Journal of Biogeography, **27**, 203–216

Cladistic biogeography of the Mexican transition zone

C. J. Marshall and J. K. Liebherr *Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853–0901, U.S.A.*

Abstract

Biogeographic relationships among nine montane areas of endemism across the transition zone between North and South America are analysed cladistically based on phylogenetic hypotheses of thirty-three resident monophyletic taxa of insects, fish, reptiles, and plants.

Areas of endemism include the Arizona mountains (AZ), Sonoran Desert (SD), Sierra Madre Occidental (OCC), southern Sierra Madre Occidental (SOC), Sierra Madre Oriental (ORI), Sierra Transvolcanica (TRAN), Sierra Madre del Sur (SUR), Chiapan-Guatemalan Highlands (CGH), and Talamancan Cordillera (TC).

Area relationships are summarized using Brooks Parsimony Analysis and Assumption 0, with the former resulting in more defensible biogeographic hypotheses.

Areas of endemism are dividable into two monophyletic groups; a northern group including AZ, SD, OCC, and ORI, and a southern group consisting of TC, CGH, TRAN, SUR, and the isolated southern regions of the Sierra Madre Occidental (SOC).

The northern set of areas are characterized by recent, probably Pleistocene, isolation and prevalent widespread species, whereas the southerly areas probably diverged after Pliocene closure of the Panamanian isthmus.

The southern areas are redundantly represented on many of the taxon-area cladograms by endemic species, indicative of much higher levels of endemism in the Sierra Transvolcanica and further south.

Use of a general area cladogram in such a transition zone permits explicit exploration of biogeographic patterns and establishes a predictive framework for taxonomy and conservation prioritization.

Keywords
Vicariance, areas of endemism, montane biota, Mexico, Central America.

INTRODUCTION

Mexico and Central America comprise one of the most biologically diverse regions of the world. This diversity, in conjunction with a complex geological history, has held the attention of biogeographers for more than a century. Soon after the recognition of the major biogeographic regions of the world (Sclater, 1858; Wallace, 1876), this area was recognized as a transition zone between the Nearctic and Neotropical biotas (Heilprin, 1887). Transition zones have been traditionally thought to be populated by groups exhibiting disparate distributional patterns. Because these disparate patterns have been the focus of most studies, distributions in one taxon have not been thought predictive or informative for other unrelated taxa. We utilize cladistic biogeography to simultaneously derive a general summary of patterns in a variety of groups occupying Mexico and Central America. We then demonstrate the utility of this general pattern for understanding the biotic diversification in the region.

A complete and detailed geological history for Mexico and Central America is not at hand. In general terms, however, we know that subduction of the Pacific and Cocos Plates under the North American Plate during the Cretaceous has produced most of the extensive orogenic activity, volcanism and uplifting characteristic of the region. Geologists paint a dynamic, almost mosaic, history of the terrestrial (emergent) topography (Morán-Zenteno, 1994). More recently, the opening of the Gulf of California as well as Pleistocene glaciation further modified the biotic patterns, especially in the north (Martin & Klein, 1984; Betancourt *et al.*, 1990; Van Devender, 1990a). Proponents of cladistic biogeography hold that the distributions of different taxa are related historically, and that they should display common patterns resulting from orogenic and widespread ecological events. Common patterns of this type are what this study seeks to uncover.

Recent biogeographic studies of Mexico and Central America are greatly influenced by Halffter (1961, 1965, 1976, 1987,

---

Correspondence: C. J. Marshall, Department of Entomology, Comstock Hall, Cornell University, Ithaca, NY14853–0901, U.S.A.

1991). The works of Halffter exemplify what can be called the transition zone approach. He delimits three overlapping biogeographic patterns: the Palaeo-American, Montane Meso-American and Nearctic Patterns. Taxa fitting the Palaeo-American Pattern display moderate levels of diversification in Middle America and have closely related taxa in South America and/or Africa. The Montane Meso-American Pattern refers to taxa that arose and diversified in Mexico and Central America. These taxa typically show their greatest diversity in the mountains of nuclear Central America, from southern Mexico and Guatemala through Nicaragua. The Nearctic Pattern encompasses taxa generally associated with montane habitats north of the Isthmus of Tehuantepec that have their closest relatives in the U.S.A. or Canada. Producing a synthesis of these different patterns is never attempted. Instead, separate histories dependent on various centres of origin are maintained as parallel explanations of biogeographic pattern.

More recently, biogeographers have made a call for explicit, scientifically testable biogeographic hypotheses for this region (Llorentes Bousquets, 1996). This study investigates patterns among areas of endemism in Mexico and Central America using cladistic biogeography. It therefore does not adopt *a priori* models of how various organisms have dispersed or speciated. Rather, we focus on the phylogenetic relationships of the taxa and their current distributions in order to infer historical relationships between specified areas of endemism (biotas). This study is modelled largely after Liebherr (1994a) in which a general biogeographic statement was produced for the region with Brooks Parsimony Analysis (BPA, Wiley, 1981; Page, 1990), using a variety of Mexican and Central American Carabidae (Insecta: Coleoptera). Although the data set contained taxa that would have been categorized as separate Halffterian biogeographic patterns, Liebherr uncovered a general biotic pattern that was not in conflict with the geological history of the region. The current analysis tests these initial results with a more extensive and phylogenetically diverse assemblage of taxa which inhabit similar areas of endemism.

Significant debates still exist between adherents of cladistic biogeography as to the justification and best methods for producing general area cladograms (Enghoff, 1996; Morrone & Carpenter, 1994). This is especially true in reference to regions for which a variety of fundamental area cladograms exist, and which are therefore held to represent transition zones, or hybrid areas. The conflicting views stem largely from the notion that incongruent fundamental area cladograms should not be combined because they represent distinct historical statements. The evidence for the uniqueness of each fundamental area cladogram is usually founded on process models of diversification, such as centres of origin, dispersal capacity or pre-existing biogeographic models. These biogeographic process models have been heavily refuted in cladistic biogeography literature (Croizat *et al.*, 1974; Platnick & Nelson, 1978; Nelson & Platnick, 1981; Wiley, 1987) for being both untestable scientifically and difficult or impossible to explicitly recognize in practice. For this reason, we do not adopt these models, and analyse the available fundamental area cladograms, searching for a pattern which is maximally congruent with all biogeographic information at hand. We see this approach as analogous to testing the homology of characters through simultaneous parsimony analysis (dePinna, 1991). In both types of analysis, no *a priori* judgements regarding the suitability of various patterns are made. Rather, the results of an analysis combining all known data are used in a reciprocal fashion to evaluate the individual constituent patterns; i.e. the reciprocal illumination of Hennig (1966). The resultant general area cladogram also has implications for conservation planning, as overall biotic relationships can be used to maximize preservation of disparate taxa and biotas (Faith, 1992a; 1992b).

MATERIALS AND METHODS

Areas of endemism

Areas of endemism are defined by overlapping species distributions (Platnick *et al.*, 1978). The areas of endemism used in this study correspond to those used by Liebherr (1994a) and were originally defined based on the concordant distributions of carabid beetles. With the exception of the Southern Sierra Madre Occidental (see below), the distributional patterns of the taxa used in this study are not significantly different. In this study, montane taxa display greater endemicity than taxa from low elevations. Hence, although our areas of endemism are centred on montane regions, they also include adjoining lowland regions such as the Yucatan peninsula (Fig. 1). Areas of endemism in this study represent subdivisions of those defined for montane forest birds (Hernández-Baños *et al.*, 1995). Our more finely defined areas are based on the generally greater endemicity of the insect, lizard, and fish taxa forming the basis of this analysis. A brief description of the geology and habitat types found in each area follows.

South-eastern Arizona (AZ)

The south-eastern corner of Arizona includes a number of small, disjunct mountain ranges presumably of Cretaceous or more recent origins. The Quaternary history of this region, based on its geology and fossilized pollen, has been reviewed by Martin (1963) and Van Devender (1990a). Some of the peaks reach heights above 2700 m and are characterized by high levels of endemism. The flora is highly variable both today and over time, containing arid desert conditions, grassland as well as oak/pine forest. This region is isolated from the Sierra Madre Occidental by the Sonoran Desert lying to the south and south–west, and from Mexico's central plateau and Sierra Madre Oriental by the Chihuahuan Desert lying to the south–east.

