106	19	19	17	365	197	-
<i>Synophis bogerti</i>	QCAZ 5072	10	8	2	157	114	19	19	17	422	219	F
<i>Synophis bogerti</i>	UMMZ 91550	11	9	2	160	103	-	19	17	529	235	F
<i>Synophis bogerti</i>	UMMZ 91551	-	8	2	161	105	-	19	17	535	230	F
<i>Synophis bogerti</i>	UMMZ 91552	-	8	2	166	106	-	19	17	153	61	F
<i>Synophis calamitus</i>	BMNH 1940.2.30.31	-	8	2	162	118	21	19	17	408	241	M
<i>Synophis calamitus</i>	CAS 23612	11	8	2	166	100	19	19	17	186	80	F
<i>Synophis calamitus</i>	KU 164208	9	8	1	163	125	21	19	17	142	73	-
<i>Synophis calamitus</i>	KU 197107	9	7	1	166	110	21	19	17	149	74	F
<i>Synophis calamitus</i>	MCZ R-164530	11	9	2	164	116	-	19	17	367	208	-
<i>Synophis calamitus</i>	MZUTI 3694	11	9	2	166	118	23	19	17	462	265	M
<i>Synophis calamitus</i>	QCAZ 10453	10	8	2	160	-	19	19	16	502	-	F

.....continued on the next page

TABLE 1. (Continued)

Species	Collection	IL	SL	PO	V	SC	D1	D2	D3	SVL	TL	Sex
<i>Synophis calamitus</i>	QCAZ 10508	10	8	2/0	165	108	19	19	17	496	260	F
<i>Synophis calamitus</i>	QCAZ 1136	10	8	2	161	120	19	19	17	328	194	-
<i>Synophis calamitus</i>	QCAZ 11931	8	8	1	165	109	19	19	17	364	196	M
<i>Synophis calamitus</i>	QCAZ 1688	10	8	2	161	-	19	19	17	408	-	M
<i>Synophis calamitus</i>	QCAZ 2807	10	8	2	160	110	19	19	17	487	255	F
<i>Synophis calamitus</i>	QCAZ 3386	10	8	2	157	107	19	19	17	391	213	F
<i>Synophis calamitus</i>	QCAZ 381	10	8	2	162	111	19	19	17	226	111	-
<i>Synophis calamitus</i>	QCAZ 3875	10	8	2	164	113	19	19	17	453	250	F
<i>Synophis calamitus</i>	QCAZ 5847	10	8	0/2	164	-	19	19	-	445	-	-
<i>Synophis calamitus</i>	QCAZ 7264	9	8	2	163	116	19	19	17	507	283	M
<i>Synophis calamitus</i>	QCAZ 8098	8	8	2/1	162	106	19	19	15	491	261	F
<i>Synophis calamitus</i>	TCWC 66209	11	8	2	160	96	21	19	17	-	-	-
<i>Synophis calamitus</i>	UMMZ 185812	10	8	2	165	105	-	19	17	144	66	-
<i>Synophis calamitus</i>	UMMZ 185813	10	8	2	162	122	-	-	-	257	147	-
<i>Synophis insulomontanus</i>	CORBIDI 9223	10/11	9	2	147	103	22	19	19	285	144	F
<i>Synophis insulomontanus</i>	CORBIDI 10418	11	9	2	149	-	22	21	19	380	88	F
<i>Synophis insulomontanus</i>	CORBIDI 13705	11	8/9	2	152	109	21	19	19	350	192	M
<i>Synophis insulomontanus</i>	CORBIDI 13940	11	8	2	151	108	20	19	19	335	181	M
<i>Synophis lasallei</i>	EPN S.974	-	-	2	156	116	-	21	-	175	90	M
<i>Synophis lasallei</i>	EPN S.975	-	-	2	155	119	-	21	-	354	201	M
<i>Synophis lasallei</i>	FHGO 6489	11	8	2	147	111	23	21	21	153	86	M
<i>Synophis lasallei</i>	FMNH 81313	-	-	2	154	112	-	21	-	292	158	F
<i>Synophis lasallei</i>	MCZ R-156873	11	7	1	147	115	-	-	-	412	206	-
<i>Synophis lasallei</i>	MLS/CJSP	-	-	2	144	101	-	-	-	300	170	M

.....continued on the next page

TABLE 1. (Continued)

Species	Collection	IL	SL	PO	V	SC	D1	D2	D3	SVL	TL	Sex
<i>Synophis lasallei</i>	MZUTI 4181	11	9	2	156	29	21	21	19	272	42	M
<i>Synophis lasallei</i>	USNM 233061	11	9	2	156	124	-	21	-	285	160	M
<i>Synophis lasallei</i>	USNM 233062	11	8	2	153	126	-	22	20	360	200	M
<i>Synophis lasallei</i>	USNM 233063	11	8	2	151	86	23	21	19	308	197	M
<i>Synophis lasallei</i>	USNM 233064	11	8	2	151	-	-	21	19	270	150	-
<i>Synophis niceforomariae</i>	MHUA 14413	12	8	2	193	127	-	19	-	-	-	-
<i>Synophis niceforomariae</i>	MHUA 14577	11	8	2	190	131	19	19	17	-	-	M
<i>Synophis niceforomariae</i>	MLS2072	11/10	8	2	184	127	-	19	17	407	210	M
<i>Synophis plectovertrebralis</i>	UVC 11580	8	8	1	144	91	19	19	17	212	100	M
<i>Synophis plectovertrebralis</i>	UVC 11858	7	7	1	147	79	19	19	17	196	76.5	F
<i>Synophis zaheri</i>	MZUTI 3353	8	8	2	166	112	19	19	17	351	184	M
<i>Synophis zaheri</i>	MZUTI 3355	9	8	2	169	111	19	19	17	372	194	M
<i>Synophis zamora</i>	FHGO 8340	11	8	2	153	88	21	19	17	415	199	M
<i>Synophis zamora</i>	MECN 11250	10	8	2	153	98	21	19	17	412	196	F
<i>Synophis zamora</i>	MECN 11262	-	8	2	154	118	21	21	17	306	145	M
<i>Synophis zamora</i>	MZUTI 4180	11	9	2	152	100	19	19	18	457	214	M
<i>Synophis zamora</i>	QCAZ 12773	9	8	2	153	111	19	19	17	331	176	M
<i>Synophis zamora</i>	QCAZ 9174	10	9	2	147	103	19	18	17	359	187	M
<i>Synophis zamora</i>	QCAZ 9175	10	8	2	151	109	19	19	17	340	186	M

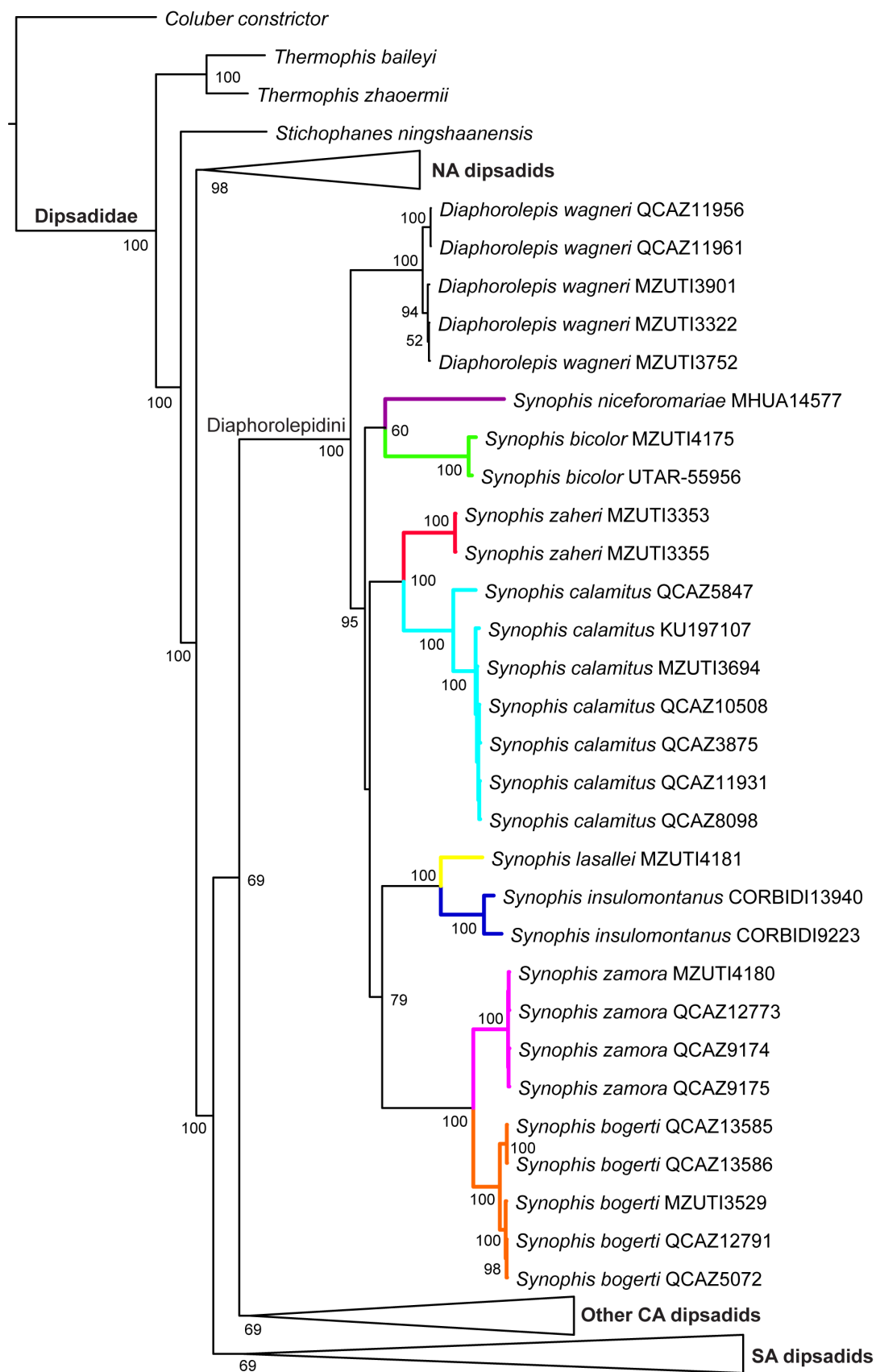


FIGURE 1. Bayesian maximum clade credibility phylogeny for Diaphorolepidini, summarized from 15 million post-burnin generations in MrBayes 3.2.5. Support values >50% are shown. Clades of primarily North American (NA), Central American (CA), and South American (SA) species other than Diaphorolepidini are collapsed.



