

# Phylogeography of *Peromyscus furvus* (Rodentia; Muridae) based on cytochrome *b* sequence data

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## Abstract

We conducted phylogenetic analyses of cytochrome *b* sequence data to assess genetic variation within and among the three allopatric segments of the distribution of *Peromyscus furvus* from the Sierra Madre Oriental in eastern Mexico. We identified 24 unique haplotypes among the 54 individuals examined and genetic distances ranged up to 0.078 substitutions per site. Populations from the central portion of the range formed a monophyletic unit, whereas samples from the southern distributional unit were polyphyletic. Furthermore, the southernmost population sampled may represent a distinct species. This high degree of genetic differentiation among populations, currently recognized as conspecific, mirrors the result of other genetic studies of highland rodents in Mesoamerica. Together these studies indicate that the region, already considered hyperdiverse on the basis of species diversity and endemism, may contain considerably greater diversity than is currently appreciated.

**Keywords:** cytochrome *b*, highlands, likelihood, Mesoamerica, parsimony, *Peromyscus furvus*, phylogeography

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## Introduction

The mountainous regions of Middle America harbour extensive biodiversity, both in terms of species diversity and levels of endemism (e.g. Fa & Morales 1993; Flores-Villéla 1993; Flores-Villéla & Gerez 1994). This is attributable, in part, to the fact there are several separate mountain systems at these tropical latitudes with correspondingly disjunct cool-adapted highland biotas. In addition to the high species diversity and endemism, genetic studies have documented extensive intraspecific differentiation as well as highly structured genetic variation in highland rodents of the region (e.g. Rennert & Kilpatrick 1986; Rogers & Engstrom 1990; Sullivan *et al.* 1997; Sullivan *et al.* 2000). However, the region has recently been subject to a great deal of habitat loss due to subsistence-based deforestation, making assessment of the phylogeographic structure and identification of evolutionarily significant units (ESU's) in endemic species particularly critical.

*Peromyscus furvus*, the Blackish deer mouse, occupies moist mid- to high-elevation subtropical forests on the eastern flanks of the Sierra Madre Oriental in east-central

Mexico. As currently understood (Carleton 1989; Harris & Rogers 1999), its distribution is composed of three allopatric units, within which habitat is relatively continuous and which are isolated from each other by low river valleys. These segments are arranged nearly linearly in a north-west–south-east fashion. Difficulties delimiting species boundaries for these groups of populations persisted for much of the 1900s, and each of these three distributional units has been described as a distinct species. Subsequent authors, however, have variously arranged these into a polytypic *P. furvus* [with the subspecific epithets *latirostris* applied to the northern unit, *angustirostris* applied to the central unit, and *furvus* to the southern unit (Musser 1964; Hooper 1968)], or treated all populations as part of a monotypic species (Hall 1971; Huckaby 1980; Carleton 1989).

Harris & Rogers (1999) used allozyme data to assess genetic variation within *P. furvus*. In general, they found moderate to high levels of variation, as measured by standard fixation indices, but the allopatric segments of the distribution did not appear to be genetically differentiated from each other. However, their data suggested low levels of gene flow and high inbreeding. They interpreted these results as consistent with the current taxonomic treatment of *P. furvus* as monotypic (Hall 1981; Carleton 1989).

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In the present paper, we use mitochondrial DNA (mtDNA) sequence data from the mitochondrial cytochrome *b* gene (*cytb*) to examine the phylogeography of *P. furvus*. These data represent independent genetic data relative to the allozyme data of Harris & Rogers (1999) and allow us to assess the relationships among lineages present in this species.

## Methods

### Samples

Many of the mice we used (Table 1) were previously examined by Harris & Rogers (1999) in their analysis of allozyme variation. Our samples include a single population from the northern distributional unit (Population 5), four populations from the central unit (Populations 1, 2, 4, and 8), and three from the southern unit (Populations 3, 6, and 7). Hooper (1968) considered *Peromyscus furvus* to be a member of the *P. mexicanus* group, a position endorsed by Huckaby (1980) and Hall (1981). Subsequently, Carleton (1989) erected the *P. furvus* species group, which included *furvus*, *P. ochraventer* and *P. maynensis*. More recently, however, Wade (1999) demonstrated that *P. furvus* and *P. ochraventer* are not closely related. Because of these uncertainties, we included samples of *P. mexicanus*, *P. ochraventer*, and *P. melanocarpus* as outgroups.

