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SYSTEMATICS OF *MYOTIS OCCULTUS* (CHIROPTERA: VESPERTILIONIDAE) INFERRED FROM SEQUENCES OF TWO MITOCHONDRIAL GENES

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The systematic relationship between *Myotis lucifugus carissima* and *Myotis occultus* has been the subject of multiple studies. Although several studies, including a recent allozyme study, concluded that *M. occultus* is a subspecies of *M. lucifugus*, this view has not been universally accepted. We reexamined the relationships of these 2 taxa by sequencing the mitochondrial cytochrome-*b* (cyt-*b*) and cytochrome oxidase II (COII) genes of specimens from the allozyme study. The results suggest that *M. occultus* represents an evolutionarily distinct monophyletic lineage and provide support to arguments that *M. occultus* is a distinct species.

Key words: cytochrome *b*, cytochrome oxidase II, maximum likelihood, molecular clock, phylogenetics

The taxonomic arrangement that best depicts the systematic relationships of *Myotis occultus* and *Myotis lucifugus* continues to elude bat systematists. *M. lucifugus* was described by Thomas (1904) before *M. occultus* was recognized. Hollister (1909) first described *M. occultus*, which ranges from southern California into Arizona, New Mexico, and south into Mexico. Miller and Allen (1928) retained specific status for *M. occultus* in their survey of bat species. *M. l. carissima* ranges across much of the western United States, and its range abuts areas of the southwest that are occupied by *M. occultus* (Hall 1981). These 2 taxa appear to overlap morphologically in northern New Mexico and southern Colorado, and it is specimens from this area that have been particularly problematic for systematists.

Findley and Jones (1967) measured 11 morphological characters from 500 specimens of *M. occultus* and *M. l. carissima* and found considerable morphological overlap in southern Colorado and northern New Mexico. Findley and Jones (1967) interpreted this overlap as intergradation, which they believed indicated that *M. occultus* and *M. l. carissima* were behaving as subspecies of a single species, *M. lucifugus*.

Barbour and Davis (1970) were not convinced that the evidence was sufficient to warrant grouping these taxonomically separate taxa into 1 species, so they reexamined the same specimens as well as additional specimens from the supposed area of intergradation. Their results also indicated the presence of morphologically intermediate specimens, and they agreed that *M. occultus* should be considered a subspecies of *M. lucifugus*.

Hoffmeister (1986) revisited the taxonomy of *M. occultus* and examined 27 cranial characters and performed principal-components and canonical-variates analyses. Some of the specimens examined by Hoffmeister (1986) were those morphologically intermediate specimens examined by Bar-

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bour and Davis (1970) and Findley and Jones (1967). Hoffmeister's (1986) results demonstrated 2 distinct groups as well as some intermediates from Eagle Nest, Colfax County, New Mexico. Hoffmeister concluded that the consistent demonstration of 2 distinct groups was sufficient evidence to tentatively warrant specific status for *M. occultus*.

In a phenetic study of the genus *Myotis*, Findley (1972) examined 48 characters for each of 60 species of *Myotis* and classified the species in this genus into species groups. His analysis used many of the same characters that Findley and Jones (1967) had used; this new analysis assigned *M. occultus* to the ''grisescens'' group, and *M. l. carissima* was assigned to an entirely different group, the ''austroriparius'' group. Findley (1972:43) concluded that either *M. occultus* had converged ''toward the grisescens group phenome or the field relationships of *carissima* and *occultus* have not been fully elucidated.''

Recently, Valdez et al. (1999) performed an allozyme analysis of *M. occultus* and *M. l. carissima* and found little or no genetic differentiation, suggesting a high degree of interconnectedness between the taxa. Although there were no significant differences among allozymic characters, Valdez et al. (1999) suggested that *M. occultus* be retained as a subspecies of *M. lucifugus* because of its considerable morphological differences from *M. l. carissima* (Hoffmeister 1986).

