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Phylogenetic measures applied to the conservation of Mexican marsupials

Medidas filogenéticas aplicadas para la conservación de los marsupiales mexicanos

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Abstract. The didelphimorphs in Mexico are found all over the country except for the Baja California Peninsula. The aim of this study was to use 3 methods to assess the phylogenetic diversity of the species *Marmosa mexicana, Tlacuatzin canescens, Caluromys derbianus, Chironectes minimus, Didelphis marsupialis, Didelphis virginiana, Metachirus nudicaudatus*, and *Philander opossum*, and to determine the potential conservation areas for these mammals. Phylogenetic information was included to measure the taxonomic weighting, taxonomic dispersion, and taxonomic distinctness within the Mexican biogeographic provinces. In addition, a gap analysis was performed to show which protected areas contain the didelphimorphs listed under a conservation category. Considering phylogenetic diversity with the former analysis, results indicate that the biogeographic provinces most important for conservation of didelphimorphs are the Gulf of Mexico, the Pacific Coast, and Oaxaca, although Soconusco and Sierra Madre del Sur also have to be considered. We also observed that not all of the richest sites corresponded with current protected areas. This study is important because it employed different conservation approaches based on phylogenetic measures and was focused on Mexican marsupials, of which 1 species is endemic and 2 are of conservation concern.

Key words: didelphimorphs, gap analysis, phylogenetic diversity, taxonomic dispersion, taxonomic distinctness, taxonomic weight.

Resumen. El orden Didelphimorphia se encuentra distribuido en todo México excepto en la península de Baja California. En este trabajo se evaluó la diversidad filogenética para las especies *Marmosa mexicana, Tlacuatzin canescens, Caluromys derbianus, Chironectes minimus, Didelphis marsupialis, Didelphis virginiana, Metachirus nudicaudatus* y *Philander opossum,* y se determinaron las áreas potenciales de conservación para estos organismos. Para realizar los análisis de peso taxonómico, dispersión taxonómica y diferenciación taxonómica se incluyó información filogenética. También se realizó un análisis de vacíos y omisiones (gap analysis) para evaluar si las áreas protegidas contienen a los didelfimorfos bajo alguna categoría de protección. Al combinar los resultados de todos los análisis se concluyó que las provincias biogeográficas más importantes en la conservación de los marsupiales son la del Golfo de México, Costa del Pacífico y Oaxaca, pero también son importantes Soconusco y la Sierra Madre del Sur. Se identificaron sitios de gran riqueza específica que no corresponden con la ubicación de áreas naturales protegidas. Por último este estudio es importante por emplear diferentes medidas filogenéticas que pueden ser usadas en conservación de los marsupiales mexicanos, de los cuales dos especies se encuentran bajo alguna categoría de conservación y una es endémica.

Palabras clave: didelfimorfos, análisis de vacíos, diversidad filogenética, dispersión taxonómica, diferenciación taxonómica, peso taxonómico.

Introduction

Over the last 30 years, conservation biology has improved the quality of information used in diversity studies. When the species is considered the unit of analysis, results can provide important information on conservation decision-making if they include phylogenetic diversity and complementarity (Eguiarte et al., 1999). Traditionally, species richness in areas was analyzed giving the same value to all the taxa. In recent times, distinct taxa have different conservation priorities when threatened; also, different conservation values are given to species when they are not part of the same phylogenetic group (Atkinson, 1989).

Didelphimorphs are American marsupials distributed along the entire American Continent. They are an ancient group present since the Cretaceous. South America has a vast number of endemic species and the highest diversity.

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In Mexico, marsupials are distributed throughout the country except Baja California Peninsula, but their highest richness and diversity is in the southern part of the country (Ceballos y Oliva, 2005). Species under protection are *Caluromys derbianus* and *Metachirus nudicaudatus* listed as threatened, and *Chironectes minimus* listed as in danger of extinction (SEMARNAT, 2010).

Conserving American marsupials is important from an evolutionary, biogeographical, ecological, and morphological point of view due to the features kept from the Australasian radiations. Different methods used to analyze taxonomic distinctness depend on spatial and taxonomic scale and the quality of data. It is important to consider that to make the best conservation decisions, priority of areas is not based only on possession of a high number of species, but also on the evolutionary history of the species (Eguiarte et al., 1999; Martin-Piera, 1999). In contrast, the method of gap analysis compares places with high biological richness with protected areas to propose new places for conservation (Scott et al., 1987; Bojórquez and Flores-Villela, 1991). The aim of this work was to determine which of the Mexican biogeographic provinces (*sensu* Arriaga et al., 1997) have the highest phylogenetic diversity of didelphimorph mammals and which of these provinces are most relevant for conservation considering different approaches. We used the taxonomic weight measure by Vane-Wright et al. (1991), the taxonomic dispersion measure proposed by Williams et al. (1991), and the taxonomic distinctness measure of Warwick and Clarke (1995). Then we used gap analysis to identify which protected areas include the highest richness of didelphimorphs, to verify whether the species are protected in any of these areas, and to identify places that should be protected.

Materials and methods

Data. A phylogenetic analysis was performed with PAUP* 4.0 b10 (Swofford, 1999). For maximum-parsimony analysis, all the characters were equally weighted based on the phylogenetic relationships inferred by Voss and Jansa (2003). Heuristic searches were performed with 1 000 random additions of taxa and a tree-bisection reconnection (TBR) algorithm was used for the branch swapping with nodal support assessed by 1 000 bootstrap replicates. *Caluromys derbianus* was added to the data matrix and the codification of characters was based on previous published descriptions (Voss and Jansa, 2003; Bucher and Hoffman, 1980).

The data matrix of 45 taxa and 71 morphological-karyological characters (Voss and Jansa, 2003; Bucher and Hoffman, 1980) is shown in Appendix. The cladogram obtained was the result of a bootstrap analysis, which was used for the taxonomic weight method.

Taxonomic dispersion, taxonomic distinctness, and gap analysis were performed based on georreferenced data from 5 electronic databases of zoological collections for the 8 species of didelphimorphs present in Mexico: *Marmosa mexicana* Merriam, 1897; *Tlacuatzin canescens* Allen, 1893, Voss and Jansa, 2003; *Caluromys derbianus* Waterhouse, 1841; *Chironectes minimus* Zimmerman, 1780; *Didelphis marsupialis* Linnaeus, 1758; *Didelphis virginiana* Kerr, 1792; *Metachirus nudicaudatus* Desmarest, 1817; and *Philander opossum* Linnaeus, 1758. Data were retrieved from SNIB (Sistema Nacional de Información sobre Biodiversidad) of CONABIO, AMNH (American Museum of Natural History), MaNis (Mammal Network Information System), GBIF (Global Biodiversity Information), and REMIB (Red Mundial de Información sobre Biodiversidad). The final data set included 1 828 records taxonomically validated by experts from each database and a georeferenced site or locality where the organism was collected. Species collection records were assigned to 16 of the19 biogeographic provinces of Mexico (Fig. 1) defined by Arriaga et al. (1997); the remaining 3 correspond to California, Baja California, and el Cabo provinces, where didelphimorphs are absent.

