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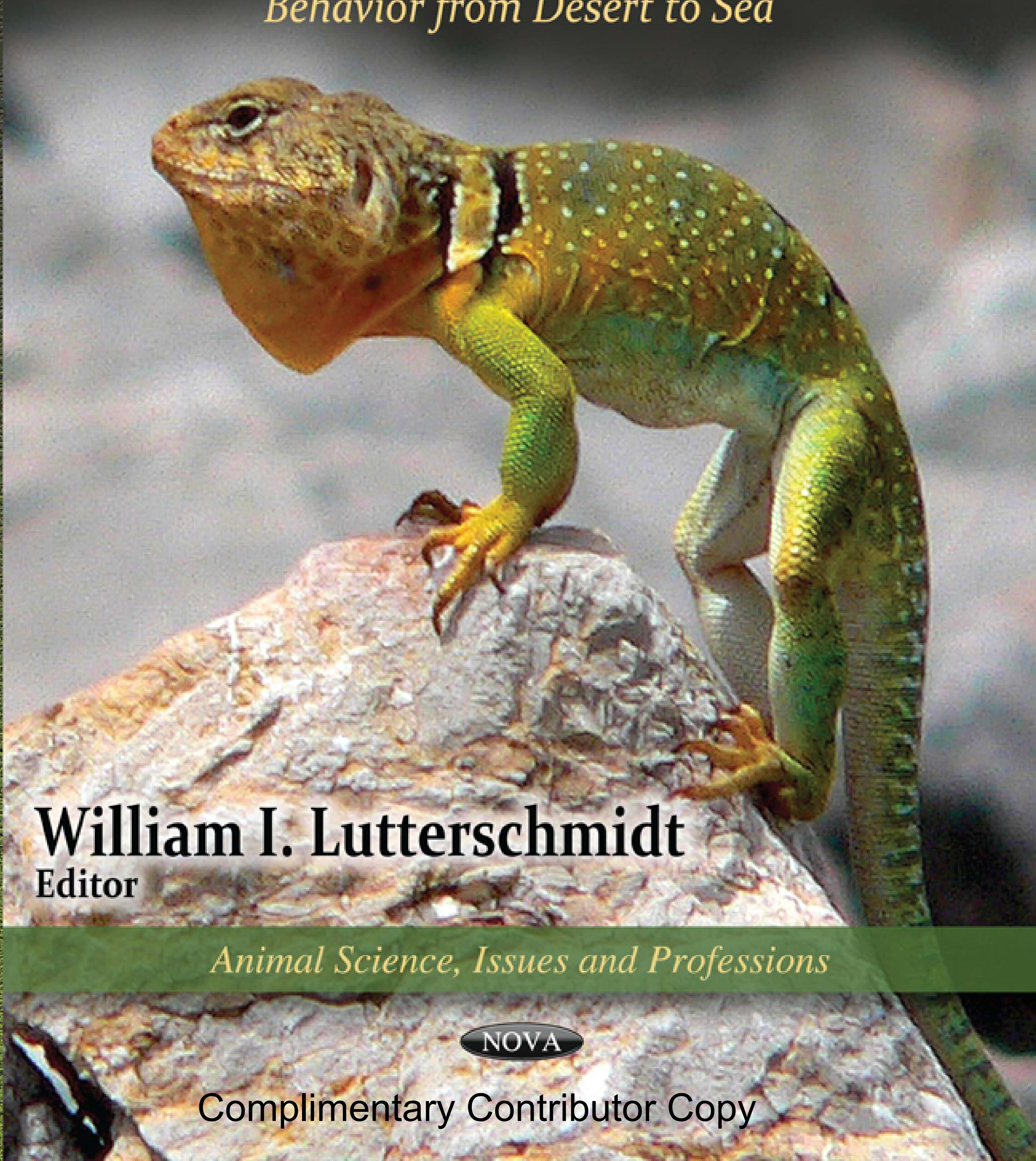

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INVESTIGATIONS OF ECOLOGY, PHYSIOLOGY, AND BEHAVIOR FROM DESERT TO SEA

WILLIAM I. LUTTERSCHMIDT, PH.D.
EDITOR

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Chapter 6

REPTILE TRACKS: AN INDICATOR FOR IDENTIFYING AREAS OF HIGH DIVERSITY IN ARID ZONES OF MEXICO

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ABSTRACT

The arid zones of México have an important species number of amphibians and reptiles, with both restricted and wide distribution. These characteristics have allowed the identification of areas of endemism in the country within greater geographic areas such as the Neartic and Neotropical regions. In central Mexico, the arid and semiarid environments are primarily located within the Transmexican Volcanic Belt (TVB), Sierra Madre Oriental (SMO), Mexican Plateau (MP), and Chihuahuan Desert Region (CDR) provinces. These geographic areas are highly regarded for the study of biogeography and conservation of many biological groups. We conducted an analysis of biogeographical tracks through panbiogeography and Parsimony Analysis of Endemism (PAE) to determine areas where distribution of several groups of reptiles. With the development of a data matrix including a total of 1690 records that belong to 106 reptile species that have their distribution in the arid provinces mentioned above, we obtained a parsimonious cladogram which reveals the existence of two main clusters or generalized tracks, one generated with species from SMO and MP, and the second cluster with species from CDR and TVB. With the development of these generalized tracks we were able to detect a panbiogeographic node, and give a possible explanation for the historical distribution of the different species of reptiles from different arid zones of central Mexico. Our results showed great similarities in the distribution of reptiles of the arid environments of Mexico compared to other studies previously published by using other biological groups. Finally, in order to know the accuracy of boundaries and the biogeographic history of arid zones from Mexico, it is desirable to analyze the distribution of several biological groups in a consistent pattern.

