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Amphibian & Reptile Conservation
15(2) [Taxonomy Section]: 289–310 (e294).

urn:lsid:zoobank.org:pub:B0980607-EBC4-4B57-A3E0-F140F2C263AA

A new species of *Geophis* (Dipsadidae) from Veracruz, Mexico, with comments on the validity of related taxa

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***Abstract.*—A new species of the *Geophis dubius* group is described from the cloud forests in the mountains north of Xalapa, Veracruz. This new species is most similar to *G. turbidus* and *G. lorancai,* from which it differs genetically as well as by a very unique color pattern, morphological characters, and habitat use. The validity of *G. fuscus*, which was described from central Veracruz, is discussed. With the description of the new species and our assessment of *G. fuscus*, the number of species in the *Geophis dubius* group increases to 14 and the number of species of *Geophis* to 52.**

Keywords. *Geophis dubius* group, *Geophis fuscus*, *Geophis lorancai*, *Geophis turbidus*, montane cloud forest, new species, Sierra de Misantla, Sierra Madre Oriental

Resumen.—Se describe una nueva especie del grupo de *Geophis dubius* del bosque mesófilo de montaña al norte de Xalapa, Veracruz. Esta nueva especie es mas parecido a *G. turbidus* y *G. lorancai*, de cuales se diferencía geneticamente y por su coloración única, carácteres morfológicas y preferencia de hábitat particular. También disuctimos la valídez de *G. fuscus*, cual también fue descrito del centro de Veracruz. Con la descripción de la nuev especies, y nuestro análisis de *G. fuscus*, el numero de especies del grupo *Geophis dubius* se aumenta a 14 y el número de especies de *Geophis* a 52.

Palabras clave. Bosque mesófilo de montaña, *Geophis fuscus*, *Geophis lorancai*, grupo de *Geophis dubius*, nueva especie, Sierra de Misantla, Sierra Madre Oriental

Citation: Grünwald CI, Ahumada-Carrillo IT, Grünwald AJ, Montaño-Ruvalcaba CE, García-Vázquez UO. 2021. A new species of *Geophis* (Dipsadidae) from Veracruz, Mexico, with comments on the validity of related taxa. *Amphibian & Reptile Conservation* 15(2) [Taxonomy Section]: 289–310 (e294).

Accepted: 14 October 2021; **Published:** 23 December 2021

Introduction

The genus *Geophis* Wagler, 1830 is one of the largest genera of Dipsadidae with 50 recognized species (Canseco-Márquez et al. 2016). Downs (1967) recognized seven species groups of *Geophis*, as the *G. chalybeus*, *G. championi*, *G. dubius*, *G. latifrontalis*, *G. omiltemanus*, *G. semidoliatus*, and *G. sieboldi* groups, and this study follows that arrangement. While the *Geophis dubius* group was considered by Downs (1967) to consist of only five species, it has received a great deal of taxonomic interest in recent decades and is currently composed of at least 12 species, with a collective range from along the Atlantic versant from southern Hidalgo to central Guatemala, and along the Pacific versant from western Oaxaca to El Salvador and Guatemala. *Geophis fuscus* (Fisher 1886) was described from "Jalapa, Mexico" and later considered synonymous with *G. dubius* by various authors (Boulenger 1894; Bogert and Porter 1966; Downs 1967; Campbell et al. 1983; Nieto-Montes de Oca 2003). Herein, we give more insight to the potential origin and validity of *G. fuscus*.

The *Geophis dubius* group is defined by having a head which is indistinct or slightly distinct from the neck; snout long and bluntly pointed; rostral prominent, its visible length is one third or more its distance from the frontal; internasals large, rounded anteriorly; prefrontal short; anterior edge of the frontal sharply angulate;

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parietal short; supraocular small, triangular and absent in *G. rhodogaster*; eye small; postnasal enlarged; loreal short; anterior temporal absent; dorsal scales smooth or keeled and in 17 rows, and scales above the vent with paired apical pits (absent in some species) according to Downs (1967).

Species of the *Geophis dubius* group are mostly dark dorsally without conspicuous patterns, although several exceptions exist. The most remarkably colored species is *G. lorancai*, which has black bands on a bright orange background. Herein, we describe a new species of the *Geophis dubius* group that is unique within the genus in possessing bright crimson red lateral stripes on a slate gray background. The only species we are aware of in Mexico with bright crimson red lateral stripes are *Gyalopion quadrangulare* (Günther, 1893) and *Sonora mutabilis* Stickel, 1943; however, both belong to Colubridae, and are white and black banded snakes from the tropical deciduous forests of western Mexico.

Materials and Methods

The specimens of the new species were compared with specimens of all species of the *Geophis dubius* group from Central Mexico, as well as the relevant information published in the literature. The specimens examined are listed in Appendix 1.

Scale nomenclature follows Downs (1967) and Savage and Watling (2008). Scale counts were performed with the aid of a dissecting microscope. Measurements were taken with a ruler or digital calipers to the nearest 0.1 mm (Truper, Mexico). Ventrals were counted as suggested by Downs (1967). Bilateral characters were scored on both sides. When the condition of a given character was not identical on both sides, the conditions on the left and right sides are given, in that order, separated by a slash (/). In some instances, the conditions on the left and right sides are given in that manner in the tables even when they do not differ. Head length was measured from the tip of the snout to the posterior end of the parietals, and head width was measured at the widest point of the head at the posterior part of the jaw. All scale dimensions were measured at their maximum. To examine dentition characters, the maxilla and ectopterygoid were removed from the skull and cleansed in a dilute solution of Proteinase K at 34 °C for approximately one hour. The diagnosis is based on both the specimens examined and the extensive data published on the *Geophis dubius* group by Canseco-Márquez et al. (2016). Data for *G. fuscus* were taken from the original description (Fischer 1886). Other relevant literature that contributed to the diagnostics includes: Bogert and Porter (1966), Downs (1967), Smith and Holland (1969), Campbell and Murphy (1977), Savage (1981), Campbell et al. (1983), Restrepo and Wright (1987), Smith and Chiszar (1992), Smith and Flores-Villela (1993), Lips and Savage (1994), Smith (1995), Wilson et al. (1998), Pérez-Higareda et al. (2001), Myers (2003), Nieto-Montes de Oca (2003), Savage and Watling (2008), Townsend (2009), Townsend and Wilson (2006), and Pavón-Vázquez et al. (2011, 2013). Abbreviations used in the text and tables are as follows: snout-vent length (SVL), tail length (TL), total length (TotL), head length (HL), head width (HW), and snout-orbit length (SL).

Molecular analysis. For DNA extraction and PCR amplification, fragments of the mtDNA gene cytochrome b (*cyt-b*) were obtained for *G. lorancai*, *G. semidoliatus*, and the holotype of the new species (Table 1). The genomic DNA was extracted from liver or muscle tissue with the use of the standard ammonium acetate protocol (Fetzner 1999), and Polymerase Chain Reaction (PCR) was used to amplify the aforementioned fragments with the primers L14919–H15716 and L15845–H16064 (Burbrink et al. 2000). PCR products were purified with polyethylene glycol (Lis 1980). Purified DNA was sequenced by Macrogen Korea (Standard-Seq of Macrogen Inc.). Sequences of *cyt-b* were obtained from GenBank for *G. juarezi*, *G. carinosus, G. turbidus,* and *G. dubius* of the *Geophis dubius* group; while five samples for the remaining five species groups of *Geophis* (*G. occabus*, *G. godmani*, *G. bicolor*, *G. omiltemanus*, and *G. latifrontalis*), and *Rhadinaea flavilata* were used as outgroup (Table 1).

The alignment was performed using the Muscle algorithm included in the software MEGA 7 (Kumar et al. 2016; Tamura et al. 2018). The best-fitting substitution models and partitioning schemes were obtained simultaneously using the Bayesian Information Criterion in the software PartitionFinder 2.1.1 (Lanfear 2016). A Bayesian phylogenetic analysis was performed with the software MrBayes 3.2 (Ronquist et al. 2011). The analysis was run for 30,000,000 generations with the default settings and tree sampling every 3,000 generations. The results were evaluated for convergence and sufficient sampling in Tracer 1.6 (Rambaut et al. 2014), and the combined trees were obtained in each run using LogCombiner 1.8.4 (Drummond et al. 2012). The maximum clade credibility (MCC) tree was annotated in TreeAnnotator 1.8.4 (Drummond et al. 2012) after specifying a burn-in of 25%. Nodes with a Posterior probability (PP) $\geq$ 0.95 were considered significantly supported (Huelsenbeck and Rannala 2004).

Results

***Geophis cansecoi* sp. nov.**
Figs. 1–6.

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Holotype (Figs. 1–2). MZFZ 4432 (field number, CIG 1161). Adult male, collected at 0.9 km south of Los Capulines, on Misantla-Chiconquiaco Hwy., Municipio

Table 1. Collection and voucher data for colubrid genetic samples used in this study. Acronyms for herpetological collections follow Sabaj (2019). JAC, CIG, RWB, and ENS are field identifiers for un-catalogued specimens being deposited in the MZFZ, MZFC-HE, and UTA.

