

Cantils (genus *Agiistrodon*) are some of the most feared snakes in Mesoamerica, as their bite and powerful venom have caused numerous human fatalities. Equipped with a large and strikingly-marked head, a stout body, and a nervous attitude that often is mistaken for aggression, these snakes usually are killed on sight. Cantils primarily are found in tropical forests that undergo a prolonged dry season, but occasionally inhabit savannas and areas that flood seasonally after heavy rains. Pictured here is a cantil from Parque Nacional Santa Rosa, in northwestern Costa Rica. Photo by Louis W. Porras.

A taxonomic reevaluation and conservation assessment of the common cantil, *Agkistrodon bilineatus* (Squamata: Viperidae): a race against time

¹Louis W. Porras, ²Larry David Wilson, ^{3,4}Gordon W. Schuett, and ⁴Randall S. Reiserer

¹7705 Wyatt Earp Avenue, Eagle Mountain, Utah, 84005, USA ²Centro Zamorano de Biodiversidad, Escuela Agrícola Panamericana Zamorano, Francisco Morazán, HONDURAS; 16010 S.W. 207th Avenue, Miami, Florida, 33187, USA ³Department of Biology and Center for Behavioral Neuroscience, Georgia State University, Atlanta, Georgia, 30303, USA ⁴The Copperhead Institute, P.O. Box 6755, Spartanburg, South Carolina 29304, USA

Abstract.—Several lines of evidence suggest that numerous populations of cantils (*Agkistrodon bilineatus*, *A. taylori*), New World pitvipers with a distribution in Mesoamerica, are in rapid decline. We examined the IUCN conservation status for *A. bilineatus*, assessed for the entire range of the species, as well as the Environmental Vulnerability Scores (EVS) provided for certain countries along its distribution. Because of pronounced disparities in these conservation assessments and notable phenotypic differences that coincide with the geographic distribution of certain cantil populations, we conduct a taxonomic reassessment of the common cantil, *Agkistrodon bilineatus* (Günther 1863), to determine if the recognized subspecies of *A. bilineatus* merit specific status. Based on our morphological assessment, biogeographical evidence, and the results of previous DNA-based studies, we elevate the three previously recognized subspecies of *A. bilineatus* to full species (*A. bilineatus*, *A. russeolus*, and *A. howardgloydii*). Given this taxonomic reassessment, we examine the conservation status of the newly elevated taxa, suggest avenues for future studies within this complex of pitvipers, and provide conservation recommendations.

Key words. Character evolution, evolutionary species, Mesoamerica, subspecies concept

Resumen.—Varias líneas de evidencia sugieren que numerosas poblaciones de cantiles (*Agkistrodon bilineatus*, *A. taylori*), víboras de foseta del Nuevo Mundo con una distribución en Mesoamérica, están en rápido declive. Examinamos los resultados sobre el estado de conservación propuestos por la UICN para *A. bilineatus*, que fueron evaluados para la distribución total de la especie, así como los resultados de los Índices de Vulnerabilidad Ambiental (en inglés, Environmental Vulnerability Scores [EVS]) que fueron determinados para esta especie en algunos países a lo largo de su distribución. Por haber disparidades pronunciadas en estas evaluaciones de conservación y diferencias fenotípicas notables que coinciden con la distribución geográfica de ciertas poblaciones de cantiles, en este trabajo realizamos una reevaluación taxonómica del cantil común, *Agkistrodon bilineatus* (Günther 1863), para determinar si las subespecies reconocidas de *A. bilineatus* merecen el estatus de especie. Basado en nuestro análisis morfológico, evidencia biogeográfica y los resultados de anteriores estudios basados en ADN, elevamos las tres subespecies de *A. bilineatus* previamente reconocidas al nivel de especie (*A. bilineatus*, *A. russeolus* y *A. howardgloydii*). Tomando en cuenta esta nueva evaluación taxonómica, examinamos el estado de conservación de los taxones aquí elevados, hacemos sugerencias para estudios futuros dentro de este complejo de víboras de foseta y ofrecemos recomendaciones para su conservación.

Palabras claves. Evolución de caracteres, especies evolutivas, Mesoamérica, concepto de subespecies

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Correspondence. Emails: ¹empub@msn.com (Corresponding author) ²bufodoc@aol.com ^{3,4}gwschuet@yahoo.com
⁴rreiserer@gmail.com

Although the restoration of tropical dry forest is still possible, humanity will not give the globe back to its wildland denizens, and old-growth tropical dry forest will never again cover large areas.

Janzen 2004: 80.

Introduction

The common cantil (*Agkistrodon bilineatus*) is a polytypic species of North American pitviper with a variably fragmented distribution extending from extreme southwestern Chihuahua and southern Sonora, Mexico, to northwestern Costa Rica, on the Pacific versant, and parts of the Yucatan Peninsula, northern Belize, Guatemala, and extreme western Honduras on the Atlantic versant; it also occurs in Las Islas Marías, an archipelago of four islands located about 100 km west of the state of Nayarit, Mexico (Gloyd and Conant 1990; Campbell and Lamar 2004; Lemos-Espinal and Smith 2007; Babb and Dugan 2008; García-Grajales and Buenrostro-Silva 2011; McCranie 2011). With few exceptions, the dominant vegetation zones occupied by *A. bilineatus* are dry forest, deciduous forest, thorn scrub, and savanna, primarily areas of low relief that have been exploited heavily for irrigated agriculture and where this species mostly has become a rare snake; the elevational range of *A. bilineatus* extends from near sea level to about 1,500 m (Gloyd and Conant 1990; Conant 1992). Along the Pacific coast of Mesoamerica, tropical dry forests were reported as the most endangered of the major tropical ecosystems, with only 0.09% of that region afforded official conservation status (Janzen 1988). A quarter of a century after Janzen's elucidative paper, aside from protected areas, dry forests throughout this region have continued to deteriorate.

In a monographic study of the *Agkistrodon* complex, Gloyd and Conant (1990) provided an extensive review of the cantils, including information on their taxonomy, morphology, distribution, and aspects of their natural history. Based on multiple lines of evidence, Parkinson et al. (2002) conducted a phylogeographic analysis of the cantils and elevated *A. b. taylori* to the rank of full species, emphasizing that the loss of forested areas in the habitat of this species underscored the need for its conservation. More recently, Wilson et al. (2010) compiled an extensive conservation assessment for the entire Mesoamerican herpetofauna, in which numerous authorities provided information on the status of cantils. Although the methodological approaches of these authors varied, it was clear from the outcome that the conservation status of *A. bilineatus* showed dramatic differences when analyzed on a country by country or regional basis, since the reported or estimated IUCN rankings for this species extended the gamut from Least Concern to Critically Endangered (Lavin-Murcio and Lazcano 2010; Sasa et al. 2010). Some authors also

provided Environmental Vulnerability Scores (EVS; a conservation measure developed and used by Wilson and McCranie 1992, 2004, and McCranie and Wilson 2002) for certain countries, and their results were more informative. This measure provides a rough gauge of the theoretical degree that herptofaunal species are vulnerable to environmental degradation; the scores at the upper end of the scale (ranging from 14 to 20) indicate a greater degree of concern (Wilson et al. 2013), and the EVS for *A. bilineatus* was reported as 15 for Honduras, Nicaragua, and Costa Rica, and as 16 for Belize (Sasa et al. 2010; Stafford et al. 2010; Sunyer and Köhler 2010; Townsend and Wilson 2010).

Based on our field experiences, recent discussions with several colleagues working in regions where cantils occur, and information from the published literature, we echo the statements of several of the aforementioned authorities that in many regions *A. bilineatus* has declined significantly, largely as a result of human activities.

Our principal goal in this paper is to reexamine the conservation status of *A. bilineatus*, inasmuch as the available information suggests that certain populations are declining or imperiled. In conservation biology the threat status of an organism typically is evaluated at the species level, so first we reevaluate the taxonomic status of the three subspecies of *A. bilineatus* (*bilineatus*, *russelous*, and *howardgloydii*) to determine if any (or all) of them shows sufficient lineage divergence to warrant full species recognition. Accordingly, our conservation assessment develops from our taxonomic conclusions.

Morphological Assessment

Gloyd and Conant (1990) and Campbell and Lamar (2004) provided an extensive amount of biological information on cantils, including excellent drawings of the scalation and pattern of the relevant taxa discussed in this paper, so we relied largely on these sources for our morphological assessment. Unlike previous views (see Gloyd and Conant 1990), the genus *Agkistrodon* now is restricted to the New World (see Molecular Assessment).

As in other pitviper genera, *Agkistrodon* (sensu stricto) is characterized by the presence of a deep facial pit, a vertically elliptical pupil, a large venom gland in the temporal region, and a canaliculated fang on the maxilla followed by a series of smaller replacement fangs. In *Agkistrodon*, however, the scales on the crown generally are large and plate-like, although often they are fragmented or contain partial sutures, and the skull is relatively broad and equipped with short fangs. Other characters include a pronounced canthus rostralis, the presence of a loreal scale in all members except *A. piscivorus*, a robust (or relatively robust) body, and a moderate to long tail. Scale characters such as supralabials, infralabials, and dorsal scale rows at midbody show little variation among the species, although the last of these characters is slightly higher in *A. piscivorus*. The

number of ventral scales is lower in *A. bilineatus* and *A. taylori* than in *A. contortrix* and *A. piscivorus*, and the number of subcaudals is slightly lower in the latter two species. In *Agkistrodon*, some or most of the subcaudal scales are divided, and the terminal spine on the tail tip is turned downward in all the taxa except *A. piscivorus*. Moderate hemipenial differences have been reported among the taxa, but the similarities are more pronounced when comparing *A. contortrix* and *A. piscivorus* to *A. bilineatus* and *A. taylori* (Gloyd and Conant 1990; Malnate 1990). The tail tip of neonates and juveniles of all species of *Agkistrodon* is brightly colored and typically is yellow, white, or pink (Gloyd and Conant 1990). The coloration of the tail tip changes as animals mature, to a faded yellow, green, gray, black, or sometimes to match the color of the dorsum. Young individuals often use their tail to lure prey (e.g., anurans, lizards) by way of vertical undulations and waving, a behavior termed “caudal luring” (reviewed by Strimple 1988, 1992; Carpenter and Gillingham 1990).

1. The cantils

Commonly known as cantils, *A. bilineatus* and *A. taylori* are thick-bodied pitvipers (Serpentes: Viperidae) with a large head and a moderately long and slender tail, and their maximum total lengths are similar. As in the other

species of *Agkistrodon*, the scale characters of cantils only show a moderately low range of variation (Table 1).

A wide range of color pattern variation is evident in *Agkistrodon*, and these characters were used to diagnose the three subspecies of *A. bilineatus* (Burger and Robertson 1951; Gloyd 1972; Conant 1984), as well to elevate *A. taylori* to the rank of full species (Parkinson et al. 2000). The coloration of the head is distinctive, as cantils are adorned with five conspicuous pale stripes, one vertically on the front of the snout and two laterally on each side of the head. The dorsal color pattern consists of crossbands, at least in juveniles, and this character shows a notable degree of geographic and ontogenetic variation. The chin color and ventral coloration also demonstrate considerable geographic variation.