Phylogenetic methods. a) Taxonomic weight and complementarity. Proposed by Vane-Wright et al. (1991), the taxonomic weight and complementarity method identifies diversity critical points. Like the taxonomic dispersion method (below), it takes into account phylogenetic and biogeographic information. This method does not consider whether species are plesiomorphic or apomorphic before the analysis is performed (Vane-Wright et al., 1991), but it considers monophyletic groups within taxa. The difference between taxonomic weight and taxonomic dispersion is that the former includes the taxonomic weight for each species and uses complementarity to detect and propose possible protected areas. Complementarity identifies the minimum number of protected areas needed to ensure the maximum number of species (Williams, 2001).

The analysis of taxonomic weight included the 45 species of didelphimorphs in order to avoid sampling error from including only the Mexican species. In this work we only presented the results for Mexican opossums. We used 4 taxonomic measures (I), (Q), (W), and (P), to evaluate the information on the cladogram. The first index (I) corresponds to the number of monophyletic groups to which each species belongs; this value reflects the number of nodes from the root of the tree to the node subtending the terminal taxon. The basal phylogenetic weight (Q) is

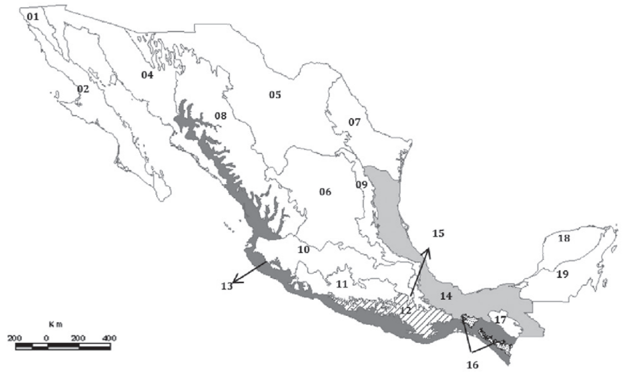


Figure 1. Mexican Biogeographic Provinces by Arriaga et al. (1997) and provinces with maximum taxonomic dispersion. 01 California (clf); 02 Baja California (bc); 03 del Cabo (cab); 04 Sonora (son); 05 Altiplano Norte (apn); 06 Altiplano Sur (aps); 07 Tamaulipeca (tam); 08 Sierra Madre Occidental (smo); 09 Sierra Madre Oriental (sme); 10 Eje Volcánico (vol); 11 Depresión del Balsas (bal); 12 Sierra Madre del Sur (sms); 13 Costa del Pacífico (pac); 14 Golfo de México (gm); 15 Oaxaca (oax); 16 Soconusco (scn); 17 Los Altos de Chiapas (chi); 18 Yucatán (yuc); and 19 Petén (ptn). The provinces with maximum taxonomic dispersion are represented in background pattern. The Pacific Coast shown in dark gray and Gulf of Mexico in light gray have the maximum taxonomic dispersion, containing all the species of didelphimorphs (8 species). The Soconusco province represented with dots and Sierra Madre del Sur with lines, follow in importance because both include at least 1 species from each node in the phylogeny of the Mexican didelphimorphs (7 species).

the sum of I divided by the smallest value of I. The number of taxa that contribute to the total diversity of the group (W), is the total sum of Q divided by the minimum value of Q. The measure (P) is the percentage of the W value for each taxon, and is the result of the multiplication of each value of W times one hundred and divided by the total of W (Vane-Wright et al., 1991). The taxonomic singularity percentage (P%) was calculated to identify areas of highest priority in didelphimorphs conservation. Areas with 100 (P%) were the best option for conservation, but also the sets of areas that summed to 100.

Once the value of W was obtained, the distributions of the didelphimorphs in the biogeographic provinces and the phylogenetic information were included to prioritize using complementarity.

b) Taxonomic dispersion (Williams et al., 1991). We constructed a data matrix of taxa *vs.* biogeographical provinces (8x16) and coded the presence or absence of taxa to identify areas with the highest number of taxa in regard to the phylogeny of didelphimorphs (Voss and Jansa, 2003; modified by Medina-Romero, 2007). Those areas that include all taxa possess the maximum dispersion. Areas of interest are those with the highest representation of species in the subclades when it is not possible to protect all species (Williams et al., 1991).

c) Taxonomic distinctness. Warwick and Clarke (1995) proposed this method to synthesize the path of relationships in a sample. They described the mean taxonomic distance between 2 organisms selected randomly in the phylogeny or in the Linnaean taxonomy for the entire species community. This method avoids the requirement of having resolved phylogenies, which are unknown for many taxonomic groups, but it is essential to have a Linnaean classification that reflects the different relationships of similarity between species (Clarke and Warwick, 1998a, b, 2001; Warwick and Clarke, 1995, 1998). We only used the average taxonomic distinctnes proposed by Warwick and Clarke (1995), because the order Didelphimorphia comprises 8 species in Mexico and no other taxa were included to strengthen the analysis.

To obtain this value, 2 matrices with the taxonomic classification of didelphimorphs were prepared in Excel. The first matrix included different Linnaean categories (species, genus, family, order, superorder, subclass, and class); the second matrix was scored for presence or absence of taxa for each of the biogeographic provinces. Fourteen provinces were included under the criteria of having 3 or more taxa in each one. The provinces of Sonora (son) and the Altiplano del Norte (apn) were not included because they contained only 2 and 1 species, respectively. The average taxonomic distinctness values and a funnel graph were obtained with the program Primer 5 (PRIMER-E, 2001; Clarke and Warwick, 2001).

d) Gap analysis. Gap analysis is a cartographic technique proposed by Scott et al. (1987) to compare areas with high species richness and location of protected areas (Miller, 1994). There are 163 protected areas in Mexico (CONANP, 2007); the map used for the analysis included only 35 areas where the highest species richness for didelphimorphs was found based on results from taxonomic dispersion, taxonomic weight, and taxonomic distinctness (Fig. 2).

