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Contributions of Cladistic Biogeography to the Mexican Transition Zone

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1. Introduction

The Mexican Transition Zone (MTZ) was defined by Halffter (1987) as the complex area where Neotropical and Nearctic biotic elements overlap, including the southern United States, Mexico and adjacent areas of Central America. The biota of this area has received the attention of several naturalists since the mid 19th century (e.g. Sclater, 1858) due to its placement between the Nearctic and Neotropical regions and its “hybrid” character (Morrone, 2005 and references therein), associated with high biotic diversity and a high degree of endemism of plant and animal taxa. This area also has received attention in conservation and biodiversity plans at a worldwide level, because its central portion, the Mesoamerican hotspot, was considered one of the main biodiversity hotspots recognized in the world (Flores-Villela & Gerez, 1994; Luna-Vega and Contreras-Medina, 2010; Mittermeier et al., 1998; Myers et al., 2000).

Recently, authors have proposed hypotheses to explain disjunct biotic patterns observed in the MTZ from different approaches and methodologies, such as panbiogeography (Álvarez & Morrone, 2004; Contreras-Medina & Eliosa-León, 2001; Escalante et al., 2004; Morrone & Márquez, 2001; Morrone & Gutiérrez, 2005), parsimony analysis of endemism (Aguilar-Aguilar et al., 2003; Espinosa et al., 2000; Luna-Vega et al., 2001; Morrone et al., 1999; Morrone & Escalante, 2002), and cladistic biogeography (Contreras-Medina et al., 2007; Espinosa et al., 2006; Flores-Villela & Goyenechea, 2001; Liebherr, 1991; Marshall & Liebherr, 2000; Rosen, 1978). The latest studies based on cladistic biogeography approaches represent the basis of this chapter.

Our goal here is to compare and discuss the different contributions made to the biogeography of the Mexican Transition Zone by applying different cladistic biogeographical methods. It is also to contrast the different areas of endemism proposed in these studies with the objective of obtaining consensus on areas of endemism to be considered in future research.

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2. Cladistic biogeography: Basis and methods

Cladistic biogeography is an approach to historical biogeography that searches for patterns of relationships among areas of endemism based on the phylogenetic relationships of the taxa inhabiting them (Crisci et al., 2000; Humphries & Parenti, 1999; Morrone & Crisci, 1995). This approach emerged as a combination of principles of phylogenetic systematics of Willi Hennig (1966) and the biogeographic ideas formulated by Léon Croizat (1958, 1964) represented in his book *Panbiogeography* (Contreras-Medina, 2006; Craw, 1988; Crisci et al., 2000; Espinosa & Llorente, 1993; Flores-Villela & Goyenechea, 2001). Cladistic biogeography is based on a close relationship among systematics and biogeography, considering that taxonomic cladograms converted into area cladograms can elucidate the fragmentation sequence of studied areas. With this procedure, it is possible to propose hypotheses on historical relationships among areas of endemism (Contreras-Medina, 2006; Morrone, 1997). Cladistic biogeographic analysis essentially looks for congruent patterns among area cladograms of different taxa (Humphries & Parenti, 1999; Page & Lydeard, 1994) showed in a general area cladogram, which represents the final result of this kind of analysis (Contreras-Medina, 2006; Morrone, 1997). Interpretation of cladistic biogeographical results usually focuses on vicariance rather than on dispersal events, because vicariance affects different groups of organisms simultaneously (Morrone & Crisci, 1995; Nelson & Platnick, 1981).

The construction of area cladograms is simple when each taxon is endemic to a single area and each area has only one taxon (Morrone, 1997). Incongruence can occur between two or more area cladograms due to three main reasons, known as redundant distributions, widespread taxa and missing areas (Morrone et al., 1996). Redundant distributions occur when an area appears more than once in an area cladogram, because two or more terminal taxa are distributed in this area; widespread taxa occur when any of the terminal taxa inhabits two or more of the areas analyzed; missing areas occur when there is not a terminal taxon distributed in one of the areas analyzed, therefore this area is not represented in the area cladograms (Morrone, 2009). One or more of the methods that have been proposed in cladistic biogeography are then applied to these area cladograms, and the final result is a general area cladogram (Morrone, 1997).