Keywords: Reptiles, Arid zones, Panbiogeography, nodes, Mexico

INTRODUCTION

In 1958, Croizat proposed the method of identifying generalized tracks (Panbiogeography) as a method for describing and understanding the biogeographic history of different biological groups in a spatio-temporal context, which could lead in turn, to the detection of various important areas of endemism with a complex biota (Morrone 2001a, Morrone 2003). These areas are traditionally considered as important and interesting units for conservation biology because they represent a complex of stories involving several biological groups (Giokas and Sfenthourakis 2008). In addition, Croizat (1958) determined that the distribution of different biological groups that are either highly philopatric or have high vagility can generate distribution patterns that can be important in time and space. Therefore, panbiogeography is a useful tool to describe distribution patterns from a historical perspective based in three methodological dimensions: form (e.g., morphology, molecular attributes, functional and ecological), space (distribution area), and time. Under these three parameters, Croizat’s (1964) achievement discerns the current distribution of various ancestral biotas from a historical-ecological perspective. However, De Candolle (1820) had previously distinguished for the first time the meaning between ecological and historical biogeography, referring mainly to the causes that act in the past and currently, and how they allowed the distribution of different biological groups such as reptiles (Smith 1941, Smith and Taylor 1966, Wilson et al. 2010).

Croizat´s (1964) panbiogeography recognizes areas of high diversity with geomorphological features, vegetation types, geological and climatic evidence, which allowed the basis to generate different biogeographic regionalization analyses in diverse biogeographic provinces of Mexico, such as arid zones (Smith 1941, Morrone 2001a). Although the panbiogeographic or tracks method is simple, it allows the generation of important information for understanding dispersion of species, which consists in locating several points of reference of the distribution of one species on a map, and these points are linked through lines and follow the minimum distance among these points (minimum routing; Morrone 2004). When the points are all linked, the direction and extent of the individual traces are identified to locate generalized tracks. These were considered by Morrone (2001a, 2001b) as ancestral geobiotic fragments (a priority for conservation), and when two or more generalized tracks they overlap form a panbiogeographic node, which is interpreted as a tectonic convergence zone and/or biotic where was originated high diversity and species richness (Craw 1988, Morrone 2004). The latter sites represent biologically and geologically complex areas (Morrone 2004). Although panbiogeography has been an effective method, it has also been subjected to evaluations. Morrone and Crisci (1993) reexamined the principles and methods of the panbiogeography and implemented the Parsimony Analysis of Endemism (PAE) as an auxiliary analysis to panbiogeography, although still there is no formal distinction between the historical and ecological biogeography components (Craw 1989, Cracraft 1991, Morrone 1994). With PAE assistance tools, we can identify important areas for conservation, mainly by determining the species number present in them. These areas are described as areas of high diversity and containing endemic species. By using these two methods (panbiogeography and PAE), we tried to identify potential areas of high species richness and endemism, mainly for central México. We identified four biogeographic provinces, Transmexican Volcanic Belt (TVB), Mexican Plateau (MP), Chihuahuna Desert

Region (CDR), and Sierra Madre Oriental (SMO), and considered these as areas of potential distribution for several species of reptiles with different affinities (Neartic and Neotropical; Figure 1). CDR and the northern part of the SMO belong to the Neartic Region, and TVB and MP belong in part to the Mexican Transition Zone (Escalante et al. 2003, Morrone 2005).

