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HISTORICAL BIOGEOGRAPHY IN NORTH AMERICAN ARID REGIONS: AN APPROACH USING MITOCHONDRIAL-DNA PHYLOGENY IN GRASSHOPPER MICE (GENUS *ONYCHOMYS*)

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Abstract.—Restriction-endonuclease-site variation of mitochondrial DNA (mtDNA) was used to investigate patterns of geographic and phylogenetic divergence within the rodent genus *Onychomys*. *Onychomys* has occupied arid habitats in the western North American deserts, shrub-steppes, and grasslands since the late Tertiary. A phylogenetic analysis of the total mtDNA restriction-site variation throughout the range of *Onychomys* suggests that the distribution of this genus has been affected by the same Quaternary pluvial-interpluvial climatic fluctuations that have resulted in the periodic fragmentation of arid habitats in western North America. *Onychomys* mtDNA haplotypes define at least five discrete geographical subsets, suggesting that there are five areas of endemism for biota restricted to arid and semiarid habitats in North America. The mtDNA-haplotype phylogeny can be used to infer an hypothesis of historical relationships among the five areas of endemism as follows: ([{(Wyoming Basin + Interior Plains + Colorado Plateaus) + (Columbia Basin + Great Basin)} + Gulf Coastal Plain] + Chihuahuan) + Western Deserts. The results of this study point to the potential use of mtDNA-haplotype phylogenies to reconstruct historical biogeographic events in Quaternary time. The utility of mtDNA variation depends in part on the ecology and distribution of the species being examined. Therefore, our hypothesized area cladogram can be tested by investigating regional relationships in other western North American taxa with distributions similar to *Onychomys*.

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A basic goal of historical biogeography is to investigate the causal relationship between earth history and biotic distribution and divergence. In general, three kinds of information are important (Platnick and Nelson, 1978; Rosen, 1978; Cracraft, 1983; Humphries and Parenti, 1986): 1) recognizable patterns of allopatric divergence of phylogenetically operational taxa, or so-called "phylogenetic species" (Nelson and Platnick, 1981; Cracraft and Prum, 1988) in areas of endemism; 2) phylogenetic hypotheses among endemically differentiated taxa, with subsequent inferences about historical relationships among the areas themselves; and 3) an evaluation of the pattern and extent of generalized vicariance through comparative analyses of independently derived phylogenetic and geologic (or climatic) historical hypotheses.

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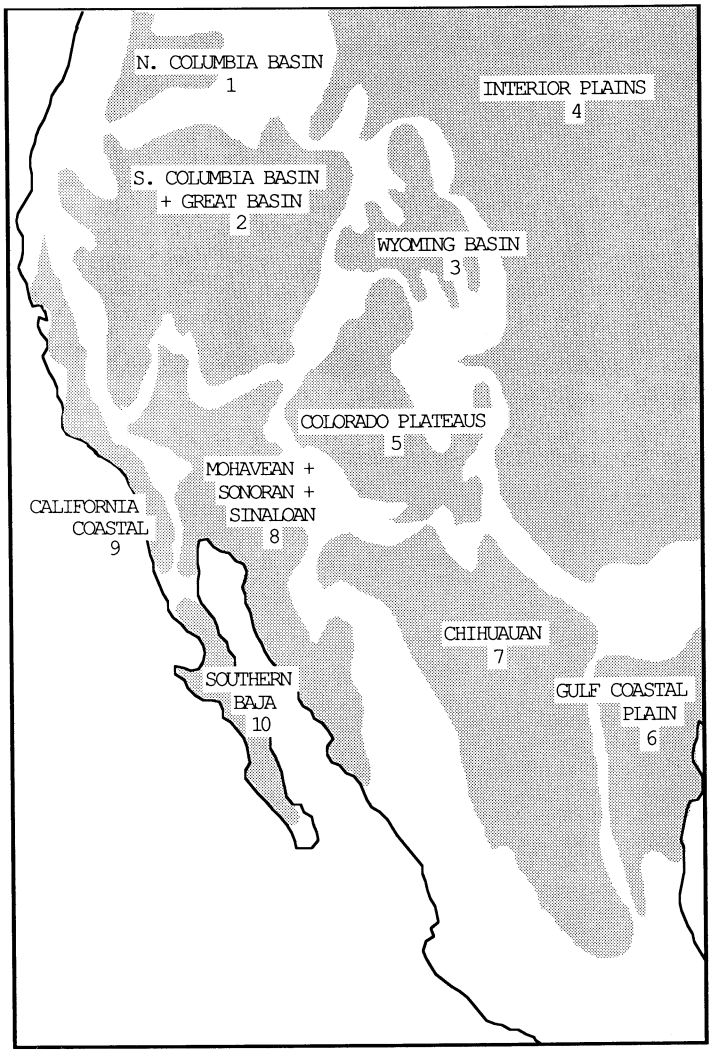

FIG. 1. Regions of desert, grassland, or shrub-steppe habitat in western North America. Regions are delineated physiographically and by relative habitat continuity. Sources include Hunt (1974) and Omernik (1987).

The desert, shrub-steppe, and grassland regions that occupy much of western North America (Fig. 1) began developing in Tertiary time as a consequence of major physiographic changes, including the uplift of principal mountain ranges (Axelrod, 1983, 1985). Since their inception, these systems have undergone distributional and compositional alterations as a result of Quaternary pluvial-interpluvial cycles (reviewed in Wright [1983]). Therefore, the expected result of such climatic cycles should be the establishment of regional endemism caused by the fragmentation of arid and semiarid habitats.