FIGURE 2. Holotype (MHUA14577) of *Synophis niceforomariae* in life.



FIGURE 3. Paratype (MHUA14133) of *Synophis niceforomariae* in preservative.

Etymology. Named after the French priest and naturalist Hermano Nicéforo María (born Antoine Rouhaire Sizaude), who established important natural-history collections at the Instituto de la Salle in Bogotá. While numerous taxa have been named *mariarum*, *nicefori*, or some derivative (see Adler 1989), he requested in a 1968 letter that he be addressed in print using his full name, Hermano Nicéforo María (Rodríguez 2002). Thus, it seems appropriate to use the specific epithet *niceforomariae*.

Diagnosis. *Synophis niceforomariae* can be differentiated from all other similar or related species by the combination of an unmodified vertebral scale row with a single weak keel; smooth nuchal scales; absence of a nuchal collar in adults; presence of a loreal; intranasals in contact; fused prefrontals; rostral concave; anal single; no apical pits; 2 postoculars; 10–12 infralabials; 8 supralabials; 184–193 ventrals; 127–131 subcaudals; and 19-19-17 dorsal scale-rows.

Description. Small-sized, long-tailed snakes (~400mm SVL, 200mm TL) with slender bodies and head distinct from neck. Eye large (>1/3 head height), bulbous, and black in life, with pupil not easily distinguishable from iris. Pupil round in preservative (though this may be an effect of fixation). Dorsum coloration grayish-brown with iridescent sheen in life and preservation, no light-colored nuchal collar in adults, and posterior supralabials mostly unpigmented (<50%). Ventral coloration primarily bright yellow, extending onto margins of ventral scales and supralabials. Anterior one-third of ventral surface yellow; posterior two-thirds to vent becomes increasingly mottled, and ventral surface of tail same color as dorsum.

Remarks. This species was referred to as *Synophis* cf. *bicolor* by Pyron *et al.* (2015). The cleared-and-stained skull of the male holotype was prepared by Martínez (2011), with illustrations of the cranium and mandible (her Figs. 15, 18, & 22), but the hemipenis was not illustrated or described in detail. Condition of the vertebrae, which are heavily modified in *Emmochliophis* and some *Synophis* (Fritts & Smith 1969; Savitzky 1974; Hillis 1990) unknown, pending skeletal preparation, micro-CT scanning, or X-rays. Has a very small known range to the east of Yarumal, Colombia, at ~1300–1600m around Campamento, Anori, and Amalfi. Two reportedly similar specimens in the Instituto de Ciencias Naturales de la Universidad Nacional de Colombia (ICN) were collected slightly to the south of the populations sampled here, at lower elevations (~900–1300m; Table 2). We did not examine these individuals, but it seems likely that they are also *S. niceforomariae*, and that the range of the species is slightly larger (Fig. 4).

With this new species and the re-assignment of numerous specimens examined by Pyron *et al.* (2015) and Torres-Carvajal *et al.* (2015), the known species limits of many *Synophis* taxa have changed. In particular, Pyron *et al.* (2015) assigned specimens of *S. bogerti*, *S. calamitus*, and *S. niceforomariae* to *S. bicolor* and assigned specimens of *S. zamora* to *S. bicolor* and *S. lasallei*. Similarly, Torres-Carvajal assigned specimens of *S. niceforomariae* to *S. bicolor*. Using the updated information from the combined datasets (Tables 1, 2), we provide a checklist with updated summaries of geographic, elevational, and external morphological data useful for classifying the 9 species of *Synophis* known to date:

1. *Synophis niceforomariae* Pyron, Arteaga, Echevarría, & Torres-Carvajal, 2016

Range. Andean highlands of north-central Colombia, Antioquia department, near Medellín, ~1300–1700m, possibly with populations south of Medellín, ~900m.

Description. Adult size ~410mm SVL and ~210mm TL in males, smooth nuchal scales; no nuchal collar; intranasals in contact; 2 postoculars; 10–12 infralabials; 8 supralabials; 184–193 ventrals; 127–131 subcaudals; and 19-19-17 dorsal scale-rows with single, weak keel.

Notes. Includes specimens referred to as *S. bicolor* and *S. cf. bicolor* by previous authors (Nicéforo -María 1970; Pyron *et al.* 2015; Torres-Carvajal *et al.* 2015).

2. *Synophis bicolor* Peracca, 1896

Range. Chocóan lowlands of northwestern Ecuador, and presumably southwestern Colombia, ~200–300m.

Description. Adult size ~360–410mm SVL and ~230–250mm TL in males, smooth nuchal scales; no nuchal collar; intranasals in contact; 2 postoculars; 9–11 infralabials; 8 supralabials; 174–183 ventrals; 129–143 subcaudals; and 19-19-17 dorsal scale-rows with single, weak keel.

TABLE 2. Vouchered localities for *Synopsis* species examined in this study. Species assignments given here for vouchered specimens should supersede previous allocations, such as those given by Pyron *et al.* (2015) and Torres-Carvajal *et al.* (2015).

Species	Collection Number	Locality	Latitude	Longitude	Elevation
<i>Synopsis bicolor</i>	MECN 6732	Tobar Donoso, Ecuador	1.189930	-78.504130	229
<i>Synopsis bicolor</i>	MECN 6733	Sendero Awa, Ecuador	1.164400	-78.507120	257
<i>Synopsis bicolor</i>	MZUTI 4175	Itapoa, Ecuador	0.464110	-79.155470	267
<i>Synopsis bicolor</i>	UTA R-55956	Ecuador, Esmeraldas, Canton San Lorenzo	1.03212	-78.613780	318
<i>Synopsis bogerti</i>	FHGO 9186	Río Zopladora, Ecuador	-2.611510	-78.472174	1677
<i>Synopsis bogerti</i>	KU 121341	Ecuador, Pastaza, Mera	-1.457452	-78.107976	1111
<i>Synopsis bogerti</i>	MECN 2220	Puyo, Ecuador	-1.466780	-77.983350	957
<i>Synopsis bogerti</i>	MZUTI 3529	Wild Sumaco, Ecuador	-0.675700	-77.601290	1463
<i>Synopsis bogerti</i>	UMMZ 91550	Ecuador, Napo-Pastaza, Abitagua	-1.383000	-78.083000	1482
<i>Synopsis bogerti</i>	QCAZ 5072	Ecuador: Napo: Wildsumaco Wildlife Sanctuary	-0.685906	-77.598592	1379
<i>Synopsis bogerti</i>	QCAZ 12791	Ecuador: Napo: Wildsumaco Wildlife Sanctuary	-0.635667	-77.522000	1085
<i>Synopsis bogerti</i>	QCAZ 13323	Ecuador: Morona Santiago: Sardinayacu, Parque Nacional Sangay	-2.071531	-77.833606	1127
<i>Synopsis bogerti</i>	QCAZ 13585	Ecuador: Pastaza: Zarentza, Parque Nacional Llanganates	-1.362631	-78.058200	1328
<i>Synopsis bogerti</i>	QCAZ 13586	Ecuador: Pastaza: Zarentza, Parque Nacional Llanganates	-1.362569	-78.057839	1336
<i>Synopsis bogerti</i>	QCAZ 3511	Guacamayos	-0.627822	-77.833606	2047
<i>Synopsis bogerti</i>	QCAZ 11070	Reservado ecologica Antisana	-0.661806	-77.791444	1643
<i>Synopsis calamitus</i>	BMNH 1940.2.30.31	Río Solaya, Ecuador	-0.010213	-78.819510	1008
<i>Synopsis calamitus</i>	CAS 23612	Chimborazo, Naranjapata, Ecuador	-2.266667	-79.083333	763
<i>Synopsis calamitus</i>	KU 164208	9 km SE Tandayapa, Pichincha Province, Ecuador	-0.047404	-78.632804	2169
<i>Synopsis calamitus</i>	KU 197107	4 km SE Tandayapa, Pichincha Province, Ecuador	-0.012514	-78.650697	1889
<i>Synopsis calamitus</i>	MCZ R-164530	Ecuador, Pichincha, Tandapi	-0.419803	-78.801132	1714
<i>Synopsis calamitus</i>	MZUTI 3694	Tambo Tanda, Ecuador	-0.020108	-78.651012	2048
<i>Synopsis calamitus</i>	QCAZ 10453	Cotopaxi: Naranjito, Bosque Integral Otonga	-0.417820	-78.988030	1655
<i>Synopsis calamitus</i>	QCAZ 10453	Naranjito, Bosque Integral Otonga (BIO)	-0.415967	-79.004800	2110
<i>Synopsis calamitus</i>	QCAZ 1136	Chiriboga	-0.224530	-78.767750	1955

.....continued on the next page

TABLE 2. (Continued)