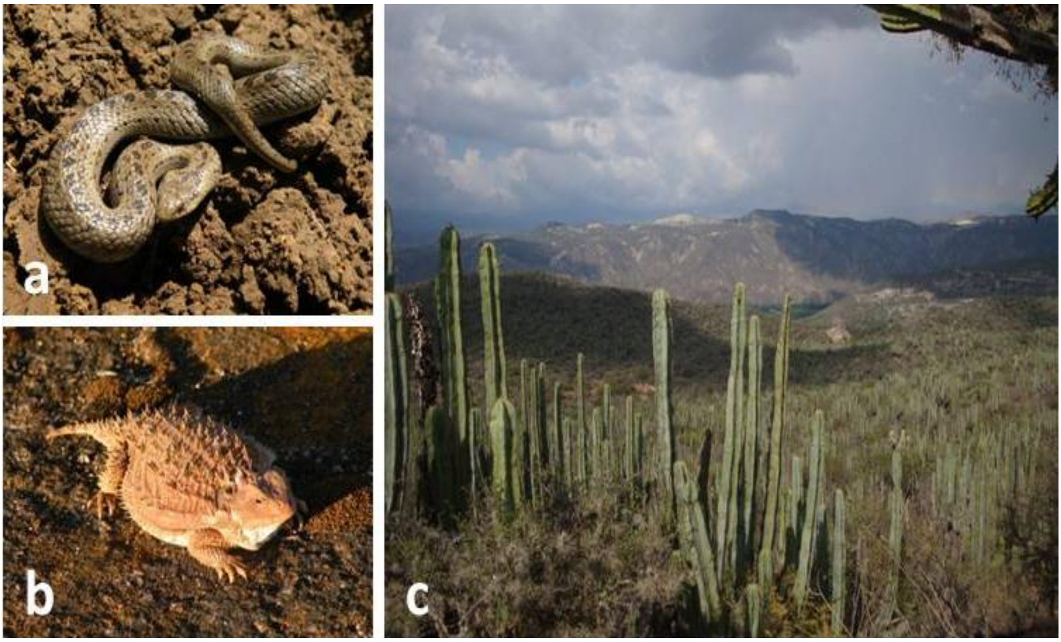

Figure 1. Shows two of species that have their distribution in arid zones of México. (a) *Conopsis lineata*, (b) *Phrynosoma orbiculare* and (c) submontane forest from Reserva de la Biosfera Barranca de Metztitán, Hidalgo, México. Photos (a) and (b) taken by Uriel Hernández-Salinas, and (c) taken by Melany Aguilar.

In consideration of the above information, the aim of this chapter is to identify areas of high species richness by using the distribution of reptiles from arid zones under the methodology of both methods.

RESEARCH METHODS

We used a database with more than 50,000 records generated by chapter author A. Ramirez-Bautista (unpubl data). Records and species number from the dabase came from several scientific collections from México and USA (Table 1). From this database, we used the records of the species only from arid zones that belong to some states that are in the analyzed provinces (Table 2), and each record was mapped using Geographic Information System (GIS) and Arcview® 3.2 software (ESRI 1999). Additionally, individuals tracks from some species with wide provincial distribution were assessed with GIS (Figures 2 and 3).

Table 1. Records used in this study from Mexican and foreign scientific collections

Collection names	**Acronym**	**Country**
Colección Nacional de Anfibios y Reptiles	CNAR-UNAM	Mexico
Instituto Politécnico Nacional	ENCB-IPN	Mexico
Instituto Tecnológico Agropecuario de Hidalgo	ITAH	Mexico
The University of Michigan Museum of Zoology	UMMZ	Estados Unidos
The University of Kansas Museum of Natural History	KU	Estados Unidos
American Museum of Natural History, Department of Herpetology	AMNH	Estados Unidos
Carnegie Museum of Natural History Collection of Herpetology	CMNH	Estados Unidos
Collection of Herpetology, Museum of Comparative Zoology, Harvard University	MCZ	Estados Unidos
Collection of Herpetology Museum Zoology Louisiana State University	LSUMZ	Estados Unidos
Collection of Herpetology, National Museum of Natural History, Smithsonian Institute.	USNMNH	Estados Unidos
Collection of Herpetology, University of Illinois Museum of Natural History	UIMNH	Estados Unidos
Collection of Herpetology, Zoology Section of Los Angeles Country Museum of Natural History	LACM	Estados Unidos
Escuela Nacional de Estudios Profesionales Iztacala, Colección Herpetológica	ENEPI	Mexico
Field Museum of Natural History, Division of Amphibians and reptiles	FMNH	Estados Unidos
Oklahoma Museum of Natural History University of Oklahoma, Collection Herpetology	OMNH	Estados Unidos
Texas Cooperative Wildlife Collection, Texas A and M University, Collection Herpetology	TCWC	Estados Unidos
Texas Natural History Collection of Herpetology	TNHC	Estados Unidos
University of California at Berkeley Museum of Vertebrate Zoology, Collection of Herpetology	MVZ	Estados Unidos
University of Texas at Arlintong, Collection of Vertebrates	UTA	Estados Unidos

We followed the proposal by Delgado and Márquez (2006), which consists in locating the species in each biogeographic province considering the locality (coordinates, elevation, vegetation type, state and municipality). Records that lacked this kind of information were excluded to avoid biased results. In order to know the limits for each biographic province in which the individual tracks are shown (Figure 4), we used a modified proposal of biogeographic regionalization for México by Espinosa-Organista et al. (2000). Generalized tracks from species of reptiles of the four biogeographic provinces were recognized with PAE (Craw et al. 1999, Luna-Vega et al. 2000, Morrone and Márquez 2003). PAE generates a set of nested areas that are constantly sharing common biota, and it is where common historical causes can be hypothesized to explain the cluster of analyzed areas (Morrone et al. 1999, Luna-Vega and Alcántara 2002).

Table 2. States that comprise each of the analyzed provinces

Provinces			
CDR	**SMO**	**TVB**	**MP**
Chihuahua*	San Luís Potosi*	Colima	Zacatecas*
Coahuila	Coahuila	Distrito Federal*	San Luís Potosi*
Durango*	Hidalgo*	Guanajuato*	Guanajuato*
Nuevo León	Nuevo León	Jalisco	Chihuahua
San Luís Potosi*	Veracruz	Hidalgo	Jalisco
Tamaulipas	Puebla	Morelos	Nuevo México
Zacatecas*	Querétaro*	Veracruz	Durango
		Puebla	Tlaxcala*
		Michoacán*	Puebla
		Querétaro*	Coahuila
		Tlaxcala*	

* Represents states with records of reptiles from arid zones used in this chapter. CDR: Chihuahuan Desert Region, MP: Mexican Plateau, SMO: Sierra Madre Oriental, TVB: Transmexican Volcanic Belt.

