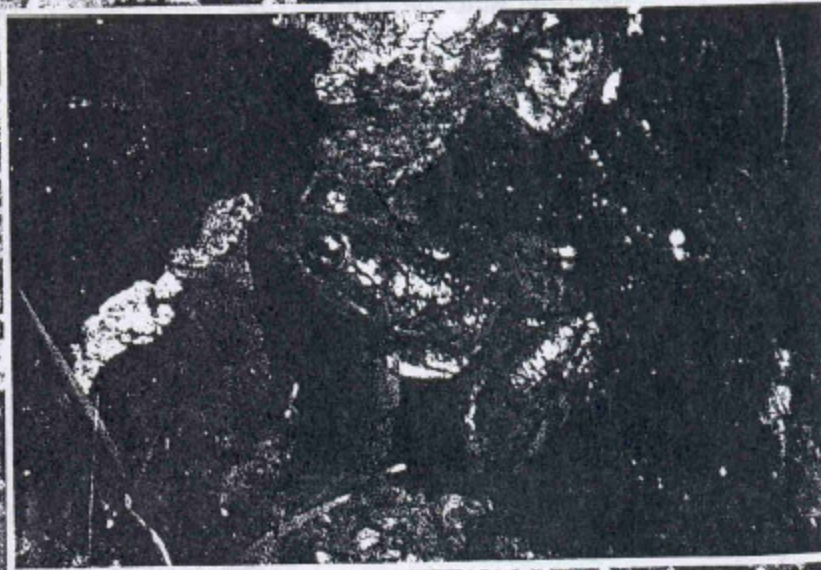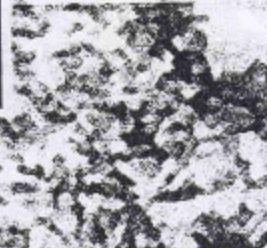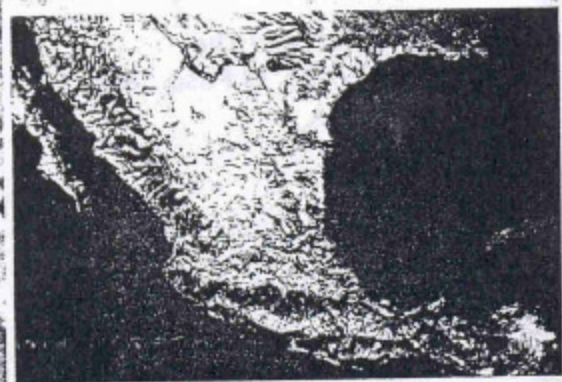# MESOAMERICAN HERPETOLOGY:

SYSTEMATICS, ZOOGEOGRAPHY, AND CONSERVATION

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THE UNIVERSITY OF TEXAS AT EL PASO

MESOAMERICAN HERPETOLOGY: SYSTEMATICS, ZOOGEOGRAPHY, AND CONSERVATION

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A COMPARISON OF HYPOTHESES OF HISTORICAL AREA RELATIONSHIPS FOR MEXICO AND CENTRAL AMERICA, OR IN SEARCH FOR THE LOST PATTERN

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ABSTRACT: A comparison of six general area cladograms (GAC's), for México and Central America, was done using the reconciled trees method of COMPONENT 2.0 (Page, 1993). The GAC's used in this study are those derived from Assumptions 0, 1 and 2 implemented in COMPONENT 2.0. For each assumption, a 50% majority rule and Nelson consensus were chosen. Each of the six GAC's was reconciled independently with 10 groups of taxa represented by beetles, lizards, snakes and frogs, to test which of the six hypotheses of area relationships explain the biogeography of each taxon. Results show that the GAC's from Assumption 0 best explain the biogeographic history of five taxa. When pruning trees to test hypotheses of dispersal, all of the cladograms explain the biogeographic history of the 10 taxa studied. One thousand random area cladograms were generated and each taxon was reconciled with the random trees. Values from this and the previous comparison with the six GAC's were tested at a $p < 0.05$ level of significance to verify that they were not a product of a random pattern. Considering the complexity of the biogeographic history of the area, each cladogram may explain portions of the geographic history for the taxa studied.

Key Words: Biogeography; Component analysis; México; Central America.

HISTORICAL biogeography contains two competing paradigms, dispersal and vicariance (panbiogeography and cladistic biogeography). Dispersal theory has dominated biogeographic thinking from the time of Darwin and Wallace through the mid 1900s. Vicariance theory originated from the works of Leon Croizat beginning during the middle of this century. Croizat's theories and principles, however, were not appreciated until scientists from the American Museum of Natural History (D. Rosen, G. Nelson and N. Platnick) rediscovered his works and championed the principles and fundamentals of panbiogeography. Later these investigators combined the principles of vicariance with the fundamentals of phylogenetic systematics of Hennig (1966) to create what is now known as cladistic biogeography (formerly labeled vicariance biogeography by its creators).

A generalized scheme of the main schools of thought in historical biogeography and its major proponents are:
(1) Dispersal Biogeography (Darwin, 1859; Wallace, 1876; Matthew, 1915; Darlington, 1957; Simpson, 1940, 1950, 1953; Mayr, 1965).
(2) Phylogenetic Biogeography or Hennigian Biogeography* (Hennig, 1966; Brundin, 1966, 1972).
(3) Panbiogeography* (Croizat, 1952,1958,1962; Craw, 1983, 1988; Page, 1987).
(4) Cladistic Biogeography* (Rosen, 1975, 1978; Nelson and Platnick, 1981; Wiley, 1981; Cracraft, 1988; Humphries and Parenti, 1986).
* All except (1) are considered to be phylogenetic biogeographies for the importance of considering monophyletic groups or supposedly monophyletic groups (Espinosa and Llorente, 1993).

Dispersal and vicariance are two separate phenomena that attempt to explain current distributions. The main differences between these two schools and some of their principles are outlined below (modified from Savage, 1982):

DISPERSAL	VICARIANCE
Explains the distribution of individual groups. Therefore there is a distinction between different kinds of biogeography, e.g. phytogeography and zoogeography.	Explains the distribution of biota in space and time. Therefore does not consider different biogeographies: there is only one.
Centers of origin are the places where a group originated and dispersed using dispersal routes.	Does not consider centers of origin, considers centers of endemism.
Does not require demonstration of a monophyletic origin for the group under analysis (paraphyly = monophyly).	Requires demonstration of a monophyletic origin for the group under study.