### Data collection

We chose to sequence *cyt b* because data from this gene have been useful for other phylogeographic studies of Middle American highland rodents both within species

and for species complexes (e.g. Sullivan *et al.* 1997; Sullivan *et al.* 2000). DNA was extracted from approximately 10 mg of liver using a modification of the DTAB/CTAB procedure of Gustincich *et al.* (1991). We used the following primers, corresponding to I and V in Palumbi (1996), to amplify an 848-bp fragment of the gene: L-14115: 5'-GATATGAAA-AACCATCGTTG-3' and H-14963: 5'-GGC-AAATAGGAA-RTATCATT-3'. The first of these primers is part of the flanking tRNA<sub>Glu</sub>, and was modified to fit *Mus*. (Bibb *et al.* 1981). Amplifications were precipitated using polyethylene glycol (PEG) as a carrier and 15–45 ng of polymerase chain reaction (PCR) product was used as a template for cycle sequencing in 10 µL reactions with the BigDye Kit (Applied Biosystems, Inc.). Sequencing reactions were cleaned via gel filtration using CentriSep columns (Princeton Separations, Inc.) and run on an ABI 377 automated sequencer using 4% Long Ranger gels. This approach consistently produced reliable sequences of approximately 650 bp; thus, approximately 90% of the region was sequenced in both directions, with the remaining sequence being within 200 bp of a sequencing primer. Sequences have been deposited in GenBank under accession nos AF270980–AF271032.

### Data Analyses

Sequence files were edited and aligned using Sequencher software (GeneCodes); alignment was unambiguous because there was no length variation detected. Phylogenetic analyses were conducted using both parsimony and likelihood as optimality criteria, and all analyses were conducted using PAUP\* (version 4.0d64-d65; written by D. L. Swofford). Parsimony analyses were conducted using equal weights. Maximum-likelihood (ML) analyses were conducted under the GTR +  $\Gamma$  model of nucleotide evolution (see e.g. Sullivan & Swofford 1997). This was chosen on the basis of likelihood-ratio tests of goodness of fit following Frati *et al.* (1997) and Sullivan *et al.* (1997); the 16 models we evaluated are the same models examined by the aforementioned authors, and the assumptions of these models are compared in Sullivan & Swofford (1997). Redundant haplotypes were eliminated from the data matrix prior to likelihood analyses. The likelihood analyses used a successive approximations approach (Swofford *et al.* 1996; Frati *et al.* 1997), in which the parameters of the chosen model were estimated on an initial parsimony tree, with subsequent searches conducted under the likelihood criterion using fixed model parameters. Model parameters were re-estimated on the resulting ML tree and a second ML search was conducted using the refined model parameters. Iteration stopped when two consecutive ML searches produced the same topology. Both parsimony and likelihood analyses utilized heuristic searches with stepwise addition (10 random addition sequences) and tree bisection-reconnection (TBR) branch swapping. Nodal support was

**Table 1** *Peromyscus furvus* samples and outgroups examined

Population	Unit*	<i>n</i> †	Locality
1	Central	7	Mexico, Hidalgo, 3 km E Tlanchinol
2	Central	8	Mexico, Hidalgo, El Portero, 10 km SW Tenango de Doria
3	Southern	9	Mexico, Puebla, Rancho El Pariso, 6 km SW Huachinango
4	Central	3	Mexico, Veracruz, La Colonia, 6.5 km W Zacualpan
5	Northern	8	Mexico, San Luis Potosí, Ejido Aguayo. 6.2 km N Xilitla
6	Southern	4	Mexico, Veracruz, Banderillas, 6 km NW Jalapa
7	Southern	12	Mexico, Oaxaca, 1.5 km S Puerto de la Soledad
8	Central	2	Mexico, Hidalgo, 21.8 km NE Metepec

\*Distributional units are based on contiguous habitat. Each of these disjunct sets of populations has been previously considered a distinct species (see text).