For PAE application, we created a matrix with records from different reptile species present in each of the four biogeographic provinces (Alzate et al. 2008). The columns of the data matrix represent each of the species and the rows represent the regions or areas. In addition, we added (to the data matrix) a column and row of zeros to represent area and hypothetical species allowing us to root the cladogram (Alzate et al. 2008). These cladograms were obtained by the Nona program (Goloboff 1993) and WinClada® 0.9.99 (Nixon 2000); the latter program was also used to construct the cladograms. To run the data matrix, a heuristic search was performed by using multiple search strategy TBR + TBR and the search parameters of 1000 trees for analysis, 100 trees per replicate and 10 replicates. Thus, the cladogram robustness was determined by a test of “bootstrap” by using 1000 replicates. The results of this test are expressed as a percentage of the reliability of the nodes of the cladograms and the relationships among species for each province (Asiain 2005, Morrone 2005).

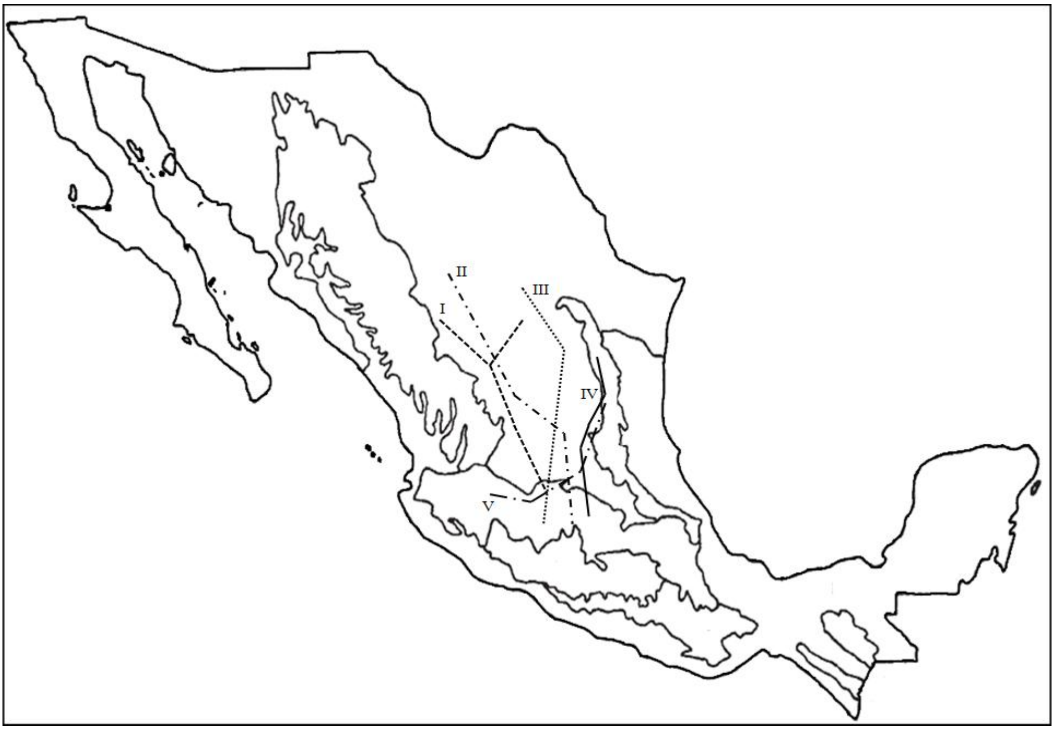

Figure 2. Individual tracks of (I) *Storeria storerioides*, (II) *Urosaurus bicarinatus*, (III) *Noorops nebulosus*, (IV) *Conopsis lineata*, (V) *Thamnophis sumichrasti*.

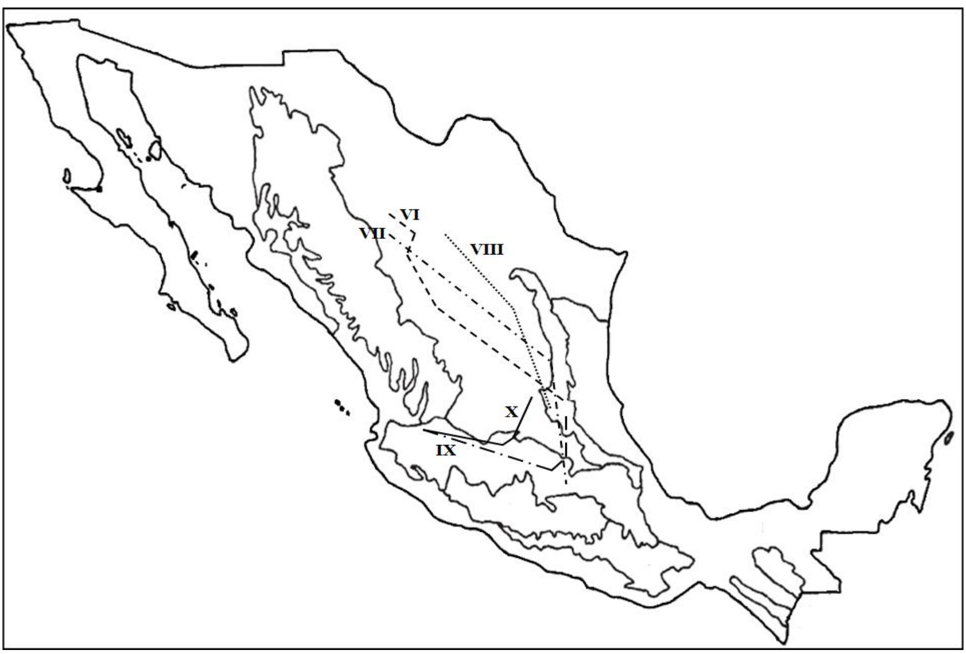

Figure 3. Individual tracks of (VI) *Leptodeira septentrionalis*, (VII) *Crotalus scutulatus*, (VIII) *Nerodia rhombifer*, (IX) *Thamnophis scalaris*, (X) *Crotalus ravus*, (XI) *Geophis semidoliatus*.

