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THE GENERA OF ASTERACEAE ENDEMIC TO MEXICO AND ADJACENT REGIONS

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ABSTRACT

The flora of Mexico includes about 119 endemic or nearly endemic genera of Asteraceae. In this study, the genera are listed and their distribution patterns among the floristic provinces of Mexico analyzed. Results indicate strong affinities of the endemic genera for mountainous and arid or semiarid regions. Since its first appearance in Mexico, the Asteraceae diversified into these kinds of habitats, which were produced mostly by recurrent orogenic and climatic phenomena. The specialized tribes Heliantheae and Eupatorieae are richly represented, a fact that places Mexico as an important secondary center of diversification for the Asteraceae.

Key words: Asteraceae, Mexico, Southwestern United States, Guatemala, endemism, floristic analysis.

INTRODUCTION

The Asteraceae contribute greatly to the floristic richness of Mexico. Of the estimated 30,000 species of vascular plants occurring in Mexico (Toledo 1988), perhaps more than 3000 belong to Asteraceae and more than 1300 of these are endemic. The generic diversity of Asteraceae in Mexico greatly exceeds that of most other areas of the world (Table 1). A concise summary of the Composite flora of Mexico at the generic level is available (Cabrera-Rodríguez and Villaseñor 1987). However, the data presented there may change rather quickly during the oncoming years, due to further systematic work and discoveries in many yet unexplored areas of the country. The aim of this paper is to summarize what is known about the endemic genera of Asteraceae of Mexico with regard to their geographical distributions, and to present plausible explanations for the generic richness found in the region.

THE GENERA OF ASTERACEAE ENDEMIC AND NEARLY ENDEMIC TO MEXICO

Any taxon with a limited geographical distribution may be considered an endemic. However, since political boundaries generally do not correspond with biogeographical borders, the argument pointed out by Major (1988) is accepted in this paper, that analyses of endemism should be based on floristic provinces or regions, and not on political units. Consequently, genera that are restricted to one or more Mexican floristic provinces, and do not occur elsewhere, are considered endemic in this paper. The floristic division of Rzedowski (1978) is used. Rzedowski (1978) divides Mexico into 17 floristic provinces (Fig. 1), based primarily on endemism, as well as on patterns of distribution of species, genera, and families of plants. He also points out the strategic position of Mexico at the confluence of the Holarctic and Neotropical kingdoms and the uneven mix that occurs in some provinces of floristic elements from both realms. Because some floristic provinces extend into the bordering southwestern United States or into

Table 1. Genera of Asteraceae in the floras of several countries or regions.

Country or region	Number of genera
United States, Canada and Greenland (Kartesz and Kartesz 1980)	346
Mexico (Cabrera-Rodríguez and Villaseñor 1987)	340
Guatemala (Nash and Williams 1976)	133
Cuba (Alain 1964)	95
Costa Rica (Standley 1938)	101
Panama (Woodson et al. 1975)	111
Colombia (Cuatrecasas 1972)	149
Venezuela (Aristiguieta 1964 *in* Cuatrecasas 1972)	137
Peru (Dillon 1980)	203
Chile (Reiche 1905)	127
Argentina (Cabrera 1961)	178
Europe (Moore et al. 1976)	181
China (Hu 1965–1969)	155
India (Hooker 1882; Calder et al. 1926)	123
Southern Africa (Dyer 1975)	209
South Australia (Cooke 1986)	137

Guatemala, and their geographical correspondence beyond Mexico is imprecise, this paper also includes "nearly endemic" genera, those which occur in floristic provinces in Mexico as well as neighboring areas, but do not extend beyond.

