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GEOGRAPHICAL  
DIVERSIFICATION OF  
TRIBES EPILOBIEAE,  
GONGYLOCARPEAE, AND  
ONAGREAE (ONAGRACEAE)  
IN NORTH AMERICA, BASED  
ON PARSIMONY ANALYSIS  
OF ENDEMICITY AND TRACK  
COMPATIBILITY ANALYSIS<sup>1</sup>

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ABSTRACT

Tribes Epilobieae, Gongylocarpeae, and Onagreae, a monophyletic branch in the family Onagraceae, comprise genera endemic to or having their major basal radiation in the Madrean Floristic Region of southwestern North America. Parsimony analysis of endemicity (PAE) and panbiogeography (track compatibility analysis) were performed in order to seek an historical explanation for the patterns of high diversity and endemicity for the group in this region. Twenty-one areas of endemism are delimited, based on previous biogeographic schemes and presence of endemic plant and animal taxa. Based on distributional data on 173 species, a strict consensus PAE cladogram shows four main groups of areas: northern North America, the central Mexican areas, western North America, and eastern North America. Track compatibility analysis resulted in two strongly supported generalized tracks: one includes eastern North America, and the other western North America. PAE and panbiogeographical analyses of the distributional patterns of these taxa suggest a close relationship of eastern and western North America, with both areas more related to the Neotropics than to the Palearctic, and a rather weak association between northern North America and Asia. The discovery of two tracks in eastern and western North America for Epilobieae, Gongylocarpeae, and Onagreae reveal little relationship of North America with Asia or other continents. These tribes display a distinct but contemporaneous biogeographical history that differs from those of the Holarctic. These eastern and western tracks show that ancestral biotas existed on each side of North America, with the species of each track sharing a common history.

*Key words:* biogeography, endemicity, Madrean, Onagraceae, panbiogeography.

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Recent developments in biogeography have highlighted the importance of the spatial distribution of organisms as a direct subject of analysis (Craw et al., 1999; Crisci, 2001; Crisci et al., 2000, 2003). The Onagraceae, a moderate-sized, sharply defined, homogeneous family, have been intensively studied (Raven, 1979, 1988; Hoch et al., 1993; Levin et al., 2003, 2004) and thus constitute an excellent group within which to develop such biogeographic studies.

The family Onagraceae includes six monogeneric tribes—Circaceae, Fuchsiaeae, Gongylocarpeae, Hauyaeae, Jussiaeae, and Lopezieae—and two larger, more diverse tribes, Epilobieae and Onagreae (Raven, 1979; Hoch et al., 1993; Levin et al., 2003). Tribes Epilobieae, Gongylocarpeae, and Onagreae, which form a monophyletic branch in the family (Levin et al., 2003), are biogeographically distinct because almost all 11 genera in these tribes are endemic to or have had their major basal ra-

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diation in western North America. A primary concentration of genera exists in the Madrean Floristic Region (Takhtajan, 1986), comprising the southwestern United States and northern Mexico. This is an area of great geological and climatological complexity with a rich and highly characteristic biota (Axelrod, 1958; Axelrod & Raven, 1985; Takhtajan, 1986).

*Gongylocarpus*, until recently included in the Onagreae, and *Xylonagra* (Onagreae) are endemic to western North America, and *Camissonia*, *Clarkia*, and *Gayophytum* (all Onagreae) have the great majority of their taxa in the region, especially in the California Floristic Province (Raven & Axelrod, 1978); each of the latter three genera also has one or two species in temperate South America. The remaining genera of Onagreae (*Calylophus*, *Gaura*, *Oenothera*, *Stenosiphon*) have centers of diversity further east in North America, although *Gaura* extends into central Mexico and *Oenothera* into Central and South America. One exception to the predominantly North American nature of these tribes is *Chamerion* (the fireweeds), a genus of Epilobieae with six of its eight species and one of two sections endemic in Europe and Asia. Tribe Epilobieae definitely has a north temperate origin, with a distribution pattern that suggests a more complex history of diversification (Raven, 1976; Baum et al., 1994). All seven sections of *Epilobium* (including the former segregate genera *Boisduvalia* and *Zauschneria*) occur in or are restricted to the Madrean Region, with the large section *Epilobium* diversified on all other continents except Antarctica.

In order to seek the historical explanations that led to the high diversity and endemicity of Epilobieae, Gongylocarpeae, and Onagreae in North America, we will analyze the patterns of distribution of species of these tribes native to North America (for a list of species and references, see Table 1). A focus on patterns of distribution requires conceptual and methodological tools that allow comparisons to be made in a meaningful and informative way. Two modern approaches that allow this kind of analysis are parsimony analysis of endemicity and track compatibility analysis (panbiogeography) (Morrone & Crisci, 1990, 1995; Crisci et al., 2000, 2003).

## MATERIALS AND METHODS

### AREAS OF ENDEMISM

An area of endemism is defined as an area of nonrandom distributional congruence among different taxa. It is identified by the congruent distributional boundaries of two or more species, where

congruence does not demand complete agreement on those limits at all possible scales of mapping, but relatively extensive sympatry is a prerequisite (Platnick, 1991).

Areas of endemism used in this analysis are defined primarily by Takhtajan (1986) and Thorne (1993) and validated by other biogeographical studies (i.e., Dice, 1943; Rzedowski, 1978; Brown et al., 1979, 1998; McLaughlin, 1989, 1992; Ayala et al., 1993; Escalante Pliego et al., 1993; Fa & Morales, 1993; Li & Adair, 1994; Liebherr, 1994a, b; Morrone et al., 1999; Marshall & Liebherr, 2000; Morrone, 2001). Because the focus of this study is on a major plant lineage that has diversified in arid North America, we have used small, closely defined areas within the Madrean area. Some taxa within this lineage have distributions that extend beyond the North American regions. For these we used the more broadly defined Neotropical, East Palearctic, and West Palearctic regions, since they fall outside of our area of focus in North America. Africa and Australia were not included because native North American species of these three tribes occur in these areas only as exotics. Table 2 lists the areas of endemism alphabetically, with taxa of the three target tribes endemic to each area. Full descriptions of each area of endemism, including sample plant and animal taxa endemic to each, are provided in Appendix 1. The areas are illustrated in Figure 1.

In some regions, the area delineations provided by Takhtajan (1986) and Thorne (1993) proved somewhat vague or difficult to interpret, and in those cases we used additional resources to determine the boundaries. For example, we used the geographical subdivisions found in *The Jepson Manual* (Hickman, 1993) to more precisely delineate the five regions in California (CAL, GBA, MOJ, SON, and VAN; see Table 2 for area acronyms). Similarly, we used the vegetational areas described in Correll and Johnston (1970) to establish the boundaries of the regions in Texas (APP, ATL, CHI, NAP, and TAM). Additional sources used for specific areas are referenced in the area description. In this way, distributional records could be placed more precisely in the appropriate area of endemicity.

### TAXA ANALYZED

The primary data for this analysis are the distributions of 173 native species of Onagraceae tribes Epilobieae, Gongylocarpeae, and Onagreae inhabiting North America (Canada, Mexico, United States; Table 1). The distributional data were taken

Table 1. List of species included in this analysis and source of distributional data (see text for details regarding unpublished data). *Gongylocarpus* is listed here in tribe Onagreae; only recently (Levin et al., 2003) it was transferred to tribe Gongylocarpeae. The number of each species corresponds with column numbers in the data matrix (Table 3). Names of taxa are those currently in use, based on recent revisions. Two of the names, *Oenothera deserticola* and *O. purpusii*, subsequently have been revised due to a nomenclatural problem (Wagner, 2004): *Oenothera purpusii* in the sense used here will become *O. deserticola*, and the current *O. deserticola* will take a new name.

| Taxa  | Source of information             |
|---|-----------------------------------|
| TRIBE ONAGREAE  |                                   |
| <b><i>Camissonia</i></b> Link                                   | Raven (1962, 1969)                |
| 1. <i>C. andina</i> (Nutt.) P. H. Raven                         |                                   |
| 2. <i>C. arenaria</i> (A. Nelson) P. H. Raven                   |                                   |
| 3. <i>C. boothii</i> (Douglas) P. H. Raven                      |                                   |
| 4. <i>C. breviflora</i> (Torr. & A. Gray) P. H. Raven           |                                   |
| 5. <i>C. brevipes</i> (A. Gray) P. H. Raven                     |                                   |
| 6. <i>C. californica</i> (Nutt. ex Torr. & A. Gray) P. H. Raven |                                   |
| 7. <i>C. campestris</i> (Greene) P. H. Raven                    |                                   |
| 8. <i>C. cardiophylla</i> (Torr.) P. H. Raven                   |                                   |
| 9. <i>C. chamaenerioides</i> (A. Gray) P. H. Raven              |                                   |
| 10. <i>C. cheiranthifolia</i> (Hornem. ex Spreng.) Raim.        |                                   |
| 11. <i>C. claviformis</i> (Torr. & Frém.) P. H. Raven           |                                   |
| 12. <i>C. confusa</i> P. H. Raven                               |                                   |
| 13. <i>C. contorta</i> (Douglas) Kearney                        |                                   |
| 14. <i>C. eastwoodiae</i> (Munz) P. H. Raven                    |                                   |
| 15. <i>C. graciliflora</i> (Hook. & Arn.) P. H. Raven           |                                   |
| 16. <i>C. guadalupensis</i> (S. Watson) P. H. Raven             |                                   |
| 17. <i>C. hilgardii</i> (Greene) P. H. Raven                    |                                   |
| 18. <i>C. hirtella</i> (Greene) P. H. Raven                     |                                   |
| 19. <i>C. ignota</i> (Jeps.) P. H. Raven                        |                                   |
| 20. <i>C. intermedia</i> P. H. Raven                            |                                   |
| 21. <i>C. kernensis</i> (Munz) P. H. Raven                      |                                   |
| 22. <i>C. lacustris</i> P. H. Raven                             |                                   |
| 23. <i>C. lewisii</i> P. H. Raven                               |                                   |
| 24. <i>C. minor</i> (A. Nelson) P. H. Raven                     |                                   |
| 25. <i>C. multijuga</i> (S. Watson) P. H. Raven                 |                                   |
| 26. <i>C. ovata</i> (Nutt. ex Torr. & A. Gray) P. H. Raven      |                                   |
| 27. <i>C. pallida</i> (Abrams) P. H. Raven                      |                                   |
| 28. <i>C. palmeri</i> (S. Watson) P. H. Raven                   |                                   |
| 29. <i>C. parvula</i> (Nutt. ex Torr. & A. Gray) P. H. Raven    |                                   |
| 30. <i>C. pterosperma</i> (S. Watson) P. H. Raven               |                                   |
| 31. <i>C. pubens</i> (S. Watson) P. H. Raven                    |                                   |
| 32. <i>C. pusilla</i> P. H. Raven                               |                                   |
| 33. <i>C. pygmaea</i> (Douglas) P. H. Raven                     |                                   |
| 34. <i>C. refracta</i> (S. Watson) P. H. Raven                  |                                   |
| 35. <i>C. robusta</i> P. H. Raven                               |                                   |
| 36. <i>C. scapoidea</i> (Torr. & A. Gray) P. H. Raven           |                                   |
| 37. <i>C. strigulosa</i> (Fisch. & C. A. Mey.) P. H. Raven      |                                   |
| 38. <i>C. subacaulis</i> (Pursh) P. H. Raven                    |                                   |
| 39. <i>C. tanacetifolia</i> (Torr. & A. Gray) P. H. Raven       |                                   |
| 40. <i>C. walkeri</i> (A. Nelson) P. H. Raven                   |                                   |
| <b><i>Calylophus</i></b> Spach                                  | Towner (1977)                     |
| 41. <i>C. berlandieri</i> Spach                                 |                                   |
| 42. <i>C. hartwegii</i> (Benth.) P. H. Raven                    |                                   |
| 43. <i>C. lavandulifolius</i> (Torr. & A. Gray) P. H. Raven     |                                   |
| 44. <i>C. serrulatus</i> (Nutt.) P. H. Raven                    |                                   |
| 45. <i>C. toumeyii</i> (Small) Towner                           |                                   |
| 46. <i>C. tubicula</i> (A. Gray) P. H. Raven                    |                                   |
| <b><i>Clarkia</i></b> Pursh                                     | Lewis & Lewis (1955, except in *) |
| 47. <i>C. amoena</i> (Lehm.) A. Nelson & J. F. Macbr.           |                                   |

Table 1. Continued.

| Taxa  | Source of information           |
|---|---------------------------------|
| 48. <i>C. biloba</i> (Durand) A. Nelson & J. F. Macbr.  |                                 |
| 49. <i>C. concinna</i> (Fisch. & C. A. Mey.) Greene   |                                 |
| 50. <i>C. cylindrica</i> (Jeps.) F. H. Lewis & M. R. Lewis  |                                 |
| 51. <i>C. dudleyana</i> (Abrams) J. F. Macbr.   |                                 |
| 52. <i>C. epilobioides</i> (Nutt. ex Torr. & A. Gray) A. Nelson & Macbr.                          |                                 |
| 53. <i>C. gracilis</i> (Piper) A. Nelson & J. F. Macbr.   |                                 |
| 54. * <i>C. heterandra</i> (Torr.) F. H. Lewis & P. H. Raven                                      | Lewis (1993)                    |
| 55. <i>C. lassenensis</i> (Eastw.) F. H. Lewis & M. R. Lewis                                      |                                 |
| 56. <i>C. modesta</i> Jeps.   |                                 |
| 57. * <i>C. mosquini</i> E. Small   | Lewis (1993)                    |
| 58. <i>C. pulchella</i> Pursh   |                                 |
| 59. <i>C. purpurea</i> (Curtis) A. Nelson & J. F. Macbr.  |                                 |
| 60. <i>C. rhomboidea</i> Douglas  |                                 |
| 61. * <i>C. rostrata</i> W. S. Davis  | Lewis (1993)                    |
| 62. <i>C. speciosa</i> F. H. Lewis & M. R. Lewis  |                                 |
| 63. * <i>C. tembloriensis</i> Vasek   | Lewis (1993)                    |
| 64. <i>C. unguiculata</i> Lindl.  |                                 |
| 65. <i>C. xantiana</i> A. Gray  |                                 |
| <b>Gaura</b> L.   | Raven & Gregory (1972)          |
| 66. <i>G. angustifolia</i> Michx.   |                                 |
| 67. <i>G. biennis</i> L.  |                                 |
| 68. <i>G. boquillensis</i> P. H. Raven & D. P. Greg.  |                                 |
| 69. <i>G. brachycarpa</i> Small   |                                 |
| 70. <i>G. calcicola</i> P. H. Raven & D. P. Greg.   |                                 |
| 71. <i>G. coccinea</i> Pursh  |                                 |
| 72. <i>G. drummondii</i> (Spach) Torr. & A. Gray  |                                 |
| 73. <i>G. filipes</i> Spach   |                                 |
| 74. <i>G. hexandra</i> Ortega   |                                 |
| 75. <i>G. longiflora</i> Spach  |                                 |
| 76. <i>G. mckelveyae</i> (Munz) P. H. Raven & D. P. Greg.   |                                 |
| 77. <i>G. mutabilis</i> Cav.  |                                 |
| 78. <i>G. neomexicana</i> Wooton  |                                 |
| 79. <i>G. parviflora</i> Douglas ex Lehm.   |                                 |
| 80. <i>G. sinuata</i> Nutt. ex Ser.   |                                 |
| 81. <i>G. suffulta</i> Engelm. ex A. Gray   |                                 |
| 82. <i>G. villosa</i> Torr.   |                                 |
| <b>Gayophytum</b> A. Juss.  | Lewis & Szweykowski (1964)      |
| 83. <i>G. decipiens</i> F. H. Lewis & Szweykowski   |                                 |
| 84. <i>G. diffusum</i> Torr. & A. Gray  |                                 |
| 85. <i>G. heterozygum</i> F. H. Lewis & Szweykowski   |                                 |
| 86. <i>G. humile</i> A. Juss.   |                                 |
| 87. <i>G. racemosum</i> Torr. & A. Gray   |                                 |
| 88. <i>G. ramosissimum</i> Torr. & A. Gray  |                                 |
| <b>Gongylocarpus</b> Cham. & Schltld. (transferred to <b>Gongylocarpeae</b> ; Levin et al., 2003) |                                 |
| 89. <i>G. rubricaulis</i> Schltld. & Cham.  | Carlquist & Raven (1966)        |
| <b>Oenothera</b> L.   |                                 |
| 90. <i>O. albicaulis</i> Pursh  | W. L. Wagner (unpublished data) |
| 91. <i>O. biennis</i> L.  | Dietrich et al. (1997)          |
| 92. <i>O. brachycarpa</i> A. Gray   | W. L. Wagner (unpublished data) |
| 93. <i>O. caespitosa</i> Nutt.  | Wagner et al. (1985)            |
| 94. <i>O. californica</i> (S. Watson) S. Watson   | W. L. Wagner (unpublished data) |
| 95. <i>O. cavernae</i> Munz   | Wagner et al. (1985)            |
| 96. <i>O. cordata</i> J. W. Loudon  | Dietrich & Wagner (1988)        |
| 97. <i>O. coronopifolia</i> Torr. & A. Gray   | W. L. Wagner (unpublished data) |
| 98. <i>O. deltoides</i> Torr. & Frém.   | W. L. Wagner (unpublished data) |

Table 1. Continued.

