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Delimitation of the Nearctic region according to mammalian distributional patterns

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The Nearctic has been recognized as a biogeographic region since the 19th century. We analyzed distributional patterns of the mammals inhabiting North and Central America, from Alaska to Panama, to delimit the boundaries of the Nearctic region. We performed 6 optimality analyses, using a grid of 4° latitude–longitude, based on families, genera, species, and combinations of these. The analysis of the matrix with the 3 taxonomic levels yielded better results in terms of the largest number of endemics and the best delimitation of the Nearctic region. We also found 3 patterns—western, eastern, and northern—within the region that coincide partially with previous biogeographic characterizations. Although mammals seem to represent appropriate taxa to delimit this region, we conclude that a more robust delimitation might be obtained by analyzing other plant and animal taxa.
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The Nearctic region was 1st delimited by Sclater (1858) and Wallace (1876), based mainly on bird and mammal taxa. It extends from North America to central Mexico, although some highlands of Chiapas (southern Mexico) and Central America previously were assigned to this region (Udvardy 1975). Few hierarchical regionalizations exist within the Nearctic region, and most of these are based on ecological features (Bailey 1998; Bailey and Cushwa 1981; Coops et al. 2009; Ricketts et al. 1999). Others are based on specific countries, for example, Canada and the United States (Hagmeier 1966; Hagmeier and Stults 1964) or Mexico (Cabrera and Willink 1973; Escalante et al. 2007b; Morrone 2001a; Smith 1941). No recent delimitations based on the concept of biogeographic homology (Morrone 2001b) have been made for the entire Nearctic region. The Mexican part of the Nearctic region has been studied extensively based on quantitative methods to find spatial homology using mammals (Escalante et al. 2003, 2004, 2007a, 2007b, 2009), but the northern boundaries of most of the Mexican biogeographic provinces, which are spread within the United States, are imperfectly known.

Wallace (1876) recognized 4 subregions within the Nearctic region, whereas Merriam (1892) proposed 6 life zones for North America. Smith (1941) published a map of the biotic provinces of Mexico, with the Nearctic region composed of 2 subregions and 16 provinces. Dice (1943) identified 29 biotic provinces in North America, from Canada and Greenland to Mexico. Schmidt (1954) revised previous regionalizations and confirmed that North America belongs to the Arctogaean realm (Holarctic region and Nearctic and Arctic subregions) and has 5 provinces. Hagmeier and Stults (1964) and Hagmeier (1966) performed 2 phenetic analyses to map zoogeographic provinces for North American mammals (United States and Canada), identifying 1 region, 4 subregions, 13 superprovinces, and 35 provinces. Cabrera and Willink (1973) regionalized Latin America into 2 regions, 1 of them the Holarctic region (equivalent to the Nearctic region in

North America) with the North American Pacific dominion and the Mountain Forest province. Udvardy (1975) recognized the Nearctic realm with 22 biogeographical provinces, following basically the concept of Dice (1943). For Takhtajan (1986), 4 regions and 11 provinces comprised North America, which belonged to the Holarctic kingdom. Ortega and Arita (1998) used a biogeographic index to determine quantitatively the boundary between the Nearctic and Neotropical regions. Morrone (2001a) and Escalante et al. (2007b) described 5 Mexican provinces and 2 dominions as part of the Nearctic region based on distributional models of mammal species. Discrepancies among these regionalizations are due to the different methods used and the taxa analyzed. Furthermore, some of them are restricted to a portion of the Nearctic region.

Mammals are 1 of the taxa traditionally included in biogeographic regionalizations because their phylogenetic relationships are relatively well known and many efforts have been made to document their distributional areas. For the Americas, some Internet portals harbor maps of their distributions (http://www.mnh.si.edu/mna/; http://www.natureserve.org/infonatura/; http://www.conabio.gob.mx/informacion/mamiferos/doctos/presentacion.html), which can be used to analyze their patterns of endemism.