No.	Voucher number	Species	Locality	GenBank accession no.
1	JAC 24684	*Geophis bicolor*	Mexico: Michoacán	JX398637
2	**MZFZ 4432**	***Geophis cansecoi* sp. nov.**	**Mexico: Veracruz: Chiconquiaco**	**MZ883108**
3	MZFC-HE 10552	*Geophis carinosus*	Mexico: Veracruz: Volcan San Martín	KC917314
4	EBUAP 1966:	*Geophis dubius*	Mexico: Oaxaca: Monte Flor	KC917318
5	MZFC-HE 16160	*Geophis dubius*	Mexico: Oaxaca: Santa María Guienagati	KC917316
6	MZFC-HE 27256	*Geophis dubius*	Mexico: Oaxaca: San Isidro Buenos Aires	KC917319
7	MZFC-HE 27257	*Geophis dubius*	Mexico: Oaxaca: San Martín Buenavista	KC917317
8	CAS 178126	*Geophis godmani*	Costa Rica: Puntarenas: Las Tablas	JQ598932
9	MZFC-HE 27525	*Geophis juarezi*	Mexico: Oaxaca: Santa Maria Alotepec	KC917315
10	RWB 7232	*Geophis latifrontalis*	Mexico: Queretaro: San Joaquin	KC917323
11	MZFC-HE 28405	*Geophis lorancai*	Mexico: Veracruz: Zongolica	MZ883110
12	MZFC-HE 28404	*Geophis lorancai*	Mexico: Puebla: Chichiquila	MZ883109
13	MZFC-HE 25528	*Geophis occabus*	Mexico: Guerrero: El Molote	KC917323
14	ENS 11496	*Geophis omiltemanus*	Mexico: Guerrero	JX398639
15	CIG 1138	*Geophis semidoliatus*	Mexico: Veracruz: Nepopoalco	MZ883111
16	MZFC-HE 27253	*Geophis turbidus*	Mexico: Puebla: Cuetzalan	KC917321
17	MZFC-HE 27254	*Geophis turbidus*	Mexico: Puebla: Cuetzalan	KC917320
18	CAS 198643	*Rhadinaea flavilata*	USA: Florida: Lake Ural	AF471078

de Yecuatla, (19.811724°, -96.824587°, datum WGS84, 1,590 m asl), Veracruz, Mexico on 5 June 2017 by Christoph I. Grünwald, André J. Grünwald, and Iván T. Ahumada-Carrillo.

Paratypes (*n* = 14, Figs. 3–6). MZFZ 4433 (CIG 01162). Adult, DOR, collected at 1.1 km south of Los Capulines, on Misantla-Chiconquiaco Hwy., Municipio de Yecuatla, (19.810740°, -96.824874°, datum WGS84, 1,626 m asl), Veracruz, Mexico, on 6 June 2017 by Christoph I. Grünwald, Iván T. Ahumada-Carrillo, and André J. Grünwald. MZFZ 4434–35 (CIG 01378–79), MZFZ 4436–38 (CIG 01393–95), INIRENA 2811–14 (CIG 01396–99), MZFZ 4448–49 (CIG 01490–91). Adults and juveniles, collected at Los Capulines, on Misantla-Chiconquiaco Hwy., Municipio de Yecuatla, (19.813360°, -96.827240°, datum WGS84, 1,570 m asl), Veracruz, Mexico, on 8 June 2019 by Christoph I. Grünwald, André J. Grünwald, and Carlos E. Montaño-Ruvalcaba. INIRENA 2815–16 (CIG 01386–87). Adults, collected at 3.7 km S of Los Capulines, on Misantla-Chiconquiaco Hwy., Municipio de Chinconquiaco, (19.793370°, -96.822970°, datum WGS84, 1,763 m asl), Veracruz, Mexico, on 8 June 2019 by Christoph I. Grünwald, André J. Grünwald, and Carlos E. Montaño-Ruvalcaba.

Diagnosis. A member of the *Geophis dubius* group, as defined by Downs (1967) and expanded by Wilson and Townsend (2007), and characterized by the following combination of traits: eye relatively small; single supraocular and postocular present on each side (with one exception, see below); no anterior temporal scale, penultimate supralabial and parietal in contact; second infralabials small, broadly separated from each other; mental scale and anterior chinshields in contact; smooth dorsal scales throughout the body arranged in 17 rows; ventrals 134–142 in females (*n* = 7), and 125–131 in males (*n* = 7); subcaudals 28–35 in females (*n* = 7), and 34–37 in males (*n* = 7), with ventral + subcaudal totals 163–173 in females (*n* = 7) and 159–165 in males (*n* = 7); tail length 11.6–16.3% of TotL in females, 16.7–19.0% of TotL in males; dorsal pattern slate gray, with crimson red lateral stripe on each side, usually on first three or four scale rows but occasionally occupying part of the fifth; venter pale cream, except on the ventral surfaces of the head and throat, which are gray; maxillary teeth 6–8.

Geophis cansecoi is distinct from all species in the *G. championi* and *G. semidoliatus* groups, as well as most species in the *G. sieboldi* group by possessing the dorsal scales arranged in 17 rows (vs. 15 rows), and from the remaining species in the *G. sieboldi* group by possessing smooth dorsal scales throughout the body (vs. dorsal scales keeled on posterior half of body). *Geophis cansecoi* differs from all species in the *G. omiltemanus* and *G. chaylybeus* groups by a small eye, 10–12% of head length (vs. >12%); furthermore, from the species in the *G. omiltemanus* group by lacking an anterior temporal scale, thus either the fourth or fifth supralabial in contact with parietal (vs. fifth supralabial separated from parietal by anterior temporal scale); from some species in the *G. chalybeus* group (*G. dugesii*, *G. nigrocinctus*, and *G. tarascae*) by possessing dorsal scales arranged in 17 rows (vs. 15 rows) and from the remaining species by

Fig. 1. Holotype of *Geophis cansecoi* **sp. nov.** MZFZ 4432 from Los Capulínes, Municipio de Yecuatla, Veracruz, Mexico. **(A)** Dorsolateral perspective in life. **(B)** Lateral perspective in life. **(C)** Ventral perspective in life.

possessing a mental and anterior chinshields in contact (vs. separated by a pair of enlarged first infralabials, which are in contact). *Geophis cansecoi* can be distinguished from members of the *G. latifrontalis* group as follows: from *G. latifrontalis* and *G. mutitorques* by lacking an anterior temporal scale and possessing the fourth or fifth supralabial in contact with parietal (vs. fifth supralabial separated from parietal by anterior temporal scale); from *G. blanchardi* and *G. latifrontalis* by possessing mental and anterior chinshields in contact (vs. separated by a pair of enlarged first infralabials which are in contact), as well as from all species by its unique color pattern of slate gray ground coloration with two crimson red lateral stripes (vs. variable ground coloration with or without bands and without lateral stripes).

Geophis cansecoi can be distinguished from species within its own *Geophis dubius* group, as follows: from *G. carinosus*, *G. juarezi*, *G. rostralis*, and sometimes *G. turbidus* by possessing smooth scales throughout the body (vs. strongly keeled dorsal scales on posterior

Fig. 2. Holotype of *Geophis cansecoi* **sp. nov.** MZFZ 4432 from Los Capulínes, Municipio de Yecuatla, Veracruz, Mexico. **(A)** Dorsal perspective in preservative. **(B)** Ventral perspective in preservative.

portion of the body or above vent); from *G. anocularis*, *G. duellmani*, and *G. rhodogaster* by usually possessing a supraocular scale (vs. supraocular scale absent); from *G. anocularis* and *G. duellmani* by possessing a postocular scale (vs. postocular scale absent); from *G. dubius* and *G. fuscus* (see below) by possessing internasal scales and prefrontal scales that are not fused (vs. fused); from *G. carinosus*, *G. dubius*, *G. immaculatus*, *G. juarezi*, *G. nephodrymus*, *G. rhodogaster*, and sometimes *G. turbidus* by first infralabial scales that are broadly separated, never in contact (vs. in contact or narrowly separated); from *G. carinosus*, *G. juarezi*, and sometimes *G. anocularis* and *G. fulvoguttatus* by possessing more than 125 ventral scales in males (vs. less than 125); from *G. anocularis* and usually from *G. carinosus* and *G. immaculatus* by possessing more than 134 ventral scales in females (vs. usually fewer); from *G. dubius* by possessing fewer than 142 ventral scales in females (vs. more than 144); from *G. carinosus*, *G. duellmani*, *G. juarezi*, *G. rhodogaster*, and *G. rostralis* by possessing fewer than 38 subcaudal scales in males (vs. 39 or more); from *G. nephodrymus* and *G. lorancai* by possessing 34 or more subcaudal scales in males (vs. 35 or less); from *G. carinosus* and *G. juarezi* by possessing fewer than 35 subcaudal scales in females (vs. 37 or more); from all species in the species group other than *G. lorancai* by possessing fewer maxillary teeth 6–8 (vs. 9 or more); from *G. annocularis*, *G. carinosus*, *G. duellmani*, *G. juarezi*, *G. rhodogaster,* and *G. rostralis* by possessing a shorter tail in males, 17–19% of TotL (vs. more than 19% of TotL); from *G. nephodrymus* by possessing a longer tail in males 17–19% of TotL (vs. less than 17% of TotL); from *G. carinosus*, *G. duellmani*, and *G. juarezi*, by possessing a shorter tail in females, 12–16% of TotL (vs. more than 16% of TotL); and from all species in the species group by its unique color pattern of slate gray ground coloration with two crimson red lateral stripes (vs. variable ground coloration with or without bands and without lateral stripes). A comparison of the diagnostic characters of all species of the *G. dubius* species group is given in Table 2. Many species of Mexican *Geophis* are poorly understood, and in many cases photographs of live individuals have not been published. For comparative purposes, we have included photos of closely related species of the *Geophis dubius* group as well as sympatrically occurring species of *Geophis* from other species groups (Figs. 7–9).