Sonoran Desert (SD)

The Sonoran region, as defined in this study, extends from the extreme southeast of California through southwestern Arizona and continues southward into the state of Sonora. It includes regions from below sea level to 1000 m in elevation. Baja California is occasionally considered part of the Sonoran Desert (Martin, 1963; Van Devender, 1990b), however, it is treated as a separate area in this study. Although Sonora boasts Mexico's oldest rock formations dating from the pre-Cambrian (Morán-Zenteno, 1994), marine fossils and sedimentary deposits indicate that most of the region was submerged

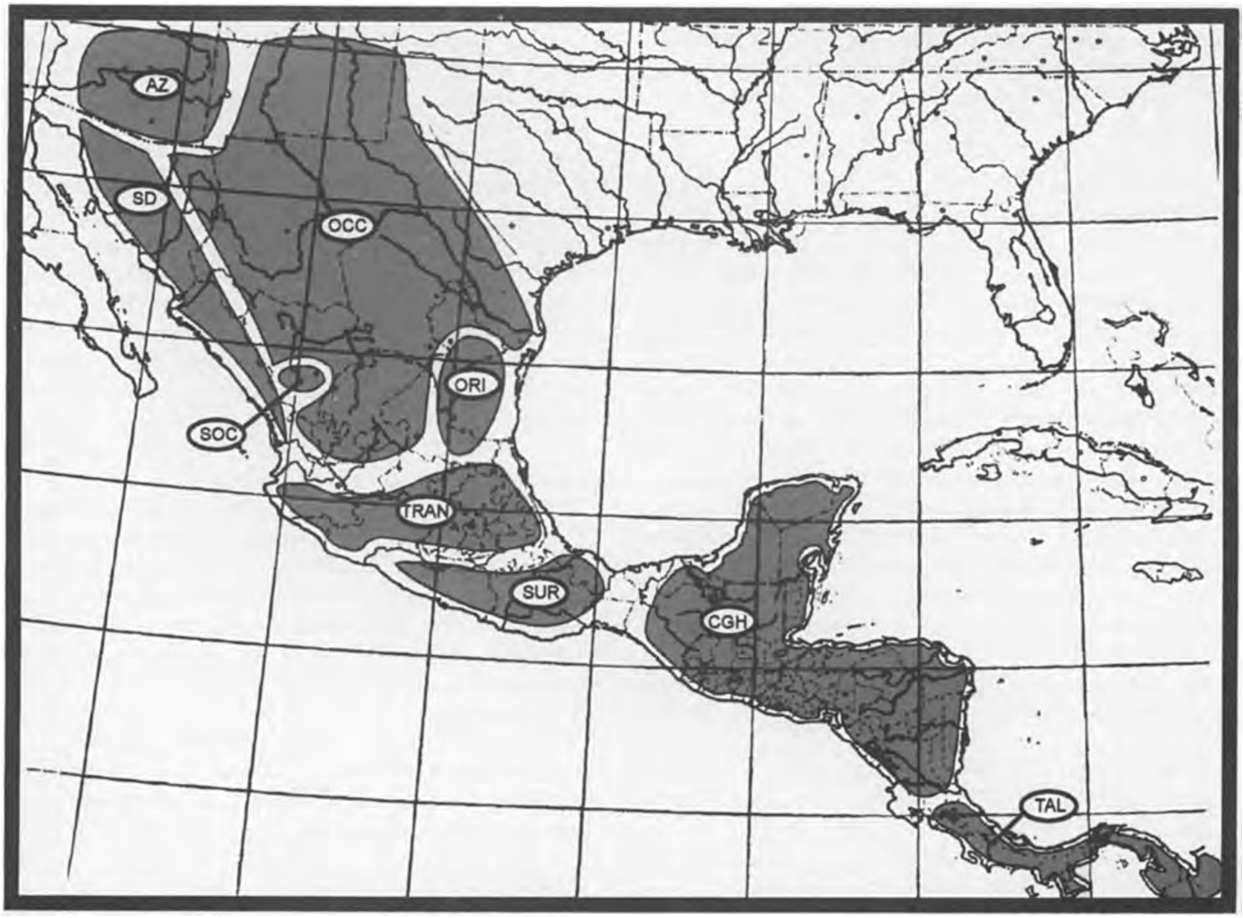

Figure 1 Areas of endemism. AZ, Arizona; CGH, Chiapan Guatemalan Highlands; OCC, Sierra Madre Occidental-Central Plateau; ORI, Sierra Madre Oriental; SD, Sonoran Desert; SOC, Southern Sierra Madre Occidental; SUR, Sierra Madre del Sur; TAL, Talamancan Cordillera; TRAN, Sierra Transvolcanica.

prior to the Jurassic, when a string of permanently emergent volcanoes formed in the north-western region (Ferrusquía-Villafranca, 1993; Morán-Zenteno, 1994). The terrestrial aspect seen today was presumably the result of general uplifting during the late Cretaceous in combination with further volcanic activity in the eastern portions during the Oligocene/Miocene (Ferrusquía-Villafranca, 1993). The opening of the Gulf of California to the west is thought to have begun at the end of the Tertiary (late Miocene), resulting in the creation of the arid environment that characterizes the region today.

Sierra Madre Occidental+Central Plateau (OCC)

This is the largest of the included areas of endemism. The Sierra Madre Occidental and the Central Plateau regions are combined into a single, large area because the taxa examined in this analysis are often distributed across the two areas. The Sierra Madre Occidental comprises a massive chain of volcanic mountains extending south from the southern border of New Mexico between the Sonoran and Chihuahuan deserts. It ranges from 200 to 2200 m elevation, and is characterized by a variety of habitats including both dry and subtropical forest at lower elevations, drier mixed forest at mid-elevations, and pine/oak forest predominating at elevations above 2000 m. Two volcanic events, one in the Cretaceous and one in the late Tertiary, are responsible for producing this sierra, both related to the subduction of the Pacific Plate under the North American Plate (Ferrusquía-Villafranca, 1993). The range terminates to the South in Jalisco and Michoacan where it meets the Sierra Transvolcanica. The Central Plateau, including the Rio Grande River drainage, rests between the Sierra Madre Occidental and the Sierra Madre Oriental and consists of two geological units: the Coahuilan and Chihuahuan subprovinces (Ferrusquía-Villafranca, 1993). Prior to the mid-Cretaceous, much of this region was submerged under epicontinental seas, but geological evidence suggests the early appearance of at least two land masses: Coahuila Island and Peninsula de Tamaulipas (Alfonso-Zwanziger, 1978). Uplifting during the Cretaceous elevated the region and the epicontinental sea retreated eastward.

Southern Sierra Madre Occidental (SOC)

This area, in the south of Durango, was initially recognized by the overlapping distributions of several endemic carabid beetles (Liebherr, 1994a). Environmentally and geologically this region is indistinguishable from the rest of the Sierra Madre Occidental to the North. The region is included in this analysis to test for potentially congruent distributional patterns in other taxa.

Sierra Madre Oriental (ORI)

The Sierra Madre Oriental is one of the most interesting and complex geological regions of Mexico. In this study, the Sierra Madre Oriental region includes the north–south lying mountains of southern Nuevo Leon, western Taumalipas and northern San Luis Potosi. A geologically related, less dense, band of mountains extends westward from Nuevo Leon across southern Coahuila. However, the endemism characteristic of this region is primarily found in the eastern, north–south mountains and therefore the western extension is not included in this area of endemism. Geologists believe that this region was submerged longer than the four regions mentioned above, given that it shows evidence of sedimentary deposition that would have resulted from an eastern regression of the Jurassic epicontinental sea. The region was eventually lifted above sea level late in the Cretaceous by the subduction of the Pacific Plate under the North American Plate, also causing the folded mountains characteristic of the region (Ferrusquía-Villafranca, 1993).

Sierra Transvolcanica (TRAN)

The Sierra Transvolcanica extends between Jalisco and Veracruz, virtually cutting Mexico into northern and southern halves. This belt is home to an incredible array of endemic species and is relatively young geologically. The western-most portion of this region could represent an older formation associated with the Sierra Madre Occidental to the north, as the western limit is not easily distinguished from the southern limits of the Sierra Madre Occidental. If so, this section of the Sierra could have originated in the Cretaceous. However, the larger more extensive mountains that extend transversely across Mexico differ in composition from those to the west and are much more recent. There is considerable debate about the time frame within which this range developed. The majority view holds that the range is a melange of Plio-Quaternary andesites, basalts, and associated sedimentary features, overlying a continuous east–west trending series of Mid-Tertiary volcanoes (Ferrusquía-Villafranca, 1993). A divergent view considers the mid-Tertiary volcanism to represent five distinct and isolated systems, with continuity of the Range only being established in the Quaternary (Demant & Robin, 1975; Demant, 1978) as a result of the subduction of the Cocos Plate under the North American Plate. The range is separated from the Sierra Madre del Sur by the Balsas Depression except in its eastern-most limits where the two mountain ranges are closely associated.

Sierra Madre del Sur (SUR)

This Sierra lies between the Balsas Depression and the expansive Isthmus of Tehuantepec. It includes the mountains of Guerrero and Oaxaca and is home to many endemic organisms. The biodiversity is supported by an assortment of habitat types representing a great variety of moisture and temperature regimes. The origin of the Sierra Madre del Sur is not well understood due to the complexity of the geological formations. However, fossil evidence indicates that this region comprised terrestrial habitat prior to, or during, the Cretaceous. The extent and persistence of this terrestrial habitat is poorly known (Ferrusquía-Villafranca, 1993), but marine regression beginning in the late Cretaceous resulted in expanding terrestrial habitats early in the Tertiary. The low elevation of the Isthmus of Tehuantepec has always been considered important biogeographically. Prior to the Miocene, this region formed a marine barrier which, even after emerging, continued to separate the habitats to either side with an ecological barrier of low elevation forest.

Chiapan/Guatemalan Highlands (CGH)

This region includes the area south of the Isthmus of Tehuantepec, and is characterized by mid- to high-elevation ridges and mountains that rise out of a generally low elevation, tropical forest habitat. The low-elevation Yucatan Peninsula shares most of the low-elevation flora and fauna with these regions, and is therefore grouped into this region even though it is geologically distinct. Stuart (1966) interprets this region as terrestrial by Late Cretaceous, however, Ferrusquía-Villafranca (1993) and Morán-Zenteno (1994) maintain that it was submerged until at least the Palaeocene. Limited post-Pliocene uplifting and volcanism are also reported for this region (Raven & Axelrod, 1974).

