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## Synopsis and taxonomic revision of three genera in the snake tribe Sonorini

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### ABSTRACT

Delimiting species is a crucial goal of integrative biology, and yet can be misled by homoplasy and high levels of morphological variation. The snake tribe Sonorini contains three genera that have long confounded taxonomists: *Chilomeniscus*, *Chionactis* and *Sonora*. Dynamic colour evolution in this group, including rampant geographic variation in colour and colour polymorphism, has led to a chaotic taxonomy. We used mitochondrial and high-throughput nuclear data (ddRADseq) and complete taxonomic sampling of each genus to reconstruct phylogenetic relationships and systematically revise the genus. Our research revealed that *Sonora* is paraphyletic with regards to *Chilomeniscus* and *Chionactis* and that at least one species (*S. semiannulata*) is paraphyletic with respect to at least one other recognized species. Additionally, we found substantial undescribed genetic diversity within multiple species which is incongruent with morphological variation in coloration. Accordingly, we proposed synonymizing *Chionactis* and *Chilomeniscus* with *Sonora*, which has taxonomic priority over both genera. As we found genetic evidence that supported some of the historically delimited diversity within multiple taxa, we revised species-level taxonomy accordingly. This new taxonomy recognizes a revised genus of *Sonora* that contains 15 species of diminutive and often brightly coloured snakes that are distributed from central Mexico to north-western USA.

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*semiannulata*

## Introduction

Delimiting species diversity is crucial for conservation assessment, to inform organismal research, and to understand the evolution of biodiversity (Rocha et al. 2014; Tewksbury et al. 2014). However, species delimitation can be misled by homoplasy and morphological variation, especially in taxa with high or unique phenotypic diversity (Burbrink 2001; Devitt

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et al. 2008; Cox et al. 2012). Both of these confounding factors are common in temperate and tropical snakes from the Western hemisphere for many reasons, including repeated origins of coral snake mimicry and associated geographic variation in colour and colour polymorphism (Davis Rabosky et al. 2016b). Integrative taxonomy seeks to resolve the tree of life and delimit species based upon multiple lines of evidence (Dayrat 2005; Fujita et al. 2012), which is an ideal approach for revising groups where substantial morphological variation has confounded previous attempts to resolve their systematics.

The snake tribe Sonorini is a clade of colubrid snakes that are found from North to South America. This group has had dynamic colour evolution, with multiple red-black banded coral snake mimics (Dowling 1975; Dowling and Duellman 1978). Traditionally, the Sonorini contains the genera of *Chilomeniscus*, *Chionactis*, *Conopsis*, *Ficimia*, *Gyalopion*, *Sonora* and *Stenorhina* (Dowling 1975; Dowling and Duellman 1978). Other authors have also included *Tantilla* and *Scolecophis*, which would also imply that the genera *Tantillita* and *Geagras* are also in Sonorini (Savitzky 1983; Greene 1997). Other molecular phylogenetic analyses have also found that the genera of *Sympholis* and *Pseudoficimia* are closely related to the Sonorini (Pyron et al. 2013; Davis Rabosky et al. 2016b). Previous research has suggested that the Sonorini exclusive of *Tantilla*, *Scolecophis*, *Geagras* and *Tantillita* is monophyletic, using phylogenetic analyses with both morphological and molecular markers (Pyron et al. 2013; Davis Rabosky et al. 2016b). Within the Sonorini, relationships within the subgroup and monophyletic clade that includes *Chionactis*, *Chilomeniscus* and *Sonora* has long confounded herpetological taxonomists because of homoplastic morphological characters, rampant colour polymorphism, and differing opinions about the taxonomic significance of unique caudal and rostral modifications (e.g. file tails and shovel noses) present only in certain species (Stickel 1938, 1943; Frost and VanDevender 1979; Frost 1983a, 1983b; Grismer et al. 2002; Wood et al. 2014). When such idiosyncratic characters cannot unite species into subgroups, the potential exists for surprising relationships among species and patterns of phenotypic evolution, convergence, and stasis.

The dynamic colour evolution and potential for morphological conservatism within the clade containing *Chilomeniscus*, *Chionactis* and *Sonora* has led to a complex and confusing taxonomic history. The genus of *Chilomeniscus* contains the sand snakes, with most scientists recognizing two species based upon morphological evidence (Grismer et al. 2002; although Holm 2008 recognizes five species). The genus *Chionactis* has received more attention recently and was found to be composed of three species that are delimited both by colour and molecular data (Wood et al. 2013, 2014). Notably, the type species within this genus was originally described as *Rhinostoma*, and has historically been assigned to *Sonora* (Stickel 1938, 1943). Finally, the genus *Sonora* as currently recognized contains four species, three of which are found in Mexico and one (*Sonora semiannulata*) that is widely distributed throughout northern Mexico and the central and western USA (Cox et al. 2012; Cox and Davis Rabosky 2013). Our goal in this study was to review and revise the taxonomic relationships within this subgroup of the Sonorini using high quality genetic data across a well-sampled phylogeny.

### **Taxonomic history of *Sonora*, *Chilomeniscus* and *Chionactis***

Of these three genera under consideration, *Sonora* Baird and Girard 1853 was the first to be formally described. Current taxonomy recognizes four species of *Sonora* (Cox et al. 2012): *S.*

*semiannulata*, *S. aemula*, *S. mutabilis* and *S. michoacanensis*. The nominate form of the genus *Sonora* was described in 1853 as *Sonora semiannulata* from specimens collected in the Santa Rita mountains in what was then Sonora, Mexico (Baird and Girard 1853; Stickel 1943). This species is the most widespread, occurring from northern Mexico in Tamaulipas to Durango and Baja California, and in the central USA from Texas and Missouri to California and Oregon in the western USA (Ernst and Ernst 2003). Notably, *S. semiannulata* is highly polymorphic in colour pattern, leading to a chaotic taxonomy, with as many as five species and six subspecies described, including *S. s. semiannulata* (Baird and Girard 1853), *S. s. blanchardi* (Stickel 1938), *S. s. gloydi* (Stickel 1938), *S. s. isozona* (Cope 1866), *S. miniata miniata* (Stickel 1938), *S. m.* (or *semiannulata*) *linearis* (Stickel 1938, 1943), *S. taylori* or *S. episcopa taylori* (Boulenger 1894; Stickel 1938, 1943), *S. episcopa* or *S.e. episcopa* (Kennicott 1859; Stickel 1938, 1943), *S. bancroftae* (Klauber 1943), and *S. mosaueri* (Stickel 1938). This taxonomy was greatly simplified by the morphological analysis of Frost (1983a), which collapsed all species and subspecies into the single species of *S. semiannulata*. A species from the west coast of Mexico in Nayarit, Sinaloa and Sonora was variously described as either *Procinura aemula* (Cope 1879; Lemos-Espinal et al. 2004b) or *Sonora aemula* (Bogert and Oliver 1945; Zweifel and Norris 1955) based on the distinctive keeled scalation on its posterior body and tail, but genetic analyses confirmed it to be nested within *Sonora* (Cox et al. 2012). *Sonora michoacanensis*, which was described by Cope (1885), is the southernmost species within *Chilomeniscus*, *Chionactis* and *Sonora*, and is found in the states Michoacán, Guerrero, Morelos, Colima, and Puebla in Mexico. Populations first described as the subspecies *S. michoacanensis mutabilis* by Stickel (1943) were elevated to species using genetic data by Cox et al. (2012). Although not currently recognized, the names *S. erythura* and *S. aequalis* were previously applied to populations and colour morphs of *S. michoacanensis* and *S. mutabilis* (Taylor 1937; Smith and Taylor 1945; Ponce-Campos et al. 2004), contributing to taxonomic confusion. *Sonora aemula*, *S. mutabilis*, *S. michoacanensis* and *S. semiannulata* all possess the red and black banded coloration of coral snake mimics (Cox et al. 2012; Davis Rabosky et al. 2016a) and all have substantial colour polymorphism, including all red individuals with no banding on the body.

There are two currently recognized species within the sand snakes of the genus *Chilomeniscus* (Grismer et al. 2002): *C. stramineus* and *C. savagei* (note that some morphological data potentially support five species; Holm 2008). All members of this genus have an elongated rostrum and are adapted to sandy, scrubby, and arid habitats in northern Mexico and south-western USA. *Chilomeniscus* was first described by Cope (1866) for the species *C. stramineus*. This species is found throughout Baja California, north-western Mexico, and south-western USA according to Grismer et al. (2002), but restricted to the southern tip of Baja California by Holm (2008). A closely related island species (*C. savagei*) is limited to Cerralvo Island off the south-eastern coast of Baja California Sur and is recognized in both recent studies (Grismer et al. 2002; Holm 2008). While most taxonomists follow Grismer et al. (2002) and only recognize two species of *Chilomeniscus* (Powell et al. 2016; Crother 2017), a later unpublished dissertation by Holm (2008) recognizes three additional species that Grismer et al. (2002) does not: *C. punctatissimus* (an island form found exclusively on Espiritu Santo and Partida Islands off of the south-eastern coast of the Baja California peninsula), *C. cinctus* (found in north-western mainland Mexico and south-western USA), and *C. fasciatus* (found from northern Baja California south to La Paz). Importantly, multiple

populations and species have colour polymorphism, including morphs with the red and black bands typical of coral snake mimics (Davis Rabosky et al. 2016b).

The three species of snakes within the genus *Chionactis* (*C. occipitalis*, *C. annulata* and *C. palarostris*) are known as shovel-nosed snakes. These were originally described as *Rhinostoma* (Hallowell 1854), *Lamprosoma* (Baird 1859) and *Sonora* (Klauber 1937), with the genus name *Chionactis* originally applied only to *C. occipitalis*. It is worth noting that *C. palarostris* was originally described as *Sonora palarostris* (Klauber 1937), *C. occipitalis* was historically assigned to *Sonora* (Stickel 1938, 1943), and junior synonyms of *S. semiannulata* have been assigned to *Chionactis* (Frost 1983b). These snakes all have an enlarged rostral scale, hence the English common name for the group. The northernmost species is *C. occipitalis*, which is found in California, Arizona and Nevada in the USA, while *C. annulata* is found in southern California, Arizona, Sonora, and northern Baja California (Wood et al. 2014). Finally, *C. palarostris* is found in north-western Mexico and south-western USA (Wood et al. 2014). All of these species exhibit coral snake mimicry (Davis Rabosky et al. 2016b), colour polymorphism and geographic colour variation, and all are limited to arid and sandy habitats.

In this study, we integrated mitochondrial sequence and genome-wide SNP data with molecular phylogenetic methods to systematically revise snakes in the genera of *Chilomeniscus*, *Chionactis* and *Sonora*. Our revision was guided by four general principles. First, we recognize that names applied in the traditional Linnaean taxonomy should represent independent lineages, which are ideally monophyletic (Hennig 1966; Farris 1983; de Queiroz and Gauthier 1992). Second, we adhered to the evolutionary species and general lineage species concepts (Ghiselin 1974; Wiley 1978; de Queiroz 1998) for making decisions regarding species level taxonomy. Third, we designed our revisions to minimize disruptions to the taxonomy of this group in order to maximize taxonomic stability, which has important repercussions for governmental and non-governmental organizations that must implement policy and strategy using current taxonomy (Simpson 1961; Pauly et al. 2009). Finally, we aimed to avoid the subjective elevation of genera when some individual species across genera are already very difficult to distinguish morphologically from one another. Using these principles and methods, we suggest a new taxonomy to recognize diversity and to accurately represent evolutionary relationships among the brightly coloured snakes currently placed in the genera *Chilomeniscus*, *Chionactis* and *Sonora*.

## Materials and methods

### *Natural history surveys for specimens*

This revision is the result of several natural history expeditions to collect specimens and tissues from Mexico and USA. Field work by ARDR and CLC in USA took place from March to July in 2008 (Texas, California, Nevada, Arizona and New Mexico), 2009 (Kansas, Missouri, Texas, Oklahoma, Colorado and New Mexico), 2010 (Oklahoma, Texas, Arizona, California and Idaho), 2011 (Texas and California), 2012 (Texas and California), 2013 (Colorado, Oklahoma and Texas), and 2016 (Missouri, New Mexico and Texas). Separate expeditions by ARDR and CLC were made to Baja California in 2010 (two separate expeditions for a total of three weeks covering Baja California and Baja California Sur) and 2011 (two weeks in northern Baja California). Additionally, CLC was part of three separate expeditions for a total of five months

throughout mainland Mexico in 2008 and 2009 (the states of Tamaulipas, Coahuila, Nuevo Leon, Veracruz, Mexico, Sinaloa, Sonora, Jalisco, Aguascalientes, Zacatecas, Colima, Michoacan, Guerrero, Oaxaca, Durango, Chihuahua, San Luis Potosi and Nayarit). Finally, many other expeditions occurred in the years prior to the inception of this study through North America by CER, JAC, ENS, JRV, OFV, and JAM.

### **Tissue selection**

We used a combination of tissue samples collected during fieldwork across the range of this group and tissue grants from natural history collections (Table 1). We selected tissue samples to have complete taxonomic coverage and to substantially cover the geographic range of each species. We note that some species, or certain geographic regions, are only rarely encountered in nature or sampled by collectors, and so for these species our sampling is necessarily sparser. Additionally, although we tried to generate mitochondrial and next-generation sequencing datasets for the same samples, we did not achieve perfect congruence between the two datasets due to limited levels of sequencing failure, mostly due to variation in tissue preservation quality.

### **Sequencing protocol**

We sequenced two mitochondrial regions (portions of the *cytb* and *ND4* genes) using primers from Cox et al. (2012) for 106 individuals. DNA was isolated using Qiagen DNeasy kits (Qiagen, Valencia, CA, USA) following standard protocols. Mitochondrial loci were amplified with 2 min denaturation at 95°C, with 35 cycles of denaturation (95°C for 30 s), annealing (50°C for 30 s), and extension (72°C for 1 min), and a final 10 min extension at 72°C. We used gel electrophoresis in 1% agarose to confirm amplification, and cleaned PCR products for sequencing using the ExoSAP-IT kit (United States Biochemical, Cleveland, OH, USA). The BigDye Terminator Cycle Sequencing Kit (Applied Biosystems Inc., Foster City, CA, USA) was used for cycle sequencing, with the products precipitated using an ethanol/sodium acetate/EDTA method and rehydrated in formamide (Hi-Di). Samples were analysed using three different ABI genetic analysers (Foster City, CA, USA) in the Genomics Core Facility at the University of Texas Arlington, the Evolutionary Genetics Laboratory at University of California, Berkeley, and the Genomic Diversity Lab and Sequencing Core at the University of Michigan.