2. Color and pattern characteristics of the ornate cantil

Among the cantils, the color pattern of *A. taylori* is the most vivid (Fig. 1). The lower facial stripe is broad and extends to cover the lower edge of the supralabials, the dorsal pattern is composed of pronounced black crossbands separated by gray or pale brown areas that often contain yellowish brown or orange, the chin is patterned with bold markings with wide white or yellow elements, and the venter contains dark gray or black markings



Fig. 1. Adult female *Agkistrodon taylori* from Aldamas, Tamaulipas, Mexico. The ornate cantil often is vividly marked. Photo by Tim Burkhardt.

Table 1. Maximum total length and selected scale characters in the three subspecies of *Agristodon bilineatus* and in *A. taylori*. Min-max values are followed by the mean (in parentheses). Data derived from Gloyd and Conant (1990).

Character	<i>A. b. bilineatus</i>	<i>A. b. russeolus</i>	<i>A. b. howardgloydii</i>	<i>A. taylori</i>
Total length	1,090 mm	1,050 mm*	960 mm	960 mm
Ventrals	127–143 (134.5)	131–141 (136.1)	128–135 (131.1)	127–138 (133.7)
Subcaudals	52–71 (61.6)	46–62 (55.4)	54–61 (58.8)	40–56 (48.3)
Supralabials	5–9 (8.1)	8–9 (8.0)	7–9 (8.0)	7–9 (8.0)
Infralabials	9–13 (10.7)	8–12 (10.8)	9–12 (10.9)	9–12 (10.4)
Dorsal scale rows (midbody)	21–25 (22.9)	23–25 (23.1)	23–25 (23.4)	21–23 (22.9)

*Specimen with an incomplete tail.

arranged in a somewhat checkerboard pattern. In contrast to juveniles, adults exhibit a subdued pattern that contains brighter colors, but older individuals of both sexes tend to become melanistic, and sexual color dimorphism is present in all age classes (Burchfield 1982). The tail tip of young individuals has been reported as sulphur yellow, ivory white, or salmon pink (Burchfield 1982; Gloyd and Conant 1990); the tail tip of most young individuals, however, is sulphur yellow (LWP, GWS, pers. observ.; Fig. 2).



Fig. 2. Neonate female *Agkistrodon taylori* born in captivity from adults collected in the state of Tamaulipas, Mexico. Sexual color pattern dimorphism is evident in all age classes, except in very old individuals that sometimes darken with age. In young males, the rhombs on the dorsum tend to form bands and the interstitial pattern is reduced. Photo by Breck Bartholomew.

3. Color and pattern characteristics of the common cantil

In *A. b. bilineatus*, both the upper and lower facial stripes are relatively broad, and the lower stripe is continuous and bordered below by dark pigment along the mouth line. From a frontal view, the vertical stripe along the rostral and mental and the lateral head stripes often meet on the tip of the snout. In adults, the dorsal ground color ranges from very dark brown to black, and if crossbands

are present often they are difficult to distinguish. The dorsal pattern consists of small white spots or streaks. The chin and throat are dark brown or black with a pattern of narrow white lines or markings, and the venter is dark brown or black with pale markings. The coloration of neonates and juveniles is some shade of brown, and consists of brown or chestnut crossbands separated by a paler ground color, with the lateral edges of the crossbands flecked with white. The crossbands gradually fade with maturity, however, as the overall dorsal coloration darkens (Fig. 3). The tail tip of neonates and juveniles has been reported in numerous publications as bright yellow (e.g., Allen 1949; Gloyd and Conant 1990). Sexual color dimorphism has not been reported in any age class.

In *A. b. russeolus*, the upper facial stripe is narrow and sometimes is intermittent posterior to the eye, and the lower stripe is broader and continuous and separated from the commissure by a band of dark pigment. From a frontal view, the vertical stripe along the rostral and mental and the two upper lateral head stripes typically meet on the tip of the snout. The dorsal ground color of adults generally is pale reddish brown, and the pattern consists of broad, deep reddish brown to brown crossbands that are separated dorsally by areas of paler coloration, and often are edged irregularly with white. The crossbands remain apparent, even in older adults. Laterally, the centers of the crossbands are paler and usually contain one or two dark spots. The pattern on the chin and throat often is reduced, with small whitish spots or lines present on a darker background. Approximately the median third of the venter lacks a pattern or contains a few markings. The coloration of a neonate (150 to 175 mm TL) collected near Mérida, Yucatán, was described from life by Howard K. Gloyd (Gloyd and Conant 1990: 83) as showing a velvety appearance, and its pattern consisted of rich chestnut-brown crossbands with rufous brown interspaces, which were edged with blackish brown and interrupted lines of white, “and the tip of the tail gray.” A neonate from Dzibilchaltún, Yucatán, showed a similar coloration except that the banding was edged intermittently only with white, and the tail tip was pale gray with faint white banding (Fig. 4). This individual was maintained in captivity and by the time it had grown to a total



Fig. 3. Young adult *Agkistrodon b. bilineatus* from Apatzingán, Michoacán, Mexico, at an elevation of 330 m. Adult individuals from much of the west coast of Mexico often lose the dorsal banding (see cover of this issue). *Photo by Javier Alvarado.*



Fig. 4. Neonate *Agkistrodon bilineatus russeolus* from Dzibilchaltún, Yucatán, Mexico. Note the pale gray tail tip with faint white banding, and the overall dorsal color pattern. *Photo by Javier Ortiz.*

length of ca. 400 mm, a marked transformation in color pattern had taken place (Fig. 5). With growth, the inner portion of the crossbands gradually turned the same pale color as the interspaces and the individual's pattern developed a more fragmented appearance; the color of the tail tip also shifted to include darker gray tones (Fig. 5). Henderson (1978) reported the dorsal pattern of a preserved young individual (ca. 380 mm) from Orange Walk Town, Orange Walk District, Belize, as faintly banded, and the tail as grayish-yellow with faint narrow bands. Although Gloyd and Conant (1990: 83) reported the tail



Fig. 5. Juvenile (ca. 400 mm TL) *Agkistrodon bilineatus russeolus* from Dzibilchaltún, Yucatán, Mexico (same individual as in Fig. 4). With growth, the inner portion of the crossbands turned the same color as the interspaces, and the snake's pattern developed a more fragmented appearance. *Photo by Javier Ortiz.*

tip of an individual from the same locality as "bright green," they did not indicate the total length of the snake and an ontogenetic color shift might have occurred. The fragmentation of the banding in *A. b. russeolus* is apparent in the photograph of an adult collected in the outskirts of Consejo, Corozal, Belize (Fig. 6). Sexual color dimorphism has not been reported in juveniles or adults of *A. b. russeolus*.

In *A. b. howardgloydii*, the upper facial stripe is narrow and the posterior part often is absent in adults, and the lower facial stripe is broader and usually divided into two



Fig. 6. Adult *Agkistrodon bilineatus russeolus* from the outskirts of Consejo, Corozal, Belize. Note the fragmented color pattern. Photo by Kevin Zansler, courtesy of Robert A. Thomas.



Fig. 7. Adult *Agkistrodon bilineatus howardgloydii* from Volcán Telica, León, Nicaragua. The color pattern of individuals from this volcanic region often contains black pigment. Photo by Nony Sonati, courtesy of Javier Sunyer.

components that sometimes meet at the suture between the second and third supralabials, and below is bordered by a dark line; the lower edges of the supralabials also are pale in color. From a frontal view, of the five facial stripes

only the top two generally meet on the tip of the snout, but in some individuals all five stripes are connected. The dorsal ground color of adults generally is reddish brown or brown. Adults with black pigment, however, are known from Reserva Natural Volcán Telica in northwest Nicaragua, with a pattern consisting of darker crossbands that contrast moderately with the dorsal ground color, and along this volcanic area adults sometimes show a dark coloration (J. Sunyer, pers. comm.; Figs. 7, 8). A cantil also was sighted on the eastern shore of Laguna de Xiloá, north of Managua (R. Earley, pers. comm.). The chin and throat are orange yellow, bright orange, or brownish orange with a pattern of a few small white spots, but this coloration terminates abruptly after the first few ventrals. The venter usually

is dark reddish brown. The dorsal coloration of juveniles is tan to reddish orange, or reddish, with distinguishable reddish brown crossbands that are edged intermittently with white and/or black, especially as they approach



Fig. 8. Young *Agkistrodon bilineatus howardgloydii* from Volcán Masaya, Masaya, Nicaragua. The color pattern of adults from this area sometimes darkens with age. Photo by Javier Sunyer.



Fig 9. Juvenile (311 mm TL) *Agkistrodon bilineatus howardgloydii* from Parque Nacional Santa Rosa, Guanacaste, Costa Rica. Note the color pattern of the tail tip, which anteriorly to posteriorly turns from very dark to pale gray with corresponding pale gray to white interspaces. Photo by Alejandro Solórzano.

the venter. The tail tip of juveniles is banded with a sequential pattern that ranges from very dark gray anteriorly to paler gray toward the tip, with the interspaces alternating from pale gray to white (Fig. 9). Although Villa (1984: 19) indicated that in Nicaragua “the bright sulphur-yellow tail of the young becomes dark in the adult,” and a photograph of a “juvenile individual” of *A. b. howardgloydii* with what is indicated as a “yellowish tail” appears on the frontispiece, the robust body features of the snake clearly show that it is not a juvenile and its tail is not yellow. We question, therefore, whether Villa might not have assumed that the tail color of *A. b. howardgloydii* would be yellow, as this information long was entrenched in literature regarding *A. b. bilineatus*. With regard to sexual color dimorphism, unlike the other subspecies of *A. bilineatus*, sub-adults and adults of *A. b. howardgloydii* show a moderate degree of sexual color dimorphism; in individuals from Costa Rica, females are distinctly banded and paler in overall coloration, whereas males tend to be darker, with their banding obscured (Figs. 10, 11). Metachrosis, the ability to change color at will or under external stimuli (such as light), was observed in the holotype of *A. b. howardgloydii* (Conant 1984). The coloration of this individual was paler at night (LWP, pers. observ.).



Fig. 10. Adult female *Agkistrodon bilineatus howardgloydii* from Colonia Jobo de la Cruz, Guanacaste, Costa Rica. The color pattern of subadults and adults is paler in females. *Photo by Louis W. Porras.*



Fig. 11. Adult male *A. b. howardgloydii* (holotype) from 0.8 kilometers north of Mirador Cañon del Tigre, Parque Nacional Santa Rosa, Guanacaste, Costa Rica. The color pattern of subadults and adults is darker in males. *Photo by Louis W. Porras.*

Molecular Assessment

Gloyd and Conant (1990) recognized 33 taxa (species and subspecies) in *Agkistrodon* (sensu lato), with a distribution in the Old World and the New World, but subsequent studies using molecular (mtDNA) methods partitioned *Agkistrodon* and demonstrated that the name applies to a monophyletic group of species restricted to the New World (Knight et al. 1992; Kraus et al. 1996; Parkinson et al. 1997, 2002; Parkinson 1999; Castoe and Parkinson 2006; Malhotra et al. 2010). *Agkistrodon* currently is viewed as containing four species, *A. bilineatus*, *A. contortrix*, *A. piscivorus*, and *A. taylori* (Parkinson et al. 2000; Campbell and Lamar 2004), although one subspecies of *A. piscivorus* and two of *A. contortrix* appear to constitute distinct species (Guher and Burbrink 2008; Douglas et al. 2009).