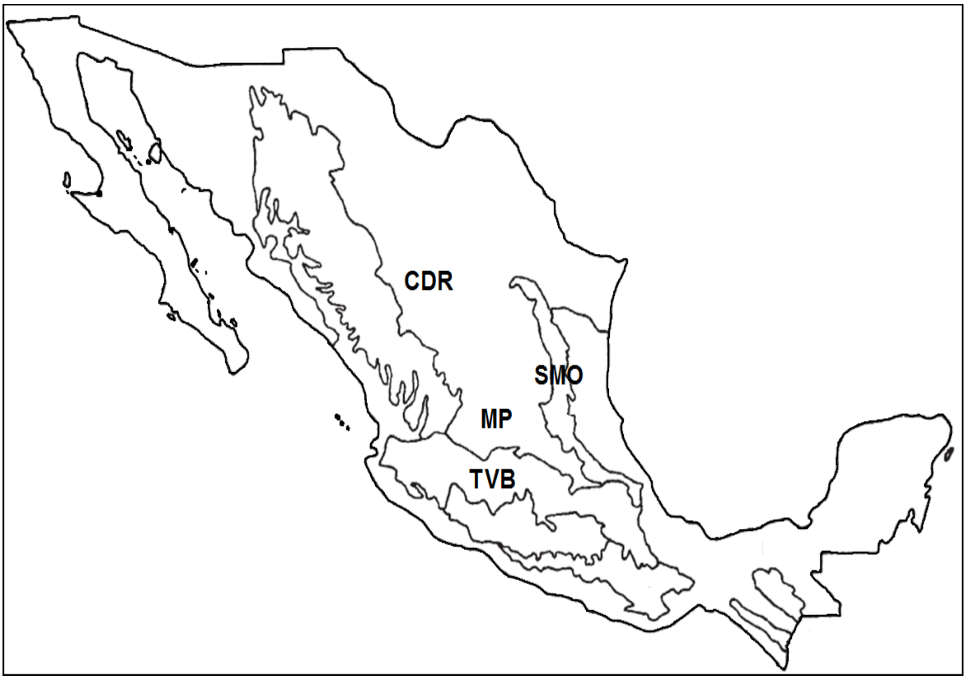

Figure 4. Biogeographic provinces of México. CDR: Chihuahuan Desert Region, MP: Mexican Plateau, SMO: Sierra Madre Oriental, TVB: Transmexican Volcanic Belt. Modified from Espinosa-Organista et al. 2000.

RESULTS AND DISCUSSION

In this chapter we used a database with 1690 records distributed in 106 species of reptiles of the arid zones that are located in the four biogeographic provinces or areas of endemism (Table 3); and a parsimonious cladogram was obtained with a length of 150 steps, consistency index of 70 and retention index of 26 (Figure 5). This cladogram revealed the existence of two main clusters or generalized tracks, whose importance has been corroborated with several biological groups, such as beetles (Morrone and Márquez 2003), plants (Contreras-Medina et al. 2001), birds (García-Trejo and Navarro 2004), and mammals (Escalante et al. 2005). The first cluster analysis was generated with interception of SMO and MP, and it is supported by seven synapomorphies (Figure 5, Table 3), and on the other hand, the second generalized track is composed with the province CDR and TVB, which support nine synapomorphies (Figures 5 and 6; Table 3), and by means of a re-sampling of the data matrix a reliability of 100% was obtained for each generalized track obtained (Figure 7). Both generalized tracks are consistent with those obtained by Morrone and Márquez (2003) to elaborate a preliminary analysis of biogeographic atlas of México and the generalized track 3 and 4 obtained by Contreras-Medina et al. (2001). The latter of which describes the affinities of distributions between Neartic and Neotropical flora and fauna and a septentrional generalized track covering a large part of the Mexican Transition Zone. This Zone was identified by Morrone and Márquez (2001) with different groups of beetles, which undoubtedly indicates that some arid zones of central Mexico represent a region with a complex evolutionary history.

