Historical and ecological biogeography of the genus *Crotalus* in Mexico

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The genus *Crotalus* is well represented in all biogeographic provinces including most major vegetation communities and climatic zones described for Mexico. For this reason, we use the assumptions of panbiogeography with the objective to establish a biogeographic framework for the 26 species of rattlesnakes native to Mexico. On the basis of 1472 records, 26 individual tracks derived from the distribution of each species resulted in two generalised tracks. The first is located in the Peninsula of Baja California, in the biogeographic provinces of California and Baja California, and is identified by three species (*C. enyo, C. mitchellii* and *C. ruber*). The second generalised track is located on the eastern portion of the Transmexican Volcanic Belt, the Balsas Basin, and Sierra Madre del Sur, supported by *C. ravus* and *C. intermedius*. An analysis of partition of variance found that vegetation explains the most variation in the distribution of species. Very similar results were obtained by analysis of ancestral reconstruction for biogeographic provinces, vegetation types and elevation. Our results are consistent with different climatic events during the Pleistocene, and tectonic events such as the lifting of the Sierra Madre Occidental and Sierra Madre Oriental. In addition, our results showed similarities with historical distributions of birds, mammals and beetles. Further studies of the distribution and phylogeography of other groups of reptiles with significant information gaps in their historical and current distribution are needed to shed further light on the biogeography and diversity of reptiles of Mexico.

Key words: biogeographic provinces, distribution, ecology, panbiogeography, Rattlesnakes

INTRODUCTION

The genus *Crotalus* belongs to the family Viperidae and is composed of 35 extant species (Wilson et al., 2013). Of these, 26 species are found in Mexico, where 22 species (63% of the total diversity in the genus) are endemic (Douglas et al., 2006; Wilson et al., 2013). Members of this genus occur in tropical lowland provinces of the Gulf of Mexico, the Pacific Coast, the Yucatán Peninsula, and the montane provinces of the Sierra de Chiapas and the Sierra Madre del Sur, as well as the temperate forests of the Sierra Madre Oriental, Sierra Madre Occidental and Transmexican Volcanic Belt, and arid areas of northern Mexico (the Sonoran, Baja California and California provinces) and the Mexican Plateau at elevations up to 4,000 m a.s.l. (Smith & Taylor, 1966; Klauber, 1972; Campbell & Lamar, 2004). The distribution of the genus *Crotalus* is of particular interest to biologists and geologists interpreting evidence of historical interglacial fluctuations, such as regional temperatures, and duration of glacial eras during the Pleistocene (Klauber, 1972; Douglas et al., 2006).

The ranges of extant *Crotalus* species have also previously been shown to resemble patterns observed in non-flying mammals for example (Bryson et al., 2011a,b, 2014; Douglas et al., 2006; Escalante et al., 2007), but studies that integrate distribution patterns with aspects of climate, vegetation and elevation are largely lacking so far. Panbiogeography is a tool that can be used to describe patterns of historical distribution of complex groups occurring in one or more geographical areas, where the presence of each species in different biogeographic provinces and vegetation types reflects its current ecological distribution (Klauber, 1972; Morrone, 2015). In this study, we analysed the historical and ecological relationships of the 26 *Crotalus* species of Mexico, using the variance partitioning method and an analysis of ancestral character state reconstruction (Morrone et al., 2002).