Genera included in this paper as "near endemics" would be found at the limits of Rzedowski's floristic provinces. Most of these near-endemic genera occur in California, south of the Sierra Nevada and the Transverse ranges, in a region that closely approximates the geographic distribution of creosote bush (*Larrea tridentata* (DC.) Coville). These near endemics also have a natural limit just south of the Mogollon Escarpment in central Arizona and generally are not found north of Albuquerque, New Mexico, an area that is roughly defined by Socorro and Guadalupe Counties. In Texas, the near-endemic genera are usually restricted to the vegetational areas defined by Correll and Johnston (1970) as the Rio Grande Plains, Edwards Plateau, and Trans-Pecos; in Guatemala they generally are found in the mountain regions west of the Department of Huehuetenango. A "near endemic" must occur in Mexico to be included in this analysis; at least 31 genera of Asteraceae with limited distributions in the peripheral states fail to meet this condition.

Recent estimates indicate the presence of about 340 genera of Asteraceae in Mexico (Cabrera-Rodríguez and Villaseñor 1987). This figure varies from 330 to 370 depending on the use of narrower or broader taxonomic criteria. A narrower generic concept than that used previously (Cabrera-Rodríguez and Villaseñor 1987) is followed in this paper. Accordingly, 78 endemic genera are recognized (Table 2), about one-fourth of the Composite genera in the flora. Inclusion of 41 near-endemic genera, which extend their geographic ranges slightly beyond Mexico, brings the total to 119 genera (Table 2), about one-third of the Composite genera in the flora.

Table 2 indicates the distribution patterns of endemic genera of Asteraceae in the 17 floristic provinces of Mexico proposed by Rzedowski (1978) and indicates which genera range farther into adjacent territories. Several regions are especially