The identification of areas of endemism is the 1st step in regionalizing a geographic area. Software NDM and VNDM implement an optimality criterion based on distribution maps that are relevant to endemism (Goloboff 2005; available at www.zmuc.dk/public/phylogeny). This method takes into account the general concept of areas of endemism (an area of nonrandom distributional congruence among different taxa), where species are scored according to how well their distributions match a given area (sets of grid cells), and the areas with higher scores are retained (Aagesen et al. 2009; Szumik et al. 2002; Szumik and Goloboff 2004). Some papers have shown that NDM performs better than other methods under certain parameters and for some taxa (Carine et al. 2009; Escalante et al. 2009). The possibility of using different taxonomic levels in endemicity analyses rarely has been explored (Casagranda et al. 2009; Morrone and Escalante et al. 2002; Vázquez-Miranda et al. 2007).

Our aim was to identify the natural limits of the Nearctic region, based on distributions of mammals at different taxonomic levels, using the optimality criterion. We believe that it might be appropriate to analyze all North American mammal taxa simultaneously and evaluate the usefulness of analyzing different taxonomic levels (e.g., genera and species).

Materials and Methods

We used a database of distributional data of 744 species belonging to 43 families and 217 genera of North and Central American mammals (Arita and Rodríguez 2004; maps available at http://conabioweb.conabio.gob.mx/website/mamiferos/viewer.htm). The map of each species was overlaid on a grid of 4° latitude–longitude (324 grid cells) and assigned to each grid cell with 0 (absent) or 1 (present). We followed the nomenclatural convention from NDM for the grid. We built 6 presence–absence binary matrices for NDM: with 43 families; with 217 genera; with 744 species; with 249 families and genera, excluding families with a single genus (to avoid bias of their distributional areas); with 850 genera and species, excluding genera with a single species; and with 882 families, genera, and species, excluding families with a single genus and genera with a single species.

The optimality method (also known as analysis of endemicity) was run in NDM/VNDM (Goloboff 2005; available at www.zmuc.dk/public/phylogeny). Each matrix was analyzed 50 times, changing the random seed and using a heuristic search in NDM. The options used were: save sets of areas with ≥ 2 endemic species, save sets with score >2.000, and retain suboptimal sets of 0.90 worst fit and using edge proportion option. The minimum score to consider an area as an area of endemism is 2.0, because this score indicates that 2 taxa coincide in their distributional areas (each taxa with an endemic index of 1.0). Sets in conflict with other sets of higher score were retained if $\geq 50\%$ of the scoring species were exclusive (Szumik and Goloboff 2004). Consensus areas were obtained using 30% similarity of species, against any of the other areas in the consensus; that is, 2 or more areas are combined if they share $\geq 30\%$ of their taxa. We obtained the number of endemic taxa for each matrix and their consensus areas of endemism.

Results

Each matrix showed different numbers of endemic taxa and areas of endemism. These results were plotted and mapped to choose the best area to represent the Nearctic region. Numbers of nonendemic and endemic taxa relative to the total number of taxa for each matrix were determined. The highest proportion of endemics was found in the matrix of families, genera, and species (Fig. 1). Areas of endemism had scores between 2.0 and 62.68 (Table 1); lower scores and lower numbers of areas of endemism and consensus areas were obtained for families, and higher values were obtained in the matrix of 3 taxonomic levels.

Families.—We identified 4 general patterns, none of them representing the boundaries of the Nearctic region. Those areas represent a restricted Neotropical, a transitional Neotropical, a wide Neotropical, and a cosmopolitan pattern.

Genera.—Nine general patterns resulted from this analysis, some of them almost representing the Nearctic region (score = 2.41–2.83), but mostly defining the Neotropical region. One area of endemism includes the United States and Canada, excluding the northern part of the Eskimoan province of Dice (1943). Two areas in the western United States and the others are different variations of the Neotropical region (restricted, wide, with or without Florida, etc.).