For high-throughput sequencing, we performed double digest Restriction Site Associated DNA (ddRAD) sequencing following the protocol developed by Peterson et al. (2012). We extracted total genomic DNA using a Qiagen Blood and Tissue spin column kit. We digested DNA using the enzymes EcoR1 and Msp1 and selected DNA fragments between 100 and 200 base pairs, and added ~200 bp of Illumina primers, adapters and barcodes. We used 24 unique barcodes and four unique indices to individually mark genomic DNA. The resulting 400–500 bp fragment was then sequenced, and all primers, adaptors and barcodes were removed bioinformatically during post-processing. Several samples failed to sequence despite several attempts, including the *Sonora michoacensis* sample (MZFC23956). We sequenced a total of 46 individuals on an Illumina HiSeq 2500 at the University of Michigan Sequencing Core with 200 base-pair paired-end reads.



**Table 1.** Localities for tissue samples used in phylogenetic analyses. Tissue ID corresponds to sample IDs on phylogenetic trees.

Tissue ID	Museum #	Taxon	Country	State	County	Localities
ANDY1S		<i>Sonora semiannulata</i>	USA	Arizona	Yavapai	Near Smith's Peak
ASDM21449	ASDM21449	<i>Sonora aemula</i>	MX	Sonora		
ASU34620	ASU34620	<i>Sonora palarostris</i>	USA	Arizona	Pima	
ASU34621	ASU34621	<i>Sonora palarostris</i>	USA	Arizona	Pima	
BAL1M		<i>Sonora semiannulata</i>	USA	Arizona	Yavapai	Near Red Rock Crossing
BEZY6661		<i>Sonora annulata</i>	USA	Arizona	Maricopa	25.9 km (by road) WSW Mobile
BTM26		<i>Sonora mutabilis</i>	MX	Jalisco		Zapopan, Barranca del Rio Santiago
CAS206503	CAS206503	<i>Sonora semiannulata</i>	USA	California	Inyo	Argus Mountains near the Defense Mine
CAS223436	CAS223436	<i>Sonora semiannulata</i>	USA	Nevada	Clark	NE side of Spring Mountains
CAS223569	CAS223569	<i>Sonora episcopa</i>	USA	Colorado	Baca	County Rd. M 3.2 km S of County Rd. 3
CER826		<i>Sonora semiannulata</i>	USA	Texas	Presidio	8.4 km west on FM 170, River Road
CJF4238	UTA R55414	<i>Sonora episcopa</i>	USA	Texas	Menard	TX HWY 190 at Clear Creek
CJF4211	UTA R55833	<i>Sonora episcopa</i>	USA	Texas	Jim Hogg	TX 624 ca. 22.4 km S of Mirando
CLC009	UTA R55720	<i>Sonora episcopa</i>	USA	Texas	Shackelford	Near Albany
CLC016	UTA R60060	<i>Sonora episcopa</i>	USA	Texas	Palo Pinto	HWY 4 next to Bridge over Brazos River
CLC075	UTA R60060	<i>Sonora episcopa</i>	USA	Texas	Randal	Buffalo Lake NWR
CLC133	UTA R57153	<i>Sonora taylora</i>	USA	Texas	Starr	Near Hebronville
CLC150	UTA R56114	<i>Sonora episcopa</i>	USA	Texas	Reeves	Lake Balmorhea
CLC166	UTA R57115	<i>Sonora episcopa</i>	USA	Oklahoma	Love	Hickory Creek WMA
CLC169	UTA R57050	<i>Sonora episcopa</i>	USA	Texas	Coleman	HWY206 2 cuts S of Cross Plains
CLC183	UTA R57388	<i>Sonora episcopa</i>	USA	Texas	Crockett	Dirt road off of 67 to the south
CLC214	UTA R57473	<i>Sonora episcopa</i>	USA	Texas	Val Verde	Pandale paved (1024)
CLC221	UTA R55714	<i>Sonora episcopa</i>	USA	Oklahoma	Comanche	HWY49, in Medicine Park
CLC225	UTA R57393	<i>Sonora episcopa</i>	USA	Texas	Fisher	Rolling Plains Quail Research Ranch (THS Field Meet)
CLC256	UTA R57471	<i>Sonora episcopa</i>	USA	Kansas	Comanche	FAS30
CLC258	UTA R57411	<i>Sonora episcopa</i>	USA	Colorado	Otero	Rourke RD (CR25) in Comanche National Grasslands
CLC280	UTA R 57469	<i>Sonora episcopa</i>	USA	New Mexico	San Miguel	Conchas Dam
CLC282	UTA R 57427	<i>Sonora episcopa</i>	USA	Oklahoma	Beckham	Sandy Sanders WMA
CLC310	UTA R 57470	<i>Sonora episcopa</i>	USA	Texas	Edward	Near Camp Wood
CLC323	UTA R57461	<i>Sonora episcopa</i>	USA	Texas	Callahan	0.8 km N of Coleman County Line on HWY283
CLC342	UTA R57474	<i>Sonora taylora</i>	USA	Texas	Dimmit	468 on way to Big Wells, abandoned railroad
CLC354	UTA R58157	<i>Sonora episcopa</i>	USA	Texas	Cooke	Moss Lake
CLC363	UTA R58168	<i>Sonora episcopa</i>	USA	Oklahoma	Carter	Rest stop off of I35N north of Ardmore
CLC365	UTA R58302	<i>Sonora episcopa</i>	USA	Texas	Edwards	CR390
CLC367	UTA R58306	<i>Sonora episcopa</i>	USA	Texas	Edwards	CR391
CLC368	UTA R58305	<i>Sonora episcopa</i>	USA	Texas	Edwards	Nueces River Bed
CLC369	UTA R58306	<i>Sonora episcopa</i>	USA	Texas	Jeff Davis	TX118 (Observatory Road)

(Continued)



Table 1. (Continued).

Tissue ID	Museum #	Taxon	Country	State	County
CLC371	UTA R59127	<i>Sonora taylora</i>	USA	Texas	Hidalgo
CLC374	UTA R59129	<i>Sonora taylora</i>	USA	Texas	Hidalgo
CLC375	UTA R59268	<i>Sonora taylora</i>	USA	Texas	Hidalgo
CLC379		<i>Sonora fasciata</i>	MX	Baja California Sur	
CLC386		<i>Sonora fasciata</i>	MX	Baja California Sur	
CLC393		<i>Sonora cincta</i>	MX	Baja California	
CLC403		<i>Sonora mosaueri</i>	MX	Baja California Sur	
CLC406		<i>Sonora cincta</i>	MX	Baja California	
CLC428	UTA R58578	<i>Sonora semiannulata</i>	USA	Arizona	Maricopa
CLC431	UTA R58602	<i>Sonora semiannulata</i>	USA	Arizona	Santa Cruz
CLC432	UTA R58603	<i>Sonora semiannulata</i>	USA	Arizona	Cochise
CLC453	UTA R58608	<i>Sonora episcopa</i>	USA	Oklahoma	Tulsa
CLC485	UTA R58620	<i>Sonora episcopa</i>	USA	Missouri	Taney
CLC493	UTA R58579	<i>Sonora episcopa</i>	USA	Oklahoma	Blaine
CLC512		<i>Sonora semiannulata</i>	USA	Arizona	Coconino
CLC645	UTA R60015	<i>Sonora taylora</i>	USA	Texas	Duval
CLC761	UTA R59322	<i>Sonora episcopa</i>	USA	Texas	Eastland
DAW11-070		<i>Sonora annulata</i>	USA	Arizona	Maricopa
DAW349		<i>Sonora occipitalis</i>	USA	California	Inyo
DAW356		<i>Sonora occipitalis</i>	USA	Nevada	Nye
EBU25		<i>Sonora semiannulata</i>	USA	New Mexico	Sierra
HIL1B		<i>Sonora semiannulata</i>	USA	Arizona	Yavapai
JAC23362	UTA R53487	<i>Sonora mutabilis</i>	MX	Jalisco	
JAC26385	UTA R53488	<i>Sonora episcopa</i>	MX	Coahuila	
JAC26373		<i>Sonora episcopa</i>	MX	Jalisco	
JAC23363		<i>Sonora mutabilis</i>	MX	Jalisco	
JAC23364		<i>Sonora semiannulata</i>	MX	Jalisco	
JAC29573		<i>Sonora semiannulata</i>	MX	Jalisco	
JAC30533		<i>Sonora mutabilis</i>	MX	Nuevo Leon	
JRM4406		<i>Sonora semiannulata</i>	USA	Jalisco	
JRM4409		<i>Sonora semiannulata</i>	USA	Arizona	Yavapai
JWS098	UTA R58496	<i>Sonora semiannulata</i>	USA	Arizona	Coconino
JWS280	UTA R58271	<i>Sonora episcopa</i>	USA	Arizona	Real
MHP11224	MHP11224	<i>Sonora episcopa</i>	USA	Texas	Kimble
MHP11237	MHP11237	<i>Sonora episcopa</i>	USA	Kansas	Barber
MHP11315	MHP11315	<i>Sonora semiannulata</i>	USA	California	Inyo
MHP12271	MHP12271	<i>Sonora episcopa</i>	USA	Kansas	Clark
			USA	Kansas	Kiowa

(Continued)

Old Military Road  
 Old Military Road  
 Old Military Road  
 1 km S of El Triunfo  
 1 km S of El Triunfo  
 Road to Las Tres Virgenes off MX1  
 Oasis at San Ignacio  
 Rancho Santa Ines 1 km off of MX1 just south of Catavina  
 8 km S of Sunflower on HWY87  
 Road to Meadow Valley off of FR58 (Harshaw Rd.)  
 Rucker/Tex Canyon Rd, NW off of HWY 80  
 HWY26 jct with E129th near Garnett  
 Glade Top Rd (FR149) in Mark Twain NF  
 10 mi N of Geary on HWY 281/270/8  
 Indian Gardens, Bright Angel Trail, Grand Canyon Park  
 Benavides:abandoned lots  
 HWY16  
 Vulture Mine Road, 3.4 rd km N Aguila Rd.  
 Ninemile Canyon Road west of Hwy 395  
 Amragosa Valley, Valley Vista Boulevard  
 1.6 km E Dam V.C. Ash Canyon  
 Hillside Road s of Jct with HWY 96  
 Municipio Bolaños: Tuxpan de Bolaños  
 Near Muzquiz  
 Near Muzquiz  
 Municipio Bolaños: Tuxpan de Bolaños  
 Municipio Bolaños: Tuxpan de Bolaños  
 Road to Pueblitos near Barranca del Rio Santiago  
 Along cornville rd., 1.9 rd km NW McGuirville  
 Along HWY89A, 1.0 rd km N Cliff Dwellers lodge  
 336 between Leakey and Prade Ranch in rock field  
 US377 between Telegraph and Ricksprings



Table 1. (Continued).

Tissue ID	Museum #	Taxon	Country	State	County
MHP7657	MHP7657	<i>Sonora episcopa</i>	USA	Kansas	Wilson
MHP8550	MHP8550	<i>Sonora episcopa</i>	USA	Kansas	Russell
MULK5CHOC		<i>Sonora occipitalis</i>	USA	California	Imperial
MVZ170844		<i>Sonora fasciata</i>	MX	Baja California Sur	La Paz
MVZ206230		<i>Sonora semiannulata</i>	USA	Arizona	Cochise
MVZ230610		<i>Sonora semiannulata</i>	USA	California	San Bernardino
MVZ236386		<i>Sonora straminea</i>	MX	Baja California Sur	La Rivera
MVZ236387		<i>Sonora straminea</i>	MX	Baja California Sur	Los Barriles
MVZ237181		<i>Sonora semiannulata</i>	USA	California	Inyo
MVZ238156		<i>Gyalopion canum</i>	USA	Texas	Brewster
MZFC23956		<i>Sonora michoacensis</i>	MX	Guerrero	
OWY4		<i>Sonora semiannulata</i>	USA	Oregon	Malheur
PAH4D		<i>Sonora palastrois</i>			
PCU729		<i>Sonora semiannulata</i>	USA	Nevada	Lincoln
RM527	UTA R55776	<i>Sonora semiannulata</i>	USA	Texas	Brewster
RM528	UTA R55777	<i>Sonora semiannulata</i>	USA	Texas	Presidio
RNF5080		<i>Sonora occipitalis</i>	USA	California	Kern
ROSENAVRA1		<i>Sonora semiannulata</i>	USA	Arizona	Pima
RWM875		<i>Sonora mosaueri</i>	MX	Baja California Sur	
SBFU1		<i>Sonora episcopa</i>	USA	New Mexico	Eddy
SOSE1		<i>Sonora semiannulata</i>	USA	Nevada	Humboldt
SOSE2		<i>Sonora semiannulata</i>	USA	Nevada	Washoe
TNH6C0972	TNH6C0972	<i>Sonora episcopa</i>	USA	Texas	Val Verde
TNHC60274	TNHC60274	<i>Sonora episcopa</i>	USA	Texas	Llano
TNHC60275	TNHC60275	<i>Sonora episcopa</i>	USA	Texas	Llano
TNHC61357	TNHC61357	<i>Sonora episcopa</i>	USA	Texas	Val Verde
TNHC66591	TNHC66591	<i>Sonora episcopa</i>	USA	Texas	Presidio
TNHC66592	TNHC66592	<i>Sonora episcopa</i>	USA	Texas	Presidio
TNHC66594	TNHC66594	<i>Sonora episcopa</i>	USA	Texas	Jeff Davis
TNHC66753	TNHC66753	<i>Sonora episcopa</i>	USA	Texas	Sutton
TNHC66762	TNHC66762	<i>Sonora episcopa</i>	USA	Texas	San Saba
TORT5		<i>Sonora semiannulata</i>	USA	Arizona	Pima
UANL4676	UANL4676	<i>Sonora episcopa</i>	MX	Coahuila	Nadadores
UANL6976	UANL6976	<i>Sonora aemula</i>	MX	Sonora	Los Alamos
UMMZ200750	UMMZ200750	<i>Sonora cincta</i>	USA	Arizona	Maricopa
UNR7645	UNR7645	<i>Sonora semiannulata</i>	USA	Nevada	Clark
UNR7646	UNR7646	<i>Sonora semiannulata</i>	USA	Nevada	Clark

(Continued)

El Sombrero Trailer Park  
Area just NW of junction 110 and HWY666N  
Near Copper Strand Mine  
Road to La Rivera

Barrel Springs, Mazourka Canyon

Along Owyhee River  
See Holm (2008)

Carp  
River Road FM170  
River Road FM170  
Dove Springs  
Vic Marana (Avra Valley)

Near Sitting Bull Falls

Black rock desert, caught in drift fence  
Moving around in a thunderstorm west of Getlach, NV