Talamancan Cordillera (TC)

Extending from the Nicaraguan Depression south to Colombia lies the Talamancan Cordillera. This volcanic mountain range began as a chain of islands which eventually coalesced, forming a land bridge between South and Central America (Coates & Obando, 1996). The date of this closure is debated, but most estimates are between 3 and 5 mya, at the Miocene/Pliocene boundary. The habitat is predominantly wet, tropical rainforest, although there are regions of drier forest in the north of Costa Rica and high elevation cloud forest throughout.

Taxa

Several criteria were used to select the taxa included in this analysis. All taxa represent hypothesized monophyletic clades with constituent species that inhabit at least two areas of endemism described above. Additionally, each taxon included in the analysis has a published phylogeny (Fig. 2) relating its species in an explicit manner (e.g. cladograms). Lastly, taxa for which no biogeographic pattern could be discerned were removed (i.e. their taxon-area cladograms resulted in completely unresolved fundamental area cladograms). This resulted in a data set based on thirty-three phylogenetically distinct clades. Distributional data for these clades were obtained through revisions, relevant faunistic surveys of Mexico and Central America, and species descriptions (see Appendix 1 for references).

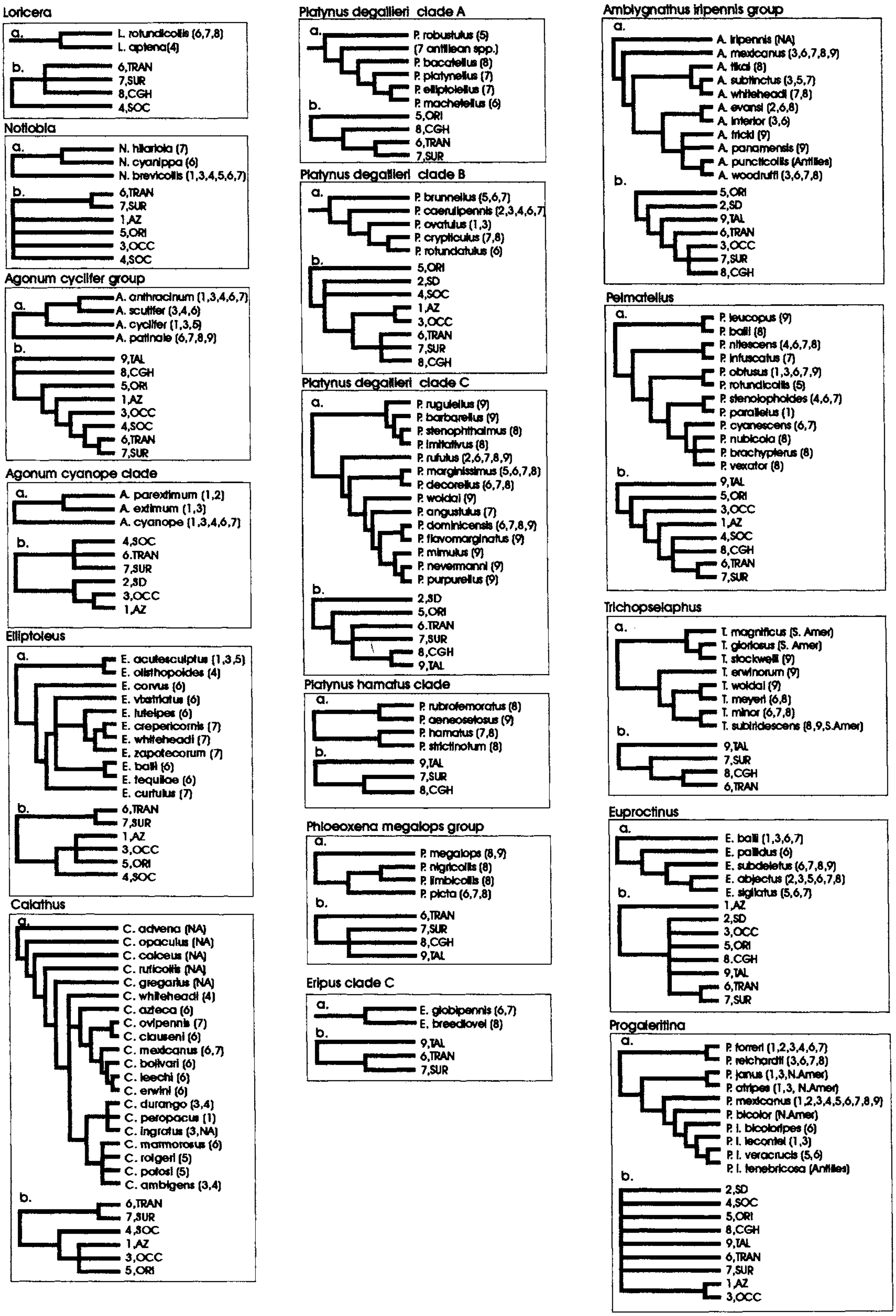

Figure 2 *caption on following page*

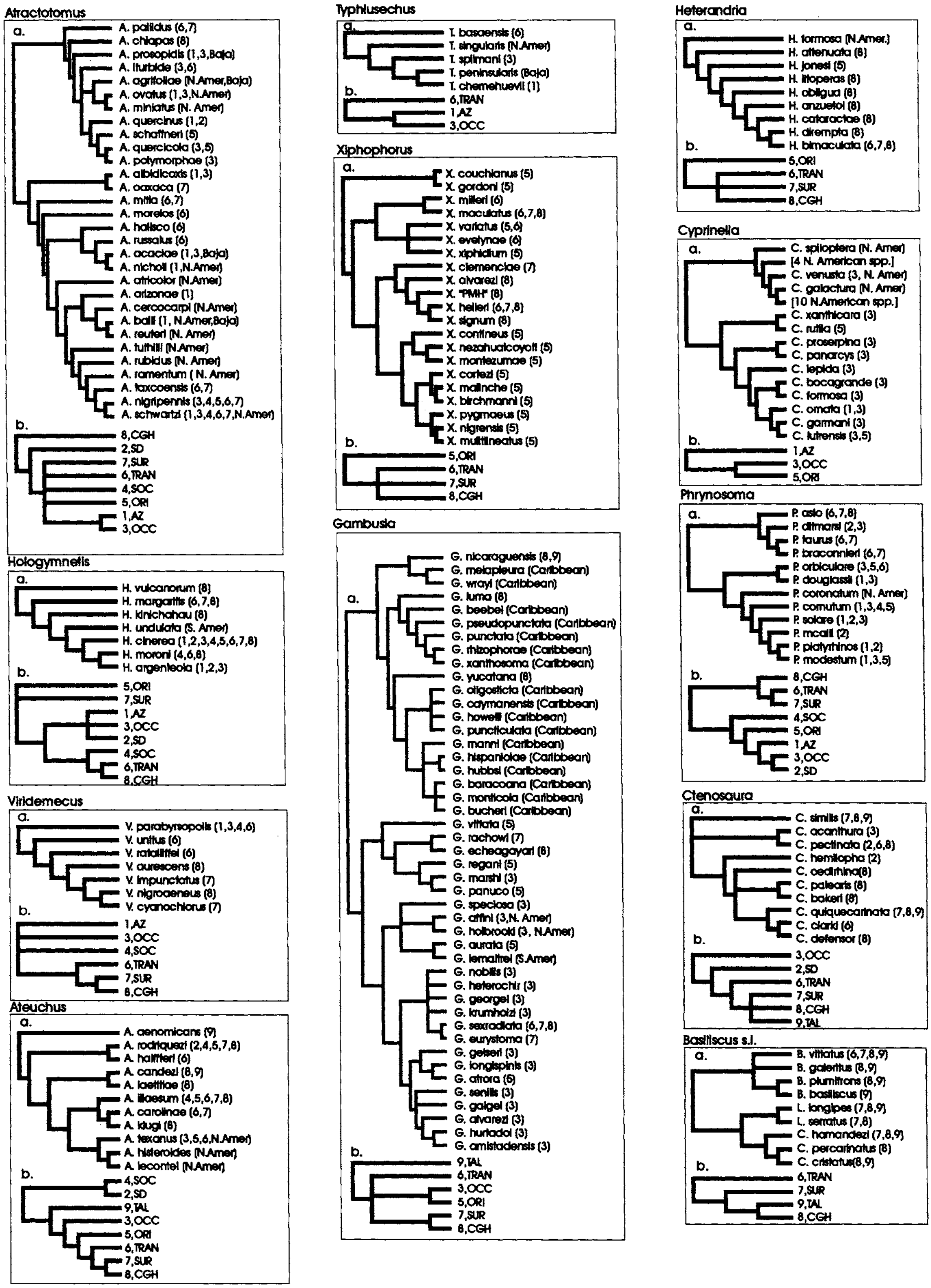

Figure 2 *caption on following page*

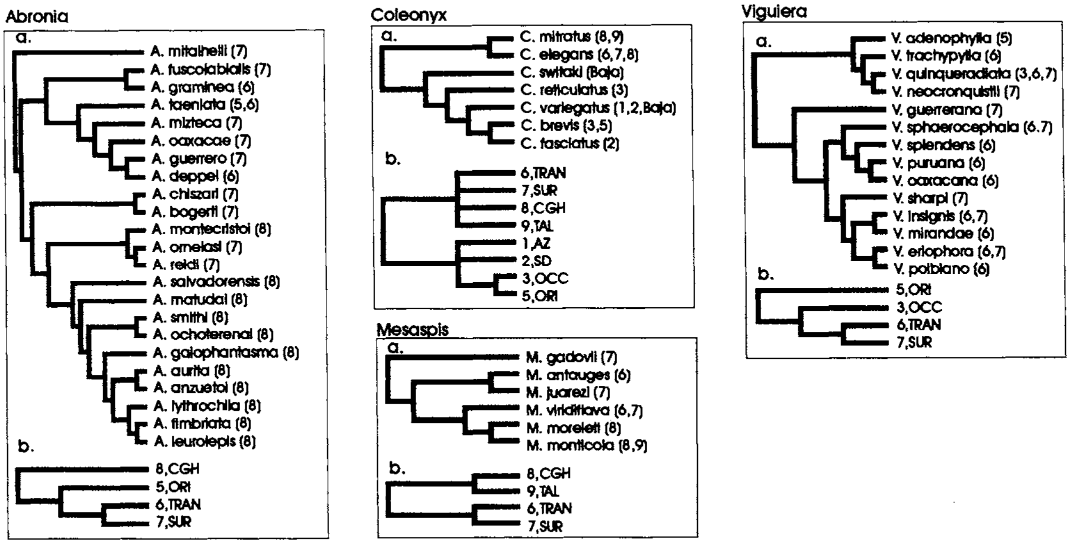

Figure 2 (a) Taxon area cladograms for study taxa. Numbers following species correspond to their distribution: 1, AZ; 2, SD; 3, OCC; 4, SOC; 5, ORI; 6, TRAN; 7, SUR; 8, CGH; 9, TAL; N. Amer., North America; S. Amer., South America; Baja, Baja California. See Appendix for references. (b) Fundamental area cladograms for corresponding taxa. See Fig. 1 legend for abbreviations.

Biogeographic methods

The phylogenetic and distributional data for each taxon were used to create fundamental area cladograms. Fundamental area cladograms were obtained using an Assumption 0 cladistic biogeographic analysis (Wiley, 1987), which treats widespread taxa as evidence of area relationships. Other methods (Assumption 1 and 2, Nelson *et al.*, 1981) utilize information from widespread taxa differently, diminishing their relative importance in determining biotic relationships (Enghoff, 1996). Unfortunately, with numerous widespread taxa these methods often lead to a great many equally parsimonious fundamental area cladograms (Nelson & Platnick, 1981) that when combined into a consensus tree (see below) often produce less resolved patterns that are not as explanatory, thereby serving as weaker tests of other biogeographic patterns. Additionally, the geological recency of many of the areas of endemism may make an Assumption 0 analysis less problematic given that widespread taxa, under these circumstances, are more likely to represent distributions in place before the isolating events producing the vicariant patterns. A strict consensus cladogram was used to summarize equally parsimonious, fundamental area cladograms. Areas peripheral to the focal area (e.g. North America, Baja California or the Caribbean) were included in the taxon area cladograms (Fig. 2), but were then removed from the resulting cladograms. This was done in order to minimize inclusion of areas outside our areas of interest in the full component matrix. Inclusion of peripheral areas, not represented in most of the taxon-area cladograms, seriously diminishes biogeographic resolution for our focal areas, as it introduces many inapplicable cells to the matrix (see below for construction of component matrix).

Two methods were employed to create general area cladograms. Both methods analyse the fundamental area cladograms under the criterion of parsimony, looking for the maximally congruent relationship(s) between the areas of endemism. Essentially, the areas of endemism are treated as taxa in a phylogenetic analysis and the fundamental area cladograms are treated as characters. A hypothetical area of all 'O's is included to serve as an outgroup for cladogram rooting. Many of the fundamental area cladograms only relate a subset of the areas of endemism. This occurs when a taxon does not possess species inhabiting one or more of the areas of endemism defined for this study. The two methods used to produce general area cladograms differ in the way these fundamental area cladograms are added to the final matrix. Brooks Parsimony Method (BPA, Wiley, 1987) adds them to the matrix by placing a '?' in each row corresponding to an inapplicable area. A second method (Zandee & Roos, 1987) scores inapplicable areas as '0', thereby indicating that lack of information regarding a taxon's occurrence is in fact, positive evidence of its absence there. This manner of treating missing taxa is called Assumption 0 (Page, 1990; Ridder-Numan, 1996).