Species.—We recovered an area of endemism that is almost equivalent to the Nearctic region (score = 2.76–3.76) and is similar to the area obtained with genera (excluding the

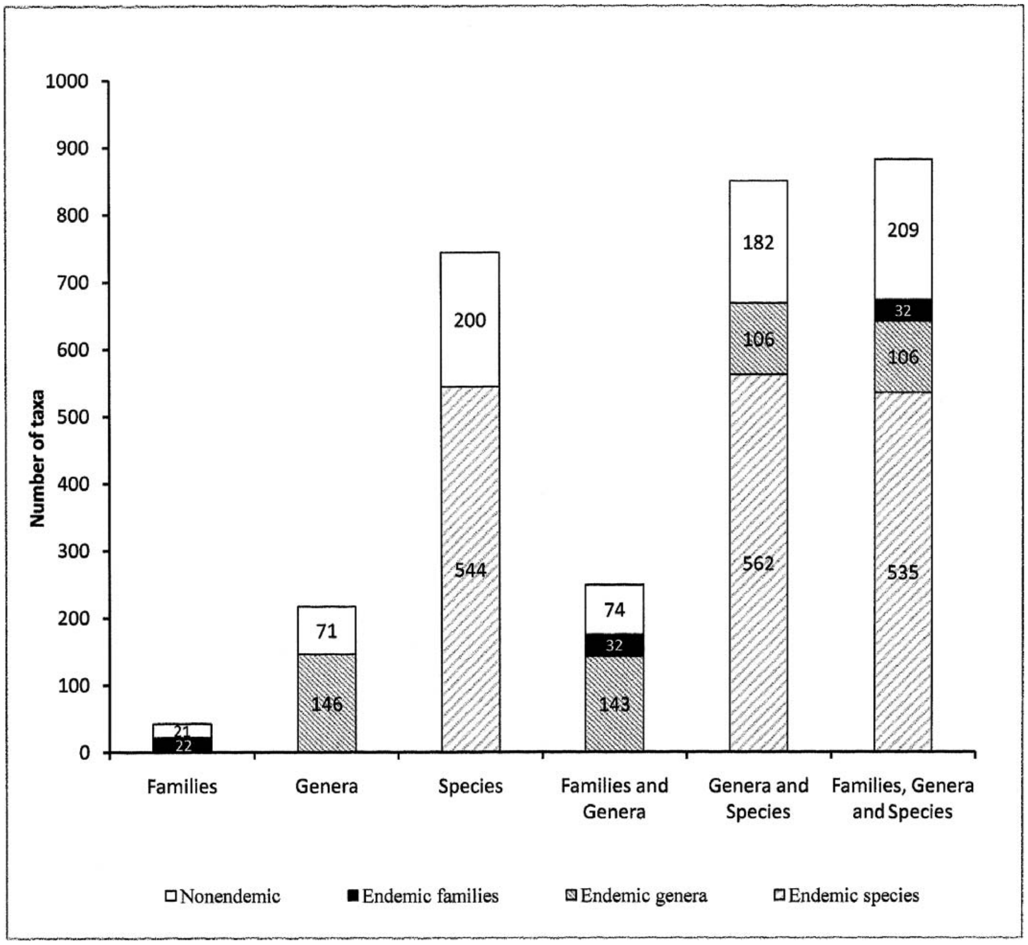

Fig. 1.—Comparison between the number of nonendemic and endemic taxa among the total number of taxa for 6 matrices.

northern islands of Canada). Another interesting pattern found is an area of endemism in northern Canada and Alaska (score = 2.71–2.96). Several small areas of endemism exist in North America, some of them including parts of Mexico and the United States, and a pattern of disjunction between western and eastern North America is evident. Additionally, we found a transitional area in Mexico that has been recognized by several authors (see Morrone 2005).

Families and genera.—We found 3 consensus areas with a pattern similar to the genera matrix for the Nearctic region (score = 2.54–2.79). We recovered the western pattern only in 3 consensus areas, 1 of them including areas of Alaska. All the remaining areas belong to the Neotropical region (9 consensus areas) and 1 to a cosmopolitan area.

Table 1.—Description of areas of endemism and consensus areas for the 6 spatial matrices generated from NDM software (www.zmuc.dk/public/phylogeny). The minimum and maximum scores represent the range of scores for all areas of endemism obtained for a taxonomic level.