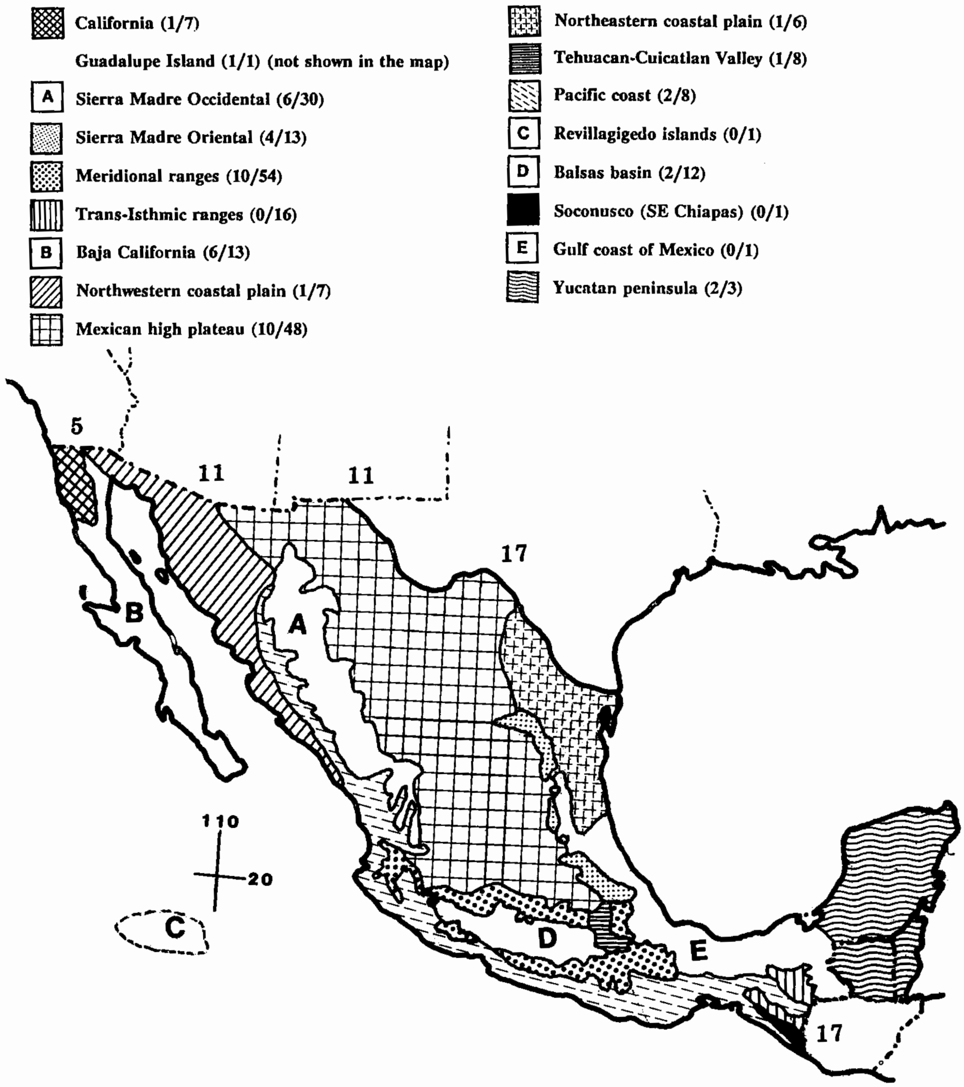

Fig. 1 Rzedowski's floristic provinces of Mexico. Figures between parentheses indicate the number of Mexican-endemic genera of Asteraceae that are restricted to the province, followed by the total found within the province. Figures for Arizona, California, New Mexico, Texas, and Guatemala indicate the number of genera of Asteraceae nearly endemic to Mexico that have range extensions into these areas (redrawn from Rezdowski 1978).

rich in these endemic genera: 1) the Meridional ranges (including the mountainous ranges of central Mexico, particularly the Eje Volcanico Transversal and the Sierra Madre del Sur); 2) the Mexican high plateau, largely consisting of the Chihuahuan Desert; 3) Baja California; 4) the Sierra Madre Occidental in northwestern Mexico; and 5) the Sierra Madre Oriental in northeastern Mexico. The montane areas, together with the arid and semiarid areas, include 61% of the endemic genera (39 and 33 genera respectively). Among the montane endemic genera for these regions are *Adenopappus, Ageratella, Arnicastrum, Axiniphyllum, Chromolepis, Digitac-*

Table 2. Genera of Asteraceae endemic to Mexico and adjacent regions and their distribution.[1]

Tribe Astereae

Dichaetophora Gray: 9, T
Geissolepis B. L. Rob.: 9
Gymnosperma Less.: 9, 11, 14, A, N, T, G
Olivaea Sch. Bip. ex Benth.: 3, 5, 9
Osbertia Greene: 4, 5, 6, G
Stephanodoria Greene: 9
Xanthocephalum Willd.: 3, 5, 8, 9, A, T

Tribe Eupatorieae

Ageratella Gray ex S. Wats.: 3, 5
Alomia Kunth: 5, 14
Amolinia King & H. Rob.: 6, G
Asanthus King & H. Rob.: 3, 9, A, N
Barroetea Gray: 5, 9, 11, 14
Carphochaete Gray: 5, 9, 14, A, N, T
Carterothamnus King: 7
Cronquistia King: 3
Decachaeta DC.: 3, 5, 12
Dyscritogyne King & H. Rob.: 5
Erythradenia (B. L. Rob.) King & H. Rob.: 5
Flyriella King & H. Rob.: 4, 9, 10, T
Jaliscoa S. Wats.: 3, 5, 12
Kyrsteniopsis King & H. Rob.: 5, 9
Malperia S. Wats.: 1, 7, C
Matudina King & H. Rob.: 12
Metastevia Grashoff: 5, 14
Mexianthus B. L. Rob.: 5, 12
Microspermum Lag.: 3, 5, 14
Neohintonia King & H. Rob.: 5
Oaxacania B. L. Rob.: 11
Phanerostylis (Gray) King & H. Rob.: 4, 5, 9
Piptothrix Gray: 3, 5, 6, G
Piqueriopsis King: 5
Pseudokyrsteniopsis King & H. Rob.: 6, G
Revealia King & H. Rob.: 5
Sartorina King & H. Rob.: 5
Shinnersia King & H. Rob.: 9, T
Steviopsis King & H. Rob.: 5
Tamaulipa King & H. Rob.: 10
Trichocoronis Gray: 1, 5, 7, 9, 10, C, T
Viereckia King & H. Rob.: 4