Devils River State Natural Area

Prairie Mts 3.2 air km SW on G. Rylander Ranch

Prairie Mts 3.2 air km SW on G. Rylander Ranch

Devils River State Natural Area

Sierra Vieja Mts, Fort Holland

Sierra Vieja Mts, Fort Holland

Miller Ranch, 0.16 rd km E of fork from Kimball House  
9.7 km west of Kimball, County Line on FM 3131

Colorado Bend State Park

Tucson

Celemania, 7.2 km E Sacramento

8 km W of Chinacos on Rd from Alamos

Trash pile SE of Sossaman Rd and Guadalupe Rd

Coyote Springs Valley on SR-169

~1.6 km. W of W entrance to Valley of Fire State Park

**Table 1.** (Continued).

Tissue ID	Museum #	Taxon	Country	State	County	Valley of Fire State Park
UNR7648	UNR7648	<i>Sonora semiannulata</i>	USA	Nevada	Clark	Valley of Fire State Park
UTEP18429	UTEP18429	<i>Sonora semiannulata</i>	USA	Texas	El Paso	Franklin Mtn. foothills near Memphis Ave. in El Paso
UTEP18436	UTEP18436	<i>Sonora episcopa</i>	USA	Texas	Sutton	FTM 3130 6.4 km. E of JCT with I10 about 45 km
UTEP18437	UTEP18437	<i>Sonora episcopa</i>	USA	Texas	Sutton	FTM 3130 6.4 km. E of JCT with I10 about 45 km
UTEP18554	UTEP18554	<i>Sonora semiannulata</i>	USA	Texas	El Paso	8811 Neptune St. El Paso TX

Museum abbreviations: ASDM, Arizona Sonora Desert Museum; ASU, Arizona State University Herpetology Collection; BTM, Bosque Tropical Mexico; CAS, California Academy of Sciences; UTA-R, University of Texas Arlington Amphibian and Reptile Diversity Research Center; MZFC, Museo Zoologico de Facultad Ciencias; MHP, Museum of the High Plains at Sternberg University; MVZ, Museum of Vertebrate Zoology at the University of California; TNHC, Texas Natural History Collection; UANL-Universidad Autonoma de Nuevo Leon Herpetology Collection; UMMZ, University of Michigan Museum of Zoology; UNR, University of Nevada Reno Herpetology Collection; UTEP, University of Texas El Paso Amphibian and Reptile Collection. Samples without a museum number are either tissue-only samples or pending accession.  
 Collector initials: CLC, Christian L. Cox; CER, Corey E. Roelke; JAC, Jonathan A. Campbell; CJF, Carl J. Franklin; JRM, Joseph R. Mendelson; JWS, Jeffrey W. Streicher; RM, Robert Makowsky; DAW, Dustin A. Wood; BEZY, Robert Bezy PAH, Peter A. Holm. Note that some tissue samples have an ID code rather than a collector initial and number.

For RADseq data, we assembled our SNP array using a pipeline developed by Singhal et al. (2017). We removed low-quality and short reads using Trimmomatic v0.35 (Bolger et al. 2014), then assembled reads within each individual using Rainbow 2.0.4 (Chong et al. 2012). We characterized low quality reads as those with a phred score of less than 20. We identified homologous loci using vsearch v.1.1.0 (Rognes et al. 2016), and aligned individual loci using bwa 0.7.12 (Li and Durbin 2009) and GATK (McKenna et al. 2010). We called SNPs using samtools 1.2 (Li et al. 2009). We used all SNPs from every locus, but we did not include SNPs with more than two alleles. The original dataset had 183,111 SNPs, which was reduced to 13,340 (~7% of total) after removing SNPs with high levels of missing data or missing taxa. Each SNP was shared by at least 42 of the 52 individuals in the alignment.

### **Phylogenetic analysis**

For both datasets, we used RAxML v7.0.3 (Stamatakis 2006) using the GTRGAMMA model to conduct maximum likelihood (ML) analysis using 100 ML tree searches and 1000 bootstrap replicates on the best scoring topology to obtain nodal support values. We elected to conduct analyses on separate, concatenated datasets to examine their individual phylogenetic signal, but acknowledge the future utility of coalescent frameworks for analysing multilocus data.

To visualize species ranges and sampling density, we downloaded species range maps from the IUCN Red List of Threatened Species ([www.iucnredlist.org](http://www.iucnredlist.org), accessed on 1 February 2015) and overlaid them with all georeferenced museum occurrence records (grey crosses) aggregated from the VertNET ([www.vertnet.org](http://www.vertnet.org)) and GBIF ([www.gbif.org](http://www.gbif.org), both accessed on 26 May 2015) data portals. We performed only minor cleaning of these occurrences to remove points more than 500 km from the known range, retaining points adjacent but not encompassed by the conservative IUCN ranges. The only exception to this workflow was the IUCN range map for *S. michoacanensis*, which did not encompass 80% of the vetted museum occurrence records. For this species, we used these known occurrences to construct a contiguous alpha hull polygon in the R package 'rangeBuilder' (Davis Rabosky et al. 2016a) encompassing 99% of the points, with a 40 km buffer to account for sampling error. We then plotted the collection localities for each of our sequenced tissue samples and colour coded them by recovered phylogenetic clade (coloured points). As we recognize that both the IUCN maps and georeferenced occurrences from museum collections may contain some errors, we plot both in the useful exercise of visualizing where and to what extent discrepancies with collection data occur (although mismatches between data types were generally minor, except for *S. michoacanensis* as above).

## **Results**

### **Phylogenetic relationships using mtDNA loci**

Our mtDNA phylogenetic analysis of *Chilomeniscus*, *Chionactis* and *Sonora* revealed that *Sonora* is paraphyletic with regards to *Chilomeniscus* and *Chionactis* and that at least one species (*S. semiannulata*) is paraphyletic with respect to at least four other currently recognized species (Figures 1, 2). The most basal dichotomy in the mtDNA phylogenetic tree was between a clade comprised of *S. mutabilis* and *S. michoacanensis* and a clade of all other taxa (Figures 1, 2). *Chilomeniscus* was monophyletic and sister to a clade comprised

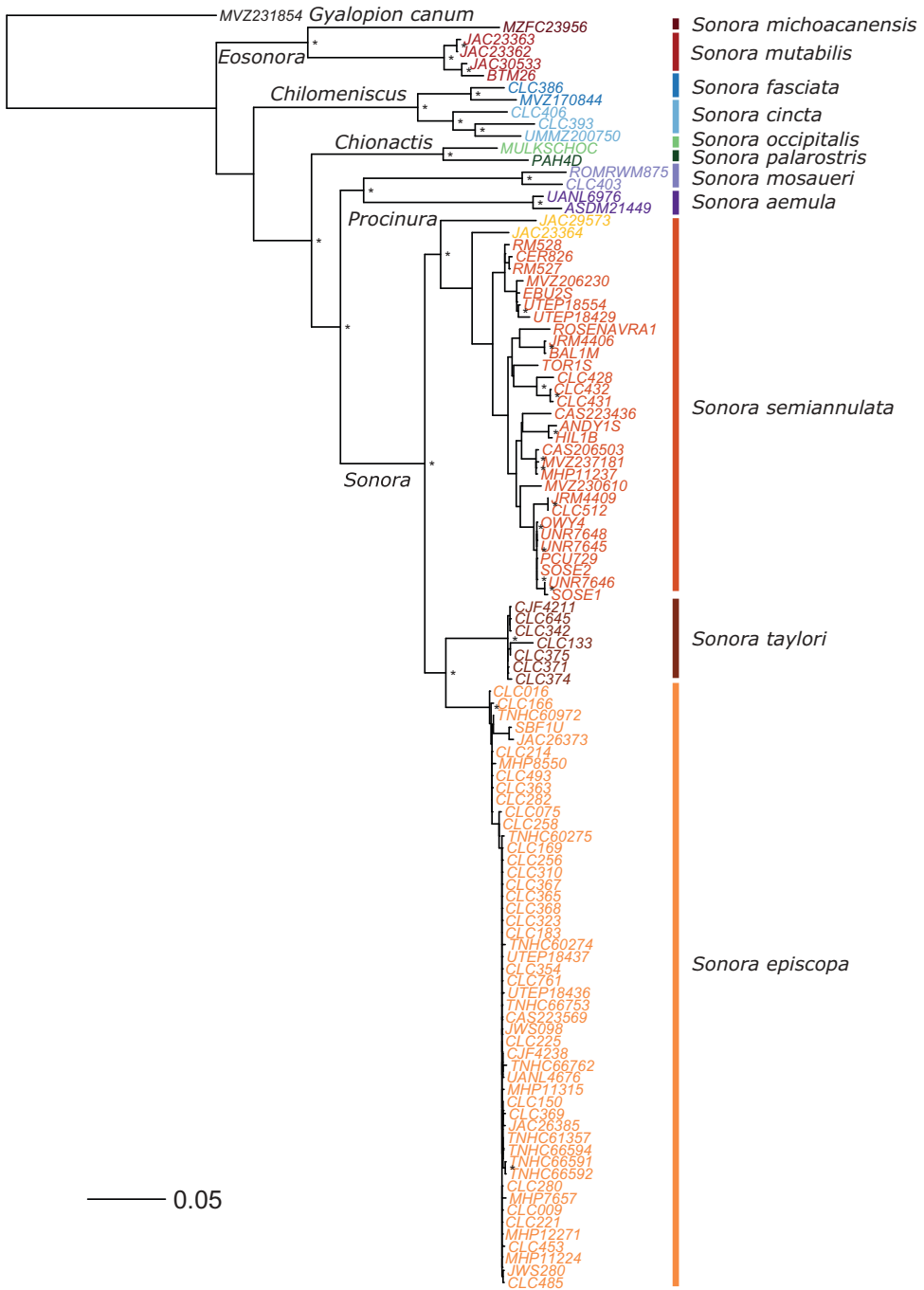
*Chionactis* and all other *Sonora* (exclusive of *S. mutabilis* and *S. michoacanensis*), while *Chionactis* was monophyletic and sister to all other remaining *Sonora*. The taxa *S. aemula* and *S. semiannulata* from southern Baja California (*S. mosaueri*) were sister to all of the remaining *S. semiannulata*, which encompassed samples from throughout North America and northern Mexico. Samples of *S. semiannulata* exclusive of Baja California were monophyletic with three large geographically circumscribed clades (Figure 3). The first clade was limited to Texas south of the Edwards Plateau and the Balcones escarpment (*S. taylori*), the second was found in western North America west of western Texas (*S. semiannulata*), and the last was comprised of samples from New Mexico, Colorado, Texas, and the states further east (*S. episcopa*).

### **Phylogenetic relationships using ddRADseq loci**

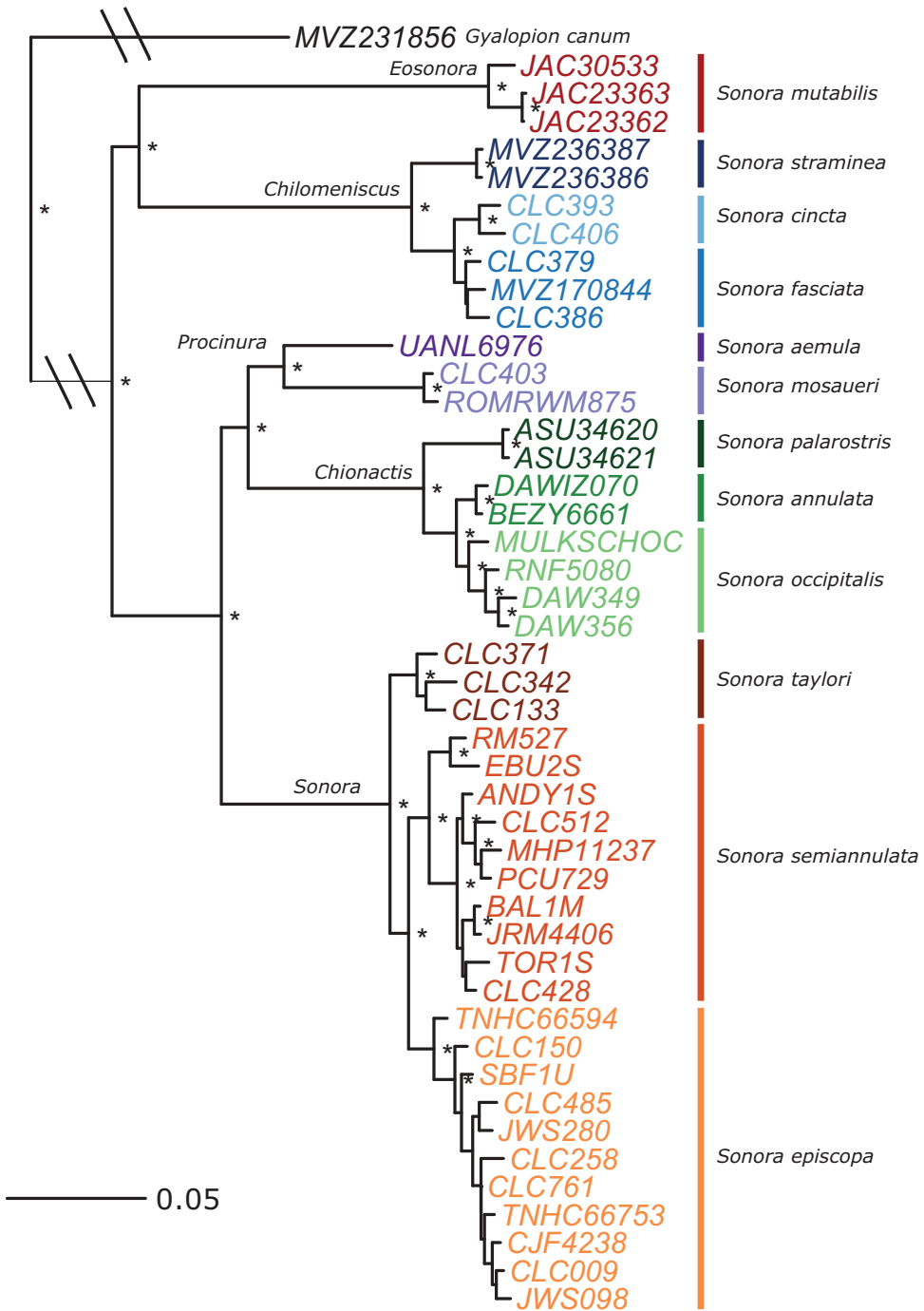
Similar to our mtDNA analysis, our phylogenetic analysis using nuclear ddRAD data revealed that *Sonora* is paraphyletic with regards to *Chilomeniscus* and *Chionactis* and that at least one species (*S. semiannulata*) is paraphyletic with respect to at least four other recognized species (Figure 2). We found that the most basal dichotomy in the phylogenetic tree was between a clade comprised of *S. mutabilis*, *S. michoacanensis* and a monophyletic *Chilomeniscus* which was sister to the rest of *Sonora*. *Chionactis* was monophyletic and sister to a clade comprised of *S. aemula* and *S. semiannulata* material from Baja California (*S. mosaueri*). This clade of *S. aemula*, *S. semiannulata* from Baja California (*S. mosaueri*) and *Chionactis* was sister to all of the remaining *S. semiannulata*, which encompassed samples from throughout North America and northern Mexico. Samples of *S. semiannulata* exclusive of Baja California were monophyletic, and represent three large geographically circumscribed clades (Figure 3). The first clade was limited to Texas south of the Edwards Plateau and the Balcones escarpment (*S. taylori*), the second was found in western North America (including north-west Mexico) west of western Texas (*S. semiannulata*), and the last was comprised of samples from north-eastern New Mexico, Colorado, Texas, and the states further east (*S. episcopa*).