MATERIAL AND METHODS

Sources of information
We obtained geographical records for members of the genus *Crotalus* from a database of amphibians and
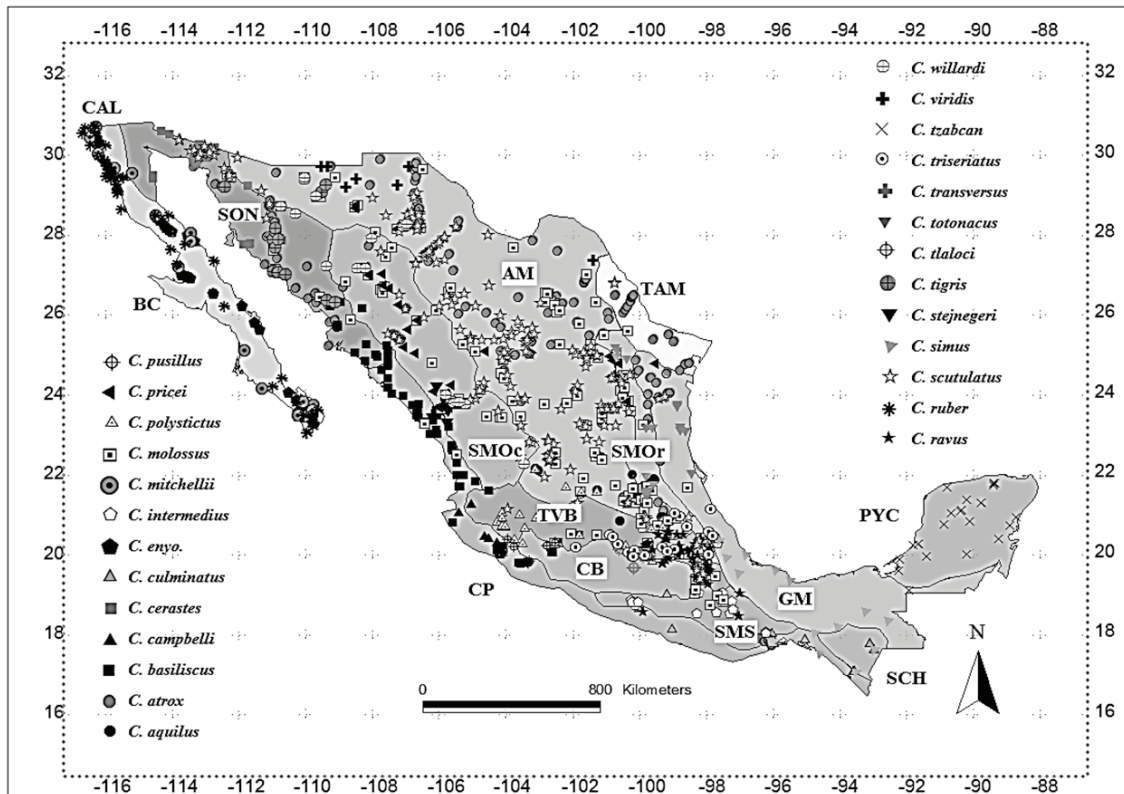
Fig. 1. General map of all species of rattlesnake distributed in Mexico. CAL=California, BC=Baja California, SON=Sonora, AM=Mexican Plateau, TAM=Tamaulipeca, SMOc=Sierra Madre Occidental, SMOr=Sierra Madre Oriental, TVB=Transmexican Volcanic Belt, CB=Balsas Basin, SMS=Sierra Madre del Sur, CP=Pacific Coasts, GM=Gulf of Mexico, PYC=Península of Yucatán, SCH=Sierra de Chiapas.

reptiles of Mexico managed by one of the authors of this study (ARB). The database provides information on all 26 species of the genus *Crotalus* occurring in Mexico (Table 1; Campbell & Lamar, 2004; Wilson et al., 2013). In addition, we consulted the database of the Global Biodiversity Information Facility (http://www.gbif.org/species; GBIF, 2008) for additional records for 11 of 26 species. All records were verified and assessed by consulting existing literature (Smith & Taylor, 1966; Klauber, 1972; Campbell & Lamar, 2004), and ambiguous records were removed.

Panbiogeographic analysis
Panbiogeographic analysis is an approach to improve our understanding of evolutionary processes underlying patterns of distribution of biological groups with wide distributions (Craw et al., 1999; Morrone, 2015). While the approach is not without criticism (e.g., Waters et al., 2013), panbiogeographic analysis provides an approach that emphasizes the spatial and geographical dimension of biodiversity based on vicariant distributions (Morrone, 2015). Combined with other methods (e.g., phylogenetic analysis: reconstructing ancestral states; ecological: variance partition), it allows for a better understanding of distribution patterns linked with evolutionary processes (Morrone & Crisci, 1995; Szumik & Goloboff, 2004; Morrone, 2015).

Our methodology was as follows: 1) Construction of individual tracks, which consists of the unification of localities for each species by lines of low geographic proximity, using the ArcView 3.2 program (ESRI, 1998); 2) Obtaining generalised tracks, which occur when there is a geographic coincidence in the direction of two or more individual tracks. In order to do so, we applied an endemicity analysis following Fernández-Badillo et al. (2014), assessing the consistency in topology, structure and direction of each individual track using the program DM/VNDM (Goloboff, 2015); 3) Identification of the nodes, i.e., points where two or more generalised traces coincide that represent a complex area in which ancestral biota and geological fragments interrelated in space and time converge (Grehan, 2011; Morrone, 2015), and we used the biogeographic regionalisation of Mexico proposed by Morrone et al. (2002) to locate each record in one or several biogeographic provinces.

Ecological analysis
Based on information obtained from Klauber (1972) and Campbell & Lamar (1989, 2004), of 26 species of the *Crotalus* genus distributed in different vegetation types in Mexico, we built a binary matrix of species for 12 vegetation types. In addition, we located the georeferenced data for each species on the digital map of climates (INEGI 1:250 000) provided by BIOTICA-CONABIO (http://www.conabio.gob.mx/biotica5/). We recorded the climate type for each georeferenced datum, and we built a binary matrix of species for 9 climate types. We assigned a 1 if the species was

Biogeography of the genus Crotalus

Table 1. Species of *Crotalus* genus in different biogeographic provinces, according to the regionalization by Morrone et al. (2002). CAL=California, BC=Baja California, SON=Sonora, AM=Mexican Plateau, TAM=Tamaulipeca, SMOc=Sierra Madre Occidental, SMOr=Sierra Madre Oriental, TVB=Transmexican Volcanic Belt, CB=Balsas Basin, SMS=Sierra Madre del Sur, CP=Pacific Coasts, GM=Gulf of Mexico, PYC=Península of Yucatán, SCH=Sierra de Chiapas.