†Number of individuals sampled at each site.

estimated via bootstrap analysis (Felsenstein 1985) with 500 and 200 replicates for parsimony and likelihood, respectively. In order to facilitate the likelihood bootstrap analyses, most model parameters were fixed to values estimated from the original data; the exception is that empirical base frequencies were used for each pseudoreplicate. In addition, MAXTREES was set to one for the likelihood bootstrap analyses in order to eliminate interminable branch swapping in replicates with little or no phylogenetic signal. Because most populations examined represented monophyletic assemblages of haplotypes, hierarchical analyses of haplotype frequencies were not conducted.

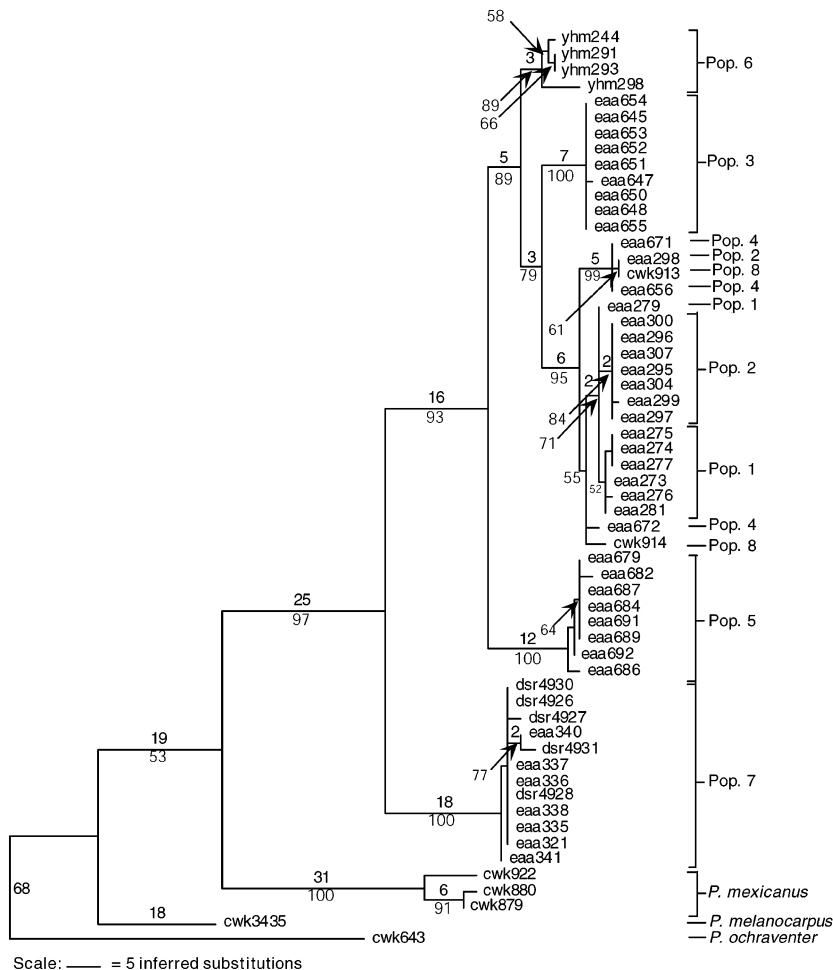
## Results

Twenty-four unique haplotypes were identified among the 54 individuals sequenced. Of the 719 sites aligned in all individuals (including outgroups), 173 were observed to vary, 125 of which were parsimony informative. Twenty-eight first codon-position sites were observed to vary (14 parsimony informative), six second codon-position