| Taxa  | Source of information                     |
|---|---|
| 99. <i>O. deserticola</i> (Loes.) Munz  | Wagner (2004, unpublished data)           |
| 100. <i>O. dissecta</i> A. Gray ex S. Watson                                  | Wagner (1984)                             |
| 101. <i>O. drummondii</i> Hook.   | Dietrich & Wagner (1988)                  |
| 102. <i>O. elata</i> Kunth  | Dietrich et al. (1997)                    |
| 103. <i>O. epilobiifolia</i> Kunth  | W. L. Wagner (unpublished data)           |
| 104. <i>O. falfurriae</i> W. Dietr. & W. L. Wagner                            | Dietrich & Wagner (1988)                  |
| 105. <i>O. flava</i> (A. Nelson) Garrett                                      | W. L. Wagner (unpublished data)           |
| 106. <i>O. fruticosa</i> L.   | Straley (1977)                            |
| 107. <i>O. grandiflora</i> L'Hér.   | Dietrich et al. (1997)                    |
| 108. <i>O. grandis</i> (Britton) Smyth  | Dietrich & Wagner (1988)                  |
| 109. <i>O. heterophylla</i> Spach   | Dietrich & Wagner (1988)                  |
| 110. <i>O. howardii</i> (A. Nelson) W. L. Wagner                              | W. L. Wagner (unpublished data)           |
| 111. <i>O. humifusa</i> Nutt.   | Dietrich & Wagner (1988)                  |
| 112. <i>O. jamesii</i> Torrey & A. Gray                                       | Dietrich et al. (1997)                    |
| 113. <i>O. kunthiana</i> (Spach) Munz   | W. L. Wagner (unpublished data)           |
| 114. <i>O. laciniata</i> Hill   | Dietrich & Wagner (1988)                  |
| 115. <i>O. latifolia</i> (Rydb.) Munz   | W. L. Wagner (unpublished data)           |
| 116. <i>O. linifolia</i> Nutt.  | Straley (1977)                            |
| 117. <i>O. longissima</i> Rydb.   | Dietrich et al. (1997)                    |
| 118. <i>O. macrocarpa</i> Nutt.   | W. L. Wagner (unpublished data)           |
| 119. <i>O. macroseles</i> A. Gray   | Dietrich et al. (1985)                    |
| 120. <i>O. mexicana</i> Spach   | Dietrich & Wagner (1988)                  |
| 121. <i>O. nuttallii</i> Sweet  | W. L. Wagner (unpublished data)           |
| 122. <i>O. nutans</i> G. F. Atk. & Bartlett                                   | Dietrich et al. (1997)                    |
| 123. <i>O. oakesiana</i> (A. Gray) J. W. Robbins ex S. Watson & J. M. Coulter | Dietrich et al. (1997)                    |
| 124. <i>O. pallida</i> Lindl.   | W. L. Wagner (unpublished data)           |
| 125. <i>O. parviflora</i> L.  | W. L. Wagner (unpublished data)           |
| 126. <i>O. pennellii</i> Munz   | W. L. Wagner (unpublished data)           |
| 127. <i>O. perennis</i> L.  | Straley (1977)                            |
| 128. <i>O. pilosella</i> Raf.   | Straley (1977)                            |
| 129. <i>O. primiveris</i> A. Gray   | Wagner (1986, unpublished data)           |
| 130. <i>O. pubescens</i> Willd. ex Spreng.                                    | Dietrich & Wagner (1988)                  |
| 131. <i>O. purpusii</i> Munz  | Wagner (2004, unpublished data)           |
| 132. <i>O. rhombipetala</i> Nutt. ex Torr. & A. Gray                          | Dietrich & Wagner (1988)                  |
| 133. <i>O. rosea</i> L'Hér. ex Aiton  | W. L. Wagner (unpublished data)           |
| 134. <i>O. spachiana</i> Torr. & A. Gray                                      | Straley (1977)                            |
| 135. <i>O. speciosa</i> Nutt.   | W. L. Wagner (unpublished data)           |
| 136. <i>O. tetraptera</i> Cav.  | W. L. Wagner (unpublished data)           |
| 137. <i>O. triloba</i> Nutt.  | W. L. Wagner (unpublished data)           |
| 138. <i>O. tubifera</i> Ser.  | W. L. Wagner (unpublished data)           |
| 139. <i>O. villosa</i> Thunb.   | W. L. Wagner (unpublished data)           |
| <b>Stenosiphon</b> Spach  |   |
| 140. <i>S. linifolius</i> (Nutt.) Heynh.                                      | Great Plains Flora Assoc. (1986)          |
| TRIBE EPILOBIEAE  |   |
| <b>Chamerion</b> (Raf.) Raf.  | Hoch (1993)                               |
| 141. <i>C. angustifolium</i> L.   | Mosquin (1966)                            |
| 142. <i>C. latifolium</i> L.  | Small (1968)                              |
| <b>Epilobium</b> L.   | Hoch (1986, 1993, unpublished (see text)) |
| 143. <i>E. anagallidifolium</i> Lam.  |   |
| 144. <i>E. arcticum</i> Sam.  |   |
| 145. <i>E. brachycarpum</i> C. Presl  |   |
| 146. <i>E. canum</i> (Greene) P. H. Raven                                     |   |
| 147. <i>E. ciliatum</i> Raf.  |   |
| 148. <i>E. clavatum</i> Hausskn.  |   |

Table 1. Continued.

| Taxa  | Source of information |
|---|-----------------------|
| 149. <i>E. coloratum</i> Spreng.                          |                       |
| 150. <i>E. davuricum</i> Fisch. ex Hornem.                |                       |
| 151. <i>E. densiflorum</i> (Lindl.) Hoch & P. H. Raven    | Raven & Moore (1965)  |
| 152. <i>E. denticulatum</i> Ruiz & Pav.                   |                       |
| 153. <i>E. foliosum</i> (Nutt. ex Torr. & A. Gray) Suksd. |                       |
| 154. <i>E. glaberrimum</i> Barbey                         |                       |
| 155. <i>E. halleanum</i> Hausskn.                         |                       |
| 156. <i>E. hornemannii</i> Rchb.                          |                       |
| 157. <i>E. lactiflorum</i> Hausskn.                       |                       |
| 158. <i>E. leptocarpum</i> Hausskn.                       |                       |
| 159. <i>E. leptophyllum</i> Raf.                          |                       |
| 160. <i>E. luteum</i> Pursh                               |                       |
| 161. <i>E. minutum</i> Lindl. ex Lehm.                    |                       |
| 162. <i>E. mirabile</i> Trel.                             |                       |
| 163. <i>E. nevadense</i> Munz                             |                       |
| 164. <i>E. obcordatum</i> A. Gray                         |                       |
| 165. <i>E. oregonense</i> Hausskn.                        |                       |
| 166. <i>E. pallidum</i> (Eastw.) Hoch & P. H. Raven       | Raven & Moore (1965)  |
| 167. <i>E. palustre</i> L.                                |                       |
| 168. <i>E. pygmaeum</i> (Speg.) Hoch & P. H. Raven        | Raven & Moore (1965)  |
| 169. <i>E. saximontanum</i> Hausskn.                      |                       |
| 170. <i>E. smithii</i> H. Lév.                            |                       |
| 171. <i>E. strictum</i> Muhl.                             |                       |
| 172. <i>E. suffruticosum</i> Nutt.                        |                       |
| 173. <i>E. torreyi</i> (S. Watson) Hoch & P. H. Raven     | Raven & Moore (1965)  |

from recent or unpublished taxonomic revisions, supplemented with specimen label data from the herbaria at MO and US (Table 3). Distribution records for *Epilobium* derive from nearly 100,000 specimens from more than 100 herbaria consulted in preparation for a revision (Hoch et al., unpublished); these records served as the basis for *Epilobium* treatments in *The Jepson Manual* (Hoch, 1993), the *Flora of the Great Plains* (Hoch, 1986), and other recent floras. Records for several sections of *Oenothera* for which taxonomic revisions are not yet published (cited in Table 1 as “Wagner, unpublished data”) are derived from several sources. All unpublished *Oenothera* distributions except for those of section *Anogra* are based on approximately 4500 collections from more than 100 herbaria borrowed for those revisions. For the 10 species of section *Anogra*, distributions derive from some 250 collections at US and MO, supplemented by additional collections examined for *The Jepson Manual* project (Wagner, 1993). We have excluded from our distributional analysis specimens that were cultivated and/or appear far outside the established range in human-disturbed habitats. Species that occur only in one area of endemism are not informative in a Parsimony Analysis of Endemism (PAE) regarding area relationships and therefore

are excluded from the analysis. However, they provide support for the delimitation of areas of endemism and are listed in Table 2. For example, the monotypic genus *Xylonagra* is endemic to Central Baja California and thus is used to circumscribe the Sonoran (SON) region.

Although almost all of the genera of Epilobieae, Gongylocarpeae, and Onagreae are endemic to or have had their major basal radiation in the Madrean Floristic Region of southwestern North America, many species of these tribes, especially in *Epilobium* and *Oenothera*, occur outside of North America. If native North American species also have a native distribution outside of North America, those distributions are included in the data matrix in the appropriate area (NE, WP, or EP). However, if a species occurs as a native only outside of North America, it has been excluded from this analysis. These excluded taxa include in Epilobieae 6 Eurasian species of *Chamerion* and 125 species of *Epilobium* (large groups endemic to South America, Eurasia, and Australasia), and in Onagreae, 1 species each of *Camissonia* (*C. dentata*), *Clarkia* (*C. tenella*), and *Gayophytum* (*G. micranthum*), and 39 species of *Oenothera*, virtually all endemic to South America. In *Epilobium* and *Oenothera*, we have excluded 9 species (*E. billardierianum* and *E. ko-*

Table 2. Alphabetical list of areas of endemism used in this analysis, and taxa of tribes Epilobieae, Gongylocarpeae, and Onagreae (Onagraceae) endemic to specific individual areas (see Table 1 for sources of distributional data). See Appendix 1 for full descriptions of the areas and references; numbers in parentheses refer to Appendix 1.

| Acronym/Area of endemism             | Endemic taxa   |
|--------------------------------------|--|
| APP/Appalachian (3)                  | <i>Gaura demareei</i> P. H. Raven & D. P. Greg.; <i>Oenothera argillicola</i> Mack.  |
| ARC/Arctic (1)                       | —  |
| ATL/Atlantic and Gulf Coastal (4)    | <i>Gaura lindheimeri</i> Engelm. & A. Gray; <i>Oenothera clelandii</i> W. Dietr., P. H. Raven & W. L. Wagner, <i>O. curtissii</i> Small  |
| CAL/Californian (9)                  | <i>Camissonia benitensis</i> P. H. Raven, <i>C. bistorta</i> (Nutt. ex Torr. & A. Gray) P. H. Raven, <i>C. hardhamiae</i> P. H. Raven, <i>C. integrifolia</i> P. H. Raven; <i>C. luciae</i> P. H. Raven, <i>C. micrantha</i> (Hornem. ex Spreng.) P. H. Raven; <i>Clarkia affinis</i> F. H. Lewis & M. R. Lewis, <i>C. borealis</i> E. Small, <i>C. bottae</i> (Spach) F. H. Lewis & M. R. Lewis, <i>C. breweri</i> (A. Gray) Greene, <i>C. davyi</i> (Jepson) F. H. Lewis & M. R. Lewis, <i>C. delicata</i> (Abrams) A. Nelson & J. F. Macbride, <i>C. franciscana</i> F. H. Lewis & P. H. Raven, <i>C. imbricata</i> F. H. Lewis & M. R. Lewis, <i>C. joloensis</i> D. R. Parn., <i>C. lewisii</i> P. H. Raven & D. R. Parn., <i>C. prostrata</i> F. H. Lewis & M. R. Lewis, <i>C. rubicunda</i> (Lindl.) F. H. Lewis & M. R. Lewis, <i>C. similis</i> F. H. Lewis & W. R. Ernst; <i>Epilobium cleistogamum</i> (Curran) P. Hoch & P. H. Raven; <i>Gayophytum oligospermum</i> F. H. Lewis & Szweyk. |
| CAN/Canadian (2)                     | —  |
| CHI/Chihuahuan (12)                  | <i>Gaura macrocarpa</i> Rothr.; <i>Oenothera havardii</i> S. Watson, <i>O. neomexicana</i> (Small) Munz, <i>O. organensis</i> Munz, <i>O. platanorum</i> P. H. Raven & D. R. Parn., <i>O. riskindii</i> W. L. Wagner, <i>O. texensis</i> P. H. Raven & D. R. Parn.   |
| EP/East Palearctic (20)              | — (some endemics, but outside of North American study group)   |
| GBA/Great Basin (8)                  | <i>Camissonia atwoodii</i> Cronquist, <i>C. confertiflora</i> (P. H. Raven) P. H. Raven, <i>C. exilis</i> (P. H. Raven) P. H. Raven, <i>C. gouldii</i> P. H. Raven, <i>C. heterocroma</i> (S. Watson) P. H. Raven, <i>C. megalantha</i> (Munz) P. H. Raven, <i>C. nevadensis</i> (Kellogg) P. H. Raven, <i>C. parryi</i> (S. Watson) P. H. Raven, <i>C. speculicola</i> (P. H. Raven) P. H. Raven  |
| MAS/Mexican Altiplano (16)           | —  |
| MOJ/Mojavean (10)                    | <i>Camissonia munzii</i> (P. H. Raven) P. H. Raven   |
| NAP/North American Prairies (5)      | <i>Gaura triangulata</i> Buckl.; <i>Oenothera canescens</i> Torr. & Frém., <i>O. coryi</i> W. L. Wagner, <i>O. engelmannii</i> (Small) Munz, <i>O. harringtonii</i> W. L. Wagner, Stockh. & W. M. Klein  |
| NE/Neotropical (19)                  | — (some endemics, but outside of North American study group)   |
| ROC/Rocky Mountain (7)               | <i>Oenothera acutissima</i> W. L. Wagner, <i>O. psammophila</i> (A. Nelson & J. F. Macbr.) W. L. Wagner, Stockh. & W. M. Klein   |
| SMO/Sierra Madre Occidental (14)     | <i>Epilobium maysillesii</i> Munz; <i>Oenothera maysillesii</i> Munz, <i>O. tamrae</i> W. Dietr. & W. L. Wagner  |
| SMR/Sierra Madre Oriental (17)       | <i>Oenothera muelleri</i> Munz, <i>O. stubbei</i> W. Dietr., P. H. Raven & W. L. Wagner  |
| SMS/Sierra Madre del Sur (18)        | —  |
| SON/Sonoran (11)                     | <i>Camissonia angelorum</i> (S. Watson) P. H. Raven, <i>C. crassifolia</i> (Greene) P. H. Raven, <i>C. proavita</i> P. H. Raven, <i>C. sceptrostigma</i> (Brandege) P. H. Raven; <i>Gongylocarpus fruticosus</i> (Benth.) K. Brandege; <i>Oenothera arizonica</i> (Munz) W. L. Wagner, <i>O. brandegeei</i> (Munz) P. H. Raven, <i>O. breedlovei</i> W. Dietr. & W. L. Wagner, <i>O. wigginsii</i> W. M. Klein; <i>Xylomagra arborea</i> (Kellogg) J. D. Smith & J. N. Rose  |
| TAM/Tamaulipan (13)                  | —  |
| TMV/Trans-Mexican Volcanic Belt (15) | —  |
| VAN/Vancouverian (6)                 | <i>Camissonia sierrae</i> P. H. Raven; <i>Clarkia arcuata</i> (Kellogg) A. Nelson & J. F. Macbr., <i>C. australis</i> E. Small, <i>C. exilis</i> F. H. Lewis & Vasek, <i>C. lingulata</i> F. H. Lewis & M. R. Lewis, <i>C. mildrediae</i> (Heller) F. H. Lewis & M. R. Lewis, <i>C. springvillensis</i> Vasek, <i>C. stellata</i> Mosquin, <i>C. virgata</i> Greene, <i>C. williamsonii</i> (Durand & Hilg.) F. H. Lewis & M. R. Lewis; <i>Epilobium howellii</i> P. Hoch, <i>E. nivium</i> T. S. Brandege, <i>E. oreganum</i> Greene, <i>E. rigidum</i> Hausskn., <i>E. septentrionale</i> (D. D. Keck) Bowman & P. Hoch, <i>E. siskiyouense</i> (Munz) P. Hoch & P. H. Raven; <i>Gayophytum eriospermum</i> Coville; <i>Oenothera wolfii</i> (Munz) P. H. Raven, <i>O. xylocarpa</i> Coville   |
| WP/West Palearctic (21)              | — (some endemics, but outside of North American study group)   |