Once a matrix of the fundamental area cladogram components was developed, it was analysed using Hennig86 (Farris, 1988) under the exact search strategy: ie* Clados (Nixon, 1991) was used to examine the resulting topologies, as well as to assess the component support for each clade.

RESULTS

Initially, thirty-three fundamental area cladograms were derived from their associated taxon-area cladograms (Fig. 2). The fundamental area cladograms yielded a final matrix of eighty-four components (Table 1). Most of the components (69%) were from insect taxa, with the second highest number coming from lizards (22%), and the remainder from fish (7.5%) and plants (1.5%).

Table 1 Component-Area Matrix analysed with Brooks Parsimony Analysis.

Components

Areas of Endemism	01 05 10	11 15 20	21 25 30	31 35 40	41 45 50	51 55 60	61 65 70	71 75 80	81 84
out	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000
OCC	?000111110	1101101111	111110001?	?0111????0	0??011000?	?????110??	111100011?	?011101000	0110
ORI	?000001??0	110110011?	1001100000	0000001??	?00011????	???01110??	000000001?	?010000000	1110
AZ	?000011110	1101101111	0011100???	?0111????0	0?????????	?????010??	????00111?	?0011010??	????
SOC	0001111001	010010011?	?000100???	?0001????0	0?????????	??????????	????01111?	???0011000	0001
TRAN	1111111001	0010010110	?000011111	1101011?0	1110010110	0101100111	0111111111	1110011101	1110
SUR	1111111001	001001011?	?000011111	1101101111	1111011110	1101100111	1111111110	1110000011	1110
CGH	1?00000???	??????000?	?000001??0	1101111111	1111011111	1010000110	1111011111	1010011111	1110
SD	???????010	??????001?	?111100???	?0001000??	??????001?	?????010??	0001??????	?010101000	0001
TAL	??00000???	??????????	??????????	?????1110?	???0001111	101??0010?	0011000000	0000???00	0010

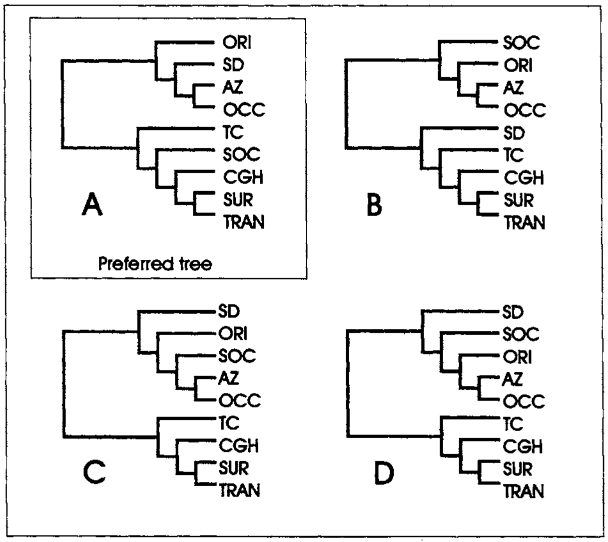

Figure 3 Resultant general area cladograms. (A) Single cladogram produced under Brooks Parsimony Analysis (BPA): length = 129, CI = 0.62, RI = 0.62; (B, C, D) three equally parsimonious cladograms produced under Assumption 0 analysis: length = 140, CI = 0.57; RI = 0.64. See text for abbreviations.

Analysis of this secondary matrix using Hennig86 produced different results depending on the form of parsimony analysis. BPA resulted in a single most parsimonious cladogram (Fig. 3a) of 129 steps, CI:0.62 and RI:0.62. Use of Zandee and Roos' Assumption 0 analysis produced three equally parsimonious topologies (Fig. 3b–d) of 140 steps, CI:0.57 and RI:0.64. All the resultant cladograms are topologically distinct although they have many components in common. They differ most notably in the position of the Sonoran desert (SD) and the Southern Sierra Madre Occidental (SOC).

The BPA cladogram (Fig. 3a) displays a basal dichotomy, yielding two clades of relatively northern and southern affinities. In the northern clade, the mountains of Arizona and the Sierra Madre Occidental/Central Plateau are the most recently diverged areas. Sister to these areas is the Sonoran Desert. The most basal area in the northern clade is the Sierra Madre Oriental. The remaining areas comprise a 'southern' clade. With the exception of the Southern Sierra Madre Occidental (SOC), these areas include or are south of the Sierra Transvolcanica. Within this southern clade, the Sierra Transvolcanica (TRAN) and the Sierra Madre del Sur (SUR) are the most recently diverged areas, with the Chiapan-Guatemalan Highlands (CGH) forming their sister area. The southern tip of the Sierra Madre Occidental forms the sister region to (CGH + (TRAN + SUR)). The Talamancan Cordillera (TC) comprises the most basal sister area within the southern clade.

In the Assumption 0 cladograms, as in the BPA cladogram, AZ is closely allied with OCC. Additionally, all area cladograms indicate CGH as the sister area of (SUR + TRAN). Unlike the BPA results, SOC is allied to the mountains north of the Sierra Transvolcanica. The Sierra Madre Oriental (ORI) is always related to (AZ + OCC), being their sister region in two of the three topologies (Fig. 3b,d) and separated from them only by SOC in the third (Fig. 3c). Cladograms 3c and 3d indicate that SD diverges from the base of the northern clade, whereas in cladogram 3b it forms the basal branch of the southern clade: SD(TC(CGH(TRAN + SUR))).