Species	Collection Number	Locality	Latitude	Longitude	Elevation
<i>Synopsis calamitus</i>	QCAZ 11931	Ecuador: Pichincha: Reserva Ecológica Santa Lucía	0.115690	-78.593540	1765
<i>Synopsis calamitus</i>	QCAZ 3386	Cerca a Chiriboga, Las Palmeras, La Soledad, Estación Científica Río Guajalito	-0.229000	-78.806000	2224
<i>Synopsis calamitus</i>	QCAZ 381	Tandapi	-0.418540	-78.799450	1612
<i>Synopsis calamitus</i>	QCAZ 3875	Ecuador: Cotopaxi: Naranjito, Bosque Integral Otonga	-0.414783	-79.000733	1894
<i>Synopsis calamitus</i>	QCAZ 452	Chiriboga, Pichincha Province, Ecuador	-0.226685	-78.771271	1790
<i>Synopsis calamitus</i>	QCAZ 5847	Ecuador: Carchi: 14 km El Chical-Gualchán	0.881006	-78.223010	1940
<i>Synopsis calamitus</i>	QCAZ 8098	Ecuador: Pichincha: El Cedral	0.114000	-78.569930	2272
<i>Synopsis calamitus</i>	TCWC 66209	Ecuador, Cotopaxi, Las Pampas	-0.348360	-79.076010	1238
<i>Synopsis calamitus</i>	UMMZ 185812	Ecuador, Cotopaxi, San Francisco de Las Pampas	-0.440357	-78.966629	1586
<i>Synopsis insulomontanus</i>	CORBIDI 9223	Perú: San Martin: Picota: Puesto de Control 16 Chambirillo (Cordillera Azul)	-7.069139	-76.015333	1143
<i>Synopsis insulomontanus</i>	CORBIDI 13940	Perú: Huánuco: Pachitea: Cordillera El Sira	-9.426172	-74.735167	1543
<i>Synopsis insulomontanus</i>	CORBIDI 13705	Distrito de Chinchao-Localidad de Miraflores	-9.677946	-75.836413	1825
<i>Synopsis lasallei</i>	EPN S.974	Ecuador, Napo-Pastaza, nr. Río Talin, headwaters of the Río Bobonaza	-1.466670	-77.883300	948
<i>Synopsis lasallei</i>	FHGO 6489	Ceploa, Ecuador	-1.339063	-77.670660	839
<i>Synopsis lasallei</i>	FMNH 81313	Colombia, Meta, Pico Renjifo, Serrania de la Macarena	2.476901	-73.794852	520
<i>Synopsis lasallei</i>	KU 164221	2 km SSW Río Reventador, Ecuador	-0.100000	-77.600000	1479
<i>Synopsis lasallei</i>	MCZ R-156873	Ecuador, Napo Prov., Incel Station, Cascada San Rafael, Río Quijos	-0.103401	-77.585487	1290
<i>Synopsis lasallei</i>	MLS/CJSP	N of Alban, cen. Cundinamarca Dept., cen. Colombia	4.883333	-74.450000	1983
<i>Synopsis lasallei</i>	MZUTI 4181	Sacha Yaku, Ecuador	-1.407882	-77.711092	974
<i>Synopsis lasallei</i>	USNM 233061	Río Arajuno, headwaters of, tributary of Río Napo, Pastaza, Ecuador	-1.400000	-77.883300	969
<i>Synopsis lasallei</i>	USNM 233062	Río Siquino, tributary of Río Villano, Upper Curaray, Pastaza, Ecuador	-1.455303	-77.714685	576
<i>Synopsis lasallei</i>	USNM 233063	Río Bobonaza, headwaters of, Ecuador	-1.512156	-77.833454	594
<i>Synopsis lasallei</i>	WWL 977-978	Colombia, Meta prov., Villavicencio	4.150000	-73.633333	539

.....continued on the next page

TABLE 2. (Continued)

Species	Collection Number	Locality	Latitude	Longitude	Elevation
<i>Synophis niceforomariae</i>	MHUA 14577	Colombia, Dpto. Antioquia, Mpio. Amalfi, V. da La Manguita, Fca. La Esperanza	6.978611	-75.044444	1394
<i>Synophis niceforomariae</i>	MLS 2072	Municipio Campamento, Departamento Antioquia, Colombia	6.979498	-75.296602	1656
<i>Synophis niceforomariae</i>	MHUA 14413	Colombia, Departamento Antioquia, Municipio Anori	6.987778	-75.044444	1320
<i>Synophis niceforomariae</i>	ICN 11171	Parque Nacional Natural Utría	6.386944	-75.022778	1289
<i>Synophis niceforomariae</i>	ICN 052567	Florencia, sitio El Estadero, orilla de quebrada	5.587500	-75.143300	865
<i>Synophis plectovertebralis</i>	UVC 11580	Haciendo San Pedro, 6km S El Queremal, Municipio Dagua, Valle del Cauca, Colombia	3.483333	-76.700000	1830
<i>Synophis zaheri</i>	MZUTI 3353	Buenaventura Lodge, Ecuador	-3.647970	-79.755070	874
<i>Synophis zaheri</i>	MZUTI 3355	Buenaventura Lodge, Ecuador	-3.648820	-79.756400	812
<i>Synophis zamora</i>	FHGO 7770	Cara del Indio, Ecuador	-3.575695	-78.451020	1207
<i>Synophis zamora</i>	FHGO 8340	El Quimi, Ecuador	-3.571852	-78.516598	752
<i>Synophis zamora</i>	MECN 11250	Paquisha Alto, Ecuador	-3.909518	-78.487244	1660
<i>Synophis zamora</i>	MECN 11262	El Pangui, Ecuador	-3.624502	-78.586510	814
<i>Synophis zamora</i>	MZUTI 4180	El Genairo, Ecuador	-4.166181	-78.940940	1212
<i>Synophis zamora</i>	QCAZ 12773	Ecuador: Zamora Chinchipe: Numbami reserve, 18 km Zamora-Romerillos	-4.173510	-78.958230	1530
<i>Synophis zamora</i>	QCAZ 13854	Ecuador: Zamora Chinchipe: Bombuscaro	-4.111939	-78.972561	1512
<i>Synophis zamora</i>	QCAZ 9174	Ecuador: Zamora Chinchipe: Las Orquídeas	-4.263200	-78.691090	1804

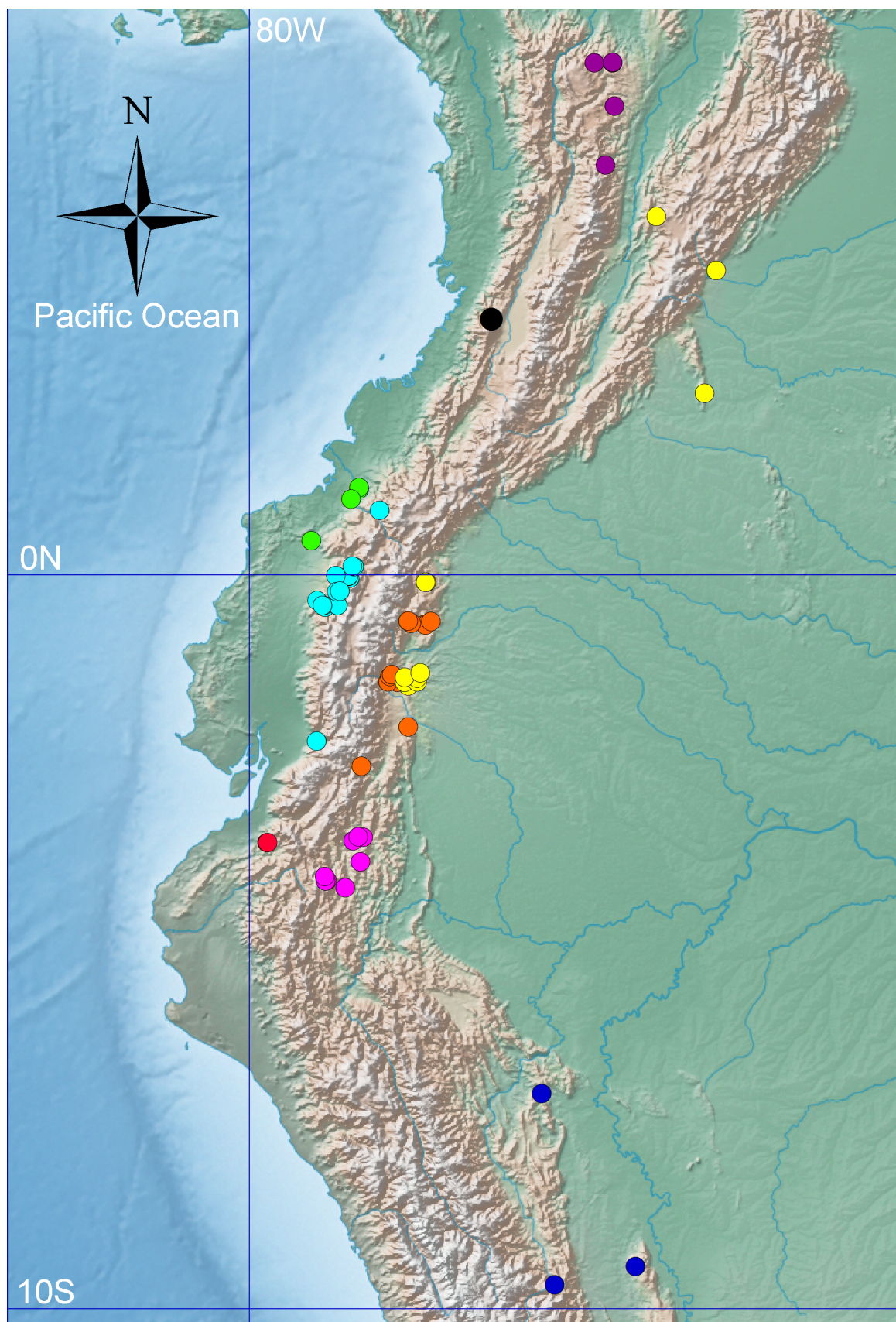


FIGURE 4. Map of verified localities for the 9 known, extant species of *Synophis*. Circles are colored by species: *S. niceforomariae* (purple), *S. lasallei* (yellow), *S. plectovertebralis* (black), *S. bicolor* (green), *S. calamitus* (teal), *S. bogerti* (orange), *S. zamora* (pink), *S. zaheri* (red), and *S. insulomontanus* (blue).

Notes. Populations representing *S. bogerti*, *S. calamitus*, *S. niceforomariae*, and *S. zamora* have previously been referred to as *S. "bicolor"* (e.g., Bogert 1964; Pyron *et al.* 2015; Torres-Carvajal *et al.* 2015).

3. *Synophis zaheri* Pyron, Guayasamin, Peñafiel, Bustamante, & Arteaga, 2015

Range. Pacific Andean slopes of southwestern Ecuador, El Oro province, ~800–900m.

Description. Adult size ~350–370mm SVL and ~180–190mm TL in males, smooth nuchal scales; no nuchal collar; intranasals in contact; 2 postoculars; 8–9 infralabials; 8 supralabials; 166–169 ventrals; 111–112 subcaudals; and 19–19-17 dorsal scale-rows with single, weak keel.

Notes. Known only from the holotype and paratype.

4. *Synophis calamitus* Hillis, 1990

Range. Pacific Andean slopes of central and northern Ecuador, primarily in Pichincha, Santo Domingo de los Tsáchilas, and Cotopaxi provinces, ~1000–2300m. Populations also occur in Carchi province (~1900m), and possibly Chimborazo province (~800m; see below).