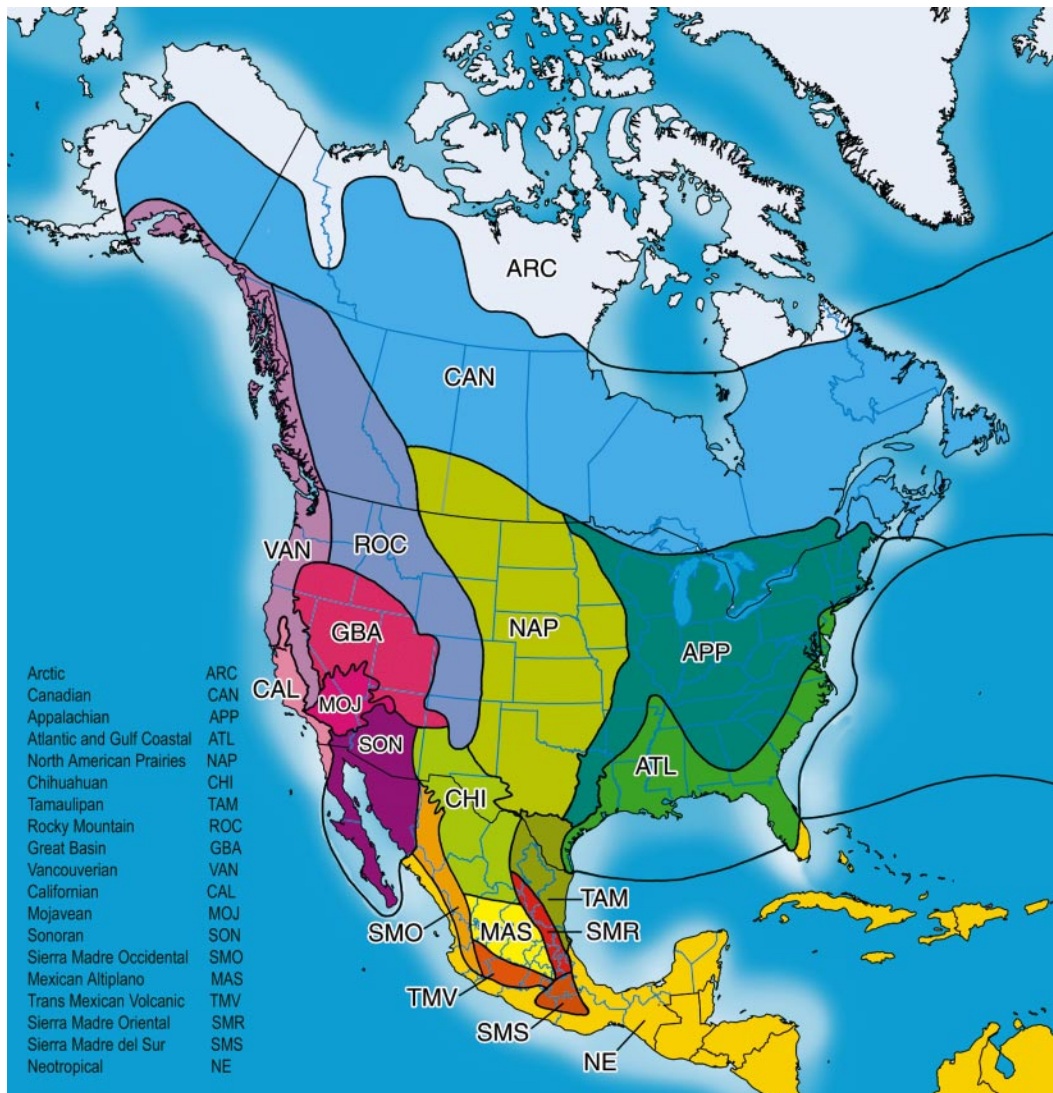


Figure 1. Areas of endemism as delimited for the historical biogeographic analysis and used to code the distributional data for each species. The areas were drawn in Photoshop 7.0 by Alice Tangerini on a base map from ArcMap 8.2 (ESRI) with a North American Lambert conformal conic projection. The floristic regions are based primarily on Takhtajan (1986) and Thorne (1993), with other modifications as described in the text.

*marovianum* from Australasia and *E. hirsutum*, *E. montanum*, *E. obscurum*, and *E. parviflorum* from Eurasia, *O. glazioviana*, a hybrid of recent origin in Europe, and *O. mollissima* and *O. stricta* from South America) because all of them clearly have been introduced into North America in historical time.

#### PARSIMONY ANALYSIS OF ENDEMICITY (PAE)

Parsimony analysis of endemism or PAE (Rosen, 1988; Rosen & Smith, 1988) is an historical biogeographical approach that seeks to identify the

distributional pattern of organisms. It classifies localities, quadrats, or areas (which are analogous to taxa) by their shared taxa (which are analogous to characters) according to the most parsimonious solution resulting in a hierarchical classification of the geographic units (Morrone & Crisci, 1995; Crisci et al., 2000, 2003). Rosen (1988) originally proposed the method using localities as study units. Craw (1988) and Cracraft (1991) presented a variation of the method using areas of endemism as study units to identify the hierarchical information contained in the geographical distribution of organ-



isms to establish area relationships. Indeed, McLaughlin (1992) suggested that areas are actually arranged in a natural hierarchy.

The variation of the methodology proposed by Craw (1988) and Cracraft (1991) using areas of endemism included taxonomic information in the matrix by adding columns for higher taxonomic categories or phylogenetic information. Thus, the resulting matrix consisted of areas  $\times$  species distributions plus generic distributions. However, as Crisci et al. (2000) observed, adding phylogenetic or taxonomic information to the matrix is a misuse of Brooks parsimony analysis (Brooks et al., 2001), which is a technique that does not utilize phylogenetic data specifically. Therefore, we use areas of endemism as our units of study and species distributions as the characters of those areas, but exclude the information on supraspecific taxa.

PAE cladograms represent nested sets of areas in which terminal dichotomies represent two areas between which the most recent biotic interchange has occurred (Morrone & Crisci, 1995). Craw (1988) suggested that "character" reversions in the cladogram could be interpreted biogeographically as extinctions, and parallelisms as dispersions. This analysis was carried out using PAUP\*, vers. 4.0b10 (Swofford, 2001), applying the branch-and-bound and deltran options. If more than one tree results from the analysis, a strict consensus tree is constructed. As proposed by Rosen (1988), the cladogram was rooted with a hypothetical area coded with all zeros. The bootstrap method (Felsenstein, 1985) was employed to evaluate the reliability of the estimates; 100 replicates were performed. We used the software MacClade 4.0 (Maddison & Maddison, 2000) to generate the data matrix and as a tool to analyze the taxa distribution on the tree(s).

#### PANBIOGEOGRAPHY (COMPATIBILITY TRACK METHOD)

Croizat (1958) postulated that geographic barriers evolve together with biotas. The panbiogeographic approach (Croizat, 1958, 1981) consists of plotting distributions of taxa on maps and connecting their separate distributional areas together with lines called individual tracks. When individual tracks coincide, the resulting summary lines are considered generalized tracks, which indicate the pre-existence of ancestral biotas that became fragmented by tectonic and/or climatic changes. At the same time, generalized tracks provide spatial criteria for biogeographic homology (Grehan, 1988a, b; Morrone & Crisci, 1995). When two or more generalized tracks intersect, that area is called a node.

Nodes are dynamic biogeographic boundaries where remnant fragments of different ancestral biotas come into contact. Nodes are biogeographically interesting because they are composite regions that represent an intersection of different biogeographical and ecological histories.

Analytical developments by McAllister et al. (1986), Page (1987), Connor (1988), Craw (1989), and Henderson (1990, 1991) used graph theory to provide objective and quantitative methods for drawing and comparing tracks, including the compatibility track method applied here. This method was developed by Craw (1988, 1989), based on the concept of distributional compatibility (Connor, 1988; Craw, 1989). Individual tracks are treated as biogeographic hypotheses of relationship among localities or distribution areas. Two or more individual tracks are regarded as being compatible only if they result in the same pairwise comparison or if one track is a subset of the other. This method is analogous to character compatibility (Meacham, 1984). However, in the track compatibility method, nonoverlapping tracks are incompatible, whereas they would be compatible under the original taxonomic concept. The compatibility track method basically consists of constructing a matrix (areas vs. taxa), where each taxon is scored as present (1) or absent (0) in each area, and applying compatibility analysis software to find the largest clique(s) of compatible tracks. The method involves finding a simple form of spanning tree linking localities or distribution areas. The tree is constructed from the largest clique of compatible distributions in a distributional compatibility matrix and is based on the original concept of compatibility (nonoverlapping tracks are also considered compatible). Therefore, using a restricted concept of compatibility (only individual tracks that are either included within or replicated by one another are compatible) the tree (= clique) could contain more than one generalized track. In this case, multiple generalized tracks (groups) found in one clique will be formed only by areas that are exclusive of each generalized track. If more than one largest clique or several cliques of considerable size are found, then a hypothesis of existence of several generalized tracks linking the localities or distribution areas in more than one way can be considered (areas can be members of more than one generalized track at the same time). Alternatively, the intersection (i.e., those individual tracks common to all the largest cliques) can also be identified as a generalized track (Craw, 1990). For more details and other applications of this method see Craw (1988, 1989), Morrone and Crisci



Table 3. Continued.

|     | 100        | 110        | 120        | 130        | 140        | 150        | 160        | 170        | 173 |
|-----|------------|------------|------------|------------|------------|------------|------------|------------|-----|
| OUT | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 000 |
| ARC | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 1111001001 | 0000011111 | 0000001010 | 000 |
| CAN | 1000000000 | 0000100000 | 0000000000 | 0010101100 | 0000000010 | 1111101011 | 0000011010 | 0000001010 | 100 |
| APP | 1000010000 | 0101011110 | 0101010101 | 1110101100 | 0101110111 | 1000101010 | 0000000010 | 0000001000 | 100 |
| ATL | 1000010000 | 1001011110 | 1101010101 | 0110101100 | 0011110010 | 1000001010 | 0000000010 | 0000001000 | 100 |
| NAP | 1010001000 | 0101110111 | 0111110100 | 1001100000 | 0101101011 | 1000101010 | 0000111010 | 0000001110 | 000 |
| VAN | 0000000100 | 0100100000 | 0000000000 | 0001000000 | 0000000010 | 1110111100 | 1011111111 | 1101111111 | 001 |
| ROC | 0010001000 | 0100100000 | 0000101000 | 1001000001 | 0000000010 | 1110111101 | 1011111111 | 1101101111 | 011 |
| GBA | 0011101100 | 0100100001 | 0000101000 | 0001000011 | 0000000010 | 1110111100 | 1001111010 | 1011111110 | 011 |
| CAL | 0001000100 | 0100100000 | 0000000000 | 0000000000 | 0000000000 | 1110111100 | 1011111010 | 1000111100 | 001 |
| MOJ | 0011101100 | 0000100001 | 0000001000 | 0000000011 | 0000000000 | 1000111000 | 0000000000 | 0010000000 | 000 |
| SON | 0110000100 | 1100100000 | 0010000000 | 0001000011 | 0010001000 | 0000111000 | 1011000000 | 0000000000 | 000 |
| CHI | 0110001001 | 0100100000 | 0111000110 | 0001010011 | 0110101011 | 1000111000 | 0000000000 | 0000000010 | 000 |
| TAM | 0100000000 | 1001000100 | 0111000010 | 0000010001 | 0010111000 | 0000000000 | 0000000000 | 0000000000 | 000 |
| SMO | 0000000000 | 0100100000 | 0010000000 | 0000000001 | 0010010100 | 0000001000 | 0000000000 | 0000000000 | 000 |
| TMV | 0000000000 | 0000000000 | 0010000000 | 0000000001 | 1010010100 | 0000001000 | 0100000000 | 0000000000 | 000 |
| MAS | 0000000011 | 0110100000 | 0110000000 | 0000000001 | 1010010100 | 0000001000 | 0100000000 | 0000000000 | 000 |
| SMR | 0000000010 | 0110000000 | 0010000000 | 0000000001 | 1010010100 | 0000001000 | 0000000000 | 0000000000 | 000 |
| SMS | 0000000000 | 0110000000 | 0010000000 | 0000000001 | 1010010000 | 0000001000 | 0100000000 | 0000000000 | 000 |
| NE  | 0000000010 | 0110000000 | 1011000000 | 0000000001 | 0010000000 | 0000001010 | 0100000000 | 0000000000 | 000 |
| WP  | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 1111000001 | 0000011000 | 0000001000 | 000 |
| EP  | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 1111001001 | 0000011000 | 0000001000 | 000 |

(1990, 1995), Craw et al. (1999), and Crisci et al. (2000, 2003).

In this analysis we use the same areas of endemism and the same data matrix (Table 3) that we used in the PAE analysis. The analysis of the data matrix of 21 areas of endemism versus individual tracks of 173 taxa (Table 3) was carried out with SECANT 2.2 (Salisbury, 1999). SECANT identifies all groups of cladistically compatible characters. Individual tracks were treated here as binary characters ordered with absence as the “ancestral” state for each (= outgroup with all zeros), and presence as state 1.

## RESULTS

### PARSIMONY ANALYSIS OF ENDEMICITY

The analysis of the data matrix (Table 3) with PAUP\*4.0b10 generated four area cladograms (Fig. 2) with 377 steps, consistency index (CI) = 0.459, and retention index (RI) = 0.619, which differed in the relationships among most Mexican areas SMO, TMV, MAS, SMR, SMS; in the relationship of the Neotropical area (NE) either with the Mexican areas (Fig. 2B–D) or with the eastern North American areas APP, ATL, NAP, CHI, and TAM (Fig. 2A); in the relationship of APP, ATL, NAP, CHI, and TAM either with the Mexican areas (Fig. 2A–B) or with the western areas VAN, CAL, ROC, GBA, SON, and MOJ (Fig. 2C–D); and in the relationship of Tamaulipas (TAM) either with Chihuahua (CHI) (Fig. 2C–D), or with APP, ATL, NAP, and CHI (Fig. 2A–B).

The strict consensus of the four trees (Fig. 3) shows the following area relationships: (1) ((Arctic, Canadian) West Palearctic, East Palearctic) forms the basalmost lineage, sister to the remaining areas; (2) (((Appalachian, Atlantic) North American Prairies) Chihuahuan, Tamaulipas); (3) (((Vancouverian, Californian) Rocky Mountains, Great Basin) Sonoran Mojavean); (4) ((Mexican Altiplano, Sierra Madre Oriental) Sierra Madre Occidental, Trans-Mexican Volcanic Belt, Sierra Madre del Sur); and (5) the Neotropical as one single branch. The last four branches (2–5) constitute a polytomy. Thus, the strict consensus cladogram generated by PAUP\*4.0b10 shows four main groups (Fig. 4): northern North America, eastern North America, western North America, and the central Mexican areas.

The percentage of 100 bootstrap replicates demonstrates that strength of support for nodes varies considerably. Many branches have less than 50% support, but others, particularly in eastern and western North America, have stronger support. The

most strongly supported branches in order are: 99% (APP—ATL), 98% (VAN—CAL), 96% (VAN, CAL, ROC, GBA), 79% (ROC—GBA), 78% (APP, ATL, NAP, CHI, TAM), 62% (VAN, CAL, ROC, GBA, SON, MOJ), 61% (APP, ATL, NAP), and 60% (ARC, CAN, WP, EP). The weakness and strength of bootstrap values may reflect the strong concentration of taxa in northern Mexico and southwestern United States, and lower concentration in areas more distant from that area.

### PANBIOGEOGRAPHY (COMPATIBILITY TRACK METHOD)

Applying the SECANT 2.2 program to the data matrix (Table 3) resulted in 4 largest cliques, each with 51 individual tracks. The intersection (those 49 individual tracks common to the 4 largest cliques) is considered as the fifth large clique. These 5 cliques contain a total of 11 generalized tracks. The first clique contains 2 generalized tracks, the second clique contains 2, the third clique contains 3, the fourth clique contains 2, and the intersection contains 2 generalized tracks. Since many of these tracks in different cliques are the same, the 11 generalized tracks can be reduced to 3 generalized tracks: 2 strongly supported (“East”/green and “West”/purple in Fig. 5), and 1 weakly supported (“South”/orange in Fig. 5). The northern regions (ARC, CAN, EP, and WP) and two areas in Mexico (SMO and TMV) are not part of these supported generalized tracks, and are shown as white in Figure 5.

The first (“East”) strong generalized track includes eastern North American areas (ATL, APP, CHI, NAP, TAM), and is strongly supported by 17 individual tracks from taxa in 3 genera, namely, *Calylophus berlandieri* (taxon 41); *Gaura biennis* (67), *G. brachycarpa* (69), *G. filipes* (73), *G. longiflora* (75), *G. sinuata* (80), and *G. suffulta* (81); and *Oenothera cordata* (96), *O. falfurriae* (104), *O. grandiflora* (107), *O. grandis* (108), *O. heterophylla* (109), *O. linifolia* (116), *O. mexicana* (120), *O. nutans* (122), *O. spachiana* (134), and *O. speciosa* (135).