Description of holotype (Figs. 1–2). MZFZ 4432. Adult male. SVL 227 mm; TL 47; TotL 274 mm. HL 8.6 mm (from tip to posterior border of parietal); HW 5.1 mm, head slightly (1.3 times) distinct from body. Snout long, SL 3.7 mm, with HL 2.3 times SL, rounded from above, obtusely pointed from lateral profile, projecting anteriorly 1.0 mm beyond the lower jaw. Rostral 1.6 times as broad as high (2.6 mm wide, 1.6 mm high), portion visible from above (1.0 mm) is 0.3 times as long as its distance from frontal (3.3 mm), 1.4 times as long as common internasal suture (0.7 mm), with posterior end approximately at level of anterior margin of nostrils; internasals as broad as long (length / width) = (1.2 mm /1.2 mm), angular anteriorly, in lateral contact with anterior and posterior nasals. Prefrontals in lateral contact with postnasal, loreal, and eye on each side, their length 2.7 mm, 73% of the length of SL, and their common suture 1.7 mm, 63% of the length of frontal. Frontal wider than long, 3.1 mm wide, 2.7 mm long, 1.2 times as wide as long. Supraocular large, in contact with prefrontal, frontal, parietal, and postocular. Postoculars moderately sized, in contact with supraocular, parietal, and fourth and fifth supralabials. Parietal 3.8 mm long, 2.7 mm wide, 1.4 times as long as wide, length of parietal 44% of HL, the common suture between parietals 2.4 mm, 89% of frontal length. Nasal divided, postnasal longer than prenasal with combined length of both nasals (2.1 mm) longer than loreal. Loreal 1.6 mm long, 1.1 mm high, longer than high, and reaching orbit. Eye small, 0.9 mm, 10% of HL. Supralabials six on both sides, first in contact with nasals, second and third in contact with loreal, third and fourth

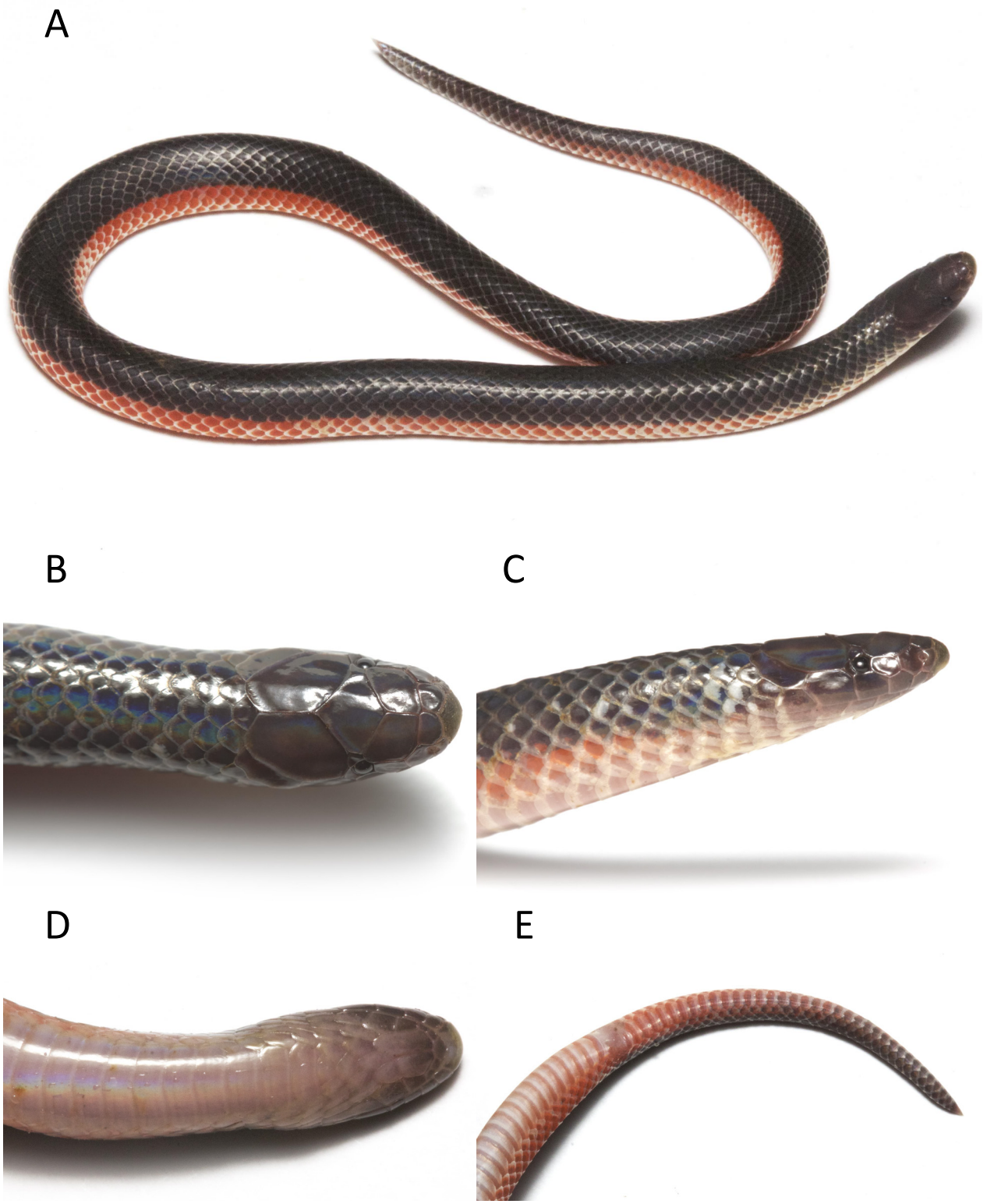

Fig. 3. Diagnostic characters of paratype *Geophis cansecoi* **sp. nov.** MZFZ 4436 from Los Capulínes, Municipio de Yecuatla, Veracruz, Mexico. **(A)** Dorso-lateral perspective in life. **(B)** Dorsal profile of head in life. **(C)** Lateral profile of head in life. **(D)** Ventral profile of head in life. **(E)** Ventral surface of tail in life.

entering orbit, fifth largest and in contact with parietal and posterior temporal. Anterior temporal absent, one posterior temporal. Four nuchal scales in contact with parietals.

Mental 1.2 times as broad as long (1.4 mm broad, 1.2 mm long), rounded anteriorly, in posterior contact with both anterior chinshields. Infralabials five left / six right, first through third in contact with anterior chinshields, and third and fourth in contact with posterior chinshields. Anterior chinshields irregular, left chinshield 2.4 mm

Table 2. Key to comparative characters of the *Geophis dubius* species group.

	G. cansecoi sp. nov.	*G. turbidus*	*G. lorancai*	*G. dubius*	*G. fuscus*	*G. rostralis*	*G. carinosus*	*G. juarezi*	*G. duellmani*	*G. anocularis*	*G. fulvoguttatus*	*G. immaculatus*	*G. nephodrymus*	*G. rhodogaster*
Extent of dorsal scale keeling	Smooth	Smooth or keeled on posterior one-fourth of body	Smooth	Smooth with keels barely visible above vent	Smooth	Keeled above vent	Strongly keeled on posterior two-thirds of body	Strongly keeled on posterior one-half to two-thirds of body	Smooth	Smooth or weakly keeled above vent	Smooth	Smooth	Smooth	Smooth
Supraoculars	Present	Present	Present	Present	Present	Present	Present	Present	Absent	Absent	Present	Present	Present	Absent
Postoculars	Present	Present	Present	Present	Present	Present	Present	Present	Absent	Absent	Present	Present	Present	Present
Prefrontals and internasals fused or not fused	Not fused	Not fused	Not fused	Fused	Fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused
Loreal length (as length/ height)	1.5	1.3	1.5	Varied	2.0	?	Long and narrow	1.1–2.0	1.5	2.0–2.5	1.4–1.7	1.5	1.1–2.0	1.4–1.8
First gular single or paired	Single	Usually single	Usually single or none	Paired	Single	?	Single	Single	?	Single or paired	?	Single	Single	?
1st pair of infralabials	Separated	In contact or narrowly separated	Separated	In contact or narrowly separated	In contact	Broadly separated	In contact	In contact	Broadly separated	Broadly separated	Separated	In contact	In contact or narrowly separated	In contact
Subcaudal coloration	Red with some light gray crossbands and darker gray on tip	Banded white and brown	Reddish or orange with darker gray on tip	Brown	Cream, yellowish	White or pale cream with mottled with dark	Brown with traces of white anteriorly	Cream with reddish brown crossbands, turning to reddish brown	White anteriorly then dark brown	Pink suffused with dark brown	—	Dark gray	Dark gray	—
Ventrals (♂)	125–131	125–139	125–130	131–149	142	126–132	116–123	114	126–133	122–126	135–137	129	122–138	131–138
Ventrals (♀)	134–142	129–140	130	137–151	—	—	125–136	118–124	134–138	123–132	145–147	130–134	128–138	136–147
Subcaudals (♂)	34–37	34–39	33–35	36–50	49	39–43	45–49	55	40–43	35–39	34–36	32	22–31	39–46
Subcaudals (♀)	28–35	26–31	25	31–41	—	—	37–43	49	32–36	29–35	24–35	27–29	24–32	29–35
Maxillary teeth	6–8	9	7	10–12	?	11	10–13	11–13	10–12	09–11	10	12	11	14–17
Tail length / total length ratio (♂)	0.17–0.19	0.14–0.18	0.15–0.18	0.17–0.21	0.16	0.20–0.21	0.23–0.24	0.25	0.20–0.21	0.21–0.22	0.16–0.18	0.17	0.12–0.165	0.22

Table 2. Key to comparative characters of the *Geophis dubius* species group.