1. Molecular studies of cantils

Parkinson et al. (2000) provided the first phylogeographic (mtDNA) analysis of cantils, and tested all of the recognized subspecies (*bilineatus*, *howardgloydii*, *russeolus*, and *taylori*). Using maximum parsimony (MP) and maximum likelihood (ML) methods, these authors recovered the clades (*taylori* + (*bilineatus* (*howardgloydii* + *russeolus*))). Furthermore, based on additional lines of evidence (e.g., biogeography, morphology) they recommended the elevation of *taylori* to full species status, whereas the remaining subspecies were thought to be more recently diverged (i.e., having shallower relationships). Using other mtDNA regions (ATPase 8 and 6), and both ML and Bayesian methods of analyses, Douglas et al. (2009) corroborated the results of Knight et al. (1992) and Parkinson et al. (2000) with respect to New World *Agkistrodon*, including the relationships of cantils, although in their study they lacked DNA samples of *A. b. russeolus*.

2. Current views of cantil systematics and taxonomy

Despite efforts by the various aforementioned authorities, a considerable gap in our understanding of the taxonomy and phylogeography of cantils remains. We attribute this outcome largely to insufficient sampling, based on the number of specimens used in their analyses and the number of localities sampled. For example, Knight et al. (1992) included only two samples of cantils (*bilineatus* and *taylori*) and both lacked locality information, although their samples of *taylori* presumably were collected in Tamaulipas, Mexico (A. Knight, pers. comm.). Similarly, Parkinson et al. (2000) reported on only seven samples of cantils, of which two lacked locality data, and their respective samples of *taylori* ($n = 2$) and *howardgloydii* ($n = 2$) each came from the same locality (see Parkinson et al. 2000: table 2). In testing phylogeographic

hypotheses in *Agkistrodon*, Guiher and Burbrink (2008) and Douglas et al. (2009) used extensive sampling of *A. contortrix* and *A. piscivorus*, and both studies used cantils as an outgroup. No new localities for cantils, however, were sampled.

Presently, only limited mtDNA-based sequence data (no nuclear genes have been tested) are available for a handful of specimens of cantils. No definitive molecular information exists for the nominate form, *A. b. bilineatus* (i.e., no study has provided precise locality information) and only one specimen of *A. b. russeolus* (Yucatán, Mexico) has been subjected to a DNA-based inquiry (Parkinson et al. 2000). Given the extensive range of cantils, the limited number of specimens sampled and tested thus far (Mexico: Tamaulipas [no specific locality], Yucatán, [no specific locality]; Costa Rica: Guanacaste Province, Santa Rosa) is inadequate to provide a robust view of their phylogeography. Nonetheless, despite these deficiencies, the available molecular (mtDNA) evidence suggests that the three subspecies of cantils (*A. b. bilineatus*, *A. b. howardgloydii*, and *A. b. russeolus*) can be diagnosed as separate evolutionary entities (per Wiley 1978, 1981).

Character Mapping

Character mapping is a powerful analytical procedure for producing information and gaining insights into character evolution, particularly with respect to origin, direction, and frequency (Brooks and McLennan 1991; Harvey and Pagel 1991; Martins 1996; Fenwick et al. 2011; Maddison and Maddison 2011). Ideally, characters (traits) should be traced onto trees constructed from an explicitly independent data set (Harvey and Pagel 1991; Maddison and Maddison 2011), such as morphological characters mapped onto trees constructed using molecules (e.g., proteins, DNA).

1. Methods

We conducted a character mapping analysis (CMA) of the cantils by using morphological data derived from the literature (Gloyd and Conant 1990; Campbell and Lamar 2004), new information presented in this paper, and unpublished personal data on all species of *Agkistrodon* (sensu stricto) (see Appendix 1). All characters were coded as binary (i.e., 0, 1) or multi-state (e.g., 0, 1, 2). Non-discrete multi-state characters (e.g., color pattern) were ordered from lowest to highest values. Character polarity was established by using two congeners (*A. contortrix* and *A. piscivorus*) as outgroups. The cottonmouth (*A. piscivorus*) is confirmed as the sister group to cantils (Douglas et al. 2009). Ten characters were selected as potential apomorphies (shared-derived traits) and were traced onto a fully resolved tree (six taxa) based on the mtDNA-markers used in Parkinson et al. (2000) and Douglas et al. (2009). Character tracing was performed

separately for each of the 10 traits using outgroup analysis and parsimony procedures in Mesquite (Madison and Madison 2011), and then combining the individual results onto a global tree.

2. Results and discussion

We found 10 morphological characters (scutellation, color pattern traits) selected for the CMA useful in providing broad support for the topology of the molecular tree, as well as robust evidence for the distinctiveness of the taxa, in particular the three subspecies of *A. bilineatus* (Table 2). We thus assign these characters as putative synapomorphies and autapomorphies for *Agkistrodon* (Fig. 12). Although we had a priori knowledge of specific and unique traits used to originally diagnose each of the subspecies, the CMA presents them in a phylogenetic and temporal framework. Accordingly, we show trait evolution with respect to origin, direction, and frequency. For example, we recovered dark dorsal coloration (dark brown or black) as the putative ancestral condition of *Agkistrodon* (Outgroup 1), which is retained in the basal-most cantils (*A. taylori* and *A. b. bilineatus*), but evolved to reddish-brown in the sister clade *A. b. howardgloydii* + *A. b. russeolus*. These types of data can be used in CMA to test explicit hypotheses concerning adaptation, such as seeking correlations of body color to climate, habitat types, and a range of other variables (e.g., Martins 1996).

Allopatry in *A. bilineatus*

In prioritizing a list of vipers for future conservation measures, Greene and Campbell (1992: 423) considered *A. bilineatus* (sensu lato) a taxon of special interest because of its “highly fragmented and biogeographically interesting distribution.” Parkinson et al. (2002) also commented on the relictual nature of the distribution of cantils, and used allopatry as one of their criteria for elevating *A. b. taylori* to species level.

As presently understood, the distribution of *A. b. bilineatus* extends along the Pacific coast of Mexico (including the offshore Las Islas Marías) and northern Central America, from extreme southwestern Chihuahua and southern Sonora to central El Salvador; inland in Mexico, this species has been recorded in northwestern and extreme southeastern Morelos, as well as in the Río Grijalva Valley (Central Depression; Johnson et al. 2010) of Chiapas (Gloyd and Conant 1990; Campbell and Lamar 2004; Castro-Franco and Bustos Zagal 2004; Herrera et al. 2006; Lemos-Espinal and Smith 2007; García-Grajales and Bueno-Rostro-Silva 2011). McCranie (2011) included a photograph of a cantil from extreme western Honduras (Copán, Copán). Based on that photograph, and others provided to us by the collector (R. Garrido, pers. comm.) taken after the animal had reached maturity, the color pattern characteristics of this individual are most similar to those of *A. b. bilineatus* (Fig. 13).

Table 2. Morphological characters used in the character mapping analysis (Fig. 12). See text for details.

Character	State	Designation
Facial striping	absent	A0
	present	A1
Upper facial stripe	absent	B0
	variable	B1
	broad	B2
	narrow	B3
Adult coloration	tan	C0
	black/dark brown	C1
	reddish-brown	C2
Adult dorsal band (same as ground color)	no	D0
	yes	D1
Adult dorsal band color (when present)	brown	E0
	black/dark brown	E1
Throat color	multi-colored	E2
	reddish-brown	E3
	ground-color	F0
	cream/white	F1
	multi-colored	F2
	dark	F3
Juvenile to adult color ontogeny	brown	F4
	yellow-orange	F5
	slight	G0
	pronounced	G1
	moderate	G2
	yellow	H0
Neonate tail-tip color	gray	H1
	slight	I0
Neonate tail pattern	moderate	I1
	pronounced	I2
Sexual color dimorphism	absent	J0
	present	J1

A photograph of what appears to be *A. b. bilineatus*, with a locality of Honduras, also appears in Köhler (2001: fig. 264). The distribution of *A. b. russeolus* primarily extends along the outer part of the Yucatan Peninsula, from west-central Campeche and the northern portion of Yucatán and Quintana Roo on the Gulf side, and in northern Belize on the Caribbean side, although isolated records are available from extreme southeastern Campeche and central Petén, Guatemala (Gloyd and Conant 1990; Campbell 1998; Campbell and Lamar 2004; Köhler 2008). The southernmost population of cantil (*A. b. howardgloydii*)

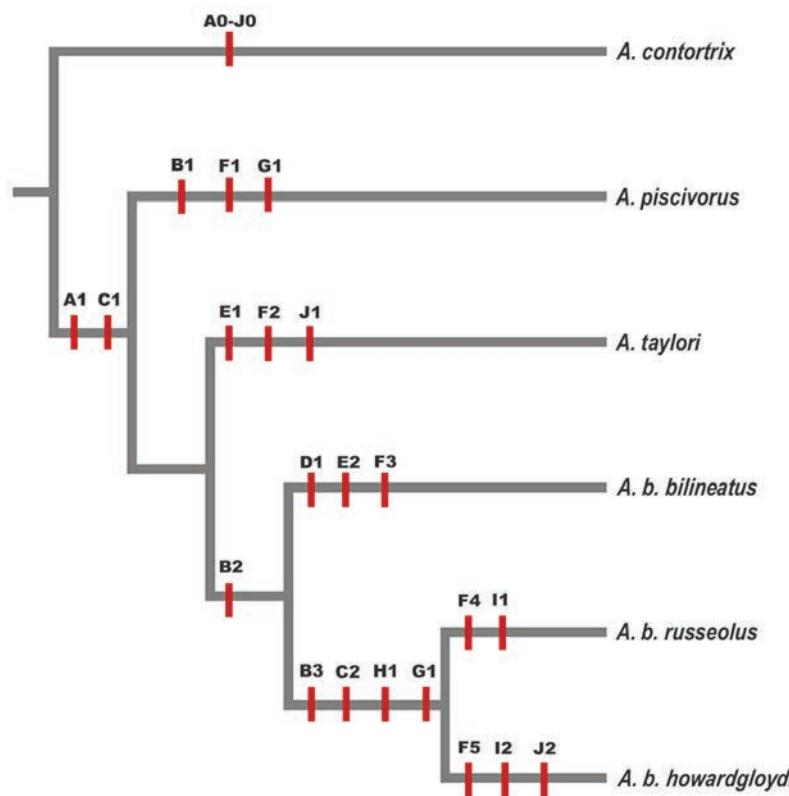


Fig. 12. Character mapping analysis of morphological traits in cantils (*A. b. bilineatus*, *A. b. howardgloydi*, *A. b. russeolus*, and *A. taylori*). Outgroup 1 = *A. piscivorus*; Outgroup 2 = *A. contortrix*. See Table 2 and Appendix 1.



Fig. 13. Young adult *Agkistrodon b. bilineatus* from La Chorcha Lodge, Copán, Honduras at an elevation of 610 m (2,000 feet). Two sightings of this species have occurred at the lodge, in 2003 and 2008. Photo by Robert Gallardo.

occurs along the Pacific coast of Central America from Isla Zacate Grande, in the Golfo de Fonseca, and the adjacent mainland of southern Honduras to the southern limit of Parque Nacional Santa Rosa Park in northwestern Costa Rica (Sasa and Solórzano 1995).