Of the organisms adapted to North American desert, shrub-steppe, and grassland habitats, some have limited geographic distributions (e.g., the rodent genus *Microdipodops,* which is restricted to the shrub-steppes of Nevada, Oregon, and western Utah), while many others are widespread throughout these arid and semiarid regions (Stebbins, 1966; Hall, 1981). Given the high incidence of shared taxa, it seems plausible that the biogeographic history of these re-

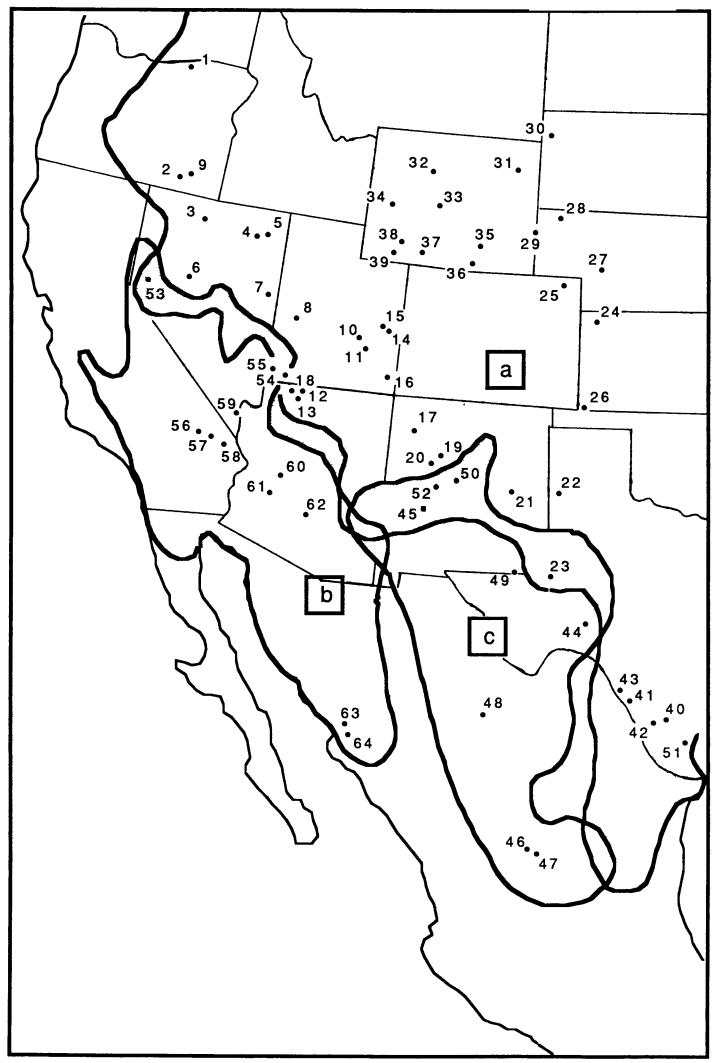

FIG. 2. Distribution of the 64 samples of *Onychomys* used in this study. The geographic distributions of the three species are outlined as follows: a) *O. leucogaster*; b) *O. torridus*; c) *O. arenicola*.

gions has resulted in the allopatric divergence of monophyletic lineages (i.e., phylogenetic species) within distinct areas of endemism. One widespread rodent taxon which seems suitable for detailed phylogenetic analysis is the genus *Onychomys*. This genus has been endemic to western North America since the Pliocene, 5 MY B.P. (Carleton and Eshelman, 1979; Savage and Russell, 1983) and contains three polytypic species (Hollister, 1914; Hinesley, 1979; Riddle and Choate, 1986; Sullivan et al., 1986) which occur in desert, shrub-steppe, and grassland habitats (Fig. 2).

Mitochondrial DNA has strong potential as a system for investigating recent intracontinental patterns of regional endemism, in which many biogeographically informative phylogenetic lineages are likely to comprise a single geographically widespread biological species or species complex (Wallace et al., 1985; Bermingham and Avise, 1986; Avise et al., 1987; MacNeil and Strobeck, 1987; Lamb et al., 1989). Importantly, the

mode of mtDNA genetic transmission (matrilineal inheritance) favors a rapid geographic sorting of haplotype lineages in the absence of gene flow (Avise et al., 1984). The consequences of such sorting lead to the biogeographic prediction (Avise et al., 1987) that all haplotypes within an area of endemism will, given sufficient time, represent a single monophyletic lineage distinct from those in other areas. Although certain population characteristics (e.g., small inbred demes, strong female philopatry) could in principle have an additional nonhistorical effect on haplotype-lineage survivorship (Avise et al., 1984), the restriction of gene flow between populations of an otherwise panmictic species should result in the geographic structuring of closely related mtDNA haplotypes, thus producing a high historical biogeographic "signal."

In this study, geographic and phylogenetic patterns of divergence are evaluated among *Onychomys* mtDNA haplotypes. These patterns of endemic divergence in *Onychomys* will allow us to construct a phylogenetically based hypothesis of general patterns of endemism and historical relationships among areas characterized by desert, shrub-steppe, and grassland habitats. This becomes a predictive framework bearing on phylogenetic affinities of organisms sharing overlapping (generalized) tracks and so, eventually, indicating the extent to which generalized patterns of vicariance may have affected the distribution and divergence of biota among these areas.

Materials and Methods

A total of 64 specimens representing three species of *Onychomys* (*O. torridus, O. leucogaster,* and *O. arenicola*) were collected throughout most of the geographical range of the genus (see Fig. 2). Mitochondrial DNA was isolated from frozen tissues (liver, heart, or kidney) using CsCl–propidium-iodide gradient centrifugation (Brown, 1980; Densmore et al., 1985). The isolated mtDNAs were digested with the following eight restriction endonucleases: *Bam*H I, *Bcl* I, *Bgl* II, *Bst*E II, *Eco*R I, *Hin*c II, *Hin*d III, and *Xba* I. Mitochondrial-DNA fragments were end-labeled with ^{32}P-dNTP using Klenow large-fragment DNA polymerase I (Brown, 1980). The labeled fragments were separated by electrophoresis through 1.2% agarose and 3.5% polyacrylamide vertical gels. *Hin*d III-digested lambda DNA and *Hin*f I digests of SV40 DNA were used as molecular-weight standards. A separate restriction-site map was produced for each restriction endonuclease. These individual site maps were derived from a combination of partial and double restriction-endonuclease digestions plus a comparison of overall site variation found for each species. All unique restriction-site patterns (or haplotypes) for each enzyme were designated by a letter, and a composite mtDNA haplotype was produced for each sample. Site maps for each restriction endonuclease are available upon request.