It would appear that there is no consensus on the systematic relationship between *M. occultus* and *M. lucifugus*. Our current understanding of the status and distribution of *M. lucifugus*, as shown in Hall (1981), is strongly rooted in the work of Miller and Allen (1928). The depictions of ranges of the subspecies of *M. lucifugus* in these references pose an array of interesting questions that demand additional study, ideally with a phylogeographic approach. Generally, we think that the limits of currently known full species in North America *Myotis* are well established and morphologically verifiable.

In this study, we examined 2 mitochondrial genes to reinvestigate the status of *M. occultus*. We sequenced the mitochondrial cytochrome-*b* (cyt-*b*) and cytochrome oxidase II (COII) genes from some of the same samples (Appendix I) examined by Valdez et al. (1999). Our framework for assessing differences among these taxa assumes reproductive isolation (Herd and Fenton 1983) among a group of similar species that are generally morphologically distinct (Findley 1972).

Materials and Methods

Specimens and DNA extraction.—Total genomic DNA was extracted from 13 ingroup specimens regarded as *M. l. carissima* or *M. occultus* and 2 outgroup specimens, *M. velifer* and *M. yumanensis*, all of which were identified by morphology and geographic distribution (Appendix I). Frozen tissues and tissue from study skins were obtained through loans from the Museum of Southwestern Biology, Albuquerque, New Mexico. DNA was extracted from tissue following a phenol–chloroform method described by Piaggio and Spicer (2000). All ingroup samples used in this study were also used by Valdez et al. (1999), although we did not include all of their samples in this analysis.

Amplification and sequencing.—Double-stranded DNA products were obtained using the polymerase chain reaction (PCR) method. Amplifications of the complete mitochondrial COII gene required external primer pairs, L7553 with H8320 (Adkins and Honeycutt 1994), which amplify a segment approximately 700 base pairs (bp) in length. Cyt *b* was initially amplified using external primer pairs, L14724 with H15915 (Kocher et al. 1989), which amplify a segment approximately 1,200 bp in length. These primers would not amplify most samples. Therefore, we designed a light-strand primer specific to *M. occultus* and *M. l. carissima*, LCB5-5′ (5′-GCC TCT ATT ATG GAT CCT-3′). This primer was designed from a section of conserved sequence found within the few samples of the entire cyt-*b* gene; therefore, the segment amplified by LCB5-5′ resulted in a partial segment of cyt *b*. When paired with H15915, a sequence of 795 bp was generated. Amplifications were carried

out in a P100 thermal-cycler (PerkinElmer, Wellesley, Massachusetts) for 33 cycles of denaturation at 94°C for 1 min, annealing at 52°C for 1 min, and extension at 72°C for 2 min. Amplified PCR products were cleaned before sequencing, using a polyethylene glycol precipitation protocol (Kusukawa et al. 1990).

All sequencing was done via dye-terminator cycle sequencing on a Catalyst 800 Molecular Biology Lab Station and followed the protocol specified by the ABI PRISM™ Dye Primer Cycle Sequencing Ready Reaction Kit (Revision B, August 1995, PerkinElmer). Primers used for sequencing reactions were the same as those used for the double-stranded amplification reactions.

Preliminary sequence analysis.—Sequences were aligned using Sequencher 3.0 (Gene Codes Corp 1995) with *Artibeus jamaicensis* (Pumo et al. 1998). Aligned sequences were submitted to GenBank (cyt *b,* AF294500–AF294514, COII, AF294565–AF294579; Appendix I). The sequences were evaluated for overall base composition bias, which was calculated using methods described by Irwin et al. (1991). Values can range from 0 to 1, 0 indicating no bias and 1 representing complete composition bias. An extreme overabundance of 1 nucleotide can increase the tendency for those sites to become saturated (Irwin et al. 1991). Base homogeneity was evaluated using the base-frequency option in the program PAUP* 4.0b2 (Swofford 1999). A nonhomogeneous bias can violate an assumption of many analyses, namely, that the proportion of bases remains stationary (Perna and Kocher 1995; Spicer 1995; Yoder et al. 1996).