### **Discussion**

Our phylogenetic analysis of the genera *Chilomeniscus*, *Chionactis* and *Sonora* revealed that *Sonora* is paraphyletic with regards to *Chilomeniscus* and *Chionactis* and that at least one species (*S. semiannulata*) is paraphyletic with respect to at least four other recognized species. Additionally, we found substantial undescribed genetic diversity within multiple species that is incongruent with morphological variation in coloration. Accordingly, we propose synonymizing *Chionactis* and *Chilomeniscus* with *Sonora*, which has taxonomic priority over both genera. As we found genetic evidence that supports some of the historically delimited taxonomic diversity is distributed across multiple lineages, we revised the species-level taxonomy accordingly. This revised genus of *Sonora* contains 15 species of diminutive and often brightly coloured snakes that are distributed from central Mexico to the north-western USA (Table 2, Figures 3–7). We address the rationale for revision of within-species diversity first, and then discuss our decision to synonymize the genera *Chionactis* and *Chilomeniscus* with *Sonora*.



**Figure 1.** Phylogenetic relationships among *Sonora* based upon mitochondrial sequence data. Nodes and tips have been labelled with our proposed taxonomy. Asterisks indicate  $\geq 85\%$  bootstrap proportions from the maximum likelihood analysis. Colours of species on branches and tips on the phylogenetic tree correspond to colours on the maps in Figures 3–7.



**Figure 2.** Phylogenetic relationships among *Sonora* based upon ddRADseq data. Nodes and tips have been labelled with our proposed taxonomy. Asterisks indicate 100% bootstrap proportions from the maximum likelihood analysis. Colours of species on branches and tips on the phylogenetic tree correspond to colours on the maps in Figures 3–7.



**Figure 3.** Map of the geographic distribution from IUCN and georeferenced occurrence records from GBIF (grey crosses) for the subgenus *Sonora*, including *S. episcopa*, *S. semiannulata* and *S. taylori*. The top of the map has images of the uniform (a), banded (b), striped (c), and mimetic (d) morphs of *Sonora episcopa*. The side panel depicts *S. taylori* without (e) and with (f) a black cap on the head. The bottom panel depicts the uniform (a), banded (b), striped (c), and mimetic (d) morphs of *S. semiannulata*. Photos by C. L. Cox (a–f, h) and A. R. Davis Rabosky (g, i, j). Colours of circular points on the map correspond to the phylogenetic tree in Figures 1 and 2.

**Taxonomic implications within species**

The geographically widespread species *S. semiannulata* as currently constituted was not monophyletic and contained substantial genetic diversity (Figures 1, 2, 3, 7). We suggest that this conflict between current taxonomy and cryptic diversity can be resolved by the elevation of four different species, which correspond to four separate molecular clades

**Table 2.** Summary of current taxonomy and proposed taxonomic revisions of the snake genus *Sonora*.

Current taxonomy	Revised taxonomy
<i>Chilomeniscus stramineus</i>	<i>Sonora straminea</i> <i>Sonora fasciata</i> <i>Sonora cincta</i> <i>Sonora punctatissima</i>
<i>Chilomeniscus savagei</i>	<i>Sonora savagei</i>
<i>Chionactis occipitalis</i>	<i>Sonora occipitalis</i>
<i>Chionactis palarostris</i>	<i>Sonora palarostris</i>
<i>Chionactis annulatus</i>	<i>Sonora annulata</i>
<i>Sonora semiannulata</i>	<i>Sonora semiannulata</i> <i>Sonora episcopa</i> <i>Sonora taylori</i> <i>Sonora mosaueri</i>
<i>Sonora aemula</i>	<i>Sonora aemula</i>
<i>Sonora mutabilis</i>	<i>Sonora mutabilis</i>
<i>Sonora michoacanensis</i>	<i>Sonora michoacanensis</i>

that are well supported by nuclear and mitochondrial data. Importantly, these four molecular clades correspond closely to previously recognized species and subspecies of *Sonora* (Stickel 1938, 1943). The most significant paraphyletic clade includes specimens from Baja California, which are not even nested within the other *S. semiannulata* clades, but rather sister to *S. aemula* and placed outside the divergence of the former *Chionactis* clade. This clade corresponds to the previously recognized *Sonora mosaueri* (Stickel 1938), and we propose resurrecting that name for this lineage. However, we note that although this paraphyly and revision are both well supported and are robust to the addition of more samples, our sampling across Baja California is sparse and limited to one sample from the Cape region and one from the mid-Peninsula, both in the state of Baja California Sur (Figure 7).

Among the three remaining genetic clades of *S. semiannulata*, we found three well-supported, reciprocally monophyletic, and geographically delimited clades; one from South Texas, another from central USA and northern Mexico, and the final in western USA and north-western Mexico (Figure 3). Fascinatingly, previous authors in past decades recognized each of these clades as subspecies or species based solely on morphological variation (Stickel 1938, 1943) before they were synonymized based on overlapping scale characters (Frost and VanDevender 1979; Frost 1983a, 1983b). The genetic clade found in South Texas corresponds to *S. episcopa taylori* (Stickel 1943), which has continued to be recognized by some authors as a subspecies of *S. semiannulata* (Dixon and Werler 2005). We recommend elevating *S. taylori* to species status as the name for this clade. Additionally, we recommend that the genetic clade found in central USA and northern Mexico can be referred to *S. episcopa*, which was long recognized by previous authors (Kennicott 1859; Stickel 1943). Finally, the clade found in western USA and NW Mexico corresponds to the original type material, and so should be referable to *S. semiannulata* Baird and Girard 1853.

Perhaps the most intriguing localities of *S. semiannulata* are the two specimens from north-central (JAC29573, Nuevo Leon) and west-central Mexico (JAC23364, Jalisco). These samples represent the earliest divergences among *S. semiannulata*, and are genetically distinct from the rest of *S. semiannulata*. Of particular note is the fact that Jalisco is from much further south than *S. semiannulata* was previously known to occur

(the closest records are from Durango), and this species was found at the same time and locality as two *S. mutabilis* (JAC23362 and JAC23363). Greater sampling in Zacatecas, northern Jalisco, and Aguascaliente could reveal cryptic genetic diversity within *S. semiannulata* and the extent of sympatry between *S. mutabilis* and *S. semiannulata*.

We found that the two most southerly distributed *Sonora* species, *S. mutabilis* and *S. michoacanensis*, were reciprocally monophyletic, a result that echoes Cox et al. (2012). It is worth noting that our sampling for both *S. mutabilis* and *S. michoacanensis* is generally sparse, and limited to a single sample in the mitochondrial dataset in the current study and a few additional loci for the same sample in Cox et al. (2012) for *S. michoacanensis*. The complex topography of central and southern Mexico has been implicated in the generation of biodiversity (Bryson et al. 2011; Streicher et al. 2014), and so additional collection within these areas can inform our understanding of diversity within these species.

We also found evidence of unrecognized diversity within the *Chilomeniscus* clade. While Holm (2008) presented evidence supporting five species within this group, most authors continue to only recognize the two species suggested by Grismer et al. (2002). Our research found genetic breaks consistent with the three of the five species recognized by Holm (2008) in Baja California and mainland North America, and so we recognize *S. cincta*, *S. fasciata* and *S. straminea* as distinct species. *Sonora cincta* is found in northern Baja California, south-western USA, and north-western Mexico (Figure 4). Both *S. fasciata* and *S. straminea* are limited to south-central and the southern tip of Baja California, respectively (Figure 4). While genetic data for the two island species (*C. punctatissimus* and *C. savagei*) is not currently available, we defer to Grismer et al. (2002) and Holm (2008) by recognizing both of these species. Future field research within this group should attempt to obtain tissue samples from Isla Cerralvo, Isla Partida, and Isla Epiru Santo as well as other islands in the Gulf of California to test the extent of island diversification within this group.

In contrast to *Sonora* and the *Chilomeniscus* clade, the *Chionactis* clade has been the subject of recent phylogenetic, population genetic, and morphological research (Wood et al. 2008, 2013, 2014). This research has found support for three different species within this clade; *S. occipitalis*, *S. annulata* and *S. palarostris*, which is congruent with our results (Figures 1, 2, 5). We defer to this previous research and continue to recognize these three species of *Sonora*.

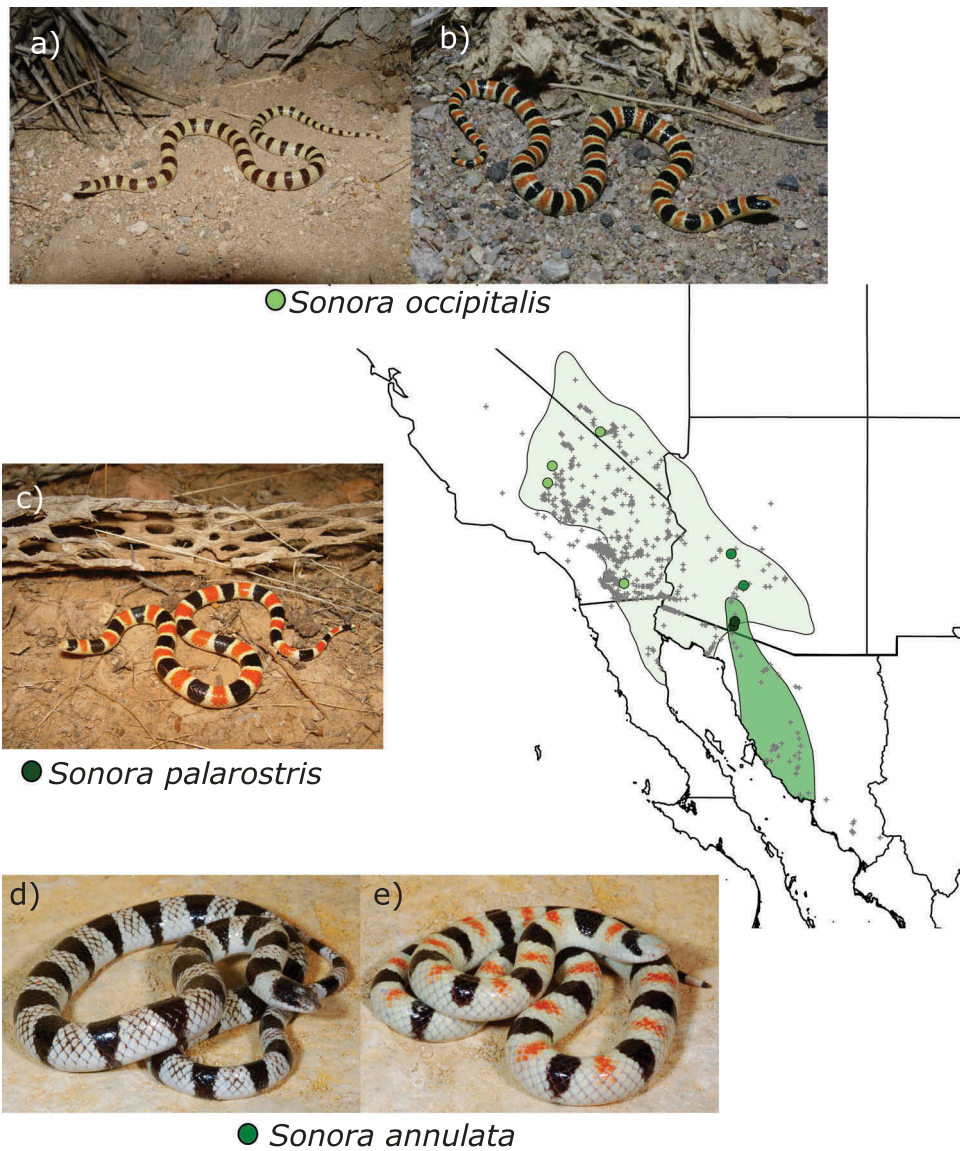
### **Generic reassignment of *Chionactis* and *Chilomeniscus***

In order to resolve the non-monophyly of *Sonora*, we suggest placing the genera *Chionactis* and *Chilomeniscus* in synonymy with *Sonora*, resulting in the recognition of *Sonora* as a monophyletic genus comprised of 15 species. We were guided by the general principle of taxonomic stability in revising this group to make all genera monophyletic (Simpson 1961; Pauly et al. 2009). This principle recognizes the necessity of taxonomic revision so that taxonomy reflects phylogeny with all superspecific groups monophyletic, and it favours taxonomic revisions that minimize disruption to current nomenclature (Simpson 1961; Pauly et al. 2009). We interpret this concept to select taxonomic revisions that solve non-monophyly of genera while minimizing total taxonomic changes (changing of names) and introducing new nomenclature (new genus names). We emphasize that we



**Figure 4.** Map of the geographic distribution from IUCN and georeferenced occurrence records from GBIF (grey crosses) for the subgenus *Chilomeniscus*, including *Sonora cincta*, *S. fasciata* and *S. straminea*. The top of the map has images of the banded (a) morph of *S. cincta*. The side panel (b) depicts *S. straminea*. The bottom panel depicts the banded (c) morph of *S. fasciata*. Photos by C. L. Cox (a) and J. A. McGuire (b, c). Colours of shaded ranges and circular points on the map correspond to the phylogenetic tree in Figures 1 and 2.

also considered the potential of a new taxonomy to accommodate changes in topology from increased molecular or taxon sampling, and so we sought to minimize future



**Figure 5.** Map of the geographic distribution from IUCN and georeferenced occurrence records from GBIF (grey crosses) for the subgenus *Chionactis*, including *Sonora occipitalis*, *S. palarostris* and *S. annulata*. The top of the map has images of the bicoloured (a), and tricoloured (b) morphs of *S. occipitalis*. The side panel (c) depicts *S. palarostris*. The bottom panel depicts the bicolour (d) and tricolour (e) morphs of *S. annulata*. Photos by T. Brennan (a, b, and c) and M. Mulks (d and e). Colours of shaded ranges and circular points on the map correspond to the phylogenetic tree in Figures 1 and 2.

taxonomic disruption. Beyond taxonomic stability, we only considered taxonomic arrangements that rendered all taxa monophyletic with both our mtDNA and ddRADseq datasets, given that we did not have identical taxon sampling for each dataset.