The taxonomic assignment of certain populations of *A. bilineatus*, however, remains problematical. A single individual of cantil was reported from north of Palma Sola, in central coastal Veracruz, an area disjunct from that of all other populations (Blair et al. 1997). Smith and Chiszar (2001) described the specimen as a new subspecies (*A. b. lemosespinali*), but Campbell and Lamar (2004: 266) indicated that this taxon “was diagnosed by several characteristics, all of which are within the normal range of variation for *A. taylori* or might be artifacts in a specimen preserved for more than 30 years.” After examining additional specimens of *A. taylori* from Hidalgo and Veracruz, however, Bryson and Mendoza-Quijano (2007) concluded that the specimen was most closely related to, if not conspecific with, *A. b. bilineatus*, but that it also differed from all of the subspecies of *A. bilineatus* in its tail length to total length ratio. Bryson and Mendoza-Quijano (2007) further commented that the presence of *A. bilineatus* in coastal Veracruz lends corroboration to the transcontinental dispersal hypothesis presented by Parkinson et al. (2002).

Another isolated population is known from the Atlantic versant of central Guatemala, from the Río Chixoy (Negro) Valley (Campbell and Lamar 1989). Gloyd and Conant (1990) commented that two specimens from this area show similarities in color pattern to each of the three populations of *A. bilineatus* occurring in Central America. Until additional specimens and/or molecular data are available, however, the taxonomic status of this allopatric population is uncertain and remains for future investigation. Similarly,

the population in the Central Depression of Chiapas, Mexico, and adjacent western Guatemala merits further examination.

In summary, the distribution of *A. bilineatus* is disjunct or fragmented throughout its extensive range, and thus we contend that three identifiable areas of its distribution are biogeographically distinct. Except for certain issues that remain unresolved (see Discussion), these regions of allopatry constitute the ranges of *A. b. bilineatus*, *A. b. russeolus*, and *A. b. howardgloydii* (see Distribution Map [Fig. 14] below).

Our Taxonomic Position

Six decades ago, Wilson and Brown (1953) discussed the recognition of subspecies in biology and were among the first to advocate, with compelling academic vigor, to halt the use of trinomials in taxonomy. Since their provocative paper was published, a flurry of literally hundreds of papers on the utility of infraspecific categories has appeared, of which many applauded the insights of Wilson and Brown (1953) and supported abandoning the recognition of subspecies (e.g., Edwards 1954; Donoghue 1985; Ball and Avise 1992; Douglas et al. 2002; Zink 2004), whereas others criticized their views as biologically short sighted (e.g., Sibley 1954; Durrant 1955; Crusz 1986; Mallet 1995). Even with the application of an integrative taxonomic approach (reviewed by Padial and de la Riva 2010), a unified concept of species and consequences for solving the problems of species delimitation (see de Queiroz 2007), or a general species concept approach as presented by Hausdorf (2011), no perfect solutions are available to resolve all of the conflicting viewpoints. Nevertheless, Padial and de la Riva (2010: 748) argued that on the basis of the evolutionary species concept, “the point of separation from [a] sister lineage is what marks the origin of a species...and neither subspecies nor ‘subspeciation’ are logically needed.” Importantly, this statement implies that there are no “stages of speciation,” i.e., subspecies are not “on their way” to becoming species. We also share the opinion of Johnson et al. (2010: 327), who asserted that the species level is “the lowest evolutionary lineage segment that should be used in a formal phylogenetically based taxonomy...In this modern taxonomic hierarchy, all taxa except for subspecies are hypothesized to consist of separate evolutionary lineages, and thus subspecies should not be recognized as a formal taxonomic unit.” Moreover, today new subspecies rarely are described in most major zoological journals, although many authors retain already-recognized subspecies as a provisional measure (e.g., Oatley et al. 2011). Here, we adopt the position on subspecies outlined by Wilson and Brown (1953) and subsequently supported by hundreds of biologists (reviewed by Burbrink et al. 2000; Douglas et al. 2002; Johnson et al. 2010).

Taxonomic Conclusions

The taxonomic overview and analysis we provide for the three putative subspecies of the common cantil (*A. b. bilineatus*, *A. b. russeolus*, and *A. b. howardgloydii*) substantiates that sufficient morphological (color and pattern), molecular (mtDNA), and ecological (biogeographical) data are available to consider these taxa as separate and diagnosable entities with their own evolutionary trajectories (see Wiley 1981; Wiley and Mayden 2000; Douglas et al. 2002). As we view it necessary to adopt and identify a species concept (Padial and de la Riva 2010), we used the evolutionary species concept (ESC) introduced by Wiley (1978, 1981). We agree with others that the ESC is preferred among the species hypotheses, since it best accommodates both morphological and molecular information (Wiley and Mayden 2000; Schwentner et al. 2011).

Accordingly, we elevate the three subspecies of *A. bilineatus* to full species and suggest the following common names: *Agkistrodon bilineatus* (common cantil), *A. russeolus* (Yucatecan cantil), and *A. howardgloydii* (southern cantil). We indicate the reported localities for all the cantils, including *A. taylori*, in a distribution map (Fig. 14).

Conservation Assessment

Up to 2006, the conservation status of *Agkistrodon bilineatus* (sensu lato) was judged by the IUCN as Least Concern, but in 2007, presumably as a result of the reptile assessment undertaken in September 2005, in Jalisco, Mexico, the status was changed to Near Threatened (IUCN Red List website; accessed 20 February 2013). Given that we elevated each of the three subspecies of *A. bilineatus* to full species, we will assess their conservation status individually.

1. Application of the IUCN rankings

The IUCN categories for assigning conservation status are the most widely used scheme for attempting to assess the degree of extinction risk for taxa at the species level (www.iucnredlist.org). The criteria used for this assessment are stipulated in the Guidelines for Using the IUCN Red List Categories and Criteria (Version 8.1; August 2010). Those with the greatest application to Mesoamerican reptile populations involve the extent of occurrence (i.e., geographic range), and at least two criteria regarding the degree of range fragmentation, the degree of decline in one of a number of distributional or populational characteristics, or the degree of fluctuations in any of these characteristics. The extent of occurrence is related to the threat categories as follows: Critically Endangered (< 100 km²); Endangered (< 5,000 km²); and Vulnerable (< 20,000 km²).



Fig. 14. Distribution map of the reported localities for cantils, including some indicated in this paper. Green is used to designate localities from where we regard the systematic status of cantils as undetermined.

Under our new taxonomic arrangement, the distribution of *A. bilineatus* (sensu stricto) is extended to include extreme western Honduras, in the vicinity of the city of Copán on the Caribbean versant (McCrane 2011). Thus, its extent of distribution well exceeds the 20,000 km² that forms the upper cutoff for a Vulnerable species; it also is greater than the 250,000 km² indicated by García (2006) as the combined extent of the six dry forest ecoregions in Pacific coastal Mexico, in addition to its range in Central America. Given its approximate geographic distribution, it clearly lies outside of the upper size limits for any of the IUCN threat categories. In addition, this species does not appear to qualify as Near Threatened, given that “the taxon should be close to qualifying for the Vulnerable category. The estimates of population size or habitat should be close to the Vulnerable thresholds, especially when there is a high degree of uncertainty” (IUCN 2010: 63). If, however, *A. bilineatus* cannot be judged as Near Threatened, only three other categories are available, viz., Extinct, Least Concern, and Data Deficient. The species is not Extinct, or as we maintain in this paper not of Least Concern, and also does not classify as Data Deficient because enough information was

available for it to be judged as Near Threatened (Lee and Hammerson 2007). In light of this information, we contend that *A. bilineatus* (sensu stricto) should be judged as Near Threatened. A broad-scale assessment of this snake’s conservation status throughout its distribution is extremely critical, however, since much of its area of occurrence has been subjected to considerable human population growth.

In Mexico, *A. bilineatus* primarily occurs in the coastal portion of nine states from Sonora to Chiapas, as well as in Morelos. According to information obtained from Wikipedia (www.wikipedia.org), here and elsewhere in this section, these 10 states have a combined human population of 33,432,935 (29.0% of the 2012 population of Mexico). With a growth rate of 1.4% for the country (Population Reference Bureau 2010) and an estimated doubling time of 50 years, if these growth rates remain comparable the population of these states will reach 66,865,870 by the year 2063. Although these figures and projections apply to an area greater than the total range of *A. bilineatus* in Mexico, they signal grave concern for the survival of these populations.

The prospects for the future of *A. bilineatus* in Guatemala and El Salvador are equally as disturbing. Guatemala is the most rapidly growing country in Central America, with a human population 13,824,463 in 2011, a growth rate of 2.8%, and an estimated doubling time of 25 years, and El Salvador already has become the most densely populated region in Mesoamerica. These statistics, therefore, portend a gloomy picture for the flora and fauna of these countries.

Consequently, in light of these data, we consider *A. bilineatus* as Near Threatened, while conceding that future population analyses might demonstrate a threatened status.

The distribution of *A. russeolus* is much greater than 100 km² (the upper cutoff point for a Critically Endangered species), but significantly less than 5,000 km² (the upper cutoff point for an Endangered species). Thus, based on the extent of occurrence, *A. russeolus* should be judged as an Endangered species. According to the maps in Gloyd and Conant (1990), Lee (1996), Campbell and Lamar (2004), and Köhler (2008), *A. russeolus* is known from up to twelve localities, depending on the level of discrimination. Most of these localities are from the state of Yucatán, from the vicinity of Mérida, Motul, and Pisté. Given this number of locations ($n = 12$), *A. russeolus* should be assessed as Vulnerable, since the criterion for this category is ≤ 10 , as opposed to Endangered, which is ≤ 5 . These records are historical, however, with some dating prior to 1895 (sensu Gloyd and Conant 1990), and to our knowledge no modern survey has been undertaken to ascertain the viability of cantil populations in these regions.

The human population of the three Mexican states occupying the Yucatan Peninsula, Campeche, Yucatán, and Quintana Roo, is over 4,000,000 (Population Reference Bureau 2010). Most of the historical records for *A. russeolus* are from the state of Yucatán, the most populous of the three with a current population of about 2,000,000. Specimens assigned to *A. russeolus* have been reported from seasonally dry forest in northern Belize, from Corozal and northern Belize Districts (Stafford and Meyer 2000), and the savanna area of central Petén, Guatemala (Campbell 1998).

Lee and Hammerson (2007) indicated that the major factor affecting the long-term viability of populations of *A. bilineatus* (sensu lato) is “the extreme pressure from persecution leading to population reductions of close to 30% over the last 15 to 30 years...” According to J. Lee (pers. comm.), this evaluation cannot be applied precisely to *A. russeolus*, but would point to a Critically Endangered status based on criterion C1, i.e., an estimate of continuing decline of at least 25% in 3 years or one generation (IUCN 2010). Lee (1996: 399) commented that, “*Agkistrodon bilineatus* [sensu lato] is a dangerously venomous snake that is widely feared by the native people of Yucatán. It is believed to be capable of

prodigious jumps and to deliver venom both through its bite and with its tail, which is thought to act as a stinger...” Lee (1996: 416) also discussed the historical and the modern attitude toward snakes in general and *A. russeolus* (as *A. bilineatus*) in particular, in his chapter on ethnoherpetology in the Yucatan Peninsula, indicating that the cantil or uolpoch (the Mayan name) “is considered by many contemporary Maya to be the most dangerous of all Yucatecan snakes.” This attitude translates into this snake being killed on sight (J. Lee, pers. comm.). Consequently, based on the available information on the conservation status of *A. russeolus*, we consider this species as Endangered. A conservation assessment needs to be undertaken, however, to determine if this categorization is appropriate, or whether the category of Critically Endangered would be more applicable.