Results

We obtained a total of 100 trees and one strict consensus cladogram for the order Didelphimorphia (Fig. 3).The resulting values for the most parsimonious trees were length= 189 steps, consistency index= 0.481 and retention index= 0.830. The hypothesis shown was strongly supported by the bootstrap analysis.

a) Taxonomic weight and complementarity. The analysis of taxonomic weight showed *C. derbianus, T. canescens*, *M. mexicana,* and *M. nudicaudatus* as the most plesiomorphic taxa with the highest taxonomic weight of 3.00 (Fig. 3), followed by *C. minimus* with a value of 2.00, *D. marsupialis*

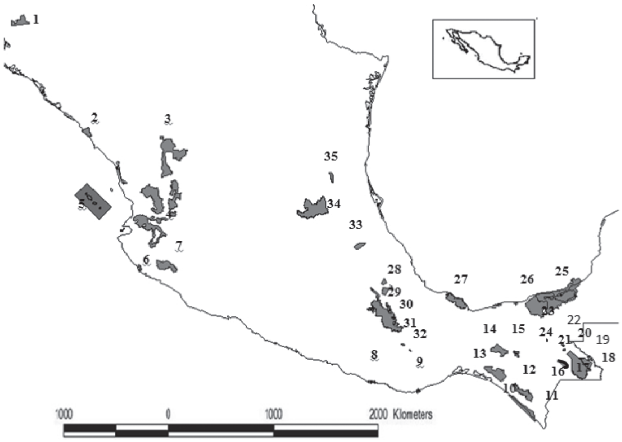


Figure 2. Protected areas used for gap analysis. (1) Sierra de Álamo, (2) Meseta de Cacaxtla, (3) La Michilia, (4) Cuenca Alimentadora del Distrito de Riego 043 del Estado de Nayarit, (5) Islas Marías, (6) Chamela-Cuixmala, (7) Sierra de Manantlán, (8) Lagunas de Chacahua, (9) Huatulco, (10) La Encrucijada, (11) volcán Tacana, (12) El Triunfo, (13) La Sepultura, (14) Selva El Ocote, (15) Cañón El Sumidero, (16) Lagunas de Montebello, (17) Montes Azules, (18) Lacan-Tun, (19) Chan-Kin, (20) Bonampak, (21) Naha, (22) Metzabok, (23) Palenque, (24) Cascada de Agua Azul, (25) Laguna de Terminos, (26) Pantanos de Centla, (27) Los Tuxtlas, (28) Pico de Orizaba, (29) Cañón de Río Blanco, (30) Tehuacan-Cuicatlán, (31) Benito Juárez, (32) Yagul, (33) Cuenca Hidrográfica del Río Necaxa, (34) Sierra Gorda, (35) Sierra del Abra-Tanchipa.

and *Philander opossum* with a value of 1.20, and the lowest taxonomic weight was for *D. virginiana* with a value of 1.00. Based on the taxonomic singularity percentage, the provinces with the highest priority were the Gulf of Mexico (gm) and the Pacific Coast (pac) with 100% of phylogenetic information (20.40), followed by Soconusco (scn) and the Sierra Madre del Sur (sms) with 85.3%. The percentages of phylogenetic information for each biogeographic province are shown in Fig. 4. The taxonomic weight index is used along with complementarity to prioritize crucial areas for conservation. Applying this, the counterpart area for the Sierra Madre del Sur (sms) province is Soconusco (scn); the former province preserves all taxa except *Metachirus nudicaudatus* with 85.3% of phylogenetic information, but this species is included in the latter province with 14.7%. In other words, these 2 provinces include all 8 species of didelphimorphs in Mexico. Another possible complementarity hypothesis is the province of Soconusco with 85.3% of phylogenetic information, which is complemented by the 14.7% of Chiapas province.

b) Taxonomic dispersion. The Gulf of Mexico (gm) and Pacific Coast (pac) provinces had the highest taxonomic dispersion (Wtotal= 20.40 equivalent to 100%; Fig. 4). All species of didelphimorphs occur in both areas (Fig. 1). Assuming that it is not always possible to protect all species, the area with the highest taxonomic dispersion is the Soconusco province (scn; Fig. 4), because it includes at least 1 species from each node in the phylogeny of the didelphimorphs and 7 of the 8 species distributed in Mexico (*C. derbianus, C. minimus, D. marsupialis, D. virginiana, P. opossum, M. nudicaudatus*, and *M. mexicana*). Another important province is the Sierra Madre del Sur (sms), because it includes the same species as Soconusco except the narrow endemic, *T. canescens*, and it also includes *M. nudicaudatus* (Fig. 1); that is why it is preferred over the rest of the biogeographic provinces.