DISPERSAL	VICARIANCE
Dispersal events and vagility of the group are key phenomena.	Dispersal events and vagility of a group are not relevant.
The fossil record is crucial in reconstructing biogeographic histories, e.g. center of origin, direction of dispersal, and age of the group.	The fossil record may be considered as a secondary source of information, but it cannot contradict evidence from recent distributions. Can support but not falsify a vicariance hypothesis.
Considers the dispersal of a group across barriers, the population goes through speciation, resulting in two allopatric sister species. The barrier is older than the disjunction.	Considers that populations are fragmented by barriers and undergo allopatric speciation resulting in the formation of sister taxa. The barrier is the cause of disjunction.
Generally does not consider that changes in geography are fundamental in explaining the actual distribution of groups. Dispersal ability is mainly responsible for this phenomenon.	Changes in geography, ecology and paleoclimatic events are principal explanations for the actual distribution of biotas. Orogeny and plate tectonics are key elements.
Phyletic speciation is a valid concept. Fossils are considered as ancestors of recent species.	Phyletic speciation is not valid. Therefore an evolutionary species concept (Simpson, 1961; Wiley, 1981) is adopted.
Spacial (allopatry, parapatry, and sympatry) relations are ambiguous.	Spacial relations are important; sympatry indicates dispersal, allopatry and parapatry indicate vicariance.
Some initial notion of the age of groups is needed, timing of geologic and climatic events and centers of origin.	No prior judgement of former history of dispersals or geologic ages of distributional events; these are discovered by analysis.
Eclectic analytical method: Equal weight is given to original historical patterns, dispersals, climatic effects, evolution in situ and interrelationships; final arbiter is usually paleontology.	Robust analytical method: Constructs area cladograms that are tested by cladograms of relationships for individual taxa; geologic history is important and novel geologic hypotheses can be found by the analysis.

A BRIEF HISTORY OF METHODS OF ANALYSIS IN CLADISTIC BIOGEOGRAPHY

Since the early 1970s there has been much controversy over which paradigm best explains historical relationships of organisms in a geographical framework. Much of the recent research has focused on the methodology of cladistic biogeography and panbiogeography. The methods of analysis that have been proposed in cladistic biogeography include: reduction of area cladograms, ancestral species maps, component analysis, Brooks parsimony analysis (BPA), and three area statements.

Rosen (1978) using his method of "reduction of area cladograms" hypothesized the biogeographic relationships of two genera of freshwater fishes (*Heterandria* and *Xiphophorus*) in southern Mexico and Central America. Rosen first produced taxonomic cladograms, then searched for the areas of endemism where these groups were found. Then he replaced the species names for the areas of distribution on the cladograms to produce area cladograms. Finally, he compared the area cladograms and eliminated incongruent information in order to find a pattern of congruency among the area cladograms (See Espinosa and Llorente, 1993 for a discussion of

this procedure). But this method can be criticized because it only finds irrefutable congruent patterns, which is not always the case in nature.

The second method, complementary to the one proposed by Rosen, is that of Wiley (1980, 1981). This method has been labeled "ancestral species maps" and attempts to determine whether area cladogram incongruencies are due to different responses to speciation events, dispersal, or peripheral isolation. This method offers a better explanation of Rosen's fishes, but can be criticized because it introduces assumptions not supported by the data (Humphries and Parenti, 1986).

The third method which also analyses incongruencies in distributional data is "component analysis" (Nelson and Platnick, 1981). Component analysis also uses taxonomic cladograms that are transformed into area cladograms. A component is equivalent to an internode in an area cladogram. For example, in Fig. 1, A and B are components and represent an hypothesis of relationships for the areas above that particular component. Thus a component can be interpreted as the distributional area of an ancestral species. When comparing two or more area cladograms, various incongruencies may arise due to: groups being compared which have historical patterns of different age, local extinction of one or more taxa in different
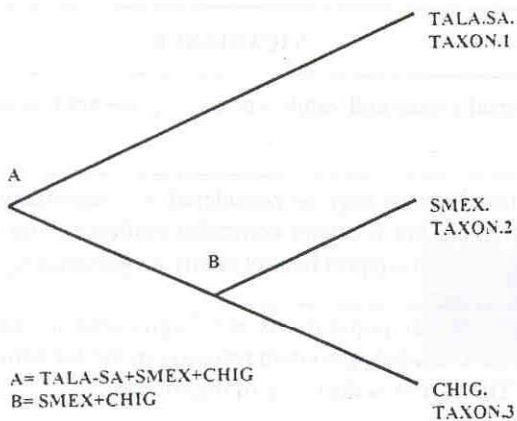
Fig. 1. — An area cladogram illustrating components A and B, see Fig. 2 and text. TALA.SA. = Talamanca ridge-South America, CHIG. = the highlands of Chiapas and Guatemala, SMEX. = Sierra Madre del Sur.

Fig. 2.—Area cladograms showing the 15 possible solutions to the probelm of Fig. 1. See text for explanation.

areas, sampling errors, widespread distribution of a taxon, redundant distributions, and erroneous determination of the taxa (Cracraft, 1988; Espinosa and Llorente, 1993; Humphries and Parenti, 1986; Morrone and Carpenter, 1994; Page, 1990). In order to resolve the incongruencies mentioned above, Nelson and Platnick (1981) proposed two methodological assumptions known as Assumptions 1 and 2. The theoretical principles of these assumptions are outlined below and are illustrated in Figs. 1 and 2.

Assumption 1: whatever is true of one occurrence of a widespread taxon, is true of other occurrences of the same widespread taxon. For example, if the population of taxon 1 in SA (Fig. 1) is found to be different from the population in TALA, then according to this assumption the relationship of these taxa and their areas will be the same with respect to the sister relationship of the areas SMEX and CHIG (Fig. 2a, 2b, 2c). Assumption 2: whatever is true of one occurrence of a widespread taxon, is not necessarily true for other occurrences of the same widespread taxon. For example, in the same case as above, the discovery of a different relationship between the taxa in TALA and SA may change the relationship of their areas and the sister relationship of SMEX and CHIG (Fig. 2a-2o). For a complete example and solutions using these assumptions, see Espinosa and Llorente (1993) and Humphries and Parenti (1986).