Agkistrodon howardgloydii is distributed in apparently fragmented populations that extend from Isla Zacate Grande in the Golfo de Fonseca and the adjacent mainland of southern Honduras (McCrane 2011), western Nicaragua in the area west of Río Tipitapa and the northwestern shore of Lago de Nicaragua (Köhler 1999, 2001), and in extreme northwestern Costa Rica from Bahía Salinas, near the Nicaraguan border, to the sectors of Santa Rosa and Guanacaste, both in Área de Conservación Guanacaste (Conant 1984; Solórzano 2004). Gloyd and Conant (1990: 92) discussed additional Nicaraguan localities that would extend the distribution northeastward into the southwestern tip of Departamento Jinotega, but this record is one of several supplied to the authors by Jaime Villa. Unfortunately, these specimens were in Villa’s “personal collection that was destroyed during the earthquake and fire that devastated Managua beginning on December 23, 1972.” Like Köhler (1999, 2001), we discounted these records until museum specimens are available from those areas to provide verification. The extent of this species’ range, therefore, apparently is greater than 100 km² but less than 5,000 km², so on the basis of its extent of occurrence it would be assessed as Endangered. With respect to the number of localities, three have been reported for Honduras, including one based on a photograph in Köhler et al. (2006), five from Nicaragua (Köhler 2001; a sight record in this paper), and five from Costa Rica (Conant 1984; Savage 2002); most of these localities in Costa Rica, however, fall within Parque Nacional Santa Rosa, so their total number could be considered as few as two. Thus the total number of localities would range from 10 to 13, which technically would place this species in the Near Threatened category, but again historical records (Nicaragua) date back to 1871 (Gloyd and Conant 1990). As a consequence, this species would appear to fall in the Vulnerable category. Furthermore, given the localized distribution of *A. howardgloydii* in Costa Rica, it is noteworthy that this species was not reported from the country until 1970 (Bolaños and Montero 1970).

Agkistrodon howardgloydii occurs in disjunct populations in Honduras, Nicaragua, and Costa Rica, in lowland dry forest—the most endangered of the major forest types in Mesoamerica (Janzen 2004). In Honduras, nearly all of this forest has been removed from the Pacific coastal plain. A telling feature in McCranie (2011: table 22) is that of the protected areas in Honduras currently supporting “some good forest,” not one contains lowland dry forest. Based on figures from 2001, the departments of Choluteca and Valle each rank among the top five in human population density in the country. As noted by Solórzano et al. (1999), M. Sasa was unsuccessful in finding this species at several localities in the Golfo de Fonseca and indicated that most of the locals were unaware of its existence. These disturbing reports and observations suggest that low population densities (or local extirpation) might be the trend. Similarly, McCranie (2011) noted that professional collectors in Choluteca failed to identify this species from photographs. Also, three of us (LWP, LDW, GWS) have been unsuccessful in finding this species on Isla Zacate Grande, in the Golfo de Fonseca, and on the adjacent mainland.

According to Sunyer and Köhler (2010: 494), similar population trends prevail in Nicaragua, since *A. howardgloydii* (as *A. bilineatus*) is restricted to lowland dry forest in the western part of the country, and “this formation has undergone severe human alteration.” Although *A. howardgloydii* apparently occurs in at least three protected areas, 75% of the protected areas in Nicaragua “contain less than 50% of their original forest cover...” (Sunyer and Köhler 2010: 505). The five known localities for this species in Nicaragua (Köhler 2001; this paper) all are from the most heavily populated region in the country, an area that likely harbored more extensive populations of this species in the past.

In Costa Rica, the conservation of *A. howardgloydii* is more promising, as most of the restricted range of this species is located within the Área de Conservación Guanacaste. In this region, populations have been reported as “relatively stable and protected” (Solórzano 2004: 622). At Parque Nacional Santa Rosa, for example, 21 individuals were obtained for study from 1993 to 1996 (Solórzano et al. 1999). Nonetheless, Sasa et al. (2010: table 8) indicated that although the distribution of this species has been reduced by slightly more than 20% from a potential distribution of 6,883 km², only a little more than 13% of that reduced distribution (5,465 km²) is located within reserves. Like other venomous snakes, we can assume that this species is killed on sight in the 87% of the reduced range outside of protected areas. An important factor in this species’ favor is that the human population growth rate of Costa Rica (1.2%) is the lowest in Central America, and that Guanacaste Province, which encompasses the snake’s entire range in Costa Rica, is the most sparsely populated of all the provinces.

Although the population of *A. howardgloydii* in protected areas of Costa Rica apparently remains stable,

throughout most of the range populations have been extirpated (or are nearing extirpation). Thus, in light of the conservation prospects for *A. howardgloydii*, we consider this species as Endangered with the understanding that a range-wide conservation assessment is required, especially in Honduras and Nicaragua.

2. Application of the EVS

The conservation status algorithm known as the Environmental Vulnerability Score (EVS) was developed by Wilson and McCranie (1992) for use with amphibians in Honduras and subsequently applied to both amphibians and reptiles in this country (Wilson and McCranie 2004). The EVS was utilized in a broader fashion in most of the chapters dealing with Central American countries in Wilson et al. (2010), and in all cases used at the country level. As noted in the Introduction of this paper, the EVS for *A. bilineatus* (sensu lato) in four Central American countries fell within the upper end of the vulnerability scale (Wilson and McCranie 2004).

Originally, the EVS algorithm was constructed for use strictly within Honduras, and thus had limited utility outside of that country. For example, the scale used for Honduras was as follows:

- 1 = widespread in and outside of Honduras
- 2 = distribution peripheral to Honduras, but widespread elsewhere
- 3 = distribution restricted to Nuclear Middle America (exclusive of Honduran endemics)
- 4 = distribution restricted to Honduras
- 5 = known only from the vicinity of the type locality

In its original form, four of the five levels of this scale could not be used outside of Honduras. For the EVS to have a broader application, therefore, it required reconstruction and this recently was accomplished for Belize (Stafford et al. 2010), Nicaragua (Sunyer and Köhler 2010), and Costa Rica (Sasa et al. 2010).

In order to use the EVS measure independent of country divisions, it requires additional reconstruction, as follows:

- 1 = distribution extending from North America (United States and Canada) to South America
- 2 = distribution extending from North America to Mesoamerica or from Mesoamerica to South America
- 3 = distribution restricted to Mesoamerica
- 4 = distribution restricted to a single physiographic region within Mesoamerica
- 5 = known only from the vicinity of the type locality

The other components of the gauge require only minimal reconstruction. The ecological distribution component can be revised as follows:

- 1 = occurs in eight or more formations
- 2 = occurs in seven formations
- 3 = occurs in six formations
- 4 = occurs in five formations

- 5 = occurs in four formations
- 6 = occurs in three formations
- 7 = occurs in two formations
- 8 = occurs in one formation

The only modification of this component is that the first level was changed from “occurs in eight formations” to “occurs in eight or more formations” (see Wilson and McCranie 2004). This change appears acceptable, since very few species in Mesoamerica occupy more than eight formations (see Wilson and Johnson 2010: table 16).

The component for the degree of human persecution in reptiles (a different measure was used for amphibians) is the same as used by Wilson and McCranie (2004), as follows:

- 1 = fossorial, usually escape human notice
- 2 = semifossorial, or nocturnal arboreal or aquatic, non-venomous and usually non-mimicking, sometimes escape human notice
- 3 = terrestrial and/or arboreal or aquatic, generally ignored by humans
- 4 = terrestrial and/or arboreal or aquatic, thought to be harmful, might be killed on sight
- 5 = venomous species or mimics thereof, killed on sight
- 6 = commercially or non-commercially exploited for hides and/or meat and/or eggs

Based on these changes to the EVS, the calculated scores for the three species of cantils are as follows:

$$\begin{aligned}
 A. \text{bilineatus: } & 3 + 5 + 5 = 13 \\
 A. \text{russeolus: } & 4 + 6 + 5 = 15 \\
 A. \text{howardgloydii: } & 4 + 8 + 5 = 17
 \end{aligned}$$

Consequently, the value for *A. bilineatus* falls at the upper end of the medium vulnerability category, and the values for *A. russeolus* and *A. howardgloydii* fall into the high vulnerability category.

In summary, the IUCN categorizations and EVS values for these three taxa are as follows: *A. bilineatus* (Near Threatened and 13); *A. russeolus* (Endangered and 15); and *A. howardgloydii* (Endangered and 17). Interestingly, the IUCN has assessed *A. taylori* as a species of Least Concern (Lavin et al. 2007), whereas the EVS for this taxon is reported as 17 (Wilson et al. 2013).

Discussion

We provided a substantive review of the taxonomy and conservation status of the common cantil (*A. bilineatus*, sensu lato). Our taxonomic assessment led us to elevate the three subspecies of *A. bilineatus* to full species (*A. bilineatus*, *A. howardgloydii*, and *A. russeolus*), based on multiple lines of evidence. Nonetheless, we are not confident that this arrangement necessarily captures the full diversity of this widely distributed group of pitvipers.

Accordingly, we identified several regions where additional sampling must be accomplished, but overall we recommend a thorough phylogeographic analysis employing morphological analyses and the use of both mtDNA and nuclear (e.g., introns, microsatellites) markers. Owing largely to the isolation of certain populations, we suspect that additional species will be discovered within this complex.

The population of *A. bilineatus* in southern Sonora and adjacent southwestern Chihuahua, Mexico, for example, occurs in a distinctive habitat (“Sonoran-Sinaloan transition subtropical dry forest” according to the WWF [see García 2006]), the color pattern of adults differs somewhat from that of typical *A. bilineatus* (Fig. 15), and a moderate hiatus exists from the closest-known population to the south (49 miles [78.8 kilometers] south of Culiacán, Sinaloa, Mexico; Hardy and McDiarmid 1969; Campbell and Lamar 2004).

Another example is the insular population on Las Islas Marías. On this offshore group of islands, two specimens collected in 1881 were reported from the “Tres Marías” (without naming a specific island), and one specimen from Isla María Grande was collected in 1897 (Boulenger 1896; Stejneger 1899; see Zweifel 1960). Interestingly, Gloyd and Conant (1990) indicated that the cantil with the greatest total length is among these specimens, as well as the *A. b. bilineatus* (sensu lato) with the lowest number of subcaudals. Gloyd and Conant (1990), however, considered this latter specimen as aberrant, but commented (p. 69) that “Whether other aberrant specimens occurred on the islands probably will never be known, inasmuch as the species may now have been extirpated from the archipelago.” Casas-Andreu (1992) indicated the presence of *A. bilineatus* on other islands of the Las Islas Marías chain (on Isla San Juanito and Isla María Magdalena). According to G. Casas-Andreu (pers. comm.), however, these records were not based on new material, as no cantils were encountered during his survey in 1986, but rather they were obtained from the literature. Inasmuch as no literature citations or museum numbers for these specimens appear in Casas-Andreu (1992), our knowledge of the distribution of *A. bilineatus* on Las Islas Marías remains sketchy. Although some areas of “good habitat” were present in the archipelago in 1986 (G. Casas-Andreu, pers. comm.), habitat destruction, a growing human population (including a large penal colony), the presence of agricultural camps and domestic animals, the outright killing of fauna, and the introduction of rats and feral cats all had become a significant problem (Casas-Andreu 1992). In 2000, the archipelago and its surrounding waters were declared an international protected area (Reserva de la Biosfera Islas Marías). In spite of the lack of information on *A. bilineatus* from these islands, the only reptiles protected under the Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT) are *Crocodylus acutus* (special protection), *Iguana iguana* (special protection), *Ctenosaura*



Fig. 15. Adult *Agkistrodon bilineatus* found by Larry Jones and Thomas Skinner in August of 2005, ca. 12 km NW of Alamos, Sonora, Mexico. This individual later was released. Photo by James C. Rorabaugh.