Species	CAL	BC	SON	AM	TAM	SMOc	SMOr	TVB	CB	SMS	CP	GM	PYC	SCH
Crotalus aquilus				X			X	X						
C. atrox			X	X	X	X	X			X		X		
C. basiliscus				X		X				X	X			
C. campbelli								X						
C. cerastes	X		X											
C. culminatus								X	X	X	X	X	X	X
C. enyo	X	X	X											
C. intermedius				X				X	X			X		
C. mitchellii	X	X	X			X								
C. molossus			X	X	X	X	X	X	X					
C. polystictus				X		X		X						
C. pricei			X	X	X	X	X							
C. pusilus								X						
C. ravus								X	X	X				
C. ruber		X												
C. scutulatus			X	X		X	X	X						
C. simus										X		X		X
C. stejnegeri						X								
C. tigris			X			X								
C. tlaloci								X						
C. totonacus					X		X					X		
C. transversus								X						
C. triseriatus				X			X	X	X					
C. tzabcan													X	
C. viridis		X		X		X								
C. willardi			X			X								

present in a certain vegetation type and climate, and a 0 if species was not present. In addition, we built a species matrix by elevation and another one by latitude-longitude. To construct the data matrices we considered that the species were placed always in the rows and the environmental variables in the columns. To analyse these data, we used a redundancy analysis of variance to identify the most important environmental variables based on georeferenced presence-absence records of *Crotalus* species in the biogeographic provinces proposed by Morrone et al. (2002). This matrix (species by biogeographic provinces) was used as the dependent variable, and environmental variables served as independent variables and covariates (Legendre et al., 2011). The distribution of variance was assessed using the canonical correspondence analysis (CCA) test using CANOCO v. 4.56 (Ter Braak & Smilauer, 2002) for Windows.

Ancestral character state reconstruction
In order to establish species distribution patterns by biogeographic provinces, vegetation types, and elevation, we constructed a phylogeny for the genus *Crotalus* based on ancestral character states using the Mesquite Program v. 2.5 (Maddison & Maddison, 2009). Ancestral character states were calculated using maximum parsimony, and a phylogeny for *Crotalus* was obtained from studies by Campbell & Lamar (2004), Pyron et al. (2013), and Bryson et al. (2014).
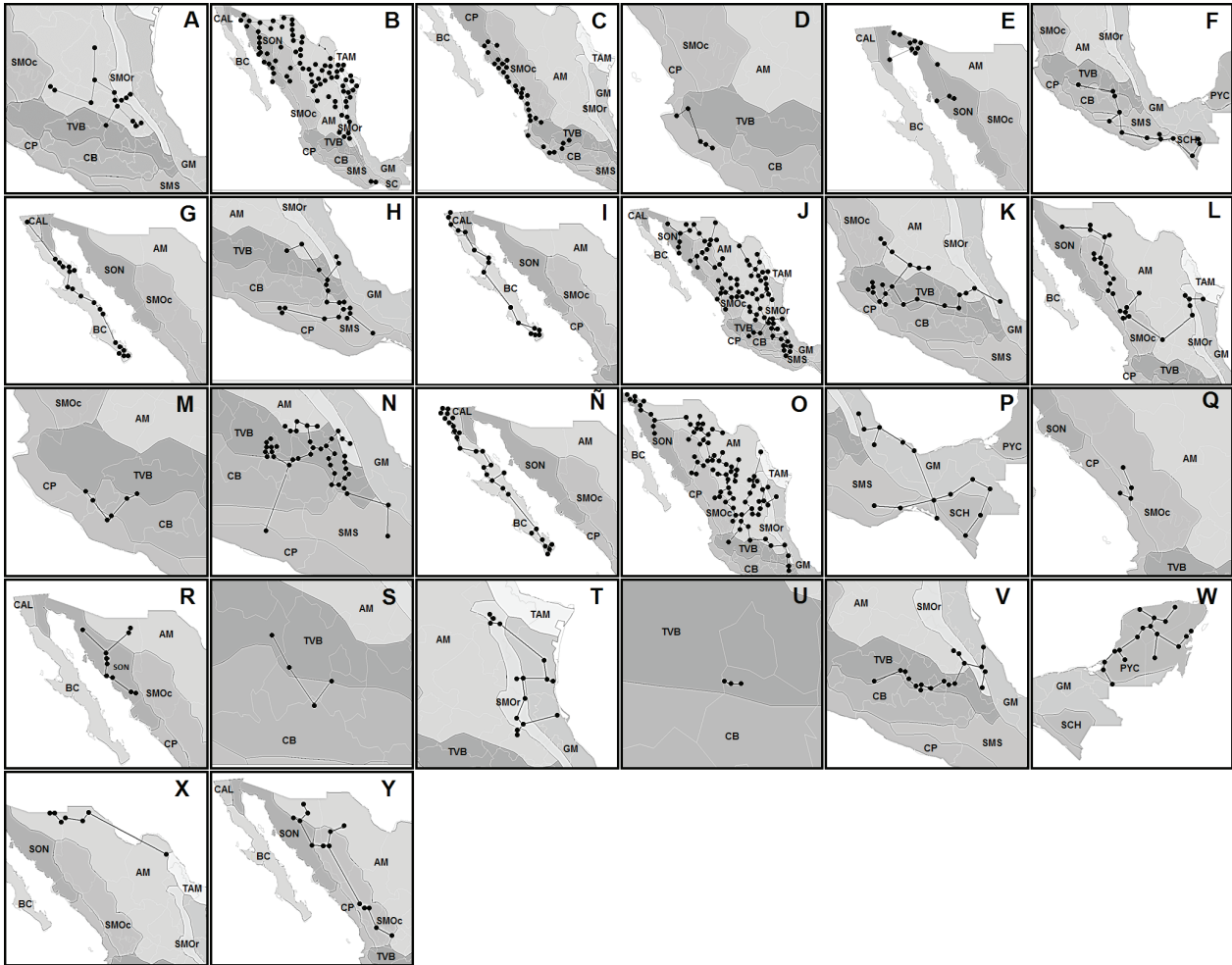
Fig. 2. Individual tracks for species of the *Crotalus* genus distributed in Mexico. A) *C. aquilus*, B) *C. atrox*, C) *C. basiliscus*, D) *C. campbelli*, E) *C. cerastes*, F) *C. culminatus*, G) *C. enyo*, H) *C. intermedius*, I) *C. mitchellii*, J) *C. molossus*, K) *C. polystictus*, L) *C. pricei*, M) *C. pusillus*, N) *C. ravus*, Ñ) *C. ruber*, O) *C. scutulatus*, P) *C. simus*, Q) *C. stejnegeri*, R) *C. tigris*, S) *C. tlaloci*, T) *C. totonacus*, U) *C. transversus*, V) *C. triseriatus*, W) *C. tzabcan*, X) *C. viridis*, Y) *C. willardi*.