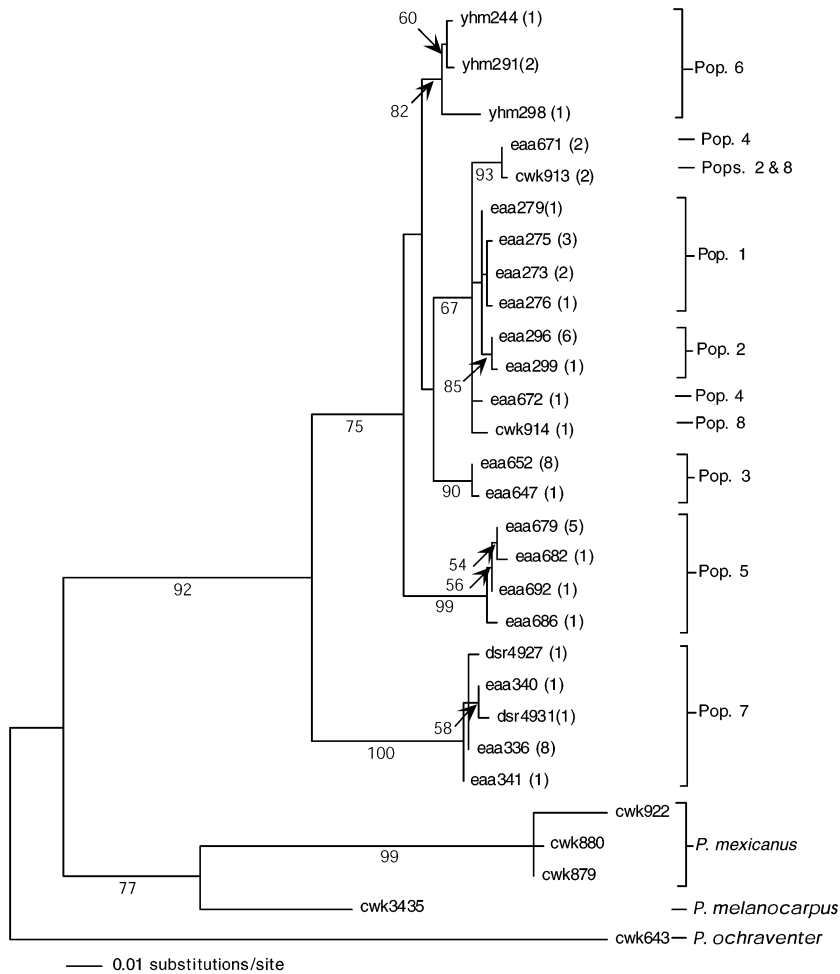
sites were observed to vary (five parsimony informative), and 139 third codon-position sites were observed to vary (106 parsimony informative). This distribution of sites observed to vary, along with the absence of stop codons, frameshift substitutions, and radical amino-acid substitutions, suggest that these sequences represent the mtDNA *cyt b* coding gene rather than a nuclear pseudogene.

Genetic distances [following Tamura & Nei (1993) for comparison to other studies of *Peromyscus cyt b*] between *P. furvus* and outgroup taxa ranged from 0.109 to 0.160 substitutions per site and from 0.000 to 0.078 substitutions per site within *P. furvus*. Population 7 is extremely divergent from the rest of the samples of *P. furvus*; its average genetic distance to the rest of the species is 0.071 substitutions per site. This level of differentiation exceeds that seen at *cyt b* between *P. leucopus* and *P. gossypinus* (within the *P. leucopus* species group; 0.039–0.046; Sullivan *et al.* 1995) and equals or exceeds that seen among *P. polionotus*, *P. keeni*, and *P. melanotis* (within the *P. maniculatus* species group; 0.056–0.071; Sullivan *et al.* 1995).

Parsimony analysis produced a single most parsimonious (MP) tree (Fig. 1) of 290 steps [consistency index (c.i.)



**Fig. 1** Maximum-parsimony tree [290 steps; consistency index (c.i.) = 0.669; retention index (r.i.) = 0.917; rescaled consistency index (r.c.) = 0.614] from analysis of *cyt b* data. Numbers above the branches are branch lengths (inferred under ACCTRAN). Internal branches with no length designation are a single step. Numbers below branches are bootstrap values (500 replicates). Branches with no bootstrap values shown were present in <50% of the replicates. Population numbers are presented in Table 1; individual designations refer to collector and catalogue numbers.