Although the three cladograms (Fig. 3b,c,d) contain the same overall amount of homoplasy, they distribute this homoplasy in different ways. Cladogram 3b has fewer homoplasious components but these components have lower CI values than the homoplasious components of either of the two remaining topologies. In other words, the homoplasy is concentrated in fewer components in cladogram 3b. Employing successive weighting (Farris, 1969; Carpenter, 1988) on the data set, which applies an *a posteriori* weight to the components based on their CI value, favours cladogram 3b.

DISCUSSION

Both the BPA and Assumption 0 analyses recovered many of the same biotic relationships. However, the BPA method produces a single pattern more in accordance with previous studies and geological evidence. This pattern differs from the Assumption 0 cladograms only in the placement of the two most ambiguous regions in the analysis: the southern extent of the Sierra Madre Occidental (SOC) and the Sonoran

Desert (SD). As a result of poor sampling (e.g. phylogenetic studies for taxa of these regions), these two regions both have many questionably scored characters in the matrix. The biogeographic information that is available for SD and SOC is provided largely by widespread taxa occupying more than two areas; each area has only three endemic species in the overall analysis (Fig. 2). In other words, there are very few components in the final matrix that specifically relate SOC or SD to other areas; they are either related equally well to several areas (information from widespread species) or ambiguous (?'s from missing data). The Assumption 0 analysis, eliminates the ambiguity by replacing the ?'s with 'O' s, but given the poor sampling of these regions, this remedy most likely replaces the ambiguity with inaccuracy. In phylogenetic studies requiring the inclusion of poorly known taxa (e.g. fossils), it has been suggested that ambiguously scored taxa be left out of the initial analysis and subsequently included by mapping them onto the topology in the most parsimonious location (Ax, 1987). Implementing this approach (under BPA or Assumption 0) with this study's matrix results in the same cladogram obtained using the BPA method. For all of the preceding reasons, the BPA cladogram (Fig. 3a) is preferred and forms the basis of the discussion to follow.

Interpretation of the preferred general area cladogram as a biogeographic history of Mexico and Central America yields several conclusions. First, there are two biogeographic assemblages in Mexico and Central America: one north of the Sierra Transvolcanica and one south, which includes the Sierra Transvolcanica and the southern Sierra Madre Occidental. This finding may not be surprising given that Mexico has always been considered a mixing area of southern and northern biotas. Perhaps novel is that the northern biotas are limited to the regions north of the Sierra Transvolcanica, not the Isthmus of Tehuantepec. The traditional focus of transition zone hypotheses on the Isthmus of Tehuantepec is likely based on its geographical prominence, and on faunal subtraction surveys (e.g. Miller & Smith, 1986) that examine the southern or northern limits of specific taxa. While it is true that many taxa corresponding to Halffter's Nearctic pattern do not extend south of the isthmus, this analysis finds that more commonly, taxa inhabiting northern regions do not extend beyond the Sierra Transvolcanica and Balsas Depression. There are components indicating affinity between the Sierra Transvolcanica and the Sierra Madre Oriental, however, these are heavily outweighed by other components linking the Sierras Transvolcanica and Madre del Sur to the Chiapan-Guatemalan highlands plus Talamancan Cordillera. These results do not deny biotic relations between the Sierra Transvolcanica and regions to the north. They indicate only that if the general pattern is interpreted using vicariant explanations, then alternatives, such as dispersal or extinction, must be invoked to explain these incongruent elements.

Inclusion of the southern Sierra Madre Occidental (SOC) with other regions to the south may be explained by this region's connection to the earlier developing portions of the western Sierra Transvolcanica (Ferrusquía-Villafranca, 1993). This interpretation suggests that the longer lasting connection between these two areas established species that subsequently speciated through vicariance but are still most closely related (e.g. *Loricera rotundicollis* Chaudoir vs. *L. aptena* Ball and Erwin, Fig. 2), or that the connection established widespread species that did not subsequently speciate (e.g. *Pelmatellus nitescens* Bates, *P. stenolophoides* Bates, Fig. 2), resulting in close area relationships under the conditions of BPA or Assumption 0.

Liebherr (1994a) likewise uncovered a northern-southern division across this transition zone, however, that division was not the oldest vicariant event of his general area cladogram. His preferred general area cladogram placed the Sierra Madre Oriental (ORI) as the sister area to all of the other areas because this relationship was represented in five of the nine equally parsimonious area cladograms derived via BPA. But, in one equally parsimonious solution ORI was the basal area in a component also including AZ, OCC, and SOC, and in a second it was allied with those three areas plus SD. Similarly, the present study emphasizes relationships of ORI to the north, as the sister area to the three northern regions AZ, OCC and SD. Its position in the general pattern stems from the basal position of this region in many of the fundamental area cladograms (e.g. *Agonum cyclifer* group, *Calathus* species, Fig. 2) in combination with components uniting this region with OCC, effectively linking this region more closely to the north than to the regions south of the Sierra Transvolcanica. This finding is consistent with conclusions of Martin (1958) and Van Devender (1990a) who propose the existence of a woodland corridor between the Sierra Madre Oriental and the Sierra Madre Occidental during the Pleistocene. If this date is accepted as the divergence date of ORI, isolation among the other regions must be even more recent. The extremely close association of AZ and OCC, which share many widespread species, supports the notion that these areas are either very recently isolated or only weakly isolated biotically.

In the preferred area cladogram (Fig. 3a) the relationship of the Sonoran desert to south-eastern AZ and OCC is somewhat problematic. Geological and meteorological evidence estimate the ecological origin (e.g. desertification) of the Sonoran region during the Miocene, thus predating the Pleistocene corridor of Martin (1958). However, as stated above, the placement of SD in this analysis is by no means stable given the general lack of montane taxa containing species representative of the region and the analytical conditions of BPA which recognize this ambiguity.

Within the southern clade the most derived biotic relationship is between the Sierra Transvolcanica (TRAN) and Sierra Madre del Sur (SUR). The geographical barriers between the four major areas of the southern clade are: (1) the Balsas Depression between TRAN and SUR (2) the Isthmus of Tehuantepec (between TRAN + SUR and CGH), and (3) the Nicaraguan Depression (between CGH and TC). All three barriers represent lowlands, which for much of Mexico's history consisted of marine habitat, and currently present ecological habitats distinct from the higher elevation, montane habitats that they separate. The isolation of TRAN and SUR via the Balsas Depression may date from the origin of the Sierra Transvolcanica itself. This could be as early as late Tertiary if the range constituted isolated volcanoes, possibly in a marine embayment, during that time. If isolation developed during the latest round of Plio-Pleistocene volcanism, this isolation could be even more recent (1–2 mya). This latter date would well explain the numerous widespread species shared between the two areas. Based on the general cladogram, the biotic division between regions north and south of the Isthmus of Tehuantepec occurred after the emergence and isolation of the Costa Rican and Panamanian Talamancan Cordillera biota (TC), itself a relatively recent event geologically speaking (2.8–3.1 mya, Coates *et al.*, 1996). Constraining the vicariance among the areas north of the Nicaragua Depression to the last 3 mya suggests a pre-existing cosmopolitan biota on either side of the Isthmus (CGH and TRAN + SUR) that was eventually isolated by the gradually elevated habitats on either side, such elevation due to either or both climatic and geological factors. Whether the shared biota initially established itself via continuous land connections or by dispersal over water is not ascertainable. The relatively basal position of a Panamanian/Costa Rican biota (TC) places a maximum age for the southern clade, and indicates that the patterns depicted most likely reflect late Tertiary geological and ecological events rather than events of the Mesozoic.

Thus the geological history in combination with the general area cladogram strongly suggests a disparity in the ages of the northern and southern sets of areas. Whereas the northern areas are very recently diverged, perhaps as late as during the Pleistocene, the southern areas appear to have diverged over the past 3 mya or so. This longer period of southern diversification is accompanied by greater biotic endemicity, perhaps best exemplified by the fishes *Heterandria* and *Xiphophorus* (Rosen, 1978, 1979; Rauchenberger *et al.*, 1990), though also exemplified by numerous sympatric species in the taxon-area cladograms from the southerly areas (Fig. 2, areas 6–9). Conversely, the more northerly taxa tend to be more widespread geographically (Fig. 2, areas 1–3), either not responding as consistently to habitat vicariance, or possessing life histories in which dispersal over barriers is necessary for the maintenance of populations.

Because we have not looked outside the nine areas of endemism for isolation events—most likely with North America—it is not possible to affix a maximum age for the isolation of the northern and southern assemblages of areas. Settling this question requires a geographically more comprehensive analysis.

General area cladograms

The biogeographic conclusions reached in this study are drawn from the general area cladogram. However, not all taxa fit the generalized pattern equally well. Much like characters in a phylogenetic analysis, there are some that fit well, while others are homoplasious. How one interprets the homoplasy, or incongruence, between the fundamental area cladograms centres on how one views biogeographic patterns in general, and what questions a biogeographic analysis is expected to answer.