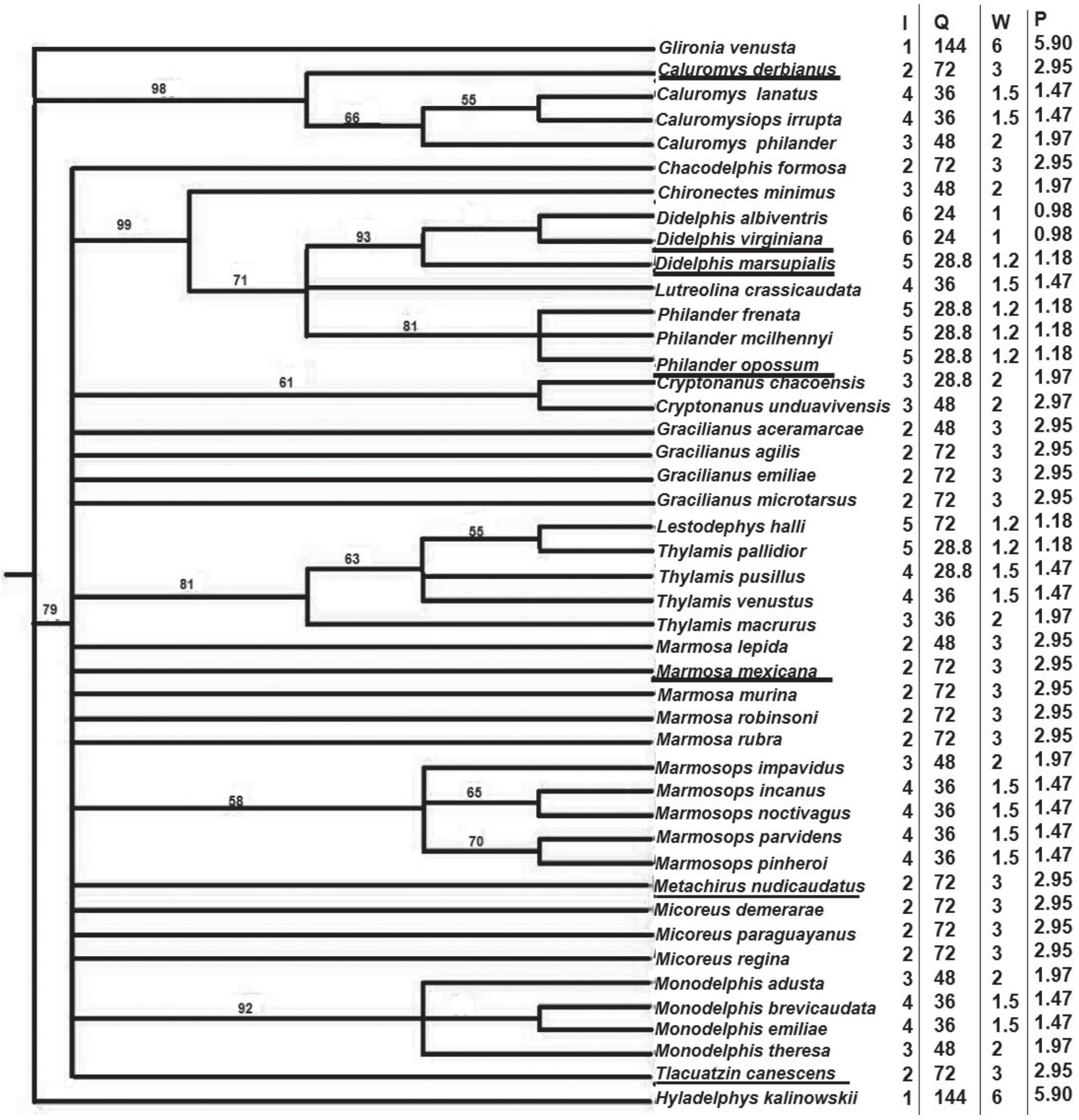
c) Taxonomic distinctness. The area with the highest taxonomic distinctness was the Oaxaca (oax) province with a value of 38.1. This province includes *C. derbianus* and *T. canescens* (endemic to Mexico), but 2 species are absent, *M. nudicaudatus* and *C. minimus,* both listed as protected (SEMARNAT, 2010). The provinces of Sonora (son) and the Altiplano del Norte (apn) were not included because they contained only 2 and 1 species, respectively.

d) Gap analysis. A total of 35 protected areas were identified within the biogeographic provinces of Pacific Coast, Gulf of Mexico, Soconusco, Sierra Madre del Sur, and Oaxaca (Table 1). The gap analysis comparing the species' shared in the protected areas (Table 2) indicates that Palenque has 5 species, and Los Tuxtlas and Cañón del Río Blanco 4 species each (Fig. 6). None of the protected areas contained all species of marsupials. Palenque had the highest number of didelphimorph species. Moreover, it included *C. minimus* and *C. derbianus*, which are listed as "protected" and "threatened" respectively (SEMARNAT, 2010).

Discussion

The application of biogeographic methods for conservation has led to a different perspective for making better proposals in this topic (Whittaker et al., 2005). Under this assumption we used different biogeographic methods to analyze and to assess priorities in conservation status for the didelphimorphs species in the natural protected areas of Mexico by combining taxonomic distinctness, taxonomic weight, taxonomic dispersion, complementarity, and gap analysis, although we are aware that there are other biogeographic and ecological methods available.

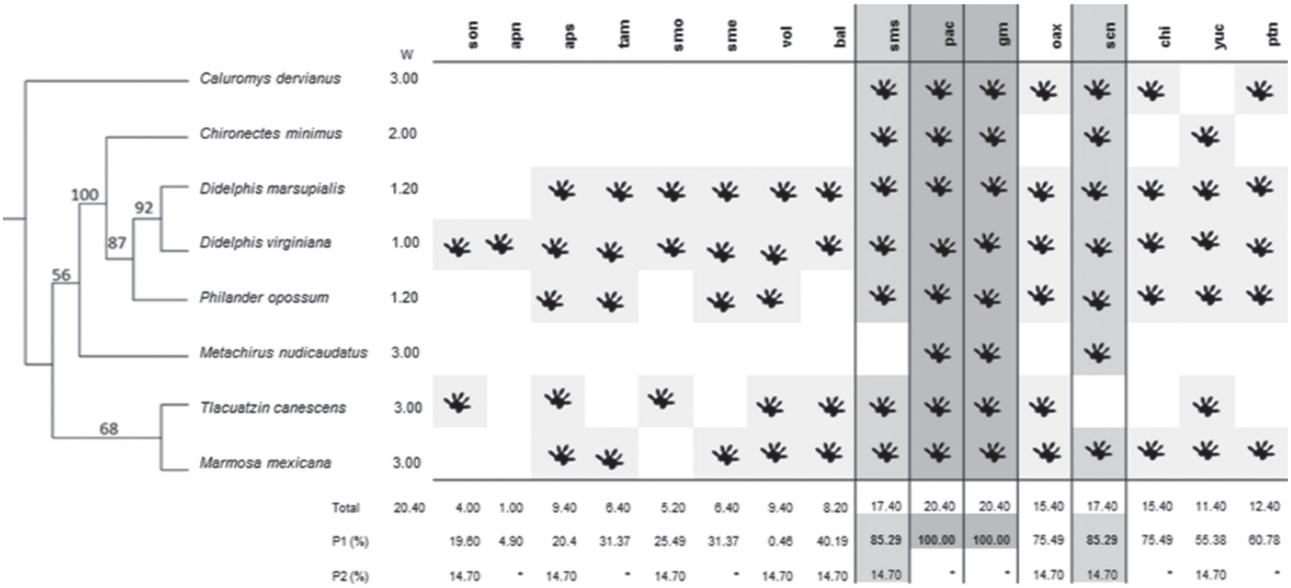
Previous studies on Mexican marsupials using taxonomic dispersion were not found even though this method integrates distribution and taxonomic relationships of didelphimorphs to establish possible areas for conservation. Taxonomic dispersion and taxonomic weight gave us similar results and indicate that the southern portions of the Gulf of Mexico and