Phylogeny reconstruction for the composite mtDNA haplotypes consisted of a parsimony analysis using the HENNIG86 program, version 1.5 (available from J. S. Farris, Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794). In this analysis, each restriction site was treated as a character and scored as present or absent. When two or more trees of equal length were found, a consensus tree reflecting the information shared by all trees was constructed using the following sequence of HENNIG86 options: mhennig*, bb*, and nelson. In addition to the cladistic analysis, divergence estimates, expressed as δ, were computed directly from mtDNA restriction-site data using equations from Nei and Li (1979). Finally, estimates of total haplotype diversity ($\hat{h}$) in various geographic regions were generated by treating each different haplotype as a separate nucleon and using equation 7 from Nei and Tajima (1981).

Results

Geographic Variation

The overall restriction-site variation uncovered in this study revealed 42 composite haplotypes, with the greatest number occurring within the range of *Onychomys leucogaster* (Table 1). A large portion of the variation within *O. leucogaster* occurs throughout the combined Colorado Plateaus, Interior Plains, and Wyoming Basin regions (see Fig. 1). The distributional patterns of site variation generated by several

enzymes (*Eco*R I, *Hin*d III, *Xba* I, and possibly *Hin*c II; Table 1) suggest that these combined regions may eventually be separable into three distinct centers of divergence. Nevertheless, the large number of sites shared among these three regions suggests two alternatives: that a great deal of postisolation dispersal has occurred or that the alleged events isolating these regions were sufficiently recent to be unresolvable using restriction endonucleases with penta- and hexanucleotide recognition sites. Future studies using restriction endonucleases that recognize tetranucleotide sites may help address these two alternatives. Although it would at first appear that lesser amounts of haplotype variation are found among samples of *O. leucogaster* to the west of the Rocky Mountain axis in the Great Basin regions (Fig. 1), as well as in *O. leucogaster* from the Gulf Coastal Plain, this observation is not supported if total haplotype diversity ($\hat{h}$) is estimated for each of these three groups of regions: Great Basin + Columbia, $\hat{h} = 0.87$; Colorado Plateaus + Interior Plains + Wyoming Basin, $\hat{h} = 0.85$; Gulf Coastal Plain, $\hat{h} = 0.80$.

No geographic pattern in restriction-site variation is yet detectable within *O. torridus* (with the possible exception of *Hin*c II; Table 1), and therefore, there is no suggestion of differentiation among the Mojavean, Sonoran, and Sinaloan regions (see Fig. 1). Samples of *O. torridus* are not yet available from California Coastal regions, and no grasshopper mice occur in southern Baja. Here again, it may be that sufficient resolution is currently lacking to address the possibility of additional geographic structure nested within this region. In a similar fashion, the question of geographic variation within *O. arenicola* is not yet tractable. Several enzymes (*Bcl* I, *Bst*E II, *Bam*H I, *Eco*R I, and *Hin*d III) separate haplotypes 23 and 24 from haplotype 25 by a minimum of six restriction-site changes (Table 1) and, therefore, demonstrate a possible pattern of differentiation among samples of *O. arenicola* in northern and southern portions of the Chihuahuan region, but current geographic coverage is insufficient to address the reality of this pattern. As was the case in *O. leucogaster,* total haplotype diversity within each of these two species appears to be high ($O.$ *torridus,* $\hat{h} = 0.94$; *O. arenicola,* $\hat{h} = 0.75$).

Restriction-site data were used to generate pairwise estimates of the percentage nucleotide sequence divergence (δ) among haplotypes. In all cases, average divergence values were considerably lower between haplotypes that occur within the same geographic area (of the five outlined in Figure 3) than were any values between haplotypes that occur in different areas (Table 2).

Phylogeny Reconstruction

In all, 71 restriction sites were mapped for the eight restriction endonucleases used in this study and were coded as present or absent for each of the 42 composite haplotypes (Table 1). These data were analyzed phylogenetically using maximum-parsimony algorithms in HENNIG86, but the character matrix was first streamlined to include only phylogenetically informative data (i.e., invariant and autapomorphic characters were deleted), leaving a total of 49 sites.

The phylogenetic trees produced through HENNIG86 are automatically rooted using a designated outgroup. Although no adequate mtDNA data are available to root the phylogeny for *Onychomys* with an informative outgroup (i.e., a closely related genus of peromyscine rodents), several lines of evidence suggest that, at the level of nominate species, *O. arenicola* and *O. leucogaster* may be each other's closest extant sister group, and therefore that *O. torridus* could be used as a "functional outgroup" to root the *O. arenicola* + *O. leucogaster* clade. The evidence includes: 1) the relatively great overall nucleotide sequence divergence of *O. torridus* mtDNA haplotypes from those of the other two species documented in this study through distance estimates (Table 2) and 2) analyses of allozymes, external morphology, and bacular morphology (Sullivan et al., 1986). We realize, however, that an outgroup is needed to verify the placement of *O. torridus.* Such a study, involving intergeneric comparisons of mtDNA divergence, will be most informative with nucleotide sequences rather than restriction sites. These studies are in progress.