As stated in the introduction, the objective of cladistic biogeography is the search for similarities between distributions of taxa. Vicariance, like the concept of homology in phylogenetics, allows biotic distributions to be compared by assuming *a priori* that organisms evolve in concert with their surrounding geographies (Nelson & Platnick, 1981; Wiley, 1987). In this manner, distributions of several species can share a common origin as do the homologous morphological structures of different species. Congruent biotic distributions, like congruent morphological features, provide evidence of biotic relationships. Biotic relationships, hypothesized in this way, are scientific in that they may be tested and refuted by new observations. Without the recognition of vicariance, each organism's distribution is unique, making intertaxonomic comparisons impossible in any meaningful way. Without vicariance, fundamental area cladograms, or any biogeographic statement, are merely descriptive in substance; neither predictive nor testable (other than at the level of an observation). Knowledge of the biogeographic pattern of one taxon, says nothing about the pattern of another. On the other hand, cladistic biogeography links the biogeographic information from one taxon to that of others and forms a predictive and testable null hypothesis. Importantly, the adoption of the vicariant null hypothesis does not require congruence between the individual patterns—general patterns can still have high levels of incongruence—it only assumes *a priori* that congruence should exist.

Various methods of creating general biogeographic patterns exist, differing in how, or if, they incorporate incongruent pieces of information. The analysis adopted here treats each piece of evidence (congruent or incongruent) as equal and searches for a pattern that is maximally congruent (most parsimonious) with all the data. Consensus techniques also yield general patterns (Page, 1988) but do not truly incorporate incongruent information, since consensus techniques treat incongruent data as ambiguity (e.g. unresolved nodes). As a result, these cladograms are necessarily less parsimonious than any of the underlying fundamental cladograms (Carpenter, 1988; Barrett *et al.*, 1991), and are therefore suboptimal as general scientific statements. Narrative biogeographic studies, such as Halffter's, are intermediate in that they attempt to minimize incongruence by creating multiple general patterns. Unfortunately, these methods potentially push the problem to a lower level. If conflict still exists between the 'similar' patterns and it is considered evidence for yet other, lower level biogeographic patterns, eventually every novel biogeographic pattern becomes its own general pattern. This undermines the utility of generating a general pattern in the first place. Furthermore, these methods present no scientific means by which taxa are to be divided into appropriate categories without adopting untestable *a priori* evolutionary models such as centres of origin. Conversely, general biogeographic patterns serve to provide limits for explanations regarding observations at hand, while simultaneously inviting predictions about observations yet to be made. The general pattern displays the biogeographic elements that can be explained by common causes (Minaka, 1987) as well as those that require unique or special explanations. Page (1990) noted that widespread taxa under BPA can produce character optimizations on the area cladogram that may be inconsistent with their original phylogenetic relationships. However, such inconsistencies are soluble via a variety of dispersal scenarios

(Brooks, 1990; Page, 1990), with ultimate understanding dependent on comparing individual taxon area relationships to the summary of data, i.e. the general area cladogram. Both types of pattern (congruent and incongruent) have scientific merit, and both can form the basis of future scientific investigations. Specific patterns that do not fit a general pattern could be indicative of specific biological qualities of the relevant organism (e.g. increased dispersal power), or unique historical events pertaining to those taxa (e.g. random dispersal or local extinction). As with homoplasious characters in phylogenetic analyses, a particularly strong general pattern used to evaluate questionably incongruent phylogenetic data may inspire re-evaluation of the validity of such data.

In addition to its utility in forming scientific explanation, the general pattern forms the basis for making scientific predictions. Faunistic prediction can be made based on the general pattern, especially if phylogenetic information is available for target taxa. The general pattern of this study predicts, for example, that based on a species found in the Sierra Transvolcanica a researcher could expect the existence of most closely related taxa in the Sierra Madre del Sur. The ability to make biogeographic predictions not only serves the purposes of taxonomists seeking taxa not yet described, but should be integrated into conservation efforts seeking a means of prioritizing various regions. A general area cladogram explicitly states the biotic affinities of the various implicated regions. As such, the pattern produced forms the best scientific hypothesis of the underlying process(es) producing biotic diversification (e.g. speciation) within the areas of study. The biogeographic pattern forms a bridge between the biotic diversity of independent taxa and thus, can allow conservationists to preserve areas inhabited by species which are least related phylogenetically (higher biodiversity) vs. regions sharing closely related taxa (lower biodiversity) (Faith, 1992a, 1992b; Nixon & Wheeler, 1992; Humphries *et al.*, 1995).

ACKNOWLEDGMENTS

This work was accomplished under the support of the National Science Foundation through grants #9208269-(JKL) and #9520759-(CJM) which is gratefully acknowledged. We would also like to thank the graduate students of the Cornell University Department of Entomology and of the Liberty Hyde Bailey Hortorium for discussions of the content and methods used in this study. Comments and corrections to an earlier version of the manuscript by Dr Mary Liz Jameson of the University of Nebraska State Museum were gratefully accepted and exceptionally helpful. Additionally, Dr David Lytle of the Section of Ecology and Systematics, Cornell University provided valuable comments with regard to the applicability of biogeographic methods to conservation efforts.

REFERENCES

Aalbu, R. I. & Andrews, F. G. (1985) New species relationships and notes on the biology of the endogean tentyrine genus *Typhlusechus* (Tenebrionidae: Stenosini). *Occasional Papers in Entomology*, 30, 1–28.

Alfonso-Zwanziger, J. A. (1978) Geología regional del sistema sedimentario cupido. *Boletín de la Asociación Mexicana de Geologos Petroleros*, 30 (1, 2).

Ax, P. (1987) *The phylogenetic system: the systematization of organisms on the basis of their phylogenesis.* Wiley, New York.

Ball, G. E. (1975) Pericaline Lebiini: notes on classification, a synopsis of the New World genera, and a revision of the genus *Phloeoxena* Chaudoir (Coleoptera: Carabidae). *Quaestiones Entomologicae*, 11, 143–242.

Ball, G. E. (1978) The species of the Neotropical genus *Trichopselaphus* Chaudoir (Coleoptera: Carabidae: Harpalini): classification, phylogeny and zoogeography. *Quaestiones Entomologicae*, 14, 447–489.

Ball, G. E. (1987) The Neotropical genus *Trichopselaphus* Chaudoir (Coleoptera: Carabidae: Harpalini): new species and a review of taxonomic and evolutionary aspects. *Transactions of the American Entomological Society*, **112**, 249–287.

Ball, G. E. & Erwin, T. L. (1969) A taxonomic synopsis of the tribe Loricerini (Coleoptera: Carabidae). *Canadian Journal of Zoology*, 47, 877–907.

Ball, G. E. & Maddison, D. R. (1987) Classification and evolutionary aspects of the species of the New World genus *Amblygnathus* Dejean, with a description of *Platymetopsis*, new genus, and notes about selected species of *Selenophorus* Dejean (Coleoptera: Carabidae: Harpalini). *Transactions of the American Entomological Society*, **113**, 189–307.

Ball, G. E. & Negre, J. (1972) The taxonomy of the Nearctic species of the genus *Calathus* Bonelli (Coleoptera: Carabidae: agonini). *Transactions of the American Entomological Society*, **98**, 412–533.

Ball, G. E. & Nimmo, A. P. (1983) Synopsis of the species of subgenus *Progaleritina* Jeannel, including reconstructed phylogeny and geographical history (Coleoptera: Carabidae: *Galerita* Fabricius). *Transactions of the American Entomological Society*, 109, 295–356.

Barrett, M., Donoghue, M. J. & Sober, E. (1991) Against consensus. *Systematic Zoology*, 40, 486–493.

Betancourt, J. L., Van Devender, T. R. & Martin, P. S. (eds) (1990) *Packrat middens. The last 40,000 years of biotic change.* University of Arizona Press, Tuscon.

Brooks, D. R. (1990) Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update. *Systematic Zoology*, 39, 14–30.

Campbell, J. A. & Frost, D. R. (1993) Anguid lizards of the genus *Abronia*: revisionary notes, descriptions of four new species, a phylogenetic analysis, and key. *Bulletin of the American Museum of Natural History*, **216**, 1–121.

Carpenter, J. M. (1988) Choosing among multiple equally parsimonious cladograms. *Cladistics*, 4, 291–296.

Coates, A. G. & Obando, J. A. (1996) The geological history of Central America. *Evolution and environment in tropical America* (ed. by J. B. C. Jackson, A. F. Budd, A. G. Coates), pp. 21–56. The University of Chicago Press, Chicago.

Croizat, L., Nelson, G. & Rosen, D. E. (1974) Centers of origin and related concepts. *Systematic Zoology*, 23, 265–287.

de Queiroz, K. (1987) A new spiny Iguana from Honduras with comments on relationships with *Ctenosaura* (Squamata: Iguania). *Copeia*, 892–902.

Demant, A. (1978) Caracteristicas del Eje Neovolcánico Transmexicano y sus problemas de interpretación. *Revista Instituto*

Geologica Universidad Nacioal Autonoma de Mexico, 2, 172–187.

Demant, A. & Robin, C. (1975) Las faces del volcanismo en México; una síntesis en relación con la evolucion geodinámica desde el Creatácico. *Revista Instituto Geologica Universidad Nacioal Autonoma de Mexico*, 75, 70–83.

dePinna, M.C.C. (1991) Concepts and tests of homology in the cladistic paradigm. *Cladistics*, 7, 367–394.

Dixon, J.R. (1970a) *Coleonyx. Catalogue of American amphibians and reptiles* (ed. by C. J. McCoy), pp. 95.1–95.2, Society of the Study of Amphibians and Reptiles, Bethesda, Md.