The first method developed in cladistic biogeography was the reduced consensus cladogram proposed by Rosen (1978), which was only used by him. Another method proposed was the Brooks parsimony analysis or BPA (Brooks, 1990; Kluge, 1988), which has been extensively used in studies developed in the MTZ (Contreras-Medina et al., 2007; Espinosa et al., 2006; Marshall & Liebherr, 2000). BPA has been criticized by some authors as a suboptimal method, because it uses both dispersal and vicariance explanations to fit taxa and areas to the same tree (e.g. Siddall & Perkins, 2003); however, other authors (e.g. Brooks et al., 2001; Van Veller & Brooks, 2001) have defended it as a valid method. Nelson & Ladiges (1996) noted that when nodes and areas are associated in order to be included in a data matrix, geographic paralogy may result because of duplication or overlap in the distribution of taxa related by paralogous nodes. To this end, another method was proposed, known as paralogy-free subtrees (Nelson & Ladiges, 1995). This method consists in the reduction of complex cladograms to paralogy-free-subtrees, that means that geographic data are associated only with the informative nodes, and areas duplicated or redundant in the descendants of each node do not exist (Morrone, 2009). Once that paralogy-free-subtrees are

obtained, these are represented in a component or a three-item matrix and analyzed with a parsimony algorithm (Crisci et al., 2000). A parsimony analysis of these paralogy-free subtrees (PAPS) may thus be used to generate a more robust hypothesis, because geographic paralogy has been removed. Another frequent method that has been cited in biogeographic literature is component analysis (Nelson & Platnick, 1981), but unfortunately this method has not been applied to the biota of the MTZ.