A third theoretical approach was developed by Zandee and Roos (1987), which was referred to as Assumption 0. The fundamentals of Assumption 0 are as follows: areas sharing the same taxon should be considered sister areas (monophyletic). For example, if the population of taxon 1 in SA (Fig. 1) is found to be different from the population in TALA, their areas should be considered sister areas (Fig. 2a). All these assumptions emphasize the problem of dealing with widespread taxa and help to resolve incongruencies when comparing different area cladograms that were derived from taxonomic cladograms. They help to explain the relationship of a group of areas of endemism. It is important to note that Assumption 2 encompasses Assumptions 0 and 1, and is considered less restrictive than the other two assumptions (Page, 1988).
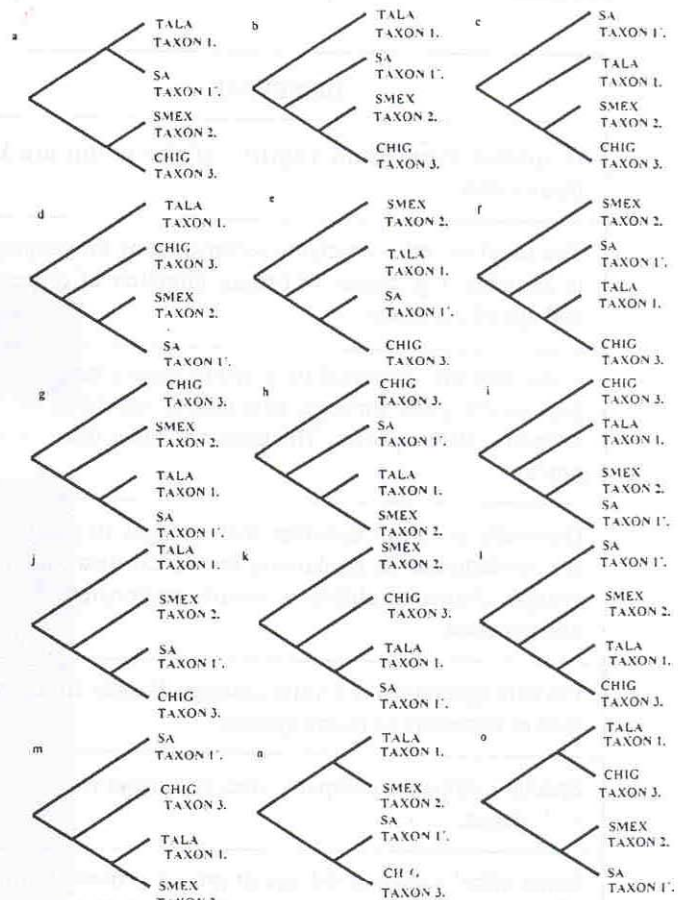
A fourth approach to solve incongruencies derived from differences in area cladograms is called "Brooks parsimony analysis" (BPA), and is similar to other parsimonious methods in biogeography (Zandee and Ross, 1987; Wiley, 1988a; Espinosa and Llorente, 1993). In BPA a binary data matrix is constructed from area cladograms using presence (1) and absence (0) of the terminal and ancestral species in the areas. Wiley proposed that these matrices can be processed under Wagner parsimony criteria using PAUP (Swofford, 1993) or Hennig86 (Farris, 1988). This method gives results that are biased to the solutions under Assumption 0 (Espinosa and Llorente, 1993; Morrone and Carpenter, 1994). It should be noted that there have been other criticisms to BPA (see Cracraft, 1988; Page, 1990), although it has been widely used to solve several biogeographic problems (Wiley, 1988a,b; Flores-Villela, 1991; Morrone and Carpenter, 1994).

The last approach, called "Three Area Statements" (TAS), was developed by Nelson and Ladiges (1991a,b), and is also considered a parsimony method in biogeography (Morrone and Carpenter, 1994). To apply this method, the distribution of clades should be coded as a group of three-area statements. A computer program (TAS) is used to implement this method, and to produce a data matrix to be analyzed by a parsimony program. TAS normally implements only Assumptions 0 and 1 but data manipulation allows for Assumption 2 to be addressed as well (Morrone and Carpenter, 1994). This method has been roundly rejected and is no longer in use (Wilkinson, 1994).
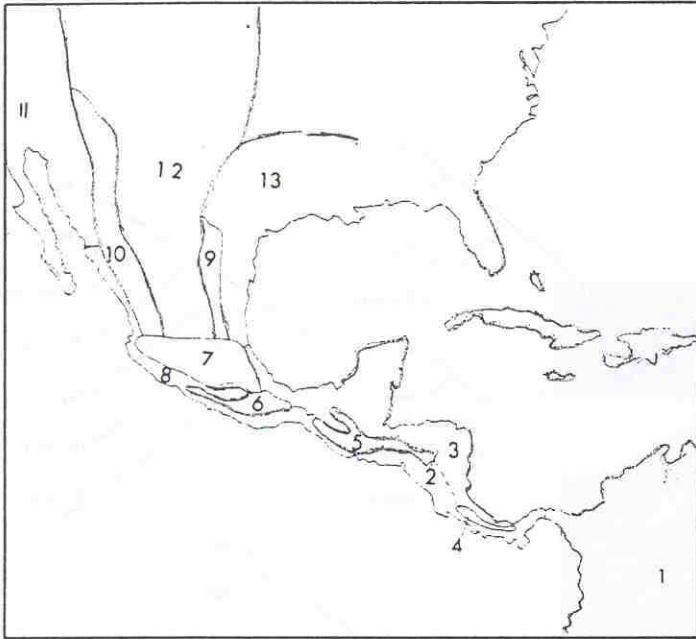
Fig. 3.—Map showing the 13 areas of endemism from Flores-Villela (1991). See text for identification of numbered areas.

Assumptions 0, 1, 2 and BPA can be implemented using computer programs, in particular COMPONENT 1.5 (Page, 1989), Hennig86 (Farris, 1988) or PAUP (Swofford, 1993) for BPA. Recently, Page (1990, 1993, 1994) has developed an alternative approach to implement assumptions 0, 1, and 2 (COMPONENT 2.0, Page, 1993). This method was originally developed by Goodman et al. (1979) for mapping gene clado-grams onto organism cladograms, and is called "reconciled trees" (Page, 1994). The advantage of the reconciled trees method is that it allows evaluation of discrepancies between area cladograms and taxonomic cladograms (duplications, leaves added, losses). These measures of fit, as Page (1994) points out, may have some biological meaning, but some of them may not and can be considered as items of error (Nelson and Platnick, 1981). The biological interpretation of meaning-ful measures of fit is that duplications may be interpreted as cospeciation events (Page, 1994), while losses may be inter-preted as extinctions or unsampled taxa (Slowinski, 1993). The importance of applying this method is that it is possible to evaluate the ad hoc assumptions to explain the differences between taxa and area cladograms.