Matrices	No. areas of endemism	No. consensus areas	Minimum–maximum scores
Families	8	4	2.50–4.78
Genera	95	12	2.00–30.37
Species	249	31	2.00–55.25
Families and genera	97	16	2.00–32.95
Genera and species	415	37	2.01–60.10
Families, genera, and species	519	43	2.01–62.68

Genera and species.—Three consensus areas represent the Nearctic region, with a score slightly higher (score = 4.48–4.73) than in previous analyses. The disjunct western–eastern patterns were more evident in this analysis, with 11 areas for the western pattern and 4 for the eastern pattern (scores = 5.11–5.59 and 8.39–8.70, respectively). We also found the transitional zone occupying almost all of Mexico, similar to the Mexican Transition Zone of Escalante et al. (2007b).

Families, genera, and species.—In this analysis we recovered most of the Nearctic region, with the exception of the northern islands of Canada, with a score of 4.43–4.68. We found all previous patterns, including the western and eastern patterns (scores = 4.82–5.20 and 8.47–8.72, respectively), a northern pattern (score = 2.71–2.96), the Neotropical region, the transitional zone, and very small areas.

Discussion

The Nearctic region could not be recovered from the matrix of families although only 2 families are restricted to this

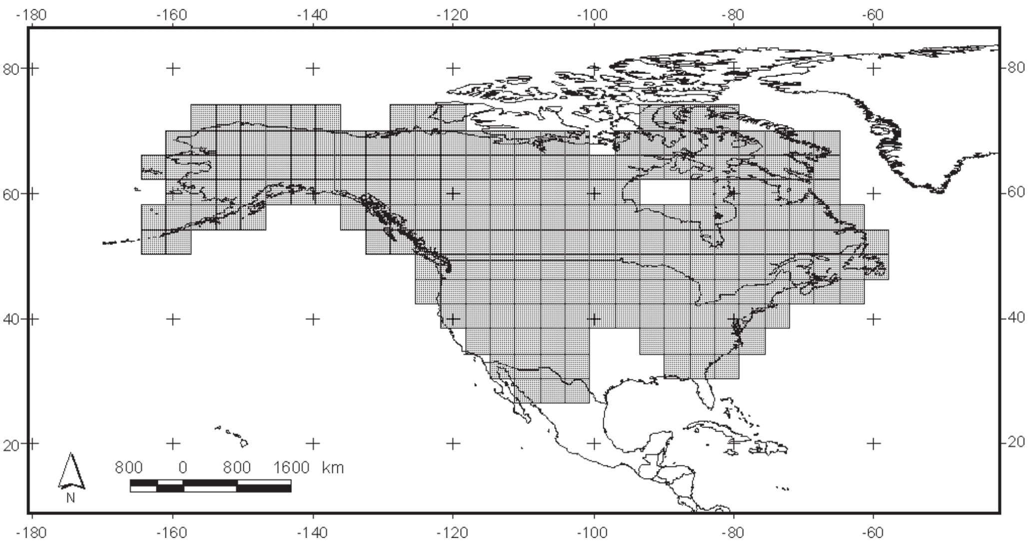

FIG. 2.—Area of endemism corresponding to the Nearctic region (consensus area 1).