Tribe Heliantheae

Achyropappus Kunth: 5, 9
Adenothamnus Keck: 1
Agiabampoa Rose ex Hoffm.: 8
Alvordia Brandeg.: 7
Amauria Benth.: 1, 7
Amblyolepis DC.: 9, T
Arnicastrum Greenm.: 3, 5
Axiniphyllum Benth.: 3, 5
Baeriopsis Howell: 2
Bartlettia Gray: 9
Chromolepis Benth.: 3, 5
Clappia Gray: 9, 10, N, T
Coreocarpus Benth.: 3, 7, 8, 13, 14, A
Correlia Powell: 3
Coulterella Vasey & Rose: 7
Damnxanthodium Strother: 3
Dicranocarpus Gray: 9, T
Dugesia Gray: 5, 9, 11
Dyscritothamnus B. L. Rob.: 9
Eryngiophyllum Greenm.: 12
Euphrosyne DC.: 5, 9
Eutetras Gray: 5, 9
Faxonia Brandeg.: 7
Goldmanella Greenm.: 17
Greenmaniella Sharp: 4
Guardiola Cerv. ex Humb. & Bonpl.: 3, 4, 5, 8, 9, 12, 14, A
Haploesthes Gray: 9, N, T
Henricksonia Turner: 9
Hybridella Cass.: 3, 5, 9
Hymenothrix Gray: 1, 3, 7, 8, 9, 14, C, A, N, T
Iostephane Benth.: 3, 5, 9
Loxothysanus B. L. Rob.: 4, 5, 6
Oteiza La Llave: 4, 5, 6, G
Oxypappus Benth.: 3, 5, 12
Parthenice Gray: 7, 8, 9, A
Perymeniopsis H. Rob.: 4
Philactis Schrader: 5, 6, 12, 15, G
Plagiolophus Greenm.: 17
Plateilema (Gray) Cockerell: 9
Plummera Gray: 9, A
Pseudoclappia Rydb.: 9, N
Rojasianthe Standl. & Steyerm.: 6, G
Sartwellia Gray: 9, N, T
Squamopappus Janzen et al.: 6, G
Stuessya Turner & Davies: 14
Tetrachyron Schlecht.: 4, 5, 6, 11, G
Trichocoryne Blake: 3
Trigonospermum Less.: 3, 5, 9, G
Varilla Gray: 9, 10, T
Venegasia DC.: 1, C
Vigethia Weber: 4

Tribe Inuleae

Gnaphaliothamnus Kirp.: 3, 5, 6, G
Pelucha S. Wats.: 7
Pseudognaphalium Kirp.: 5, 6, G

Tribe Lactuceae

Marshalljohnstonia Henrickson: 9
Pinaropappus Less.: 3, 5, 8, 9, 11, A, N, T, G

Tribe Liabeae

Liabellum Rydb.: 5, 9

Tribe Senecioneae

Digitacalia Pippen: 5, 6
Nelsonianthus H. Rob. & Brettell: 6, G
Odontotrichum Zucc.: 3, 5, 6, 9, A

Table 2. Continued.

Pericalia Cass.: 3, 5	*Hydrodyssodia* Turner: 9
Pippenalia McVaugh: 3	*Hydropectis* Rydb.: 3, 9
Pittocaulon H. Rob. & Brettell: 5, 9, 14	*Leucactinia* Rydb.: 9
Psacaliopsis H. Rob. & Brettell: 5, G	*Nicolletia* Gray: 1, 7, 9, C, N, T
Psacalium Cass.: 3, 5, 9, G	*Strotheria* Turner: 9
Tribe Tageteae	*Urbinella* Greenm.: 3
Adenopappus Benth.: 5	Tribe Vernonieae
Boeberastrum (Gray) Rydb.: 7	*Bolanosa* Gray: 5
Boeberoides (DC.) Strother: 14	*Harleya* Blake: 16, 17, G
Chrysactinia Gray: 4, 9, 10, 11, N, T	*Leiboldia* Schlecht. ex Gleason: 4, 5
Gymnolaena (DC.) Rydb.: 5, 6, 11	*Stramentopappus* H. Rob. & Funk: 5