RESULTS

Panbiogeographic analysis: Individual and generalised tracks

In this study we obtained 1472 records for all 26 species of the genus *Crotalus* in Mexico, and used these records to build 26 individual tracks (Figs. 1 and 2). We excluded the species *C. catalinensis*, *C. angelensis*, *C. muertensis* and *C. tortuguensis* because they are endemic to small islands. We identified two consensus areas of endemism analogous to generalised tracks (Fig. 3). The first generalised track is located in the biogeographic provinces of California and Baja California. This generalised track is formed by the overlapping of three tracks corresponding to the species *C. enyo*, *C. mitchellii*, and *C. ruber* (Fig. 3A). These species are adapted to desert environments, but can also be found in chaparral, desert scrub and rocky areas.

Generalised track 2 is located in the eastern Transmexican Volcanic Belt, Balsas basin, and central Sierra Madre del Sur. This generalised track is comprised by the superimposition of two individual tracks that correspond to *C. ravus* and *C. intermedius* (Fig. 3B). These species inhabit pine-oak forest and cloud forest,

although *C. ravus* also has been found in tropical dry forest, tropical deciduous forest, mesquite and desert scrub.

Ecological analysis: Redundancy analysis

The redundancy analysis revealed that vegetation represents 73.5% (2.17 of the variation is explained for vegetation; Monte Carlo test, $F=2.69$, $p=0.0010$) of the variation in the distribution of the 26 species of *Crotalus* (total inertia of 2.95 in the presence-absence matrix of the species present in the analysed provinces). Climate explained 66.1% of variation (1.95 of the variation; Monte Carlo test, $F=0.75$, $p=0.67$), followed by elevation with 57.2% (1.69 of variation; Monte Carlo test, $F=1.03$, $p=0.40$). Latitude and longitude together explained 18.6% (0.55 of variation; Monte Carlo test, $F=2.31$, $p=0.0050$). The proportions do not add to 2.95 or 100% because none of the variables examined was independent from the others.