The second (“West”) strong generalized track includes the western North American areas (CAL, GBA, MOJ, ROC, SON, VAN), and is supported by 31 individual tracks from taxa in 4 genera, namely, *Camissonia boothii* (taxon 3), *C. campestris* (7), *C. graciliflora* (15), *C. lacustris* (22), *C. ovata* (26), and *C. pubens* (26); all species of *Clarkia* (47–65) except for *C. epilobioides* (52), *C. pulchella* (58), and *C. purpurea* (59); *Gayophytum decipiens* (83) and *G. heterozygum* (85); and *Epilobium clavatum* (148), *E.*

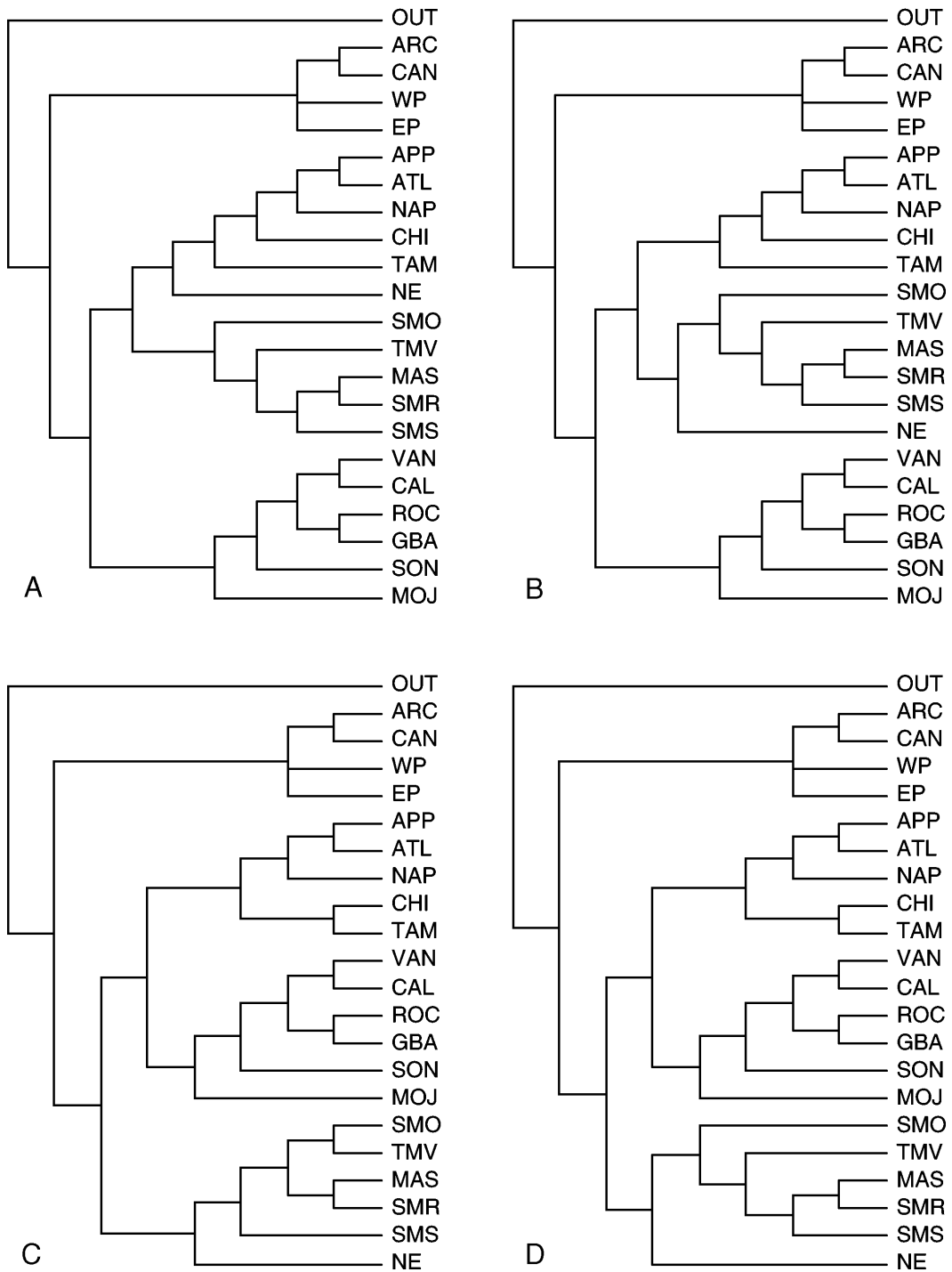


Figure 2. Four most parsimonious cladograms (A–D) resulting from the parsimony analysis of endemicity (PAE) analysis after applying PAUP\* vers. 4.0b10. Trees are 377 steps, CI = 0.459, and RI = 0.619. Area acronyms correspond to those in Figure 1 and Table 2.

Strict

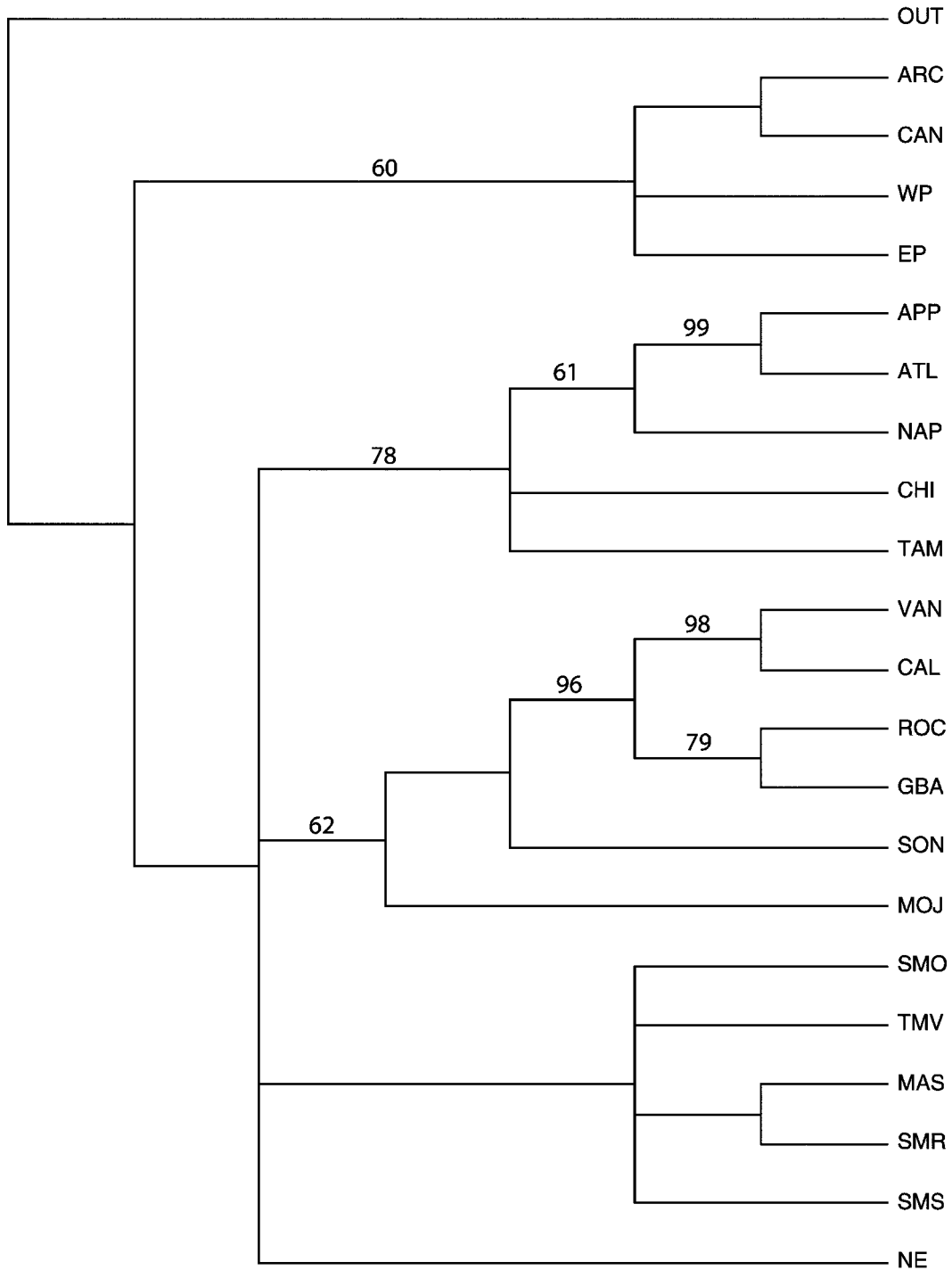


Figure 3. Strict consensus cladogram of the four cladograms obtained in the parsimony analysis of endemity (PAE). Bootstrap support values are shown above the branches. Area acronyms correspond to those in Figure 1 and Table 2.

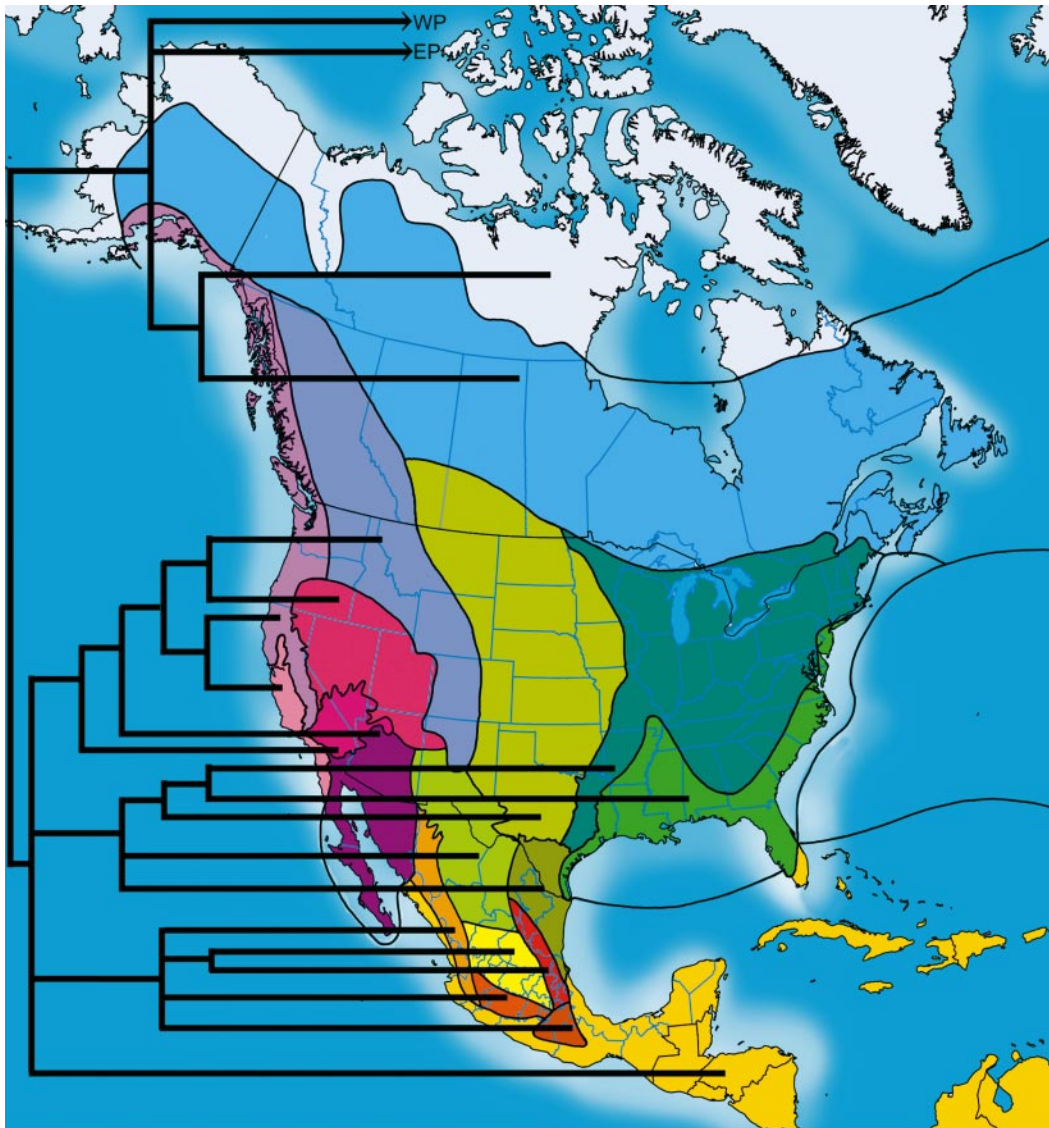


Figure 4. Strict consensus cladogram of the four cladograms obtained in the parsimony analysis of endemism superimposed onto the map with the areas of endemism. The tree branches delineate four main groups of areas: northern (ARC, CAN, EP, WP), eastern North America (APP, ATL, NAP, CHI, TAM), western North America (VAN, CAL, ROC, GBA, SON, MOJ), and southern North America (SMO, TMV, MAS, SMR, SMS). Areas correspond to those in Figure 1 and Table 2.

*densiflorum* (151), *E. glaberrimum* (154), *E. minutum* (161), *E. oregonense* (165), *E. pallidum* (166), and *E. torreyi* (173).

The third (“South”) generalized track includes some of the Mexican areas (MAS, SMR, SMS) and the Neotropical area (NE), with support from only 2 individual tracks, of *Oenothera deserticola* (taxon 99) and *O. epilobiifolia* (103). The South generalized track is considerably weaker than the previous two, since it is supported by many fewer individual

tracks. The Neotropical area is supported as part of the East generalized track by *Oenothera laciniata* (taxon 114). The Trans-Mexican Volcanic Belt (TMV) is supported as part of the South generalized track by *Oenothera kunthiana* (taxon 113). Several Mexican areas (SMS, TMV, MAS) are supported as part of the East generalized track by *Gaura drummondii* (taxon 72) and *Oenothera jamesii* (112). As noted above, the Sierra Madre Occidental (SMO) does not form part of any generalized track.

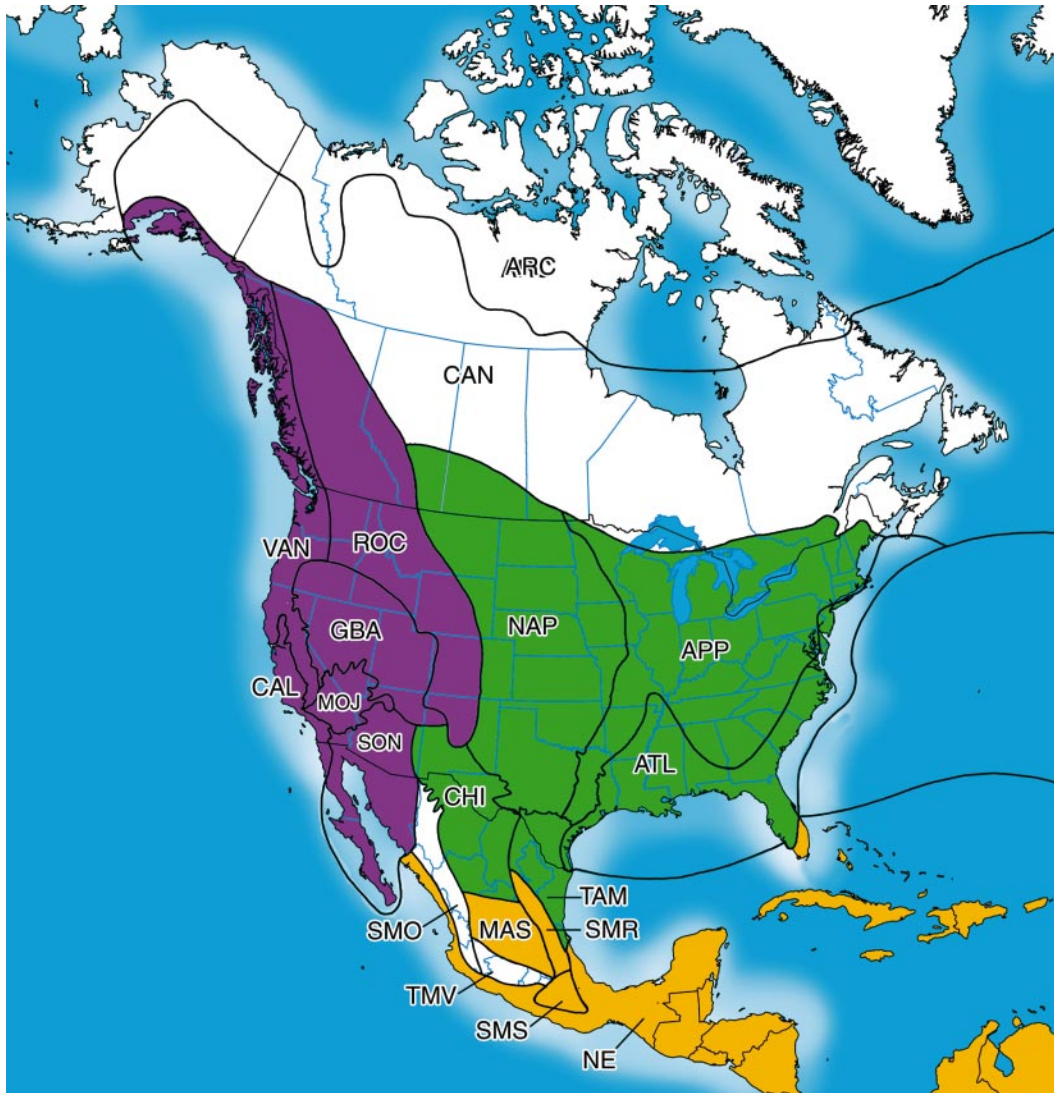


Figure 5. Distributional patterns after applying track compatibility analysis: a strongly supported Eastern generalized track including APP, ATL, CHI, NAP, and TAM, shown in green; a strongly supported Western generalized track, including CAL, GBA, MOJ, ROC, SON, and VAN, shown in purple; and a weakly supported Mexican and Neotropical generalized track including MAS, NE, SMR, and SMS, shown in orange. The areas ARC, CAN, SMO, and TMV, shown in white, and the two non-North American areas EP and WP, do not form part of any generalized track. Area acronyms correspond to those in Figure 1 and Table 2.

These data weakly support the Neotropical area (NE) as a panbiogeographic node in the distributional history of Onagreae, Gongylocarpeae, and Epilobieae, since there is some support for its inclusion in both the East and South generalized tracks.

The program SECANT 2.2 also found 9 cliques each with 50 individual tracks. The analysis of these 9 cliques resulted in the same generalized tracks that we found among the five largest cliques, with the exception of one generalized track found

in only one of the 9 cliques. This additional track includes the areas CHI and TAM, supported by *Gaura boquillensis* (taxon 68), *Oenothera macrosceles* (119), and *O. pennellii* (126).

Most of the genera of Epilobieae and Onagreae support at least one of the generalized tracks found in this analysis, i.e., *Calylophus*, *Gaura*, and *Oenothera* belong to the East track, and *Camissonia*, *Clarkia*, *Gayophytum*, and *Epilobium* to the West track. Several other genera, including *Chamerion* (Epilobieae; two species), *Gongylocarpus* (Gongy-



locarpeae; two species), and *Stenosiphon* (Onagreae; one species) do not form part of any generalized track.