The main objective of this paper is to compare different hypotheses of area relationships (for México and Central America) constructed using reconciliation methods of COM-PONENT 2.0 under cladistic biogeographic assumptions, and to explore which of these implies a lesser number of ad hoc explanations.

METHODS

Thirteen areas of endemism were chosen for analysis (Fig. 3) based on the biogeographic scenarios of Morafka (1977) and Savage (1982). These areas are identified in Flores-Villela (1991): 1) northern South America (SA), 2) the eastern Central American Atlantic lowlands (ELL), 3) the

western Central American Pacific lowlands (WLL), 4) Talamanca ridge, Central America (TALA), 5) the highlands of Chiapas, México and Guatemala (CHIG), 6) the Sierra Madre del Sur highlands of Southern México (SMEX), 7) the Transvolcanic Axis of central México (TVA), 8) the Pacific lowlands of México and Balsas depression (PCBAL), 9) the Sierra Madre Oriental of eastern México (SMOR), 10) the Sierra Madre Occidental of western México (SMOC), 11) the Sonoran Desert (DSON), 12) the Chihuahuan Desert (DCHI), and 13) the semiarid lands of Tamaulipas, México and Southern Texas (TAMS).

Six general area cladograms (Fig.5a-f) were constructed using COMPONENT 2.0 (Page, 1993) using the method of reconciled trees (Page, 1994) and implementing Assumptions 0, 1, and 2. Even though 16 taxonomic cladograms were avail-able after splitting the cladogram from the lizards of the family Xantusiidae (Bezy and Sites, 1987), into two cladograms of *Xantusia* and *Lepidophyma*, (just using information of *Lepidophyma*), only 10 were used to produce the general area cladograms (GAC's) under study (Fig. 4). The criterion for eliminating some of the area cladograms was primarily due to the fact that five of the monophyletic groups have extensive distributions outside the area under consideration, and others have endemic species in Baja California which is not consid-ered in this analysis.

The following taxonomic cladograms were used with COMPONENT 2.0 implementing Assumptions 0, 1, and 2 to build six GAC's (Fig. 5a to 5f): *Abronia* (Campbell and Frost, 1993), lizards of the family Corytophanidae (Lang, 1989), *Lepidophyma* (Bezy and Sites, 1987), *Mesaspis* (Good, 1988), *Rana palmipes* (Hillis and De Sá, 1988), the *R. pipiens* com-plex (Hillis et al., 1983), *Ateuchus* (Kohlmann and Halffter, 1988), *Elliptoleus* (Liebherr, 1991), *Bothriechis* (Crother et al., 1992), and frogs of the *Eleutherodactylus gollmeri* group (Savage, 1987). These ten taxonomic-area cladograms are shown in Figs. 4a-4j.

Since Assumption 2 is not directly implemented with COMPONENT 2.0, results derived from this assumption should be viewed with discretion. To implement Assumption 2, areas in each cladogram were chosen so that the majority of areas were fixed and the others were allowed to float during the analysis (see Page, 1993, pp 8-26).

After the implementation of Assumptions 0, 1, and 2 a consensus was performed with the resulting GAC's. Fifty per-cent Majority Rule (MR) and Nelson consensus were chosen for comparison with the hypothetical area cladogram.

All six of the GAC's were separately compared with each of the taxonomic cladograms, using the method of reconciled trees (Page, 1994), with the routine "Map Trees (Map onto all trees)" and implementing Assumptions 0, 1, and 2. This was done to find the best historical biogeographic hypotheses for the taxa under investigation. Also a similar routine was per-formed using the option of pruning the taxon-leaves, and implementing Assumptions 0, 1, and 2. This method allows one to find which taxa on a cladogram may represent dispersal events. When the values of the comparison between clado-grams are significantly low (when pruning one taxon), this suggests the possibility of a dispersal event; therefore the
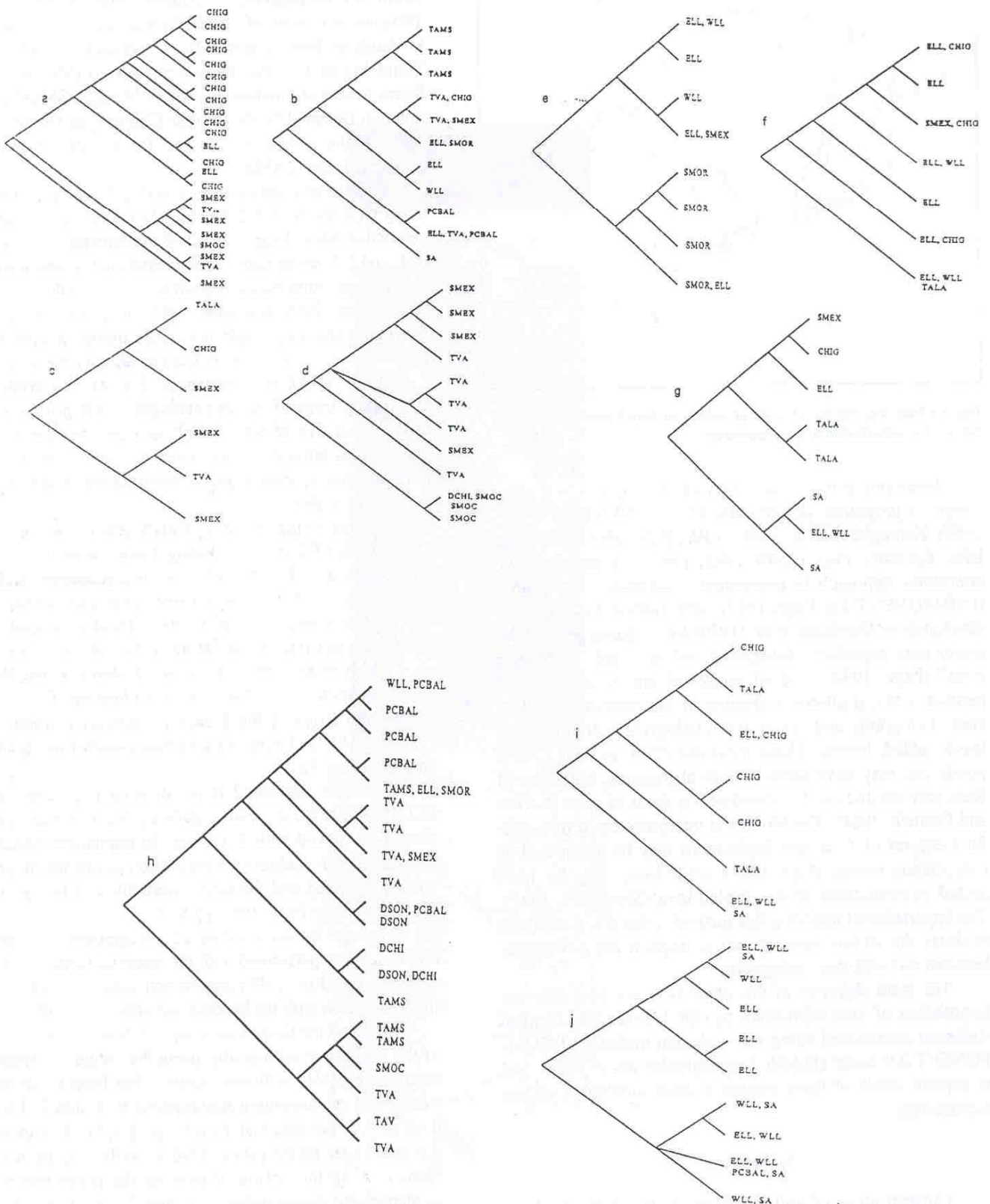
Fig. 4—Ten area cladograms used with COMPONENT 2.0 to produce the GAC's from Assumptions 0, 1, and 2. 4a. *Abronia* (Campbell and Frost, 1993). 4b. *Ateuchus* (Kohlmann and Halffter, 1988). 4c. *Mesaspis* (Good, 1988). 4d. *Elliptoleus* (Liebherr, 1991). 4e. *Lepidophyma* (Bezy and Sites, 1987). 4f. *Eleutherodactylus gollmeri* group (Savage, 1987). 4g. *Rana palmipes* group (Hillis and De Sá, 1988). 4h. *R. pipiens* complex (Hillis et al., 1983). 4i. *Bothriechis* (Crother et al., 1992). 4j. Corytophanidae (Lang, 1989).