However, we recognize that there are several arrangements that would render all genera monophyletic. Our solution, which is to synonymize *Chionactis* and *Chilomeniscus* with *Sonora*,

entails changing the scientific names of five currently recognized species (not including five newly recognized species, which will remain constant in all taxonomic schemes), and would not create or elevate new genera. Other solutions would be (1) to retain *Chionactis* and *Chilomeniscus*, and to generate new genera for the clades containing *S. michoacanensis* and *S. mutabilis* and *S. aemula* and *S. mosaueri* (two new genera, four name changes); (2) to retain *Chionactis* and *Chilomeniscus*, generate a new genus for *S. michoacanensis* and *S. mutabilis*, and put *S. aemula* and *S. mosaueri* into *Chionactis* (one new genus, four name changes); or (3) to retain *Chilomeniscus*, place *Chionactis* into synonymy with *Sonora*, and generate a new genus for *S. michoacanensis* and *S. mutabilis* (five name changes, one new genus). Note that all of these taxonomic arrangements result in similar number of changes (4–5 name changes, sinking of 0–2 genera and either creation or re-elevation of 0–2 genera). Our preferred solution does not require that we create multiple new genera (either with completely novel names or names that were never in wide usage) with only a few species, and only a modest number of taxonomic changes that are similar to other possible options. It is important to note that elevating genera essentially requires proving a negative – that any new sample added to the dataset from within the broader clade would not render the putative genera paraphyletic, or otherwise complicate the taxonomy. In contrast, collapsing genera requires only that the genera being synonymized are nested in the broader genus. This method can be reliably inferred from existing sampling, and so requires no speculation about the systematic and taxonomic impact of future sampling, thus resulting in a more stable taxonomy.

Beyond strict taxonomic stability, collapsing *Chilomeniscus* and *Chionactis* into *Sonora* has several other advantages. First, it is consistent with historical taxonomy, as multiple species of *Chionactis* (but not *Chilomeniscus*) were historically placed into *Sonora* (Stickel 1938). Second, this recognizes the biogeographic and ecological similarities among the 15 species now in *Sonora*. Biogeographically, all species are found from central and western USA to central Mexico, in habitats ranging from seasonally semiarid to arid (Figure 8). From a phylogenetic perspective, all 15 species form a cohesive clade, without any other particularly close relatives. Colour polymorphism is rampant within all clades within this genus, while coral snake mimicry likely evolved early in this group and has been lost multiple times (Davis Rabosky et al. 2016b). Additionally, species that approach maximal genetic divergence within the clade are very difficult to reliably distinguish morphologically (e.g. *S. semiannulata* and *S. mutabilis*), and have long been considered congeners (Stickel 1943). Our preferred solution also does not create groups of small and morphologically dissimilar genera (e.g. Alternative 1, combining *S. mosaueri* and *S. aemula*; Alternative 2, combining *S. mosaueri* and *S. aemula* with *S. annulata*, *S. occipitalis* and *S. plarostris*), but rather creates a moderately sized genus with morphological diversity.

To help maintain continuity with current taxonomy and aid the recognition of unique morphological diversity, we suggest that the major clades of the genus *Sonora* can be recognized using subgeneric nomina. There are multiple solutions to recognizing phylogenetic structure below the level of genera within the Linnaean classification system, and these include species groups (i.e. in the former *Eleutherodactylus*; Streicher et al. 2009), sections (i.e. in plant taxonomy; Schenk 2013), and subgenera (i.e. amphibian groups such as bolitoglossine salamanders; McCranie and Townsend 2011). We have elected to use subgenera to denote major clades within *Sonora*, which allows us to maintain nomenclatural continuity with previous taxonomies for researchers that wish to go beyond the Linnaean binomial names. Therefore, we propose the name *Chionactis* as a subgenus for the clade including *S. annulata*,

*S. occipitalis*, and *S. palarostris*, the name of their former genus. The clade composed of *S. cincta*, *S. fasciata*, and *S. straminea* can also be recognized as their former genus name of *Chilomeniscus*. Beyond these two clades, we have also recovered three other reciprocally monophyletic clades within *Sonora*, which are (1) *S. episcopa*, *S. taylori* and *S. semiannulata*; (2) *S. mosaueri* and *S. aemula*; and (3) *S. michoacanensis* and *S. mutabilis*. We suggest that the clade of *S. episcopa*, *S. taylori* and *S. semiannulata* form the subgenus of *Sonora*, in recognition of the fact that *S. semiannulata* is the nominate species of this genus. The genus name *Procinura* has been used previously for *S. aemula*, and so is available for the subgenus name for the clade *S. aemula* and *S. mosaueri*. Finally, *S. michoacanensis* and *S. mutabilis* reach the southern extent of the geographic range of *Sonora*, and represent the earliest dichotomous branch in the genus. In recognition of this early split, we propose using the name *Eosonora* as the subgenus for this clade, with *eo* indicating early or dawn *Sonora*.

### **Phenotypic evolution across the genus**

Much of the scientific attention on *Sonora* has been focused on colour pattern, both to understand the evolutionary drivers of colour pattern and to clarify taxonomy (Stickel 1943; Wood et al. 2008, 2014; Cox et al. 2013; Cox and Chippindale 2014; Davis Rabosky et al. 2016a). Interestingly, our taxonomic revisions that are based upon a broader phylogenetic perspective also highlight the rapid evolution of other morphological traits. Given the topology and divergence estimates of our new phylogeny, the 'ancestral' bauplan of a generalized small colubrid appears in multiple places on the tree: the subgenus *Eosonora*, *S. mosaueri*, and the subgenus *Sonora*. From this morphology, there have been repeated origins of rostral adaptations, with the elongated rostrum of the subgenus *Chilomeniscus* and the shovel-like rostrum of the subgenus *Chionactis*. One member of the subgenus *Procinura* (*Sonora aemula*) has also evolved the caudal adaptation of a file-like tail, despite its close genetic affiliation with *S. mosaueri* that lacks this feature. While the rostral adaptations of the subgenera *Chionactis* and *Chilomeniscus* are thought to be important for navigating the gravel and sandy soils in their habitat (Ernst and Ernst 2003), the function of the tail of *S. aemula* is unknown. This morphological diversity despite only modest phylogenetic divergences suggests the potential for rapid morphological evolution of cephalic and caudal structures as well as colour pattern.

### **Limitations of the current study and future research**

This work certainly represents the largest molecular study to date on *Sonora*, with correspondingly representative and fine-scale geographic sampling. However, there are still outstanding taxonomic problems that cannot be resolved without additional work. First, our revision has focused on using genetic data in this group of snakes where morphology has confounded taxonomy. However, future research could work to identify morphological traits that could be useful for species that we are currently not able to diagnose morphologically. Second, our sampling cannot resolve the borders and contact zones between several lineages, including *Sonora mosaueri* and *S. semiannulata* in Baja California, *S. cincta*, *fasciata* and *S. straminea* in Baja California, *S. episcopa* and *S. semiannulata* in New Mexico, and *S. episcopa*, *S. semiannulata* and *S. taylori* in extreme north-eastern Mexico (e.g. Tamaulipas). Third, we did not have tissue samples for Espirtu, Partida, or Cerralvo Islands, and so we are unable to evaluate the

phylogenetic position of *S. punctatissima* or *S. savagei*. Fourth, we currently cannot evaluate the phylogenetic placement of specimens formerly assigned to *S. semiannulata* from Baja California Norte, which have previously been described as *S. bancroftae* (from San Jorge near the San Telmo River) and have a distinctive grey banding pattern (Klauber 1943). This taxon was subsequently collapsed into *Sonora* by Frost (1983a) based upon non-diagnosable morphological variation. Given the cryptic diversity in *Sonora* (this study), whether these specimens are part of the *S. mosaueri* group or the *S. semiannualata* group, and the precise location of the contact zone in Baja, are both unknown without increased sampling across the entire peninsula. Finally, specimens of *S. aemula*, *S. mutabilis* and *S. michoacanensis* are generally rare in natural history collections, and genetic resources even more rare. Given the surprising finding of a *Sonora semiannulata* as far south as northern Jalisco (which was identified in the field as *S. mutabilis*, and only diagnosed as *S. semiannulata* based upon molecular data), increased sampling in mainland Mexico has the potential to generate new insight about the evolution of diversity among snakes of the genus *Sonora* in North America.

### Species accounts

Below we provide species accounts for all species of the genus *Sonora*, including those previously assigned to *Chionactis* and *Chilomeniscus*. We note that we relied upon previously published species accounts for morphological diagnoses (Grismer et al. 2002; Holm 2008; Cox et al. 2012; Wood et al. 2014). Species accounts are not provided for currently recognized subspecies, but we refer to the authorities that define subspecies. When constructing synonymies, we did not necessarily aim for an exhaustive list of all sources that have used each name, but rather tried to highlight the important taxonomic changes in the taxonomy. Finally, colour pattern has long confounded taxonomists in this group, and some genetically distinct species are not diagnosable using morphological variation (Frost and VanDevender 1979; Frost 1983a; Grismer et al. 2002). In cases where morphology cannot diagnose species, we use geography as a guide to species identity in both the dichotomous key and species accounts.

### Key to species of the genus *Sonora*

- 1. Snout normal, not elongate or spade-like ..... 2  
    Snout elongate or spade-like..... 3
- 2. Tail normal, does not have spines or a file-like appearance ..... 4  
    Tail with distinctly raised tubercular scales or caudal spines creating a ‘file-like’ tail appearance..... *Sonora aemula*
- 3. Snout elongated..... 5  
    Snout spade-like, with an enlarged rostral scale ..... 6
- 4. Distributed south of Sinaloa and Zacatecas in Mexico ..... 7  
    Distributed north of Sinaloa and Zacatecas in Mexico ..... 8
- 5. Distributed on Cerralvo, Isla Partida, or Espiritu Santo Islands off of the coast of Baja California..... 9  
    Distributed in Baja California peninsula, mainland Mexico, and the USA..... 10

- 6. Less than 23 crossbands..... *Sonora palarostris*  
Greater than 23 crossbands ..... 11
- 7. Absence of banding on the tail..... *Sonora michoacensis*  
Tail completely banded..... *Sonora mutabilis*
- 8. Distributed south and east of the Balcones Escarpment in Texas, lacks banding or a red longitudinal stripe, 13 midbody scale rows..... *Sonora taylori*  
Distributed north and west of the Balcones Escarpment, including northern Mexico ..... 12
- 9. Distributed on Cerralvo Island, Baja California Sur..... *Sonora savagei*  
Distributed on Espiritu Santo or Partida Islands, Baja California Sur *Sonora punctatissima*
- 10. Apical maculations on dorsal body scales..... *Sonora straminea*  
No apical maculations on dorsal body scales ..... 13
- 11. Brown colour of crossbands, usually without red crossbands... .. *Sonora occipitalis*  
Black crossbands..... *Sonora annulata*
- 12. Distributed in Oregon, California, Idaho, Nevada, Utah, Arizona in the USA and Chihuahua, western Texas along the Rio Grande,<sup>1</sup> extreme south-western New Mexico,<sup>2</sup> Sonora, Durango, northern Baja California,<sup>3</sup> and Jalisco in Mexico,<sup>4</sup> crossbands on banded individuals square-shaped and not saddle-like.....  
..... *Sonora semiannulata*  
Distributed in Kansas, Oklahoma, Missouri, Arkansas, and in Texas north of the Balcones Escarpment, west Texas,<sup>1</sup> and north-eastern New Mexico,<sup>2</sup> crossbands on banded individuals saddle-shaped..... *Sonora episcopa*
- 13. Distribution at in the south-western USA in Arizona, California, and Arizona, the state of Sonora in Mexico, and Bahia Concepcion or further north in Baja California,<sup>5</sup> number of body bands (excluding tail) on banded individuals less than 21..... *Sonora cinctus*  
Distributed south of Bahia Concepcion,<sup>5</sup> number of body bands (excluding tail) on banded individuals numbering 23 or greater..... *Sonora fasciata*

<sup>1</sup>The precise contact zone of *S. episcopa* and *S. semiannulata* in west Texas is not known, and specimens of *S. semiannulata* from west Texas cannot be distinguished morphologically from *S. episcopa*. See species accounts for details.

<sup>2</sup>The precise contact zone of *S. episcopa* and *S. semiannulata* in central New Mexico is not known, and specimens of *S. semiannulata* from central New Mexico cannot be distinguished morphologically from *S. episcopa*. See species accounts for details.

<sup>3</sup>The precise contact zone of *S. mosaueri* and *S. semiannulata* in northern Baja California is not known, and specimens of *S. semiannulata* from northern Baja California cannot be distinguished morphologically from *S. mosaueri*. See species accounts for details.

<sup>4</sup>The precise contact zone of *S. mutabilis* and *S. semiannulata* in southern Mexico is not known, and it is not known whether specimens of *S. semiannulata* can be distinguished morphologically from *S. mutabilis*. See species accounts for details.

<sup>5</sup>The precise contact zone of *S. cincta* and *S. fasciata* in Baja California is unknown, and it is not known whether specimens of *S. cincta* can be reliably distinguished morphologically from *S. fasciata*. See species accounts and Holm (2008) for details.

### Subgenus *Sonora*

#### *Sonora episcopa* (Kennicott 1859)

*Lamprosomum episcopum* Kennicott 1859:22. Holotype: The syntypes are in the US National Museum (USNM) 2042 and 2045, specimen 2042 was designated the lectotype by Stickel (1938). Type locality: The type locality is listed as 'Eagle Pass', Maverick County, Texas. However, Stickel (1943) speculates that this may have been only an intermediate shipping locality, rather the collection locality.

*Contia episcopa episcopa* Cope 1880:21

*Contia episcopa torquata* Cope 1880:21 Holotype: Syntypes are in the Academy of Natural Sciences in Philadelphia 10995 and 10996. Type locality: 'North-western Texas'.