	I	Q	W	P
Glironia venusta	1	144	6	5.90
Caluromys derbianus	2	72	3	2.95
Caluromys lanatus	4	36	1.5	1.47
Caluromysiops irrupta	4	36	1.5	1.47
Caluromys philander	3	48	2	1.97
Chacodelphis formosa	2	72	3	2.95
Chironectes minimus	3	48	2	1.97
Didelphis albiventris	6	24	1	0.98
Didelphis virginiana	6	24	1	0.98
Didelphis marsupialis	5	28.8	1.2	1.18
Lutreolina crassicaudata	4	36	1.5	1.47
Philander frenata	5	28.8	1.2	1.18
Philander mcilhennyi	5	28.8	1.2	1.18
Philander opossum	5	28.8	1.2	1.18
Cryptonanus chacoensis	3	28.8	2	1.97
Cryptonanus unduavivensis	3	48	2	2.97
Gracilianus aceramarcae	2	48	3	2.95
Gracilianus agilis	2	72	3	2.95
Gracilianus emiliae	2	72	3	2.95
Gracilianus microtarsus	2	72	3	2.95
Lestodephys halli	5	72	1.2	1.18
Thylamis pallidior	5	28.8	1.2	1.18
Thylamis pusillus	4	28.8	1.5	1.47
Thylamis venustus	4	36	1.5	1.47
Thylamis macrurus	3	36	2	1.97
Marmosa lepida	2	48	3	2.95
Marmosa mexicana	2	72	3	2.95
Marmosa murina	2	72	3	2.95
Marmosa robinsoni	2	72	3	2.95
Marmosa rubra	2	72	3	2.95
Marmosops impavidus	3	48	2	1.97
Marmosops incanus	4	36	1.5	1.47
Marmosops noctivagus	4	36	1.5	1.47
Marmosops parvidens	4	36	1.5	1.47
Marmosops pinheroi	4	36	1.5	1.47
Metachirus nudicaudatus	2	72	3	2.95
Micoreus demerarae	2	72	3	2.95
Micoreus paraguayanus	2	72	3	2.95
Micoreus regina	2	72	3	2.95
Monodelphis adusta	3	48	2	1.97
Monodelphis brevicaudata	4	36	1.5	1.47
Monodelphis emiliae	4	36	1.5	1.47
Monodelphis theresa	3	48	2	1.97
Tlacuatzin canescens	2	72	3	2.95
Hyladelphys kalinowskii	1	144	6	5.90

Figure 3. Didelphimorph phylogenetic relationships (species underlined represent marsupials present in Mexico) with bootstrap values indicated above the branches of the tree. Taxonomic weight measures are showed in columns. (I), number of taxonomic groups; (Q), basal phylogenetic weight; (W), number of taxa that contribute to the total diversity of the group, and (P), percentage of the W value for each taxon. The total value for (I) was 144, for (Q) 2240.8, and for (W) 101.7.

the Pacific Coast, followed by the Soconusco and the Sierra Madre del Sur, are important for didelphimorphs conservation. The taxonomic distinctness analysis shows that the province of Oaxaca stands out as the most important area for didelphimorphs conservation. Areas with maximum taxonomic dispersion were the Gulf of Mexico and the Pacific Coast. These provinces have a large territorial extension, and the 8 didelphimorphs species were located only in the southern portion of these areas. If it is not always possible to protect all species, the Soconusco and the Sierra Madre del Sur provinces should be the subsequent conservation areas considered in order



	W	son	apn	aps	tam	smo	sme	vol	bal	sms	pac	gm	oax	scn	chi	yuc	ptn
Caluromys dervianus	3.00									●	●	●	●	●	●		●
Chironectes minimus	2.00									●	●	●		●		●	
Didelphis marsupialis	1.20			●	●	●	●	●	●	●	●	●	●	●	●	●	●
Didelphis virginiana	1.00	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Philander opossum	1.20			●	●		●	●		●	●	●	●	●	●	●	●
Metachirus nudicaudatus	3.00										●	●		●			
Tlacuatzin canescens	3.00	●		●		●		●	●	●	●	●	●			●	
Marmosa mexicana	3.00			●	●		●	●	●	●	●	●	●	●	●	●	●
Total	20.40	4.00	1.00	9.40	6.40	5.20	6.40	9.40	8.20	17.40	20.40	20.40	15.40	17.40	15.40	11.40	12.40
P1 (%)		19.60	4.90	20.4	31.37	25.49	31.37	0.46	40.19	85.29	100.00	100.00	75.49	85.29	75.49	55.38	60.78
P2 (%)		14.70	-	14.70	-	14.70	-	14.70	14.70	14.70	-	-	14.70	14.70	-	14.70	-