Description. Adult size ~330–510mm SVL and ~190–280mm TL (assuming >330mm SVL is adult), smooth nuchal scales; no nuchal collar; intranasals usually in contact but occasionally divided by rostral; usually 2 postoculars but occasionally 0 or 1; 8–11 infralabials; 7–9 supralabials; 157–166 ventrals; 96–125 subcaudals including possibly truncated tails, 100–113 in females, 109–118 in males; and (19–23)-19-17 dorsal scale-rows with single, weak keel.

Notes. Includes a much larger range of specimens identified as *Synophis* aff. *bicolor* from the western Andes by Pyron *et al.* (2015). The specimen from Carchi province in northern Ecuador (QCAZ5847) is morphologically identical to other *S. calamitus* populations (Torres-Carvajal *et al.* 2015), but genetically distinct from the central Ecuadorean populations (Figs. 1, 4). There is thus intraspecific genetic diversity in *S. calamitus*, possibly related to the Río Mira as a geographic barrier to gene flow. The southernmost specimen, from Chimborazo province (CAS23612; Fig. 4), resembles both *S. calamitus* and *S. zaheri*. We refer it here to *S. calamitus*, for which it is a southern range extension, but it may represent a northern range extension for *S. zaheri* or a new species. Collecting effort in this locality should be a priority.

5. *Synophis lasallei* (Nicéforo-María, 1950)

Range. Amazonian Andean slopes, from central Colombia to central Ecuador, ~500–1500m. The type locality ("N of Albán, cen. Cundinamarca Dept., cen. Colombia") is difficult to georeference accurately for precise location and elevation.

Description. Adult size ~270–410mm SVL and ~150–210mm TL (assuming >270mm SVL is adult and MZUTI4181 and USNM233063 have truncated tails), keeled nuchal scales; no nuchal collar; intranasals in contact; usually 2 postoculars, but occasionally 1; 11 infralabials; 7–9 supralabials; 144–156 ventrals; 101–126 subcaudals omitting truncated tails, 111–126 not including holotype MLS/CJP with 101, which may also be truncated but was not examined; and (21–23)-(21–22)-(19–20) dorsal scale-rows with single, heavy keel.

Notes. Some specimens of *S. bogerti* and *S. zamora* were referred to *S. lasallei* by Pyron *et al.* (2015), prior to the description of those taxa. The only specimen of *S. lasallei* sequenced here is from the southernmost known population in Ecuador. It is possible that additional cryptic species are present in this taxon, such as the Colombian or northern Ecuadorean populations.

6. *Synophis insulomontanus* Torres-Carvajal, Echevarría, Venegas, Chávez, & Camper, 2015

Range. Amazonian Andean slopes of central Peru, ~1100–1800m.

Description. Adult size ~340–380mm SVL and ~180–190mm TL (assuming >340mm SVL is adult, and

CORBIDI10418 has a truncated tail), keeled nuchal scales; no nuchal collar; intranasals in contact; 2 postoculars; 10–11 infralabials; 8–9 supralabials; 147–152 ventrals; 103–109 subcaudals; and (20–22)–(19–21)–19 dorsal scale-rows, with single, heavy keel.

Notes. Known only from the holotype and paratypes.

7. *Synophis zamora* Torres-Carvajal, Echevarría, Venegas, Chávez, & Camper, 2015

Range. Amazonian Andean slopes of southeastern Ecuador, Zamora and Morona-Santiago provinces, ~800–1800m.

Description. Adult size ~310–460mm SVL and ~150–210mm TL, keeled nuchal scales; no nuchal collar; intranasals in contact; 2 postoculars; 9–11 infralabials; 8–9 supralabials; 147–154 ventrals; 88–118 subcaudals; and (19–21)–(18–21)–(17–18) dorsal scale-rows with single, heavy keel.

Notes. Includes several specimens referred to *S. bicolor* and *S. lasallei* by Pyron *et al.* (2015).

8. *Synophis bogerti* Torres-Carvajal, Echevarría, Venegas, Chávez, & Camper, 2015

Range. Amazonian Andean slopes of central Ecuador, ~1000–2000m.

Description. Adult size ~370–410mm SVL and ~180–200mm TL in males and 420–540mm SVL and 220–240mm TL in females (assuming >370mm SVL is adult), keeled nuchal scales; no nuchal collar; intranasals in contact; 2 postoculars; 10–11 infralabials; 8–9 supralabials; 157–168 ventrals; 103–117 subcaudals; and 19–(17–19)–17 dorsal scale-rows at midbody, with single, heavy keel.

Notes. Includes specimens historically and recently referred to *S. bicolor*, *S. aff. bicolor* (eastern Andes), and *S. lasallei* by previous authors (Bogert 1964; Pyron *et al.* 2015).

9. *Synophis plectovertebrales* Sheil & Grant, 2001

Range. Pacific Andean slopes of Valle del Cauca, Colombia, ~1800m.

Description. Adult size ~200–210mm SVL and ~80–100mm TL, smooth nuchal scales; nuchal collar; intranasals in contact; 1 postocular; 7–8 infralabials; 7–8 supralabials; 144–147 ventrals; 79–91 subcaudals; and 19–19–19 dorsal scale-rows at midbody, with single, weak keel.

Notes. Known only from the holotype and paratype. Not included in our phylogenetic analyses (Fig. 1); its placement is thus unknown.

With this re-assessment of species boundaries and taxonomic reassignment of nearly all known specimens of *Synophis* (Figs. 1–4, Tables 1,2), the morphological limits and geographic ranges of the known, extant species are tentatively stabilized. There are likely additional cryptic species in some taxa (e.g., *S. lasallei*), and there are almost certainly additional new species to be discovered. Our results here should clarify lingering confusion over most species limits, and provide a robust basis for future work.

The known species can be informally grouped into at least three species groups. The first is the *S. bicolor* group (*S. bicolor*, *S. niceforomariae*), distributed in the northern Andes, with higher ventral and subcaudal counts (174–193 and 127–143), weak keels, more slender bodies and lighter colorations (Figs. 2, 3; see Fig. 4 in Pyron *et al.* 2015). The second is the *S. calamitus* group (*S. zaheri*, *S. calamitus*), distributed on the Pacific Andean slopes of Ecuador, with intermediate counts (157–169 and 96–125), stronger keels, more robust bodies, and both lighter (*S. zaheri*) and darker (*S. calamitus*) colorations (see Figs. 3, 8, & 9 from Pyron *et al.* 2015 and Fig. 5 from Torres-Carvajal *et al.* 2015). The third is the *S. lasallei* group (*S. lasallei*, *S. insulomontanus*, *S. zamora*, and *S. bogerti*), with lower to intermediate counts (144–168 and 88–126), heavy keels, and darker colorations (see Figs. 3 & 9 from Pyron *et al.* 2015 and Fig. 5 from Torres-Carvajal *et al.* 2015). The placement of *S. plectovertebrales* is uncertain, and we suggest it may form a fourth group with small body sizes (~200mm SVL), low counts (144–147 and 79–91), nuchal collars, and weak keels. The phylogenetic placement of this group is not known, and it could potentially include *Emmochliophis* (*E. miops* was originally described in *Synophis*), which also have low counts and nuchal collars, but lack a loreal.

The first three groups are also at least partially distinguishable by hemipenial morphology. In all known diaphorolepidine species, the hemipenis is bilobed, semicalyculate, and semicapitate, relatively stout and bulbous, and covered in large spines or hooks near the base. The organ is not markedly different between *Diaphorolepis wagneri*, *Synophis bogerti* and *S. lasallei* (Bogert 1964; Zaher 1999), and thus does not appear to strongly differentiate individual species, though no quantitative analysis sampling multiple individuals per species has been performed. The organ has also not been described in detail or illustrated for any species in the *S. bicolor* or *S. plectovertebralis* groups.

In the *S. calamitus* group (*S. calamitus* QCAZ452; *S. zaheri* MZUTI3353, 3355), the lobes are stout and blunt, approximately one-half the length of the hemipenial body, which is ornamented with numerous spines, none of which are noticeably enlarged. In contrast, the *S. lasallei* group is diagnosed by lobes which are more slender than the hemipenial body, and approximately equal to its length. All species have a significantly enlarged spine near the base of the hemipenial body, either on the right side in sulcate view (*S. lasallei* USN233062; *S. insulomontanus* CORBIDI13940) or the left side (*S. zamora* QCAZ9174; *S. bogerti* QCAZ12791). An extensive comparison of more hemipenial material may reveal more significant differences that are useful for diagnosing species.

Similarly, the vertebral condition of many of the newer species is not known. Diaphorolepidine species are generally characterized by heavy modification of the pre- and post-zygapophyses (Bogert 1964; Fritts & Smith 1969; Savitzky 1974; Hillis 1990; Sheil & Grant 2001). Examining this condition requires either destructive dissection, or expensive microCT scanning. A comparative analysis of material using the latter technique will likely prove invaluable for diagnosing species and determining species boundaries, as well as perhaps understanding the function of this unique adaptation.

Finally, snakes in the genus *Synophis* have recently been referred to as "fishing snakes" by various sources, such as the Reptile Database (<http://www.reptile-database.org/>), the IUCN Red List (<http://www.iucnredlist.org/>), Torres-Carvajal *et al.* (2015), and various news outlets covering the discoveries of Pyron *et al.* (2015) and Torres-Carvajal *et al.* (2015). However, the origin of this name is unclear, as no known species are ichthyophagous. The name appears to originate from *The Elsevier Dictionary of Reptiles* (Wrobel 2004), but no etymology is given. The only known diet items are gymnophthalmid lizards in *Emmochliophis miops* and *Synophis plectovertebralis* (Sheil 1998; Sheil & Grant 2001).