Fig. 5.—The six area cladograms used in this study. Cladograms 5a and 5b are majority rule and Nelson consensus respectively, derived from Assumption 0; cladograms 5c and 5d majority rule and Nelson consensus respectively derived from Assumption 1; and cladograms 5e majority rule and 5f Nelson consensus from Assumption 2.

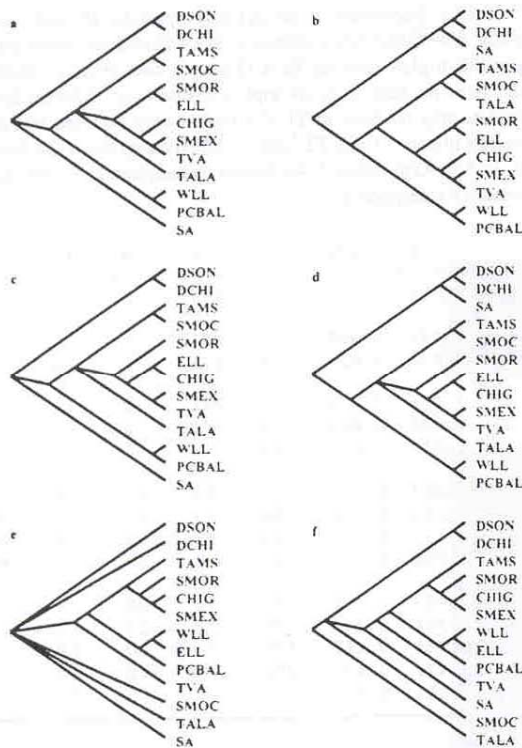**Table 1.**—General values for area cladograms using the method of reconciled trees with Assumption 0 (Page, 1993, 1994). Asterisk denotes values that deviate significantly from random trees at $p < 0.05$. Underline boldface values indicate the lowest reconciliation values for each taxon.

TAXA	AS-0/MR/NE			AS-1/MR/NE			AS-2/MR/NE		
	DU	LA	LO	DU	LA	LO	DU	LA	LO
Abronia	17	22	18	17	16	12*	17	23	23
Corytophanidae	8	24	14	8	24	14	8	24	16
Lepidophyma	6	12	9	6	13	9	7	16	13
Mesaspis	3	8	7	3	8	7	3	9	9
Bothriechis	5	13	9	5	13	9	5	16	9
							5	19	11
E. gollmeri grp.	6	24	14	6	23	17	6	23	12
R. palmipes	3	11	5*	4	14	9	3	11	5
							3	10	5*
R. pipiens	15	71	31*	15	71	35*	15	91	37*
Ateuchus	6	27	13*	7	33	18*	8	48	24
Elliptoleus	8	12	7	8	12	7	8	14	8

MR= 50% majority rule consensus, NE= Nelson consensus, DU= duplications, LA= leaves added, LO= losses.

Table 2.— General values for area cladograms using the method of reconciled trees with Assumption 0. pruning each taxon-leaf to find taxa that supposedly dispersed (Page, 1993; Slowinski, 1993). Values in this table represent the lowest value after pruning each taxon-leaf. Asterisk denotes values that are significant at $p < 0.05$ from random trees. Underline boldface values indicate the lowest reconciliation values for each taxon; abbreviations are defined as in Table 1.

TAXA	AS-0/MR/NE			AS-1/MR/NE			AS-2/MR/NE		
	DU	LA	LO	DU	LA	LO	DU	LA	LO
Abronia	17	17	13	16	7	6*	17	18	18
Corytophanidae	7	14	9*	7	14	9*	7	14	9*
Lepidophyma	5	9	6*	6	9	6*	6	8	5*
Mesaspis	2	3	3	2	3	3	2	3	3
Bothriechis	4	7	5*	4	7	5*	4	7	5*
E. gollmeri grp.	5	16	11*	5	15	16*	4	16	8*
R. palmipes	2	0	0*	3	3	3*	2	0	0*
							5		
R. pipiens	13	52	26*	13	52	30*	15	74	31*
Ateuchus	5	20	9*	6	25	13*	7	35	17*
Elliptoleus	6	1	1*	6	1	1*	6	1	1*

resulting reconciled cladogram should have lower values in the reconciliation analysis (Page, 1993; Slowinski, 1993).