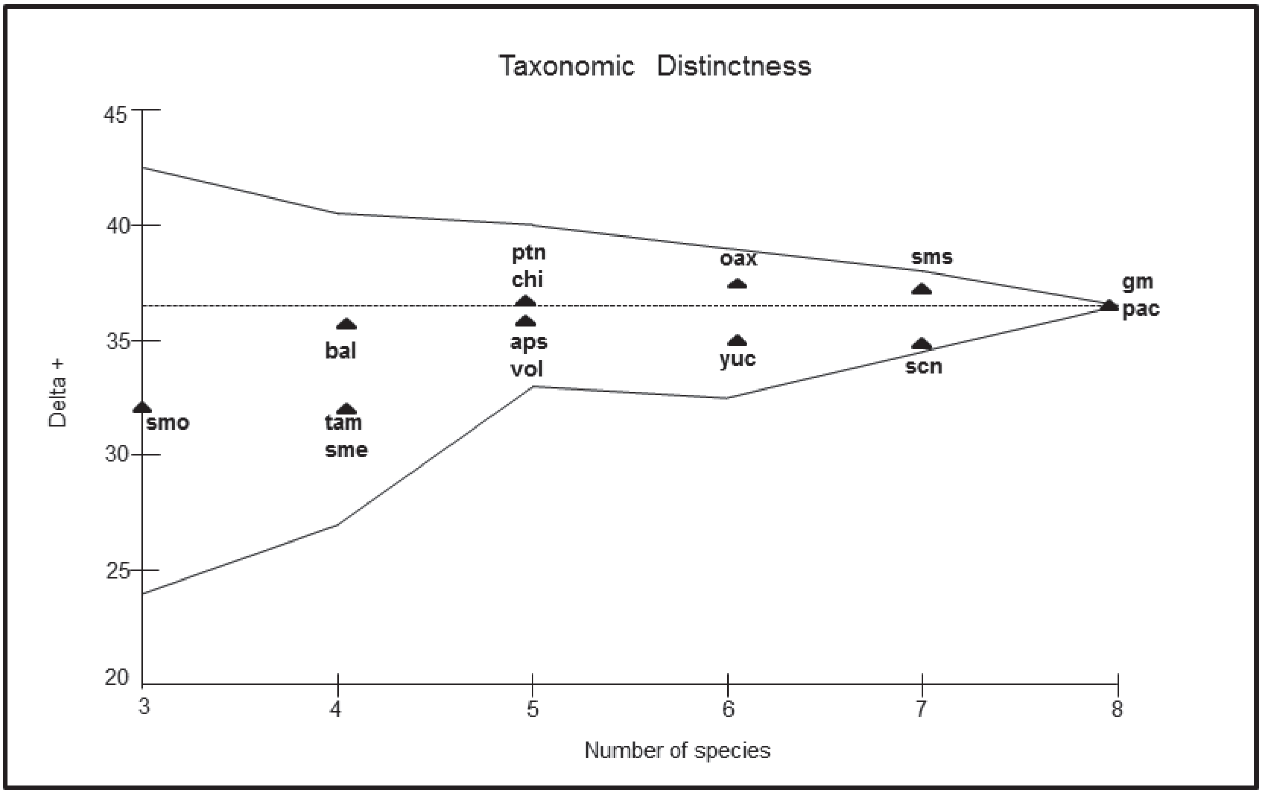
Figure 4. Taxonomic weight, taxonomic dispersion, and priority conservation areas for the Mexican species of didelphimorphs. The phylogenetic relationships of Mexican didelphimorphs and bootstrap values (Voss and Jansa, 2003; modified by Medina-Romero, 2007) are shown on the left. The distribution of each taxon by biogeographic province is given on the right. The letter W corresponds to the taxonomic weight obtained on fig 2. P1 indicates the percentage of taxonomic weight for each area, P2 shows the taxonomic weight without first choice areas; this means areas that lack taxa. The biogeographic provinces are abreviated as follows: Sonora (son), Altiplano Norte (apn), Altiplano Sur (aps), Tamaulipeca (tam), Sierra Madre Occidental (smo), Sierra Madre Oriental (sme), Eje Volcanico (vol), Depresion del Balsas (bal), Sierra Madre del Sur (sms), Costa del Pacífico (pac), Golfo de México (gm), Oaxaca (oax), Soconusco (scn), Los Altos de Chiapas (chi), Yucatán (yuc), and Petén (ptn). Dark gray areas show maximum taxonomic dispersion; those delimited with a line follow in order of importance.

of importance, where at least 1 taxon from each node of the cladogram is found, even though *M. nudicaudatus* is not included within the Sierra Madre del Sur. Gap analysis showed that most of the didelphimorphs richness is found in protected areas, including *C. derbianus* and *C. minimus*, which are in risk of extinction. Nevertheless we can propose to establish a biological corridor connecting the protected areas, focusing on those of the most southern part of the country, to strengthen dispersal among these mammals and to guarantee the protection of *M. nudicaudatus* and *C. minimus*, both with distributions restricted to the area mentioned above.

Taxonomic distinctness measures have been applied to conservation biology in different ways. Bhat and Magurran (2006), working with fish, argued that these measures have a vast potential for environmental evaluation and conservation biology. García-Marmolejo et al. (2008) employed these measures to establish conservation priorities for Neotropical mammals. They determined that Oaxaca and Chiapas were the areas with the highest specific diversity. Our results show that Oaxaca is also an area with high taxonomic distinctness for marsupials. García-Marmolejo et al. (2008) evaluated the overlapping of panbiogeographic nodes with protected areas, and found that 1 site of highest diversity richness for mammals was found in Los Altos de Chiapas, which included 2 didelphimorphs, *M. mexicana* and *C. derbianus*. This information partially coincides with our results where Palenque is considered the richest area for didelphimorphs. These results from Mexican marsupials represent another example of the usage of these measures to assess terrestrial mammal conservation biology.

Using gap analysis and herpetofauna data, Ochoa-Ochoa and Flores-Villela (2006) found that approximately 40% of the protected areas of Mexico coincided with places of high richness for these organisms. Additionally, Urbina-Cardona and Flores-Villela (2010) found that the hotspot areas were concentrated in the southeast part of Mexico, which is congruent with our results for marsupials. The above results also agree with the latitudinal and richness patterns proposed by Ceballos and Oliva (2005) and Ceballos (2007), who established that the highest richness of Mexican marsupials occurs in southern Mexico, and that the reserves with the highest species number are located in tropical forest areas.

Based on the results of our work, we noticed that it is better to combine different methods to make decisions, because a better conservation proposal can



Provinces	aps	tam	smo	sme	vol	bal	sms	pac	gm	pac	scn	chi	yuc	ptn
Species	5	4	3	4	5	4	7	8	8	6	7	5	6	5
Delta +	35.71	33.33	33.33	33.33	35.71	35.71	37.41	36.73	36.73	36.1	35.37	37.14	35.24	37.14

Figure 5. Funnel graph obtained with Primer 5, on the x-axis the species richness and on the y-axis the taxonomic distinctness or delta plus values. Triangles correspond to the biogeographic provinces where didelphimorphs are distributed. The maximum taxonomic richness is in the provinces of Gulf of Mexico and Pacific Coast; the maximum taxonomic distinctness is located in the Oaxaca province with a value of 38.1. The table below shows the values of the delta+ and the richness for each biogeographic province.

Table 1. Protected areas located in the biogeographic Mexican provinces employed for the gap analysis

Biogeographic province	*Protected Areas*
Pacific Coast	Sierra de Álamo, Meseta de Cacaxtla, La Michilia, Cuenca Alimentadora del distrito de riego 043 del estado de Nayarit, Islas Marías, Chamela-Cuixmala, Sierra de Manantlán, Lagunas de Chacahua, Huatulco, La Encrucijada, Lagunas de Montebello
Gulf of Mexico	Selva el Ocote, Cañón El Sumidero, Montes Azules, Lacan-tun, Chan-kin, Bonampak, Naha, Metzabok, Palenque, Cascada de Agua Azul, Laguna de Terminos, Pantanos de Centla, Los Tuxtlas, Cuenca Hidrográfica del Río Necaxa, Sierra Gorda, Sierra del Abra-Tanchipa
Soconusco	Volcán Tacana, El Triunfo, La Sepultura
Sierra Madre del Sur	Tehuacan-Cuicatlán, Benito-Juárez, Yagul
Oaxaca	Pico de Orizaba, Cañón de Río Blanco

Areas underlined correspond to areas that protect didelphimorph species (see Fig. 6).