#### DISCUSSION

The historical biogeography of North America has long been a focus of botanists attempting to find general patterns of relationships within North America and between North America and other continents. The present-day geographical distribution of Epilobieae, Gongylocarpeae, and Onagreae and the biogeographic patterns generated by those distributions may provide clues to understanding the high diversity and endemism of these three tribes in North America, as well as the history of the areas involved.

#### DISTRIBUTIONAL PATTERNS

The application of Parsimony Analysis of Endemism (PAE) to the species distribution of Epilobieae, Gongylocarpeae, and Onagreae delimits four major regions: northern North America; eastern North America; western North America; and central Mexico (Fig. 4). Three of them (eastern North America, western North America, and central Mexico) are also found in the compatibility track analysis. Comparison of these with the higher regional floristic categories in the schemes of Takhtajan (1986) and Thorne (1993) suggests the following differences and similarities. (1) Our northern North American region coincides with the Circumboreal region of Takhtajan and Thorne. (2) Our eastern North American region corresponds to the North American Atlantic region of Takhtajan and Thorne, with the addition of the Tamaulipas (TAM) and Chihuahua (CHI) areas. Miranda and Sharp (1950) proposed such an affinity from distributions of many plant species, and they and Berry (1930) suggested that this shared flora was derived from the Eocene Wilcox flora of the Mississippi Embayment. (3) The Rocky Mountain and Madrean regions of Takhtajan and Thorne show different affinities in our analysis. Their regions proposed close affinities between ROC and VAN, and among CAL, GBA, and the Sonoran Province, whereas our results link VAN with CAL and ROC with GBA. Raven and Axelrod (1978) considered the Vancouverian (VAN) and Californian (CAL) areas to be closely related since they share a flora comprising a mixture of northern temperate elements and xeric, southern elements, with a very high degree of endemism. Furthermore, Axelrod and Raven (1985) also considered the Rocky Mountains (ROC) and Great Basin (GBA) areas to be close because Cor-

dilleran taxa spread into the western Great Basin largely after 14 m.y. ago as the climate became drier, summer rains decreased, and eastern exotic taxa were eliminated. (4) Our central Mexican areas coincide with the Mexican Highlands Province of Takhtajan and Thorne. The lower level of resolution among the central Mexican areas observed in the consensus PAE cladogram is most likely due to the relatively few species of Epilobieae, Gongylocarpeae, and Onagreae distributed there.

The relationships of the Madrean and other North American regions to the Neotropical (NE) are particularly complex, which is reflected in the ambiguous position of NE in the four shortest trees (Fig. 2). Indeed, NE could be considered a panbiogeographic node in our study. Three species (*Gaura angustifolia* [taxon 66], *Oenothera humifusa* [111], and *O. laciniata* [114]) otherwise restricted to the East region reach NE only at the southern tip of Florida, and another eastern species, *Epilobium coloratum* (149), occurs on Hispaniola (in NE), apparently by long-distance dispersal. These taxa provide support for NE as sister to the East region (Fig. 2A). A single species, *Gayophytum humile* (86), found primarily in the western region (VAN-CAL-ROC-GBA), also occurs in NE, apparently as a result of long-distance dispersal to central Chile and Argentina (Lewis & Szweykowski, 1964). Most of the connections of North American regions with NE, however, are through the Mexican region (Fig. 2B–D), almost always by close adjacent dispersal in western and southern Mexico, extending south to Central and sometimes South America. Recent phylogenetic analysis of Onagraceae (Levin et al., 2003, 2004) suggests the following: (1) the immediate sister clade to the Gongylocarpeae + Epilobieae + Onagreae is a branch with *Lopezia* (Lopezieae) and *Megacorax* (unplaced), both found primarily or exclusively in the central Mexican region, with some *Lopezia* species extending to NE; and (2) each of the three successive basal clades of the family, namely *Fuchsia* + *Circaea*, *Hauya*, and *Ludwigia*, have primary or exclusive distributions in NE. *Circaea*, with its circumboreal distribution and absence from NE, is a notable exception; however, it forms a strongly supported clade with *Fuchsia*. A detailed analysis of biogeographical patterns in Onagraceae using phylogenetic information is now in progress.

The distributions of numerous species do not coincide with the major patterns found in the PAE and track compatibility analysis. In general, these inconsistencies can result from one of three types of processes, namely, dispersal, vicariance, or extinction affecting one or few species. The predom-

inant process in our study appears to be short-distance dispersal into geographically contiguous but unrelated areas. This may involve large-scale dispersal, but more often involves only a few or even one population(s) in the adjacent area. For example, many species with distributions in the East North American region often extend into the CAN area [North region; e.g., *Oenothera biennis* (91), *O. fruticosa* (106), *O. parviflora* (125)], or into ROC [West region; e.g., *Calylophus serrulatus* (44), *Oenothera nuttallii* (121)], or to the south into the Mexican region [e.g., *Gaura drummondii* (72), *Oenothera jamesii* (112)]. Similarly, some western species reach CAN [*Camissonia breviflora* (4)] or even ARC [along the southwest coast of Alaska; *Epilobium leptocarpum* (158), *E. luteum* (160)] in the northern region, or CHI [*Camissonia chamaenerioides* (9), *Epilobium canum* (146)] or NAP [*Camissonia andina* (1), *C. subacaulis* (38), *Gayophytum ramosissimum* (88)] in the East region. One particularly clear example of adjacent dispersal concerns *Oenothera primiveris* (129); in the West region of primary distribution (GBA, SON, MOJ), most populations are large-flowered and outcrossing (including some that are self-incompatible), whereas the populations in CHI (East region) are small-flowered and autogamous (Wagner, unpublished data).

Some distributions that seem to represent adjacent dispersal may in fact have another explanation. For example, *Oenothera villosa* (taxon 139) occurs widely in both the western and eastern regions, suggesting adjacent dispersal. However, genome and cytological analysis (Dietrich et al., 1997) of this permanent translocation heterozygote species shows that populations in the western and eastern regions, which currently are treated as subspecies, derived independently from different populations of *Oenothera elata* (102). Nevertheless, they intergrade so extensively in the transition area between ROC and NAP that they are best treated as subspecies of a single species.

Several taxa may represent examples of long-distance dispersal. For example, *Epilobium saximontanum* (169), found primarily in the western region (ROC, GBA, VAN) with near outliers in the eastern region (NAP, CHI), also occurs in eastern CAN (Newfoundland) and ARC (Ungava Bay, Quebec) in the northern region. This highly disjunct pattern is not found in other species and seems best explained as a case of long-distance dispersal. The distribution of *Calylophus lavandulifolius* (43) is unusual in several ways: it appears “bimodal,” with concentrations of populations in NAP (eastern) and GBA (western) and relatively few populations in intervening areas. In addition, the apparently normal

distribution in NAP + CHI + TAM in the eastern region masks a long-distance disjunction between populations in northern CHI and southern TAM.

Certain recurring inconsistent distribution patterns may represent vicariance events. One pattern [found in *Clarkia pulchella* (58) and three *Epilobium*—*E. hornemannii* (156), *E. lactiflorum* (157), and *E. saximontanum* (169)] concerns the occurrence of outlier populations of western taxa (in ROC and VAN) in the Black Hills of South Dakota in NAP (East region). The Black Hills, home to numerous disjunct montane and northern taxa (e.g., Asteraceae: *Balsamorhiza sagittata*; Pinaceae: *Pinus contorta*, *P. flexilis*; Ranunculaceae: *Aconitum columbianum*; Van Bruggen, 1976; Great Plains Flora Association, 1986), have become isolated as the climate warmed in postglacial times; the pattern seems best explained as an example of vicariance. Similarly, at least six taxa (*Camissonia confusa* [12], three *Clarkia*—*C. epilobioides* [52], *C. purpurea* [59], and *C. rhomboidea* [60], and two *Epilobium*—*E. foliosum* [153] and *E. glaberrimum* [154]) show strongly disjunct distributions from southern California (CAL and/or VAN) to south-central Arizona (SON), mirroring a “trans-Sonoran Desert” vicariance event described by Axelrod (1979).

Finally, the absence of taxa from certain areas in which they may otherwise be anticipated may represent cases of local extinction. These are, however, difficult to prove, and in some cases clearly do not represent extinctions. For example, some species [4 of *Camissonia*—*C. brevipes* (5), *C. claviformis* (11), *C. pallida* (27), and *C. refracta* (34) and 2 of *Oenothera*—*O. californica* (94) and *O. deltoidea* (98)] otherwise widespread in the western region are missing in ROC. Yet their absence in ROC cannot be considered extinctions, since all of these are desert taxa with southwestern distributions quite distant from the ROC boundaries. On the other hand, many taxa with the CAL + VAN (17 taxa) or CAL + VAN + SON (3 taxa) distribution patterns may have become extinct in the adjacent MOJ area, which has become progressively more extreme in Holocene time, and progressively inhospitable to many species (Axelrod, 1979). The absence of many taxa in the MOJ region may have forced MOJ into the position as the sister group to the rest of the western region, when it may in fact be a more recently derived area (Van Devender & Spaulding, 1979).

The establishment of western and eastern North American major regions found by PAE and track compatibility analysis agrees with many previous analyses (e.g., Li, 1952; Croizat, 1965; Graham, 1972; Iltis, 1983; Xiang et al., 1998, 2000; Wen,

1999; Guo & Ricklefs, 2000; Donoghue et al., 2001; Sanmartín et al., 2001). These analyses have defined the two broad biogeographic units based on the distributions of many taxa, some of which were evaluated in a phylogenetic context. In many of those analyses, however, there exists a relationship of these areas with East Asia. Disjunct North American–Asian taxa have been considered as Tertiary relics with former widespread distributions during the Paleogene. This “Arcto-Tertiary geoflora” (Wolfe, 1978; Larsen, 1980) resulted from migrations between eastern Asia and North America through Beringia or across the north Atlantic. The distributional patterns of Epilobieae, Gongylocarpeae, and Onagreae show a close relationship between eastern and western North America, with both areas more related to the Neotropics than to the Palearctic, and a weak association between northern North America and Asia. Our results do not reject other hypotheses of such continental connections. The taxa of Onagraceae chosen for our analysis—the tribes Epilobieae, Gongylocarpeae, and Onagreae—display a biogeographical history that may differ from those of other taxa, but that can coexist at the same time. Our analysis does not disprove the migration of taxa (including Epilobieae, Gongylocarpeae, and Onagreae) through the Bering and Atlantic northern land bridges, or through the Panama isthmus. The East and West tracks show that two ancestral biotas existed on both sides of North America, with the species of each track sharing a common distributional history.

#### CORRELATION OF BIOGEOGRAPHIC PATTERN WITH GEOLOGIC AND PALEOCLIMATIC EVIDENCE

The geological and climatic processes in the past provide at least partial explanations for the current biogeographical patterns in North America of Epilobieae, Gongylocarpeae, and Onagreae. Major historical events in this area include orogenic processes such as the uplifting of the Rocky Mountains, the Sierra Madre, and western Cordillera, and the most recent glaciations (summary in Graham, 1999).

The uplifting of the Rocky Mountains together with the uplifting of the Sierra Madre Occidental in the early Tertiary remarkably changed the biota of western North America, creating a barrier for floristic exchanges between eastern and western North America. This had two main effects on the flora of western North America: significant extinction of taxa because of the increasingly dry climate, and accelerated speciation and diversification of new taxa (Qian, 2001). Indeed, the area of the

southern Rocky Mountains and the Sierra Madre Occidental was an important center for the evolution of the Madro-Tertiary geoflora (Axelrod, 1958). The early diversification of Onagraceae tribe Onagreae was postulated to have taken place in the Madrean vegetation of western North America (Raven & Axelrod, 1978). Until recently, tribe Gongylocarpeae, also endemic to the Madrean region, was considered to be the basal branch of Onagreae (Carlquist & Raven, 1966). Tribe Epilobieae also may have originated in western North America as part of the Madro-Tertiary geoflora (Raven, 1976; Baum et al., 1994), but evidence from fossil pollen is equivocal, and the distribution of *Chamerion* and its position as sister to *Epilobium* (Baum et al., 1994) suggest a possible origin in western Eurasia (Raven & Raven, 1976). The strong association of *Epilobium* to the western track, and the endemism of the near-basal species *E. rigidum* (Baum et al., 1994; Levin et al., 2004) in the VAN region, support an origin of the genus in western North America. The Madro-Tertiary geoflora had already appeared on the drier borders of the North American tropics by the Middle Eocene, and probably occupied much of the southwestern United States and adjacent Mexico by the close of the Oligocene. It extended its range in all directions in response to the expanding aridity in the succeeding Miocene epoch (Axelrod, 1958; Valliente-Banuet et al., 1998). Major expansion of Onagraceae tribes Onagreae, Gongylocarpeae, and Epilobieae may have occurred during the Miocene and Pliocene (Raven & Axelrod, 1974; Raven & Raven, 1976; Raven, 1979).

From the late Oligocene (25 mya) through the Pliocene, new orogeny gave rise to the present western Cordilleran System, including major deformation and uplift of the Rocky Mountains, Sierra Nevada, Sierra Madre Occidental, and Sierra Madre Oriental (Axelrod & Raven, 1985; Wing, 1987; Graham, 1993). This resulted in cooler and drier climates that precipitated the development of grasslands in central North America (Sanmartín et al., 2001), being thus a third event differentiating the western and the eastern floras. However, Wen (1999) noted that the close biogeographic relationship between western and eastern North America suggests that the Cordilleran range was not an effective barrier to exchange between these two floristic regions.

In the Quaternary period, the flora of North America experienced late Pleistocene full-glacial conditions (20,000–15,000 yr. b.p.), late-glacial climatic amelioration (15,000–10,000 yr. b.p.), and Holocene interglacial conditions of the last 10,000

years (Graham, 1999). The Quaternary can be characterized more by changes in the distributions of plant taxa than by the evolution of new genera and species (Delcourt & Delcourt, 1993). During times of glacial maxima, fragmented populations may have undergone genetic differentiation within isolated refugia. With the onset of interglacial conditions, migration and expansion of distributional ranges would reestablish genetic exchanges between populations within species and among closely related species that were formerly isolated. Grichuk (1984) proposed the term "migration flora" to denote floras that moved into a given region after the preceding flora was eliminated by glacial or periglacial conditions. Delcourt and Delcourt (1993) suggested that the individual elements of such migration floras could move hundred to thousands of kilometers as they differentially responded to changing climatic and competitive conditions. Different groups and species of Onagraceae tribes Epilobieae, Gongylocarpeae, and Onagreae appear to have participated in such Quaternary migrations into western and eastern North America, apparently from areas in the southwestern part of the continent. We hope that this scenario may be tested using other groups of plants and animals, as well as other analytical tools including phylogenetic methods.