*Contia torquatus* Boulenger 1894:265

*Chionactis episcopus* Cope 1900:937

*Chionactis episcopus episcopus* Cope 1900:938

*Chionactis episcopus torquatus* Cope 1900:939

*Contia nuchalis* Schenkel 1901:162

*Sonora episcopa* van Denburgh and Slevin 1913b:412

*Sonora episcopa* Stickel 1938:184

*Sonora episcopa episcopa* Stickel 1943:121

*Sonora semiannulata episcopa* Frost and VanDevender 1979:6

*Sonora semiannulata* Frost 1983b:333.1

### Diagnosis

This species is distinct from *Sonora cincta*, *S. fasciata*, *S. straminea*, *S. aemula*, *S. annulata*, *S. occipitalis* and *S. palastrois* by the lack of rostral or caudal adaptations. *Sonora episcopa* can potentially be confused with *S. semiannulata* and *S. taylori*, both of which with it is either sympatric or narrowly allopatric. The *S. semiannulata* species group has been historically difficult to define using morphological characteristics, and in fact it was this lack of clear colour pattern or meristic characters delimiting species that led Frost and VanDevender (1979) to synonymize *S. episcopa* with *S. semiannulata*. However, our genetic data show clear reciprocal monophyly of *S. episcopa*, *S. taylori* and *S. semiannulata*. Perhaps the best way to distinguish *S. episcopa* from *S. taylori* and *S. semiannulata* is by geographic range (see below). Beyond geographic range, the expression of colour pattern in morphs that express black crossbands seems to distinguish *S. episcopa* and *S. semiannulata*. *Sonora semiannulata* generally has rectangular black crossbands, while *S. episcopa* has oval-shaped saddles. Besides geographic range, Dixon and Werler (2005) suggests that *S. episcopa* can be distinguished from *S. taylori* based upon 14 or 15 midbody scale rows (13 in *S. taylori*).

### Variation

This is one of the most spectacularly variable snakes in North America and is one of the most variable in the genus *Sonora*. Populations can be polymorphic for the presence or absence of black crossbands, a red, longitudinally oriented dorsal stripe, a single nuchal band, or a black cap on the head. Some individuals have a longitudinal stripe that does not have any red pigment, but lacks maculation that is present on the remaining dorsal scales. Banded individuals can vary greatly in appearance, with bands ranging in expression from complete saddles to broken bands or symmetrical dorsolateral dots. Bands often change in appearance from the head to the tail, becoming broken or absent on the tail and distal surfaces of the body. Ground colour can range from grey, to tan, to brown, to russet or red. The presence of maculations on the scales can vary tremendously, ranging from a barely detectable dot to a large marking that encompasses most of the scale.

### Distribution

*Sonora episcopa* has an extensive geographic range, from the glades of central Missouri and northern Arkansas to the tablelands of Colorado and New Mexico (Figure 3). All of the subgenus *Sonora* material from Kansas, Colorado, Oklahoma, Missouri, and Arkansas is unequivocally *S. episcopa*. All populations of the subgenus *Sonora* in Texas north and west of the Balcones escarpment in Texas are *S. episcopa*, except for those along the Rio Grande in extreme southern Brewster and Presidio counties and throughout El Paso County (which are *S. semiannulata*). Generally, specimens from north-eastern New Mexico are *S. episcopa* and those from south-western New Mexico are *S. semiannulata*, but the precise contact zone between these lineages is unknown. Any populations south and east of the Balcones escarpment are *S. taylori*.

### Remarks

The precise range boundaries of *S. episcopa*, *S. taylori* and *S. semiannulata* are not well known, although we have not yet recovered any examples of hybridization or introgression between these lineages. This species is in the subgenus *Sonora* with *S. episcopa* and *S. taylori*.

### *Sonora semiannulata* (Baird and Girard 1853)

*Sonora semiannulata* Baird and Girard 1853:117. Holotype: USNM 2109. Type locality: 'Sonora, Mexico'. The type specimen was collected by John H. Clark during the USA and Mexico Boundary Survey that occurred between 1848 and 1855 (Goetzmann 1958; James 1969) and described by Spencer F. Baird and Girard (1853). Stickel (1943) assigned the type locality to the Santa Rita mountain range of southern Arizona, based on historical records from the expedition. However, this locality was in the Mexican state of Sonora prior to the Gadsden Purchase in 1854. While Baird and Girard seem to attribute the collection to James D. Graham but the preface specifies that the collector was John H. Clark (Baird and Girard 1853; Degenhardt et al. 1996). The collection date is unknown (Frost 1983b), but was likely in 1851 or 1852, the only two years that Graham was present during the survey.

*Contia isozona* Cope 1866:304. Holotype: The holotype is in the USNM 11417. Type locality: Arizona, Ft. Whipple.

*Contia episcopa isozona* Cope 1880:21

*Chionactis episcopus isozonus* Cope 1900

*Chionactis isozonus* Richardson 1915:426

*Sonora semiannulata semiannulata* Stickel 1938:185

*Sonora semiannulata blanchardi* Stickel 1938:185. Holotype: University of Michigan Museum of Zoology (UMMZ) 83122. Type locality: 'north-eastern slopes of the Chisos Mountains, Brewster County, Texas'.

*Sonora semiannulata gloydi* Stickel 1938:186. Holotype: University of Michigan Museum of Zoology (UMMZ) 83754. Type locality: 'Bright Angel Trail, Lower Sonoran Level of the Grand Canyon, Grand Canyon National Park, Arizona'.

*Sonora miniata miniata* Stickel 1938:187. Holotype: Chicago Academy of Sciences 5139. Type locality: '2 miles north-west of Mesa, Arizona'.

*Sonora miniata linearis* Stickel 1938:189. Holotype: San Diego Museum of Natural History (SDNHM) 2013. Type locality: 'Seeley, Imperial County, California'.

*Sonora semiannulata semiannulata* Stickel 1943:119

*Sonora semiannulata isozona*, Stickel 1943:120

*Sonora semiannulata linearis*, Stickel 1943:121

*Sonora semiannulata blanchardi*, Stickel 1943:121

*Sonora bancroftae* Klauber 1943:69. Holotype: San Diego Museum of Natural History (SDNHM) 3077. Type locality: 'San Jorge, Lower California, Mexico'.

*Sonora semiannulata semiannulata* Frost and VanDevender 1979:6

*Sonora semiannulata* Frost 1983b:333.1

### Diagnosis

This species is distinct from *S. cincta*, *S. fasciata*, *S. straminea*, *S. aemula*, *S. annulata*, *S. occipitalis* and *S. parastrois* by the lack of rostral or caudal adaptations. *Sonora episcopa* can be potentially confused with *S. semiannulata*, *S. mosaeri*, *S. mutabilis* and *S. michoacanensis*. The *S. semiannulata* species group has been historically difficult to define using morphological characteristics, and in fact it was this lack of clear colour pattern or meristic characters delimiting species that led Frost and VanDevender (1979) and Frost (1983a, 1983b) to synonymize many different species and subspecies into *S. semiannulata*. However, our genetic data show clear reciprocal monophyly of *S. episcopa*, *S. taylori*, *S. mosaueri* and *S. semiannulata*. Perhaps the best way to distinguish *S. semiannulata* from *S. episcopa*, *S. mosaeri*, *S. mutabilis* or *S. michoacanensis* is by geographic range (see below). Beyond geographic range, the expression of colour pattern in morphs that express black crossbands seems to distinguish *S. episcopa* and *S. semiannulata*. *Sonora semiannulata* generally has rectangular black crossbands, while *S. episcopa* has oval-shaped saddles. There are no other consistent meristic or qualitative characters that seem to separate these species, despite deep evolutionary divergences.

### Variation

Along with *S. episcopa*, *S. semiannulata* is one of the most variable in the genus *Sonora*. Populations can be polymorphic for the presence or absence of black crossbands, a red, longitudinally oriented dorsal stripe, a single nuchal band, or a black cap on the head. Bands often change in appearance from the head to the tail, becoming broken or absent on the tail and distal surfaces of the body. Ground colour can range from grey, to tan, to

brown, to russet or red. Some individuals that are found in west Texas have distinctively grey crossbands, rather than the normal black crossbands.

### **Distribution**

*Sonora semiannulata* has an extensive geographic range, from Oregon and California in the west to Texas and New Mexico in the east (Figure 3). All of the *Sonora* subgenus material from Idaho, Oregon, California, Utah, Nevada and Arizona in the USA and both Chihuahua and Sonora in Mexico is unequivocally *S. semiannulata*. The only records of *S. semiannulata* in Texas are from along the Rio Grande in extreme southern Brewster and Presidio counties and throughout El Paso County. The situation in New Mexico is more complex, with populations in the north-east of the state assignable to *S. episcopa* and those in the south and west to *S. semiannulata*, but the precise contact zone is unknown. Populations of *S. semiannulata* species group material in extreme northern Baja California in Mexico are also likely *S. semiannulata*, although we have no genetic information for these populations.

### **Remarks**

Despite the similarity in appearance and proximity of geographic ranges, we have not uncovered any evidence of sympatry or hybridization among *S. semiannulata* or *S. episcopa*. This species is in the subgenus *Sonora* with *S. episcopa* and *S. taylori*.

### ***Sonora taylori* (Boulenger 1894)**

*Contia taylori* Boulenger 1894:265. Holotype: Syntypes are in the Natural History Museum of London (1946.1.5.57–1946.1.5.5). Type locality: Duval County, Texas. Stickel (1943) notes that the original description reports both Duval County, Texas and the Mexican state of Nuevo Leon as collection localities, but restricts the type to Duval County, Texas.

*Chionactis taylorii* Cope 1900:936

*Sonora taylori* Stejneger and Barbour 1917:92

*Sonora episcopa taylori* Stickel 1943:122

*Sonora semiannulata taylori* Frost and VanDevender 1979:6

*Sonora semiannulata* Frost 1983b:333.1

### **Diagnosis**

This species is distinct from *Sonora cincta*, *S. fasciata*, *S. straminea*, *S. aemula*, *S. annulata*, *S. occipitalis* and *S. palastrotris* by the lack of rostral or caudal adaptations. *Sonora taylori* can be potentially confused only with *S. episcopa*, with which it is either sympatric or narrowly allopatric. The *S. semiannulata* species group has been historically difficult to define using morphological characteristics, and in fact it was this lack of clear colour pattern or meristic characters delimiting species that led Frost and VanDevender (1979) to synonymize many different species and subspecies into *S. semiannulata*. However, our genetic data show clear reciprocal monophyly of *S. episcopa* and *S. taylori*. Perhaps the best way to distinguish *S. episcopa* from *S. taylori* is by geographic range (see below). Besides geographic range, Dixon and Werler (2005) suggest that *S. taylori* can be distinguished from *S. episcopa* based upon the presence of 13 midbody scale rows (compared to 14 or 15 in *S. episcopa*).

### Variation

*Sonora taylori* is one of only three species in the genus that do not have bands or stripes, and so lack polymorphism and coral snake mimicry. This uniformly brown snake has some slight variation in ground colour from grey to tan, buff or brown, and Dixon and Werler (2005) have noted that the maculated scales often give the impression of light longitudinal lines. In addition, this species does have polymorphism for the black cap on the head (Figure 3).

### Distribution

*Sonora taylori* is found south and west of the Edwards Plateau and Balcones Escarpment of south Texas (Figure 3). Stickel (1943) suggested that specimens from Tamaulipas and Nuevo Leon could be considered *S. taylori*, but we did not have any samples from north-eastern Mexico and this should be tested with additional samples.

### Remarks

This species is in the subgenus *Sonora* with *S. episcopa* and *S. semiannulata*.

### Subgenus *Chilomeniscus* *Sonora cincta* (Cope 1861)

*Chilomeniscus cinctus* Cope 1861:303. Holotype: Museum of Comparative Zoology (MCZ)

24. Type locality: near the town of Guaymas, Sonora, Mexico.

*Chilomeniscus ephippicus* Cope 1867:85. Holotype: USNM 8997. Type locality: Arizona or Owens Valley, California.

*Chilomeniscus cinctus* Banta and Leviton 1963:321

*Chilomeniscus stramineus* Grismer et al. 2002:28

*Chilomeniscus cinctus* Holm 2008:29

### Diagnosis

*Sonora cincta* can be distinguished from all other *Sonora* except for *S. fasciata* and *S. straminea* by the presence of an elongated rostrum. Unlike *S. straminea*, *S. cincta* does not have apical maculations on dorsal body scales (Holm 2008). There are no simple morphological measurements to distinguish *S. fasciata* and *S. cincta*, but Holm (2008) presents a formula that uses a pattern of head squamation to distinguish these two taxa. Geographic range may in fact be the most reliable way to distinguish *S. fasciata* from *S. cincta* (see below).

### Variation

There is considerable variation in *Sonor cincta* squamation, summarized in Holm (2008). Individuals can be either uniform or with red or orange and black or brown crossbands. Bands can take the form of complete bands that reach the ventral scales, saddles that reach the lateral dorsal surface, or dorsal spots. There is also variation in presence of a dark black cap on the head.

### **Distribution**

*Sonora cincta* is distributed in the Sonoran desert and dry forests of southern Arizona, western Sonora south to Sinaloa and on the northern Baja California Peninsula at least as far south as Bahia Concepcion. They can be found from sea level to 1000 m in elevation (Figure 4).

### **Remarks**

This species is in the subgenus *Chilomeniscus* along with *S. fasciata* and *S. straminea*.

### ***Sonora fasciata* (Cope 1892)**

*Chilomeniscus stramineus fasciatus* Cope 1892:595. Holotype: USNM 12630. Type locality: La Paz, Baja California Sur, Mexico.

*Chilomeniscus stramineus esterensis* Hoard 1939:45–46. Holotype: LMK 30368. Type locality: Estero Salina, Baja California Sur.

*Chilomeniscus stramineus fasciatus* Cope 1892:595:

*Chilomeniscus cinctus* Banta and Leviton 1963:321

*Chilomeniscus stramineus* Grismer et al. 2002:28

*Chilomeniscus fasciatus* Holm 2008:31

### **Diagnosis**

*Sonora fasciata* can be distinguished from all other *Sonora* except for *S. straminea* and *S. cincta* by the presence of an elongated rostrum. *Sonora fasciata* is sympatric or narrowly allopatric with *S. straminea* and *S. cincta*. *Sonora fasciata* can be distinguished from *S. straminea* by the lack of apical maculations. There are no simple morphological measurements to distinguish *S. fasciata* and *S. cincta*, but Holm (2008) presented a formula of head squamation to distinguish these two taxa. Geographic range may in fact be the most reliable way to distinguish *S. fasciata* from *S. cincta* (see below).

### **Variation**

This snake has both geographic colour pattern variation and colour polymorphism. In southern populations, both banded and unbanded specimens can be found in a single population. All specimens from Baja California Norte are banded.