[1] Floristic provinces of Mexico [total genera per province]: 1—California [7]; 2—Guadalupe island [1]; 3—Sierra Madre Occidental [30]; 4—Sierra Madre Oriental [13]; 5—Meridional ranges [54]; 6—Trans-Isthmic ranges [16]; 7—Baja California [13]; 8—Northwestern coastal plain [7]; 9—Mexican high plateau [48]; 10—Northeastern coastal plain [6]; 11—Tehuacan-Cuicatlan valley [8]; 12—Pacific coast [8]; 13—Revillagigedo islands [1]; 14—Balsas basin [12]; 15—Soconusco (SE Chiapas) [1]; 16—Gulf coast [3]; 17—Yucatan peninsula [3]. Adjacent regions [total genera per region]: C—California [5]; A—Arizona [11]; N—New Mexico [11]; T—Texas [17]; G—Guatemala [17].

alia, Greenmaniella, Leiboldia, Loxothysanus, Microspermum, Pippenalia, and *Piptothrix.* The endemic genera found in semiarid and arid environments include *Adenothamnus, Alvordia, Amauria, Chrysactinia, Dicranocarpus, Dugesia, Dyscritothamnus, Geissolepis, Gymnosperma, Haploesthes, Malperia, Marshalljohnstonia, Nicolletia, Oaxacania, Sartwellia, Stephanodoria, Varilla,* and *Venegasia.* About a third of the endemic genera show a broader pattern of distribution, and are found on both montane and semiarid to arid environments.

GEOHISTORICAL SCENARIO

Of great importance in understanding current distribution patterns of Asteraceae in Mexico are the geohistorical events that have occurred since the Cretaceous. At the end of the Paleozoic, the Mexican region experienced extensive tectonic activity (De Cserna 1974), cresting uplifts that provided the varied habitats where the rich Mexican flora evolved.

The Sierra Madre Oriental in eastern Mexico was uplifted at the end of the Cretaceous and the beginning of the Tertiary (Guzmán and De Cserna 1963; Maldonado-Koerdell 1964; De Cserna 1974). By the Middle Tertiary, the Sierra Madre del Sur of southern Mexico was formed. At the end of the Oligocene and during the Miocene, the Sierra Madre Occidental was uplifted in northwestern Mexico. At the end of the Miocene the Gulf of California was formed, thus separating the peninsula of Baja California from the mainland. Finally, the physiography of Mexico reached its present condition in the Pliocene with the appearance of the Eje Volcanico Transversal in central Mexico and with the elevation of the Yucatan peninsula.

Fossils of Asteraceae have been identified with confidence as early as the Oligocene (Muller 1981; Raven and Axelrod 1974); Mexican Asteraceous fossils have been confidently identified from the Upper Miocene (Graham 1976). A widespread Mexican distribution for the family can be assumed by this time, because the family was present by the Middle Miocene in southern California as a member of the Madro-Tertiary Geoflora (Axelrod 1958). Orogenesis had taken place in both eastern and western Mexico by this time, as well as in southern Mexico. Continuing volcanic activity may have been an important isolating factor in the evolution of the family, fragmenting populations and producing many of the apparent vicariant taxa of the Mexican flora (Ramamoorthy and Lorence 1987). In the Asteraceae, some of the vicariant genera are *Agiabampoa* and *Alvordia*; *Hofmeisteria* Walp, *Carterothamnus,* and *Oaxacania*; and *Arnicastrum, Jamesianthus* Blake & Sherff, and *Arnica* L. The last two genera are found only in North America.

Paleoclimatic data (Dorf 1960) suggest for the Upper Miocene a prevailing warm climate in Mexico; lowlands were dominated mainly by tropical or subtropical vegetation. Asteraceae are not richly represented in modern tropical forests (Rzedowski 1972); however, temperate forests of fir and oak are documented for middle and higher elevations (Graham 1976). And a semiarid climate was already present in northwestern Mexico, where a distinctive, mostly microphyllous or sclerophyllous flora developed (Axelrod 1958). Temperate forests and semiarid or arid lands are at present, and presumably also in the past, among the most favored plant communities for members of Asteraceae (Rzedowski 1972).