Because cyt *b* and COII are linked genes, we assume that these genes reflect homogeneous evolutionary histories; consequently, we can combine the data sets. To test this assumption, we ran the partition homogeneity test in PAUP* 4.0b2 (Swofford 1999), excluding constant characters.

Parsimony analyses were performed by using the computer program PAUP* 4.0b2 (Swofford 1999). These analyses were accomplished by using the branch-and-bound algorithm, which guarantees the shortest tree. In order to assess robustness of the branching patterns, bootstrap analyses were performed (Felsenstein 1985), using a search set to 500 iterations of a branch-and-bound search. Distance analyses were calculated using the Kimura 2-parameter distance (Kimura 1980) and clustered by using the heuristic search invoking the minimum-evolution criterion.

Maximum-likelihood methods were used to evaluate the fit of the data to the parsimony and distance topologies. This was done by using the 2-parameter model for unequal base frequencies of Hasegawa et al. (1985), with a discrete approximation to the Γ-distribution, the ratio of transitions to transversions (ti/tv) and the shape parameter estimated according to the model. We used a total of 10 rate categories as described by Yang (1994), and an average rate of each category was represented by the mean (Felsenstein 1993). The maximum-likelihood model was also used to test the null hypothesis that the sequences were evolving at constant rates and therefore fit a molecular clock.

RESULTS

We sequenced the complete COII gene in both directions, which resulted in 683 bp, consisting of 113 variable sites of which 87 were phylogenetically informative. We also sequenced part of the cyt-*b* gene in both directions, which yielded 795 bp (including 18 bp of the t-RNA-thr), consisting of 150 variable sites of which 130 were phylogenetically informative. Base composition biases were calculated for both genes separately for each codon position (1st, 2nd, and 3rd), all positions combined, all characters, only variable characters, and among phylogenetically informative characters (Table 1).

Results from the partition homogeneity test (1,000 replications, $P = 1.0$) confirm our assumption that COII and cyt *b* reflect homogeneous evolutionary histories. Therefore, we combined the sequence data from COII and cyt *b* in our analyses, which provides us with 1,478 combined base pairs. This combined data set includes 263 variable characters of which 217 are parsimony informative.

The COII and cyt-*b* sequences were first analyzed by using parsimony, which resulted in 9 most parsimonious trees (length L = 295 steps), with a consistency index (CI) = 0.902 and a retention index (RI) = 0.939. However, when the collapse branches op-

TABLE 1.—Percentage of base composition and bias within *Myotis occultus* and *M. l. carrissima* mitochondrial DNA sequence. Percentages are calculated for cytochrome oxidase subunit II (COII), cytochrome *b* (cyt *b*), and both combined. Values are calculated according to coding position (1st site, 2nd site, and 3rd site) for all characters and for variable characters. Values are also calculated as all positions (sites) combined for all characters, variable characters, and phylogenetically informative characters. Bias is calculated using the formula of Irwin et al. (1991).

	All characters				Variable characters				Phylogenetically informative characters
	All sites	1st site	2nd site	3rd site	All sites	1st site	2nd site	3rd site	All sites
COII									
No. of base pairs (bp)	683	229	229	229	113	21	1	91	87
A	0.321	0.297	0.259	0.410	0.164	0.049	1.0	0.190	0.132
C	0.233	0.234	0.245	0.217	0.341	0.489		0.311	0.348
G	0.138	0.236	0.1118	0.060	0.134	0.078		0.139	0.158
T	0.308	0.234	0.378	0.314	0.361	0.385		0.359	0.362
Bias	0.172	0.061	0.183	0.299	0.269	0.497	1.0	0.227	0.280
cyt *b*									
No. of bp	795	265	265	265	150	28	5	117	130
A	0.300	0.278	0.200	0.422	0.190	0.195	0.189	0.188	0.167
C	0.261	0.262	0.249	0.270	0.366	0.336	0.216	0.380	0.398
G	0.130	0.235	0.122	0.033	0.083	0.126	0.041	0.074	0.076
T	0.310	0.225	0.429	0.275	0.362	0.343	0.554	0.358	0.359
Bias	0.160	0.053	0.239	0.289	0.303	0.239	0.405	0.317	0.343
COII and cyt *b*									
No. of bp	1,478	494	494	494	263	49	6	208	217
A	0.309	0.286	0.227	0.416	0.179	0.133	0.191	0.189	0.153
C	0.248	0.249	0.247	0.245	0.355	0.401	0.180	0.350	0.378
G	0.134	0.236	0.120	0.045	0.105	0.106	0.169	0.103	0.109
T	0.309	0.229	0.406	0.293	0.361	0.361	0.461	0.359	0.360
Bias	0.157	0.048	0.208	0.280	0.288	0.348	0.280	0.280	0.317