### **Distribution**

*Sonora fasciata* is found from the central Baja California Peninsula at least as far north as Las Tres Virgenes to southern Baja California Sur near El Triunfo (Figure 4).

### **Remarks**

This species is in the subgenus *Chilomeniscus*.

### ***Sonora punctatissima* (Van Denburgh and Slevin 1921)**

*Chilomeniscus punctatissimus* van Denburgh and Slevin 1921:98. Holotype: The holotype is the California Academy of Sciences (CAS 49156). Type locality: The type locality is listed as 'Isla Partida, Espiritu Santo Island, Gulf of California, Mexico', suggesting a type locality of Partida Island.

*Chilomeniscus punctatissimus* Banta and Leviton 1963:322

*Chilomeniscus stramineus* Grismer et al. 2002:28

*Chilomeniscus punctatissimus* Holm 2008:34

### Diagnosis

*Sonora punctatissima* can be distinguished from all other *Sonora* except for *S. fasciata*, *S. cincta*, *S. stramineus* and *S. savagei* by the presence of an elongated rostrum. Perhaps the best way to distinguish *S. punctatissima* from *S. fasciata*, *S. cincta*, *S. stramineus* and *S. savagei* is by geographic location; *S. punctatissima* is the only member of the genus *Sonora* on Partida and Espiritu Santo Islands. However, *S. punctatissima* can be distinguished from *S. stramineus* by lacking apical maculations on dorsal body scales (Holm 2008), although Grismer et al. (2002) noted the presence of blotches on scales of some morphs. *Sonora punctatissima* can be distinguished from *S. savagei* by having less than 127 ventral scales, compared to greater than 127 for *S. savagei* (Holm 2008). *Sonora punctatissima* can be distinguished from *S. fasciata* and *S. cincta* by either a gap between the internasals, possessing less than 35 bands and variation in ventral and subcaudal scale numbers summarized in Holm (2008).

### Variation

This is a variable species, especially given the limited geographic range, with Grismer et al. (2002) describing four main pattern classes and individuals with intermediate pattern types. This species can be banded or unbanded, and the expression of bands in the banded individuals varies between a clearly demarcated black bands to grey or brown bands with indistinct margins.

### Distribution

*Sonora punctatissima* is only known from Partida and Santu Espiritu Islands off of the south-eastern coast of Baja California Sur.

### Remarks

*Sonora punctatissima* is recognized based upon clear scutellation differences from other members of the subgenus *Chilomeniscus*, but we did not have access to tissue samples for this study. Future research that provides genetic samples of *S. punctatissima* can confirm the phylogenetic position of this species.

### *Sonora savagei* (Cliff 1954)

*Chilomeniscus savagei* Cliff 1954:71. Holotype: The holotype is in the California Academy of Sciences (CAS-SU 14031). Type locality: 'south-west coast of Cerralvo Island' Baja California Sur, Mexico.

*Chilomeniscus savagei* Banta and Leviton 1963:322

*Chilomeniscus savagei* Grismer et al. 2002:27

*Chilomeniscus savagei* Holm 2008:36

### Diagnosis

*Sonora savagei* can be distinguished from all other *Sonora* except for *S. fasciata*, *S. cincta*, *S. stramineus* and *S. punctatissimus* by the presence of an elongated rostrum. *Sonora savagei* can be distinguished from *S. fasciata*, *S. cincta*, *S. stramineus*, and *S. punctatissimus* by the lack of dark spots in pale bands, broad contact of the internasals with the frontal scale (Holm 2008), separated and reduced prefrontal scales, an enlarged frontal scale, and (Grismer et al. 2002). *Sonora savagei* is the only member of the genus *Sonora* on Isla Cerralvo.

### Variation

*Sonora savagei* possesses dark bands on a light background.

### Distribution

*Sonora savagei* is only known from Cerralvo Island off of the south-eastern coast of Baja California Sur.

### Remarks

*Sonora savagei* is recognized based upon clear scutellation differences from other members of the subgenus *Chilomeniscus*, but we did not have access to tissue samples for this study. Future research that provides genetic samples of *Sonora savagei* can confirm the inclusion of this species in the subgenus *Chilomeniscus*.

### *Sonora straminea* (Cope 1860b)

*Chilomeniscus stramineus* Cope 1860b:339. Syntypes: The type series is in the USNM (4674 and 6495). Type locality: 'Cape St. Lucas, Lower California [Baja California Sur]'.  
*Chilomeniscus stramineus stramineus* Banta and Leviton 1963:323  
*Chilomeniscus stramineus* Grismer et al. 2002:28  
*Chilomeniscus stramineus* Holm 2008:37

### Diagnosis

*Sonora straminea* can be distinguished from all other *Sonora* except for *S. fasciata* and *S. cincta* by the presence of an elongated rostrum. *Sonora straminea* is sympatric or narrowly allopatric only with *S. fasciata*, which shares the elongated rostrum. *S. fasciata* can be distinguished from *S. straminea* by the lack of apical maculations.

### Variation

*Sonora straminea* is one of only three species of *Sonora* that lack coloured bands or stripes, and is uniformly brown. Accordingly, this species lacks colour polymorphism and coral snake mimicry.

### Distribution

*Sonora straminea* is found only in the extreme southern tip of Baja California Sur, Mexico (Figure 4). Holm (2008) restricts this species to east of the Sierra de la Laguna and south of the Sierra de La Gata.

### Remarks

While *Sonora straminea* is morphologically and genetically distinct from *S. fasciata*, the potential for hybridization and contact is not well known, and the northern extent of the range of *S. straminea* (and southern extent for *S. fasciata*) bears further study. This species is in the subgenus *Chilomeniscus* with *S. fasciata* and *S. cincta*.

### Subgenus *Chionactis* *Sonora annulata* (Baird 1859)

*Lamprosoma annulatum* Baird 1859. Holotype: In the USNM (two cotypes 2105–2106).

Type locality: Colorado Desert, California.

*Chionactis occipitalis annulatus* Stickel 1943:128

*Chionactis occipitalis annulatus* Mahrtdt et al. 2001a:731.1

*Chionactis annulata* Wood et al. 2014:10

### Diagnosis

*Sonora annulata* can be distinguished from all other *Sonora*, excepting *S. occipitalis* and *S. palarostris*, by the presence of a flattened, spadelike rostrum. Wood et al. (2014); distinguish *S. annulata* from *S. occipitalis* by the presence of black crossbands (as opposed to brown crossbands in *S. occipitalis*) and the presence of a red secondary crossband. *Sonora annulata* can be distinguished from *S. palarostris* by having more than 23 crossbands (as opposed to less than 23 in *S. palarostris*) according to Wood et al. (2014).

### Variation

Wood et al. (2014) recognize two different subspecies of *S. annulata*, *S. a. annulata* and *S. a. klauberi*. *Sonora a. annulata* is distinguished from *S. a. klauberi* by the absence of maculations on dorsal scales and the lower proportion of maculations in the centre of scales. *Sonora a. annulata* is restricted to the Colorado Desert basin, while *S. a. klauberi* is restricted to the remainder of the Sonoran desert.

### Distribution

*Sonora anunulata* is found in the Colorado and Sonoran Deserts of Arizona and California in the USA, and in the states of Baja California and Sonora in Mexico (Figure 5).

### Remarks

This species is in the subgenus *Chionactis* with *S. occipitalis* and *S. palarostris*.

### *Sonora occipitalis* (Hallowell 1854)

*Rhinostoma occipitale* Hallowell 1854:95. Holotype: According to Mahrtdt et al. (2001a), the holotype has been lost or is misplaced. Drawings based upon the holotype are on plate IV of Hallowell (1854). Type locality: 'Mohave Desert' of California, which Mahrtdt

et al. (2001a) suggest is 'in the region of the Mojave River, western San Bernardino County, California'.

*Lamprosoma occipitale* Hallowell 1856:311

*Chionactis occipitale* Cope 1860a:241

*Chionactis occipitalis* Cooper 1870:66

*Holasoma occipitale* Muller 1882:125

*Contia occipitalis* Garman 1884:91

*Contia occipitale* Brown 1901:68

*Sonora occipitalis* van Denburgh and Slevin 1913a:412

*Sonora occipitalis* Stickel 1938:183

*Chionactis occipitalis occipitalis* Stickel 1943:128

*Chionactis occipitalis occipitalis* Mahrtdt et al. 2001a:731.1

*Chionactis occipitalis* Wood et al. 2014:10

### Diagnosis

*Sonora occipitalis* can be distinguished from all other *Sonora*, except *S. annulata* and *S. palarostris*, by the presence of a flattened, spadelike rostrum. *Sonora occipitalis* can generally be distinguished from both *S. annulata* and *S. palarostris* by the lack of red crossbands (usually present in both *S. palarostris* and *S. annulata*) and the brown coloration of crossbands. Additional morphological differences among *S. occipitalis*, *S. palarostris* and *S. annulata* are summarized in Wood et al. (2014).

### Variation

Most *S. occipitalis* lack red crossbands, but some populations have individuals with red crossbands (less than 10%). There is variation in the number of black crossbands, but there are usually more than 45.

### Distribution

Wood et al. (2014) restrict this species to the Mojave desert in south-eastern California, south-western Nevada, and north-western Arizona (Figure 5).

### Remarks

This species is in the subgenus *Chionactis* along with *S. annulata* and *S. palarostris*.

### *Sonora palarostris* (Klauber 1937)

*Sonora palarostris* Klauber 1937:363. Holotype: In the San Diego Natural History Museum, SDNHM Herps 26771. The holotype is an adult male that was collected by George Lindsay. Type locality: Five miles south of Magdalena, Sonora.

*Chionactis occipitalis palarostris* Stickel 1943:123

*Chionactis palarostris palarostris* Klauber 1951:175

*Chionactis palarostris palarostris* Klauber 1951:178

*Chionactis palarostris palarostris* Mahrtdt et al. 2001b:732.1

*Chionactis palarostris organica* Mahrtdt et al. 2001b:732.1

### Diagnosis

*Sonora palarostris* can be distinguished from all other *Sonora*, except *S. occipitalis* and *S. palarostris*, by the presence of a flattened, spadellike rostrum. Whereas both *S. occipitalis* and *S. annulata*, have more than 23 crossbands, *S. palarostris* has fewer than 23 crossbands.

### Variation

This species is monomorphic for a mimetic phenotype with both red and black crossbands on a buff or tan background, giving the appearance of a tricoloured snake. There are currently two subspecies that are recognized: *Chionactis palarostris palarostris* and *Chionactis palarostris organica*.

### Distribution

*Sonora palarostris* is found in the Sonoran Desert of extreme southern Arizona and northern Sonora, Mexico (Figure 5).

### Remarks

This species is in the subgenus *Chionactis* with *S. annulata* and *S. occipitalis*.

## Subgenus *Eosonora*

### *Sonora michoacanensis* Dugès in Cope (1885)

*Contia michoacanensis* Dugès in Cope 1885:178–179. Holotype: Neotype British Museum of Natural History (BMNH) 1903.3.21, now 1946.1.14.65. The original holotype from the Museo Alfredo Dugès was lost (Stickel 1943; Flores-Villela et al. 2016); a specimen collected in Michoacan with no additional locality information was designated as neotype by Stickel (1943). Type locality: Given as ‘from the state of Michoacan’ in Dugès in Cope (1885). Neotype locality is given as ‘Michoacán’ (Stickel 1943). Restricted to ‘Apatzingan, Michoacán’ by Smith and Taylor (1950), but they did not provide any evidence for this restriction.

*Elapomorphus michoacanensis* Cope 1895:218

*Homalocranium michoacanense* Gunther 1895:150

*Chionactis michoacanensis* Cope 1896:1024

*Scolecophis michoacanensis* Boulenger 1896:211–212

*Sonora erythura* Taylor 1937:69–71. Holotype: University of Illinois Museum of Natural History (UIMNH) 25063. Type locality: ‘16 km S of Taxco, Guerrero’.

*Sonora michoacanensis michoacanensis* Stickel 1943:113

*Sonora michoacanensis* Ponce-Campos et al. 2004:144–148

*Sonora michoacanensis* Cox et al. 2012:102

### Diagnosis

This species is distinct from *Sonora cincta*, *S. fasciata*, *S. straminea*, *S. aemula*, *S. annulata*, *S. occipitalis*, and *S. palarostris* by the lack of rostral or caudal adaptations. This species can be distinguished from *S. mutabilis* based on the almost invariable absence of banding on the tail, and from *S. aemula* based on the absence of a file-like tail

(Figure 5). We note that one specimen from the University of Michigan Museum of Zoology (UMMZ 109904) has a single narrow band on the tail.

### Variation

This species is extremely variable in colour pattern, ranging from uniform red to a banded tricoloured pattern (Echternacht 1973). In tricoloured animals, the number of bands and shape of bands varies greatly (Echternacht 1973). In some individuals, the black and yellow bands appear as black-bordered yellow spots. Morphological measurements and meristic characters are mostly overlapping between *S. mutabilis* and *S. michoacanensis*. The hemipenis is depicted in Cope (Cope 1895; Plate XXIX, Figure 6).

### Distribution

This species is found on the Pacific coast and Balsas Basin in the Mexican states of Colima, Guerrero, Michoacan, Morelos, and Puebla (Figure 6).

### Remarks

This species is in the subgenus *Eosonora* along with *S. mutabilis*.

## *Sonora mutabilis* (Stickel 1943)

*Sonora michoacanensis mutabilis* Stickel 1943:116. Holotype: The holotype is in the Field Museum of Natural History (FMNH) 105257, with paratypes FMNH 105296, British Museum of Natural History (BMNH) BMNH 1946.1.14.63–BMNH 1946.1.14.64 and American Museum of Natural History (AMNH) 19714–19716 (Stickel 1943; Echternacht 1973). Type locality: ‘Magdalena, Jalisco’ (Stickel 1943).

*Sonora aequalis* Smith and Taylor 1945:128. Holotype: Museum of Comparative Zoology (MCZ) 6444. Type locality: Originally given as ‘Matagalpa, Nicaragua’ (Stickel 1943), later concluded it to be ‘within or somewhat to the east of the ranges of *mutabilis* and *michoacanensis*, on the southern part of the Mexican plateau or in the surrounding mountains’ (Stickel 1943; Echternacht 1973).

*Sonora michoacanensis mutabilis* Echternacht 1973:8–9

*Sonora aequalis* Ponce-Campos et al. 2004:144–148

*Sonora mutabilis* Ponce-Campos et al. 2004:144–148

*Sonora mutabilis* Cox et al. 2012:103

### Diagnosis

This species is distinguished from *Sonora cincta*, *S. fasciata*, *S. straminea*, *S. aemula*, *S. annulata*, *S. occipitalis*, and *S. palarostris* by the lack of rostral or caudal adaptations. Both bicoloured and tricoloured forms of this species can be distinguished from *S. michoacanensis* based on complete banding on the tail.