The Asteraceae therefore found, after their arrival in Mexico, two of their most favored environments. Vulcanism cleared many areas, making them suitable for aggressive invaders by producing an innumerable array of microhabitats where a rich generic flora could evolve. It formed, with the elevation of mountain ranges, the many endorheic basins (basins with only interior drainage,) found mainly in northern Mexico, which are host to a great number of endemics. One example is the Bolson de Cuatro Cienegas Region in Coahuila, an area floristically studied by Pinkava (1979–1981).

Glacial events in the Quaternary allowed boreal forests to achieve a broader distribution. The desert conditions that developed during the Quaternary, as in, for example, the Chihuahuan Desert (Wells 1974) or the Tehuacan-Cuicatlan Valley (Brunet 1967), confirm again the presence in recent epochs of habitats especially suitable for the diversification of the Asteraceae. According to Brunet (1967), the Tehuacan-Cuicatlan Valley floristic province did not form until the Quaternary, when the erosion and rupture of the Sierra Madre Oriental (caused by the Rio Santo Domingo, a tributary of the Rio Papaloapan) drained a former lake. This lake had occupied what is now most of the floristic province. The eventual drainage of the lake was caused by subsidence of the underground water reservoirs. The rain shadow caused by the Sierra Madre Oriental aided this process. Floristically, the province harbors at least 238 species of Asteraceae (Villaseñor 1982), approximately 29% of which are endemic to the province. The high percentage of endemism shown in this area exemplifies the great capability of the Asteraceae to thrive and diversify explosively when suitable environments are available.

The large number of genera belonging to the tribes Heliantheae and Eupatorieae suggests that, if not the center of origin for the Asteraceae, Mexico played a very significant role in the explosive evolution of the family, as a most important secondary center of diversification.

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LITERATURE CITED

Alain, Hermano (E. E. Loigier). 1964. Flora de Cuba. Tomo V. Publicación de la Asociación de Estudiantes de Ciencias Biológicas. La Habana, pp. 175–362.

Axelrod, D. I. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. 24:433–509.

Brunet, J. 1967. Geologic studies, pp. 66–90. *In* D. S. Byers [ed.], The prehistory of the Tehuacan Valley. Vol. I. Environment and subsistence. Univ. of Texas Press, Austin, Tex.

Cabrera, A. L. 1961. Compuestas Argentinas. Clave para la determinación de los géneros. Rev. Mus. Arg. Ci. Nat. "Bernardino Rivadavia" 2:291–362.

Cabrera-Rodríguez, L., and J. L. Villaseñor. 1987. Revisión bibliográfica sobre el conocimiento de la familia Compositae en México. Biótica 12:131–147.

Calder, C. C., V. Narayanaswami, and M. S. Ramaswami. 1926. List of species and genera of Indian phanerogams not included in Sir J. D. Hooker's Flora of British India. Records of the Botanical Survey of India 11:1–157.

Cooke, D. A. 1986. Compositae (Asteraceae), pp. 1423–1658. *In* J. P. Jessop and H. R. Toelken [eds.], Flora of South Australia. Part III. South Australian Government Printing Division, Adelaide.

Correll, D. S., and M. C. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Tex. 1881 p.

Cuatrecasas, J. 1972. Algo sobre Compositae en la flora de Colombia. I Congreso Latinoamericano y V Mexicano de Botánica. Memorias de Symposia, pp. 157–166.

De Cserna, Z. 1974. La evolución geológica del panorama fisiográfico actual de México, pp. 21–56. *In* El escenario geográfico. Introducción ecológica (primera parte). I.N.A.H. Departamento de Prehistoria. México, D.F.

Dillon, M. O. 1980. Family Compositae: Part I. Introduction to family, pp. 12–21. *In* J. F. MacBride and collaborators, Flora of Peru. Fieldiana, Bot. New Series. No. 5. Publ. No. 1314.

Dorf, E. 1960. Climatic changes of the past and present. Amer. Sci. 48:341–364.