This analysis generated more than 1,808 trees of equal length, and the points of agreement among these trees are summarized

TABLE 1. Summary of *Onychomys* mtDNA haplotype patterns (specific localities given in Appendix and shown in Fig. 2). Each composite haplotype is designated with a unique number (see Fig. 3) and set of letters, with each letter representing a particular restriction-site pattern for a given enzyme (the order of the lettering is the same as that of the enzymes shown in this table), and followed by sample numbers in parentheses. Geographic regions are numbered as in Figure 1. Restriction-site characters are designated as present (1), absent (0), or undetermined (?) for each of the 42 haplotypes.

Species	Haplotype	Region	Enzyme							
			Bcl I	*Bam*H I	*Bgl* II	*Bst*E II	*Eco*R I	*Hind* III	*Xba* I	*Hinc* II
O. leucogaster	01 afabaaab (1)	1	11111011	1101110	10000	10011	1000010100100	10100010000	1110101	110010010011100
	02 agaaaaaa (2,3,9)	2	11111011	1001110	10000	10001	1000010100100	10100010000	1110101	110010110011100
	03 akaaaaaa (4)	2	11111011	1011110	10000	10001	1000010100100	10100010000	1110101	110010110011100
	04 agbaaaaa (5)	2	11111011	1001110	10001	10001	1000010100100	10100010000	1110101	110010110011100
	05 agaaaaab (6)	2	11111011	1001110	10000	10001	1000010100100	10100010000	1110101	110010010011100
	06 agaaabab (7,8)	2	11111011	1001110	10000	10001	1000010100100	11100110000	1110101	110010010011100
	07 bccbbccc (10,11)	5	11111001	1000110	10101	10011	1000000100101	11100010000	1100101	110010000011100
	08 ccdbbccd (12,18)	5	11011001	1000110	11101	10011	1000000100101	11100010000	1100101	110110000011100
	09 bcdbbdae (17)	5	11111001	1000110	11101	10011	1000000100101	11100110010	1110101	110010000001100
	10 bcebbdbc (19)	5	11111001	1000110	11001	10011	1000000100101	11100110010	1110100	110010000011100
	11 dcdbbebc (20)	5	10111001	1000110	11101	10011	1000000100101	11100100010	1110100	110010000011100
	12 ccebdfac (21)	4	11011001	1000110	11001	10011	1000001100101	11100010010	1110101	110010000011100
	13 bcdbdfac (22,23)	4	11111001	1000110	11101	10011	1000001100101	11100010010	1110101	110010000011100
	14 ccdbbfac (27,30,33)	3, 4	11011001	1000110	11101	10011	1000000100101	11100010010	1110101	110010000011100
	15 bbdbbfac (29,34,36)	3, 4	11111001	1000100	11101	10011	1000000100101	11100010010	1110101	110010000011100
	16 ccgbbhac (31)	3	11011001	1000110	11111	10011	1000000100101	11100000010	1110101	110010000011100
	17 cbcbhgaf (32,37)	3	11011001	1000100	10101	10011	1000000100111	11100010100	1110101	110010000111100
	18 bccbdcac (25)	4	11111001	1000110	10101	10011	1000001100101	11100010000	1110101	110010000011100
	19 cbcbhgag (35)	3	11011001	1000100	10101	10011	1000000100111	11100010100	1110101	110010000111110
	20 cccbhgaf (38)	3	11011001	1000110	10101	10011	1000000100111	11100010100	1110101	110010000111100
	21 chbbjidh (40)	6	11011001	1001010	10001	10011	1010000000101	11110110000	1101101	111010001001100
	22 cdbbkidh (41)	6	11011001	1101010	10001	10011	1100000000101	11110110000	1101101	111010001001100
	33 bcdbbdbc (14,15)	5	11111001	1000110	11101	10011	1000000100101	11100110010	1110100	110010000011100
	34 bcdbcccd (16)	5	11111001	1000110	11101	10011	1000000000101	11100010000	1100101	110110000011100
	35 bchbbccd (13)	5	11111001	1000110	01101	10011	1000000100101	11100010000	1100101	110110000011100
	36 bbdbdfcb (26,28)	4	11111001	1000100	11101	10011	1000001100101	11100010010	1100101	110010010011100
	37 ccdbhfac (39)	3	11011001	1000110	11101	10011	1000000100111	11100010010	1110101	110010000011100
	38 cdbbpiah (42,43)	6	11011001	1101010	10001	10011	1000000000101	11110110000	1110101	111010001001100
	41 cdbbji?h (51)	6	11011001	1101010	10001	10011	1010000000101	11110110000	???????	111010001001100
	42 bcdbbfac (24)	4	11111001	1000110	11101	10011	1000000100101	11100010010	1110101	110010000011100
O. arenicola	23 cebclkbi (44,50,52)	7	11011001	1000000	10001	11011	1001000001101	11111000010	1110100	110010000011101
	24 cebcljbi (45,48,49)	7	11011001	1000000	10001	11011	1001000001101	11111110010	1110100	110010000011101
	25 eibdmlbi (46,47)	7	11011101	1000010	10001	11111	1000100001101	11111100000	1110100	110010000011101
O. torridus	26 faaanmej (53,59)	8	11001001	1101011	10000	10001	1000010000000	01111100001	0101110	100001000011100
	27 faaannek (54,57,58)	8	11001001	1101011	10000	10001	1000010000000	01111101001	0101110	110011000011100

TABLE 1. Continued.