A set of 1,000 random cladograms was constructed, and each taxon was compared with this group of random cladograms using the method of reconciled trees with Assumptions 0, 1, and 2 (Page, 1994), with the routine "Map Trees" (Map onto all trees). Frequency distribution histograms for two of the reconciliation values of the trees (leaves added and losses) were used to compare the results of the best hypotheses of biogeographic relationships, using all data and pruned leaf-taxon (data in Tables 1 and 2). Statistical values of significance ($p < 0.05$) were used to determine which relationships are likely due to chance. The lowest values, for all comparisons mentioned above, were found consistently for Assumption 2. Although the value of significance for the results from Assumptions 0 and 2 were the same for the same taxa, we preferred using the results from Assumption 0 because Assumption 2 is not well implemented in the program, and these were used to compare all of the trees (Tables 1 and 2).

The six GAC's were compared to each other with the COMPONENT "trees, tree-to-tree distances, by triplets routine" (the best method for rooted trees, Page, 1993). These results give some indication of the differences in the area cladograms (Table 3).

The procedure followed in this paper can be abbreviated below: 13 areas of endemism were chosen (Fig.3); ten taxonomic cladograms were converted to area cladograms mapping the 13 areas of endemism onto the cladogram (Fig.4); GAC's were obtained using COMPONENT 2.0 with Assumptions 0, 1 and 2; 50% majority rule and Nelson consensus were performed to obtain six GAC's (two for each assumption; Fig. 5); each taxonomic-area cladogram was reconciled with each of the six GAC's (Table 1); each taxonomic-area cladogram was pruned to test for taxa that may have dispersed and reconciled with each of the six GAC's (Table 2); 1,000 random trees were generated and were reconciled with each of the ten taxonomic-area cladograms, both with the original trees and with the pruned trees (asterisk in Tables 1 and 2); the six GAC's were compared to each other to check how different they are (Table 3).

RESULTS

The area cladograms compared in this study are shown in Fig. 5. None of the six GAC's are identical, although all of them share several features. The Sonoran (DSON) and Chihuahuan (DCHI) deserts share a strong relationship that is evident in all of the cladograms. There is a strong relationship between the western lowlands (WLL) and the Pacific lowlands-Balsas depression (PCBAL) in the four cladograms derived from Assumptions 0 and 1, as well as between Tamaulipas-Texas (TAMS) and the Sierra Madre Occidental (SMOC). The Sierra Madre del Sur (SMEX) and the Transvolcanic Axis (TVA) are closely related in the cladograms derived from Assumptions 0 and 1. There are other rela-

tionships that are consistent in some of the GAC's but those above are the most obvious. A MR consensus (not shown) for all of the GAC's produces a polytomy showing only the sister relationships of the areas mentioned above, with the exception of Tamaulipas-Texas and the Sierra Madre Occidental.

In Table 1 the values are derived from the comparison of reconciling the taxonomic cladograms with each of the GAC's. It is important to notice that only for the GAC from Assumption 0 was the comparison among the MR and Nelson consensus different for *Bothriechis* and the *Rana palmipes* group. These results show that the GAC derived from Assumption 0 is the cladogram that represents the fewest assumptions for the majority of taxa (*Lepidophyma, Mesaspis, Bothriechis, Rana pipiens* group, and *Ateuchus*). The GAC from Assumption 1 presented low values for the lizards of the genera *Abronia* and *Mesaspis*, and the vipers of the genus *Bothriechis*. The GAC from Assumption 2 has lower values for the frogs of the *Eleutherodactylus gollmeri* group, and *Rana palmipes* group. In the latter the Nelson consensus has the lower values. Only the hypothetical area cladogram has lower values for the lizards of the family Corytophanidae.

After pruning all the taxon-leaves and comparing the results with all of the six GAC's the results are about the same (Table 2). All taxa retain the same GAC for the explanation of their biogeographical relationships. In summary, the GAC from Assumption 0 is the best hypothesis for the majority of groups under study.

The same values generated for Assumption 1 (not shown), were higher or the same compared to those from Assumption 0 (Tables 1 and 2). Although values from Assumption 2 (not shown) were lower than those in Tables 1 and 2, the lowest and those statistically different from random are almost the same as for Assumption 0.

After generating 1,000 random trees and reconciling them with each of the taxonomic groups separately using Assumption 0, comparison was made between the values from Table 1 with the above results. The GAC's from Assumptions 0 and 1 show more values that are significantly not random (at $p < 0.05$), even though some of them were not the lowest values following reconciliation with the taxonomic groups. When the reconciliation values from pruned trees are compared with the random generated values, the number of taxa as well as the GAC's have more significantly nonrandom values. The GAC from Assumption 1, for example, has significant values for all taxa except *Mesaspis*.

Table 4 summarizes the distribution of taxa that may have dispersed. Seven areas deserve attention, CHIG, DSON, DCHI, SMEX, TAMS, TVA, and TALA. These areas all included taxa that essentially had not dispersed, and the ELL and WLL have several examples of widespread taxa. Remaining areas are considered intermediate between these extremes.

Table 3 shows comparisons between all pairs of trees by triplets. There are 286 possible triplets for trees with 13 branches. It is evident that when comparing two trees derived from the same assumption, they reflect the lowest dissimilarity values, and therefore are not discused in this part of the analysis. The two trees that are more similar are the Nelson consen-

Table 3.—Tree-to-tree distances using triplets for all GAC's considered in this study. SD= Symmetric Difference, SJA= Strict Joint Assertions, Q= maximum possible triplets resolved for a 13-branch cladogram, s= triplets resolved and the same for both trees, d= triplets resolved and different for both trees, r1= triplets only resolved in T1, r2= triplets only resolved in T2, u= unresolved triplets in both T1 and T2. Tree 1= MR Assumption 0, 2= Nelson Assumption 0, 3= MR Assumption 1, 4= Nelson Assumption 1, 5= MR Assumption 2, 6= Nelson Assumption 2.