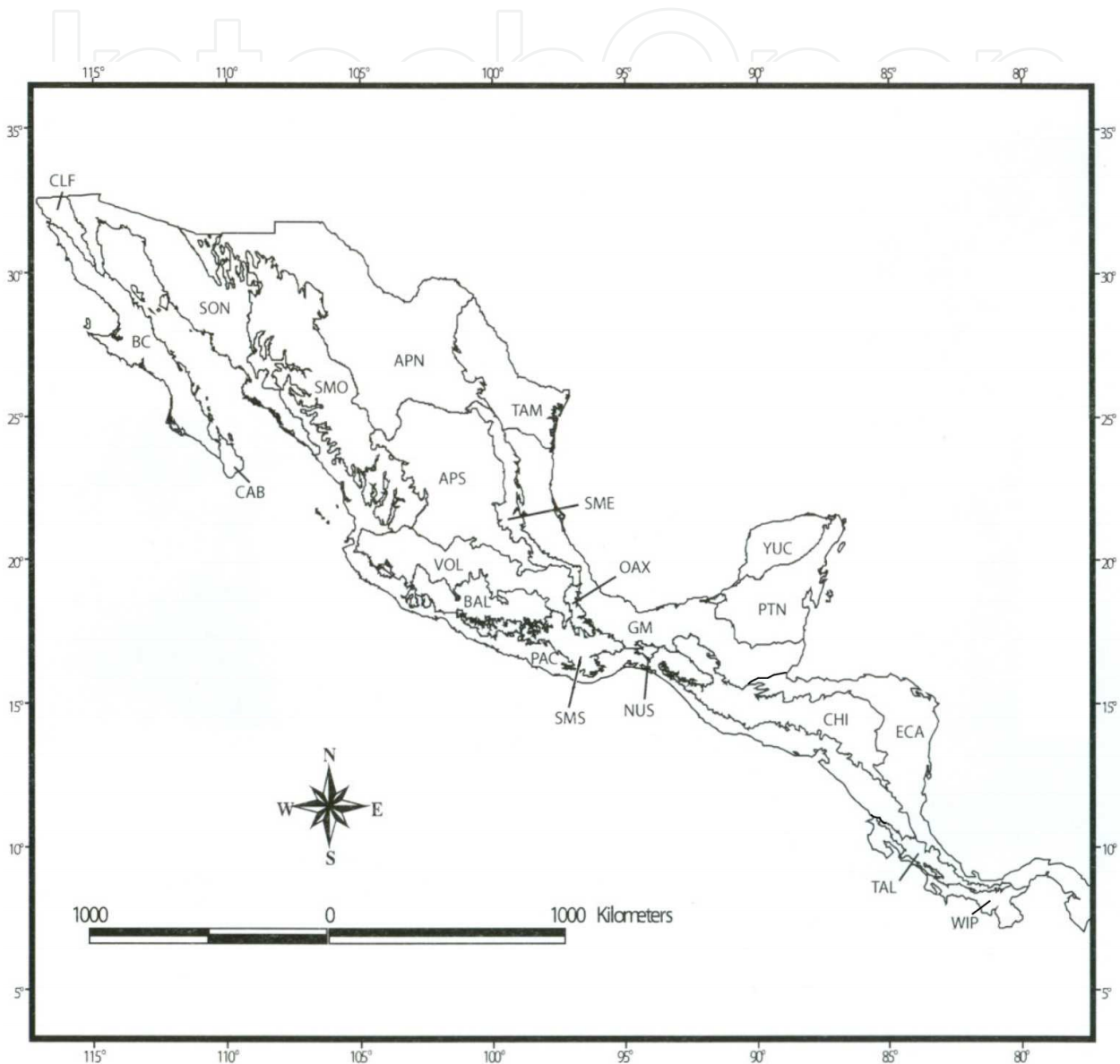


Fig. 1. The 19 biogeographic provinces of Mexico according to Arriaga et al. (1997). Abbreviations are: APN = Altiplano Norte, APS = Altiplano Sur, BAL = Depresión del Balsas, BC = Baja California, CLF = California, CAB = Del Cabo, CHI = Los Altos de Chiapas, GM = Golfo de México, NUS = Soconusco, OAX = Oaxaca, PAC = Costa del Pacífico, PTN = Petén, SME = Sierra Madre Oriental, SMO = Sierra Madre Occidental, SMS = Sierra Madre del Sur, SON = Sonorenses, TAM = Tamaulipeca, VOL = Eje Volcánico, YUC = Yucatán. The provinces of Central America from Morrone (2001) are: CHI= Los Altos de Chiapas, ECA= Eastern Central America, WIP= Western Isthmus of Panamá, and TAL = Sierra de Talamanca.

3. Areas of endemism in the Mexican Transition Zone

Areas of endemism are defined by the overlapped distributions of endemic taxa (Contreras-Medina, 2006; Morrone, 1994). These kinds of areas represent the basic units in cladistic biogeography (Contreras-Medina et al., 2001); for this reason, the recognition and delimitation of areas of endemism represent a prerequisite to carry out cladistic biogeographic studies (Morrone, 1997).

Some proposals on regionalization of the Mexican Transition Zone have been suggested based on different criteria. One of the most supported schemes was that proposed by the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) (National Commission for the Knowledge and Use of Biodiversity, Mexico), which represents the effort of a set of several specialists on geology, vascular plants, reptiles and mammals working together to provide different proposals on regionalization of the Mexican territory with different points of view. Nineteen Mexican biogeographic provinces were recognized through this workshop (Arriaga et al., 1997). An important regionalization proposal for Central America also was made by Morrone (2001). This scheme was also followed in this study, and was also used to compare the areas of endemism found in the different revised studies on cladistic biogeography of the Mexican Transition Zone.

In the study of Espinosa et al. (2006), the parsimony analysis of endemism (PAE) method (Rosen, 1988) was used in order to generate the 23 areas of endemism that were used later in the cladistic biogeography section of this paper. The areas of endemism were obtained by merging those areas supported by endemic (synapomorphic) species from PAE following the proposed provinces of Morrone (1994).

In many cases, the Mexican mountain ranges coincide with the areas of endemism (Fig. 2), so their recognition and delimitation represent necessary tools in future cladistic biogeographic studies. The origin and development of these mountain chains have strongly