Dixon, J.R. (1970b) *Coleonyx brevis. Catalogue of American amphibians and reptiles* (ed. by C. J. McCoy), pp. 88.1–88.2, Society of the Study of Amphibians and Reptiles, Bethesda, Md.

Dixon, J.R. (1970c) *Coleonyx reticulatus. Catalogue of American amphibians and reptiles* (ed. by C. J. McCoy), pp. 89.1, Society of the Study of Amphibians and Reptiles, Bethesda, Md.

Dixon, J.R. (1970d) *Coleonyx variegatus. Catalogue of American amphibians and reptiles* (ed. by C. J. McCoy), pp. 96.1–96.4, Society of the Study of Amphibians and Reptiles, Bethesda, Md.

Enghoff, H. (1996) Widespread taxa, sympatry, dispersal, and an algorithm for resolved area cladograms. *Cladistics*, 12, 349–364.

Etheridge, R. E. (1982) Checklist of the Iguaninae and Malagasy Iguanid lizards. *Iguanas of the World* (ed. by G. M. Burghardt and A. S. Rand), pp. 7–34. Noyes Publications, Park Ridge, NJ.

Faith, D. P. (1992a) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61, 1–10.

Faith, D. P. (1992b) Systematics and conservation: on predicting the feature diversity of subsets of taxa. *Cladistics*, 8, 361–373.

Farris, J. S. (1969) A successive approximation approach to character weighting. *Systematic Zoology*, 18, 374–385.

Farris, J. S. (1988) HENNIG86, Version 1.5 (a cladistics computer program obtained from the author at 41 Admiral St., Port Jefferson Station, NY. 11776 USA).

Ferrusquía-Villafranca, I. (1993) Geology of Mexico: a synopsis. *Biological diversity of Mexico: origins and distributions* (ed. by T. P. Ramamoorthy, R. Bye, A. Lot and J. Fa), pp. 3–108. Oxford University Press, New York.

Funk, R. S. (1981) *Phrynosoma mcallii. Catalogue of American amphibians and reptiles* (ed. by C. J. McCoy), pp. 281.1–281.2, Society of the Study of Amphibians and Reptiles, Bethesda, Md.

Good, D. A. (1987) A phylogenetic analysis of cranial osteology in gerrhonotine lizards (Lacertilla: aguidae). *Journal of Herpetology*, 21, 283–295.

Good, D. A. (1988) Phylogenetic relationships among gerrhonotine lizards (Squamata: anguidae). *Herpetologica*, 44, 154–162.

Good, D. A. (1989) Allozyme variation and phylogenetic relationships among the species of *Mesaspis* (Squamata: anguidae). *Herpetologica*, 45, 227–232.

Goulet, H. (1974) Classification of the North and Middle American species of the genus *Pelmatellus* Bates (Coleoptera: Carabidae: Harpalini). *Quaestiones Entomologicae*, 10, 80–102.

Grismer, L. L. (1988) Phylogeny, taxonomy, classification, and biogeography of eublepharid geckos. *Phylogenetic relationships of the lizard families* (ed. by R. Estes, G. Pregill), pp. 369–464. Stanford University Press, Stanford, CA.

Grismer, L. L. (1990a) *Coleonyx fasciatus. Catalogue of American amphibians and reptiles* (ed. by A.H. Price), pp. 463.1–463.2. Society of the Study of Amphibians and Reptiles, Bethesda, Md.

Grismer, L. L. (1990b) *Coleonyx switaki. Catalogue of American amphibians and reptiles* (ed. by A. H. Price), pp. 464.1–464.2. Society of the Study of Amphibians and Reptiles, Bethesda, Md.

Halffter, G. (1961) Explicacion preliminar de la distribucion geografica de los Scarabaeidae Mexicanos. *Acta Zoologica Mexicana (N S)*, 5, 1–17.

Halffter, G. (1965) Algunas ideas acerca de la zoogeografia de America. *Revista Sociedad Mexicana de Historia Natural*, XXVI. 1–16.

Halffter, G. (1976) Distribucion de los insectos en la zona de transicion mexicana. Relaciones con la entomofauna de Norteamerica. *Folia Entomologica Mexicana*, 1–61.

Halffter, G. (1987) Biogeography of the montane entomofauna of Mexico and Central America. *Annual Review of Entomology*, 32, 95–114.

Halffter, G. (1991) Feeding, bisexual cooperation and subsocial behavior in three groups of Coleoptera. *Advances in coleopterology* (ed. by M. Zunino, X. Belles and M. Blas), pp. 281–296, AEC, Barcelona.

Heilprin, A. (1887) *The geographical and geological distribution of animals*, 435 pp. D. Appleton, New York.

Hennig, W. (1966) *Phylogenetic systematics*. University of Illinois Press, Urbana.

Hernández-Baños, Peterson, A. T., Navarro-Sigüenza, A. G. & Escalante-Pliego, B. P. (1995) Bird faunas of the humid montane forests of mesoamerica: biogeographic patterns and priorities for conservation. *Bird Conservation International*, 5, 251–277.

Humphries, C. J., Williams, P. H. & Vane-Wright, R. I. (1995) Measuring biodiversity value for conservation. *Annual Review of Ecology and Systematics*, 26, 93–111.

Jameson, M. L. (1990) Revision, phylogeny and biogeography of the genera *Parabyrsopolis* Ohaus and *Viridimicus*, new genus (Coleoptera: Scarabaeidae: Rutelinae). *Coleopterists Bulletin*, 44, 377–422.

Kohlmann, B. & Halffter, G. (1988) Cladistic and biogeographical analysis of *Ateuchus* (Coleoptera: Scarabaeidae) of Mexico and the United States. *Folia Entomologica Mexicana*, 74, 109–130.

Lang, M. (1989) Phylogenetic and biogeographical patterns of basiliscine inguanas (Reptilia: Squamata: 'Iguanidae'). *Bonner Zoologische Monographien*, 28, 5–171.

Liebherr, J. K. (1986) Cladistic analysis of North American Platynini and revision of the. *Agonum extensicolle* species group (Coleoptera: Carabidae). *University of California Publications in Entomology*, 106, 1–198.

Liebherr, J. K. (1988) Redefinition of the *Platynus jaegeri* group and a taxonomic revision of the Mexican and Central American species (Coleoptera: Carabidae: Platynini). *Transactions of the American Entomological Society*, 114, 167–214.

Liebherr, J. K. (1991) Revision and phylogeny of the *Anchomenus* clade: the genera *Tetraleucus*, *Anchomenus*, *Sericoda* and *Elliptoleus* (Coleoptera: Carabidae: Platynini). *Bulletin of the American Museum of Natural History*, 202, 1–167.

Liebherr, J. K. (1992) Phylogeny and revision of the *Platynus degallieri* species group (Coleoptera: Carabidae: Platynini). *Bulletin of the American Museum of Natural History*, 214, 1–115.

Liebherr, J. K. (1994a) Biogeographic patterns of montane Mexican and Central American Carabidae (Coleoptera). *Canadian Entomologist*, 126, 841–860.

Liebherr, J. K. (1994b) Identification of the New World *Agonum*, review of the Mexican fauna, and description of *Incagonum*, new genus, from South America (Coleoptera: Carabidae: Platynini). *Journal of New York Entomological Society*, 102, 1–55.

Llorentes Bousquets, J. (1996) Biogeografía de artrópodos de México: ¿Hacia un nuevo enfoque? Biodiversidad, taxonomía y biogeografía de artrópodos de México. *Hacia Una Síntesis de Su Conocimiento* (ed. by J. Llorentes Bousquets, A. N. García Aldrete and E. González Soriano), pp. 41–56. Instituto de Biología, Universidad nacional Autónoma de México, Mexico D.F.

Martin, P. S. (1958) A biogeographic of reptiles and amphibians in the Gomez Farias region, Tamaulipas, Mexico. *Miscellaneous Publications of the University of Michigan Museum of Zoology*, 101.

Martin, P. S. (1963) *The last 10,000 years a fossil pollen record of the American Southwest.* The University of Arizona Press, Tucson, AZ.

Martin, P. S. & Klein, R. G. (1984) *Quaternary extinctions: a prehistoric revolution.* University of Arizona Press, Tucson, AZ.

Mayden, R. L. (1989) Phylogenetic studies of North American minnows with emphasis on the genus Cyprinella, new genus, new status (Teleostei: Cypriniformes). *University of Kansas Museum of Natural History Miscellaneous Publications*, 80, 1–189.

Miller, R. R. & Smith, M. L. (1986) Origin and geography of the fishes of Central Mexico. *The zoogeography of North American freshwater fishes* (ed. by C. H. Hocutt and E. O. Wiley), pp. 487–518. John Wiley & Sons, New York.

Minaka, N. (1987) Branching diagrams in Cladistics: their definitions and implications for biogeographic analyses. *Bulletin of the Biogeographical Society of Japan*, 42, 65–78.

Montanucci, R. R. (1987) A phylogenetic study of the horned lizards, genus *Phrynosoma*, based on skeletal and external morphology. *Natural History Museum of Los Angeles County, Science Series*, 390, 1–36.

Morán-Zenteno, D. (1994) *The geology of the Mexican Republic; AAPG Studies in Geology*, 39. (trans. by J. L. Wilson, L. Sanchez-Bareda). American Association of Petroleum Geologists, Tulsa, OK.