Species	Haplotype	Region	Enzyme								
			Bcl I	*Bam*H I	*Bgl* II	*Bst*E II	*Eco*R I	*Hind* III	*Xba* I	*Hinc* II
	28 faaannfk (60)	8	11001001	1101011	10000	10001	10000100000000	01111101001	0101100	11001100001100
	29 gaaannem (62)	8	11001101	1101011	10000	10001	10000100000000	01111101001	0101110	11001100001101
	30 gjaannek (63)	8	11001101	1001011	10000	10001	10000100000000	01111101001	0101110	11001100001100
	31 gaaannek (64)	8	11001101	1101011	10000	10001	10000100000000	01111101001	0101110	11001100001100
	32 faaannej (56)	8	11001001	1101011	10000	10001	10000100000000	01111101001	0101110	10000100001100
	39 faaaonek (55)	8	11001001	1101011	10000	10001	10000100100000	01111101001	0101110	11001100001100
	40 faaann?! (61)	8	11001001	1101011	10000	10001	10000100000000	01111101001	???????	11001100001010

with the nelson consensus tree (Fig. 4), which depicts five main groups of haplotypes that geographically delineate those same regions previously demonstrated with the distance-based estimates (δ) of geographic variation (Fig. 3). The overall topology of this tree is strongly supported by a high character-retention index (RI = 0.85; defined as RI = [maximum number of steps (on worst-case tree) − actual number of steps]/[maximum number of steps − minimum number of steps]). The large number of trees that were initially generated resulted from branch-swapping among groups of haplotypes that are very similar to one another and comprise the principal geographic regions (demonstrated in the consensus tree as unresolved clusters of terminal taxa), and the phylogenetic ambiguity in these parts of the tree resulted in a relatively low consistency index (CI = 0.53). This phylogeny identifies all haplotypes that occur in *O. leucogaster* as monophyletic with respect to *O. arenicola* and *O. torridus* and further identifies each of three geographic groups within *O. leucogaster* as monophyletic with respect to one another. If overlaid on a map, this tree graphically demonstrates a phylogenetically oriented hypothesis of historical affinities among regional groupings of grasshopper mice (Fig. 5).

DISCUSSION

Areas of Potential Endemism

A fundamental assumption of vicariance biogeography is that phylogenetically differentiated lineages have remained essentially associated with the geographic region in which they originated (Humphries and Parenti, 1986; Simberloff, 1987). Given the cyclical nature of Quaternary climatic oscillations, a potential problem faced by biogeographers working on an intracontinental scale is that dispersal among regions of endemism (possibly combined with subsequent extinction in the original region) will erase any record of the original pattern of allopatric divergence. However, a number of consistent regional groups appear to be present, as indicated by geographic and phylogenetic analyses of *Onychomys* mtDNA (Figs. 3, 4). The hypothesis can thus be presented that each of these regional groups

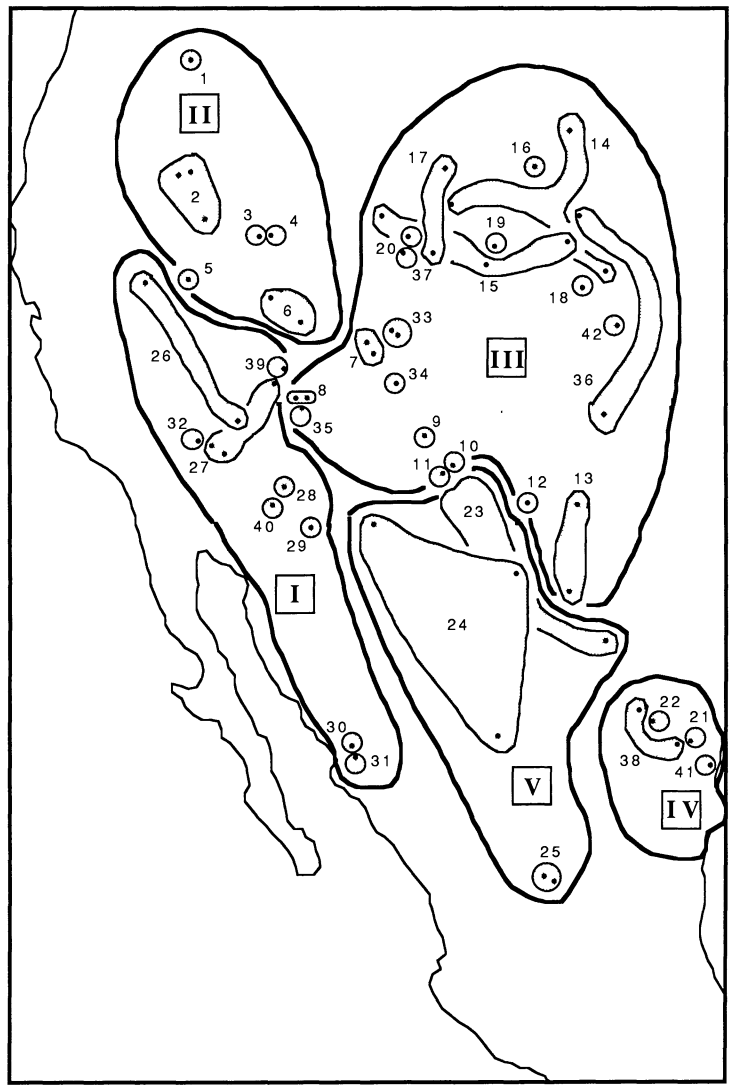

FIG. 3. Distribution of composite haplotypes (numbered as shown in Table 1). Roman numerals depict a regional grouping of haplotypes based on patterns of geographic variation as described in the text and summarized in Table 2. Each group includes species and primary geographic areas (see Fig. 1) as follows: I) *O. torridus,* Mohavean + Sonoran + Sinaloan; II) *O. leucogaster,* Northern Columbia Basin + Southern Columbia Basin/ Great Basin; III) *O. leucogaster,* Wyoming Basin + Interior Plains + Colorado Plateaus; IV) *O. leucogaster,* Gulf Coastal Plain; V) *O. arenicola,* Chihuahuan.

represents a distinct area of endemism or nested set of such areas (Fig. 4). As stated previously, the potential for further endemism of mtDNA haplotypes within area III (on the Colorado Plateaus and in the Wyoming Basin; see Fig. 3) is currently being evaluated. It may also be the case that additional areas of endemism are nested within other areas outlined here; for example, within area II (Fig. 3), the northern Columbia Basin (see Fig. 1) may be distinct from the southern Columbia Basin and Great Basin (specimens from each of these regions are morphologically distinct [Riddle and Choate, 1986]), and further distinction may exist as well within area I (Fig. 3). Nevertheless, the broadly outlined areas depicted in this study through the geographic pat-

TABLE 2. Range and mean (in parentheses) of divergence estimates (δ) summarized for all mtDNA haplotypes by geographic region. Each region is designated as shown on Figure 3.