Thus, we suggest the Standard English Name Andean Shadow Snakes and Standard Spanish Name Culebras Andinas de la Sombra for the genus *Synophis*, based on their dark color, nocturnal habits, and secretive nature. For the species, the Standard English Names would be Nicéforo María's Shadow Snakes (*S. niceforomariae*), Bicolored Shadow Snakes (*S. bicolor*), Zaher's Shadow Snakes (*S. zaheri*), Calamitous Shadow Snakes (*S. calamitus*), La Salle's Shadow Snakes (*S. lasallei*), Mountain Shadow Snakes (*S. insulomontanus*), Zamoran Shadow Snakes (*S. zamora*), Bogert's Shadow Snakes (*S. bogerti*), and Braided Shadow Snakes (*S. plectovertebralis*). Suggested Standard Names in Spanish are, respectively, Culebras Andinas de la Sombra de Nicéforo María, Culebras Andinas de la Sombra bicolores, Culebras Andinas de la Sombra de Zaher, Culebras Andinas de la Sombra calamitosas, Culebras Andinas de la Sombra de La Salle, Culebras Andinas de la Sombra monteses, Culebras Andinas de la Sombra de Zamora, Culebras Andinas de la Sombra de Bogert, and Culebras Andinas de la Sombra trenzadas.

Key to the species of Diaphorolepidini

1	Expanded intervertebral scale row with double keels	2
-	Intervertebral scale row not expanded; single keels	3
2	Genus <i>Diaphorolepis</i> . Fewer than 180 ventrals; weak keels on dorsal scales	<i>D. laevis</i>
-	More than 180 ventrals; strong keels on dorsal scales	<i>D. wagneri</i>
3	Loreal absent	4
-	Loreal present	5
4	Genus <i>Emmochliophis</i> . Nuchal collar absent; 2 postoculars	<i>E. fugleri</i>
-	Nuchal collar present; 1 postocular	<i>E. miops</i>
5	Genus <i>Synophis</i> . Nuchal collar present in immature individuals, 7 or 8 infralabials and infralabials, fewer than 148 ventrals	<i>S. plectovertebralis</i>
-	Nuchal collar absent in immature specimens, more than 8 infralabials or supralabials OR more than 157 ventrals	6
6	More than 173 ventral scales	7
-	Fewer than 174 ventral scales	8
7	Ventral scales 174–183	<i>S. bicolor</i>

-	Ventral scales 184–193	<i>S. niceforomariae</i>
8	Smooth nuchal scales; weak dorsal keels	9
-	Keeled nuchal scales; heavy dorsal keels	10
9	Ventrals 166–169; 2 postoculars; intranasals in contact; light brown dorsum in life	<i>S. zaheri</i>
-	Ventrals 157–166; potentially 0 or 1 postoculars but usually 2; intranasals potentially separated but usually in contact; dark brown or black dorsum in life	<i>S. calamitus</i>
10	Posterior dorsal scales in 19 or 20 rows; enlarged spine on right side of hemipenial base in sulcate view	11
-	Posterior dorsal scales in 17 or 18 rows; enlarged spine on left side of hemipenial base in sulcate view	12
11	Subcaudals usually 111–126; midbody dorsal scale rows 21 or 22	<i>S. lasallei</i>
-	Subcaudals 103–109; midbody dorsal scale rows usually 19	<i>S. insulomontanus</i>
12	Ventrals 147–154	<i>S. zamora</i>
-	Ventrals 157–168	<i>S. bogerti</i>

Acknowledgments

This research was funded in part by GWU and US NSF grants DBI-0905765 and DEB-1441719 to RAP and facilitated by the GWU Colonial One HPC initiative. OTC received funds from SENESCYT. We thank J. Daza, J. Arredondo, F. Grazziotin, and H. Zaher for sequence and morphological data from *S. niceforomariae* specimens, and J. Savage for comments on the manuscript.

References

- Bogert, C.M. (1964) Snakes of the genera *Diaphorolepis* and *Synophis* and the colubrid subfamily Xenoderminae. *Senckenbergiana Biologica*, 45, 509–531.
- Boulenger, G.A. (1898) An account of the reptiles and batrachians collected by Mr. Rosenberg, W.F.H., in western Ecuador. *Proceedings of the Zoological Society of London*, 1898, 107–126.
<http://dx.doi.org/10.1111/j.1096-3642.1898.tb03134.x>
- Cantino, P.D., de Queiroz, K. (2007) International Code of Phylogenetic Nomenclature. Version 4. Available from: <http://www.ohiou.edu/phylocode/> (Accessed 27 Sept. 2016)
- Fritts, T.H. & Smith, H.N. (1969) A new genus and species of snake from western Ecuador. *Transactions of the Kansas Academy of Science*, 72, 60–66.
<http://dx.doi.org/10.2307/3627049>
- Grazziotin, F.G., Zaher, H., Murphy, R.W., Scrocchi, G., Benavides, M.A., Zhang, Y.P. & Bonatto, S.L. (2012) Molecular phylogeny of the New World Dipsadidae (Serpentes: Colubroidea): a reappraisal. *Cladistics*, 28, 437–459.
<http://dx.doi.org/10.1111/j.1096-0031.2012.00393.x>
- Hillis, D.M. (1990) A new species of xenodontine colubrid snake of the genus *Synophis* from Ecuador and the phylogeny of the genera *Synophis* and *Emmochliophis*. *Occasional Papers of the Museum of Natural History, University of Kansas*, 135, 1–9.
- International Commission on Zoological Nomenclature (1999) *International code of zoological nomenclature = Code internationale de nomenclature zoologique*. International Trust for Zoological Nomenclature, London, 306 pp.
- Jan, G. (1863) *Elenco Sistematico degli Ofidi descritti e disegnati per l'Iconografia Generale*. A. Lombardi, Milano, 143 pp.
<http://dx.doi.org/10.5962/bhl.title.106683>
- Jenner, J.V. (1981) A zoogeographic study and the taxonomy of the xenodontine snakes. PhD thesis. New York University, New York, 354 pp.
- Katoh, K. & Standley, D.M. (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution*, 30, 772–780.
<http://dx.doi.org/10.1093/molbev/mst010>
- Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: Combined Selection of Partitioning Schemes and Substitution Models for Phylogenetic Analyses. *Molecular Biology and Evolution*, 29, 1695–1701.
<http://dx.doi.org/10.1093/molbev/mss020>
- Martinez, P.M.S. (2011) Comparative anatomy of the tribe Nothopsini (Serpentes, Dipsadidae), Thesis mestrado. Universidade de Sao Paulo, Sao Paulo, 159 pp.
- Nicéforo -María, H. (1950) Contribucion al conocimiento de los ofidios de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 7, 518–527.
- Nicéforo -María, H. (1970) Contribucion al conocimiento de los ofidios de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 210, 1–6.
- Peracca, M.G. (1896) Nuovo genere di Colubride aglifo dell'America meridionale. *Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino*, 11, 1–2.

- Pyron, R.A., Burbrink, F.T., Colli, G.R., de Oca, A.N.M., Vitt, L.J., Kuczynski, C.A. & Wiens, J.J. (2011) The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Molecular Phylogenetics and Evolution*, 58, 329–342.
<http://dx.doi.org/10.1016/j.ympev.2010.11.006>
- Pyron, R.A., Burbrink, F.T. & Wiens, J.J. (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *Bmc Evolutionary Biology*, 13, 93.
<http://dx.doi.org/10.1186/1471-2148-13-93>
- Pyron, R.A., Guayasamin, J.M., Penafiel, N., Bustamante, L. & Arteaga, A. (2015) Systematics of Nothopsini (Serpentes, Dipsadidae), with a new species of *Synophis* from the Pacific Andean slopes of southwestern Ecuador. *Zookeys*, 109–147.
<http://dx.doi.org/10.3897/zookeys.541.6058>
- Rodriguez, G. (2002) El naturalista Antoine Rouhaire (Hermano Nicéforo María) y el desarrollo de zoología sistemática en Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 26, 229–238.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. *Systematic Biology*, 61, 539–542.
<http://dx.doi.org/10.1093/sysbio/sys029>
- Savitzky, A.H. (1974) *The relationships of the xenodontine colubrid snakes related to Ninia*. MS thesis. University of Kansas, Lawrence, Kansas, 64 pp.
- Sheil, C.A. (1998) *Emmochliophis miops*: Redescription of *Synophis miops* (Boulenger, 1898). *Journal of Herpetology*, 32, 604–607.
<http://dx.doi.org/10.2307/1565222>
- Sheil, C.A. & Grant, T. (2001) A new species of colubrid snake (*Synophis*) from western Colombia. *Journal of Herpetology*, 35, 204–209.
<http://dx.doi.org/10.2307/1566109>
- Society for the Study of Amphibians and Reptiles. & Adler, K. (1989) *Contributions to the history of herpetology*. S.S.A.R., Oxford, Ohio, 202 pp.
- Torres-Carvajal, O., Echevarría, L.Y., Venegas, P.J., Chávez, G. & Camper, J.D. (2015) Description and phylogeny of three new species of *Synophis* (Colubridae, Dipsadinae) from the tropical Andes in Ecuador and Peru. *Zookeys*, 153–179.
<http://dx.doi.org/10.3897/zookeys.546.6533>
- Vidal, N., Delmas, A.S., David, P., Cruaud, C., Coujoux, A. & Hedges, S.B. (2007) The phylogeny and classification of caenophidian snakes inferred from seven nuclear protein-coding genes. *Comptes Rendus Biologies*, 330, 182–187.
<http://dx.doi.org/10.1016/j.crv.2006.10.001>
- Wrobel, M. (2004) *Elsevier's dictionary of reptiles: in Latin, English, German, French and Italian*. Elsevier, Amsterdam; Oxford, 758 pp.
- Zaher, H. (1999) Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bulletin of the American Museum of Natural History*, 1–168.
- Zaher, H., Grazziotin, F.G., Cadle, J.E., Murphy, R.W., de Moura, J.C. & Bonatto, S.L. (2009) Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. *Papeis Avulsos de Zoologia*, 49, 115–153.
<http://dx.doi.org/10.1590/S0031-10492009001100001>

APPENDIX I. GenBank accessions for new and existing sequences analyzed in this study (Fig. 1).