	G. cansecoi *sp. nov.*	*G. turbidus*	*G. lorancai*	*G. dubius*	*G. fuscus*	*G. rostralis*	*G. carinosus*	*G. juarezi*	*G. duellmani*	*G. anocularis*	*G. fulvoguttatus*	*G. immaculatus*	*G. nephodrymus*	*G. rhodogaster*
Tail length / total length ratio (♀)	0.12–0.16	0.12–0.13	—	—	—	0.15	0.18–0.195	0.22	0.17	0.155	0.11	0.14	0.12–0.15	0.135–0.17
Dorsal coloration pattern	Dark slate gray dorsal coloration with red lateral stripes	Grayish-brown, unmarked, one juvenile with a pink collar	Dark gray crossbands on a red or orange background	Brownish or slate gray, unmarked	Brownish or slate gray, unmarked	Gray (?), unmarked	Dark brownish or slate gray, unmarked	Dark brown	Dark saddles on a red or white background	Dark slate gray	Red orange middorsal spots on a dark grayish brown background, darker posteriorly	Brownish	Gray background, ranging from unpatterned to extensively marked with bands, laterally offset partial bands, and lateral blotches that range from pale grayish cream to brick red	Grayish to reddish brown
Ventral coloration	White with reddish outlines	Pale Cream	Reddish or orange	White	Cream, yellowish	Unmarked, white or pale cream	Cream with brown anterior borders	Cream, with narrow crossbands	Unmarked, red or white	Pink	Whitish, lateral edges mottled with dark pigment	White with brown on anterior and lateral edges of ventrals	Cream, yellowish with brown outlines	Reddish orange or yellow
Geographic distribution	Sierra Madre Oriental, west-central Veracruz	Sierra Madre Oriental, east-central Hidalgo and northern Puebla, Mexico	Sierra de Zongolica, west-central Veracruz, and Sierra de Quimixtlán, east-central Puebla, Mexico	Central Oaxaca, Mexico	Xalapa, Veracruz?	Sierra Madre del Sur, southern Oaxaca, Mexico	Northern Chiapas and southern Veracruz, Mexico to western Guatemala	Sierra de Juárez and Sierra Mixe, northern Oaxaca, Mexico	Sierra de Juárez, northern Oaxaca, Mexico	Sierra Mixe, eastern Oaxaca, Mexico	Northwestern El Salvador to southwestern Honduras	Southeastern Chiapas, Mexico and southwestern Guatemala	Sierra de Omoa, northwestern Honduras	Eastern Chiapas, Mexico through southern Guatemala to southwestern Honduras and northwestern El Salvador
Habitat	Cloud forest	Cloud forest and pine forest	Cloud forest	Cloud forest and pine-oak forest	Unknown	Humid pine-oak forest	Cloud forest, pine-oak forest, and wet forest	Wet forest and cloud forest ecotone	Cloud forest	Cloud forest	Cloud forest	Cloud forest and wet forest	Cloud forest	Humid pine-oak forest

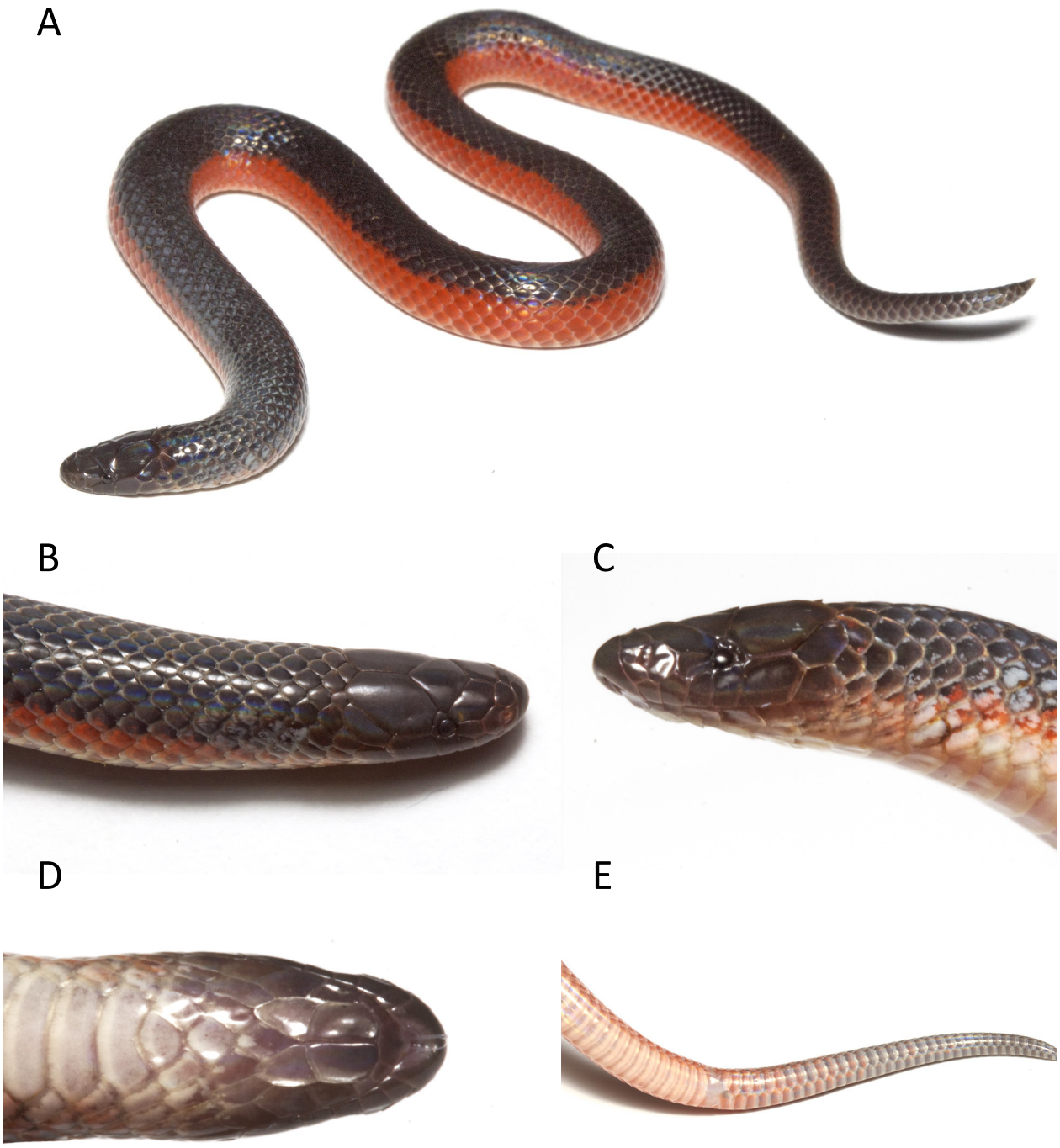

Fig. 4. Diagnostic characters of paratype *Geophis cansecoi* **sp. nov.** MZFZ 4437 from Los Capulínes, Municipio de Yecuatla, Veracruz, Mexico. **(A)** Dorso-lateral perspective in life. **(B)** Dorsal profile of head in life. **(C)** Lateral profile of head in life. **(D)** Ventral profile of head in life. **(E)** Ventral surface of tail in life.

long and 1.0 mm wide (2.4 times as long as wide) and right anterior chinshield 2.1 mm long and 1.0 mm wide (2.1 times as long as wide). Left posterior chinshield 1.4 mm long and 1.0 mm wide (1.4 times as long as wide) and right posterior chinshield 1.7 mm long and 1.1 mm wide (1.5 times as long as wide). Three midgular scales. Infralabials and scales in chin region smooth. Dorsal scales in 17-17-17 rows, smooth throughout body; no evident apical pits. Ventrals 125; cloacal plate single; subcaudal scales paired, 34 on both sides.

Coloration in life (Fig. 1). Dorsal coloration of head and mid-dorsal region of body and tail slate gray, with one crimson red lateral stripe on each side. The red lateral stripe restricted to scale rows 1 and half of 2 at one head length behind the neck, then expanding to cover scale rows 1–3 and lower portions of 4 at mid-body, and continuing to cover scale rows 1–3 and lower portions of 4 above vent. Dorsal coloration of tail slate gray, and red lateral stripe continues on scale 1 and half of 2 (with some speckling on 3) on anterior half of tail, and then

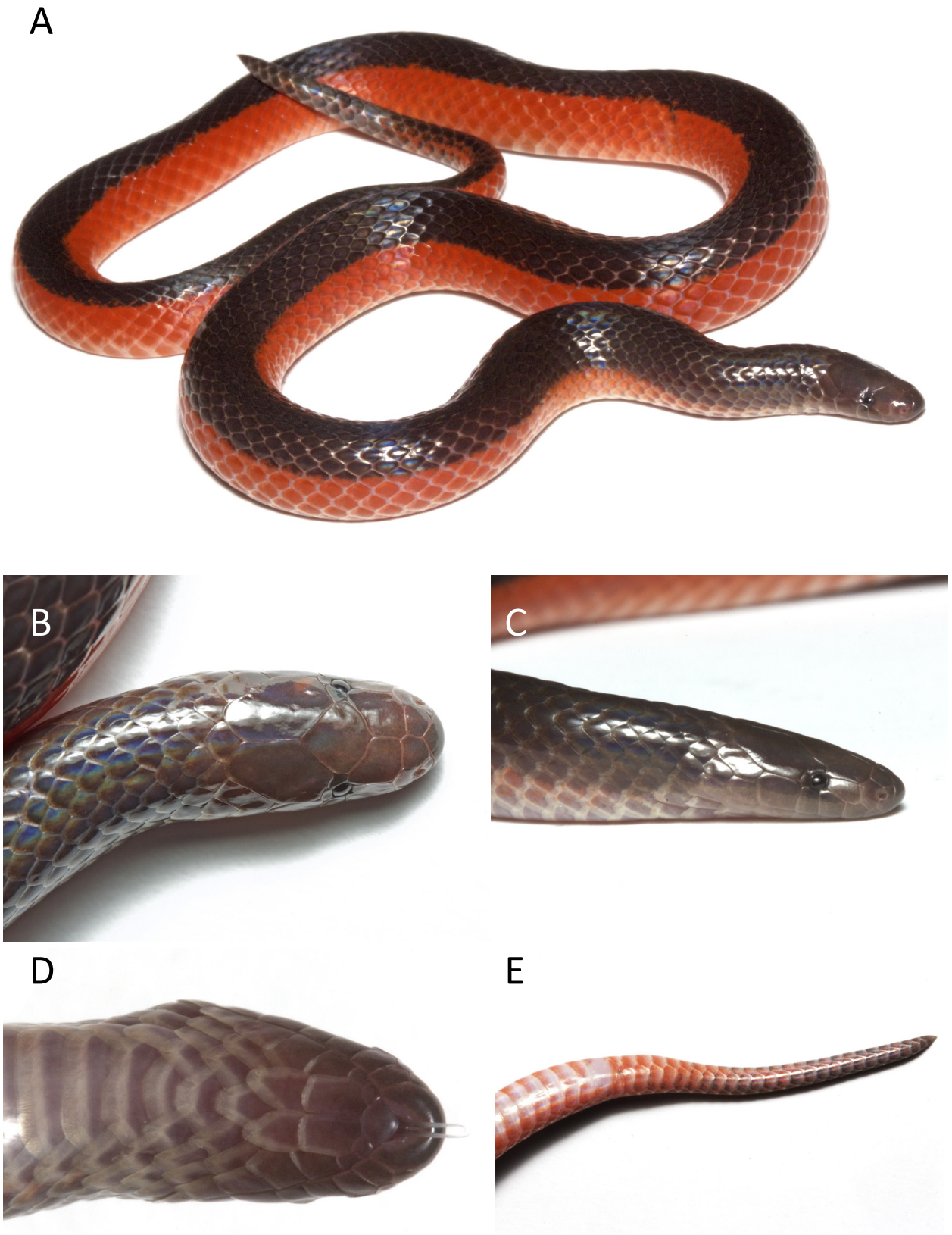

Fig. 5. Diagnostic characters of paratype *Geophis cansecoi* **sp. nov.** INIRENA 2814 from Los Capulínes, Municipio de Yecuatla, Veracruz, Mexico. **(A)** Dorso-lateral perspective in life. **(B)** Dorsal profile of head in life. **(C)** Lateral profile of head in life. **(D)** Ventral profile of head in life. **(E)** Ventral surface of tail in life.