Ancestral character state reconstruction

The analysis based on ancestral traits for rattlesnake species in different biogeographic provinces showed that most species exhibit a distribution in montane
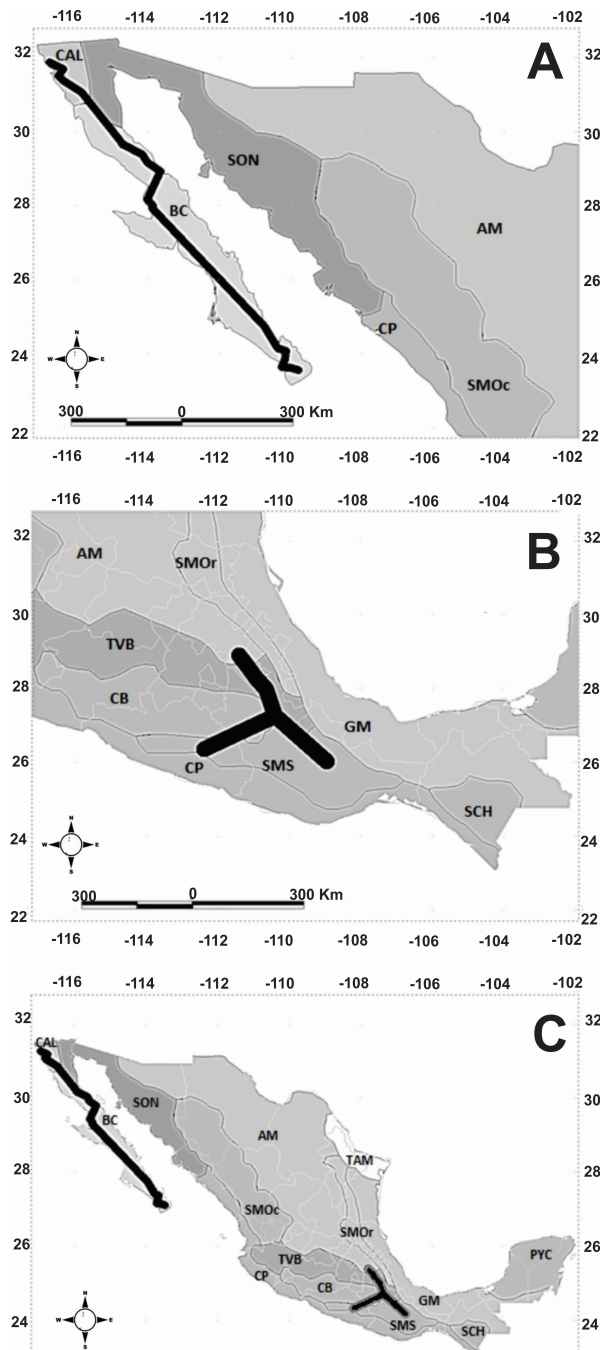
Fig. 3. Generalised tracks. A) Generalised track 1 formed by the provinces of California and Baja California, B) generalised track 2 formed by the biogeographic provinces of Transmexican Volcanic Belt, Balsas Basin, and central Sierra Madre del Sur, and C) both tracks generalised.

temperate environments (e.g., the Sierra Madre Occidental: Fig. 4J), and arid and semiarid zones (e.g., the Mexican Plateau, Transmexican Volcanic Belt, and Sonora province: Figs. 4A, F, and M), mainly for the species *C. aquilus* and *C. triseriatus* (Fig. 4A-N). Likewise, *C. tzabcan*, *C. simus* and *C. culminatus* have their distribution in Peninsula of Yucatán, Sierra de Chiapas, and province of Gulf of Mexico (Fig. 4G, H and I).

According to vegetation types (Fig. 5), most species are represented better in montane temperate environments such as oak-pine, pine and pine-oak forests (Figs. 5A, C

and D), as compared with other environments (Fig. 5A-H). Thirteen species occur at medium elevations (Fig. 6), eight species at low elevations, and five species in high elevations (species of *triseriatus* group; Fig. 6).

DISCUSSION

Available information in the pioneering studies by Smith & Taylor (1966) and Klauber (1972) on distribution of the Mexican species of *Crotalus*, together with panbiogeographic analysis developed in this study show the affinity of members of this genus with arid regions, and a distribution centered in northern Mexico and the southern United States (Douglas et al., 2006; Bryson et al., 2014). The generalised tracks shown in this study provide insights into the distribution historical and current of rattlesnakes in Mexico.

There are biogeographic regions, such as California and Baja California, with few records of species of the *Crotalus* genus; however, despite the scant information, both provinces form the first generalised track for this study, which is supported by the distributions of *C. enyo*, *C. mitchellii* and *C. ruber*, showing parallels with other generalised tracks obtained for mammals (Findley, 1969; Alroy et al., 2000; Hafner & Riddle, 2005), birds (Álvarez-Mondragon & Morrone, 2004), and beetles (Morón & Márquez, 2012). These similarities allow us to understand better the biotic consistency in the distribution of these groups during the possible vicariance events that occurred when the Chihuahuan and Sonoran Deserts were formed in the Pleistocene, regions considered to be centres of evolution and diversification (Hubbard, 1973; Riddle & Hafner, 2006). Both generalised tracks coincide broadly as mentioned by Murphy (1983), Pook et al. (2000), and Douglas et al. (2006), who pointed out that most species of *Crotalus* with distributions in the arid zones of California and Baja California evolved by vicariance events. The above confirms the hypothesis by Riddle & Hafner (2006), which establishes that the deserts from northern Mexico are the sites of origin of a complex biota where the Sea of Cortes and Sierra Madre Occidental originated in the late Miocene and Pliocene, leading to arid sites with high species richness of squamate reptiles (Savage, 1960; Douglas et al., 2006).