Table 3. Assigned species to each biogeographic provinces of this chapter

Taxa		**Provinces**			
Order **Family**	**Species**	**CDR**	**SMO**	**TVB**	**MP**
REPTILIA					
TESTUDINES					
Kinosternidae	41.- *Kinosternon herrerai*	X	X		X
	42.- *K. hirtipes*	X	X	X	X
	43.- *K. integrum*		X	X	X
SQUAMATA					
SAURIA					
Anguidae	1.- *Abronia taeniata*	X	X	X	X
	11.- *Barisia imbricata*	X	X	X	X
	12.- *B. levicollis*	X			X
	107.- *Gerrhonotus liocephalus*	X	X	X	X
Corytophanidae	44.- *Laemanctus serratus*	X	X		
Dibamidae	3.- *Anelytropsis papillosus*	X	X		
Iguanidae	27.- *Ctenosaura acanthura*		X	X	
Phrynosomatidae	17.- *Cophosaurus texanus*	X			
	61.- *Phrynosoma cornutum*	X	X	X	
	62.- *P. modestum*	X	X		
	63.- *P. orbiculare*	X	X	X	X
	71.- *Sceloporus aeneus*	X	X	X	X
	72.- *S. anahuacus*			X	X
	73.- *S. bicanthalis*		X	X	X
	74.- *S. formosus*		X	X	
	75.- S. grammicus	X	X	X	X
	76.- *S. horridus*			X	X
	77.- *S. jarrovi*	X	X	X	X
	78.- *S. megalepidurus*		X	X	X
	79.- *S. merriami*	X			
	80.- *S. minor*		X		X
	81.- *S. mucronatus*		X	X	X

Taxa Order Family	Species	Provinces			
		CDR	**SMO**	**TVB**	**MP**
	82.- *S. parvus*		X	X	X
	83.- *S. poinsetii*	X	X	X	X
	84.- *S. scalaris*	X	X	X	X
	85.- *S. spinosus*	X	X	X	X
	86.- *S. torquatus*	X	X	X	X
	87.- S. variabilis	X	X		X
	105.- *Urosaurus bicarinatus*	X		X	
	106.- *Uta stansburiana*	X		X	
Dactyloidae	4.- *Anolis nebulosus*	X		X	
	5.- *A. sericeus*	X	X		X
Scincidae	65.- *Plestiodon brevirostris*	X			X
	66.- *P. lynxe*	X	X	X	X
	67.- *P. tetragrammus*	X	X		X
	88.- *Scincella lateralis*	X	X		
	89.- *S. silvicola*	X	X	X	X
Teiidae	2.- *Holcosus undulata*	X	X	X	
	6.- *Aspidoscelis costata*	X		X	
	7.- *A. deppii*			X	
	8.- *A. exanguis*	X			
	9.- *A. gularis*	X	X	X	X
	10.- *A. guttata*				X
Xantusiidae	48.- *Lepidophyma gaigeae*	X	X	X	X
	49.- *L. occulor*	X	X		
	50.- *L. sylvaticum*		X		X
SERPENTES					
Colubridae	13.- *Coluber constrictor*	X		X	
	14.- *Conopsis biserialis*			X	X
	15.- *C. lineata*		X	X	X
	16.- *C. nasus*	X	X	X	X
	29.- *Drymarchon melanurus*	X	X	X	X
	30.- *Drymobius margaritiferus*	X	X	X	X

Table 3. (Continued)

Taxa Order Family	Species	Provinces CDR	 SMO	 TVB	 MP
	31.- *Ficimia hardyi*		X	X	X
	32.- *F. olivacea*		X	X	
	33.- *F. streckeri*	X	X		
	45.- *Lampropeltis mexicana*	X		X	
	46.- *L. ruthveni*			X	X
	47.- *L. triangulum*	X	X	X	X
	58.- *Mastigodryas melanolomus*	X	X	X	X
	64.- *Pituophis deppei*	X	X	X	X
	69.- *Salvadora bairdi*	X	X	X	X
	70.- *S. grahamiae*	X	X	X	X
	90.- *Senticolis triaspis*	X	X	X	X
	94.- *Tantilla bocourti*	X	X	X	
	95.- *T. rubra*	X		X	X
	104.- *Trimorphodon tau*	X	X	X	X
Viperidae	18.- *Crotalus aquilus*			X	X
	19.- *C. atrox*	X	X	X	X
	20.- *C. durissus*		X	X	X
	21.- *C. ornatus*	X	X	X	X
	22.- *C. polystictus*			X	
	23.- *C. pricei*	X			
	24.- *C. ravus*			X	X
	25.- *C. scutulatus*	X	X		X
	26.- *C. triseriatus*	X	X	X	X
Dipsadidae	28.- *Diadophis punctatus*	X		X	X
	34.- *Geophis dubius*		X	X	
	35.- *G. dugesi*	X		X	
	36.- *G. latifrontalis*	X	X	X	X
	37.- *G. mutitorques*	X	X	X	
	38.- *G. semidoliatus*			X	X
	39.- *G. tarascae*			X	X
	40.- *Hypsiglena torquata*	X	X	X	X
	51.- *Leptodeira annulata*	X	X	X	
	52.- *L. cussiliris*		X		X
	53.- *L. septentrionalis*	X	X		X
	54.- *Leptophis diplotropis*		X		

Taxa Order	Species	Provinces CDR	SMO	TVB	MP
	55.- *Masticophis flagellum*	X	X	X	X
	56.- *M. mentovarius*	X		X	X
	57.- *M. taeniatus*	X	X	X	X
	68.- *Rhadinaea gaigeae*		X		X
Elapidae	59.- *Micrurus tener*	X	X	X	X
Natricidae	60.- *Nerodia rhombifer*	X	X		X
	91.- *Storeria dekayi*	X	X		X
	92.- *S. hidalgoensis*	X	X		X
	93.- *S. storerioides*	X		X	X
	96.- *Thamnophis cyrtopsis*	X	X	X	X
	97.- *T. eques*	X	X	X	X
	98.- *T. marcianus*	X			X
	99.- *T. melanogaster*	X	X	X	X
	100.- *T. proximus*	X	X	X	X
	101.- *T. scalaris*		X	X	X
	102.- *T. scaliger*		X	X	
	103.- *T. sumichrasti*		X		X

CDR: Chihuahuan Desert Region, MP: Mexican Plateau, SMO: Sierra Madre Oriental, TVB: Transmexican Volcanic Belt.