Fig. 6. Paratypes of *Geophis cansecoi* **sp. nov.** in life. **(A–B)** MZFZ 4435; **(C–D)** INIRENA 2812; **(E)** INIRENA 2814; **(F)** MZFZ 4434; all from the vicinity of Los Capulínes, Municipio de Yecuatla, Veracruz, Mexico.

remnants of red lateral stripes continue on scale 1 and parts of 2 on posterior half of the tail, with the tail tip slate gray. The ventral coloration in life of the head and neck is dark gray on the mental and anterior chinshields and infralabials, light gray on the posterior chinshields, gulars, and first 15 ventral scales, fading after the ninth ventral. The ventral coloration on the body is white/pale cream. The ventral scales are outlined in pink, which represents the remnants of the red lateral stripe which fades out on the ventrals. The pink ventral scale outlines intensify in color towards the posterior portion of body and become wider, enclosing the pale cream coloration present on the ventral scales; and the last three ventral scales, as well as the cloacal plate, are crimson red. Subcaudals are crimson red, barely outlined in white/cream on anterior three-fourths of tail and then outlined in slate gray on posterior eight subcaudal pairs. Tail tip is slate gray above and below.

Coloration in preservative (Fig. 2). General coloration bicolor. Dorsal surfaces of head, body, and tail predominately dark gray; ventral surfaces of body and tail predominately pale cream, with dark gray stippling

Table 3. Morphological and mensural variation among *Geophis cansecoi* **sp. nov.** specimens. See text for descriptions of acronym abbreviations.

Specimen	MZFZ 4432	MZFZ 4434	MZFZ 4435	INIRENA 2815	INIRENA 2816	MZFZ 4436	MZFZ 4437	MZFZ 4438	INIRENA 2811	INIRENA 2812	INIRENA 2813	INIRENA 2814	MZFZ 4448	MZFZ 4449
Sex	Male	Female	Male	Female	Female	Male	Male	Female	Male	Female	Male	Female	Male	Female
TotL (mm)	274	294	187	302	239	174	182	264	169	199	198	311	180	158
SVL (mm)	227	254	153	262	200	141	159	229	140	169	165	275	148	136
TL (mm)	47	40	34	40	39	33	33	35	29	30	33	36	32	22
EL (mm)	0.9	0.8	0.75	0.9	7.1	0.7	0.8	1	0.6	0.8	0.8	0.8	0.8	0.7
HL (mm)	8.6	8	7.3	7.8	0.7	6.4	6.9	8.2	6.3	6.7	6.9	8.3	6.5	6.3
EL/HL	0.105	0.100	0.103	0.115	10.143	0.109	0.116	0.122	0.095	0.119	0.116	0.096	0.123	0.111
TL/TotL	0.172	0.136	0.182	0.132	0.163	0.190	0.181	0.133	0.172	0.151	0.167	0.116	0.178	0.139
TL/SVL	0.207	0.157	0.222	0.153	0.195	0.234	0.208	0.153	0.207	0.178	0.200	0.131	0.216	0.162
Dorsal scale rows	17	17	17	17	17	17	17	17	17	17	17	17	17	17
Ventrals	125	141	126	142	136	126	131	138	129	134	130	135	127	135
Subcaudals	34	32	37	31	35	36	34	28	35	29	35	30	37	28
Total scales	159	173	163	173	171	162	165	166	164	163	165	165	164	163
Extent of dorsal keeling	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth
Maxillary teeth	7 and 6	6	—	—	—	—	—	—	—	—	—	—	—	—
Prefrontals and internasals fused or not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused	Not fused
Supralabials	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 5 R	6 L / 5 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R
Midgulars	3	4	3	3	3 and 4	3	3	3	3	3	3	3	3	4
Infralabials	5 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R	6 L / 6 R
Mental in contact with chinshields	In contact	In contact	In contact	In contact	In contact	In contact	In contact	In contact	In contact	In contact	In contact	In contact	In contact	In contact
Postocular	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1
Supraocular	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1	1 and 0	1 and 1	1 and 1	1 and 1	1 and 1	1 and 1
Anterior temporal	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Prefontal contacting parietal	No	No	No	No	No	No	No	No	Barely on one side due to lack of supraocular	No	No	No	No	No
Number of sides to frontal	6	6	6	6	6	6	6	6	6	6	6	6	6	6
1st pairs	Broadly Separated	Broadly separated	Broadly separated	Broadly separated	Broadly separated	Broadly separated	Broadly separated	Broadly separated	Broadly separated	Broadly separated	Broadly separated	Broadly separated	Broadly separated	Broadly separated

Fig. 7. Comparative photos of sympatric or nearly sympatric species of *Geophis* living in close proximity of *Geophis cansecoi* **sp. nov. (A)** Dorsal perspective of juvenile *Geophis turbidus* from vicinity of El Damo, Municipio de Tenango de Doria, Hidalgo. *Photo by L. Fernández-Badillo*. **(B)** Dorsal perspective of juvenile *Geophis turbidus* from vicinity of La Viejita, Municipio de Tenango de Doria, Hidalgo (CIB 04451). *Photo by R. Cruz-Elizalde*. **(C)** Dorsal perspective of *Geophis semidoliatus* from the vicinity of La Joya, Municipio de Tezonapa, Veracruz. UTA 52611. *Photo by J.A. Campbell*. **(D)** Ventral perspective of *Geophis semidoliatus* from the vicinity of La Joya, Municipio de Tezonapa, Veracruz. UTA 52611. *Photo by J.A. Campbell*. **(E)** Dorsal perspective of *Geophis mutitorques* from the vicinity of Chiconquiaco, Veracruz. CIG 1156. **(F)** Ventral perspective of *Geophis mutitorques* from the vicinity of Chiconquiaco, Veracruz. CIG 1156.

on subcaudals, increasing towards tip of tail. Lateral surfaces of body pale cream on first and lower portions of second scale rows on anterior third of body, increasing to first, second, third, and very bottom of fourth scale rows on latter two-thirds of body. Light lateral stripe on latter two-thirds of body variable but with slight amounts of light salmon, remnants of the red lateral stripe in life.

Variation. Morphological variations observed on 13 specimens are as follows: MZFZ 4436–37 has only five supralabials on the right side (supralabials 3 and 4 are fused or partially fused). Four midgulars in MZFZ 4434 and MZFZ 4449, and irregularly split in INIRENA 2816, where it can be understood to represent either three or four midgulars between the posterior chinshields and first ventral. Supraocular absent on the right side of the head in INIRENA 2811. Meristic variation is given in Table 3.

Color in life. An adult female paratype had the following coloration. Dorsal coloration of head and mid-dorsal region of body and tail slate gray, with one

Fig. 8. Comparative photos of similar species of the *Geophis dubius* group from southern Mexico. **(A)** Dorsal perspective of *Geophis dubius* from the vicinity of Santa María Tlahuitoltepec, Oaxaca. CIG 00723. **(B)** Ventral perspective of *Geophis dubius* from the vicinity of Santa María Tlahuitoltepec, Oaxaca. CIG 00723. **(C)** Dorsal perspective of *Geophis dubius* from the vicinity of La Cumbre, Municipio de Santa Catarina Ixtepejí, Oaxaca. UTA 38826 (JAC 17793). *Photo by J.A. Campbell*. **(D)** Ventral perspective of *Geophis dubius* from the vicinity of La Cumbre, Municipio de Santa Catarina Ixtepejí, Oaxaca. UTA 38826 (JAC 17793). *Photo by J.A. Campbell*. **(E)** Dorsal perspective of *Geophis anocularis* from vicinity of Totontepec, Municipio de Totontepec Villa de Morelos, Oaxaca. CIG 00725. **(F)** Ventral perspective of *Geophis anocularis* from vicinity of Totontepec Villa de Morelos, Oaxaca. CIG 00725.

crimson red lateral stripe on each side. The red lateral stripe restricted to scale rows 1 and 2 at one headlength behind the neck, then expanding to cover scale rows 1–4 and lower portions of 5 at midbody, and continuing to cover scale rows 1–4 and lower portions of 5 above vent. Dorsal coloration of tail slate gray, and lateral stripe dissipates on anterior one-fourth of tail; however, remnants of red lateral stripes continue to outline some of the lower dorsal scales on the tail onto the anterior three-fourths of the tail. The ventral coloration in life dark gray on the mental and anterior portions of the chinshields, light gray on the remaining gulars and first

Fig. 9. Comparative photos of similar species of the *Geophis dubius* group from southern Mexico and Guatemala. **(A)** Dorsal perspective of *Geophis lorancai* from the vicinity of Zongolica, Veracruz. ITSZ 025. **(B)** Ventral perspective of *Geophis lorancai* from the vicinity of Zongolica, Veracruz. MZFC ITSZ 025. **(C)** Dorsal perspective of *Geophis nasalis* from the vicinity of Quetzaltenango, Guatemala. UTA 20800. **(D)** Ventral perspective of *Geophis nasalis* from the vicinity of Quetzaltenango, Guatemala. UTA 20800. **(E)** Dorsal perspective of *Geophis rhodogaster* from vicinity of Guatemala, Guatemala. UTA28347. **(F)** Ventral perspective of *Geophis rhodogaster* from the Department of Quetzaltenango, Guatemala (UTA 22752). *Photos by M.A. de la Torre Loranca* (*A–B*) *and J.A. Campbell* (*C–F*).

seven ventral scales, and then off white/pale cream on the remaining ventral scales of the anterior one-third of the body, changing to off white/pale cream with orange outline on sides and borders on the remaining two-thirds of body. Dorsal coloration of anterior half of tail red with slate gray outlines on sides and borders, posterior half of tail slate gray.