region, Aplodontiidae and Antilocapridae (Vaughan et al. 2000). Neither of these families was identified as part of an area of endemism because they are not sympatric. Sclater (1897) pointed out that the Nearctic region does not have enough distinctive and indigenous forms to recognize it separately from the Palearctic region, and it contains fewer total genera and species than other regions. For example, the Nearctic region (sensu Sclater 1858) has only 660 ''peculiar'' species of birds, whereas the Neotropical region has 2,250. Moreover, Cabrera and Willink (1973) considered that the Holarctic region, including the Nearctic of North America, is characterized by a rather poor fauna compared to others. When we analyzed all taxonomic levels, we found that the Nearctic region was better delimited. Regarding the matrix of families, genera, and species combined, we found the highest score for the consensus area that best resembles the Nearctic region (consensus area 1; Fig. 2). All of Canada, Alaska, the United States, and northern Mexico, plus the northern part of the Mexican Plateau and Sierra Madre Occidental, are included; the Baja California Peninsula, Texas, Louisiana, Oklahoma, Arkansas, and Florida are excluded. The Nearctic region was identified by 2 genera (*Myodes* and *Tamiasciurus*) and 5 species (*Sorex cinereus*, *Lepus americanus*, *Tamiasciurus hudsonicus*, *Microtus pennsylvanicus*, and *Erethizon dorsatum*). Another area defining this region is the consensus area 0, with Dipodidae, *Marmota*, *Martes* (although these 3 taxa are also Palearctic), *Zapus*, *Sorex palustris*, and *Martes americana*. We hypothesize that our results are due to species sharing their distributional areas with those of other taxonomic levels (families or genera) belonging to unrelated taxa, which may correspond to different cenocrons (sets of taxa sharing the same biogeographic story—Morrone 2009).

The western pattern (consensus area 10; Fig. 3) includes British Columbia, Alberta, and Saskatchewan (Canada), from the western coast to 100° longitude in the United States, and the Alto Delta on Mexico. It does not coincide with any dominion identified by previous authors, except with the meridional limit between the ecological dominions of Bailey (1998). The endemic species that define this area are *Sorex merriami*, *Ochotona princeps*, *Brachylagus idahoensis*, *Sylvilagus nuttallii*, *Marmota flaviventris*, *Spermophilus columbianus*, *Spermophilus elegans*, *Spermophilus lateralis*, *Tamias amoenus*, *Tamias ruficaudus*, *Perognathus parvus*, *Thomomys talpoides*, *Thomomys townsendii*, *Lemmiscus curtatus*, *Microtus montanus*, and *Microtus richardsoni*.

The eastern pattern (consensus area 22; Fig. 4) extends from 100° longitude in United States to the eastern coast, except for the northern states (Minnesota, Wisconsin, Michigan, New York, Vermont, Rhode Island, Maine, and New Hampshire). In Mexico it includes part of the Mexican Plateau, Tamaulipas, and the northern part of the Mexican Gulf biogeographic province, and it is not completely included within the Nearctic pattern (consensus areas 0 and 1). This pattern is similar to the Allechamy dominion of Wallace (1876) and the eastern portion of the humid temperate domain, coinciding also with the south-central Nearctic region of Abbott and Stewart (1998). The endemic species are *Blarina carolinensis*, *Sorex longirostris*, *Lasiurus seminolus*, *Nycticeius humeralis*, *Corynorhinus rafinesquii*, *Myotis austroriparius*, *Myotis sodalis*, *Sylvilagus aquaticus*, *Microtus pinetorum*, *Ochrotomys nuttalli*, *Peromyscus gossypinus*, *Reithrodontomys humulis*, *Oryzomys palustris*, and *Canis lupus rufus*.

Some authors previously recognized a similar boundary at 100–110° longitude (Dice 1943; Hagmeier 1966; Wallace 1876) between different biogeographic entities (subregions, superprovinces, or provinces); other taxa should be considered to refine this boundary.

The northern pattern (consensus area 37; Fig. 5) includes all of Canada, from 54° to 78° latitude, and all of Alaska. It is similar to the Canadian dominion of Wallace (1876), the Boreal life zone of Merriam (1892), and the Circumboreal