Fig. 16. Young cantil from Aldea La Laguna, Nentón, Huehuetenango, Guatemala. The specific allocation of this population remains uncertain (see Fig. 14). Photo by Manuel Acevedo.

pectinata (threatened), and *Eretmochelys imbricata* (in danger of extinction) (Anonymous 2007). A determination of the actual distribution and population status of *A. bilineatus* on Las Islas Marías, therefore, is a conservation priority.

The taxonomic status of *A. b. lemosespinali*, which tentatively was assigned to *A. b. bilineatus* by Bryson and Mendoza-Quijano (2007), remains unresolved. Known from a single specimen from Palma Sola, in coastal central Veracruz, Mexico, this area was noted

by Smith and Chizar (2001: 133) as highly agricultural and located next to a nuclear power plant regarded by “many local residents and environmentalists in general as having contaminated the surrounding area with radioactivity.” These authors further indicated that if “*A. b. lemosespinali* ever occurred in that area, it is likely now to be extinct, or it likely would have been found [again] long ago.”

Other disjunct populations of cantils merit a closer examination at both morphological and molecular levels, such as those from the Central Depression of Chiapas and the headwaters of the Río Grijalva that extend into northwestern Guatemala (Fig. 16), the Río Chixoy and Motagua valleys of Guatemala, as well as isolated populations of *A. russeolus* (Gloyd and Conant 1990; Campbell and Lamar 2004; McCranie 2011).

Assigning protected areas for the conservation of cantil populations is not simply a matter of determining regions that exist within the range of the three species, as these have been shown to vary in their level of protection. Jaramillo et al. (2010: 650) presented a model that could be used to analyze systems of protected areas in Mesoamerica, and based on six requisites concluded that the system of protected areas in Panama is impressive due to the number of areas included and their collective territory; a detailed examination of the features, however, demonstrated that all but one of the 97 areas failed, to some degree, “in meeting the necessary requirements for the long-term protection of its biotic resources.” In Honduras, McCranie (2011) indicated that, “at

first glance, Honduras appears to have in place a robust system of protected areas, especially when compared to nearby countries. However, most of those areas exist on paper only.” Similarly, Acevedo et al. (2010) stated that, “the existing system of protected areas in Guatemala is insufficient to protect the country’s herpetofauna, because most of the legally designated areas must be considered as ‘paper parks.’” Essentially the same story can be told about systems of protected areas in other countries where cantils occur (see various chapters in Wilson

et al. 2010), an unfortunate aspect of reality in ongoing efforts to conserve biodiversity.

Unfortunately, because of the continuing destruction of natural habitats and the potential for the extirpation of cantil populations, the answers to some of the aforementioned questions are on the brink of being lost forever, if not lost already. This problem is critical, and we view it as a race against time to generate the necessary information that could help set aside protected areas to conserve disjunct and relictual populations of cantils for posterity.

Conservation Recommendations

Our recommendations for the long-term conservation of *A. bilineatus*, *A. howardgloydii*, *A. russeolus*, and *A. taylori* are as follows:

1. In light of the paucity of information regarding the relative health of populations of these species, it will be essential to undertake population assessments for all the cantils at or near localities where they have been recorded, most critically for *A. howardgloydii* and *A. russeolus* because of their relatively limited geographic ranges.
2. Once these surveys are completed, a conservation management plan should be developed to ascertain if populations of all four species are located within established protected areas, or if new areas should be considered. Such a plan is critical to the survival of cantils, especially since outside of protected areas these snakes generally are killed on sight or otherwise threatened by persistent habitat destruction or degradation.
3. Inasmuch as not all protected areas can be expected to provide adequate levels of protection to support viable populations of cantils, long-term population monitoring will be essential.
4. Given the elevation of these taxa to full species, conservation agencies can now use these vipers as “flagship species” in efforts to publicize conservation efforts in their respective countries at all levels of interest and concern, including education and ecotourism.
5. We recommend the establishment of zoo conservation (e.g., AZA) and outreach programs, such as those currently in progress for the venomous Guatemalan beaded lizard (e.g., www.ircf.org; see Domínguez-Vega et al. 2012) and a wide variety of highly endangered anuran species (e.g., www.zooatlanta.org). Captive assurance colonies might help maximize future options for the recovery of wild populations.

6. One major conclusion of this paper is that our knowledge of the taxonomy and phylogeography of cantils remains at an elementary level. Thus, as conservation assessments proceed, it will be important to obtain tissue samples from a sufficiently broad array of populations to allow for more robust molecular analyses. Similarly, we need more detailed morphological assessments and more sophisticated levels of analyses, such as geometric morphometric approaches (Davis 2012).

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*This paper is part of a special issue of *Amphibian & Reptile Conservation* that deals with the herpetofauna of Mexico. In addition to Dr. Conant’s seminal work on *Agkistrodon* (with Dr. Howard K. Gloyd), readers should be reminded that he also produced important works on this country’s *Nerodia* (then *Natrix*) and *Thamnophis*.

Literature Cited

Acevedo M, Wilson LD, Cano EM, Vásquez-Almazán C. 2010. Diversity and conservation status of the Guatemalan herpetofauna. Pp. 406–435 In: *Conservation of Mesoamerican Amphibians and Reptiles*. Editors, Wilson LD, Townsend JH, Johnson JD. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Allen ER. 1949. Observations on the feeding habits of the juvenile cantil. *Copeia* 1949: 225–226.

Anonymous. 2007. *Programa de conservación y manejo Reserva de la Biosfera Islas Marías*. Comisión Nacional de Áreas Naturales Protegidas, Secretaría de Seguridad Pública. Draft, October 2007. 1–150 pp.

Babb RD, Dugan EA. 2008. Geographic Distribution. *Agkistrodon bilineatus* (cantil). México: Sonora. *Herpetological Review* 39: 110.

Ball RM, Avise JC. 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. *The Auk* 109: 626–636.

Blair KB, Killebrew FC, Smith HM, Chiszar D. 1997. Mexican amphibians and reptiles in the West Texas A & M University Natural History Museum. *Bulletin of the Chicago Herpetological Society* 32: 174–177.

Bolaños R, Montero JR. 1970. *Agkistrodon bilineatus* Günther from Costa Rica. *Revista de Biología Tropical* 16: 277–279.

Boulenger GA. 1896. *Catalogue of the Snakes in the British Museum (Natural History)*. Volume 3. London, United Kingdom.

Brooks DR, McLennan DA. 1991. *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology*. The University of Chicago Press, Chicago, Illinois, USA.

Bryson RW Jr., Mendoza-Quijano F. 2007. Cantils of Hidalgo and Veracruz, Mexico, with comments on the validity of *Agkistrodon bilineatus lemosespinali*. *Journal of Herpetology* 41: 536–539.

Burbrink FT, Lawson R, Slowinski JB. 2000. Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept. *Evolution* 54: 2107–2118.

Burchfield PM. 1982. Additions to the natural history of the crotaline snake *Agkistrodon bilineatus taylori*. *Journal of Herpetology* 16: 376–382.

Burger WL, Robertson WB. 1951. A new subspecies of the Mexican moccasin, *Agkistrodon bilineatus*. *University of Kansas Science Bulletin* 24: 213–218.

Campbell JA. 1998. *Amphibians and Reptiles of Northern Guatemala, the Yucatán, and Belize*. University of Oklahoma Press, Norman, Oklahoma, USA.

Campbell JA, Lamar WW. 1989. *The Venomous Reptiles of Latin America*. Comstock Publishing Associates, Cornell University Press, Ithaca, New York, USA.

Campbell JA, Lamar WW. 2004. *The Venomous Reptiles of the Western Hemisphere* (2 volumes). Comstock Publishing Associates, Cornell University Press, Ithaca, New York, USA.

Carpenter CC, Gillingham JC. 1990. Ritualized behavior in *Agkistrodon* and allied genera. Pp. 523–531 In: *Snakes of the Agkistrodon Complex: A Monographic Review*. Editors, Gloyd HK, Conant R. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA.

Casas-Andreu G. 1992. Anfibios y reptiles de Las Islas Marías y otras islas adyacentes a la costa de Nayarit, México. Aspectos sobre su biogeografía y conservación. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México (Serie Zoología)* 63: 95–112.

Castoe TA, Parkinson CL. 2006. Bayesian mixed models and the phylogeny of pitvipers (Viperidae: Serpentes). *Molecular Phylogeny* 39: 91–110.

Castro-Franco R, Bustos Zagal MG. 2004. Additional records and range extensions of reptiles from Morelos, México. *Herpetological Review* 35: 196–197.

Conant R. 1984. A new subspecies of the pit viper *Agkistrodon bilineatus* (Reptilia: Viperidae) from Central America. *Proceedings of the Biological Society of Washington* 97: 135–141.

Conant R. 1992. Comments on the survival status of members of the *Agkistrodon* complex. Pp. 29–33 In: *Contributions in Herpetology*. Editors, Strimple PE, Strimple JL. Greater Cincinnati Herpetological Society, Cincinnati, Ohio, USA.

Crusz H. 1986. Report of the Society for Researches on Native Livestock. *Tokyo* 11: 65–80.

Davis MA. 2012. *Morphometrics, Molecular Ecology and Multivariate Environmental Niche Define the Evolutionary History of the Western Rattlesnake (*Crotalus viridis*) complex*. Ph.D. Dissertation, University of Illinois at Urbana-Champaign, Illinois, USA.

de Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology* 56: 879–886.

Domínguez-Vega H, Monroy-Vilchis O, Balderas-Valdivia CJ, Geinger CM, Ariano-Sánchez A. 2012. Predicting the potential distribution of the beaded lizard and identification of priority areas for conservation. *Journal for Nature Conservation* 20: 247–253.

Donoghue MJ. 1985. A critique of the Biological Species Concept and recommendations for a phylogenetic alternative. *Bryologist* 88: 172–181.

Douglas ME, Douglas MR, Schuett GW, Porras LW, Holycross AT. 2002. Phylogeography of the western rattlesnake (*Crotalus viridis*) complex, with emphasis on the Colorado Plateau. Pp. 11–50 In: *Biology of the Vipers*. Editors, Schuett GW, Höggren M, Douglas ME, Greene HW. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Douglas ME, Douglas MR, Schuett GW, Porras. LW. 2009. Climate change and evolution of the New World pitviper genus *Agkistrodon* (Viperidae). *Journal of Biogeography* 36: 1164–1180.