Species	12S	16S	CYTB	ND4	BDNF	CMOS	DNAH3	HOXA13	NT3
<i>Adelphicos quadrivirgatum</i>	-	-	GQ895853	-	-	GQ895796	-	-	-
<i>Alsophis antiquae</i>	AF158455	AF158524	-	-	-	-	-	-	-
<i>Alsophis antillensis</i>	FJ416691	FJ416702	FJ416726	FJ416800	JQ599005	-	-	-	-
<i>Alsophis manselli</i>	-	AF158528	FJ416727	FJ416801	-	-	-	-	-
<i>Alsophis rijgersmaei</i>	FJ416697	FJ416708	FJ416729	FJ416803	-	-	-	-	-
<i>Alsophis rufiventris</i>	FJ416698	FJ416709	FJ416730	FJ416804	-	-	-	-	-
<i>Alsophis sajdaki</i>	-	-	FJ416731	FJ416805	-	-	-	-	-
<i>Alsophis sibonius</i>	FJ416692	FJ416703	FJ416728	FJ416802	-	-	-	-	-
<i>Amastridium sapperi</i>	-	-	GQ334479	GQ334580	-	-	GQ334557	-	GQ334663
<i>Apostolepis albicollaris</i>	JQ598793	JQ598856	-	-	-	JQ598965	-	-	-
<i>Apostolepis assimilis</i>	GQ457781	GQ457724	-	-	JQ599007	GQ457843	-	-	-
<i>Apostolepis cearensis</i>	JQ598794	JQ598857	-	-	-	JQ598966	-	-	-
<i>Apostolepis dimidiata</i>	GQ457782	GQ457725	JQ598917	-	JQ599008	GQ457844	-	-	-
<i>Apostolepis flavotorquata</i>	JQ598795	JQ598858	GQ895854	-	-	GQ895798	-	-	-
<i>Arrhyton dolichura</i>	AF158438	AF158507	FJ416721	FJ416795	-	-	-	-	-
<i>Arrhyton procerum</i>	AF158452	AF158521	FJ416723	FJ416797	-	-	-	-	-
<i>Arrhyton redimitum</i>	AF158439	AF158508	FJ416720	FJ416794	-	-	-	-	-
<i>Arrhyton supernum</i>	AF158436	AF158505	FJ416718	FJ416792	-	-	-	-	-
<i>Arrhyton taeniatum</i>	AF158453	AF158522	FJ416717	FJ416791	-	-	-	-	-
<i>Arrhyton tanyplectum</i>	AF158446	AF158516	FJ416722	FJ416796	-	-	-	-	-
<i>Arrhyton vittatum</i>	AF158437	AF158506	FJ416719	FJ416793	-	-	-	-	-
<i>Atractus albuquerquei</i>	GQ457783	GQ457726	JQ598918	-	JQ599009	GQ457845	-	-	-
<i>Atractus badius</i>	AF158425	AF158485	-	-	-	-	-	-	-
<i>Atractus duboisi</i>	-	KT944041	-	KT944059	-	-	-	-	-
<i>Atractus dunni</i>	-	KT944038	KT944050	KT944057	-	-	-	-	-
<i>Atractus elaps</i>	-	-	EF078536	EF078584	-	-	GU353244	-	GU353273
<i>Atractus flammeigerus</i>	AF158402	AF158471	-	-	-	-	-	-	-
<i>Atractus gigas</i>	-	KT944043	KT944053	KT944061	-	-	-	-	-
<i>Atractus iridescens</i>	-	KT944039	KT944051	KT944058	-	-	-	-	-

.....continued on the next page

APPENDIX 1. (Continued)

Species	12S	16S	CYTB	ND4	BDNF	CMOS	DNAH3	HOXA13	NT3
<i>Atractus major</i>	-	KT944045	-	-	-	-	-	-	-
<i>Atractus resplendens</i>	KT944036	KT944042	KT944055	KT944060	-	-	-	-	-
<i>Atractus reticulatus</i>	JQ598798	JQ598886	-	-	-	JQ598970	-	-	-
<i>Atractus schach</i>	JQ598799	AF158486	-	-	-	JQ598971	-	-	-
<i>Atractus trihedrurus</i>	GQ457784	GQ457727	JQ598919	-	JQ599010	GQ457846	-	-	-
<i>Atractus typhon</i>	-	KT944044	KT944054	KT944062	-	-	-	-	-
<i>Atractus wagleri</i>	-	-	GQ334480	GQ334581	-	-	GQ334558	-	GQ334664
<i>Atractus zebrinus</i>	JQ598800	JQ598861	-	-	-	JQ598972	-	-	-
<i>Atractus zidoki</i>	AF158426	AF158487	-	-	-	-	-	-	-
<i>Boiruna maculata</i>	GQ457785	JQ598862	GQ895855	-	JQ599011	GQ895799	-	-	-
<i>Borikenophis portoricensis</i>	FJ416696	AF158517	AF471085	U49308	JQ599012	AF471126	-	-	-
<i>Borikenophis variegatus</i>	FJ416700	FJ416711	FJ416734	FJ416808	-	-	-	-	-
<i>Caceteboia amarali</i>	GQ457807	GQ457747	JQ598921	-	-	GQ457867	-	-	-
<i>Calamodontophis paucidens</i>	GQ457786	GQ457728	-	-	-	GQ457848	-	-	-
<i>Caraiiba andreae</i>	AF158442	AF158511	FJ416743	FJ416817	-	-	-	-	-
<i>Carphophis amoenus</i>	AY577013	AY577022	AF471067	-	-	DQ112082	-	-	-
<i>Carphophis vermis</i>	-	-	FTB_ADD	-	-	-	-	-	-
<i>Clelia clelia</i>	AF158403	AF158472	-	-	-	JQ598973	-	-	-
<i>Coniophanes fissidens</i>	-	-	EF078538	EF078586	-	-	GU353245	-	GU353274
<i>Conophis lineatus</i>	GQ457788	JQ598865	JQ598924	-	JQ599016	JQ598975	-	-	-
<i>Conophis vittatus</i>	-	-	GQ895861	-	-	GQ895805	-	-	-
<i>Contia longicauda</i>	-	-	GU112407	GU112427	GU112372	-	-	-	-
<i>Contia tenuis</i>	AY577021	AY577030	GU112401	AF402658	GU112363	AF471134	-	-	-
<i>Crisantophis nevermanni</i>	GU018152	GU018169	-	-	-	-	-	-	-
<i>Cryophis hallbergi</i>	-	-	GQ895863	EF078544	-	GQ895807	GQ334559	-	GQ334666
<i>Cubophis cantherigerus</i>	AF158405	AF158475	AF544669	FJ416818	FJ433999	AF544694	-	EF144034	FJ434100
<i>Cubophis caymanus</i>	FJ416693	FJ416704	FJ416745	FJ416820	-	-	-	-	-
<i>Cubophis fuscicauda</i>	FJ416695	FJ416706	FJ416747	FJ416822	-	-	-	-	-
<i>Cubophis ruttayi</i>	FJ416699	FJ416710	FJ416746	FJ416821	-	-	-	-	-
<i>Cubophis vudii</i>	AF158443	AF158512	FJ416744	FJ416819	-	-	-	-	-

.....continued on the next page

APPENDIX 1. (Continued)

Species	12S	16S	CYTB	ND4	BDNF	CMOS	DNAH3	HOXA13	NT3
<i>Dipsas catesbyi</i>	JQ598805	Z46496	JQ598926	EF078585	JQ599021	JQ598977	GU353248	-	GU353277
<i>Dipsas indica</i>	GQ457789	GQ457730	-	-	-	GQ457850	-	-	-
<i>Dipsas neivai</i>	GQ457790	GQ457731	-	-	-	GQ457851	-	-	-
<i>Dipsas prattii</i>	-	-	GQ334482	GQ334583	-	-	GQ334560	-	GQ334667
<i>Dipsas variegata</i>	AF158406	AF158476	-	-	-	-	-	-	-
<i>Drepanoides anomalus</i>	GQ457791	GQ457732	GQ895866	-	-	GQ895810	-	-	-
<i>Echinanthera melanostigma</i>	JQ598806	GU018174	JQ598928	-	-	-	-	-	-
<i>Echinanthera undulata</i>	JQ598807	JQ598870	JQ598929	-	JQ599022	JQ598978	-	-	-
<i>Elapomorphus quinqueineatus</i>	GQ457794	GQ457735	JQ598930	-	JQ599023	GQ457855	-	-	-
<i>Erythrolamprus aesculapii</i>	GQ457795	GQ457736	GQ895871	-	JQ599024	GQ895814	-	-	-
<i>Erythrolamprus almadensis</i>	JQ598808	JQ598871	-	-	-	JQ598979	-	-	-
<i>Erythrolamprus atraventer</i>	JQ598809	JQ598872	-	-	-	JQ598980	-	-	-
<i>Erythrolamprus breviceps</i>	AF158464	AF158533	-	-	-	-	-	-	-
<i>Erythrolamprus ceii</i>	JQ598810	JQ598873	-	-	-	JQ598981	-	-	-
<i>Erythrolamprus cursor</i>	JX905310	JX905314	-	-	-	-	-	-	-
<i>Erythrolamprus epinephelus</i>	GU018158	GU018176	-	-	-	-	-	-	-
<i>Erythrolamprus jaegeri</i>	GQ457809	GQ457749	-	-	-	GQ457869	-	-	-
<i>Erythrolamprus juliae</i>	AF158445	AF158514	-	-	-	-	-	-	-
<i>Erythrolamprus miliaris</i>	JQ598811	AF158480	JQ598931	-	JQ599025	JQ598982	-	-	-
<i>Erythrolamprus mimus</i>	GU018157	GU018175	-	-	-	-	-	-	-
<i>Erythrolamprus poecilogyrus</i>	JQ598812	JQ598875	-	-	-	-	-	-	-
<i>Erythrolamprus pygmaeus</i>	GU018154	GU018172	-	-	-	-	-	-	-
<i>Erythrolamprus reginae</i>	JQ598813	JQ598876	-	-	-	JQ598983	-	-	-
<i>Erythrolamprus typhlus</i>	GQ457811	GQ457751	-	-	-	GQ457871	-	-	-
<i>Farancia abacura</i>	Z46467	Z46491	U69832	DQ902307	-	AF471141	-	-	-
<i>Farancia erythrogramma</i>	AY577017	AY577026	FTB_ADD	-	-	-	-	-	-
<i>Geophis carinosus</i>	-	-	GQ895872	-	-	GQ895815	-	-	-
<i>Geophis dubius</i>	-	-	KC917319	-	-	-	-	-	-
<i>Geophis godmani</i>	JQ598814	JQ598877	JQ598932	-	JQ599026	-	-	-	-
<i>Geophis juarezi</i>	-	-	KC917315	-	-	-	-	-	-

.....continued on the next page

APPENDIX 1. (Continued)