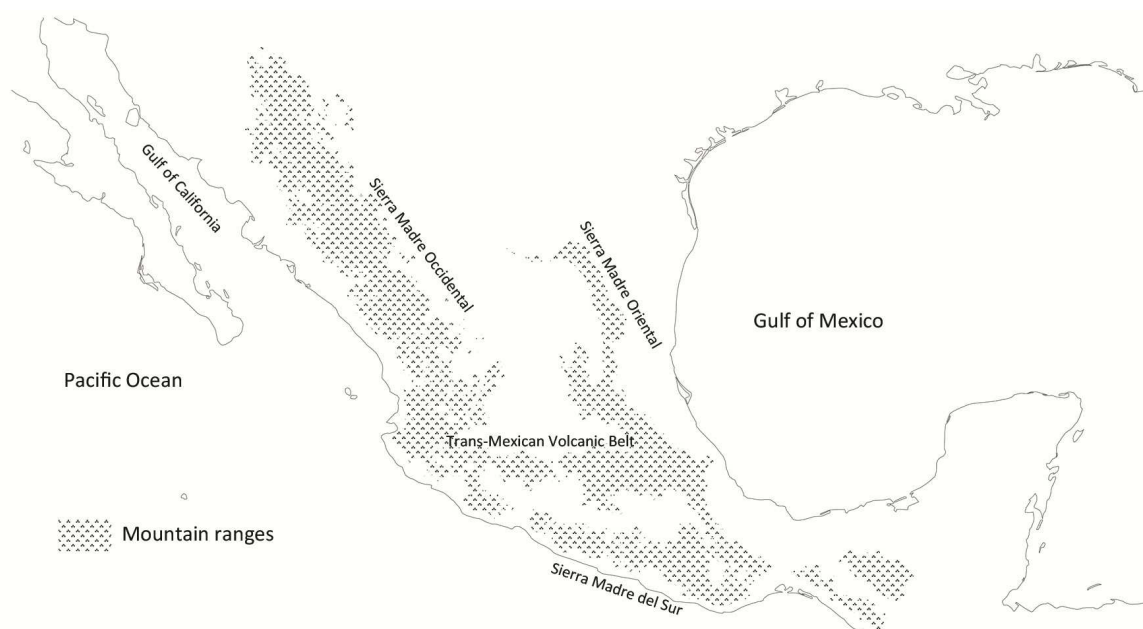


Fig. 2. The main Mexican mountain chains.

Biogeographic provinces	Marshall & Liebherr (2000)	Espinosa et al. (2006)	Flores-Villela & Goyenechea (2001)	Contreras-Medina et al. (2007)
CLF				Californian
BC				Baja California
CAB		El Cabo		Baja California
SON	Sonoran Desert	Sonora	Sonoran Desert	Planicie Costera del Noroeste
SMO	Sierra Madre Occidental plus Central Plateau		Sierra Madre Occidental	Sierra Madre Occidental
APN	Sierra Madre Occidental plus Central Plateau		Chihuahuan Desert	Altiplano
APS	Sierra Madre Occidental plus Central Plateau		Chihuahuan Desert	Altiplano
TAM	Sierra Madre Occidental plus Central Plateau		Semiarid lands of Tamaulipas	Planicie Costera del Noreste
SME	Sierra Madre Oriental		Sierra Madre Oriental	Sierra Madre Oriental
VOL	Sierra Transvolcánica		Transvolcanic Axis of Central Mexico	Serranías Meridionales
BAL		W and E Balsas	Balsas Depression	Balsas Basin
SMS	Sierra Madre del Sur	Tehuantepec	Sierra Madre del Sur	Serranías Meridionales
OAX		Tehuacán-Cuicatlán Valley	Transvolcanic Axis of Central Mexico	Tehuacán-Cuicatlán Valley
GM				Costa del Golfo de México
PAC		Tuito, Papagayo, Armería-Coahuayana and Tehuantepec	Pacific lowlands of Mexico plus Balsas Depression	Costa Pacífica
NUS				Soconusco

Biogeographic provinces	Marshall & Liebherr (2000)	Espinosa et al. (2006)	Flores-Villela & Goyenechea (2001)	Contreras-Medina et al. (2007)
YUC	Chiapan Guatemalan Highlands			Yucatán Península
PTN	Chiapan Guatemalan Highlands			Yucatán Península
CHI	Chiapan Guatemalan Highlands		Highlands of Chiapas	Serranías Transísmicas
ECA	Chiapan Guatemalan Highlands		Eastern Central American Atlantic lowlands	Eastern Central America
WIP	Talamancan Cordillera		Western Central American Pacific lowlands	Costa Pacífica
TAL	Talamancan Cordillera		Talamanca ridge	

NOTES: When the same name of an area of endemism appears in two or more cells, it means that this area in this particular study is very large and includes two or more biogeographic provinces. Empty cells mean that the biogeographic province was not included or considered in our study.