Durrant SD. 1955. In defense of subspecies. *Systematic Zoology* 4: 186–190.

Edwards JG. 1954. A new approach to infraspecific categories. *Systematic Zoology* 3: 1–20.

Fenwick AM, Greene HW, Parkinson CL. 2011. The serpent and the egg: Unidirectional evolution of reproductive mode in vipers? *Journal of Zoological Systematics and Evolutionary Research* 50: 59–66.

García A. 2006. Using ecological niche modeling to identify diversity hotspots for the herpetofauna of Pacific lowlands and adjacent interior valleys of Mexico. *Biological Conservation* 120: 25–46.

García-Grajales J, Buenrostro-Silva A. 2011. Ampliación del área de distribución geográfica de *Oxybelis fulgidus* (Serpentes: Colubridae) y *Agkistrodon bilineatus* (Serpentes: Viperidae) en la planicie costera central de Oaxaca, México. *Acta Zoológica Mexicana* (n.s.) 27: 491–495.

Gloyd HK. 1972. A subspecies of *Agkistrodon bilineatus* (Serpentes: Crotalidae) on the Yucatan Peninsula, Mexico. *Proceedings of the Biological Society of Washington* 84: 327–334.

Gloyd HK, Conant R. 1990. *Snakes of the Agkistrodon Complex: A Monographic Review*. Society for the Study of Amphibians and Reptiles, Contributions in Herpetology, Number 6, Ithaca, New York, USA.

Greene HW, Campbell JA. 1992. The future of pitvipers. Pp. 421–427 In: *Biology of the Pitvipers*. Editors, Campbell JA, Brodie ED Jr. Selva, Tyler, Texas, USA.

Guíher TJ, Burbrink FT. 2008. Demographic and phylogeographic histories of two venomous North American snakes of the genus *Agkistrodon*. *Molecular Phylogenetics and Evolution* 48: 543–553.

Günther A. 1863. Third account of new species of snakes in the collection of the British Museum. *The Annals and Magazine of Natural History* (3rd Series) 12: 348–365.

Hardy LM, McDiarmid RW. 1969. The amphibians and reptiles of Sinaloa, México. *University of Kansas Publications, Museum of Natural History* 18: 39–252.

Harvey PH, Pagel MD. 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, New York, USA.

Hausdorf B. 2011. Progress toward a general species concept. *Evolution* 64: 923–931.

Henderson RW. 1978. Notes on *Agkistrodon bilineatus* (Reptilia, Serpentes, Viperidae) in Belize. *Journal of Herpetology* 12: 412–413.

Herrera N, Henríquez V, Vaquerano R. 2006. Herpetofauna del Bosque Seco de El Salvador: nuevos registros de distribución. *Mesoamericana* 19(4): 37–43.

IUCN. 2010. Guidelines for using the IUCN Red List Categories and Criteria. Version 8.1. Available: www.iucnredlist.org [Accessed 22 July 2011].

Janzen DH. 1988. Tropical dry forests: the most endangered major tropical ecosystem. Pp. 130–137 In: *Biodiversity*. Editor, Wilson EO. National Academy Press, Washington, DC, USA.

Janzen DH. 2004. Ecology of dry-forest wildland insects in the Área de Conservación Guanacaste. Pp. 80–96 In: *Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest*. Editors, Frankie GW, Mata A, Vinson SB. University of California Press, Berkeley, California, USA.

Jaramillo C, Wilson LD, Ibáñez R, Jaramillo F. 2010. The herpetofauna of Panama: distribution and conservation status. Pp. 604–673 In: *Conservation of Mesoamerican Amphibians and Reptiles*. Editors, Wilson LD, Townsend JH, Johnson JD. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Johnson JD, Mata-Silva V, Ramírez-Bautista A. 2010. Geographic distribution and conservation of the herpetofauna of southeastern Mexico. Pp. 323–360 In: *Conservation of Mesoamerican Amphibians and Reptiles*. Editors, Wilson LD, Townsend JH, Johnson JD. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Knight A, Densmore LD, Rael ED. 1992. Molecular systematics of the *Agkistrodon* complex. Pp. 49–69 In: *Biology of the Pitvipers*. Editors, Campbell JA, Brodie ED Jr. Selva, Tyler, Texas, USA.

Köhler G. 1999. The amphibians and reptiles of Nicaragua: a distributional checklist with keys. *Courier Forschungsinstitut Senckenberg* 213: 1–121.

Köhler G. 2001. *Anfibios y Reptiles de Nicaragua*. Herpeton, Verlag Elke Köhler, Offenbach, Germany.

Köhler G. 2008. *Reptiles of Central America* (2nd edition). Herpeton, Offenbach, Germany.

Köhler G, Veselý M, Greenbaum E. 2006. *The Amphibians and Reptiles of El Salvador*. Krieger Publishing Company, Malabar, Florida, USA.

Kraus F, Mink DG, Brown WB. 1996. Crotaline intergeneric relationships based on mitochondrial DNA sequence data. *Copeia* 1996: 763–773.

Lavin-Murcio PA, Lazcano D. 2010. Geographic distribution and conservation of the herpetofauna of northern Mexico. Pp. 274–301 In: *Conservation of Mesoamerican Amphibians and Reptiles*. Editors, Wilson LD, Townsend JH, Johnson JD. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Lavin P, Mendoza-Quijano F, Hammerson GA. 2007. *Agkistrodon taylori*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. Available: www.iucnredlist.org [Accessed: 01 March 2013].

Lee JC. 1996. *The Amphibians and Reptiles of the Yucatán Peninsula*. Comstock Publishing Associates, Cornell University Press, Ithaca, New York, USA.

Lee JC, Hammerson GA. 2007. *Agkistrodon bilineatus*. In: IUCN 2012. IUCN Red List of Threatened

Species. Version 2012.2. Available: www.iucnredlist.org [Accessed 20 February 2013].

Lemos-Espinal JA, Smith HM. 2007. *Anfibios y Reptiles del Estado de Chihuahua, México / Amphibians and Reptiles of the State of Chihuahua, Mexico*. Universidad Nacional Autónoma de México, Tlalnepantla, México, and Comisión Nacional Para el Conocimiento y Uso de la Biodiversidad (CONABIO), México, DF, Mexico.

Maddison WP, Maddison DR. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75. Available: www.mesquiteproject.org [Accessed 12 March 2013].

Malhotra A, Creer S, Pook CE, Thorpe RS. 2010. Inclusion of nuclear intron sequence data helps to identify the Asian sister group of New World pitvipers. *Molecular Phylogenetics and Evolution* 54: 172–178.

Mallet J. 1995. A species definition for the Modern Synthesis. *Trends in Ecology & Evolution* 10: 294–299.

Malnate EV. 1990. A review and comparison of hemipenial structure in the genus *Agkistrodon* (sensu lato). Pp. 583–588 In: *Snakes of the Agkistrodon Complex: A Monographic Review*. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology, Number 6, Ithaca, New York, USA.

Martins EP. 1996. *Phylogenies and the Comparative Method in Animal Behavior*. Oxford University Press, New York, USA.

McCranie JR. 2011. *The Snakes of Honduras: Systematics, Distribution, and Conservation*. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology, Volume 26, Ithaca, New York, USA.

McCranie JR, Wilson LD. 2002. *The Amphibians of Honduras*. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology, Volume 19, Ithaca, New York, USA.

Outley G, Bowiel RCK, Crowe TM. 2011. The use of subspecies in the systematics of southern African white-eyes: historical entities or eco-geographic variants. *Journal of Zoology* 284: 21–30.

Padial JM, de la Riva I. 2010. A response to recent proposals for integrative taxonomy. *Biological Journal of the Linnean Society* 101: 747–756.

Parkinson CL. 1999. Molecular systematics and biogeographical history of pitvipers as determined by mitochondrial ribosomal DNA sequences. *Copeia* 1999: 576–586.

Parkinson CL, Moody SM, Ahlquist JE. 1997. Phylogenetic relationships of the “*Agkistrodon* complex” based on mitochondrial DNA sequence data. Pp. 63–78 In: *Venomous Snakes: Ecology, Evolution and Snakebite*. Editors, Thorpe RS, Wüster W, Malhotra A. Clarendon Press, Oxford, United Kingdom.

Parkinson CL, Zamudio KR, Greene HW. 2000. Phylogeography of the pitviper clade *Agkistrodon*: historical ecology, species status, and conservation of cantils. *Molecular Ecology* 9: 411–420.

Parkinson CL, Campbell JA, Chippindale P. 2002. Multigene phylogenetic analysis of pitvipers, with comments on their biogeography. Pp. 93–110 In: *Biology of the Vipers*. Editors, Schuett GW, Höggren M, Douglas ME, Greene HW. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Population Reference Bureau. 2010 World Population Data Sheet. Available: www.prb.org [Accessed: 27 January 2012].

Sasa M, Chaves G, Porras LW. 2010. The Costa Rican herpetofauna: conservation status and future perspectives. Pp. 510–603 In: *Conservation of Mesoamerican Amphibians and Reptiles*. Editors, Wilson LD, Townsend JH, Johnson JD. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Sasa M, Solórzano A. 1995. The reptiles and amphibians of Santa Rosa National Park, Costa Rica, with comments about the herpetofauna of xerophytic areas. *Herpetological Natural History* 3: 113–125.

Savage JM. 2002. *The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, between Two Seas*. The University of Chicago Press, Chicago, Illinois, USA.

Schwentner M, Timms BV, Richter S. 2011. An integrative approach to species delineation incorporating different species concepts: a case study of *Limnadopsis* (Branchiopoda: Spinicaudata). *Biological Journal of the Linnean Society* 104: 575–599.

Sibley CG. 1954. The contribution of avian taxonomy [to a symposium on subspecies and clines]. *Systematic Zoology* 3: 105–110, 125.

Smith HM, Chiszar D. 2001. A new subspecies of cantil (*Agkistrodon bilineatus*) from central Veracruz, Mexico (Reptilia: Serpentes). *Bulletin of the Maryland Herpetological Society* 37: 130–136.

Solórzano A. 2004. *Serpientes de Costa Rica: Distribución, Taxonomía, e Historia Natural / Snakes of Costa Rica: Distribution, Taxonomy, and Natural History*. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

Solórzano A, Romero M, Gutierrez JM, Sasa M. 1999. Venom composition and diet of the cantil *Agkistrodon bilineatus howardgloydii* (Serpentes: Viperidae). *Southwestern Naturalist* 44: 478–483.

Stafford PJ, Meyer JR. 2000. *A Guide to the Reptiles of Belize*. Academic Press, San Diego, California, USA.

Stafford PJ, Walker P, Edgar P, Penn MG. 2010. Distribution and conservation of the herpetofauna of Belize. Pp. 370–405 In: *Conservation of Mesoamerican Amphibians and Reptiles*. Editors, Wilson LD, Townsend JH, Johnson JD. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Stejneger L. 1899. Reptiles of the Tres Marias and Isabel Islands. *North American Fauna* 14: 63–77.

Strimple P. 1988. Comments on caudal luring in snakes with observations on this behavior in two subspecies of cantils, *Agkistrodon bilineatus* ssp. Notes from Noah, *The Northern Ohio Association of Herpetologists* 15(6): 6–10.