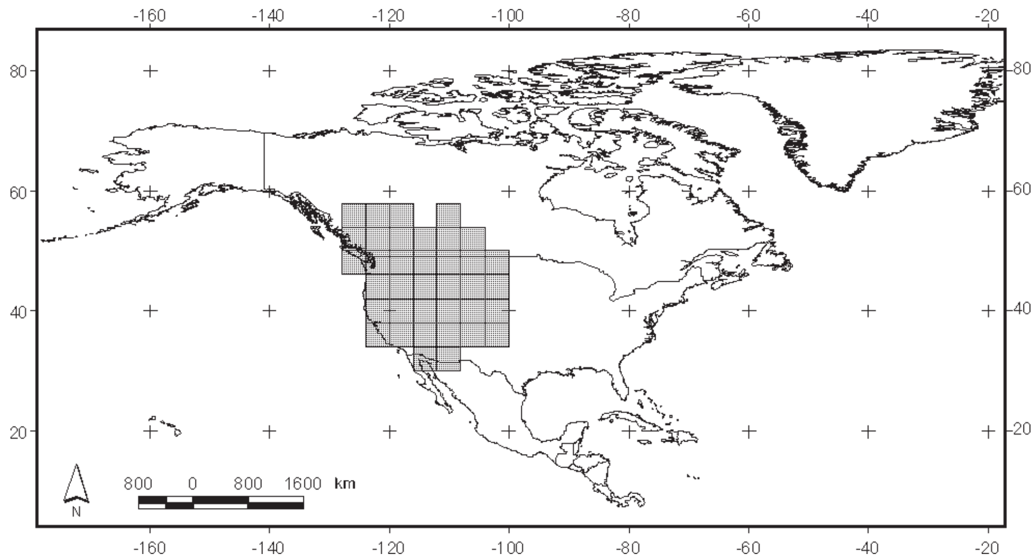

Fig. 3.—Western pattern (consensus area 10).

region of Takhtajan (1986). It has 3 endemic species, *Spermophilus parryii*, *Myodes rutilus*, and *Lemmus sibiricus*.

The Nearctic region has been delimited and regionalized in several forms. Without delimiting a precise southern boundary, some authors regionalized North America without considering Mexico (Dice 1943; Hagmeier 1966; Hagmeier and Stults 1964) or the United States (Cabrera and Willink 1973, Morrone 2001a). For other authors the boundary might be in central, southern, or northern Mexico (Fig. 6). Sclater (1858), Wallace (1876), Merriam (1892), Smith (1941), Schmidt (1954), Takhtajan (1986), and Ortega and Arita (1998) drew the boundary in middle Mexico, avoiding both coasts. Takhtajan (1986) recognized a Madrean region that extends from southeastern Oregon and the Snake River Plains of Idaho to the Sierra Madre del Sur, but excludes the Balsas Basin. Moreover, his North American Atlantic region excludes the southernmost tropical part of the Florida Peninsula. The boundary recognized by Udvardy (1975) is the most extreme because he considers the Nearctic region to reach Honduras and Nicaragua in Central America.

Following some authors, Cabrera and Willink (1973) delimited the Holarctic region in America northward starting from 30° latitude in Baja California Peninsula. This boundary is similar to boundaries of our consensus area 0, which begins at 30° latitude, although our consensus area 1 begins at 26° (Fig. 6), and consensus area 22 begins at 22°. Morrone (2006) did not recognize a boundary but delimited a Transition Zone encompassing most of central Mexico. This Mexican Transition Zone includes part of the Nearctic region, but only 5 provinces of Mexico (Fig. 6) can be considered strictly Nearctic. Our analyses suggest that the Nearctic region includes all of North America, although some northern islands are not included. The southern boundary occurs in northern Mexico, considered part of the Nearctic in the following provinces recognized by Morrone (2001a): the northern Mexican Plateau, northern Sierra Madre Occidental, Sonora,