Table 1. Comparison among the areas of endemism of the Mexican Transition Zone used in some of the studies cited in this chapter, in relation to the biogeographic provinces of Arriaga et al. (1997) and Morrone (2001).

influenced the geographic distribution of the biota of the MTZ. The geological evolution of Mexico and Central America during the Cretaceous and Cenozoic has had a significant influence on the processes controlling the composition of their biota (Cevallos-Ferriz & González-Torres, 2005). The primary geological events shaping Mexico and Central America during these time intervals include the following: (1) the development of large magmatic provinces (Sierra Madre Occidental, Trans-Mexican Volcanic Belt, and Sierra Madre del Sur); (2) the fragmentation and displacement of continental segments including the opening of the Gulf of California (the separation of the Baja California Peninsula from the mainland) and the displacement of the Chortis Block to northern Central America; (3) the marine regression that outlined the current shape of Mexico; and (4) the formation and rise of an eastern orogenic belt known as the Sierra Madre Oriental (Cevallos-Ferriz & González-Torres, 2005; Ortega-Gutiérrez et al., 1994).

In Table 1 (above), two additional studies merit comment. Liebherr (1991) did not name areas of endemism, but designated them by letters, making it difficult to compare his areas with those of other authors. Rosen (1978) identified very small areas of endemism, only

including small parts of the MTZ - these areas were mainly in Chiapas, eastern Central America, Petén, and Golfo de México.

4. Cladistic biogeography studies in the Mexican Transition Zone

Rosen (1978) was the first to apply a cladistic biogeography approach to the MTZ. In his biogeographic research, the author included the phylogenies of two fresh water fish of the genera *Heterandria* and *Xiphophorus*. Rosen (1978) recognized three coincidences of historical relationships, indicating the existence of a common ancestral distributional area that had been fragmented twice and that currently constitutes the basins of the Bravo River (in northern Mexico), the Pánuco River (in northeastern Mexico), and the Grijalva River (on the border between Mexico and Guatemala).

Another pioneering cladistic biogeographic study in the MTZ is that of Liebherr (1991). This author analyzed the history the mountain biota based on the phylogenies of two Coleoptera genera (*Elliptoleus* and *Calathus*). The complexity of the geologic history of southern Mexico is noted in the general area cladogram obtained, showing an ancient primary fragmentation that separated extra-tropical from tropical biota. Liebherr (1991) obtained a first clade that was divided in two subgroups, the first formed by the Sierra Madre Oriental and the second by the Sierra Madre Occidental and part of the Mexican Plateau. The tropical clade included the southern portions of the Sierra Madre Occidental, Sierra Madre Oriental and other Mexican mountain chains such the Sierra Madre del Sur and the Trans-Mexican Volcanic Belt.

Marshall & Liebherr (2000) published a cladistic biogeography study applying BPA and Assumption 0 methods based on 33 taxa (beetles, reptiles, fish and one plant genus) and using nine areas of endemism; they obtained four general area cladograms, one with BPA and three with Assumption 0. The congruence among these cladograms is shown in the relationships among the Arizona Mountains plus the Sierra Madre Occidental in one clade, and the Sierra Madre del Sur plus the Trans-Mexican Volcanic Belt related with the Chiapan-Guatemalan Highlands in another clade. Unfortunately, their approach included methodological confusion regarding the Assumption 0: the missing taxa option (or missing areas) in the matrix is treated by them as '0', indicating the lack of information regarding a taxon's occurrence. However, the Assumption 0 approach considers missing areas to be uninformative, as well as the other two assumptions (1 and 2) in a component analysis method (Morrone, 1998), so missing areas are located in all possible positions in the resolved area cladograms. Assumption 0 in BPA implies that areas inhabited by a widespread taxon are considered as sister areas (Morrone, 1997).

Flores-Villela & Goyenechea (2001) used 10 animal taxa in their biogeographical study (beetles, lizards, snakes and frogs) distributed in 13 areas of endemism; the method of reconciled trees implementing assumptions 0, 1, and 2 was applied in this study. The authors obtained six general area cladograms, but they did not achieve a consistent pattern of relationships among these cladograms. They concluded that each cladogram could only explain portions of the geographic history of the taxa studied, and that the results obtained were due to the geological complexity of the area under study.

