PRELIMINARY CLASSIFICATION OF THE MEXICAN BIOGEOGRAPHIC PROVINCES: A PARSIMONY ANALYSIS OF ENDEMICITY BASED ON PLANT, INSECT, AND BIRD TAXA

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Mexico is a country of megadiversity, with complex biogeographical patterns that result from a combination of factors. Congruent distributional patterns of plant and animal taxa can be organized into a hierarchical system of kingdoms, regions, subregions, domains, provinces, and districts (Cabrera and Willink, 1973). Since the beginning of the past century, several authors have proposed biogeographic regionalizations of Mexico (Martens and Galeotti, 1842; Fournier, 1899; Galeotti, 1899; Grisebach, 1899; Hemsley, 1899; Ramírez, 1899; Smith, 1941; Dice, 1943; Goldman and Moore, 1945; Stuart, 1964; Cabrera and Willink, 1973; Rzedowski, 1978; Kohlman and Sánchez, 1984; Casas-Andreu and Reyna-Trujillo, 1990; Ferrusquía-Villafranca, 1990; Ramírez-Pulido and Castro-Campillo, 1990). A recent workshop (Arriaga et al., 1997) resulted in a consensus about the provinces recognized for the Mexican terrestrial biota; however, there is no agreement about their classification into regions and subregions.

Our purpose is to examine the distributional patterns of species and subspecies of plants, insects, and birds, to classify the Mexican biogeographic provinces, applying the parsimony analysis of endemicity technique (Rosen, 1988). In addition, although only the simultaneous analysis of all the data maximize cladistic parsimony (Nixon and Carpenter, 1996), we undertake separate analyses of the three data sets to determine their incongruence.

The areas of the analysis were the following Mexican biogeographic provinces (Fig. 1) that resulted from a recent workshop (Arriaga et al., 1997); Altiplano Norte (apn), Altiplano Sur (aps), Depresión del Balsas (bal), Baja California (bc), Cabo (cab), Chiapas (chi), California (clf), Golfo de México (gm), Soconusco (nus), Oaxaca (oax), Costa del Pacífico (pac), Petén (ptn), Sonora (son), Sierra Madre Oriental (sme), Sierra Madre Occidental (smo), Sierra Madre del Sur (sms), Tamaulipas (tam), Eje Neovolcánico (vol), and Yucatán (yuc).

Distributional data were taken from monographs and revisions (Vaurie, 1966, 1970, 1981, 1982; Herman, 1972, 1975, 1976; Whitehead, 1976; Gundersen, 1977; Clark, 1978, 1982; Zimmerman, 1982; Bright, 1981, 1994; Frank, 1981; Howden, 1982, 1996; Schuh and Schwartz, 1985; Burke and Kovarik, 1986; LeSage, 1986; Ball and Maddison, 1987; Anderson, 1987; Burke and Anderson, 1989; Carlton, 1989; Kuschel, 1989; Spangler and Perkins, 1989; Wibmer, 1989; Jameson, 1990; Lanteri, 1990, 1995; Nelson and Wescott, 1991, 1995; Hamilton, 1992, 1997; Ratcliffe and Deloya, 1992; Henry, 1993; Morón, 1995; Keffer, 1996; Chemsack and McCarty, 1997; Howden, 1997; Llorente et al., 1998; Will, 1997; Hespenheide, 1998; Rifkind, 1998) and data bases from Conabio. The species and subspecies analyzed were from the following taxa: Plants—Arecales (Arecaceae), Asterales (Asteraceae), Caryophyllales (Cactaceae), Coniferales (Pinaceae), Cornales (Nyssaceae), Ericales (Ericaceae), Fabales (Fabaceae), Gentianales (Apocynaceae), Juglandales (Juglandaceae), Liliales (Agavaceae), Magnoliales (Annonaceae), Mal-