Strimple P. 1992. Caudal-luring: a discussion on definition and application of the term. Pp. 49–54 In: *Contributions in Herpetology*. Editors, Strimple PD, Strimple JL. Greater Cincinnati Herpetological Society, Cincinnati, Ohio, USA.

Sunyer J, Köhler G. 2010. Conservation status of the herpetofauna of Nicaragua. Pp. 488–509 In: *Conservation of Mesoamerican Amphibians and Reptiles*. Editors, Wilson LD, Townsend JH, Johnson JD. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Townsend JH, Wilson LD. 2010. Conservation of the Honduran herpetofauna: issues and imperatives. Pp. 460–487 In: *Conservation of Mesoamerican Amphibians and Reptiles*. Editors, Wilson LD, Townsend JH, Johnson JD. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Villa JD. 1984. The venomous snakes of Nicaragua: a synopsis. *Contributions in Biology and Geology, Milwaukee Public Museum* 59: 1–41.

Wiley EO. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* 27: 17–26.

Wiley EO. 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. Wiley-Interscience, New York, USA.

Wiley EO, Mayden RL. 2000. The Evolutionary Species Concept. Pp. 70–89 In: *Species Concepts and Phylogenetic Theory: A Debate*. Editors, Wheeler QD, Meier R. Columbia University Press, New York, New York, USA.

Wilson EO, Brown WL. 1953. The subspecies concept and its taxonomic application. *Systematic Zoology* 2: 97–111.

Wilson LD, Johnson JD. 2010. Distributional patterns of the herpetofauna of Mesoamerica, a biodiversity hotspot. Pp. 30–235 In: *Conservation of Mesoamerican Amphibians and Reptiles*. Editors, Wilson LD, Townsend JH, Johnson JD. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Wilson LD, Mata-Silva V, Johnson JD. 2013. A conservation reassessment of the reptiles of Mexico based on the EVS measure. *Amphibian & Reptile Conservation* 7(1): 1–47 (e61).

Wilson LD, McCranie JR. 1992. *Status of amphibian populations in Honduras*. Unpublished report to the task force on Declining Amphibian Populations. 14 pp.

Wilson LD, McCranie JR. 2004. The conservation status of the herpetofauna of Honduras. *Amphibian & Reptile Conservation* 3: 6–33.

Wilson LD, Townsend JH, Johnson JD. 2010. *Conservation of Mesoamerican Amphibians and Reptiles*. Editors, Wilson LD, Townsend JH, Johnson JD. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Zink RM. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proceedings of the Royal Society of London B* 271: 561–564.

Zweifel RG. 1960. Results of the Puritan-American Museum of Natural History expedition to western Mexico. 9. Herpetology of the Tres Marías Islands. *Bulletin of the American Museum of Natural History* 119 (article 2): 77–128.

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Taxonomy and conservation of the common cantil



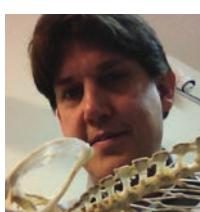
Louis W. Porras is President of Eagle Mountain Publishing, LC, a company that has published *Biology of the Vipers* (2002), *Biology of the Boas and Pythons* (2007), *Amphibians, Reptiles, and Turtles in Kansas* (2010), *Conservation of Mesoamerican Amphibians and Reptiles* (2010), and *Amphibians and Reptiles of San Luis Potosí* (2013). For many years Louis served as Vice-President and President of the International Herpetological Symposium, and during his tenure was instrumental (along with Gordon W. Schuett) in launching the journal *Herpetological Natural History*. A native of Costa Rica, Porras has authored or co-authored over 50 papers in herpetology. During the course of his studies he has traveled extensively throughout the Bahamas and Latin America. Two taxa, *Sphaerodactylus nigropunctatus porrasi*, from the Ragged Islands, and *Porthidium porrasi*, from Costa Rica, have been named in his honor.



Larry David Wilson is a herpetologist with lengthy experience in Mesoamerica, totaling six collective years (combined over the past 47). Larry is the senior editor of the recently published *Conservation of Mesoamerican Amphibians and Reptiles* and a co-author of seven of its chapters. He retired after 35 years of service as Professor of Biology at Miami-Dade College in Miami, Florida. Larry is the author or co-author of more than 290 peer-reviewed papers and books on herpetology, including the 2004 *Amphibian & Reptile Conservation* paper entitled “The conservation status of the herpetofauna of Honduras.” His other books include *The Snakes of Honduras*, *Middle American Herpetology*, *The Amphibians of Honduras*, *Amphibians & Reptiles of the Bay Islands and Cayos Cochinos, Honduras*, *The Amphibians and Reptiles of the Honduran Mosquitia*, and *Guide to the Amphibians & Reptiles of Cusuco National Park, Honduras*. He also served as the Snake Section Editor for the Catalogue of American Amphibians and Reptiles for 33 years. Over his career, Larry has authored or co-authored the descriptions of 69 currently recognized herpetofaunal species and six species have been named in his honor, including the anuran *Craugastor lauraster* and the snakes *Cerrophidion wilsoni*, *Myriopholis wilsoni*, and *Oxybelis wilsoni*.



Gordon W. Schuett is an evolutionary biologist and herpetologist who has conducted extensive research on reptiles. His work has focused primarily on venomous snakes, but he has also published on turtles, lizards, and amphibians. His most significant contributions to date have been studies of winner-loser effects in agonistic encounters, mate competition, mating system theory, hormone cycles and reproduction, caudal luring and mimicry, long-term sperm storage, and as co-discoverer of facultative parthenogenesis in non-avian reptiles. He served as chief editor of the peer-reviewed book *Biology of the Vipers* and is presently serving as chief editor of an upcoming peer-reviewed book *The Rattlesnakes of Arizona* (rattlesnakesofarizona.org). Gordon is a Director and scientific board member of the newly founded non-profit *The Copperhead Institute* (copperheadinstitute.org). He was the founding Editor of the journal *Herpetological Natural History*. Dr. Schuett is an adjunct professor in the Department of Biology at Georgia State University.



Randall S. Reiserer is an integrative biologist whose research focuses on understanding the interrelationships among ecology, morphology, and behavior. Within the broad framework of evolutionary biology, he studies cognition, neuroscience, mimicry, life-history evolution, and the influence of niche dynamics on patterns of evolutionary change. His primary research centers on reptiles and amphibians, but his academic interests span all major vertebrate groups. His studies of behavior are varied and range from caudal luring and thermal behavior in rattlesnakes to learning and memory in transgenic mice. His studies of caudal luring in snakes established methods for studying visual perception and stimulus control. He commonly employs phylogenetic comparative methods and statistics to investigate and test evolutionary patterns and adaptive hypotheses. Dr. Reiserer is an editor of the upcoming peer-reviewed book, *The Rattlesnakes of Arizona*.

Appendix 1. Morphological characters of the subspecies of *Agkistrodon bilineatus* (ingroup) and two outgroups (*A. contortrix* and *A. piscivorus*) used for character mapping analysis in this study. Unless otherwise indicated, characters are based on adult stages. *Not used in analysis.

Ingroup (cantils)

Agkistrodon bilineatus bilineatus

Upper facial stripe (lateral view): relatively broad and white.

Lower facial stripe (lateral view): relatively broad and continuous with dark pigment below; white.*

Dorsal coloration of adults: very dark brown to black; crossbands usually absent; if present, difficult to distinguish; pattern composed of small white spots or streaks.

Chin and throat: dark brown or black, with narrow white lines or markings.

Venter: dark brown or black with pale markings.*

Coloration of neonates/juveniles: some shade of brown with crossbands separated by a paler ground color; lateral edges of crossbands flecked with white.

Tail tip of neonates: bright yellow.

Sexual color dimorphism: absent.

Agkistrodon bilineatus howardgloydii

Upper facial stripe (lateral view): narrow and white; posterior portion often absent in adults.

Lower facial stripe (lateral view): broader than upper stripe, and divided into two components; stripe bordered below by dark line, followed by pale pigment to lower edge of supralabials; white.*

Dorsal coloration of adults: reddish brown or brown; pattern of dark crossbands contrasts moderately with dorsal ground color.

Chin and throat: orange yellow, bright orange, or brownish orange with few white spots.

Venter: dark reddish brown.*

Coloration of neonates/juveniles: tan to reddish orange, or reddish, with reddish brown crossbands edged intermittently with white and/or black, especially as they approach venter.

Tail tip of neonates/juveniles: banded with sequential pattern ranging from very dark gray anteriorly to paler gray toward the tip, with interspaces alternating from pale gray to white.

Sexual color dimorphism: moderate sexual color dimorphism present in sub-adults and adults.

Agkistrodon bilineatus russeolus

Upper facial stripe (lateral view): narrow and white; sometimes intermittent posterior to eye.

Lower facial stripe (lateral view): broader than upper stripe and continuous, with narrow band of dark pigment below; white.*

Dorsal coloration of adults: pale reddish brown; broad deep reddish brown to brown crossbands separated by paler areas, and strongly edged irregularly with white; crossbands remain apparent, even in older adults; laterally, centers of crossbands paler and usually contain one or two dark spots.

Chin and throat: pattern often reduced; small whitish spots or lines evident on a darker background.

Venter: approximately the median third is not patterned.*

Coloration of neonates/juveniles: pattern of brown crossbands with paler brown interspaces; banding intermittently edged with white; with growth, inner portion of crossbands turns same color as interspaces, thereby developing a highly fragmented pattern.

Tail tip of neonates/juveniles: pale gray with faint white banding; darker gray tones evident with growth.

Sexual color dimorphism: absent.

Agkistrodon taylori

Upper facial stripe (lateral view): relatively broad and white.

Lower facial stripe (lateral view): broad and continuous, and extends to lower edge of supralabials.

Dorsal coloration of adults: pronounced black crossbands separated by gray, pale brown, or lavender areas that often contain yellow-brown or orange.*

Chin and throat: bold markings, with white, yellow and or orange elements.

Venter: dark gray or black markings arranged in a somewhat checkerboard pattern.

Coloration of neonates/juveniles: strongly patterned, but with markings like those of adults but less intense.

Tail tip of neonates/juveniles: yellow (rarely, white).

Sexual color dimorphism: present in all age classes; sometimes difficult to detect in older adults that darken.

Outgroups

Agkistrodon piscivorus (outgroup 1)

Upper facial stripe (lateral view): variable in size and appearance; pale but not white.

Lower facial stripe (lateral view): relatively broad and continuous with dark pigment below.*

Dorsal coloration of adults: very dark brown to black; crossbands present in some populations, difficult to distinguish; pattern composed of small white spots or streaks.

Chin and throat: pale, cream to white.

Venter: dark brown or black with pale markings.*

Coloration of neonates/juveniles: pale ground color with pronounced bands; strong ontogenetic change

Tail tip of neonates: bright yellow.

Sexual color dimorphism: absent.

Agkistrodon contortrix (outgroup 2)

Upper facial stripe (lateral view): absent.

Lower facial stripe (lateral view): absent.*

Dorsal coloration of adults: light tan ground color; brown crossbands of varying size present.

Chin and throat: tan; typically same as ground color of face and dorsum.

Venter: pale tan with dark tan markings.*

Coloration of neonates/juveniles: ground color pale tan; similar to adults but subdued.

Tail tip of neonates: bright yellow.

Sexual color dimorphism: absent.