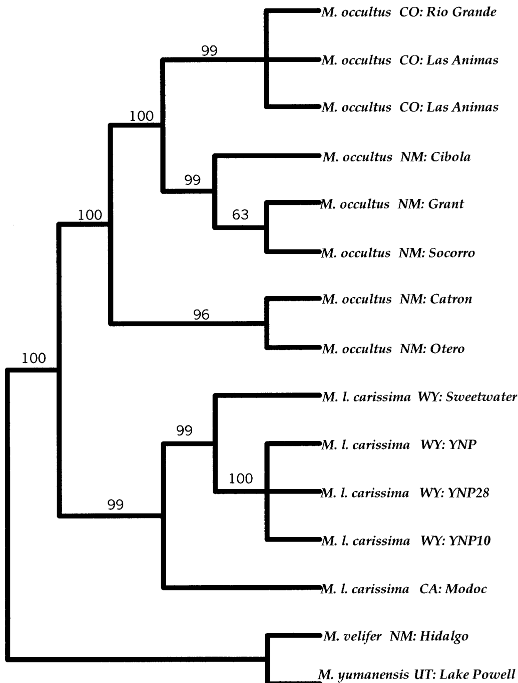

FIG. 1.—Combined cytochrome oxidase II (COII) and cytochrome-*b* (cyt-*b*) sequence data from *Myotis occultus* and *M. l. carissima* and outgroup taxa (*M. velifer* and *M. yumanensis*) were analyzed using branch-and-bound parsimony, which resulted in 1 most parsimonious tree (length L = 295 steps). Results of 500 replicates of a bootstrap analysis are included on the nodes of this tree. Legend: CO = Colorado, NM = New Mexico, WY = Wyoming, CA = California, and UT = Utah.

tion is in effect, this results in only 1 most parsimonious tree being produced. This is because there is only 1 haplotype for the specimens of *M. occultus* from Colorado, and only a single haplotype for the specimens of *M. l. carissima* from Yellowstone National Park in Wyoming. Consequently, those haplotype taxa result in unresolved trichotomies. Results of 500 replicates of a bootstrap analysis are included on the nodes of the strict consensus tree and indicate strong support at most nodes (Fig. 1).

We also performed a Kimura 2-parameter distance analysis (Kimura 1980) to partially correct for multiple substitutions. The heuristic minimum-evolution search of the Kimura 2-parameter distance analysis generated 2 trees, which were identical to the parsimony tree (L = 0.216, parsimony equivalent L = 295, CI = 0.902, RI = 0.939).

Using the 9 most parsimonious trees, a maximum-likelihood model was built to test the substitution model that best fit the data. To determine the best fit model, a series of nested hypotheses (the null hypothesis [H_0] is a special case of the alternative hypothesis [H_1]) were performed on various nucleotide substitution models. A likelihood ratio test was then performed (Goldman 1993) using the test statistic as $2(\ln L_0 - \ln L_1) = -2 \ln \lambda$, where L_0 and L_1 are the likelihood values under the null and alternative hypotheses, respectively. We then calculated the associated probability, using a chi-square distribution, with the degrees of freedom equal to the difference in number of free parameters between the 2 models.