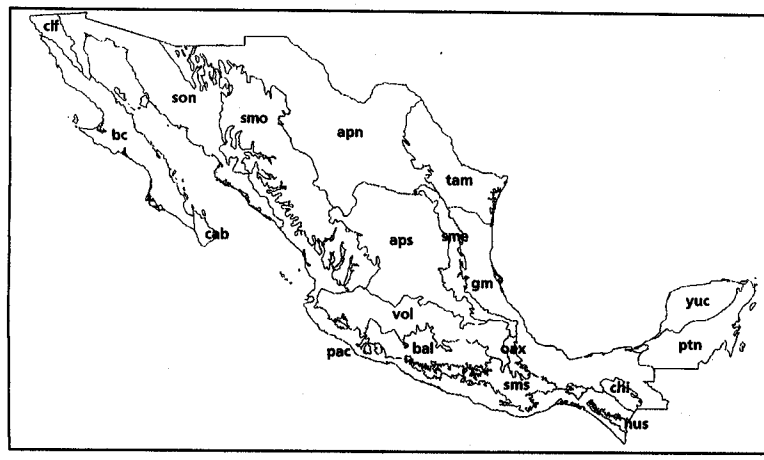

FIG. 1—Mexican biogeographic provinces considered in the analysis. apn: Altiplano Norte, aps: Altiplano Sur, bal: Depresión del Balsas, bc: Baja California, cab: Cabo, chi: Chiapas, clf: California, gm: Golfo de México, nus: Soconusco, oax: Oaxaca, pac: Costa del Pacífico, ptn: Petén, son: Sonora, sme: Sierra Madre Oriental, smo: Sierra Madre Occidental, sms: Sierra Madre del Sur, tam: Tamaulipas, vol: Eje Neovolcánico, yuc: Yucatán.

vales (Bombacaceae), Myrtales (Combretaceae), Polygalales (Vochysiaceae), Sapindales (Anachardiaceae, Burseraceae, and Meliaceae), Theales (Theaceae), Urticales (Moraceae), Violales (Fouquieriaceae); Insects—Coleoptera (Attelabidae, Buprestidae, Carabidae, Cerambycidae, Chrysomelidae, Cleridae, Curculionidae, Dryophthoridae, Dytiscidae, Elmidae, Hydrophilidae, Nemonychidae, Pselaphidae, Scarabeidae, and Staphylinidae), Ephemeroptera, Heteroptera (Miridae and Nepidae), and Lepidoptera (Papilionidae and Pieridae); Birds—Coraciiformes (Momotidae), Craciformes (Cracidae), Cuculiformes (Cuculidae), Galliformes (Phasianidae), Passeriformes (Certhiidae, Corvidae, Fringillidae, Muscicapidae, Sturnidae, and Tyrannidae), Piciformes (Picidae), Psittaciformes (Psittacidae), Strigiformes (Caprimulgidae and Strigidae), Trochiliformes (Trochilidae), and Trogoniformes (Trogonidae).

The parsimony analysis of endemicity or PAE, originally proposed by Rosen (1988) and further modified by Cracraft (1991) and Morrone (1994), classifies areas (analogous to taxa) by their shared taxa (analogous to characters) according to the most parsimonious cladogram. PAE data consist of area by taxa matrices and the resulting cladograms represent nested sets of areas (Morrone and Crisci, 1995). Species and subspecies were coded for their absence (0) or presence (1) in each area in the data matrix (available upon request to the senior author). Cladistic analyses were carried out with Hennig86 (Farris, 1989), applying options mh* (which calculates cladograms by multiple passes through the data) and bb* (which applies branch swapping to find multiple equally parsimonious trees). The cladograms obtained were rooted with a hypothetical area coded all zeros. Incongruence between data sets was investigated by calculating Mickevich and Farris' (1981) index for separate matrices and 3,000 partitions selected randomly into matrices of the three original sizes (see details in Farris et al., 1995), using the program Arnie of the package Random Cladistics (Siddall, 1995).

The parsimony analysis considering the total evidence available yielded a single most parsimonious cladogram with 1,961 steps, consistency index of 0.40, and retention index of 0.50 (Fig. 2a). This cladogram presents two major clades: 1) Cabo, California, Baja California, Tamaulipas, Altiplano Norte, Sierra Madre Occidental, and Sonora provinces; and 2) Yucatán, Petén, Soconusco, Golfo de México, Chiapas, Sierra Madre Oriental, Altiplano Sur, Oaxaca, Sierra Madre del Sur, Depresión del Balsas, Costa del Pacífico, and Eje Neovolcánico provinces. The significance of the incongruence between the three data sets gave a *P*-value of