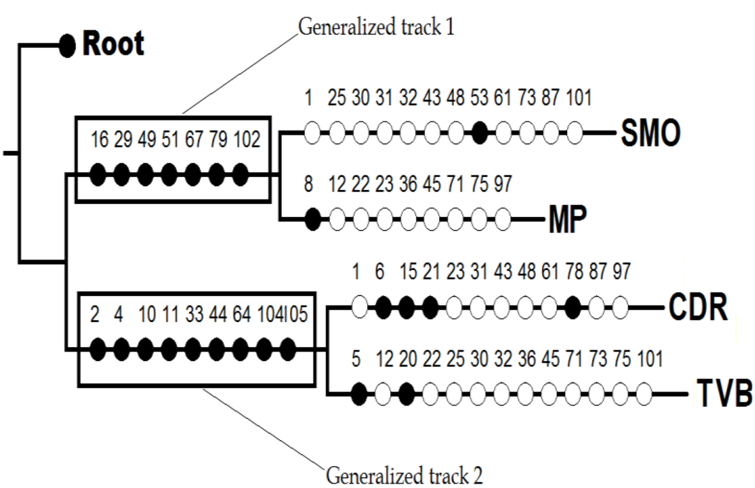

Figure 5. Cladogram result of PAE for the reptile species from arid zones. Black circle (sharing species; sinapomorphies), white circles (species with wide distribution; homoplasies), and number on the circles are the species (see Table 3), CDR: Chihuahuan Desert Region, MP: Mexican Plateau, SMO: Sierra Madre Oriental, TVB: Transmexican Volcanic Belt.

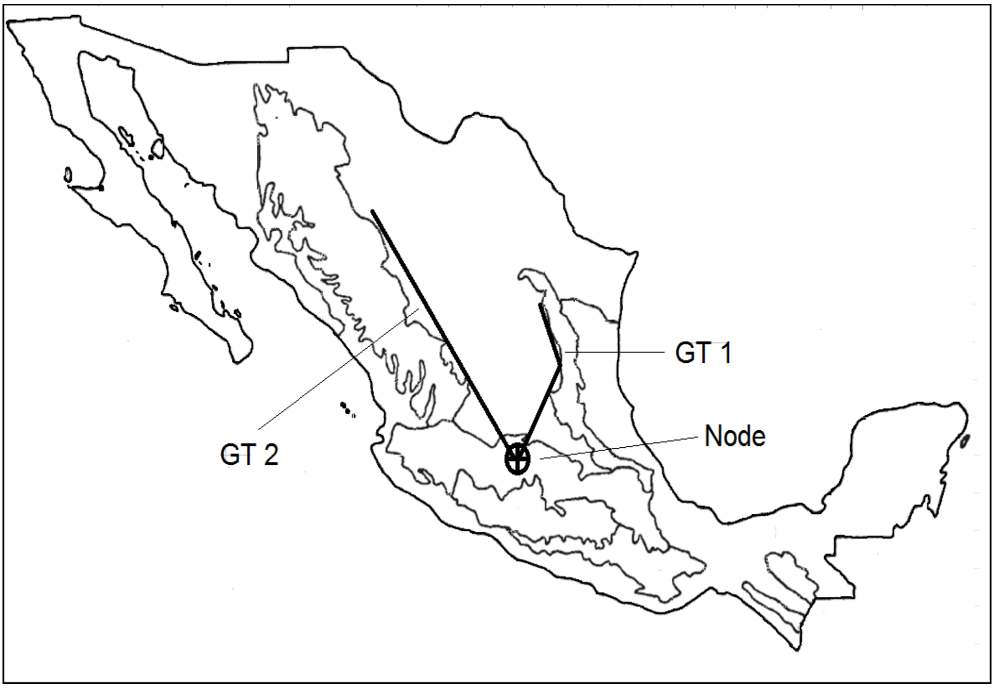

Figure 6. Generalized tracks (GT1 and 2) and nodes of the reptile species that have their distribution in the biogeographic provinces of arid environments from central Mexico.