First, the ti/tv ratios were held at an equal rate; the base frequencies were adjusted to frequencies of the combined data set found among the variable sites (Table 1). All equal rate trees had log-likelihood scores (−ln likelihood = 3,670.379) greater than the log-likelihood score of the trees in which ti/tv was estimated and were significantly lower than the model where ti/tv was held at equal rates (−ln likelihood = 3,461.058, ti/tv = 14.40, $\chi^2 = 418.642$, *d.f.* = 1, $P < 0.0001$). The lowest log-likelihood indicates the best fit; therefore, the ti/tv ratio is an important factor in this data set and must be taken into account. We also tested the fit of the data to a Poisson and gamma distribution. To test this distribution, the shape parameter (α) of the gamma distribution was estimated (10 rate categories) along with the ti/tv ratio because they are interdependent (ln likelihood = 3,447.943, ti/tv = 18.270, $\alpha = 0.457$, $\chi^2 = 26.23$, *d.f.* = 1, $P < 0.0001$). This is a significantly lower log-likelihood score than when ti/tv was estimated alone. Therefore,

these data better fit a gamma distribution than a Poisson distribution.

Using the maximum-likelihood estimates of ti/tv and α of the parsimony tree, we tested the null hypothesis of constant rates of evolution among the taxa by enforcing a molecular clock (−ln likelihood = 3,452.561). Because the null hypothesis tree does not differ significantly (χ^2 = 9.236, *d.f.* = 13, *P* = 0.755) from the unrestricted maximum-likelihood estimates, we can assume clock-like evolution (Fig. 2). The maximum-likelihood molecular-clock tree is based on a model that accounts for actual biological factors that influence the data set, so we will use the clock tree to discuss the phylogenetic relationships among these taxa because the clock tree reflects our best estimate of the divergences among the taxa in relation to each other.

Discussion

Our results suggest that *M. occultus* represents an evolutionarily distinct monophyletic lineage and that it is separated from *M. l. carissima* by sufficient genetic distance to be considered a separate species (Fig. 2). Although we cannot estimate the actual dates of divergences between these taxa because we do not have fossil dates to apply to the taxa in the tree, we inferred time between divergences by using genetic distances. For example, the maximum-likelihood, molecular-clock–corrected sequence divergence between the outgroup taxa, *M. velifer* and *M. yumanensis*, is 3.0% (Kimura 2-parameter sequence divergence = 2.6%). These 2 taxa are widely recognized as distinct species (Findley 1972; Hall 1981; Harris 1974). Graphically, this level of divergence can be seen as the line dissecting the clades on the tree (Fig. 2). The corrected sequence divergence between *M. occultus* and *M. l. carissima* is 6.1% (Kimura 2-parameter sequence divergence = 5.1%), twice as great as that between *M. velifer* and *M. yumanensis*. Although we found the sequence divergence values between *M. l. carissima* and *M. occultus* intriguing, we do not mean to imply that there is a standard "metric" that applies in a phylogenetic evaluation of other taxa. Among samples of *M. l. carissima*, the corrected sequence divergence is 2.6% (Kimura 2-parameter sequence divergence = 2.2%). This value may reflect the geographic distances between our samples (e.g., California and Wyoming), or it is possible that this value indicates undescribed variation within *M. lucifugus* in California (Harris 1974).