## Literature Cited

- Aiken, S. G., M. J. Dallwitz, L. L. Consaul, C. L. McJannet, L. J. Gillespie, R. L. Boles, G. W. Argus, J. M. Gillett, P. J. Scott, R. Elven, M. C. LeBlanc, A. K. Brysting & H. Solstad. 1999 onward. Flora of the Canadian Arctic Archipelago: Descriptions, Illustrations, Identification, and Information Retrieval. Version: 29th April 2003. (<http://www.mun.ca/biology/delta/arctic/>).
- Axelrod, D. I. 1958. Evolution of the Madro-Tertiary geoflora. *Bot. Rev.* 24: 433–509.
- . 1979. Age and origin of Sonoran desert vegetation. *Occas. Pap. Calif. Acad. Sci.* 132: 1–74.
- & P. H. Raven. 1985. Origins of the Cordilleran flora. *J. Biogeogr.* 12: 21–47.
- Ayala, R., T. L. Griswold & S. H. Bullock. 1993. The native bees of Mexico. Pp. 179–131 in T. P. Ramamoorthy, R. Bye, A. Lot & J. Fa (editors), *Biological Diversity of Mexico: Origins and Distribution*. Oxford Univ. Press, New York, Oxford.
- Barbour, M. G. & N. L. Christensen. 1993. Vegetation. Pp. 97–131 in *Flora of North America, North of Mexico, Vol. 1*. Oxford Univ. Press, Oxford, New York.
- Baum, D. A., K. J. Sytsma & P. C. Hoch. 1994. A phylogenetic analysis of *Epilobium* (Onagraceae) based on nuclear ribosomal DNA sequences. *Syst. Bot.* 19: 363–388.
- Berry, E. W. 1930. Revision of the Lower Eocene Wilcox flora of the southeastern states. *U.S. Geol. Surv. Prof. Paper* 156.
- Boufford, D. E. 1982 [1983]. The systematics and evolution of *Circaea* (Onagraceae). *Ann. Missouri Bot. Gard.* 69: 804–994.
- Brooks, D. R., M. G. P. van Veller & D. A. McLennan. 2001. How to do BPA, really. *J. Biogeogr.* 28: 345–358.
- Brown, D. E., C. H. Lowe & C. P. Puse. 1979. A digitized classification system for the biotic communities of North America, with community (series) and association examples for the southwest. *J. Ariz.-Nev. Acad. Sci.* 14 (Suppl. 1): 1–16.
- , F. Reichenbacher & S. E. Franson. 1998. A classification of North American biotic communities. Univ. Utah Press, Salt Lake City.
- California Academy of Sciences. 2003. Entomology. World Wide Web site: ([www.calacademy.org/research/entomology/](http://www.calacademy.org/research/entomology/)).
- Carlquist, S. & P. H. Raven. 1966. The systematics and anatomy of *Gongylocarpus* (Onagraceae). *Amer. J. Bot.* 53: 378–390.
- Chen, C. J., P. C. Hoch & P. H. Raven. 1992. Systematics of *Epilobium* (Onagraceae) in China. *Syst. Bot. Monogr.* 34: 1–209.
- Connor, E. F. 1988. Fossils, phenetics and phylogenetics: Inferring the historical dynamics of biogeographic distributions. Pp. 254–269 in J. K. Liebherr (editor), *Zoogeography of Caribbean Insects*. Cornell Univ. Press, Ithaca.
- Correll, D. S. & M. C. Johnston. 1970. *Manual of the Vascular Plants of Texas*. Texas Research Foundation, Renner, Texas.
- Cracraft, J. 1991. Patterns of diversification within continental biotas: Hierarchical congruence among the areas of endemism of Australian vertebrates. *Austral. Syst. Bot.* 4: 211–427.
- Craw, R. C. 1988. Continuing the synthesis between panbiogeography, phylogenetic systematics and geology as illustrated by empirical studies on the biogeography of New Zealand and the Chatham Islands. *Syst. Zool.* 37: 291–310.
- . 1989. Quantitative panbiogeography: Introduction to methods. *New Zealand J. Zool.* 16: 485–494.
- . 1990. New Zealand biogeography: A panbiogeographic approach. *New Zealand J. Zool.* 16: 527–547.
- , J. R. Grehan & M. J. Heads. 1999. *Panbiogeography: Tracking the history of life*. Oxford Biogeography series n. 11. Oxford Univ. Press, New York, Oxford.
- Crisci, J. V. 2001. The voice of historical biogeography. *J. Biogeogr.* 28: 157–168.
- , L. Katinas & P. Posadas. 2000. *Introducción a la teoría y práctica de la biogeografía histórica*. Sociedad Argentina de Botánica, Buenos Aires, Argentina.
- & ———. 2003. *Historical Biogeography: An Introduction*. Harvard Univ. Press, Cambridge, Massachusetts.
- Croizat, L. 1958. *Panbiogeography, Vols. I, Ila, and IliB*. Published by the author, Caracas, Venezuela.
- . 1965. On approaching the subgeneric classification of *Euphorbia papilion* and *E. tetrapora*. *SouthW. Naturalist* 10: 241–247.
- . 1981. Biogeography: Past, present, and future. Pp. 501–523 in G. Nelson & D. E. Rosen (editors), *Vicariance Biogeography: A Critique*. Columbia Univ. Press, New York.
- Delcourt, P. A. & H. R. Delcourt. 1993. Paleoclimates, paleovegetation, and paleofloras during the late Quaternary. Pp. 71–94 in *Flora of North America, North of Mexico, Vol. 1*. Oxford Univ. Press, Oxford, New York.
- Dice, L. R. 1943. *The Biotic Provinces of North America*. Univ. Michigan Press, Ann Arbor.

- Dietrich, W. & W. L. Wagner. 1988. Systematics of *Oenothera* section *Oenothera* subsection *Raimannia* and subsection *Nutantigemma*. Syst. Bot. Monogr. 24: 1–91.
- , P. H. Raven & W. L. Wagner. 1985. Revision of *Oenothera* sect. *Oenothera* subsect. *Emersonia* (Onagraceae). Syst. Bot. 10: 29–48.
- , W. L. Wagner & P. H. Raven. 1997. Systematics of *Oenothera* section *Oenothera* subsection *Oenothera* (Onagraceae). Syst. Bot. Monogr. 50: 1–234.
- Donoghue, M. J., C. D. Bell & J. Li. 2001. Phylogenetic patterns in northern hemisphere plant geography. Int. J. Plant. Sci. 162 (6 Suppl.): S41–S52.
- Escalante Pliego, P., A. G. Navarro Sigüenza & A. Townsend Peterson. 1993. A geographic, ecological, and historical analysis of land bird diversity in Mexico. Pp. 281–307 in T. P. Ramamoorthy, R. Bye, A. Lot & J. Fa (editors), Biological Diversity of Mexico: Origins and Distribution. Oxford Univ. Press, New York, Oxford.
- Fa, J. E. & L. M. Morales. 1993. Patterns of mammalian diversity in Mexico. Pp. 319–361 in T. P. Ramamoorthy, R. Bye, A. Lot & J. Fa (editors), Biological Diversity of Mexico: Origins and Distribution. Oxford Univ. Press, New York, Oxford.
- Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783–791.
- Froese, R. & D. Pauly (editors). 2003. FishBase. Version: 12 November 2003. (www.fishbase.org).
- Frost, D. R. 2002. Amphibian Species of the World: An Online Reference. V2.21 (15 July 2002). (<http://research.amnh.org/herpetology/amphibia/index.html>).
- Graham, A. 1972. Outline of the origin and historical recognition of floristic affinities between Asia and eastern North America. Pp. 1–18 in A. Graham (editor), Floristics and Paleofloristics of Asia and Eastern North America. Elsevier, New York.
- . 1993. History of the vegetation: Cretaceous (Maastrichtian)—Tertiary. Pp. 57–70 in Flora of North America, North of Mexico, Vol. 1. Oxford Univ. Press, New York, Oxford.
- . 1999. Late Cretaceous and Cenozoic History of North American Vegetation (North of Mexico). Oxford Univ. Press, Oxford.
- Great Plains Flora Association. 1986. Flora of the Great Plains. Univ. Press Kansas, Lawrence.
- Grehan, J. R. 1988a. Panbiogeography: Evolution in space and time. Riv. Biol., Biol. Forum 81: 469–498.
- . 1988b. Biogeographic homology: Ratites and the southern beeches. Riv. Biol., Biol. Forum 81: 577–587.
- Grichuk, V. P. 1984. Late Pleistocene vegetation history. Pp. 155–178 in A. A. Velichko (editor); H. E. Wright & C. W. Barnosky (editors, English ed.), Late Quaternary Environments of the Soviet Union. Univ. Minnesota Press, Minneapolis.
- Guo, Q. & R. E. Ricklefs. 2000. Species richness in plant genera disjunct between temperate eastern Asia and North America. Bot. J. Linn. Soc. 134: 401–423.
- Henderson, I. 1990. Quantitative biogeography: An investigation into concepts and methods. New Zealand J. Zool. 16: 495–510.
- . 1991. Biogeography without areas? Austral. Syst. Bot. 4: 59–71.
- Hickman, J. C. (editor). 1993. The Jepson Manual: Higher Plants of California. Univ. California Press, Berkeley and Los Angeles.
- Hoch, P. C. 1986. *Epilobium*. Pp. 504–509 in Flora of the Great Plains. Univ. Press Kansas, Lawrence.
- . 1993. *Epilobium*. Pp. 793–798 in J. C. Hickman (editor), The Jepson Manual: Higher Plants of California. Univ. California Press, Berkeley and Los Angeles.
- , J. V. Crisci, H. Tobe & P. E. Berry. 1993. A cladistic analysis of the plant family Onagraceae. Syst. Bot. 18: 31–47.
- Iltis, H. H. 1983. Biogeographical relationships between temperate eastern Asia and temperate eastern North America. Pp. 49–51 in Proceedings of U.S.–Japan Scientific Seminar on the Origin of the Eastern Asian and North American Floras from Arctotertiary Precursors. U.S.–Japan Cooperative Science Program, New York.
- Larsen, J. A. 1980. The Boreal Ecosystem. Academic Press, New York.
- Lepage, D. 2003. AviBase. ([www.bsc-eoc.org/avibase](http://www.bsc-eoc.org/avibase)).
- Levin, R. A., W. L. Wagner, P. C. Hoch, M. Nepokroff, J. C. Pires, E. A. Zimmer & K. J. Sytsma. 2003. Family-level relationships of Onagraceae based on chloroplast *rbcL* and *ndhF* data. Amer. J. Bot. 90: 107–115.
- , ———, ———, W. J. Hahn, A. Rodriguez, D. A. Baum, L. Katinas, E. A. Zimmer & K. J. Sytsma. 2004. Paraphyly in tribe Onagreae: Insights into phylogenetic relationships of Onagraceae based on nuclear and chloroplast sequence data. Syst. Bot. 29: 147–164.
- Lewis, H. 1993. *Clarkia*. Pp. 786–793 in J. C. Hickman (editor), The Jepson Manual: Higher Plants of California. Univ. California Press, Berkeley and Los Angeles.
- & M. E. Lewis. 1955. The genus *Clarkia*. Univ. Calif. Publ. Bot. 20: 241–392.
- & J. Szwejkowski. 1964. The genus *Gayophytum* (Onagraceae). Brittonia 16: 343–391.
- Li, H. 1952. Floristic relationships between eastern Asia and eastern North America. Trans. Amer. Philos. Soc. 42: 371–429.
- Li, S. & K. T. Adair. 1994. Species pools in eastern Asia and North America. Sida 16: 281–299.
- Liebher, J. K. 1991a. Phylogeny and revision of the *Anchomenus* clade: The genera *Tetraleucus*, *Anchomenus*, *Sericoda*, and *Elliptoleus* (Coleoptera: Carabidae: Platynini). Bull. Amer. Mus. Nat. Hist. 202: 1–163.
- . 1991b. A general area cladogram for montane Mexico based on distributions in the Platynine genera *Elliptoleus* and *Calathus* (Coleoptera: Carabidae). Proc. Entomol. Soc. Wash. 93: 390–406.
- . 1992. Phylogeny and revision of the *Platynus degallieri* species group (Coleoptera: Carabida: Platynini). Bull. Amer. Mus. Nat. Hist. 214: 1–115.
- . 1994a. Identification of New World *Agonum*, review of the Mexican fauna, and description of *Incagonum*, new genus, from South America (Coleoptera: Carabidae: Platynini). J. Entomol. Soc. 102: 1–55.
- . 1994b. Biogeographic patterns of montane Mexican and Central American Carabidae (Coleoptera). Canad. Entomol. 126: 841–860.
- Llorente-Bousquets, J. & A. Luis-Martínez. 1993. Conservation-oriented analysis of Mexican butterflies: Papilionidae (Lepidoptera, Papilionoidea). Pp. 147–178 in T. P. Ramamoorthy, R. Bye, A. Lot & J. Fa (editors), Biological Diversity of Mexico: Origins and Distribution. Oxford Univ. Press, New York, Oxford.
- MacMahon, J. A. 2000. Warm deserts. Pp. 285–322 in M. G. Barbour & W. D. Billings (editors), North American Terrestrial Vegetation. Cambridge Univ. Press, Cambridge.
- Maddison, D. R. & W. P. Maddison. 2000. MacClade 4: Analysis of Phylogeny and Character Evolution. Vers. 4.0. Sinauer, Sunderland, Massachusetts.

- Marshall, C. J. & J. K. Liebherr. 2000. Cladistic biogeography of the Mexican transition zone. *J. Biogeogr.* 27: 203–216.
- McAllister, D. E., S. P. Platania, F. W. Schueler, M. E. Baldwin & D. S. Lee. 1986. Ichthyofaunal patterns on a geographic grid. Pp. 17–51 in C. H. Hocutt & E. O. Wiley (editors), *The Zoogeography of North American Freshwater Fishes*. John Wiley & Sons, New York.
- McLaughlin, S. P. 1989. Natural floristic areas of the western United States. *J. Biogeogr.* 16: 239–248.
- . 1992. Are floristic areas hierarchically arranged? *J. Biogeogr.* 19: 21–32.
- Meacham, C. 1984. Evaluating characters by character compatibility analysis. Pp. 152–165 in T. Duncan & T. F. Stuessy (editors), *Cladistic: Perspectives on the Reconstruction of the Evolutionary History*. Columbia Univ. Press, New York.
- Miranda, F. & A. J. Sharp. 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. *Ecology* 31: 313–333.
- Morrone, J. J. 2001. Toward a cladistic model for the Caribbean subregion: Delimitation of areas of endemism. *Caldasia* 23: 43–76.
- & J. V. Crisci. 1990. Pangioecografía: Fundamentos y métodos. *Evolución Biológica (Bogotá)* 4: 119–140.
- & ———. 1995. Historical biogeography: Introduction to methods. *Ann. Rev. Ecol. Syst.* 26: 373–401.
- , D. Espinosa Organista, C. Aguilar Zuñiga & J. Llorente Bousquets. 1999. Preliminary classification of the Mexican biogeographic provinces: A parsimony analysis of endemicity based on plant, insect, and bird taxa. *SouthW. Naturalist* 44: 507–544.
- Mosquin, T. 1966. A new taxonomy for *Epilobium angustifolium* L. (Onagraceae). *Brittonia* 18: 167–188.
- Nowak, R. M. 1997. *Walker's Mammals of the World*. Johns Hopkins Univ. Press. ([www.press.jhu.edu/books/walkers\\_mammals\\_of\\_the\\_world/](http://www.press.jhu.edu/books/walkers_mammals_of_the_world/)).
- Page, R. D. M. 1987. Graphs and generalized tracks: Quantifying Croizat's panbiogeography. *Syst. Zool.* 36: 1–17.
- Platnick, N. I. 1991. On areas of endemism. *Austral. Syst. Bot.* 4 [Commentary].
- Qian, H. 2001. Floristic analysis of vascular plant genera of North America north of Mexico: Spatial patterning of phytogeography. *J. Biogeogr.* 28: 525–534.
- Ramamoorthy, T. P., R. Bye, A. Lot & J. Fa. 1993. *Biological Diversity of Mexico: Origins and Distribution*. Oxford Univ. Press, New York.
- Raven, P. H. 1962. Systematics of *Oenothera* subgenus *Chylisma*. *Univ. Calif. Publ. Bot.* 34: 1–122.
- . 1969. A revision of the genus *Camissonia* (Onagraceae). *Contr. U.S. Natl. Herb.* 37: 161–396.
- . 1976. Generic and sectional delimitation in Onagraceae, tribe Epilobieae. *Ann. Missouri Bot. Gard.* 63: 326–340.
- . 1979. A survey of reproductive biology in Onagraceae. *New Zealand J. Bot.* 17: 575–593.
- . 1988. Onagraceae as a model of plant evolution. Pp. 85–107 in L. D. Gottlieb & S. K. Jain (editors), *Plant Evolutionary Biology*. Chapman & Hall, London and New York.
- & D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539–673.
- & ———. 1978. Origin and relationships of the California flora. *Univ. Calif. Publ. Bot.* 72: 1–134.
- & D. P. Gregory. 1972. A revision of the genus *Gaura* (Onagraceae). *Mem. Torrey Bot. Club* 23: 1–96.
- & D. M. Moore. 1965. A revision of *Boisdewalia* (Onagraceae). *Brittonia* 17: 233–254.
- & T. E. Raven. 1976. The genus *Epilobium* (Onagraceae) in Australasia: A systematic and evolutionary study. *New Zealand Dept. Sci. Industr. Res. Bull.* 216: 1–321.
- Ricketts, T. H., E. Dinerstein, D. M. Olson, C. J. Loucks, W. Eichbaum, D. DellaSala, K. Kavanagh, P. Hedao, P. T. Hurley, K. M. Carney, R. Abell & S. Walters. 1999. *Terrestrial Ecoregions of North America: A Conservation Assessment*. Island Press, Washington, D.C.
- Rosen, B. R. 1988. From fossils to earth history: Applied historical biogeography. Pp. 437–481 in A. A. Myers & P. S. Giller (editors), *Analytical Biogeography: An Integrated Approach to the Study of Animal and Plant Distributions*. Chapman & Hall, New York.
- & A. B. Smith. 1988. Tectonics from fossils? Analysis of reef-coral and sea-urchin distributions from Late Cretaceous to Recent, using a new method. Pp. 275–306 in M. G. Audley-Charles & A. Hallam (editors), *Gondwana and Tethys*. Oxford Univ. Press, Oxford.
- Rzedowski, J. 1978. *Vegetación de México*. Editorial Limusa, D. F., México.
- Salisbury, B. A. 1999. SECANT: Strongest Evidence Compatibility Analytical Tool. Vers. 2.2. Department of Ecology & Evolutionary Biology, Yale University, New Haven.
- Sanmartín, I., H. Enghoff & F. Ronquist. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biol. J. Linn. Soc.* 73: 345–390.
- Small, E. 1968. The systematics of autopolyploidy in *Epilobium latifolium* (Onagraceae). *Brittonia*: 169–181.
- Straley, G. B. 1977 [1978]. Systematics of *Oenothera* sect. *Kneiffia* (Onagraceae). *Ann. Missouri Bot. Gard.* 64: 381–424.
- Swofford, D. L. 2001. PAUP\*: Phylogenetic Analysis Using Parsimony. Vers. 4.0b10. Sinauer, Sunderland, Massachusetts.
- Takhtajan, D. H. 1986. *Floristic Regions of the World*. Univ. California Press, Berkeley.
- Thorne, R. F. 1993. *Phytogeography*. Pp. 132–153 in *Flora of North America, North of Mexico*. Oxford Univ. Press, New York, Oxford.
- Towner, H. F. 1977. The biosystematics of *Calylophus* (Onagraceae). *Ann. Missouri Bot. Gard.* 64: 48–120.
- Uetz, P., R. Chenna, T. Etzold & J. Hallermann. 2003. The EMBL Reptile Database. ([www.reptile-database.org/](http://www.reptile-database.org/)).
- Valliente-Banuet, A., N. Flores Hernandez, M. Verdu & P. Davila. 1998. The chaparral vegetation in Mexico under non-Mediterranean climate: The convergence and Madrean-Tethyan hypotheses reconsidered. *Amer. J. Bot.* 85: 1398–1408.
- Van Bruggen, T. 1976. *The Vascular Plants of South Dakota*. Iowa State Univ. Press, Ames.
- Van Deventer, T. R. & W. G. Spaulding. 1979. Development of vegetation and climate in the southwestern United States. *Science* 204: 701–710.
- Wagner, W. L. 1984 [1985]. Reconsideration of *Oenothera* subg. *Gauropsis* (Onagraceae). *Ann. Missouri Bot. Gard.* 71: 1114–1127.
- . 1986. New taxa in *Oenothera* (Onagraceae). *Ann. Missouri Bot. Gard.* 73: 475–480.
- . 1993. Onagraceae. Pp. 776–804 in J. C. Hick-