Species	12S	16S	CYTB	ND4	BDNF	CMOS	DNAH3	HOXA13	NT3
<i>Gomesophis brasiliensis</i>	GQ457796	GQ457737	-	-	-	-	-	-	-
<i>Haitiophis anomalus</i>	FJ666091	FJ666092	-	-	-	-	-	-	-
<i>Helicops angulatus</i>	GQ457797	GQ457738	AF471037	-	JQ599027	AF471160	-	-	-
<i>Helicops carinicaudus</i>	JQ598815	-	-	-	-	JQ598984	-	-	-
<i>Helicops gomesi</i>	GQ457798	GQ457739	-	-	-	GQ457858	-	-	-
<i>Helicops hagmanni</i>	JQ598816	JQ598878	-	-	-	JQ598985	-	-	-
<i>Helicops infrataeniatus</i>	GQ457799	GQ457740	JQ598933	-	-	GQ457859	-	-	-
<i>Heterodon nasicus</i>	GQ457801	AY577027	FTB_ADD	-	-	GQ457861	-	-	-
<i>Heterodon platirhinos</i>	AY577019	AY577028	GU112412	AF402659	EU402641	JQ598986	EU402749	-	GU353271
<i>Heterodon simus</i>	AY577020	AY577029	AF217840	DQ902310	-	AF471142	-	-	-
<i>Hydrodynastes bicinctus</i>	GQ457802	GQ457742	JQ598935	-	JQ599030	GQ457862	-	-	-
<i>Hydrodynastes gigas</i>	GQ457803	GQ457743	GQ895873	-	JQ599031	GQ895816	-	-	-
<i>Hydromorphus concolor</i>	-	-	GQ895874	-	-	GQ895817	-	-	-
<i>Hydrops triangularis</i>	GQ457804	GQ457744	AF471039	-	JQ599032	AF471158	-	-	-
<i>Hypsigena affinis</i>	-	-	GU353241	EU363055	-	-	GU353249	-	GU353278
<i>Hypsigena chlorophaea</i>	EU728577	EU728577	EU728577	EU728577	-	-	FJ455227	-	FJ455198
<i>Hypsigena jani</i>	EU728592	EU728592	EU728592	EU728592	-	-	FJ455225	-	FJ455193
<i>Hypsigena ochrorhyncha</i>	EU728578	EU728578	EU728578	EU728578	-	-	FJ455231	-	FJ455202
<i>Hypsigena slevini</i>	EU728584	EU728584	EU728584	EU728584	-	-	FJ455223	-	FJ455191
<i>Hypsigena tanzeri</i>	-	-	EU728588	EU363044	-	-	-	-	-
<i>Hypsigena torquata</i>	EU728591	EU728591	EU728591	EU728591	-	AF471159	FJ455224	-	FJ455192
<i>Hypsirhynchus callilaemus</i>	AF158440	AF158509	FJ416737	FJ416811	-	-	-	-	-
<i>Hypsirhynchus ferox</i>	AF158447	AF158515	GQ895875	FJ416816	-	GQ895818	-	-	-
<i>Hypsirhynchus funereus</i>	AF158451	AF158520	FJ416739	FJ416813	-	-	-	-	-
<i>Hypsirhynchus parvifrons</i>	AF158441	AF158510	FJ416740	FJ416814	JQ599006	-	-	-	-
<i>Hypsirhynchus polylepis</i>	AF158450	AF158519	FJ416738	FJ416812	-	-	-	-	-
<i>Hypsirhynchus scalaris</i>	AF158449	AF158518	FJ416741	FJ416815	-	-	-	-	-
<i>Ialtris dorsalis</i>	AF158456	AF158525	FJ416735	FJ416809	-	-	-	-	-
<i>Ialtris haetianus</i>	AF158458	AF158527	FJ416736	FJ416810	-	-	-	-	-
<i>Imantodes cenchoa</i>	EU728586	EU728586	EU728586	EU728586	EU402643	GQ457865	EU402750	-	EU390923

.....continued on the next page

APPENDIX 1. (Continued)

Species	12S	16S	CYTB	ND4	BDNF	CMOS	DNAH3	HOXA13	NT3
<i>Imantodes lentiferus</i>	AF158463	AF158532	KC176252	EF078561	-	-	-	-	-
<i>Leptodeira annulata</i>	GQ457806	GQ457746	FJ416713	FJ416787	FJ433998	AF544690	GQ334563	EF144033	FJ434099
<i>Leptodeira bakeri</i>	-	-	GQ334518	GQ334618	-	-	GQ334566	-	GQ334673
<i>Leptodeira frenata</i>	-	-	EF078532	EF078580	-	-	FJ810228	-	FJ810242
<i>Leptodeira maculata</i>	-	-	GQ334524	GQ334623	-	-	GQ334567	-	GQ334674
<i>Leptodeira nigrofasciata</i>	-	-	GQ334526	EF078581	-	-	GQ334569	-	GQ334681
<i>Leptodeira polysticta</i>	EU728590	EU728590	EU728590	EU728590	-	-	GQ334575	-	GQ334679
<i>Leptodeira punctata</i>	-	-	EF078530	EF078577	-	-	GQ334571	-	GQ334682
<i>Leptodeira rubricata</i>	-	-	GQ334527	GQ334631	-	-	-	-	-
<i>Leptodeira septentrionalis</i>	GU018148	GU018163	KC176243	KC176255	-	-	FJ455220	-	FJ455188
<i>Leptodeira splendida</i>	-	-	EF078521	EF078569	-	-	GQ334576	-	GQ334680
<i>Leptodeira uribei</i>	-	-	EF078531	EF078579	-	-	FJ810229	-	FJ810243
<i>Lygophis anomalus</i>	JQ598817	JQ598879	-	-	-	-	-	-	-
<i>Lygophis elegantissimus</i>	GQ457808	GQ457748	-	-	-	GQ457868	-	-	-
<i>Lygophis flavifrenatus</i>	JQ598818	JQ598880	-	-	-	-	-	-	-
<i>Lygophis lineatus</i>	-	-	-	-	DQ469795	DQ469789	-	-	DQ469793
<i>Lygophis meridionalis</i>	GQ457810	GQ457750	-	-	-	GQ457870	-	-	-
<i>Lygophis paucidens</i>	JQ598819	-	-	-	-	JQ598987	-	-	-
<i>Magliophis exiguum</i>	FJ416694	AF158526	AF471071	FJ416798	-	AF471117	-	-	-
<i>Magliophis stahli</i>	-	-	FJ416725	FJ416799	-	-	-	-	-
<i>Manolepis putnami</i>	JQ598820	JQ598881	JQ598936	-	JQ599035	JQ598988	-	-	-
<i>Mussurana bicolor</i>	GQ457787	GQ457729	-	-	-	GQ457849	-	-	-
<i>Ninia atrata</i>	GQ457814	JQ598882	JQ598937	GQ334659	JQ599037	GQ457874	GQ334577	-	GQ334683
<i>Nothopsis rugosus</i>	GU018159	KR814760	KR814770	KR814779	-	KR814768	-	-	-
<i>Oxyrhopus clathratus</i>	GQ457815	GQ457754	-	-	-	GQ457875	-	-	-
<i>Oxyrhopus formosus</i>	JQ598821	AF158482	-	-	-	-	-	-	-
<i>Oxyrhopus guibei</i>	JQ598822	JQ627291	JQ598938	-	JQ599038	JQ598989	-	-	-
<i>Oxyrhopus melanogenys</i>	JQ598823	AF158489	-	-	-	JQ598990	-	-	-
<i>Oxyrhopus petolaris</i>	GU018144	GU018170	GQ334554	GQ334660	-	-	GQ334578	-	GQ334684
<i>Oxyrhopus rhombifer</i>	GQ457816	GQ457755	-	-	-	GQ457876	-	-	-

.....continued on the next page

APPENDIX 1. (Continued)

Species	12S	16S	CYTB	ND4	BDNF	CMOS	DNAH3	HOXA13	NT3
<i>Phalotris lativittatus</i>	JQ598825	JQ598885	-	-	-	JQ598991	-	-	-
<i>Phalotris lemniscatus</i>	GQ457817	GQ457756	JQ598941	-	JQ599039	GQ457877	-	-	-
<i>Phalotris mertensi</i>	JQ598826	-	-	-	-	-	-	-	-
<i>Phalotris nasutus</i>	GQ457818	GQ457757	GQ895880	-	-	GQ895822	-	-	-
<i>Philodryas aestiva</i>	GQ457819	GQ457758	-	-	-	GQ457879	-	-	-
<i>Philodryas agassizii</i>	GQ457823	GQ457762	GQ895883	-	-	GQ457883	-	-	-
<i>Philodryas argentea</i>	GQ457842	GQ457780	JQ598944	-	JQ599040	GQ457899	-	-	-
<i>Philodryas baroni</i>	JQ598828	JQ598888	-	-	-	-	-	-	-
<i>Philodryas georgeboulengeri</i>	-	-	GQ895898	-	-	GQ895838	-	-	-
<i>Philodryas mattogrossensis</i>	GQ457820	GQ457759	-	-	-	GQ457880	-	-	-
<i>Philodryas nattereri</i>	JQ598829	JQ598889	AF236806	-	-	JQ598992	-	-	-
<i>Philodryas olfersii</i>	JQ598830	AF158484	JQ598945	-	JQ599041	JQ598993	-	-	-
<i>Philodryas patagoniensis</i>	GQ457821	JQ627296	AF236808	-	-	GQ457881	-	-	-
<i>Philodryas psammophidea</i>	GU018149	GU018168	-	-	-	-	-	-	-
<i>Philodryas viridissima</i>	AF158419	AF158474	AF236807	-	-	-	-	-	-
<i>Phimophis guerini</i>	GQ457822	GQ457761	-	-	-	GQ457882	-	-	-
<i>Pseudalsophis dorsalis</i>	JQ598832	JQ598892	JQ598946	-	-	JQ598994	-	-	-
<i>Pseudalsophis elegans</i>	AF158401	AF158470	JQ598947	-	JQ599042	JQ598995	-	-	-
<i>Pseudoboa coronata</i>	GQ457824	GQ457763	-	-	-	GQ457884	-	-	-
<i>Pseudoboa neuwiedii</i>	AF158423	AF158490	GQ895884	-	-	GQ895825	-	-	-
<i>Pseudoboa nigra</i>	AF544775	GQ457764	JQ598948	-	JQ599043	AF544729	-	-	-
<i>Pseudoeryx plicatilis</i>	GQ457826	GQ457765	GQ895885	-	-	GQ895826	-	-	-
<i>Pseudoleptodeira latifasciata</i>	EU728579	EU728579	EU728579	EU728579	-	-	FI455222	-	FI455190
<i>Pseudotomodon trigonatus</i>	GQ457827	GQ457766	-	-	-	GQ457887	-	-	-
<i>Psomophis genimaculatus</i>	GQ457828	GQ457767	-	-	-	GQ457888	-	-	-
<i>Psomophis joberti</i>	GQ457829	GQ457768	GQ895887	-	JQ599046	GQ895828	-	-	-
<i>Psomophis obtusus</i>	JQ598836	JQ598896	-	-	-	-	-	-	-
<i>Psychophis flavovirgatus</i>	GQ457830	GQ457769	-	-	-	GQ457890	-	-	-
<i>Rhachidelus brazili</i>	JQ598837	JQ598897	JQ598952	-	JQ599048	-	-	-	-
<i>Rhadinaea flavilata</i>	-	-	AF471078	-	-	AF471152	-	-	-