The convergence of individual tracks into the first generalised track, together with vegetation types and their distribution in the phylogeny, allows us to generate hypotheses regarding historical and ecological distributions (Klauber, 1972). This could help explain why vegetation is more related with variation in species distributions, aside from representing one of the three dimensions of the ecological niche of any species (Pianka & Huey, 1978). The second generalised track is more closely associated with the distribution observed in birds (generalised tracks 2 and 6; Álvarez-Mondragon & Morrone, 2004), and with the generalised track "septentrional" by Morrone & Márquez (2003) in beetles. This suggests that these species are representatives of an ancestral biota widely distributed throughout arid and semiarid areas of central Mexico. Vicariance
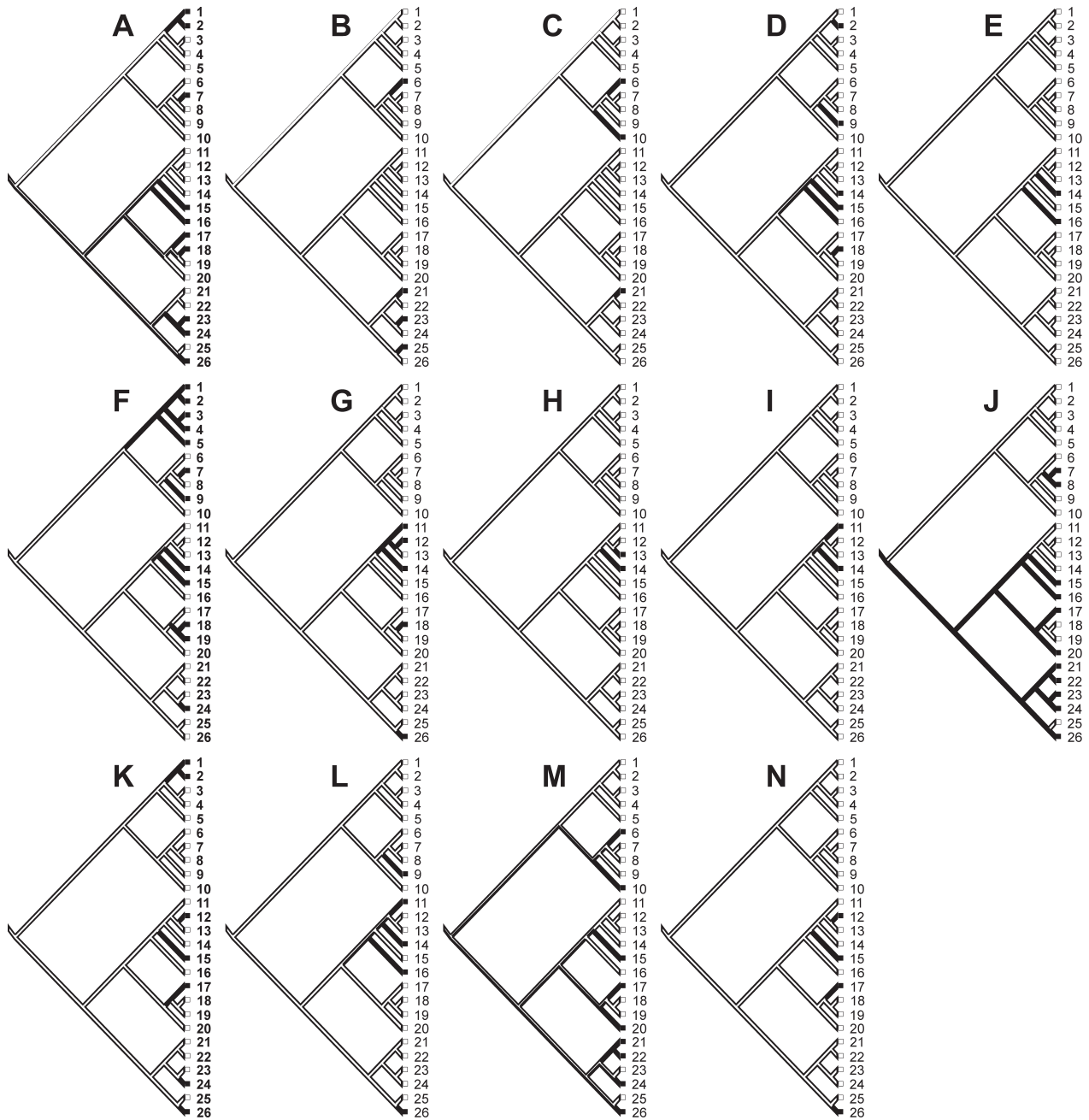
Fig. 4. Ancestral character state reconstruction in species of *Crotalus* genus (1=*C. aquilus*, 2=*C. triseriatus*, 3=*C. tlaloci*, 4=*C. pusillus*, 5=*C. campbelli*, 6=*C. enyo*, 7=*C. polystictus*, 8=*C. stejnegeri*, 9=*C. ravus*, 10=*C. cerastes*, 11=*C. simus*, 12=*C. totonacus*, 13=*C. tzabcan*, 14=*C. culminatus*, 15=*C. molossus*, 16=*C. basiliscus*, 17=*C. pricei*, 18=*C. intermedius*, 19=*C. transversus*, 20=*C. willardi*, 21=*C. mitchellii*, 22=*C. tigris*, 23=*C. viridis*, 24=*C. scutulatus*, 25=*C. ruber* and 26=*C. atrox*) for biogeographic provinces (A=Mexican Plateu, B=Baja California, C=California, D=Balsas Basin, E=Pacific Coasts, F=Transmexican Volcanic Belt, G=Gulf of Mexico, H=Península of Yucatán, I=Sierra de Chiapas, J=Sierra Madre Occidental, K=Sierra Madre Oriental, L=Sierra Madre del Sur, M=Sonora, N=Tamaulipan).