- man (editor), *The Jepson Manual: Higher Plants of California*. Univ. California Press, Berkeley and Los Angeles.
- . 2004. Resolving a nomenclatural and taxonomic problem in Mexican *Oenothera* sect. *Hartmannia* (tribe Onagreae, Onagraceae). *Novon* 14: 124–133.
- , R. E. Stockhouse & W. M. Klein. 1985. The systematics and evolution of the *Oenothera caespitosa* complex (Onagraceae). *Monogr. Syst. Bot. Missouri Bot. Gard.* 12: 1–103.
- Wen, J. 1999. Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. *Ann. Rev. Ecol. Syst.* 30: 421–455.
- Wilson, D. E. & D. M. Reeder (editors). 1993. *Mammal Species of the World*. Smithsonian Institution Press. ([www.nmnh.si.edu/msw/](http://www.nmnh.si.edu/msw/)).
- Wing, S. L. 1987. Eocene and Oligocene floras and vegetation of the Rocky Mountains. *Ann. Missouri Bot. Gard.* 74: 748–784.
- Wolfe, J. A. 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *Amer. Sci.* 66: 694–703.
- Xiang, Q. Y., D. E. Soltis & P. S. Soltis. 1998. The eastern Asian and eastern and western North America floristic disjunction: Congruent phylogenetic patterns in seven diverse genera. *Molec. Phylogenet. Evol.* 10: 178–190.
- , ———, ———, S. R. Manchester & D. J. Crawford. 2000. Timing the Eastern Asian–Eastern North American floristic disjunction: Molecular clock corroborates paleontological estimates. *Molec. Phylogenet. Evol.* 15: 462–472.
- APPENDIX 1.
- North American areas of endemism used in this analysis; see text for sources and explanation. References for plant endemics generally follow Takhtajan (1986); these are supplemented in some areas by Barbour & Christensen (1993), in Canada by Aiken et al. (1999: ([www.mun.ca/biology/delta/arctic/](http://www.mun.ca/biology/delta/arctic/))); in California by Hickman (1993), and in Mexico by Rzedowski (1978) and Ramamoorthy et al. (1993). Names were checked against the on-line *Flora of North America* database (<http://hua.huh.harvard.edu/FNA>). Endemic animals are arranged in the following order: fish, amphibians, reptiles, birds, mammals, invertebrates; within groups, alphabetical by family. References for animal endemics are as follows: <sup>1</sup>Ricketts et al. (1999); <sup>2</sup>*Mammals of the World* (Wilson & Reeder, 1993: ([www.nmnh.si.edu/msw/](http://www.nmnh.si.edu/msw/))); <sup>3</sup>Avibase (Lepage, 2003: ([www.bsc-eoc.org/avibase/](http://www.bsc-eoc.org/avibase/))); <sup>4</sup>*Amphibian Species of the World* (Frost, 2002: ([research.amnh.org/herpetology/amphibia/](http://research.amnh.org/herpetology/amphibia/))); <sup>5</sup>*Walker's Mammals of the World* (Nowak, 1997: ([www.press.jhu.edu/books/walkers\\_mammals\\_of\\_the\\_world/](http://www.press.jhu.edu/books/walkers_mammals_of_the_world/))); <sup>6</sup>*Fishbase* (Froese & Pauly, 2003: ([www.fishbase.org/](http://www.fishbase.org/))); <sup>7</sup>Reptile database (Uetz et al., 2003: ([www.reptile-database.org/](http://www.reptile-database.org/))); <sup>8</sup>entomology (California Academy of Sciences, 2003: ([www.calacademy.org/research/entomology/](http://www.calacademy.org/research/entomology/))).
1. *Arctic* (ARC): includes most of coastal Alaska, northern coastal Canada, all of the ice-free Canadian Archipelago, and Greenland. The flora is depauperate in a nearly tree-less region of tundra and polar desert, with fewer than 1000 species of vascular plants. Endemism at the species level is moderate (Aiken et al., 1999), e.g.: Asteraceae: *Taraxacum hyparcticum*; Brassicaceae: *Braya thorild-wulfii*, *Parrya arctica*; Caryophyllaceae: *Cerastium regelii*, *Silene sorensenis*; Orobanchaceae: *Castilleja arctica*; Polemoniaceae: *Phlox richardsonii*. Endemic fauna include Mammals [Cervidae] *Rangifer tarandus pearyi* (Peary caribou)<sup>1,5</sup>; [Leporidae] *Lepus arcticus* (arctic hare)<sup>1,2</sup>; [Soricidae] *Sorex pribilofensis* (Pribiloff Island shrew)<sup>1,5</sup>.
  2. *Canadian* (CAN): forms a broad band across Canada and Alaska, south of ARC and north of Rocky Mountain (ROC) and Appalachian (APP) regions, including extreme northern New England, Michigan, and Minnesota. Consists primarily of taiga and coniferous boreal forests, with dominant tree species in *Abies*, *Betula*, *Larix*, *Picea*, *Pinus*, and *Populus*. Some endemic plants include Asteraceae: *Aster yukonensis*; Boraginaceae: *Cryptantha shakletteana*; Brassicaceae: *Erysimum aspernum*; Caryophyllaceae: *Silene williamsii*; Fabaceae: *Astragalus ecosmus*; Orobanchaceae: *Castilleja annua*; Polygonaceae: *Eriogonum flavum*; Portulacaceae: *Claytonia bostockii*; Primulaceae: *Douglasia gormanii*. Endemic fauna include Mammals: [Soricidae] *Sorex gaspensis* (Gaspé shrew)<sup>2,5</sup>; Insects: [Lepidoptera] *Coenonympha nepisiquit* (maritime ringlet butterfly)<sup>1</sup>.
  3. *Appalachian* (APP): includes a small part of southern Ontario and Quebec, Canada, and most of the eastern United States, excluding the Atlantic and Gulf Coastal region (ATL) to the south. Extends from central Maine, southern Canada, and Minnesota to central Georgia, central Alabama, the Ozark Plateau and the Quachita Mts. in Missouri and Arkansas, and eastern Texas. In Texas, corresponds to the “Post Oak Savannah” and “Blackland Prairies” areas of Correll and Johnston (1970). Dominant climax vegetation is the eastern deciduous forest, with dominant tree species in *Acer*, *Aesculus*, *Betula*, *Fagus*, *Magnolia*, *Quercus*, and *Tilia*. Many endemic plant species, including Magnoliaceae: *Magnolia fraseri*; Menispermaceae: *Menispermum canadense*; Pinaceae: *Abies fraseri*; Ranunculaceae: *Aconitum reclinatum*, *Anemone acutiloba*; Rosaceae: *Prunus alleghanensis*; Ulmaceae: *Ulmus serotina*. Endemic fauna include Amphibians: [Plethodontidae] *Desmognathus welten* (Black Mountain salamander)<sup>1,4</sup>; Reptiles: [Emydidae] *Clemmys muhlenbergii* (bog turtle)<sup>1</sup>; Birds: [Emberizidae] *Dendroica kirtlandii* (Kirkland’s warbler)<sup>1,3</sup>; Annelids: [Acanthodrilidae] *Diplocardia meansi* (earthworm)<sup>1</sup>.
  4. *Atlantic and Gulf Coastal* (ATL): occupies the geologic coastal plain of the Atlantic and Gulf Coast states of the United States, from Massachusetts and New Jersey to Florida and west to south-central Texas. In Texas, corresponds to the “Pineywoods” and “Gulf Prairies and Marshes” areas of Correll and Johnston (1970). Also extends across the lower Mississippi River valley to southern Missouri and Illinois. Much of the coastal plain is characterized by extensive forests of *Pinus*, replaced in some areas by *Carya*, *Fagus*, and/or *Quercus*, and in wetter areas by *Taxodium distichum* and species of *Nyssa* and *Fraxinus*. Endemic taxa include Onagraceae (tribe Jussiaeae): *Ludwigia lanceolata*, *L. pilosa*, *L. ravenii*, and *L. suffruticosa*, and several hundred species including Annonaceae: *Asimina incana*; Iridaceae: *Iris hexagona*; Lauraceae: *Persea palustris*; Pinaceae: *Pinus eliottii*; Salicaceae: *Salix floridana*; Simaroubaceae: *Leitneria floridana*; Taxaceae: *Taxus floridana*, *Torreya taxifolia*. Endemic fauna include Reptiles [Testudinidae] *Gopherus polyphemus* (gopher tortoise)<sup>1</sup>; Birds: [Corvidae] *Aphelocoma coerulescens coerulescens* (Florida scrub jay)<sup>1,3</sup>; [Picidae] *Picoides borealis*

- (red-cockaded woodpecker)<sup>1,3</sup>; Mammals: [Ursidae] *Ursus americanus floridanus* (Florida black bear)<sup>5</sup>.
5. *North American Prairies* (NAP): includes prairies and plains between the eastern deciduous forest of APP on the east, the coniferous forests of ROC on the west and CAN on the north, and the arid semi-deserts of CHI and TAM to the southwest. Corresponds for the most part with the "Great Plains" (Great Plains Flora Assoc., 1986), but in Texas also includes the "Edwards Plateau," "Rolling Plains," and "High Plains" areas of Correll and Johnston (1970). Grasses are dominant in this region, with a rich mix of perennial forbs, and forest trees in some areas near rivers. No endemic families, few endemic genera, and some endemic species, including the bryophyte Pottiaceae: *Aschisma kansanum*; and Agavaceae: *Yucca rupicola*; Brassicaceae: *Lesquerella angustifolia*; Fabaceae: *Astragalus gracilis*, *Psoralea cuspidata*; Polygonaceae: *Eriogonum correllii*; Valerianaceae: *Valeriana texana*. Endemic fauna include Amphibians: [Plethodontidae] *Typhlomolge (Eurycea) rathbuni* (Texas blind salamander)<sup>1,4</sup> and *T. robusta* (Blanco blind salamander)<sup>1,4</sup>; Birds: [Phasianidae] *Tympanuchus cupido* (greater prairie chicken)<sup>1,3</sup>; Mammals: [Canidae] *Vulpes velox* (swift fox)<sup>1,2</sup>.
  6. *Vancouverian* (VAN): extends as a coastal strip from Kodiak Island in Alaska to coastal British Columbia, widening in Washington and Oregon to include the Cascade, Olympic, and Coast Ranges, extending into California through the Klamath and Northern Coast ranges in the west and through the southern Cascades into the Sierra Nevada to its terminus in southern California. In California, VAN corresponds to the NW, CW, CaR, and SN regions of *The Jepson Manual* (Hickman, 1993). Conifers dominate the climax vegetation, along with some broad-leaved species of *Acer*, *Alnus*, *Cornus*, *Fraxinus*, *Populus*, and *Quercus*. There are endemic genera and some 500 to 600 endemic species, including Apiaceae: *Lomatium bradshawii*; Asteraceae: *Aster paludicola*, *Erigeron cervinus*, *Senecio clarkianus*; Iridaceae: *Iris bracteata*; Sarraceniacae: *Darlingtonia californica*; Taxodiaceae: *Sequoia sempervirens*, *Sequoiadendron giganteum*. Endemic fauna include Fishes: [Catostomidae] *Catostomus rimiculus* (Jenny Creek sucker)<sup>1,6</sup>; [Cyprinidae] *Gila bicolor bicolor* (Tui chub)<sup>1,6</sup>; Amphibians: [Dicamptodontidae] *Dicamptodon ensatus* (Pacific giant salamander)<sup>1,4</sup>; Birds: [Strigidae] *Strix occidentalis caurina* (northern spotted owl)<sup>1,3</sup>; Insects: [Lepidoptera] *Colias behrii* (Sierra sulfur butterfly)<sup>1</sup>.
  7. *Rocky Mountain* (ROC): includes the Rocky Mountains and associated inland ranges from northern British Columbia and southwestern Yukon to central Oregon, south-central Idaho, extreme northeastern Utah, and north-central New Mexico, bounded on the west by VAN and GBA and on the east by CAN and NAP. In the extreme south, ROC borders the deserts of CHI. Also includes some associated outlier ranges, especially extending to the east and south of the main cordillera. Vegetation is zoned vertically, with *Pinus ponderosa* dominant in the lowest zones, and species of *Abies*, *Juniperus*, *Picea*, *Pinus*, *Populus*, and *Pseudotsuga* dominant at higher zones. Some endemic plant species include Apiaceae: *Angelica ampla*, *Lomatium tuberosum*; Brassicaceae: *Draba grayana*; Fabaceae: *Astragalus arrectus*; Orobanchaceae: *Castilleja christii*; Plantaginaceae: *Penstemon elegantulus*; Polemoniaceae: *Phlox colubrina*. Endemic fauna include Fishes: [Cyprinidae] *Gila cypha* (humpback chub)<sup>1,6</sup>; [Salmonidae] *Oncorhynchus clarki lewisi* (westslope cutthroat trout)<sup>1,6</sup>; Mammals: [Mustelidae] *Mustela negripes* (black-footed ferret)<sup>1,2,3</sup>; [Sciuridae] *Cynomys leucurus* (white-tailed prairie dog)<sup>1,2</sup>.
  8. *Great Basin* (GBA): bounded on the west by the Cascade-Sierra Nevada axis (VAN), on the east by ROC, and on the south by the desert regions of MOJ, SON, and CHI. In California, the boundaries correspond to those of the MP and SNE (including the White and Inyo Mountains) regions of *The Jepson Manual* (Hickman, 1993). Includes the Snake River Plains of southern Idaho and most of the Colorado Plateau, and consists of many north-south trending mountain ranges separated by broad, alkaline basins without external drainage, with much of the area above 1300 m. Characterized by diversity of species of *Artemisia*, Chenopodiaceae, and at higher elevations by some combination of species of *Acer*, *Populus*, *Quercus*, *Juniperus*, and *Pinus*. The region has numerous endemic species, including Asteraceae: *Chaetodelpha wheeleri*, *Erigeron mancus*; Loasaceae: *Mentzelia packardiae*; Papaveraceae: *Canbya aurea*; Plantaginaceae: *Penstemon compactus*; Primulaceae: *Primula maguirei*. Endemic fauna include Fishes: [Cyprinidae] *Ptychocheilus lucius* (Colorado pikeminnow)<sup>1,6</sup>; Mammals [Heteromyidae] *Microdipodops pallidus* (pale kangaroo mouse)<sup>1,2</sup>.
  9. *Californian* (CAL): occupies a large part of the state of California, including the Central Valley, the Coast Ranges from the San Francisco region south into northwestern Baja California Norte, Mexico, and the Transverse Ranges of southern California. Bounded on the northwest, north, and east by VAN, and on the southeast by MOJ and SON (Raven & Axelrod, 1978). Corresponds to the GV, CW, and SW regions of *The Jepson Manual* (Hickman, 1993). The vegetation varies altitudinally, from treeless grassland in lower areas to chaparral and mixed forests of *Aesculus*, *Platanus*, *Populus*, *Quercus*, *Salix*, and conifers at higher levels. Numerous endemic plant genera and species include Asteraceae: *Erigeron sanctarum*; Fagaceae: *Quercus douglasii*; Ophioglossaceae: *Ophioglossum californicum*; Papaveraceae: the genus *Romneya*; Polygonaceae: the genus *Hollisteria*. Endemic fauna include Fishes: [Cyprinidae] *Gilia bicolor mojaveensis* (Mohave Tui chub)<sup>1,6</sup>; Reptiles: [Colubridae] *Masticophis flagellum ruddocki* (San Joaquin whipsnake)<sup>1,7</sup>; Mammals: [Canidae] *Urocyon littoralis* (Island gray fox)<sup>1,2</sup>; [Heteromyidae] *Dipodomys ingens* (giant kangaroo rat)<sup>1,2</sup>, *D. venustus* (narrow-faced kangaroo rat)<sup>1,2</sup>; *Perognathus inornatus* (San Joaquin pocket mouse)<sup>1,2</sup>; Insects [Lepidoptera, Pieridae] *Euphydryas editha quino* (Quino checkerspot butterfly)<sup>1</sup>.
  10. *Mojavean* (MOJ): small but complex region borders VAN and CAL on west, GBA on north, and SON on south and east. Includes Death Valley, adjacent desert ranges, and large desert region of southeastern California, to base of Transverse ranges, corresponding to DMOJ region of *The Jepson Manual* (Hickman, 1993). Extends to east through southern Nevada and northwestern Arizona to extreme southwestern Utah (MacMahon, 2000). Predominately shrubby desert dominated by endemic Joshua-tree *Yucca brevifolia* (Agavaceae), with saltbush (*Atriplex*) scrub characteristic of alkaline basins. Other characteristic species