Two juvenile paratypes, a male and a female, had a dorsal coloration of head and mid-dorsal region of body and tail dark gray, with one crimson red lateral stripe present on each side. The red lateral stripe was confined to scale rows 1 and 2 at one head length behind the neck, expanding to scale rows 1–3 and the very bottom edge of 4 at mid-body, and reducing to scale rows 1–3 above vent. Dorsal coloration of tail dark gray with red lateral stripes fading out on anterior one-fourth of the tail. Ventral coloration in life dark gray on the mental and anterior portions of the chinshields, then light gray on the gulars and first two ventral scales, changing to cream/off white on the remaining ventrals. Ventrals on the latter one-third

Fig. 10. Type locality of *Geophis cansecoi* **sp. nov.** at Los Capulínes, Municipio de Yecuatla, Veracruz. **(A)** Exact location where type specimen was collected. **(B)** General photo of type locality. **(C)** Decomposing log in clearing in cloud forest where several of the type specimens were collected.

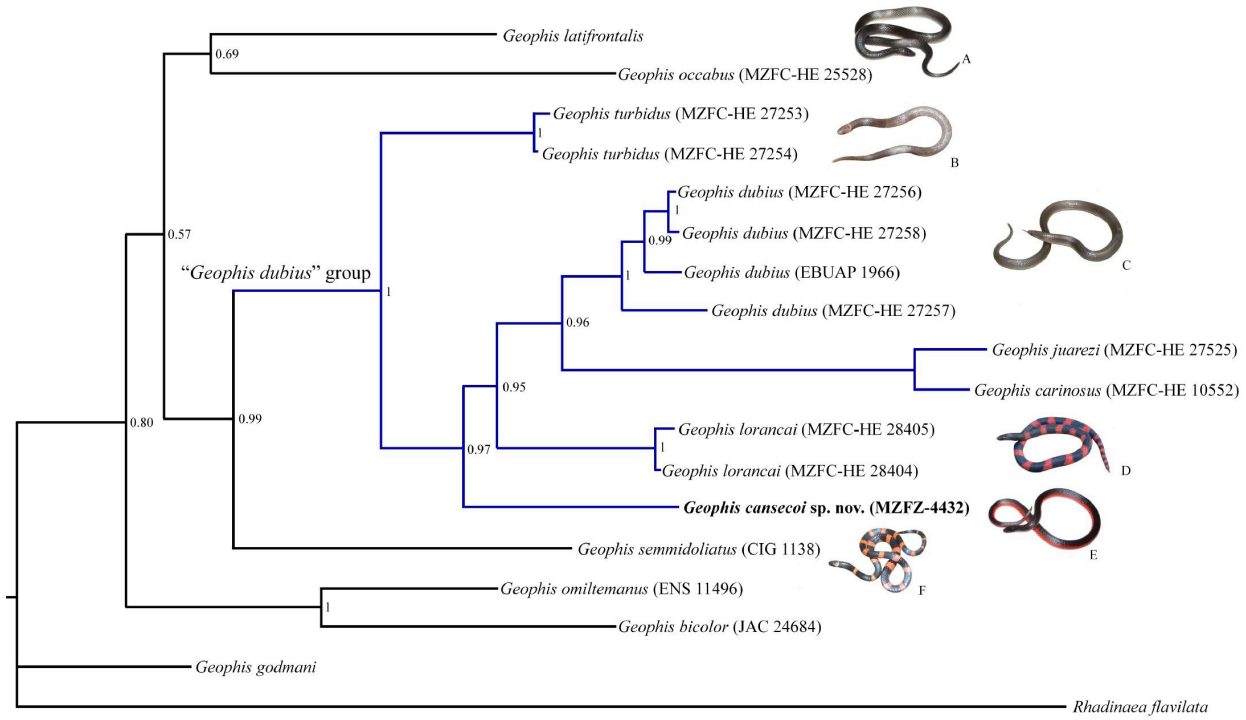

Fig. 11. Bayesian phylogenetic inference of several members of the *Geophis dubius* group based on the mitochondrial loci 16S rRNA. Black circles represent nodes with a posterior support of 1. All nodes with support of less than 0.5 are collapsed. **(A)** *Geophis occabus*, **(B)** *G. turbidus*, **(C)** *G. dubius*, **(D)** *G. lorancai*, **(E)** *G. cansecoi*, **(F)** *G. semmidoliatus*. *Photos by Christoph I. Grünwald (A, C, E, F), Raciel Cruz-Elizalde (B), and Miguel A. de la Torre-Loranca (D).*

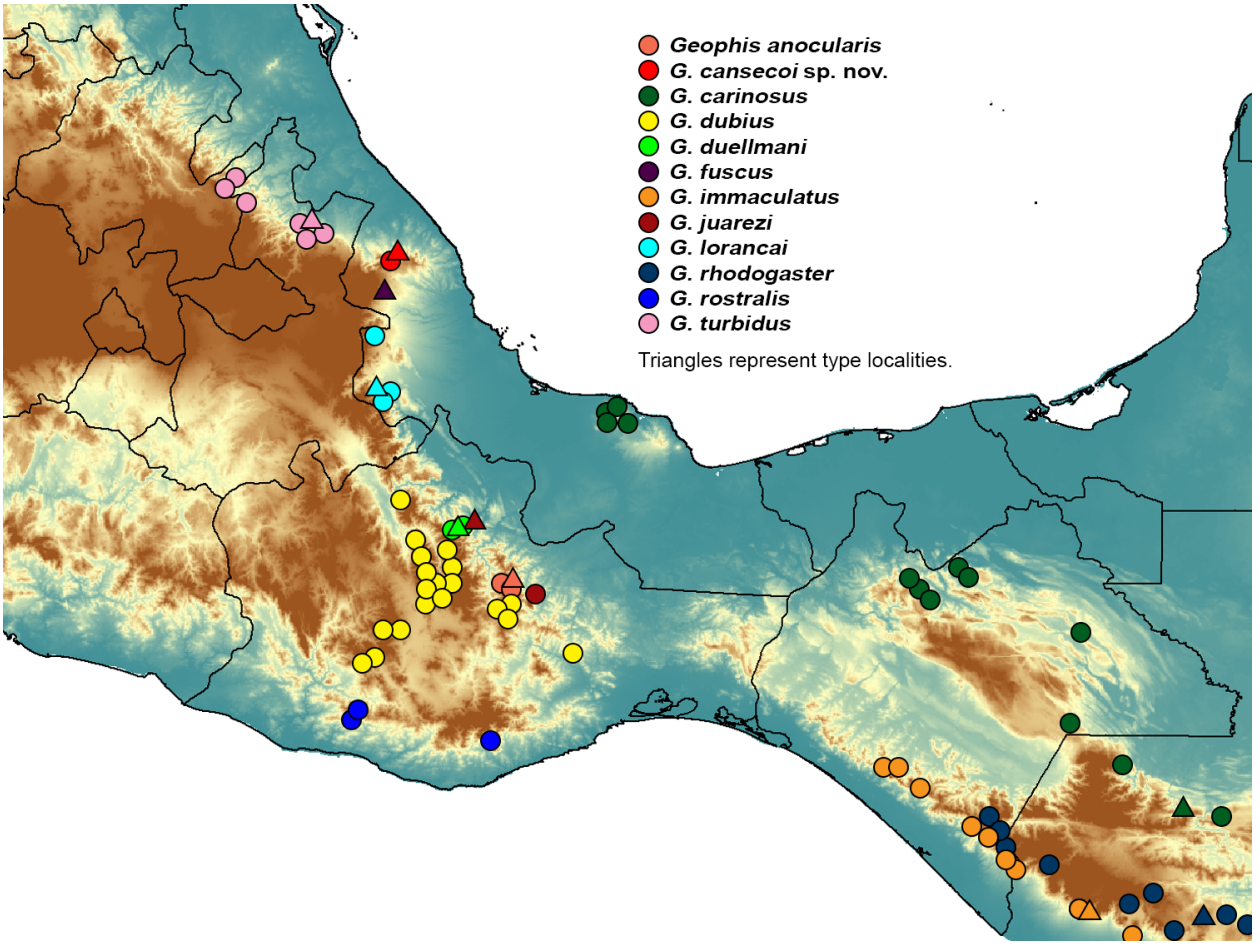

Fig. 12. Map showing the type localities and distribution of the *Geophis dubius* group members in southern Mexico and adjacent Guatemala. Circles represent localities and triangles represent known type localities. Type localities which are not known or not exact are not shown.

of the body on the male outlined in red. Subcaudals of the tail red with dark gray outlines, turning completely dark gray toward the tip of the tail.

Dentition. An adult female paratype (MZFZ 4434) had six teeth visible and two spaces, which probably represented missing teeth. The anterior maxillary tooth was opposite the first supralabial. The holotype appears to have 6–8 maxillary teeth visible; however, we did not remove the jaw.

Distribution, habitat, and ecology. This species appears to be restricted to the immediate vicinity of the type locality in the Sierra de Misantla portion of the Sierra Madre Oriental of Veracruz, Mexico (Fig. 10). It has been collected between 1,550–1,763 m asl in mesic cloud forest. Specimens were found beneath a variety of decomposing logs, trash, and rocks, and also crossing the road at night. All specimens were collected in the month of June.

Etymology. The specific epithet honors to Luis Canseco-Márquez, a Mexican herpetologist who has dedicated a portion of his career to the study of snakes of the genus *Geophis*.