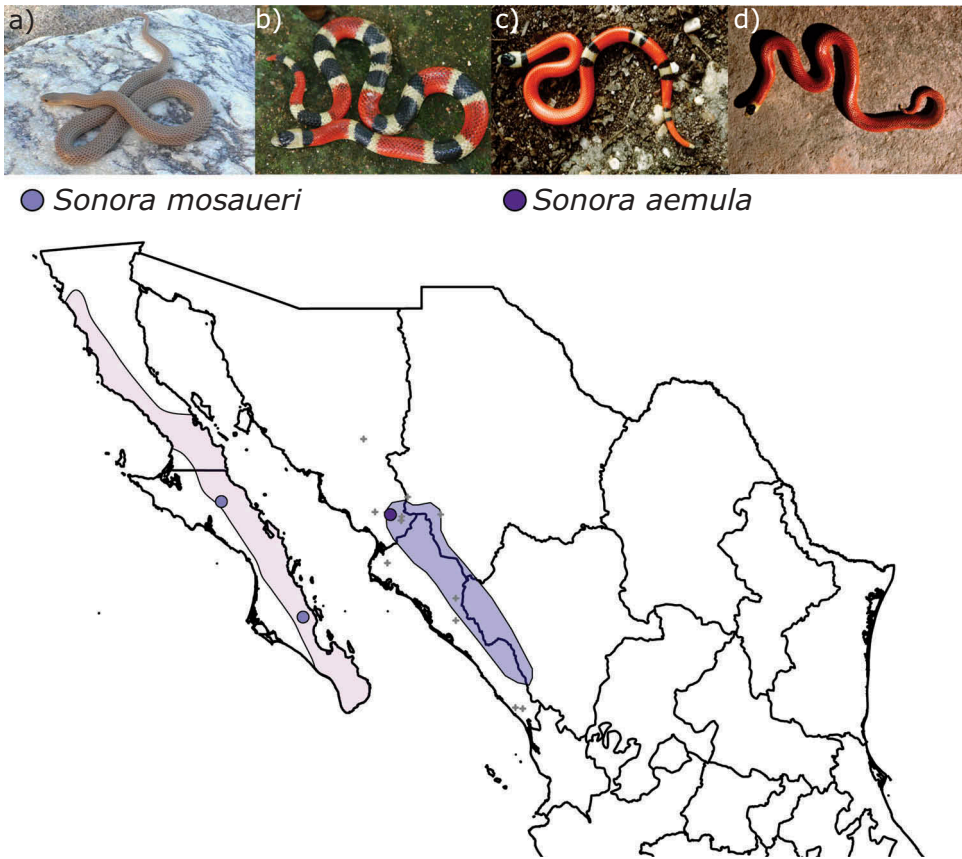
### Variation

*Sonora mutabilis* possesses bicoloured (red and black) and tricoloured (red, black, and yellow) morphs (Echternacht 1973). In tricolour morphs, the extent of black interspaces between bands may be quite variable, and bands may have red dorsal or lateral inclusions. Bands may be regular, irregular, or absent ventrally. Morphological



**Figure 6.** Map of the geographic distribution from IUCN and georeferenced occurrence records from GBIF (grey crosses) for the subgenus *Eosonora*, including *Sonora mutabilis* and *S. michoacensis*. The top of the map has images of the bicolour (a) and tricolour (b and c) morphs of *S. mutabilis*. The bottom panel depicts the tricolour morphs (d and e) of *S. michoacensis* that vary in the expression and number of bands. Photos by C. Grunwald (a), C. L. Cox (b), J. Reyes-Velasco (c), A. Mendoza (d) and O. Medina-Aguilar (e). Colours of shaded ranges and circular points on the map correspond to the phylogenetic tree in Figures 1 and 2.

measurements and meristic characters are mostly overlapping between *S. mutabilis* and *S. michoacensis*. The hemipenis of *S. michoacensis* was described by Stickel (1943). His description was based on one specimen of *S. michoacensis* and one of *S. mutabilis*. Cox et al. (2012) describe the hemipenis of *S. mutabilis* (Figure 6) and compare it to that of *S. michoacensis* (Cope 1895).



**Figure 7.** Map of the geographic distribution from IUCN and georeferenced occurrence records from GBIF (grey crosses) for the subgenus *Procinura*, including *Sonora mosaueri* and *S. aemula*. The top of the map has images of the *S. mosaueri* (a) and the tricolour (b and c) and uniform (d) morphs of *S. aemula*. Photos by C. L. Cox (a), C. Rodriguez (b), and C. M. Bogert (c, d). Colours of shaded ranges and circular points on the map correspond to the phylogenetic tree in Figures 1 and 2.

**Distribution**

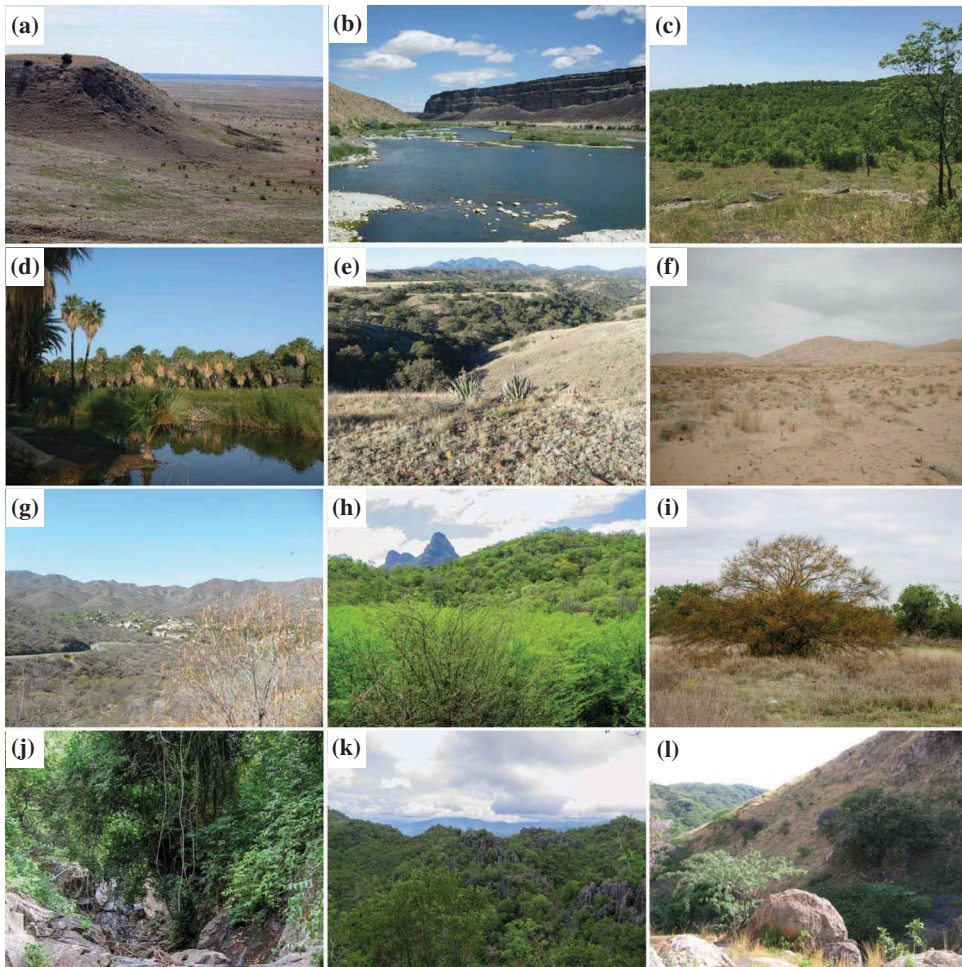
*Sonora mutabilis* is found in the Mexican states of Aguascalientes, Jalisco, Nayarit, southern Zacatecas and extreme southern Sinaloa (Figure 6).

**Remarks**

This species is in the subgenus of *Eosonora* with *S. michoacensis*.

**Subgenus *Procinura***  
***Sonora aemula* (Cope 1879)**

*Procinura aemula* Cope 1879:262 Holotype: Academy of Natural Sciences in Philadelphia (ANSP) 11614 (Bogert and Oliver 1945). Type locality: 'Batopilas, Chihuahua' (Cope 1879).  
*Contia aemula* Garman 1884:92  
*Scolecophis aemulus* Cope 1900:1109



**Figure 8.** Examples of habitat of the snake genus *Sonora* from across their geographic range. (a) Shortgrass prairie in the south-western table-lands of south-eastern Colorado near La Junta, habitat of *S. episcopa*. (b) Great Basin desert in the Snake River Valley in Idaho, near the northern extent of the range of *S. semiannulata* and the genus *Sonora*. (c) A glade in the Ozarks of southern Missouri at the eastern extent of the range of *S. episcopa*. (d) The oasis at San Ignacio, Baja California Sur, habitat for *S. mosaueri* and *S. cincta*. (e) The Huachuca Mountains of south-central Arizona, habitat of *S. semiannulata*. (f) Kelso Sand Dunes of San Bernardino County, California, habitat of *S. occipitalis*. *Sonora semiannulata* occurs in nearby rocky areas. (g) Arid tropical scrub in the southern Baja California peninsula near the town of El Triunfo, habitat of *S. fasciata* and *S. mosaueri*. (h) Tropical dry forest near Alamos, Sonora in Mexico, habitat for *S. aemula* and near the southern extent of the geographic range of *S. cincta* in mainland Mexico. (i) Tamaulipan thornscrub in south Texas, Duval County, habitat for *S. taylori*. (j) Moist tropical forest on a stream near the Barranca del Rio Santiago in Jalisco, Mexico, habitat for *S. mutabilis*. (k) Submontane tropical forest in Guerrero near Chilpancingo, habitat for *S. michoacanensis*. (l) Oak savannah near Guadalajara, Jalisco, Mexico, habitat for *S. mutabilis*. Photos by C. L. Cox (a, c, d, g–l) and A. R. Davis Rabosky (b, e, f).

*Scolecophis aemulae* Gadow 1905:225

*Scolecophis aemulus* do Amaral 1929:218

*Sonora aemula* Bogert and Oliver 1945:371

*Procinura aenula* Smith and Taylor 1945:326

*Procinura aenula* Maldonado-Koerdell 1953:124

*Sonora aemula* Zweifel and Norris 1955:244

*Procinura aemula* Lemos-Espinal et al. 2004a

*Procinura aemula* Smith et al. 2006:820.1

*Sonora aemula* Cox et al. 2012:102

### Diagnosis

This species can be distinguished from all other species of *Sonora* by the presence of distinctly raised tubercular scales or caudal spines creating a 'file-like' tail (Bogert and Oliver 1945).

### Variation

This species is extremely variable in colour pattern, ranging from a uniformly red to banded tricoloured pattern (Bogert and Oliver 1945; Zweifel and Norris 1955; Nickerson and Heringhi 1966). In tricoloured animals, the number and arrangement of triads can vary greatly (Bogert and Oliver 1945; Zweifel and Norris 1955; Nickerson and Heringhi 1966). A more detailed description of meristic characters and a hemipenial description are found in Bogert and Oliver (1945).

### Distribution

This species is found on the Pacific versant of the Mexican states of Chihuahua, Sonora and Sinaloa (Figure 7).

### Remarks

This species is in the subgenus *Procinura* along with *Sonora mosaueri*. It is worth noting that while the name *Procinura* has historically been applied to *Sonora aemula*, this name was only briefly in use after synonymy with *Sonora* in 1945 (Bogert and Oliver 1945) from 1945–1955 (Smith and Taylor 1945; Maldonado-Koerdell 1953; Zweifel and Norris 1955) and from 2004–2012 (Lemos-Espinal et al. 2004a, 2004b, 2004c; Smith et al. 2006; Cox et al. 2012).

### *Sonora mosaueri* Stickel 1938

*Sonora mosaueri* Stickel 1938:187. Holotype: The holotype is in the Museum of Vertebrate Zoology (MVZ 13772) with paratypes MVZ 13770–71 and 13773. Type locality: Comondu, Baja California Sur.

*Sonora semiannulata* Frost 1983a:35–36

### Diagnosis

This species is distinct from *Sonora cincta*, *S. fasciata*, *S. straminea*, *S. aemula*, *S. annulata*, *S. occipitalis* and *S. palarostris* by the lack of rostral or caudal adaptations. There are no clear morphological differences between *S. mosaueri* and *S. semiannulata*, whose geographic ranges may overlap in the northern state of Baja California. This lack of meristic characters distinguishing the various species and subspecies of the *S. semiannulata* species group is what led Frost (1983a) to synonymize all of

these nomen with *S. semiannulata*. However, we found substantial molecular evidence that material formerly assigned to *S. semiannulata* from the southern half of the Baja California Peninsula is not even nested with *S. semiannulata* from the USA and northern mainland Mexico, but is instead sister to *S. aemula*. We recommend that geographic range be used to distinguish *S. mosaueri* from *S. semiannulata* (see below).

### Variation

*Sonora mosaueri* is not polymorphic, and all individuals are brown, grey, or tan uniform in appearance. Individuals of this species often have prominent maculations on the dorsal scales, and have the largest body size of the *S. semiannulata* species group.

### Distribution

The complete geographic range of *S. mosaueri* is unclear, given the general paucity of specimens and tissues for genetic analysis. The description of this taxon only included animals in the type series from near Comondu, although Stickel (1938) speculates that other specimens from near Santa Rosalia could also be assigned to *S. mosaueri*. Our genetic work has revealed that *S. mosaueri* extends at least as far north as San Ignacio (Mulege Municipality), and as far south as near La Paz, Baja California Sur (Figure 7). It is likely that *S. mosaueri* extends to the southern tip of Baja California Sur, but its northern limit is unknown.

### Remarks

Future work should attempt to acquire material from north of San Ignacio, to clarify the contact zone between *Sonora semiannulata* and *S. mosaueri* and assess the validity of *S. semiannulata bancroftae*. In addition, because *S. mosaueri* is more closely related to *S. aemula* than other material formerly assigned to *S. semiannulata*, the presence and extent of sympatry with *S. semiannulata* could be revealed by focused sampling in northern Baja California. This species is part of the subgenus *Procinura* with *S. aemula*.

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## Data availability

Data for this study is archived in the Dryad Data Repository (<https://datadryad.org/>). Mitochondrial sequence data are available at <https://doi.org/10.5061/dryad.vt00811>. ddRADseq sequence data are available at <https://doi.org/10.5061/dryad.8jt2694>.

## Disclosure statement

No potential conflict of interest was reported by the authors.

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