Espinosa et al. (2006) generated hypotheses on the historical biogeography of tropical Mexico using the flowering plant genus *Bursera*. This study was based on the geographic distribution of 104 species in this genus analyzed with the BPA method. The consensus

general area cladogram obtained was formed by two main clades: the first included different areas of the Greater Antilles, and the second 12 Mexican areas of endemism. In this second clade all the areas located on the Pacific slope are included in one group, and the basal branch of this clade is constituted by the unique area located on the Gulf of Mexico slope. This general area cladogram shows the proposed historical relationships among tropical areas of Mexico.

The study of Contreras-Medina et al. (2007) was based on 81 gymnosperm species of the genera *Ceratozamia*, *Dioon* and *Pinus*, applying BPA and paralogy-free subtrees methods. In the case of the Mexican provinces, the unique relationship of both general area cladograms was the Mexican Plateau plus the Sierra Madre Oriental related with the Sierra Madre Occidental; the lowland provinces were mostly related, as in the study of Espinosa et al. (2006) with *Bursera*. Contreras-Medina and collaborators considered that both peninsulas of Mexico (Baja California and Yucatán) had a different history in relation to the continental portion of the country.

5. Conclusions

The MTZ represents a challenge for cladistic biogeography, due (in part) to its location at the boundaries between the Nearctic and Neotropical biogeographic regions, allowing the mixture of different biotic elements (Escalante et al., 2007), as suggested by previous studies from panbiogeographic approach (Contreras-Medina & Eliosa-León, 2001; Escalante et al. 2004; Morrone & Márquez, 2001). Also from a tectonic perspective, this region has formed through the convergence of three tectonic plates (North American, Cocos, and Caribbean), contributing to its geological complexity (Ortega et al., 1994).

After discussing the differences derived from applying different methods to carry out cladistic biogeographic analyses, Morrone & Carpenter (1994) concluded that when the data are “clean” (including few widespread taxa, redundant distributions, and missing areas), the results obtained using different methods are consistent. Some MTZ vicariance patterns, particularly those influenced by widespread taxa, redundant distributions and missing areas, appear to be ambiguous or the result of biogeographic noise. It remains difficult to select appropriate cladistic biogeographic methods because all have advantages and disadvantages, and all of them have been criticized (Morrone, 2009). One suggestion is to apply several methods and compare their differences and similarities (i.e., Contreras-Medina et al., 2007).

In addition, differences among the size and number of areas of endemism used in the different studies carried out in the MTZ make the search for congruent patterns of area relationships difficult. Unfortunately, it is not possible to make generalizations and comparisons among some clades obtained from the different studies commented upon here because, for example, some of the areas included in a clade of one study were not included in another, or in some studies wider units of analysis (areas of endemism) were used than those used in other studies. In some cases, different studies can be complementary, as occurred in the case of Marshall and Liebherr (2000) and Espinosa et al. (2006): the former was based mainly on mountainous taxa, whereas the latter was based mainly on lowland taxa. Notwithstanding, incongruent patterns should not be taken as signs of dispersal; they

may be the result of more than one vicariance pattern and/or to the reticulate biogeographic history in areas of endemism (Morrone, 2009).

A much needed analysis in the near future is consensus on the unification of areas of endemism in the MTZ. This will greatly strengthen cladistic biogeography interpretation, as well as the generation of new morphological and molecular phylogenies of the biota of the MTZ. Both activities represent a challenge, but it is the only way to advance in the comprehension of the complicated historical biogeography of this region. As Flores-Villela & Goyenechea (2001) noted in the title of their paper, we are still “seeking the lost pattern of the biota inhabiting the Mexican Transition Zone.”

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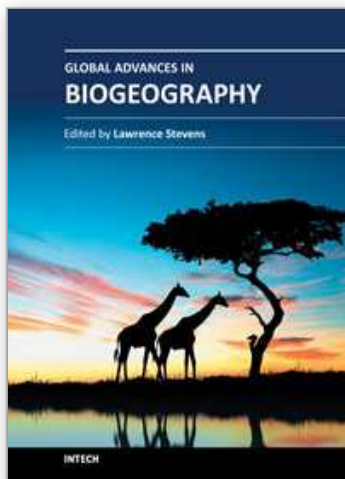
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