Relationships of *Geophis cansecoi*. The final sequence alignment consisted of 1,055 bp. The partitions and models that best fit the data were GTR+G for the first and second codon positions, and GTR+G+I for the third codon position. The phylogenetic hypotheses support the morphological data, which places *G. cansecoi* in the *Geophis dubius* group and supports the genetic distinctiveness of this species from other congeners in Mexico and northern Central America (Fig. 11). In the Maximum Credibility Tree, the sequence of *Geophis* from this population forms a strongly supported clade (Pp = 1.0) with other species currently placed in the *Geophis dubius* group (*G. carinosus*, *G. dubius*, *G. lorancai*, *G. juarezi,* and *G. turbidus*). Furthermore, our results suggest that *Geophis cansecoi* forms a strongly supported clade (Pp = 0.97) with its sister group, which includes *G. carinosus*, *G. dubius*, *G. lorancai,* and *G. juarezi*. *Geophis turbidus* appears to form the sister taxon to all the remaining haplotypes of the *Geophis dubius* group.

Discussion

On the validity of *G. fuscus* Fischer, 1886. *Geophis fuscus* was described by Fischer (1886) based on a specimen collected by Mr. Kienast from "Jalapa"

Fig. 13. Holotype of *Geophis fuscus* (BMNH 1946.1.6.48) from "Jalapa," Mexico. **(A)** Dorsal perspective in preservative. **(B)** Ventral perspective in preservative. *Photos by Jeff Streicher*.

(=Xalapa?), Mexico (Fig. 12). Generally, it has been assumed that this specimen originated from near Xalapa, Veracruz. Fischer (1886) recognized *G. fuscus* as being closely related to *G. dubius* since the internasal scales were fused with the prefrontals. He distinguished *G. fuscus* from *G. dubius*, however, by having a longer loreal scale, possessing a first pair of infralabials in contact with each other, and having a single gular scale as opposed to a pair of midgular scales as in *G. dubius*. For the coloration, he described the ventral coloration of both the body and tail as unmarked pure yellow, as opposed to that of *G. dubius*, which he described as having a ventral coloration peppered with brown (Fischer 1886). Bogert and Porter (1966) considered *G. fuscus* conspecific with *G. dubius*. They proposed that since there are numerous towns in Mexico with the name Jalapa, including several in Oaxaca, and the specimen might have come from Oaxaca. However, the collector was M. Kienast-Zolly of Zurich, Switzerland, a Swiss diplomat who lived for many years on Pico de Orizaba, Veracruz, and made various botanical collections, specifically of orchids, in the immediate vicinity of his residence (Boyle 2019). Thus, a central Veracruz origin of the type specimen of *G. fuscus* is more likely. Downs (1967) included the type specimen of *G. fuscus* in his definition of *G. dubius*, as he did specimens of *G. rostralis, G. chalybeus*, and *G. anocularis*. The confusion of these related taxa as one species by Downs (1967) renders his definition of *G. dubius* inaccurate. Furthermore, Downs (1967) ignored several of the diagnostic characters Fischer (1886) listed in his description of *G. fuscus*, such as the first pair of infralabials being in broad contact, the 49 subcaudal scales, and the brown subcaudal coloration.

The snakes of the *Geophis dubius* group are very habitat specific, and often partition mountain ranges amongst species by habitat and rainfall. A few examples of this pattern between closely related species can be seen in northern Puebla, where *G. turbidus* inhabits humid pine-oak woodland and pine forest, whereas an undescribed *Geophis* sp. (Canseco-Márquez, Pers. Comm.) inhabits cloud forest; in the Sierra Juárez of Oaxaca where *G. dubius* inhabits moist pine-oak and pine woodland, whereas *G. duellmani* inhabits cloud forest; and in the Sierra Mixe, Oaxaca where *G. dubius* inhabits

moist pine-oak and pine woodland while *G. anocularis* inhabits cloud forest (Pavón-Vázquez et al. 2013; Canseco-Márquez et al. 2016; Canseco-Márquez, Pers. Comm.). In the portion of Sierra Madre Oriental roughly between Xalapa, Veracruz, and the Oaxacan border, the only member of the *Geophis dubius* group that has been reported is the recently described *G. lorancai*, which is restricted to cloud forest at intermediate elevations (Canseco-Márquez et al. 2016). Whether any species of the *Geophis dubius* group inhabits the moist pine-oak and pine woodland in this region remains unknown but should be considered likely.

We propose that the dismissal of the suggestion by Bogert and Porter (1966) of a central Veracruz origin of the type of *G. fuscus* was unwarranted. Taking into consideration the presently known diversity of the *Geophis dubius* group in the Sierra Madre Oriental, the geographical distance between central Veracruz and the closest known specimens of *G. dubius* in Oaxaca (Sierra Mazateca) (Fig. 12), and evidence that relatively minor morphological differences are generally indicative of significant genetic divergence (Pavón-Vázquez et al. 2013), we consider *G. fuscus* as valid.

Geophis cansecoi can be readily distinguished from *G. fuscus* as follows (character states of *G. fuscus* in parenthesis): internasals and prefrontals separate (vs. fused); second infralabials broadly separated (vs. in broad contact); TL/TotL ratio in males 0.17–0.19 (vs. 0.16); ventral scales in males 125–131 (vs. 142); subcaudal scales in males 34–36 (vs. 49) (Fig. 13B).

Conservation of *Geophis cansecoi.* Despite collection localities in two different municipalities, all known individuals of this species originate from a radius of about 2.5 km from the type locality, which happens to be located near the boundary of Yecuatla and Chiconquiaco municipalities. Extensive collection efforts and the revision of DOR specimens above and below the type locality failed to locate any additional specimens of this species. We suspect that this species, while locally abundant, might have an extremely restricted range. *Geophis cansecoi* might be endemic to a narrow band of extremely mesic cloud forest on the northern slopes of the Sierra de Misantla, which we understand to be the eastern-most extension of the Mexican Trans-Volcanic Belt in Veracruz running east-west between the cities of Misantla and Xalapa then dropping off into the Atlantic Coastal Plain. This extremely small distribution, coupled with moderate habitat modification at the type locality, should merit the highest level of conservation attention possible.

Acknowledgements.—We thank the lovely people of Los Capulínes, Veracruz, for their help in the field; Luis Canseco-Márquez for generously tutoring us on how to correctly measure *Geophis* and giving valuable insight on the manuscript; and Jacobo Reyes-Velasco and Larry D. Wilson for help in reviewing the manuscript. For providing photos, we thank Jonathan Campbell, Leo Badillo, Raciel Cruz-Elizalde, and especially Jeff Streicher who provided the highly detailed photographs of the type specimen of *G. fuscus*. Biencom Real Estate, Biodiversa A.C., and Herp.mx A.C. provided important funding for the field work. Support for lab work and general funding was provided by grants from Dirección General de Apoyo al Personal Académico, Universidad Nacional Autónoma de Mexico (PAPIIT grant number IN-216619) and Consejo Nacional de Ciencia y Tecnología (CONACyT A1-S-37838) to UOGV. Permits were issued by Secretaria de Media Ambiente y Recursos Naturales (SEMARNAT) to UOGV.

Literature Cited

Bogert CM, Porter AP. 1966. The differential characteristics of Mexican snakes related to *Geophis dubius* (Peters). *American Museum Novitates* 2277: 1–19.

Boulenger GA. 1894. *Catalogue of Snakes in the British Museum* (*Natural History*). British Museum, London, United Kingdom. 382 p.

Boyle F. 1901. *The Woodlands Orchids, Described and Illustrated: with Stories of Orchid-Collecting*. MacMillan, London, United Kingdom. 274 p.

Burbrink FT, Lawson R, Slowinski JB. 2000. Mitochondrial DNA phylogeography of the North American Rat Snake (*Elaphe obsoleta*): a critique of the subspecies concept. *Evolution* 54: 2,107–2,118.

Campbell JA, Murphy JB. 1977. A new species of *Geophis* (Reptilia, Serpentes, Colubridae) from the Sierra de Coalcoman, Michoacan, Mexico. *Journal of Herpetology* 11: 397–403.

Campbell JA, Ford LS, Karges JP. 1983. Resurrection of *Geophis anocularis* Dunn with comments on its relationships and natural history. *Transactions of the Kansas Academy of Sciences* 86: 38–47.

Canseco-Márquez L, Pavón-Vázquez CJ, López-Luna MA, Nieto-Montes de Oca A. 2016. A new species of Earth Snake (Dipsadidae, *Geophis*) from Mexico. *ZooKeys* 610: 131–145.

Downs FL. 1967. Intrageneric relationships among colubrid snake genus *Geophis* Wagler. *Miscellaneous Publications Museum of Zoology, University of Michigan* 131: 1–193.

Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Phylogenetics and Evolution* 29: 1,969–1,973.

Fetzner Jr JW. 1999. Extracting high-quality DNA from shed reptile skins: a simplified method. *Biotechniques* 26(6): 1,052–1,054.

Fischer JG. 1886. Herpetologische Notizen. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 9: 1–19.

Huelsenbeck JP, Rannala B. 2004. Frequentist properties

of Bayesian posterior probabilities. *Systematic Biology* 53: 904–913.

Kumar S, Stecher G, Tamura K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis Version 7 for bigger datasets. *Molecular Biology and Evolution* 33: 1,870–1,874.

Lanfear R, Frandsen PB, Wrigth AM, Senfeld T, Calcott B. 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetics analyses. *Molecular Biology and Evolution* 34: 772–773.

Lips KR, Savage JM. 1994. A new fossorial snake of the genus *Geophis* (Reptilia: Serpentes: Colubridae) from the Cordillera de Talamanca of Costa Rica. *Proceedings of the Biological Society of Washington* 107: 410–416.

Lis JT. 1980. Fractionation of DNA fragments by polyethylene glycol induced precipitation. *Methods in Enzymology* 65: 347–353.

Myers CW. 2003. Rare snakes—five new species from eastern Panama: reviews of northern *Atractus* and sourthern *Geophis* (Colubridae: Dipsadinae). *American Museum Novitates* 3391: 1–47.

Nieto-Montes de Oca A. 2003. A new species of the *Geophis dubius* group (Squamata: Colubridae) from the Sierra de Juárez of Oaxaca, Mexico. *Herpetologica* 59: 572–585.