events (tectonic shifts, mountain and lake formation, climate change; Grehan, 2011) that gave rise to current distributions can be compared with distributions from other groups, using climatic data, elevation, phylogeny, and geoposition (latitude and longitude, Grehan, 2011).

In addition, panbiogeographic analysis of *Crotalus* species supports the idea that geological and paleoclimatic events fragmented species distributions and contributed to the formation and/or diversification of new species, and helps to explain not only the high species richness, but also the high number of endemic

species from the deserts of northern Mexico. In a biogeographic context, patterns of geographic variation of the species of the genus *Crotalus* from Mexico is related to the vegetation types, climate, elevation, and latitude-longitude, and is consistent with what López-González et al. (2012) observed about the distribution of Mexican bats. The foregoing indicates that the distribution is a result of variation at the landscape level (Klauber, 1972) and that climate shapes vegetation types, which influence the distribution of reptile species. Ord et al. (2010) and Ochoa-Ochoa &
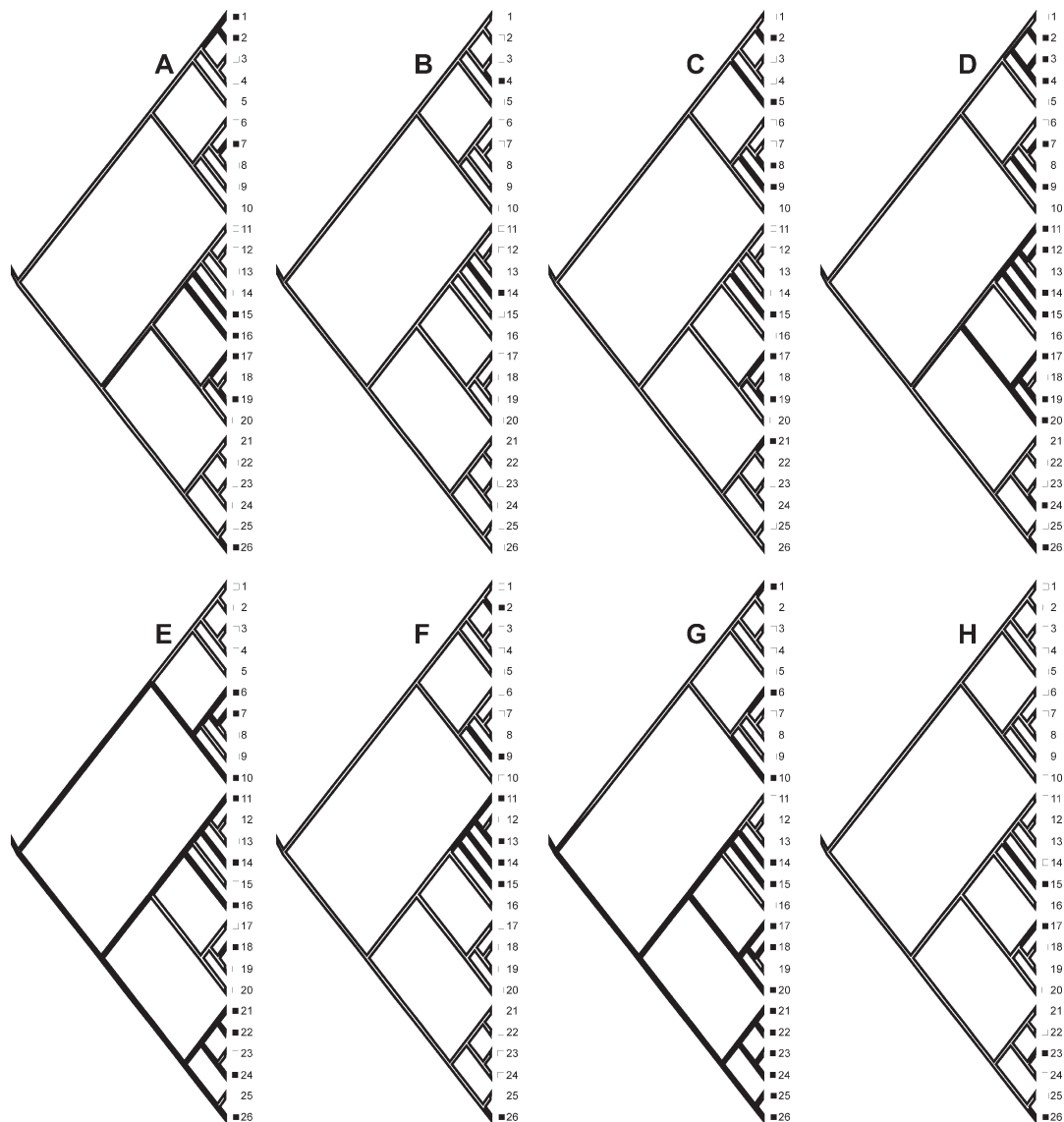
Fig. 5. Ancestral character state reconstruction in species of *Crotalus* (numbers represents the species, see Fig. 1 and 4 caption) for vegetation types (A=oak forest, B=cloud forest, C=pine forest, D=pine-oak forest, E=tropical deciduous forest, F=tropical evergreen forest, G=xeric shrub, H=pastureland).