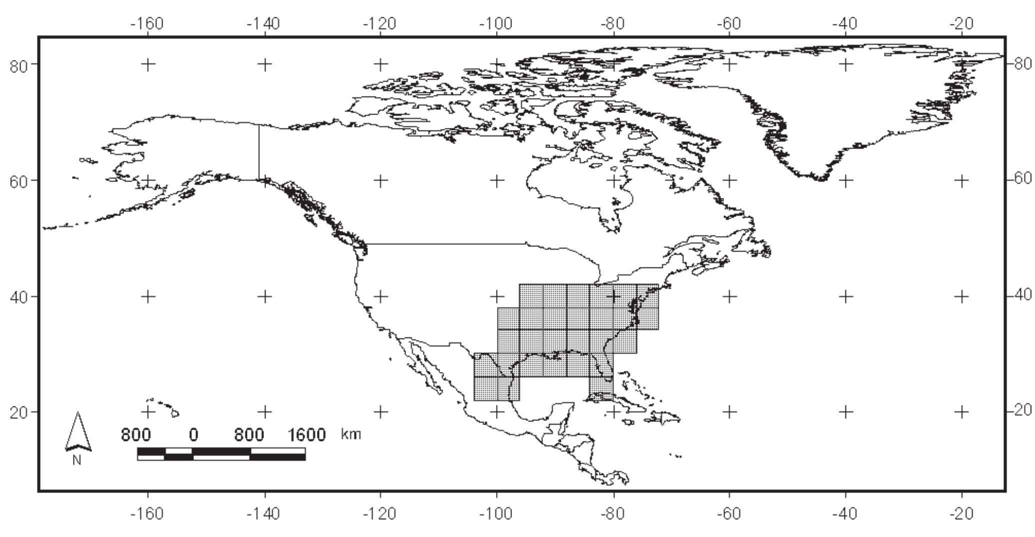

Fig. 4.—Eastern pattern (consensus area 22).

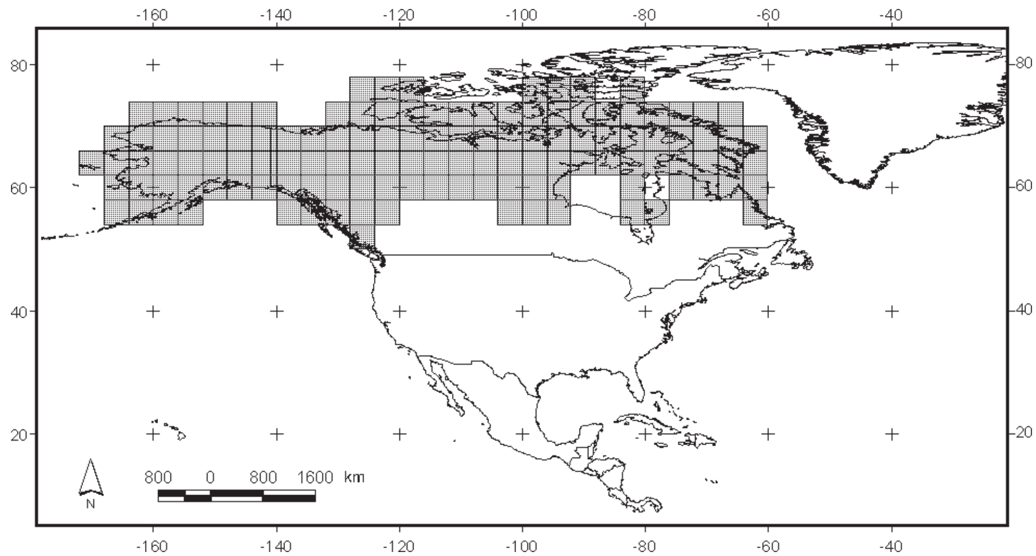

Fig. 5.—Northern pattern (consensus area 37).

and part of California and Tamaulipas provinces. Eastern Texas and Florida are excluded.

A final consideration should be made with respect to the scale of our analyses. Our grid cells could be too big to find more refined patterns, such as the Baja California Peninsula and Florida. Baja California is included in some grid cells joining it to the continent, whereas grid cells of Florida can include part of the Antilles. The use of smaller grid cells (e.g., 2° latitude–longitude) might allow us to discover and delimit better these areas of endemism.