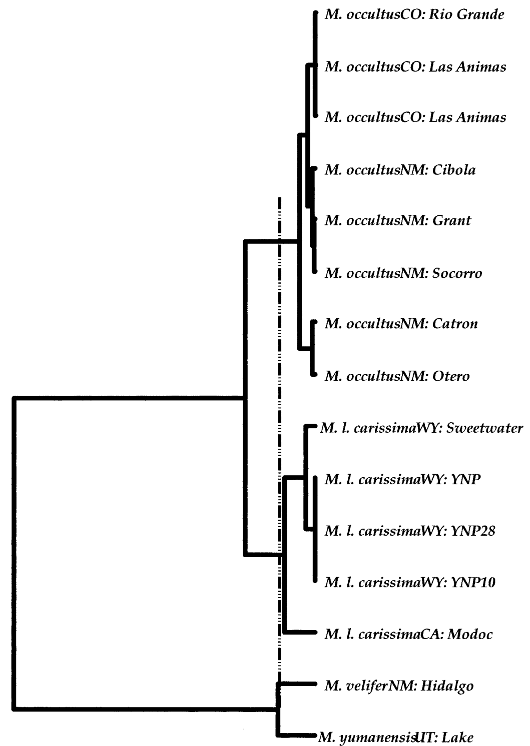

FIG. 2.—Maximum-likelihood molecular-clock tree of the combined cytochrome oxidase II (COII) and cytochrome-*b* (cyt-*b*) sequence data from *Myotis occultus* and *M. l. carissima*. This tree includes a line depicting the genetic divergence between the 2 outgroup taxa, *M. yumanensis* and *M. velifer*. These 2 taxa are considered separate species and therefore give us a measure of genetic divergence between other *Myotis* species to compare with the divergence between *M. occultus* and *M. l. carissima*. Legend: CO = Colorado, NM = New Mexico, WY = Wyoming, CA = California, and UT = Utah.

We believe that sufficient evidence exists

to corroborate specific status for the taxa in our analysis (Findley 1972; Herd and Fenton 1983). In addition, Valdez and Parkinson (pers. comm.) examined allozymic variation in the same samples of *M. l. carissima* and *M. yumanensis* from California reported here. They found the same 3 fixed allelic differences that Herd and Fenton (1983) reported, thus reinforcing the likelihood that no hybridization occurs between these 2 species. The various interpretations of morphological differences and the apparent intergradation of characters in certain geographic areas have made it difficult to reconcile the taxonomy and systematics of *M. occultus*. Findley and Jones (1967) noted that the best characters for differentiating *M. occultus* and *M. l. carissima* are number of upper premolars, length of maxillary toothrow, presence or absence of sagittal crest, and pelage coloration. Other morphological characters that may distinguish these taxa are rostrum length and slope of forehead (Hoffmeister 1986). However, Barbour and Davis (1970), Findley and Jones (1967), and Hoffmeister (1986), all believe that a zone of intergradation exists in southern Colorado and northern New Mexico. Our samples from Rio Grande and Las Animas counties, Colorado, are from this area. We identified these bats initially as *M. occultus* because they had the reddish pelage typical of that species. However, these animals are morphologically intermediate in having no sagittal crest and a complete set of premolars, as in typical *M. l. carissima*. Nonetheless, in our analysis, these specimens group consistently with *M. occultus* from New Mexico.

Our data cannot confirm or deny hybridization because we only used mitochondrial genes, which are inherited matrilineally. Hybridization can only be revealed by analyses of nuclear gene sequences. However, another possible explanation for the presence of apparent intergrades in an area is that the 2 species have converged morphologically because of some ecological factor or factors. Our data on mitochondrial gene sequences suggest that *M. occultus* and *M. lucifugus* are genetically distinct, and this may lend support to the concept of convergence over hybridization.

Harris (1974) provides insightful comments on the possible distributions and relationships of *M. l. carissima* and *M. occultus* in the late Pleistocene and Holocene and also compares their distributions to those of *M. velifer* and *M. yumanensis*. In particular, he discusses 2 different scenarios that might have occurred during the late Pleistocene. He reasons that if *carissima* and *occultus* were subspecies, then *M. occultus* must have occupied higher (montane) elevations in the southwest, to the exclusion of *M. l. carissima*, although the 2 subspecies would have interbred to the north; this scenario is the most likely to have maintained differences at the subspecific level. Our results suggest that these taxa are 2 different species, and it is his 2nd scenario that is of more interest. In this case he notes (Harris 1974:603) "If the two taxa actually are species, then *carissima*-like bats would be expected to have invaded the higher elevations, retreating north again at the end of the Pleistocene." Whereas *carissima*-like bats were at higher elevations in the southwest, *occultus*-like bats would have occupied lower elevations in the southwest, and any interbreeding between the 2 presumably would have been precluded. Interestingly, this scenario may have resulted in the Pleistocene range of *M. occultus* being divided, with bats in the Rio Grande Valley isolated from those in Arizona.