Dyer, R. A. 1975. The genera of Southern African flowering plants. Vol. I. Dicotyledons. Department of Agricultural Technical Services, Republic of South Africa, Pretoria. 756 p.

Graham, A. 1976. Studies in Neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. Ann. Missouri Bot. Gard. 63:787–842.

Guzmán, E. J., and Z. De Cserna. 1963. Tectonic history of Mexico, pp. 113–129. *In* The backbone of the Americas. Tectonic history from Pole to Pole. A symposium. Memoir No. 2. The Amer. Assoc. of Petroleum Geologists.

Hooker, J. D. 1882. The flora of British India. Vol. III. L. Reeve & Co., Ashford, Kent, pp. 219–419.

Hu, S. 1965–1969. The Compositae of China. Quart. J. Taiwan Mus. 18:1–136, 233–333; 19:1–73, 203–301; 20:1–77, 283–339; 21:1–52, 127–179; 22:1–56.

Kartesz, J. T., and R. Kartesz. 1980. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. The biota of North America. Vol. II. The Univ. of North Carolina Press, Chapel Hill. 500 p.

Major, J. 1988. Endemism: a botanical perspective, pp. 117–146. *In* A. A. Myers and P. S. Giller [eds.], Analytical biogeography. Chapman and Hall, New York.

Maldonado-Koerdell, M. 1964. Geohistory and paleogeography of Middle America, pp. 3–32. *In* R. C. West [ed.], Natural environment and early cultures. Univ. of Texas Press, Austin, Tex. Vol. I.

Moore, D. M., T. G. Tutin, and S. M. Walters [eds.]. 1976. Compositae, pp. 103–410. *In* Flora Europaea. Vol. IV. Cambridge Univ. Press, London.

Muller, J. 1981. Fossil pollen records of extant angiosperms. Bot. Rev. 47:1–142.

Nash, D. L., and L. O. Williams. 1976. Compositae. *In* Flora of Guatemala. Fieldiana, Bot. 24(Part XII):1–603.

Pinkava, D. J. 1979–1981. Vegetation and flora of the Bolson of Cuatro Cienegas region, Coahuila, Mexico. Parts I–III. Bol. Soc. Bot. México 38:35–74; 39:107–127; 41:127–151.

Ramamoorthy, T. P., and D. H. Lorence. 1987. Species vicariance in the Mexican flora and description of a new species of *Salvia* (Lamiaceae). Bull. Mus. Hist. Nat. (Paris), Series IV, 9: 167–175.

Raven, P. H., and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61:539–673.

Reiche, C. 1905. La distribución geográfica de las Compuestas de la flora de Chile. Anales Mus. Nac. Chile, Segunda Sección, Botánica. Entrega No. 17. 45 p.

Rzedowski, J. 1972. Contribuciones a la fitogeografía florística e histórica de México. III. Algunas tendencias en la distribución geográfica de las Compositae Mexicanas. Ciencia (México) 27: 123–132.

———. 1978. Vegetación de México. Ed. Limusa, México. 432 p.

Standley, P. C. 1938. Flora of Costa Rica. Publ. Field Mus. Nat. Hist., Bot. Ser. 18:1418–1538.

Toledo, V. M. 1988. La diversidad biológica de México. Ciencia y Desarrollo (México) 81:17–30.

Villaseñor, J. L. 1982. Las Compositae del Valle de Tehuacán-Cuicatlán. Flora genérica. Bachelor's Thesis. U.N.A.M. Fac. de Ciencias. México, D.F. 174 p.

Wells, P. V. 1974. Post-glacial origin of the present Chihuahuan Desert less than 11,500 years ago, pp. 67–83. *In* R. H. Wauer and D. H. Riskind [eds.], Transactions of the symposium on the biological resources of the Chihuahuan Desert region, United States and Mexico. Sul Ross State Univ., Alpine, Tex.

Woodson, R. E., R. W. Schery, and collaborators. 1975. Compositae. *In* Flora of Panama. Part IX. Ann. Missouri Bot. Gard. 62:835–1322.