Pavón-Vázquez CJ, García-Vázquez UO, Blancas-Hernández JC, Nieto-Montes de Oca A. 2011. A new species of the *Geophis sieboldi* group (Squamata: Colubridae) exhibiting color pattern polymorphism from Guerrero, Mexico. *Herpetologica* 67: 332–343.

Pavón-Vázquez CL, Canseco-Márquez L, Nieto-Montes de Oca A. 2013. A new species in the *Geophis dubius* group (Squamata: Colubridae) from northern Puebla, Mexico. *Herpetologica* 69: 358–370.

Pérez-Higareda G, Smith HM, López-Luna MA. 2001. A new *Geophis* (Reptilia: Serpentes) from southern Veracruz, Mexico. *Bulletin of the Maryland Herpetological Society* 37: 42–48.

Rambaut A, Drummond AJ, Suchard M. 2014. Tracer v1.6. Available: http://beast.bio.ed.ac.uk [Accessed: 6 December 2020].

Restrepo TJH, Wright JW. 1987. A new species of the colubrid snake genus *Geophis* from Colombia. *Journal of Herpetology* 21: 191–196.

Ronquist F, Teslenko M, Van der Mark P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3): 539–542.

Sabaj MH. 2019. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 7.1. Available: http://asih.org/sites/default/files/documents/symbolic_codes_for_collections_v6.5_2016.pdf [Accessed: 21 March 2019].

Savage JM. 1981. A new species of the secretive colubrid snake genus *Geophis* from Costa Rica. *Copeia* 1981: 549–553.

Savage JM, Watling JI. 2008. Not so rare snakes: a revision of the *Geophis sieboldi* group (Colubridae: Dipsadinae) in lower Central America and Colombia. *Zoological Journal of the Linnean Society* 153: 561–599.

Smith EN. 1995. *Geophis rhodogaster* (Colubridae), an addition to the snake fauna of Mexico. *The Southwestern Naturalist* 40: 123–124.

Smith HM, Chiszar D. 1992. A second locality for *Geophis sallei* (Reptilia: Serpentes). *Bulletin of the Maryland Herpetological Society* 28: 16–18.

Smith HM, Flores-Villela O. 1993. Variation in two species (*Geophis bicolor*, *Geophis duellmani*) of Mexican Earth Snakes (*Geophis*). *Bulletin of the Maryland Herpetological Society* 29: 20–23.

Smith HM, Holland RL. 1969. Two new snakes of the genus *Geophis* from Mexico. *Transactions of the Kansas Academy of Sciences* 72: 47–53.

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S. 2018. MEGA7: Molecular Evolutionary Genetics Analysis, version 7.0. *Molecular Biology and Evolution* 30: 2,725–2,729.

Townsend JH. 2009. Morphological variation in *Geophis nephodrymus* (Squamata: Colubridae), with comments on conservation of *Geophis* in eastern Nuclear Central America. *Herpetologica* 65: 292–302.

Townsend JH, Wilson LD. 2006. A new species of snake of the *Geophis dubius* group (Reptilia: Squamata: Colubridae) from the Sierra de Omoa of northwestern Honduras. *Proceedings of the Biological Society of Washington* 119: 150–159.

Wilson LD, Townsend JH. 2007. A checklist and key to the snakes of the genus *Geophis* (Squamata: Colubridae: Dipsadinae), with commentary on distribution and conservation. *Zootaxa* 1395: 1–31.

Wilson LD, McCranie JR, Williams KL. 1998. A new species of *Geophis* of the *sieboldi* group (Reptilia: Squamata: Colubridae) from northern Honduras. *Proceedings of the Biological Society of Washington* 111: 410–417.

Christoph I. Grünwald is a German-Mexican herpetologist who specializes in conservation through research in the field. Chris leads expeditions for the Herp.mx Field Team which have resulted in numerous range extensions and state records, descriptions of 16 new species, and re-discoveries of several "extinct" species. He has studied rattlesnakes and pitvipers for years, and many important discoveries have involved this group. Recently, Chris has turned his focus the poorly known Dipsadidae snakes, many of which are known from just a few specimens and have no associated molecular data. Understanding the extent of biodiversity is crucial to conservation, and Chris is currently making a push for collecting snakes that are difficult to find in herpetologically under-sampled regions, such as the mountainous areas of central Veracruz. As a co-founder of Biodiversa A.C., an anti-extinction non-profit, Chris is working on developing a system of "micro-reservas" to help conserve the most vulnerable high-endemism localities in Mexico.

Iván T. Ahumada-Carrillo is a Mexican herpetologist from Guadalajara, who received his degree from the University of Guadalajara (CUCBA) in Mexico. Currently, Iván is an independent investigator focusing on the biogeography of reptiles and amphibians in western Mexico, and he has discovered dozens of range extensions and state records. He has authored and co-authored various papers on biogeography, as well as the book *Anfibios y Reptiles del Bosque La Primavera*. With an interest in wildlife photography, his work has been published throughout Mexico in educational materials, web sites, scientific magazines, and books. Iván has now co-authored 12 new species descriptions, as well as numerous range extensions and state records in Mexico.

André J. Grünwald was born in Guadalajara, Mexico in 2009. André was born into a family of herpetologists and became the original "Herp.mx kid." Since an early age, André has been participating in exploratory field trips around Mexico, searching for "missing" species and novel taxa. He has participated in numerous field trips and collected several undescribed taxa. Currently in junior high school at Instituto Loyola in Chapala, Mexico, André has not quite decided on his course of study, although he has already proven himself as a valuable asset in herpetological field work. This is his first species description, and André was one of the three people on the 2017 exploratory trip into the herpetologically un-sampled swathes of cloud forest in the mountain ranges of central Veracruz which produced the type specimen of this new species. He, his father, and Carlos returned to the type locality in 2019 to collect the entire type series. Now he can't wait to get back to Veracruz and discover another new species!

Carlos Montaño-Ruvalcaba is a biology student at the University of Colima in Mexico. Originally from Colima, he has focused on the ecology, natural history, and conservation of amphibians and reptiles of western Mexico. His current research efforts focus on an *ex-situ* conservation project of rare, endemic, and threatened Mexican pitvipers such as *Mixcoatlus browni*, *Crotalus lannomi*, *C. ericsmithi*, *Ophryacus sphenophrys,* and *O. smaragdinus*. Carlos is one of the first biologists in the world to work with these species. Carlos is very skilled in the lab, and he is currently participating in the descriptions of several new species of Mexican herpetofauna. His other projects include an extended study of the ecology and natural history of the enigmatic Long-tailed Rattlesnakes *C. stejnegeri*, *C.ericsmithi,* and *C. lannomi*.

Uri O. García-Vázquez is a renowned Mexican herpetologist originally from Tlaxacala, Mexico, and currently holds a professorship at the Universidad Nacional Autónoma de Mexico on the FES-Zaragoza Campus. Uri's research interests focus on the phylogenetic relationships and biogeography of North American amphibians and reptiles. Having spent the last 10 years studying the evolutionary relationships of Mexican colubrids, skinks, and gerrhonotid lizards, Uri has authored or co-authored more than 100 publications on the herpetofauna of Mexico.

Appendix 1. List of *Geophis* specimens examined in this study. Museum acronyms follow Sabaj (2019), except ITSZ = Instituto Tecnológico Superior de Zongolica in Zongolica, Mexico, INIRENA = Instituto de Investigaciones sobre los Recursos Naturales (INIRENA) of the Universidad Michoacana de San Nicolás de Hidalgo (UMSNH) in Morelia, Mexico, and MZFZ = Museo de Zoología, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de Mexico. JAC, CIG, RWB, and ENS are field identifiers for un-catalogued specimens being deposited in the MZFZ, MZFC-HE, and UTA.

Geophis anocularis (9 specimens): MEXICO: Oaxaca: CIG 00725–729, CIG 00797, MZFC-HE 11591, MZFC-HE 16178, MZFC-HE 16180.

Geophis bicolor (1 specimen): MEXICO: Michoacán: JAC 24684.

Geophis carinosus (1 specimen): MEXICO: Veracruz: MZFC-HE 10552.

***Geophis cansecoi* sp. nov.** (15 specimens): MEXICO: Veracruz: MZFZ 4432–38, 4448–49, INIRENA 2811–16.

Geophis dubius (12 specimens): MEXICO: Oaxaca: CIG 00723–724, CNAR 6732, EBUAP 1966, MZFC-HE 13887, MZFC-HE 16160, MZFC-HE 16193, MZFC-HE 16547, MZFC-HE 27255–258.

Geophis duellmani (4 specimens): MEXICO: Oaxaca: MZFC-HE 4525–527, MZFC-HE 5081.

Geophis fuscus (1 specimen): MEXICO: Veracruz: BMNH 1946.1.6.48.

Geophis godmani (1 specimen): COSTA RICA: Puntarenas: CAS 178126.

Geophis immaculatus (5 specimens): MEXICO: Chiapas: CIG 00786–787, CIG 01228, MZFC-HE 7259–260.

Geophis juarezi (2 specimens): MEXICO: Oaxaca: MZFC-HE 2236, MZFC-HE 27525.

Geophis latifrontalis (1 specimen): RWB 7232.

Geophis lorancai (8 specimens): MEXICO: Puebla: MZFC-HE 28404; Veracruz: ITSZ 025, ITSZ 071, ITSZ 217, MZFC-HE 28401–403, MZFC-HE 28405.

Geophis occabus (1 specimen): MEXICO: Guerrero: MZFC-HE 25528.

Geophis omiltemanus (1 specimen): MEXICO: Guerrero: ENS 11496.

Geophis rhodogaster (4 specimens): MEXICO: Chiapas: CIG 00130, SMR 1831, SMR 1847, SMR 1873.

Geophis semidoliatus (2 specimens): MEXICO: Veracruz: CIG 01138, CIG 01375.

Geophis turbidus (8 specimens): MEXICO: Puebla: CNAR 6886–889, CNAR 8233, KU 39642, MZFC-HE 27253–254.