Geographic region	Geographic region				
	II	III	IV	V	I
II	0.002–0.010 (0.006)	0.026–0.048 (0.036)	0.038–0.057 (0.050)	0.055–0.072 (0.064)	0.058–0.083 (0.073)
III		0.002–0.032 (0.014)	0.029–0.051 (0.040)	0.029–0.062 (0.043)	0.075–0.108 (0.091)
IV			0.008–0.010 (0.009)	0.035–0.051 (0.043)	0.054–0.068 (0.063)
V				0.005–0.018 (0.014)	0.062–0.079 (0.073)
I					0.002–0.013 (0.007)

terning of *Onychomys* mtDNA may indicate a more general pattern of endemism for organisms adapted to arid and semiarid regions in western North America.

Lamb et al. (1989) have recently used patterns of mtDNA variation to infer a history of isolation and subsequent divergence among populations of the desert tortoise (*Xerobates agassizi*). Three separate groups of mtDNA haplotypes, corresponding to the Mohavean, the Sonoran, and the Sinaloan regions, were recognized for this species (see Fig. 1). These three groups correspond to area I (Fig. 2) occupied by *O. torridus*. The greater level of geographic structuring that was obtained for tortoise haplotypes is interesting in that mtDNA variation was assayed with a set of hexa- and pentanucleotide restriction endonucleases, each of which would be expected to provide an equivalent estimate of restriction-site variation to that provided by the set of restriction endonucleases used to assay patterns of *O. torridus* mtDNA variation. The differences in resolution provided by the tortoise and grasshopper-mouse data sets could be accounted for in two ways. First, patterns of geographic structuring of haplotypes may in fact be equivalent between the two taxonomic groups, but a greater level of resolution (as provided, for example, with tetranucleotide restriction endonucleases) may be required to uncover equivalent patterns of variation in *O. torridus*. If this is correct, then it would mean either that intrinsic differences in rates of mtDNA evolution exist between desert tortoises and grasshopper mice or that each group has responded to temporally different isolating events. The latter possibility may be a common feature of continental historical biogeography in general (Cracraft, 1988). Second, these differences could be a consequence of different population-level attributes, in that it seems very likely that grasshopper mice will disperse more readily across larger geographic areas than will desert tortoises. As such, it may be that *O. torridus* mtDNA geographic structuring represents a case of secondary hybridization among those areas of endemism that can be inferred using *X. agassizi* mtDNA.

Phenetic biotic similarities are often indirectly invoked in the common assumption that both the Wyoming Basin and the Colorado Plateaus represent eastward extensions of the Great Basin cold desert shrub-steppes (Hunt, 1974; Turner, 1982). The data presented in this study do not support this relationship in an historical biogeographic context, but conflicting signals (see Hafner [1981] on *Ammospermophilus* phylogeny) suggest that overlapping generalized tracks may be common on the Colorado Plateaus. However, such cases of partial discordance in the delimitation of areas should not be surprising, given the presence of taxa with different ecologies or dispersal abilities (Cracraft, 1985).

It should be noted that the concept of endemic areas proposed here does not imply that an entire extant geographic range has been continuously occupied by a suite

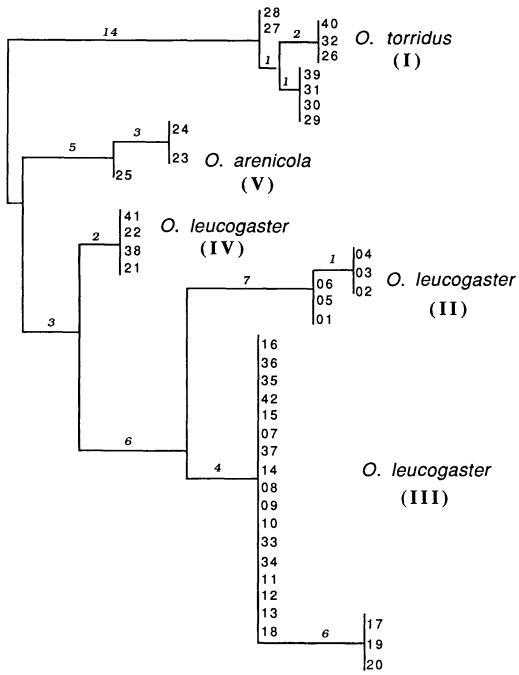

FIG. 4. Nelson consensus tree for *Onychomys* mtDNA haplotypes produced using the HENNIG86 program, drawn with branch lengths proportional to the number of character-state changes (shown above each branch). Groups of haplotypes are identified by their occurrence in a particular species of *Onychomys* and by geographic region of occurrence (roman numerals identify regions as described in the legend of Fig. 3).

of desert or grassland organisms. An array of paleobiological data suggests that, for example, much of the northern Great Plains (Wells, 1983*b*), the northern Great Basin and Columbia Basin (Thompson and Mead, 1982; Wells, 1983*a*), and a portion of the Colorado Plateaus (Spaulding et al., 1983) were covered with distinctly nonarid biota during Quaternary pluvial intervals. All that is implied is that an area of allopatric differentiation occurred somewhere within the existing range of a particular phylogenetic lineage. Furthermore, if a particular hypothesis of endemic areas is generalized across a set of taxa with overlapping distributions, all that is being investigated is the likelihood of common responses to a set of geologic or climatic events, which are represented in a modern landscape by certain physiographic or ecological features considered in the context of current or former barriers, and not the specific overlapping of microgeographic ranges.