	SD	SJA	Q	s	d	r1	r2	u
1|	0.055	0.000	286	256	0	30	0	0
1|	0.020	0.020	286	251	5	0	0	30
2|	0.074	0.020	286	251	5	0	30	0
1|	0.056	0.020	286	251	5	20	0	10
2|	0.036	0.018	286	271	5	0	10	0
3|	0.038	0.000	286	256	0	20	0	10
1|	0.429	0.325	286	129	62	5	65	25
2|	0.465	0.342	286	129	67	0	90	0
3|	0.434	0.330	286	128	63	5	65	25
4|	0.453	0.330	286	128	63	5	85	5
1|	0.462	0.412	286	141	99	29	16	2
2|	0.484	0.466	286	143	125	0	18	0
3|	0.466	0.417	286	140	100	28	16	2
4|	0.478	0.450	286	142	116	10	18	0
5|	0.155	0.000	286	196	0	72	0	19

Table 4.—Number of times an area is considered to host a taxon that may have dispersed according to data in Table 2. Only those taxa having a $p < 0.05$ siginificance from random trees are considered.

AREA	AS-0	AS-1	AS-2
DSON	1	1	1
DCHI	1	1	1
TAMS	–	–	–
TVA	1	–	–
WLL	5	4	3
ELL	6	6	6
PCBAL	3	2	2
SMOR	1	2	2
SMEX	–	1	1
SMOC	1	2	1
CHIG	–	–	1
TALA	–	–	–
SA	2	2	2

sus trees from Assumptions 0 and 1, and the next most similar are the GAC's derived from the MR consensus from Assumption 1 as compared to the MR and Nelson consensus trees from Assumption 0. All of the other comparisons show dissimilarity values higher than these.

DISCUSSION AND CONCLUSIONS

Six possible hypotheses of area relationship were studied for the 13 areas of endemism (Fig. 5). These results can be interpreted in two ways. One interpretation is the unmodified data in Table 1 which implies that each of the six GAC's may have a different explanation for the biogeographic scenarios for each of the taxa individually compared. In other words,

those GAC's tell us parts of the history. If only the lowest values are taken as the best explanation, Assumption 0 better explains the biogeographic scenario for seven of the ten taxa, Assumption 1 for five taxa, and Assumption 2 for three taxa. Some of these values are identical for more than one GAC, but again Assumption 0 explains three taxa that have no other alternative explanation. Table 2 shows that after pruning trees (assuming some dispersal for some of the taxa), some of the GAC's present the same values for the same taxa, and Assumption 0 explains the biogeographic history of eight taxa but only three taxa are explained by this GAC and no other GAC. Pruning trees makes the values more uniform and opens the possibility of more alternative explanations for each taxon.

Since no consistent pattern of relationships was found among the six GAC's, robustness was tested for the results shown in Fig 5, by implementing Assumptions 0 and 1 using frogs of the *Rana pipiens* group and vipers of the genus *Bothriechis*, because these two groups are represented in all of the 13 areas under study. We added one group after each analysis and compared the resulting cladograms sequentially until six groups were included (*Ateuchus, Elliptoleus, Rana palmipes* group, and lizards of the family Corytophanidae were added consecutively). The results show that at least the sister relationships of the Sonoran and Chihuahuan deserts, western lowlands and Pacific lowlands-Balsas depression, Tamaulipas-Texas and Sierra Madre Occidental appear invariable since the first analysis. The relationship of the Transvolcanic Axis, the Sierra Madre del Sur, and the Chiapas-Guatemalan highlands appears in a trichotomy once a third group is added to the analysis.

After doing the analysis with the *Rana pipiens* group and vipers of the genus *Bothriechis*, addition of a third group produces cladograms with three main nodes: node I is represented by the Sonoran and Chihuahuan deserts, node II can be subdivided in two subgroups a) Tamaulipas-Texas and the Sierra Madre Occidental, and b) the Transvolcanic Axis, Sierra Madre del Sur, eastern lowlands, Chiapas-Guatemalan highlands, and Sierra Madre Oriental; and node III includes the western lowlands and the Pacific-Balsas lowlands. South America is either part of the node I or is located as the basal branch of the whole cladogram. The Talamancan highlands float as part of subnode (a) or (b) of node II. All of these nodes are essentially the same as those in Fig. 5 for the MR and Nelson consensus cladograms under assumptions 0 and 1. However none of these nodes is equivalent to the other four GAC's in Fig. 5.

It is difficult to interpret hypotheses of interrelationships when the GAC's are different. For example, Morrone and Carpenter (1994) in discussing the differences derived from applying several methods of biogeographic analysis, concluded that when the data are "clean" (few widespread taxa, redundant distributions and missing areas), results are consistent when applying different methods. This statement is based on the assumption that taxonomic work done previous to the biogeographic analysis is correct. As pointed out by Cracraft (1988) taxa may have only one history, but the areas inhabited by them may have more than one history relative to their biotas.

Two examples illustrate this point. In lizards of the genus *Abronia*, there are two phylogenies available, one proposed by Good (1988) and a second by Campbell and Frost (1993). In these two papers the authors use almost the same approach for characterization and coding of external morphological features for phylogenetic inference. However, Campbell and Frost made an extensive analysis of all the characters used by Good, and criticized the use of some of them. Both phylogenies are very similar, but when applying them to Assumptions 0 and 1 with COMPONENT 2.0 the resulting area cladograms are very different. The phylogenetic hypothesis of Good (1988) results in three area cladograms, whereas that of Campbell and Frost (1993) results in a single cladogram for area relationships, under both assumptions. It is important to notice that this group of lizards does not have widespread species in the areas used for this study.

The second example is illustrated by the two available hypotheses of relationships for lizards of the genus *Urosaurus*. The earliest proposal of taxonomic relationships was published by Mittleman (1942), but a more recent cladistic analysis by Wiens (1993) drastically altered species relationships. Both phylogenies analyzed under Assumptions 0 and 1 resulted in three area cladograms for the Wiens' hypothesis, and either 111 (Assumption 0) or 315 (Assumption 1) area cladograms with Mittleman's hypothesis. Interestingly, the biogeographic results using Wiens' phylogeny are more concordant with the known biogeographical history for the region of Baja California and the coast of western México (Murphy, 1983; Wiens, 1993), placing Baja California as the sister area of western México (WLL, PCBAL). None of the consensus analyses performed with the area cladograms derived from Mittleman's phylogeny produced these biogeographic relationships.