Morrone, J. J. & Carpenter, J. M. (1994) In search of a method for cladistic biogeography: an empirical comparison of component analysis, Brooks parsimony anlaysis, and three area statements. *Cladistics*, 10, 99–153.

Nelson, G. & Platnick, N. I. (1981) *Systematics and biogeography: cladistics and vicariance.* Columbia University Press, New York.

Nixon, K. C. (1991) CLADOS (a phylogenetic character/topology viewing computer program obtained from the author at Bailey Hortorium, Plant Science Cornell University, Ithaca, NY 14853).

Nixon, K. C. & Wheeler, Q. D. (1992) Measures of phylogenetic diversity. *Extinction and phylogeny* (ed. by M. J. Novacek, Q. D. Wheeler), pp. 216–234. Colombia University Press, New York.

Noonan, G. R. (1986) Distribution of insects in the northern hemisphere: Continental drift and epicontinental seas. *Bulletin of the Entomological Society of America*, 32, 80–84.

Page, R. D. M. (1988) Quantitative cladistic biogeography: constructing and comparing area cladograms. *Systematic Zoology*, 37, 254–270.

Page, R. D. M. (1990) Component analysis: a valiant failure? *Cladistics*, 6, 119–136.

Panero, J. L. & Schilling, E. E. (1988) Revision of *Viguiera* section *Maculatae* (Asteraceae: Helianthea). *Systematic Botany*, 13, 371–406.

Parker, W. S. (1974) *Phrynosoma solare. Catalogue of American amphibians and reptiles* (ed. by C. J. McCoy), pp. 162.1–162.2. Society of the Study of Amphibians and Reptiles, Bethesda, Md.

Perrill, R. H. (1983) Phrynosoma ditmarsi. *Herpetological Review*, 14, 123.

Pianka, E. R. (1991) *Phrynosoma platyrhinos. Catalogue of American amphibians and reptiles* (ed. by A. H. Price), pp. 517.1–517.4. Society of the Study of Amphibians and Reptiles, Bethesda, Md.

Platnick, N. I. & Nelson, G. (1978) A method for analysis of historical biogeography. *Systematic Zoology*, 27, 1–16.

Price, A. H. (1990) *Phrynosoma cornutum. Catalogue of American amphibians and reptiles* (ed. by J.D. Villa), pp. 469.1–469.7. Society of the Study of Amphibians and Reptiles, Bethesda, Md.

Ratcliffe, B. C. & Deloya, A. C. (1992) The biogeography and phylogeny of *Hologymnetis* (Coleoptera: Scarabaeidae: Cetoniinae) with a revision of the genus. *Coleopterists Bulletin*, 46, 161–202.

Rauchenberger, M., Kallman, K. D. & Morizot, D. C. (1990) Monophyly and geography of the Río Pánuco Basin swordtails (genus *Xiphophorus*) with descriptions of four new species. *American Museum Novitates*,, 2975, 1–41.

Raven, P. H. & Axelrod, D. I. (1974) Angiosperm biogeography and past continental movements. *Annals of Missouri Botanical Gardens*, 61, 539–673.

Reeve, W. L. (1952) Taxonomy and distribution of the horned toad lizard genus *Phrynosoma. University of Kansas Science Bulletin*, 34, 817–960.

Ridder-Numan, J. W. A. (1996) Historical biogeography of the Southeast Asian genus *Spatholobus* (Legum.—Papilionoidea and its allies.). *Blumea*, 0 (Suppl. 10), 1–144.

Rosen, D. E. (1978) Vicariant patterns and historical explanation in biogeography. *Systematic Zoology*, 27, 159–188.

Rosen, D. E. (1979) Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative geography. *Bulletin of the American Museum of Natural History*, 162, 275–376.

Savage, J. M. & Villa, J. D. (1986) An introduction to the Herpetofauna of Costa Rica. *Society for the Study of Amphibians and Reptiles Contributions in Herpetology*, 3, 1–207.

Sclater, P. L. (1858) On the general geographical distribution of members of the class Aves. *Journal of Linnean Society of Zoology*, 2, 130–145.

Shpeley, D. (1986) Genera of the subtribe Metallicina and classification, reconstructed phylogeny and geographical history of the species of *Euproctinus* Leng and Mutchler (Coleoptera: Carabidae: Lebiini). *Quaestiones Entomoloicae*, 22, 261–218.

Smith, H. M. (1991) Range extension of three reptile species in Northern Mexico. *Bulletin of the Maryland Herpetological Society*, 27, 216–218.

Stonedahl, S. L. (1990) Revision and cladistic analysis of the Holartic genus *Atractotomus* Fieber (Heteroptera: Miridae: Phylinae). *Bulletin of the American Museum of Natural History*, 198, 1–88.

Straneo, S. L. & Ball, G. E. (1989) Synopsis of the genera and subgenera of the tribe Peleciini and revision of the Neotropical and Oriental species (Coleoptera: Carabidae). *Insecta Mundi*, 3, 73–178.

Stuart, L. C. (1963) A checklist of the Herpetofauna of Guatemala. *Miscellaneous Publications of the Museum of Zoology of the University of Michigan*, **122**, 1–150.

Stuart, L. C. (1964) Fauna of Middle America. *Handbook of Middle American Indians* (ed. by R. Wauchope), pp. 316–362. University of Texas Press, Austin, TX.

Stuart, L. C. (1966) The environment of the Central American cold-blooded Vertebrate fauna. *Copeia*, 4, 684–699.

Van Devender, T. R. (1990a) Late Quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. *Packrat middens: the last 40,000 years of biotic change* (ed. by J. L. Betancourt, T. R. Van Devender and P.S. Martin), pp. 104–133. The University of Arizona Press, Tuscon, AZ.

Van Devender, T. R. (1990b) Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. *Packrat middens: the last 40,000 years of biotic change* (ed. by J. L. Betancourt, T. R. Van Devender and P. S. Martin), pp. 134–165. The University of Arizona Press, Tuscon, AZ.

Villa, J. D. (1983) *Nicaraguan fishes, amphibians and reptiles: checklist and bibliography*. Universidad Centroamericana, Managua.

Wallace, A. R. (1876) *The geographical distribution of animals*. Macmillan, London.

Wiley, E. O. (1981) *Phylogenetics: the theory and practice of phylogenetic systematics*. Wiley and Sons, New York.

Wiley, E. O. (1987) Methods in vicariance biogeography. *Systematics and evolution: a matter of diversity* (ed. by P. Hovenkamp), pp. 283–306, Institute of Systematic Botany, Utrecht University.

Zandee, R. & Roos, M. C. (1987) Csomponent-compatibility in historical biogeography. *Cladistics*, 3, 305–332.

Appendix 1. References used to derive taxon-area cladograms.
Carabidae: *Loricera* (Ball *et al.*, 1969); *Notiobia* (Noonan, 1986); *Agonum cyclifer* group (Liebherr, 1994b); *Agonum cyanope* clade (Liebherr, 1986; 1994b); *Elliptoleus* (Liebherr, 1991); *Calathus* (Ball *et al.*, 1972); *Platynus degallieri* group (Liebherr, 1992); *Platynus hamatus* clade (Liebherr, 1988); *Phloeoxena megalops* group (Ball, 1975); *Eripus* (Straneo *et al.*, 1989); *Amblygnathus iripennis* group (Ball, 1987); *Pelmatellus* (Goulet, 1974); *Trichopselaphus* (Ball, 1978, 1987); *Euproctinus* (Shpeley, 1986); *Progaleritina* (Ball *et al.*, 1983).
Other insects: *Atractotomus* (Stonedahl, 1990); *Hologymnetis* (Ratcliffe *et al.*, 1992); *Viridimecus* (Jameson, 1990); *Ateuchus* (Kohlmann *et al.*, 1988); *Typhlusechus* (Aalbu *et al.*, 1985).
Fishes: *Heterandria* (Rosen, 1978, 1979); *Xiphophorus* (Rosen, 1978, 1979; Rauchenberger *et al.*, 1990); *Cyprinella* (Mayden, 1989).
Lizards: *Phrynosoma*, phylogeny (Montanucci, 1987), localities (Reeve, 1952; Parker, 1974; Funk, 1981; Perrill, 1983; Price, 1990; Pianka, 1991; Smith, 1991); *Ctenosaura*, phylogeny (de Queiroz, 1987), localities (Etheridge, 1982); *Basiliscus sensu* lato (Lang, 1989); *Mesaspis*, phylogeny (Good, 1987, 1988), localities (Stuart, 1963, 1964; Villa, 1983; Savage & Villa, 1986; Good, 1989); *Abronia* (Campbell *et al.*, 1993); *Coleonyx*, phylogeny (Grismer, 1988), localities (Dixon, 1970a, 1970b, 1970c, 1970d; Grismer, 1990a, 1990b; Villa, 1983).
Plants: *Viguiera* (Panero *et al.*, 1988).

BIOSKETCHES

Christopher J. Marshall is a graduate student working on his PhD at Cornell University, investigating the phylogenetic relationships and biogeography of bess beetles in the genus Verres (Coleoptera: Passalidae: Proculini). His academic interests centre around the systematics and comparative biology of the New World Passalidae and other Scarabaeoidea.

James K. Liebherr is Professor of Entomology and Curator of the Cornell University Insect Collection. He focuses on systematics and biogeography of carabid beetles inhabiting subtropical and tropical montane forests. His current project involves taxonomic revision of the approximately 300 endemic carabid beetles of the Hawaiian Islands.