Table 2. Results obtained from the gap analysis indicating the protected areas with the maximum richness and didelphimorph's species found there

Protected areas	*Didelphimorph's species*	*Number of species*
Palenque	*Marmosa mexicana, Chironectes minimus, Caluromys derbianus, Didelphis marsupialis, Philander opossum*	5
Los Tuxtlas	*Philander opossum, Caluromys derbianus, Didelphis marsupialis, Didelphis virginiana*	4
Cañón del Río Blanco	*Marmosa mexicana, Caluromys derbianus, Philander opossum, Didelphis virginiana*	4

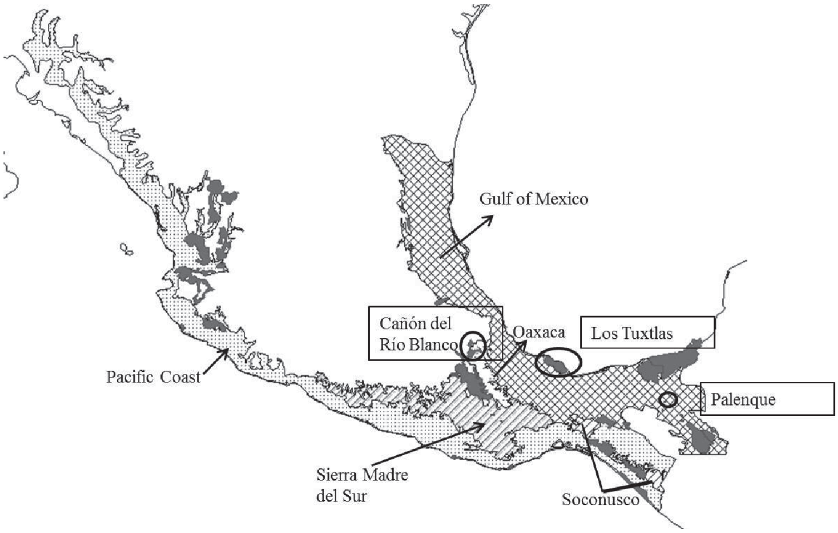


Figure 6. Combination of the results of all analyses: taxonomic weighting, taxonomic dispersion, taxonomic distinctness, and gap analysis indicating the biogeographic provinces with its highest species number: Pacific Coast (8 species), Gulf of Mexico (8 species), Sierra Madre del Sur (7 species), Soconusco (7 species), and Oaxaca (delta value of 38.1). In dark gray are showed the protected areas contained in the biogeographic provinces mentioned above; circled are the Protected areas containing maximum number of didelphimorph species for conservation: Palenque (5 species), Los Tuxtlas and Cañón de Río Blanco (4 species each; see table 2).

be obtained. This approach has been applied in different works; for example, Torres-Miranda et al. (2011) used complementarity, richness, and endemism patterns of red oaks in Mexico and Central America, and Vázquez and Valenzuela-Galván (2009) studied mammals with the same methods. Both studies coincide with our results in locating the highest richness area for plants and mammals in southern Mexico. Also the results of Vázquez et al. (2009) employing complementarity with mammals are congruent with our results in that the Pacific Coast, Sierra Madre del Sur, and Soconusco are the most species rich areas in the country. Finally, our results partially coincide with Escalante et al. (2009), who used optimality criterion, parsimony analysis of endemicity, and niche modelling methods and concluded that the regions of the central Pacific Coast, Chiapas, Transmexican volcanic belt, and the Yucatán Peninsula should be considered as endemism areas which partially correspond to similar areas in our study.

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Appendix. Characters used by Voss and Jansa (2003) and data matrix of characters and taxa for this analysis 0 indicates absence, 1 and 2 presence, -innaplicable character, ? missing data.

Characters

1 Rhinarium / with_2_grooves with_1_groove,
2 Midrostral_stripe / absent present,
3 Mask_1 / absent present,
4 Mask_2 / like_Marmosa polymorphic like_Metachirus,
5 Spot__above_eye / absent present,
6 Gular_gland / absent present,
7 Dorsal_fur_markings / unpatterned dark_bars scapular_stripes median_and_lateral_stripes red_flanks red_head_and_rump tricolored,
8 Dorsal_underfur / dark white,
9 Dorsal_guard_hairs / short long,
10 Manual_digits / III_longest 'III_=_IV' IV_longest,
11 Central_palmar_surface / 'smooth-sparsely_tubercular' densely_tubercular sandpapery,
12 Lateral_carpal_tubercles / absent present_in_adult_males,
13 Medial_carpal_tubercles / absent present_in_adult_males,
14 Pedal_digits / III_longest subequal IV_longest,
15 Interdigital_webbing / absent present,
16 'Plantar pelage (pes)' / tarsus_naked tarsus_hairy,
17 Pouch_1 / absent present,
18 Pouch_2 / opens_medially opens_anteriorly opens_posteriorly,
19 Mammae / 'inguinal-abdominal_only' 'thoracic-pectoral_too',
20 Cloaca / present absent,
21 Body_pelage_on_tail / longer_dorsally subequal none,
22 Caudal_coloration / uniform_or_variable 'black-and-white',
23 Caudal_scales / annular intermediate spiral,
24 Base_of_tail / smooth_scales raised_tubercles,
25 Tail_tip / not_prehensile prehensile,
26 Caudal_hairs_1 / 3_per_scale 4_or_more,
27 Caudal_hairs_2 / all_hairs_alike middle_hair_thickest,
28 Tail_incrassate / no yes,
29 Rostral_proc._premaxillae / absent present,
30 Palatal_proc._premaxillae / reach_C1_alveoli 'don''t_reach_C1_alveoli',
31 Maxilloturbinals / elaborately_branched simple_scrolls,
32 Nasal_tips / above_or_anterior_to_I1 posterior_to_I1,
33 Nasal_shape / widest_posteriorly subparallel,
34 Postorbital_process_frontals / absent_or_indistinct 'Caluromys-like' 'Didelphis-like',
35 Sagittal_crest / absent_or_small large,
36 Parietal_and_alisphenoid / in_contact separated,
37 Petrosal_exposure / not__exposed polymorphic exposed_laterally,
38 Maxillopalatine_fenestrae / absent_or_indistinct polymorphic present,
39 Palatine_fenestrae / absent present,
40 Maxillary_fenestrae / absent present,
41 'Post.-lat. palatal foramina' / behind_M4s lingual_to_M4s,
42 Posterior_palatal_morphology / '"Caluromys"_type' '"Didelphis"_type',
43 'Max.-alisph. contact' / absent polymorphic present,
44 Transverse_canal_foramen / absent present,
45 Secondary_foramen_ovale / absent 'formed_by_ant.-med._strut' formed_by_lamina,
46 Ectotympanic_suspension / from_skull from_malleus_only,
47 Fenestra_cochleae / exposed concealed,
48 Paraoccipital_process / adnate_to_petrosal erect,
49 Dorsal_margin_for._magnum / 'supra-_and_exoccipitals' exoccipitals_only,
50 Mental_foramina / two one,
51 Angular_process / 'acute-strongly_inflected' 'obtuse-weakly_inflected',
52 'Shape I2-I5 crowns.' / symmetrical_rhomboids asymmetrical,
53 Upper_canine / simple post.__cusp ant.__and_post.__cusps,
54 P1_size / large small_or_absent,
55 'Height P2, P3' / P2__taller subequal P3_taller,
56 P3_cutting_edges / anterior_and_posterior posterior_only,
57 'M1--M4 widths' / M1_wider_than_M4 M4_wider_than_M1,
58 Centrocrista / linear 'weakly_V-shaped' 'strongly_V-shaped',
59 'Ectoflexus on M1-M3' / absent present,
60 'Anterior cingulum (M3)' / complete incomplete,
61 Upper_molar_eruption / M4_before_P3 M4__and_P3_together P3_before_M4,
62 Lower_incisors / with_lingual_cusp without_lingual_cusp,
63 'Height p2, p3' / p2__taller subequal p3__taller,
64 dp3_trigonid / tricuspid bicuspid,
65 m3_hypoconid_position / labially_salient lingual_to_protoconid,
66 Entoconid_size / large small_and_indistinct,