In conclusion, the Nearctic region can be delimited according to the distributional patterns of mammals using total evidence for different taxonomic levels (families, genera, and species). This region has its southern boundaries in northern Mexico up to the Mexican Plateau and can be divided into 3 general patterns, western, eastern, and northern, that may correspond to the dominion level in the biogeographical hierarchy. Postulating that the Nearctic region corresponds to an area of endemism constitutes a hypothesis of primary biogeographic homology (Morrone 2009), which suggests a common biogeographic history; that is, that all taxa are integrated spatiotemporally in a biotic component. Although the North American craton (Laurentia), which is almost equivalent to North America, had an isolated evolution for an

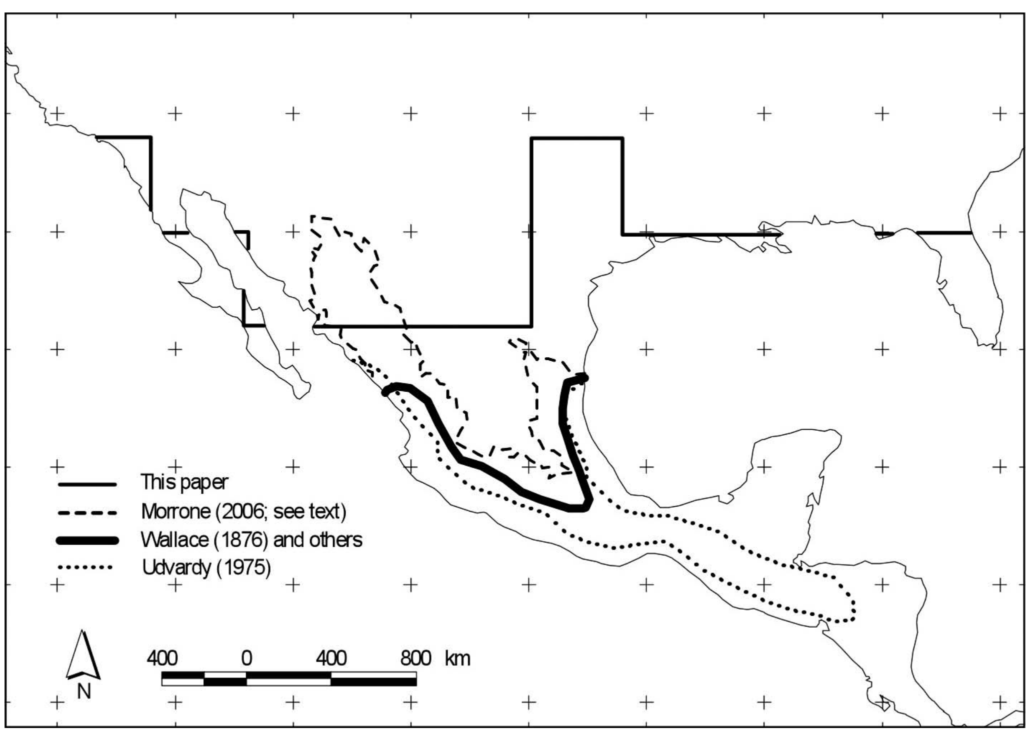

Fig. 6.—Different southern boundaries of the Nearctic region, including ours (consensus areas 0 and 1).

extended period of time (Sloss 1988), generating a particular biota, recent biotic interchanges have modified the original biota (Vermeij 1991). Nevertheless, it is possible to diagnose it as an area of endemism separately from other areas. Although mammals seem to be an appropriate group to test the potential validity of areas of endemism, only partial agreement is reached with regionalizations based on other taxa. Additional detailed studies based on other plant and animal taxa, and at even smaller geographic scales, are needed.

Resumen

La región Neártica ha sido reconocida como una región biogeográfica desde el siglo XIX. En este trabajo, analizamos los patrones de distribución de los mamíferos que habitan América del Norte y Central, desde Alaska hasta Panamá, con el fin de delimitar los límites de la región Neártica. Realizamos 6 análisis de optimización, usando una cuadrícula de 4° de latitud–longitud, basada en familias, géneros y especies, y en combinaciones de éstos. El análisis de la matriz con los 3 niveles taxonómicos dio mejores resultados en términos del mayor número de taxones endémicos y la mejor delimitación de la región Neártica. También encontramos tres patrones—oeste, este y norte—dentro de la región, los cuales coinciden parcialmente con caracterizaciones biogeográficas anteriores. Aunque los mamíferos parecen representar taxones apropiados para delimitar esta región, concluimos que una delimitación más robusta podría obtenerse analizando otros taxones de plantas y animales.

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