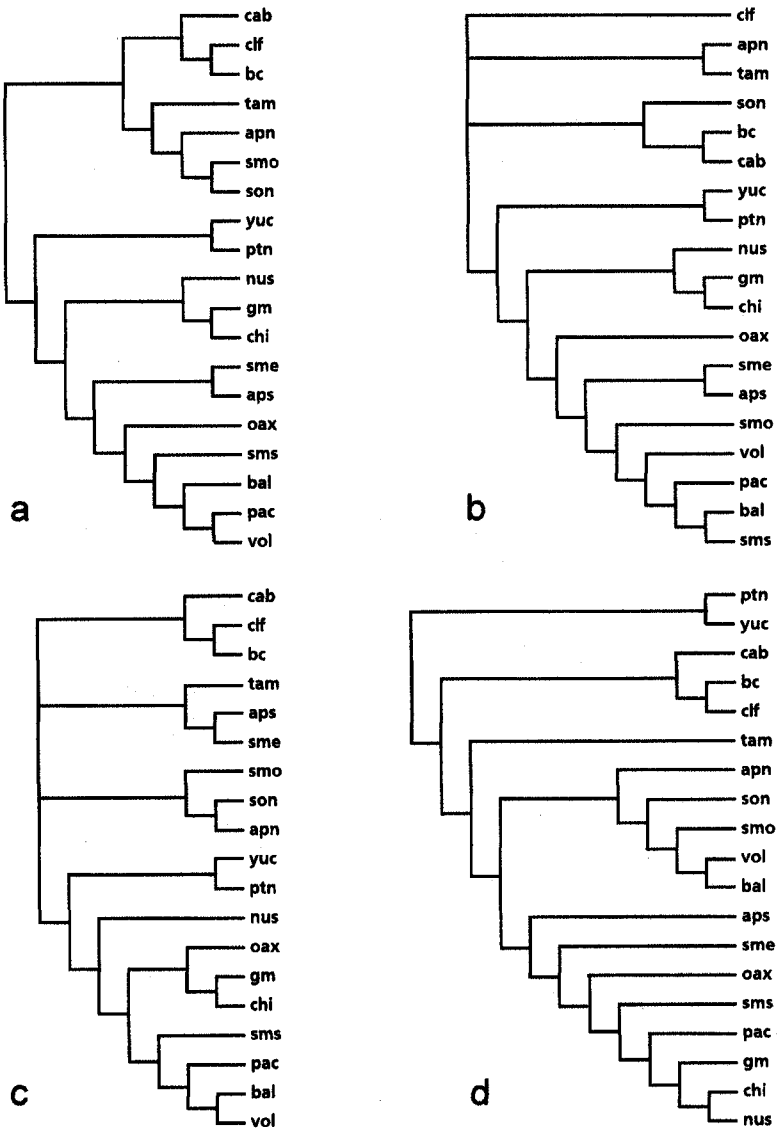

FIG. 2—Alternative cladistic hypotheses concerning the biogeographic classification of the Mexican biogeographic provinces: a. total data set; b. plant taxa; c. insect taxa; d. bird taxa. References as in Fig. 1.

0.000333, showing that disagreement between them is smaller than disagreement within each data set, so we can conclude that plant, insect, and bird data are relatively congruent.

The analysis considering only plant taxa yielded two most parsimonious cladograms with 848 steps, consistency index of 0.45, and retention index of 0.50. In the consensus cladogram (Fig. 2b), a basal polytomy leads to four clades: 1) California province; 2) Altiplano Norte and Tamaulipas provinces; 3) Sonora, Baja California, and Cabo provinces; and 4) Yucatán, Petén, Soconusco, Golfo de México, Chiapas, Oaxaca, Sierra Madre Oriental, Altiplano Sur, Sierra Madre Occidental, Eje Neovolcánico, Costa del Pacífico, Depresión del Balsas, and Sierra Madre del Sur provinces.

The analysis considering only insect taxa

yielded four most parsimonious cladograms with 553 steps, consistency index of 0.44, and retention index of 0.51. In the consensus cladogram (Fig. 2c), a basal polytomy leads to four clades: 1) Cabo, Baja California, and California provinces; 2) Tamaulipas, Altiplano Sur, and Sierra Madre Oriental provinces; 3) Sierra Madre Occidental, Sonora, and Altiplano Norte provinces; and 4) Yucatán, Petén, Soconusco, Oaxaca, Golfo de México, Chiapas, Sierra Madre del Sur, Costa del Pacífico, Depresión del Balsas, and Eje Neovolcánico provinces.

The analysis considering only bird taxa yielded a single most parsimonious cladogram with 450 steps, consistency index of 0.37, and retention index of 0.63 (Fig. 2d). This cladogram presents a basic dichotomy leading to: 1) Petén and Yucatán provinces; and 2) Cabo, Baja California, California, Tamaulipas, Altiplano Norte, Sonora, Sierra Madre Occidental, Eje Neovolcánico, Depresión del Balsas, Altiplano Sur, Sierra Madre Oriental, Oaxaca, Sierra Madre del Sur, Costa del Pacífico, Golfo de México, Chiapas, and Soconusco provinces.

Comparison of cladograms reveals that some clades persist even when considering partial evidence, e.g., the clade Yucatán-Petén in the three separate analyses; or the clade including Cabo, Baja California, and California provinces in the analyses based only on insect or bird data.