Appendix. Continues.

67 Hypoconulid / twinned_with_entoconid in_midline,
68 ‘RES {a1+ a5, m1}’ / metacentric acrocentric,
69 ‘RES {a2+a8, m2}’ / metacentric acrocentric,
70 ‘RES {a3+a10, m3}’ / metacentric acrocentric,
71 ‘RES {a6+a9, m4}’ / metacentric acrocentric,

Matrix

Caluromys_derbianus	0110000000200020011001100100011000100000000000110001101000100000000000000
Caluromys_lanatus	0110000000200020011000021100011000100000000000110001101000100000000000000
Caluromys_philander	0110000000200020010001020100011000100000000000110001101000100000000000000
Caluromysiops_irrupta	000–0020020002001?0000211000010001100000000002110001101000000000000001????
Chacodelphys_formosa	?0100100001??200????200000000000010002211010100000000000011211?00?110????
Chironectes_minimus	10120010002002101201112000000001021002000101210101000021111121000001111
Cryptonanus_chacoensis	00100100010102000–00200010000000000002210010100000000102112110000000????
Cryptonanus_unduaviensis	0010010001010200???0200010000000000002210010100000000202112100002000????
Didelphis_albiventris	10100001100001001100112010000001021002100101210110010021111121000001111
Didelphis_marsupialis	10100001100002001100112010000001021002100101210110010021111121000001111
Didelphis_virginiana	10100001100001001100112010000001021002100101210110010021111121000001111
Glironia_venusta	00100?00010??2000–0000–11??000000100010000010000000100101110000?000????
Gracilinanus_aceramarcae	00100100010102000–0020001000100000002211010110000000000111210?00?000????
Gracilinanus_agilis	0010010001010200???020001000100000002211010110000000000111210?0020000000
Gracilinanus_emiliae	00100100010102000–00201010001000000022110101100000000101112100002000????
Gracilinanus_microtarsus	0010010001010200???020001000100001002211010110000000000111210000?0000000
Hyladelphys_kalinowskii	00100000010002000–00201010000000000000100010100000101000011100002000????
Lestodelphys_halli	10100100001000010–1020000?010000000012101101101000000021121100221000000
Lutreolina_crassicaudata	100–0000000000001200112001000001021002100121210110010021111121000001111
Marmosa_lepida	00100000010102000–0020201000100001000200010100000000101112100002000????
Marmosa_mexicana	00100100010112000–002010100010000100021001010000000000011121000020000000
Marmosa_murina	00100000010002000–002020100010000100020001010000000000011121000020000000
Marmosa_robinsoni	00100100010112000–002010100010000100020001010000000000011121000020000000
Marmosa_rubra	?0100000010112000–0?2020100010000000002000101001000000001112100002000????
Marmosops_impavidus	00100000000102000–0020201010100000000221001011000000000111211000000000000
Marmosops_incanus	00100100000102000–1020201010?0001000121001011000000000111211000?0000000
Marmosops_noctivagus	00100100000102000–002020101010000000121001011000000000111211000000000000
Marmosops_parvidens	00100000000102000–00202010101000000002200010110000000201112100000000????
Marmosops_pinheiroi	00100000000102000–00202010101000000002200010110000000201112110000000????
Metachirus_nudicaudatus	10121100000002000–00201000000000000010200010110011000001112111000000000000
Micoureus_demerarae	00100000010112000–002020100010000100020001010000000000011121000020000000
Micoureus_paraguayanus	0 0100000010112000–?010201000100 0010002000101000000000011210?00?0000000
Micoureus_regina	00100000010112000–002020100010000100020001010000000000011121000020000000
Monodelphis_adusta	100–0100000000000–002000000000100000020001210000000000211211001?110????
Monodelphis_brevicaudata	100–0100000000000–00000000000010000002000121000000000021121110101100101
Monodelphis_emiliae	100–0100000000000–0000000000001000000200012100100000000211211?0201100101
Monodelphis_theresa	100–000000000000???0200000000001000000200012120000000000211211?01?110????
Philander_frenata	1011100000000020011001120110000010210021001012101100100211111?10?0001111
Philander_mcilhennyi	10121000000002001100112011000001021002100101210110010021111121000001111
Philander_opossum	10121000000002001100112011000001021002100101210110010021111121000001111
Thylamys_macrurus	00100100001002010–1020001000000010002211010110100000000211211001?0000000
Thylamys_pallidior	1010010000100201???02000100100001000221011011010000000021121100120000000

Appendix. Continues.

Matrix

Thylamys_pusillus	00100100001002010–10200010010000100022111101101000000021121100110000000
Thylamys_venustus	0010010000100201???020001001000010002211110110100000002112110012000000 0
*Tlacuatzin_canescen*s	00100000010102000–00200010000000001000201010100000000000111210000 20001111