.....continued on the next page

APPENDIX 1. (Continued)

Species	12S	16S	CYTB	ND4	BDNF	CMOS	DNAH3	HOXA13	NT3
<i>Sibon nodulamina</i>	-	KP209376	-	-	-	-	-	-	-
<i>Sibynomorphus mikanii</i>	GQ457832	JQ627297	JQ598954	-	JQ599050	GQ457892	-	-	-
<i>Sibynomorphus newiiedi</i>	JQ598838	JQ598898	-	-	-	-	-	-	-
<i>Sibynomorphus turgidus</i>	JQ598839	JQ598899	-	-	-	-	-	-	-
<i>Sibynomorphus ventrimaculatus</i>	JQ598840	JQ598900	-	-	-	JQ598997	-	-	-
<i>Siphlophis cervinus</i>	JQ598841	JQ598901	GQ895888	-	-	JQ598998	-	-	-
<i>Siphlophis compressus</i>	GQ457833	GQ457772	-	-	-	GQ457893	-	-	-
<i>Siphlophis longicaudatus</i>	JQ598842	JQ598902	-	-	-	JQ598999	-	-	-
<i>Siphlophis pulcher</i>	GQ457834	GQ457773	JQ598955	-	JQ599051	GQ457894	-	-	-
<i>Sordellina punctata</i>	JQ598843	JQ598903	JQ598956	-	JQ599052	JQ599000	-	-	-
<i>Tachymenis peruviana</i>	GQ457835	GQ457774	-	-	JQ599054	GQ457895	-	-	-
<i>Taeniophallus affinis</i>	JQ598844	JQ598905	JQ598957	-	JQ599055	GQ457853	-	-	-
<i>Taeniophallus brevirostris</i>	GQ457793	GQ457734	JQ598958	-	JQ599056	GQ457854	-	-	-
<i>Taeniophallus nicagus</i>	JQ598845	JQ598906	-	-	-	JQ599001	-	-	-
<i>Tantalophis discolor</i>	-	-	EF078541	EF078589	-	-	FJ810226	-	FJ810240
<i>Thalesius viridis</i>	AF158468	AF158538	-	-	-	-	-	-	-
<i>Thamnodynastes hypoconia</i>	JQ598846	-	-	-	-	-	-	-	-
<i>Thamnodynastes lanei</i>	GQ457836	GQ457775	-	-	-	-	-	-	-
<i>Thamnodynastes pallidus</i>	GU018155	GU018166	-	-	-	-	-	-	-
<i>Thamnodynastes rutilus</i>	GQ457837	GQ457776	-	-	-	GQ457896	-	-	-
<i>Thamnodynastes strigatus</i>	JQ598847	JQ598907	JQ598959	-	JQ599057	-	-	-	-
<i>Tomodon dorsatum</i>	GQ457838	GQ457777	GQ895892	-	JQ599059	GQ895833	-	-	-
<i>Tretanorhinus nigroluteus</i>	-	-	GQ895893	-	-	GQ895834	-	-	-
<i>Trimetopon gracile</i>	GU018160	GU018178	-	-	-	-	-	-	-
<i>Tropidodipsas sartorii</i>	-	-	EF078540	EF078588	-	-	-	-	-
<i>Tropidodryas serra</i>	JQ598848	JQ598908	JQ598961	-	-	-	-	-	-
<i>Tropidodryas straticiceps</i>	GQ457839	GQ457778	AF236811	-	JQ599060	-	-	-	-
<i>Uromacer catesbyi</i>	AF158454	AF158523	FJ416714	FJ416788	-	-	-	-	-
<i>Uromacer frenatus</i>	AF158444	AF158513	FJ416715	FJ416789	-	-	-	-	-

.....continued on the next page

APPENDIX 1. (Continued)

Species	12S	16S	CYTB	ND4	BDNF	CMOS	DNAH3	HOXA13	NT3
<i>Xenodon histricus</i>	GQ457813	GQ457753	JQ598962	-	JQ599061	GQ457873	-	-	-
<i>Xenodon matogrossensis</i>	JQ598850	JQ598910	-	-	-	-	-	-	-
<i>Xenodon merremi</i>	GQ457840	JQ598911	JQ598963	-	JQ599062	GQ457898	-	-	-
<i>Xenodon nattereri</i>	JQ598851	JQ598912	-	-	-	-	-	-	-
<i>Xenodon newwiedii</i>	GQ457841	GQ457779	AF236814	-	-	-	-	-	-
<i>Xenodon pulcher</i>	JQ598852	JQ598913	-	-	-	-	-	-	-
<i>Xenodon semicinctus</i>	GU018156	GU018173	GQ895877	-	-	-	-	-	-
<i>Xenodon severus</i>	JQ598853	Z46474	JQ598964	-	JQ599063	-	-	-	-
<i>Xenopholis scalaris</i>	JQ598854	JQ598915	-	-	-	JQ599002	-	-	-
<i>Xenopholis undulatus</i>	JQ598855	JQ598916	-	-	-	JQ599003	-	-	-
Outgroups	-	-	-	-	-	-	-	-	-
<i>Thermophis baileyi</i>	-	-	EU864148	KF595097	-	EU496922	-	-	-
<i>Thermophis zhaoermii</i>	GQ166168	GQ166168	GQ166168	GQ166168	-	KF514882	-	-	-
<i>Stichophanes ningshaanensis</i>	KJ719252	KJ719252	KJ719252	KJ719252	-	KJ638718	-	-	-
<i>Coluber constrictor</i>	L01765	L01770	EU180432	AY487040	JQ599015	AY486937	EU402743	EF456660	EU390914
Diaphorolepidini	-	-	-	-	-	-	-	-	-
<i>Diaphorolepis wagneri</i> MZUTI 3322	-	KR814752	-	KR814775	-	KR814764	-	-	-
<i>Diaphorolepis wagneri</i> MZUTI 3752	-	KR814753	-	KR814777	-	KR814766	-	-	-
<i>Diaphorolepis wagneri</i> MZUTI 3901	-	KR814754	-	KR814778	-	KR814767	-	-	-
<i>Diaphorolepis wagneri</i> QCAZ 11956	-	KT345343	KT345360	KT345377	-	-	-	-	-
<i>Diaphorolepis wagneri</i> QCAZ 11961	-	KT345344	KT345361	KT345378	-	-	-	-	-
<i>Synophis bicolor</i> MZUTI 4175	-	KT944046	-	KT944063	-	KT944067	-	-	-
<i>Synophis bicolor</i> UTA R-55956	-	-	JX398697	JX398557	-	-	JX293900	-	JX398820
<i>Synophis bogerti</i> MZUTI 3529	-	KR814759	KR814771	KR814780	-	KR814762	-	-	-
<i>Synophis bogerti</i> QCAZ 12791	-	KT345348	KT345365	KT345382	-	-	-	-	-
<i>Synophis bogerti</i> QCAZ 13323	-	KT345351	KT345368	KT345385	-	-	-	-	-

.....continued on the next page

APPENDIX 1. (Continued)

Species	12S	16S	CYTb	ND4	BDNF	CMOS	DNAH3	HOXA13	NT3
<i>Synophis calamitus</i> KU 197107	KR814622	KR814640	KR814697	KR814711	-	KR814663	-	-	-
<i>Synophis calamitus</i> MZUTI 3694	-	KR814755	-	KR814774	-	KR814765	-	-	-
<i>Synophis calamitus</i> QCAZ 10508	-	KT345345	KT345362	KT345379	-	-	-	-	-
<i>Synophis calamitus</i> QCAZ 11931	-	KT345346	KT345363	KT345380	-	-	-	-	-
<i>Synophis calamitus</i> QCAZ 3875	-	KT345354	KT345371	KT345388	-	-	-	-	-
<i>Synophis calamitus</i> QCAZ 5847	-	KT345356	KT345373	KT345390	-	-	-	-	-
<i>Synophis calamitus</i> QCAZ 8098	-	KT345357	KT345374	KT345391	-	-	-	-	-
<i>Synophis insulomontanus</i> CORBIDI 13940	-	KT345350	KT345367	KT345384	-	-	-	-	-
<i>Synophis insulomontanus</i> CORBIDI 9223	-	KT345349	KT345366	KT345383	-	-	-	-	-
<i>Synophis lasallei</i> MZUTI 4181	-	KT944047	-	KT944064	-	KT944068	-	-	-
<i>Synophis niceforomariae</i> MHUA 14577	KR814751	KR814758	KR814773	-	KX672829	KR814769	-	KX672830	KX672831
<i>Synophis zaheeri</i> MZUTI 3353	-	KR814756	-	KR814776	-	KR814761	-	-	-
<i>Synophis zaheeri</i> MZUTI 3355	-	KR814757	-	KR814781	-	KR814763	-	-	-
<i>Synophis zamora</i> MZUTI 4180	-	KT944048	-	KT944065	-	KT944069	-	-	-
<i>Synophis zamora</i> QCAZ 12773	-	KT345347	KT345364	KT345381	-	-	-	-	-
<i>Synophis zamora</i> QCAZ 9174	-	KT345358	KT345375	KT345392	-	-	-	-	-
<i>Synophis zamora</i> QCAZ 9175	-	KT345359	KT345376	KT345393	-	-	-	-	-