Fig. 6. Ancestral character state reconstruction in species of *Crotalus* (numbers represents the species, see Fig. 1 and 4 caption) for elevation.

Whittaker (2014) found that temperature, humidity and vegetation types are involved in the composition and structure of species assemblages at the local and landscape level (e.g., the subspecies of *Crotalus viridis* mostly distributed in the central and southern parts of the United States of America; Pook et al., 2000). The observed range borders of *Crotalus* species are defined as the product of interactions among physiology, phenology, reproduction, behaviour and predation within the habitats they occupy (Klauber, 1972; Prugh et al., 2008).

Elevation and latitude-longitude, explaining a smaller proportion of the variation in the distribution of Mexican rattlesnakes, represent environmental conditions that restrict the distribution of species in mountains that can be considered as areas of endemism promoting speciation (Bryson et al., 2014). Species distribution is non-random; it follows patterns that respond to different environmental factors; in addition to the environmental factors analysed in this study, such as habitat fragmentation, over harvesting and the

introduction of exotic species can further affect species distributions (Wilson et al., 2013).

One of the major questions in biogeography is why some clades occupy different geographic areas than do others (Wiens & Graham, 2005). The phylogeny used in this study indicates that most Mexican *Crotalus* species occupy arid or semiarid environments, as well as temperate and tropical zones similar to other regions from Central and South America (see e.g. Wüster et al., 2005). For example, *C. durissus* has a wide but discontinuous distribution similar to other species such as *C. simus* and *Bothrops asper*. Wüster et al. (2005) identified that the *Crotalus durissus* complex shows an ancient cladogenesis originated in central Mexico during the Miocene and early Pliocene, revealing a scenario of progressive colonisation from Mexico to South America. On the other hand, Webb & Rancy (1996) and Burnham & Graham (1999) suggested that the colonisation pattern of the *C. durissus* complex is related to the climatic and vegetational changes during the late Pliocene and Quaternary.

The fossil record and phylogeographic analysis suggest biogeographical relationships among rattlesnakes distributed in Mexico, the United States of America and Canada with a Nearctic origin (*C. triseriatus*, *C. intermedius*; Bryson et al., 2011a,b,c; Douglas et al., 2006; see also Klauber, 1972). Campbell & Lamar (2004) mentioned that geographic isolation of the genus occurred during the Pliocene in the highlands of Mexico, mainly in Sierra Madre Oriental, Sierra Madre Occidental and Sierra Madre del Sur, explaining the high species richness in temperate mountains environments of central and north of Mexico, consistent with our results (Klauber, 1972; Campbell & Lamar, 2004).

McDonald (1993) mentioned that similarities in rattlesnake species distributions with those of other snake clades reflect a shift of vegetation from mountain environments toward less highlands during glacial periods, causing a merging of the Mexican Plateau with areas of the Chihuahuan Desert, leading to the origin of species such as *C. intermedius* (Bryson et al., 2011a) and *C. triseriatus* (Bryson et al., 2011b), and harbouring species such as *C. cerastes*, *C. tigris*, *C. ruber* and *C. mitchellii* (Bryson et al., 2011c), revealing vicariance during the Pliocene and late Miocene, allopatric segregation induced by the climatic changes during the Pliocene, and genetic diversification as a result of climatic changes during late Pleistocene (Douglas et al., 2006).

Current distributions of species reflect their evolutionary history, leading to niche conservatism (Wiens et al., 2010). Only certain lineages of species will occupy particular environments that over time have the potential to lead to diversification events, as is the case for the *C. triseriatus* and *C. durissus* groups (Bryson et al., 2014).

Further work is required to confirm the existence of vicariant historical events in the early Pleistocene and Miocene that led to the radiation of *Crotalus* on the American mainland (Klauber, 1972; Campbell & Lamar, 2004).

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