Based on our analysis, we propose to classify the Mexican biogeographic provinces as follows:

Nearctic Region
  North American Pacific Subregion
    Cabo Province
    California Province
    Baja California Province
    Tamaulipas Province
    Altiplano Norte Province
    Sierra Madre Occidental Province
    Sonora Province
Neotropical Region
  Caribbean Subregion
    Yucatán Province
    Petén Province
    Soconusco Province
    Golfo de México Province
    Chiapas Province
    Sierra Madre Oriental Province
    Altiplano Sur Province
    Oaxaca Province
    Sierra Madre del Sur Province
    Depresión del Balsas Province
    Costa del Pacífico Province
    Eje Neovolcánico Province

Our results partially agree with some recent classifications (see Fig. 3). The basic distinction between Nearctic and Neotropical provinces is consistent with the schemes of Ramírez-Pulido and Castro-Campillo (1990) and Ferrusquía-Villafranca (1990), although they place the Sierra Madre Oriental, Altiplano Sur, and Eje Neovolcánico provinces in the Nearctic region. Rzedowski (1978) considers the California province as the only Nearctic Mexican province, and places the "mountain" provinces (Sierra Madre Oriental, Sierra Madre Occidental, Sierra Madre del Sur, and Chiapas) in a single transitional region. Our analysis contrasts with both hypotheses, because we found the California province more closely related to the Baja California and Cabo provinces, whereas one mountain province (Sierra Madre Occidental) is placed in the Nearctic region and the others in the Neotropical region. Furthermore, within the Neotropical provinces, different affinities for these latter provinces are apparent: e.g., the Sierra Madre Oriental is related to the Altiplano Sur; the Sierra Madre del Sur province to the Depresión del Balsas, Costa del Pacífico, and Eje Neovolcánico provinces; and the Chiapas province to the Golfo de México and Soconusco provinces.

Within both subregions there are smaller groups of provinces in the cladogram that could be possibly recognized as domains; however, we consider these results as preliminary because they are based only on a relatively small number of plant, insect, and bird taxa. A more accurate biogeographic classification should be undertaken in the future by considering a larger data set, and incorporating more taxa.

Resumen—Se llevó a cabo un análisis de parsimonia de endemismos basado en los patrones de distribución de 801 especies y subespecies de plantas (388), insectos (244) y aves (169) distribuidas en 19 provincias biogeográficas mexicanas, con el objeto de determinar sus relaciones y contrastar clasificaciones previas. Dos grupos resultaron del análisis, uno en

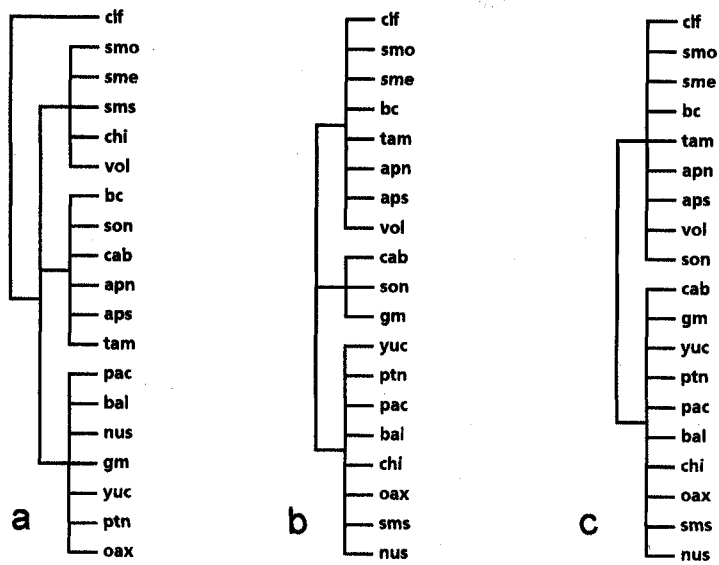

FIG. 3—Recent classifications of the Mexican biogeographic provinces: a. Rzedowski (1978); b. Ferrusquía-Villafranca (1990); c. Ramírez-Pulido and Castro-Campillo (1990). References as in Fig. 1.

el norte incluyendo las provincias del Cabo, California, Baja California, Tamaulipas, Altiplano Norte, Sierra Madre Occidental y Sonora; y otro en el sur incluyendo las provincias de Yucatán, Petén, Soconusco, Golfo de México, Chiapas, Sierra Madre Oriental, Altiplano Sur, Oaxaca, Sierra Madre del Sur, Depresión del Balsas, Costa del Pacífico y Eje Neovolcánico. Se concluye que las provincias biogeográficas mexicanas pueden clasificarse preliminarmente en dos subregiones: las provincias del norte en la subregión Norteamericano Pacífica (perteneciente a la región Neártica) y las del sur en la subregión Caribe (perteneciente a la región Neotropical).

We thank J. Cracraft and two anonymous reviewers for useful comments and the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Conabio) for access to its cartographic data bases. Economic support was provided by project Q-054 from Conabio and DGAPA IN 211397 and IN 207995 from UNAM.

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Submitted 11 September 1998. Accepted 1 February 1999. Associate editor was Charles R. Brown.