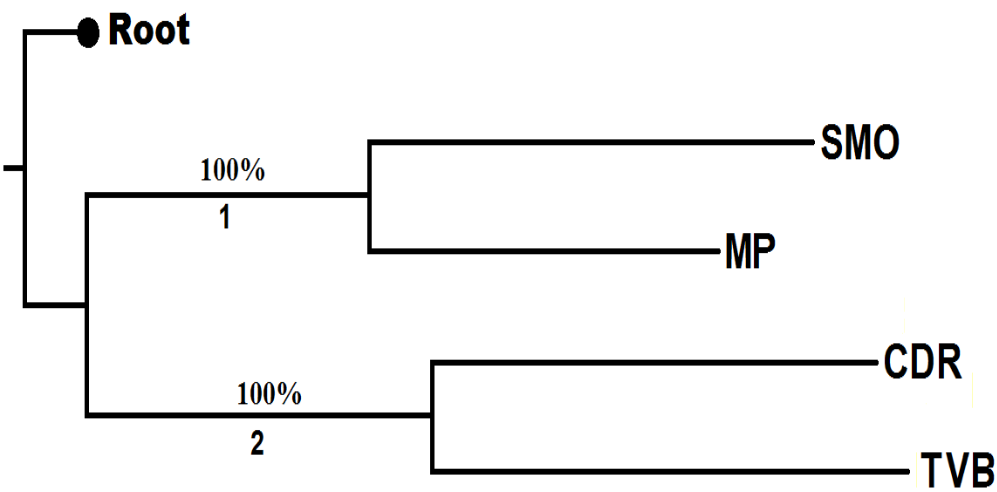

Figure 7. Cladogram from PAE for reptile species from arid zones. Values (in percentage) indicate bootstrap analysis (1000 replicates). The number below the value of boostrap makes reference to the obtained generalized tracks. 1= generalized track 1, 2 = generalized track 2. CDR: Chihuahuan Desert Region, MP: Mexican Plateau, SMO: Sierra Madre Oriental, TVB: Transmexican Volcanic Belt.

It is worth mentioning that all the species making up the generalized track 1 show affinities to both Neartic and Neotropical species, mainly for species that have distributions in SMO. This is the case because most of the records were part of the generalized track 1 that was reported in desert scrub, submontane and thorny forest ecosystems, which are associated with oak and tropical deciduous forests that have their distribution in the SMO (Rzedowski 1973). Moreover, the affinities of the species distributed in MP are mostly Neartic. The proximity to the SMO and CDR and the high temperatures found in the northern region of México favor arid vegetation types, such as thorn scrub and coastal dunes with affinities completely Neartic (Lavin-Murcio and Lazcano 2010). In contrast, the species that comprise the generalized track 2, show Neartic affinities because their distribution extend beyond the arid north of México, and these areas are very similar to those arid and semi-arid zones analyzed by Rzedowski (1973). This indicates that in México there are two important biogeographic arid elements: the first is located in the Neartic region, and the second is restricted to central and north of México, thereby providing evidence of the species richness and endemism in the arid zones of Mexico. Finally, the generalized tracks in this study are also strongly related to the American-Caribbean tracks (Rosen 1978), formed mainly for the arrival of North American faunas which were concentrated as megafauna and were subsequently fragmented during Tertiary to generate the current faunal elements in Mexico and Central America.

Furthermore, we detected a panbiogeographic node at the intersection of two generalized tracks obtained by PAE (Figure 6). This node is remarkable because currently there are few nodes that represent a complex area in arid zones of Mexico, particularly for reptiles. However, the use of other biological groups as models has represented various complex zones from the species richness point of view in central Mexico (Cabrera and Willink 1973, Rzedowski 1973, Halffter 1987), which has generated a panbiogeographic knowledge base for Mexico (Morrone 2005). From this node, we can hypothesize the historical distribution of different reptile species which are pooled and distributed toward central México. Although, it is important to note that not all species that are part of the generalized tracks are included in the panbiogeographic node (e.g., 9, 27, 28, 106, and 107; Table 3).

A significant number of reptile species used in this study, show a distribution in the CDR, which may extend into Sierra Madre Occidental and the arid lands of North America (see Lavin-Murcio and Lazcano 2010). Unfortunately, the lack of information about the distribution of species from arid zones of North America affects the understanding of the biogeographic history of the deserts of northern Mexico and southern United States. However, in Savage´s (1982) analysis on the origin of the Mexican herpetofauna, he mentions that arid zones of North America from a biogeographic point of view, gave rise to most of the deserts in northern Mexico, and consequently a large number of amphibians and reptiles species. These species are suggested to mainly stem from the northern portion of the Sonoran Desert and CDR, validating Croizat´s (1958) ideas about the land and biota evolving together. Thus, it is possible that during the formation of these deserts various events of extinction and emergence have resulted in several endemic reptiles groups, such as *Gopherus* and *Uma* (not included here), which some authors see as paleoendemism (Legler 1990).

The emergence of several endemic groups in Mexican deserts has been previously documented by Morafka (1977) and Savage (1982), indicating that both Sonoran and CDR together with their herpetofauna, have undergone various vicariance events which gave rise to the species in the Sierra Madre Occidental. In addition is the emergence of an exclusive northern herpetofauna which contains many species that are distributed along the Pacific coast and some areas of the Sierra Madre Oriental and TVB, such as species of the genus *Heloderma*, *Sceloporus*, *Crotalus*, and *Aspidoscelis*. Furthemore, it would be interesting to know the relationship of the historical biogeographic events with groups of low dispersion (e.g., frog and salamander species that inhabit colder areas of north-central Mexico), the formation of a series of mountains during the Pliocene result in vicariant processes which consequently lead to an interesting biogeographic history that resulted in coevolution in space and time of several groups of amphibians (Morafka 1977).

Finally, we acknowledge that unfortunately information on the current distribution of some species of reptiles from arid areas of Mexico is incomplete, and therefore studies on species distribution are regarded as preliminary. A greater sampling effort would help to substantiate the fragments of remaining reptile distributions from the arid zones of central Mexico. In so doing, the role of panbiogeography could be more effective technique to identify panbiogeographic nodes; those areas of high evolutionary value with diverse histories of dispersal or areas of high diversity and endemism, and conclude with this a robust key for a conservation plan to the arid zones of Mexico.

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