A concept associated with areas of endemism is that of refugia (Cracraft, 1985), a common theme in reconstructions of intracontinental biogeography (Haffer, 1982; Mayr and O'Hara, 1986). In western North America, for example, scenarios of southern desert refugia during Quaternary pluvial periods have commonly been invoked (Wells and Hunziker, 1976; Cole, 1986), although paleobiotic data do not necessarily support these concepts (Mead et al., 1983). One implication of the refugial notion is that areas become relatively small and compressed, and, as such, population sizes are drastically reduced for a period of time. Given the strong influence of effective population size in models of haplotype-lineage survivorship (Avise et al., 1984), an hypothesis of past refugia would lead to the prediction that haplotype diversities should be greatly reduced within each postulated area of endemism. Although sample sizes are generally small, estimates of $\hat{h}$ presented in this study do not currently point to a severe reduction in haplotype diversity within any of the five areas postulated. However, the possibility that one or more of these areas may actually be further divisible into additional nested areas suggests the need to evaluate such possible patterns before further addressing the existence of former refugia.

Onychomys *mtDNA Phylogeny and a Biogeographic History of North American Arid Regions*

If the topology of the mtDNA haplotype phylogeny provided in Figure 4 is true (that is, if *O. arenicola* and *O. leucogaster* are sister taxa in relation to *O. torridus*), then a phylogenetically based orientation of arid and semiarid regions will produce an hypothesis of area relationships as shown in Figure 5. This hypothesis provides a phylogenetic basis supporting a generalized track that unites arid fauna of the Chihuahuan region with that of the Gulf Coastal and Interior Plains grasslands and the northern shrub-steppes. This is perhaps at least as significant an historical component of the extant fauna of this region as is the track uniting the Chihuahuan and collective west-

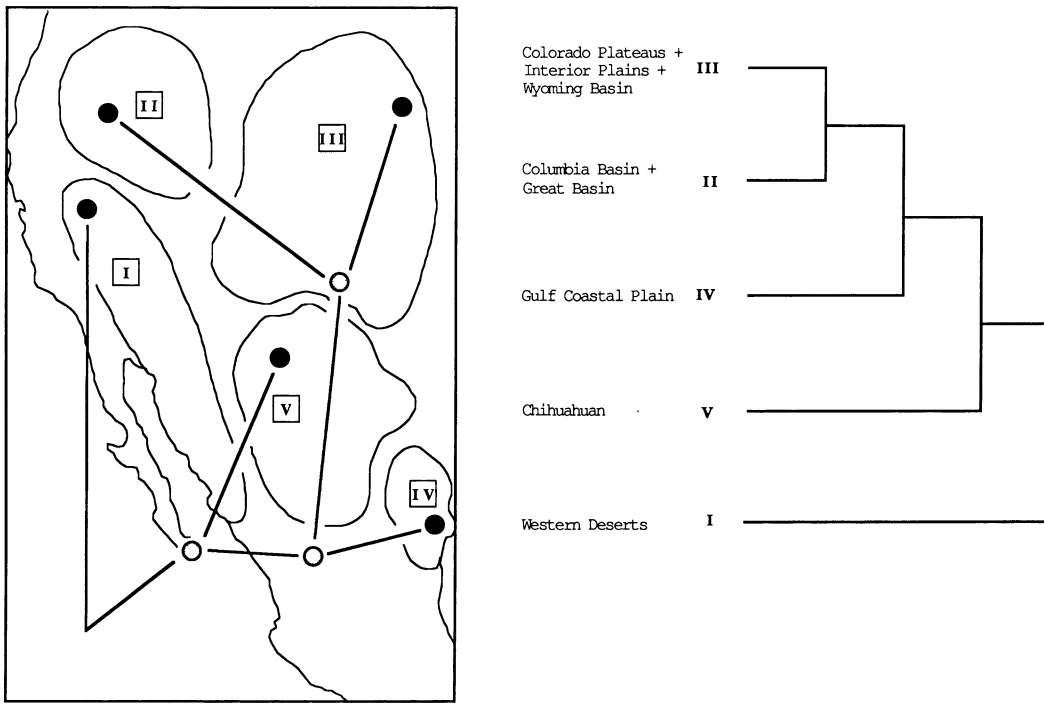

FIG. 5. Simplified phylogenetic tree redrawn from Figure 4 as an hypothesis of historical biogeographic area relationships among arid and semiarid regions of North America (roman numerals identify regions as described in the legend of Fig. 3).

ern "hot" deserts (Mohavean, California Coastal, Baja, Sonoran, and Sinaloan). The strength of the support provided by the *Onychomys* mtDNA data for this hypothesis is still problematic until such time as a more secure basal rooting (i.e., with a peromyscine rodent outgroup) is available for the phylogenetic tree, although the alternative hypotheses of (*O. torridus* + *O. leucogaster*) + *O. arenicola* or (*O. torridus* + *O. arenicola*) + *O. leucogaster* would require an assumption of greatly increased variability in mtDNA evolutionary rates across species. Nevertheless, the current phylogenetic tree supports the hypothesis that all endemically divergent lineages within the nominate species *O. leucogaster* are monophyletic in relation to both of the southern hot desert lineages (*O. arenicola* and *O. torridus*). The large internodal distances among regions within *O. leucogaster* suggest that range fragmentation has occurred in response to past biogeographic events, with mtDNA lineages sorting in allopatry.