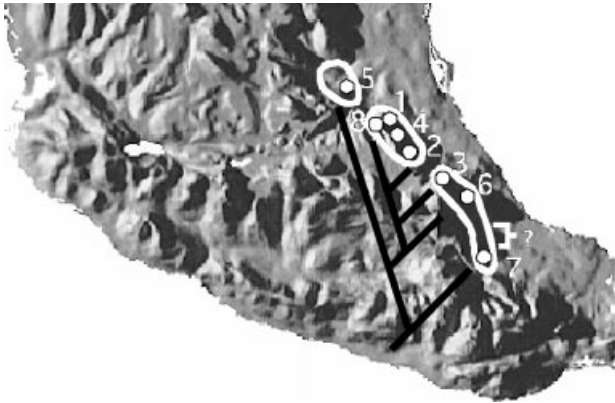
**Fig. 2** The single maximum-likelihood tree ( $\ln L = -2336.88119$ ) for nonredundant haplotypes. Numbers in parentheses indicate number of individuals which exhibited each haplotype. Numbers above each branch indicate bootstrap values. Bootstrap analysis consisted of 200 replicates, with MAXTREES set to one, and model parameters fixed to values estimated from the original data.

= 0.669, retention index (r.i.) = 0.917, rescaled consistency index (r.c.) = 0.614]. There are five major clades of haplotypes within *P. furvus*. The basal bifurcation splits Population 7 (in the southern unit) from the rest of the samples and each of these clades is well supported. Within the clade containing the rest of the samples, a bifurcation splits Population 5 (northern unit) from the remaining samples, and again each clade is well supported (Fig. 1). A third bifurcation splits Population 6 (southern unit), and Population 3 (southern unit) is sister group to all the samples of the central-unit populations (Populations 1, 2, 4, and 8). Within this central-unit clade, samples from Populations 1, 2, 4, and 8 are interdigitated, suggesting recent interchange of mitochondrial lineages among these populations. The results of the likelihood analyses are similar to those of the parsimony analyses (Fig. 2); the ML tree ( $\ln L = -2336.88119$ ) has the same basic topology and there are similar levels of nodal support. Differences between parsimony and likelihood trees are resolution among outgroup taxa and branch length estimates.

## Discussion

### Phylogeography

Several phylogeographic inferences can be made from the phylogenetic analyses of *cyt b* sequence data. First, the southern distributional unit is not a monophyletic assemblage of haplotypes (Fig. 3). The southernmost population (Population 7) is basal, whereas the other populations sampled from this unit (Populations 3 and 6) form a paraphyletic grade basal to the monophyletic assemblage of haplotypes from the central distributional unit (Populations 1, 2, 4, and 8; Fig. 3). All samples from Population 5, the sole representative of the northern distributional unit, form a well-supported monophyletic clade, which is the sister group to the Population 3/Population 6/central-unit clade. Thus, within *Peromyscus furvus* as currently defined, there appear to be five identifiable ESU's based on mtDNA sequences. Populations 3, 5, 6, and 7 each appear to represent distinct ESU's and



**Fig. 3** Phylogeography of *Peromyscus fuvvus* superimposed on its range map. The three distributional units are indicated by the white lines, and collection localities are indicated (see Table 1 for locality details). The region indicated by the question mark represents an area from which this no *fuvvus*-like mice have been collected.

Populations 1, 2, 4, and 8 (the central distributional unit) comprise the fourth.

Harris & Rogers (1999) used allozyme data to discern genetic structure in *P. fuvvus* and concluded that this species lacks significant differentiation among the formerly recognized taxa ( $F_{ST} = 0.20$ ), which are equivalent to the distributional units. However, they found that populations within the southern distributional unit exhibited more extensive differentiation ( $F_{ST} = 0.40$ ) than was estimated among the three distributional units. Given that the mtDNA suggest the southern unit is a composite of three ESU's, the possibility arises that the lack of significant differentiation among subdivisions inferred by Harris & Rogers (1999) is a spurious result stemming from their treatment of these three ESU's as a single unit.

#### Taxonomic considerations

The extremely high level of genetic differentiation observed in the mtDNA data between the southernmost Population 7 and the rest of the *P. fuvvus* samples raises questions regarding the inclusion of this population within *P. fuvvus*. Certainly, extreme genetic distances alone are insufficient arbiters of taxonomic rank. However, the presence of reciprocally monophyletic and strongly diverged mtDNA haplotypes observed here is paralleled by near fixation of a unique derived allele at the PGDH locus (Harris & Rogers 1999). These two independent data sets are congruent in differentiating Population 7 from the rest of *P. fuvvus*. Following a genealogical concordance (Baum & Shaw 1995) species concept, we hypothesize that these two genetically differentiated lineages represent distinct species. Such a distinction would make sense biogeo-