In this study, it is difficult to choose the hypothesis of area relationships that best explains the historical distributional patterns of a biota. As mentioned previously, other authors have faced the same problem (Cracraft, 1988; Morrone and Carpenter, 1994) when studying different groups of taxa in other regions. Morrone and Carpenter (1994) compared all of the available implementations of component analysis, and found that all of them were unsatisfactory. Even considering these limitations, the reconciliation method seems the best for comparing hypotheses of relationships for areas and taxa, since it is possible to compare solutions using items of error as a parameter. Page (1994) points out that some of these measures of congruence do not have a direct biological interpretation. In awaiting a better method to deal with the problems that obscure biogeographic patterns (widespread taxa, redundant distributions and extinctions), reconciliation of trees helps to understand and quantify them. For widespread taxa and redundant distributions, component analysis seems to be the best method of analysis, despite the fact that Assumption 2 is not well implemented in the available computer programs for biogeography (See Morrone and Carpenter, 1994 and Page, 1993). According to Humphries (1989) and Morrone and Carpenter (1994), Assumption 2 is probably the best way to deal with dispersal (which causes widespread taxa mainly), but extinction is poorly understood in a biogeographic context.

and is difficult to incorporate into an historical biogeographic model (Grimaldi, 1992).

Considering the multiple patterns that the six GAC's represent, an obvious conclusion is that the biogeographic history of Central America, and the adjacent lands to the south and to the north, is complex. Croizat (1958) predicted this when he discovered that generalized tracks overlap in southern México and Central America. Savage (1982) constructed a biogeographic scenario that implied some dispersal as well as vicariant events of different ages. If dispersal of many taxa is responsible for the ambiguity found here, the vicariance patterns will be obscured and difficult to recover. The data in Table 2, indicate that dispersal seems to be the dominant factor influencing the biogeographic patterns for the biota of México and Central America. If we accept this hypothesis, then the role of the lowlands in dispersal events has been very important (see Table 4), since they harbor many widespread species, whereas the highlands show more restricted distributions and higher localized endemism (see Flores-Villela, 1993 and references therein). Looking at the species that would have to be removed from a cladogram due to dispersal, with the exception of the lizards of the genera *Abronia* and *Mesaspis* (that do not have widespread species), in all of the other cladograms the taxa removed mostly have widespread distributions, except for the beetles of the genus *Ateuchus*.

On the other hand, if more than one vicariant event occurred between North America and South America a⁻ proposed by Savage (1982), then multiple lineages are probably involved, and these different vicariant histories preclude the possibility of a single dominant biogeographic pattern in this region. The problem of detecting different ages for speciation events still awaits a better solution (see discussion in Morrone and Carpenter, 1994, and references therein). Nevertheless, relying on dispersal and multiple lineages is still an ad hoc conclusion. If there is a pattern to explain the biogeographic history of this part of the world, it is yet to be found.

RESUMEN

Se hizo una comparación entre seis cladogramas generales de área (CGA) para México y Centro América usando el método de reconciliación de cladogramas en el programa COMPONENT versión 2.0 (Page, 1993). Los CGA que se usaron en este estudio son seis cladogramas derivados de la implementación de las suposiciones 0, 1 y 2 con el programa COMPONENT 2.0. Para cada una de las suposiciones de arriba se hizo un CGA por consenso utilizando los consensos de 50% de mayoría y de Nelson. Cada uno de los seis CGA fue reconciliado independientemente con 10 grupos taxonómicos (escarabajos, lagartijas, serpientes y ranas), esto se hizo con la finalidad de ver cuál de los CGA se ajustaba mejor a la historia biogeográfica de cada taxón. Los resultados mostraron que el CGA derivado de la suposición 0 era el que mejor explica la historia biogeográfica de cinco de los 10 taxones. Cuando se hizo un análisis removiendo una rama con un taxón para probar hipótesis de dispersión, los resultados indican que todos los CGA explican la historia biogeográfica de los 10 taxones estudiados. Se generaron mil cladogramas generalizados de área al azar y cada taxón se reconcilió con estos cladogramas.

Los valores resultantes de los dos ensayos anteriores se compararon con los histogramas de frecuencia de los items de error ($p < 0.05$) para eliminar la probabilidad de que los seis CGA son producto del azar. Considerando la complejidad biogeográfica del área de estudio, se concluye que cada cladograma puede explicar parte de la historia biogeográfica de cada uno de los taxones estudiados.

LITERATURE CITED

Bezy, R. L. and J. W. Sites. 1987. A preliminary study of allozyme evolution in the lizard family Xantusiidae. Herpetologica 43:280-292.

Brundin, L. 1966. Transantartic relationships and their significance as evidenced by chironomid midges. Svenska Vetensk. Handl. 11:1-472.

_____. 1972. Phylogenetics and biogeography. Syst. Zool. 21:69-79.

Campbell, J. A. and D. R. Frost. 1993. Anguid lizards of the genus *Abronia*: revisionary notes, descriptions of four new species, a phylogenetic analysis, and key. Bull. Amer. Mus. Nat. Hist. 216:1-121.

Cracraft, J. 1988. Deep-history biogeography: Retrieving the historical pattern of evolving continental biotas. Syst. Zool. 37:219-236.

Craw, R. C. 1983. Panbiogeography and vicariance cladistics: Are they truly different? Syst. Zool. 32:431-437.

_____. 1988. Panbiogeography: Method and synthesis in biogeography. *In* A.A. Myers and P.S. Giller (Eds.). Analytical Biogeography. Chapman & Hall. London.

Croizat, L. 1952. Manual of phytogeography, or an account of plant dispersal throughout the world. W. Junk, The Hague.

_____. 1958. Panbiogeography. Vol. 2b. Published by the author. Caracas, Venezuela.

_____. 1962. Space, Time, Form: The Biological Synthesis. Published by the author. Caracas, Venezuela.

Crother, B. J., J. A. Campbell, and D.M. Hillis. 1992. Phylogeny and historical biogeography of the palm-pitvipers, genus *Bothriechis*: biochemical and morphological evidence. Pp 1-19. *In* J. A. Campbell and E. D. Brodie Jr. (Eds.). Biology of the Pitvipers. Selva Publs., Tyler, Texas.

Darlington, P. J. 1957. Zoogeography: The Geographical Distribution of Animals. John Wiley & Sons, Inc., New York.