The oriented phylogenetic tree of *Onychomys leucogaster* mtDNA haplotypes indicates that grasshopper mice from the Interior Plains + Wyoming Basin + Colorado Plateaus (region III in Fig. 5) have shared a common ancestor more recently with those from the Great Basin + Columbia Basin (region II) to the west than either has with those from the Gulf Coastal Plain (region IV). Nevertheless, the anagenetic divergence between these two lineages is relatively large, suggesting that there has been a considerable period of allopatric evolution. If the traditional calibration of roughly 2% nucleotide sequence divergence per million years is used, the δ distance estimates (Table 2) suggest that the isolation between the Great Basin + Columbia Basin and the Interior Plains + Wyoming Basin + Colorado Plateaus lineages predates the Wisconsin pluvial period. In addition, the Gulf Coastal Plain lineage is the least divergent form of *O. leucogaster* in relation to *O. arenicola*. Although this lineage has a large body size, comparable to Interior Plains and

Colorado Plateaus animals (Hollister, 1914), cursory examination suggests that several morphological characteristics, other than size, are more similar to those of the smaller *O. arenicola.* The possibility exists that these Gulf Coastal animals represent a distinct and currently unrecognized biological species (with a relatively plesiomorphic morphology).

Historical Biogeography in Evolutionary Biology

Cracraft (1986) and Cracraft and Prum (1988) have recently emphasized the importance (and primacy) of addressing phylogenetic and historical biogeographic events within the context of the evolution of continental faunas. To the extent that taxa with overlapping geographic distributions share concordant patterns of endemic differentiation as well as corroborating phylogenetic (and hence, historical biogeographic) orientations among areas, hypotheses of generalized vicariant events offer the most plausible explanations for the inception and maintenance of independent phylogenetic lineages. As Templeton (1981) has argued, the allopatric mode of adaptive speciation is in fact complementary with various microevolutionary population-genetic theories (notably, Wright's [1932] shifting-balance model) of evolutionary divergence and adaptation. Other evolutionary biologists have recently recognized the importance of establishing an historical null hypothesis within which to frame comparative evolutionary investigations (Cheverud et al., 1985; Felsenstein, 1985). In short, the explicit formulation of historical biogeographic hypotheses has an increasingly important role in current evolutionary biology, and this is not only a result of rethinking the connections between macro- and microevolutionary phenomena (Vrba and Eldredge, 1984), but also of the trend toward construction of phylogenetic trees among molecules (Wilson et al., 1985), which may demonstrate a history of geographic structuring independent of criteria used to recognize "biological species" boundaries.

By demonstrating a pattern of intra- and interspecific endemism in a widespread taxon, the results of this study support the contention that climatic cycles (probably in the late-Tertiary and Quaternary, a time-frame that is generally supported here with overall estimates of divergence [δ]) have served to fractionate arid and semiarid habitats on a continental scale, rather than simply to obliterate habitat from the majority of extant regions. In other words, although individualized biotic dispersal may have been an important component in the periodic reshuffling of community compositions (Cole, 1981; Graham, 1985; Van Devender, 1985), *Onychomys* mtDNA geography and phylogeny suggest that dispersal has been spatially bounded to the extent that different regions of desert, grassland, or shrub-steppe have each had independent histories of temporal and spatial dynamics. Thus, even for a relatively recent time-frame (i.e., late Quaternary), evolutionary biologists and community ecologists need to be aware of the historical component to evolution and community organization. Finally, these results suggest that future studies focusing on the investigation of the generalized nature of these patterns across many independent taxa should be informative and enlightening.

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APPENDIX

Specimens of grasshopper mice examined in this study identified by state (or country) and county are given in the table below. Numbers listed for each species correspond to collecting localities depicted in Figure 2. Additional locality data are available from the authors upon request.

Species	Specimen number	State or country	County
Onychomys leucogaster	1	Oregon	Morrow
	2, 9	Oregon	Harney
	3	Nevada	Humboldt
	4, 5	Nevada	Elko
	6	Nevada	Lander
	7	Nevada	White Pine
	8	Utah	Beaver
	10, 11	Utah	Wayne
	12, 13, 18	Arizona	Mojave
	14, 15	Utah	Grand
	16	Utah	San Juan
	17	New Mexico	McKinley
	19	New Mexico	Sandoval
	20	New Mexico	Bernalillo
	21	New Mexico	DeBaca
	22	Texas	Lamb
	23	Texas	Winkler
	24	Kansas	Rawlins
	25	Colorado	Logan
	26	Kansas	Morton
	27	Nebraska	Keith
	28	Nebraska	Dawes
	29	Wyoming	Goshen
	30	South Dakota	Harding
	31	Wyoming	Campbell
	32	Wyoming	Hot Springs
	33	Wyoming	Fremont
	34	Wyoming	Sublette
	35, 36	Wyoming	Carbon
	37, 38, 39	Wyoming	Sweetwater
	40, 42	Texas	Duval
	41, 43	Texas	Dimmit
	51	Texas	Kennedy
Onychomys arenicola	44	Texas	Crockett
	46, 47	Mexico	Zacatecas
	48	Mexico	Chihuahua
	49	New Mexico	Eddy
	45	New Mexico	Sierra
	50	New Mexico	Valencia
	52	New Mexico	Socorro
Onychomys torridus	53	Nevada	Churchill
	54, 55	Utah	Washington
	56, 57, 58	California	San Bernardino
	59	Nevada	Clark
	60	Arizona	Yavapai
	61	Arizona	Maricopa
	62	Arizona	Pinal
	63, 64	Mexico	Sonora