graphically because this extreme southern population is separated from the rest of the species by a region from which there are no records of *P. fuvvus* (Fig. 3). We predict that a rigorous morphological analysis will uncover other characters for which these lineages have fixed differences. However, pending such evidence, formal recognition of *P. fuvvus*-like forms from northern Oaxaca (represented here by Population 7) as a distinct species would be premature. Nevertheless, the geographical isolation of Population 7 probably was even more extreme during glacial cold periods throughout the Pleistocene, during which times alpine communities in Mexico were elevationally depressed (McDonald 1993).

We believe that this basal divergence of haplotypes dates to the early Pleistocene. A likelihood-ratio test (Felsenstein 1988), using the best fit GTR +  $\Gamma$  model, indicates that the *P. fuvvus* *cyt b* data fit the molecular clock hypothesis ( $\delta_{22} = 2[-1603.2199 - (-1619.5306)] = 32.6214$ ;  $P > 0.10$ ). Calibration of the molecular clock is always difficult, but certainly must account for rate heterogeneity among sites in calculation of genetic distances, even for studies among relatively closely related sequences (i.e. Arbogast & Slowinski 1998). We used *Mus* and *Rattus* *cyt b* sequences and a range of divergence dates from 10 to 14 million years (e.g. Catzeflis *et al.* 1992) as a calibration. Under the GTR +  $\Gamma$  model, we derived an evolutionary rate of 0.0629–0.0881 substitutions/site/million years for the portion of *cyt b* we sequenced. Using this calibration, and an average GTR +  $\Gamma$  distance of 0.112 substitutions per site, we estimate that the Population 7 haplotype diverged from the rest of *P. fuvvus* haplotypes approximately between 1.27 and 1.79 million years BP. However, application of this calibration to our data is somewhat tenuous for two reasons. First, it was based on *Mus* and *Rattus*; although *Peromyscus* is in the same family (Muridae), murines and peromyscines are not particularly closely related. Second, the complex model required to fit the data has a large variance and the estimate of divergence time will have a correspondingly large confidence interval. Thus, our estimate of divergence time should be treated cautiously. However, because this calibration accounts for rate heterogeneity among sites of the magnitude we observe in our data, it is the best available and the very large mtDNA divergence observed between Population 7 and the rest of the species is certainly consistent with an early Pleistocene divergence of these haplotypes. This is an earlier divergence than expected.

#### Patterns of mtDNA variation in Mesoamerican highland rodents

Although we are aware of no phylogeographic studies of species with a distribution similarly restricted to the eastern flanks of the Sierra Madre Oriental, a number of studies have examined levels of mtDNA variation within

more broadly distributed Mesoamerican highland rodent species. These include examinations of *P. aztecus* (Sullivan *et al.* 1997), *P. mexicanus* (PJVC de Groot and MD Engstrom, unpublished data) and *Reithrodontomys sumichrasti* (Sullivan *et al.* 2000). Each of these studies has found that currently named taxa contain very high levels of mtDNA differentiation, and in some cases these results have caused the authors to question the conspecific nature of the samples examined. Furthermore, these studies have revealed a common pattern, in that allopatric segments of species frequently represent monophyletic assemblages of mitochondrial haplotypes. Thus, it is becoming apparent that the actual levels of genetic diversity and endemism in this region (which is already considered hyperdiverse) are even higher than is currently appreciated. This exacerbates the need for examination of genetic variation in other highland taxa in the region, as well as the need for conservation measures focused on preservation of genetic diversity in addition to those based on diversity indices derived from current taxonomy.

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- This paper represents an extension of the MS thesis of Danny Harris, which was conducted in the laboratory of Duke Rogers. Danny was working in Jack Sullivan's laboratory towards completion of a PhD on comparative phylogeography of several northern Rocky Mountain rodents at the time of his death. Both the Rogers Laboratory and the Sullivan Laboratory conduct ongoing research on the comparative phylogeography of highland conifer forest-dwelling taxa. Sullivan also conducts research in theoretical molecular systematics, especially in the assessing the performance of heuristic strategies for model-based estimation of phylogeny from DNA sequence data.
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