- include Agavaceae: *Yucca schidigera*; Asteraceae: *Ambrosia dumosa*; Cactaceae: *Echinocactus polycephalus*, *Ferocactus achantoides*; and Zygophyllaceae: *Larrea divaricata* subsp. *tridentata*. Some endemic plants include Agavaceae: *Yucca brevifolia*; Asteraceae: *Amphipappus fremontii*; Caryophyllaceae: *Scopolophila rixfordii*; Cactaceae: *Opuntia chlorotica*; Plantaginaceae: *Penstemon calcareus*; Polygonaceae: *Gilmania luteola*. Endemic fauna include Reptiles: [Phrynosomatidae] *Uma scoparia* (Mojave fringe-toed lizard)<sup>1,7</sup>; Mammals: [Muridae] *Microtus californicus scirpensis* (Amargosa vole)<sup>1</sup>; [Sciuridae] *Spermophilus mohavensis* (Mojave ground squirrel)<sup>1,2</sup>; Insects: [Orthoptera, Stenopelmata] *Ammopelmatus kelsoensis* (Kelso Dunes Jerusalem cricket)<sup>1,8</sup>.
11. **Sonoran (SON)**: ranges from the southern border of the MOJ in southeastern California, south throughout Baja California, Mexico, east through most of southwestern Arizona, and southeast through Sonora, Mexico. Very characteristic plants of the region include columnar cacti such as *Carnegiea gigantea* (saguaro) and *Pachycereus pringlei* (Cactaceae), trees such as *Yucca valida* (Agavaceae), *Cercidium floridum*, and *C. microphyllum* (Cercidiphyllaceae), and shrubs such as *Acacia greggii* (Fabaceae), *Krameria grayi* (Krameriaceae), and *Larrea divaricata* subsp. *tridentata* (Zygophyllaceae). Endemic plant taxa include Onagraceae (tribe Lopezieae): *Lopezia clavata*, and species in various other families, including Agavaceae: *Agave aurea*; Cactaceae: *Opuntia rosarica*; Fabaceae: *Acacia brandegeana*, *A. goldmanii*, *Erazurizia benthamii*; Fouquieriaceae: *Fouquieria columnaris*; Lamiaceae: *Hyptis laniflora*; Sapindaceae: *Aesculus parryi*; Sapotaceae: *Sideroxylon peninsulare*. Endemic fauna include Birds: [Emberizidae] *Aimophila carpalis* (rufous-winged sparrow)<sup>1,3</sup>; [Hydrobatidae] *Oceanodroma macarodactyla* (Guadalupe storm petrel, possibly extinct)<sup>1,3</sup>; Insects: [Coleoptera, Carabidae] *Calathus peropacus* (ground beetle; Liebherr, 1991b), *Pelmattellus parallelus* (ground beetle)<sup>1,3</sup>; [Hymenoptera, Anthophoridae] *Agapanthinus* (digger bees; Ayala et al., 1993).
  12. **Chihuahuan (CHI)**: borders SON and SMO on west, GBA and ROC on north, NAP and TAM on east, and MAS on south. Extends from eastern Arizona and central New Mexico through trans-Pecos Texas and south into Mexico, including most of Chihuahua and Coahuila, eastern Durango, and northern Zacatecas. Cooler desert than the Sonoran Desert, dominated by shrubby *Larrea divaricata* subsp. *tridentata* and species of *Acacia*, *Agave*, *Dalea*, *Ephedra*, *Flourensia*, *Fouquieria*, and *Jatropha*, among others. Trees, mainly species of *Yucca* and *Opuntia*, are found only along larger streambeds. Endemic plant species include Asteraceae: *Ambrosia johnstoniorum*, *Flaveria anomala*, *Gaillardia gypsophila*; Chenopodiaceae: *Meiomeria stellata*; Fabaceae: *Dalea filiciformis*; Hydrophyllaceae: *Phacelia gypsogenia*. Endemic fauna include Fishes: [Cyprinidae] *Camptostoma ornatum* (Mexican stoneroller)<sup>1,6</sup>, *Notropis chihuahua* (Chihuahua shiner)<sup>1,6</sup>; Reptiles: [Teiidae] *Cnemidophorus tigris variolosus*<sup>1,7</sup>; Insects [Coleoptera, Carabidae] *Agonum extimum* (ground beetle; Liebherr, 1991a).
  13. **Tamaulipan (TAM)**: ranges from southeastern Texas to western Coahuila and most of Nuevo León and Tamaulipas in Mexico, excluding southern parts of these states. Bounded on west by CHI and SMR and on north in southern Texas by complex interface with NAP, APP, and ATL. In Texas, corresponds to "South Texas Plains" area of Correll and Johnston (1970). Characterized mostly by thornscrubs or mesquite-grasslands, moister than CHI desert to the west. Vegetation is largely open shrub- and grasslands with *Acacia*, *Aloysia*, *Celtis*, *Condalia*, *Prosopis*, *Ziziphus*, and other spiny species. Endemic plant species include Boraginaceae: *Heliotropium torreyi*; Ebenaceae: *Diospyros palmeri*; Euphorbiaceae: *Croton torreyanus*; Fabaceae: *Acacia rigidula*, *Mimosa malacophylla*; Lauraceae: *Phoebe tampicensis*; Lentibulariaceae: *Pinguicula gracilis*; Plantaginaceae: *Leucophyllum frutescens*; Polygalaceae: *Polygala glandulosa*; Rhamnaceae: *Condalia hookeri*; Rutaceae: *Amyris cordata*. Endemic fauna include Fishes: [Cichlidae] *Cichlasoma cyanoguttatum* (Rio Grande cichlid)<sup>1,6</sup>; Mammals: [Sciuridae] *Cynomys mexicanus* (Mexican prairie dog; Fa & Morales, 1993)<sup>2</sup>; [Talpidae] *Scalopus montanus* (Coahuila mole)<sup>1</sup>; Insects: [Coleoptera, Carabidae] *Platynus bacatellus* (ground beetle; Liebherr, 1992).
  14. **Sierra Madre Occidental (SMO)**: borders SON and a coastal strip of the Central American Neotropical area (NE) on west, and CHI, the Altiplano of central Mexico (MAS), and the Trans-Mexico Volcanic (TMV) regions on the east and south. Starts near U.S.–Mexico border and extends southeast through western Chihuahua, Durango, a small part of Zacatecas, eastern Sinaloa and Nayarit, to central Jalisco. The main cordillera consists of an extensive volcanic terrain from 200 to 2200 m, with a pronounced eastern tilt. The region is characterized by a variety of habitats including both dry and subtropical forests at lower elevations, dry mixed forests at mid-elevations, and pine/oak forests above 2000 m. Endemic plants include Onagraceae (tribe Lopezieae): *Lopezia ciliatula*, *L. conjugens*, *L. gentryi*, *L. laciniata*, *L. lopezioides*, *L. ovata*, *L. semeiandra*, *L. sinaloensis*, and *L. suffrutescens*, and species in various other families, including Asteraceae: *Alvordia congesta*, *Hofmeisteria sinaloensis*, *Perityle grandifolia*; Cactaceae: *Ferocactus schwarzii*, *Mamillaria rubidea*, *Stenocereus martinii*; Crassulaceae: *Echeveria kinnachii*, *Sedum copalense*; Ericaceae: *Arbutus madrensis*; Euphorbiaceae: *Ditaxis sinaloae*; Polygonaceae: *Ruprechtia occidentalis*. Endemic fauna include Birds: [Picidae] *Campephilus imperialis* (imperial woodpecker)<sup>1,3</sup>; Insects: [Coleoptera, Carabidae] *Elliptoleus olisthopoides* (ground beetle; Liebherr, 1991a); [Neuroptera, Myrmeleontidae] *Maracandula apicalis* (antlion)<sup>8</sup>.
  15. **Trans-Mexican Volcanic Belt (TMV)**: extends in narrow, slightly northwest to southeast band in central Mexico, from central Jalisco and Guerrero through southern Estado Mexico barely to Puebla. Borders SMO and the coastal NE strip on west and south, MAS on north, and a transitional montane area between SMR and SMS on east. Major volcanic peaks (3900–4000 m) covered by *Pinus hartwegii* and coarse bunchgrasses *Festuca tolucensis*, *Calamagrostis tolucensis*, and *Muhlenbergia quadridentata*. Other characteristic taxa included species of *Achillea*, *Alchemilla*, *Arenaria*, *Cerastium*, *Geranium*, *Ranunculus*, and *Trifolium*. Among the very large number of endemic plant species are Onagraceae (tribe Lopezieae): *Lopezia longiflora*; at least seven endemic alpine species of Asteraceae: *Cirsium nivale*, *Gnaphalium sarmentosum*, *G. vulcanicum*, *Senecio calcarius*,

- S. gerberaeifolius*, *S. procumbens*, and *S. roseus*; and many other taxa, including Garryaceae: *Garrya longifolia*; Meliaceae: *Cedrela saxatilis*; Orchidaceae: *Pleurothallis nigriflora*; Oxalidaceae: *Oxalis stolonifera*, *O. cuernavacana*. Endemic fauna include Amphibians: [Ambystomidae] *Ambystoma (Rhyacosiredon) rivularis* (Michoacán stream salamander)<sup>4</sup>; Mammals: [Muridae] *Neotomodon altstoni* (Mexican volcano mouse)<sup>2</sup>; *Reithrodontomys chrysopsis* (volcano harvest mouse)<sup>2</sup>; Insects: [Coleoptera, Carabidae] *Calathus azteca*, *Elliptoleus corvus*, *E. luteipes* (ground beetles; Liebherr, 1991b), *Platynus machetellus* (ground beetle; Liebherr, 1992); [Hymenoptera, Anthophoridae] *Loxoptilus* (digger bees; Ayala et al., 1993).
16. *Mexican Aльтиplano* (MAS): in central Mexico lies between CHI on north, the mountains of SMO on the west and SMR on the east, and TMV on the south. Includes central and southern Zacatecas, southeastern Durango, eastern Jalisco and Michoacán, northern Estado México, western San Luis Potosí and Hidalgo, the Federal District, Aguascalientes, Guanajuato, and Querétaro. This region is characterized by mixed, less xeromorphic tree communities of *Acacia*, *Ipomoea*, and *Opuntia*. Endemic plant species include Agavaceae: *Yucca queretaroensis*; Asteraceae: *Acourtia elizabethiae*; Berberidaceae: *Berberis albicans*; Cactaceae: *Lophophora diffusa*, *Mammillaria camptotricha*; Fabaceae: *Acacia sororia*; Lentibulariaceae: *Pinguicula agnata*. Endemic fauna include Insects: [Coleoptera, Carabidae] *Agonum suturale* (ground beetles; Liebherr, 1991a); [Hymenoptera, Halictidae] *Paragapostemon* (halictic bees; Ayala et al., 1993).
17. *Sierra Madre Oriental* (SMR): borders CHI and MAS on west and TAM on east, including parts of southern Coahuila and Nuevo León, eastern Zacatecas, San Luis Potosí and Hidalgo, most of Tlaxcala, western Puebla, and a small part of western Veracruz and southwestern Tamaulipas. A geologically complex montane area with high levels of endemism in the relatively moist eastern part; lower elevations in the southeast support tropical evergreen forest. At middle to higher elevations (1000–2000 m), strips of warm-temperate to subtropical mesophytic forest occur, with deciduous/semi-evergreen species. Pine and/or oak forest occur at highest elevations. The mixed forest contains genera characteristic of the Appalachian region, such as *Carpinus*, *Cornus*, *Fagus*, *Hamamelis*, *Liquidambar*, *Pinus*, *Platanus*, and *Quercus*, as well as more typically tropical elements, like *Eugenia*, *Meliosma*, *Rapanea*, and *Turpinia*. Among the very large number of endemic plants are Onagraceae (tribe Lopezieae): *Lopezia nuevoleonis*; and many other taxa, including Caprifoliaceae: *Viburnum cuneifolium*; Celastraceae: *Wimmeria concolor*; Clethraceae: *Clethra pringlei*; Crossosomataceae: *Velascoa*; Fagaceae: *Fagus mexicana*, *Quercus germana*, *Q. rysophylla*; Juglandaceae: *Juglans mollis*; Oleaceae: *Forestiera racemosa*; Sabiaceae: *Meliosma alba*. Endemic fauna include Reptiles: [Anguidae] *Abronia graminea* (terrestrial arboreal alligator lizard)<sup>7</sup>, *A. taeniata* (bromeliad arboreal alligator lizard)<sup>7</sup>; Insects [Coleoptera, Carabidae] *Calathus rotgeri*, *C. potosi* (ground beetles; Liebherr, 1991b), *Platynus robustulus* (ground beetle; Liebherr, 1992); [Lepidoptera, Papilionidae; Llorente-Bousquets & Luis-Martínez, 1993] *Parides alexiares* (Oaxacan swallowtail), *Priamides erostratinus* (swallowtail), *Protesilaus epidaus tepicus* (swallowtail).
18. *Sierra Madre del Sur* (SMS): east-west oriented mountain area, ranging from 1200 to 3500 m, including eastern Guerrero, northwestern Oaxaca, and southern Puebla and Morelos. Connects to north with TMV, MAS, and SMR, but mostly surrounded by lowland NE, and as such is southernmost part of the Madrean Region (Takhtajan, 1986). Includes mesic habitats with temperate evergreen forests and woodlands. The diversity of these woodlands is very high, including species of *Quercus* and *Juniperus*, as well as genera of more southern, tropical derivation. Endemic plants include Onagraceae: (tribe Fuchsieae) *Fuchsia ravenii* and (tribe Lopezieae): *Lopezia smithii*, as well as Agavaceae: *Yucca mixtecana*; Lauraceae: *Mocinnodaphne cinnamomoidea*; Malvaceae: *Hibiscus tenorii*; Melastomataceae: *Miconia teotepecensis*; Rusaceae: *Maianthemum amoenum*, *M. macrophyllum*, *M. comaltepecense*. Endemic fauna include Amphibians: [Plethodontidae] *Thorius grandis* (grand minute salamander), *T. infernalis* (Atoyac minute salamander); Reptiles: [Anguidae] *Abronia deppii* (alligator lizard); Insects: [Coleoptera, Carabidae] *Calathus ovipennis*, *Elliptoleus crepericornis*, *E. whiteheadi* (ground beetles; Liebherr, 1991b), *Platynus platynellus* (ground beetle; Liebherr, 1992).
19. *Neotropical* (NE): large region, essentially the Neotropical Kingdom of Takhtajan (1986), comprises everything south of the Madrean and North American regions. For purposes of this analysis, NE includes a broad spectrum of tropical sub-regions, from the southernmost, tropical part of the Florida Peninsula through the islands of the Caribbean region, most of the coastal plains of Mexico, and all of Central America to most of South America. Among the very large number of endemic plant taxa are Onagraceae, tribe Hauyeeae and numerous species of *Fuchsia* (tribe Fuchsieae) and *Ludwigia* (tribe Jussieae), and the plant families Brunelliaceae, Cyclanthaceae, Desfontainiaceae, and Marcgraviaceae. Endemic fauna include Amphibians: [Hylidae] *Gastrotheca (Notodelphis) ovifera* (giant marsupial frog)<sup>4</sup>; Reptiles: [Boidae] subfamily Boinae (boas and constrictors)<sup>7</sup>; Birds: family Rheidae (rheas)<sup>3</sup>; Mammals<sup>2,5</sup>: [Camelidae] *Lama* (alpacas, guanacos, llamas); family Caviidae (cavies, guinea pigs); family Chinchillidae (chinchillas and viscachas); [marsupials, Microbiotheriidae] *Dromiciops* (monitos del monte).
20. *East Palearctic* (EP): defined here to include the northeast Asian parts of the Circumboreal Region and essentially all of the diverse Eastern Asiatic Region of Takhtajan (1986), including the eastern Himalayas, most of China, the Korean Peninsula, Japan and the north Pacific Ocean island series. The flora of this region is enormous and very rich in endemics, including in Onagraceae several species of *Circaea* (tribe Circaeae; Boufford, 1982) and *Epilobium* (tribe Epilobieae; Chen et al., 1992), as well as the endemic families Cephalotaxaceae, Ginkgoaceae, and Trochodendraceae, and more than 300 endemic genera [e.g., Apiaceae: *Tetrapanax*; Berberidaceae: *Nandina*; Cornaceae: *Aucuba*; Lardizabalaceae: *Akebia*; Rosaceae: *Chaenomeles*; Rutaceae: *Poncirus*; Taxodiaceae: *Cryptomeria*]. Endemic fauna include Fishes: [Siluridae] *Silurus asotus* (Amur catfish)<sup>6</sup>; Reptiles–Crocodilians: family Gavialidae (gharial)<sup>7</sup>; Birds [Phasianidae] *Gal-*

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- lus gallus* (red jungle fowl, chicken)<sup>3</sup>; Mammals<sup>2,5</sup>; order Dermoptera (flying lemurs); family Hylobatidae (gibbons and lesser apes); [Leporidae] *Pentalagus* (Ryukyu rabbit).
21. *West Palearctic* (WP): defined here to include European and west Asian parts of the Circumboreal Region (Takhtajan, 1986), essentially everything west of EP in Eurasia. The flora includes many endemic plants, including Apiaceae: *Agasyllis*, *Endressia*, *Thorella*; Asteraceae: *Berardia*; Boraginaceae: *Megacaryon*, *Trigonocaryum*; Brassicaceae: *Microstigma*, *Pseudovesicaria*; Fabaceae: *Petteria*; Gesneriaceae: *Haberlea*. Endemic fauna include Fishes: [Siluridae] *Silurus aristotelis* (Aristotle's catfish)<sup>6</sup>; Amphibians: [Pelobatidae] *Pelobates* (European spadefoot toads)<sup>4</sup>; Mammals: [Bovidae] *Ovis musimon* (mouflon sheep)<sup>2,5</sup>.