Many questions remain about the distribution of these taxa in the southwest. Harris (1974) noted that in Arizona, *M. occultus* is distributed predominantly in the highlands and upper stream reaches and that the lower Colorado River appears to support the only populations occurring at low elevations in the western part of its range (at least historically). In the lower Colorado River area, *M. occultus* would be sympatric

with both *M. yumanensis* and *M. velifer*. We echo Harris' (1974) suggestion that the identification of these low-elevation animals should be carefully rechecked. Mollhagen and Bogan (1997) suggested that *M. lucifugus* is absent from much of southern Utah (Harris [1974] implies the same) and that older specimens from that area be reexamined. The absence of *M. lucifugus* in southern Utah creates a hiatus between the range of that species in Utah and *M. occultus* in northern Arizona. In New Mexico, *M. occultus* is known from low-elevation riparian areas in the Rio Grande Valley and montane highlands, although in recent netting by two of us (EWV, MAB) at various locations in northern New Mexico, we failed to capture this species. There is only 1 record of *M. lucifugus* (=*occultus*) in Texas, from Fort Hancock in Hudspeth County, and authorities differ on the possible occurrence of the species in western Texas (Schmidly 1991; Yancey 1997). The distribution of *M. occultus* in Mexico remains enigmatic. It is unknown from Sonora, although it should be expected in the Sierra Madre Occidental (Bogan 1999), but is known from several localities in Chihuahua (Anderson 1972). Additional records occur to the south, including one from 5 km NW Texcoco, Mexico (7,600 feet, about 2,300 m) that was reported as *M. l. carissima* by Hall and Kelson (1959); this specimen has the full complement of premolars and no sagittal crest. Findley and Jones (1967) indicate that the specimen from Texcoco was especially close to the supposed intergrades between *M. lucifugus* and *M. occultus* from northern New Mexico.

We admit that there is an intuitive appeal to our results, as they accord with the known and apparent morphological variation of the 2 taxa, although questions regarding apparent convergence of the 2 species in southern Colorado and northern New Mexico remain unanswered. Correspondingly, this intuitive appeal was lacking in results of Valdez et al. (1999), who found no allozymic variation between *M. lucifugus* and *M. occultus* but suggested that *M. occultus* be retained as a subspecies because of the known morphological differences. Additional studies that include samples of all subspecies of *M. lucifugus* and from more geographic localities may help resolve lingering questions about the relationships of the 2 taxa. Although questions remain about these relationships, perhaps it is more meaningful to ask whether these results in any way affect the conservation status of these bats, and we think they do. The results of this paper make a somewhat more forceful case that *M. occultus* is a southwestern endemic, albeit relatively widespread in distribution (e.g., *M. auriculus*). It may, in fact, have an origin distinct from that of *M. lucifugus*, a situation that Findley's (1972) results seem to have foretold. Given this, we think it would be a mistake to assume that if population declines of *M. occultus* occur, they are inconsequential because they merely represent some small portion of the total population of *M. lucifugus*. Our results suggest that declines in *M. occultus* might jeopardize a unique southwestern species.

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APPENDIX I

Specimen, museum identification number and catalog number, GenBank accession number, and collection locality for cytochrome oxidase II (COII) gene and cytochrome-*b* (cyt-*b*) gene. All tissues are liver samples from the Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico. YNP = Yellowstone National Park and NK = Museum of Southwestern Biology catalog number.

Species	Catalog no.	GenBank accession no.		Locality
		COII	cyt *b*	
M. occultus	NK 34602	AF294565	AF294500	CO: Rio Grande Co.
M. occultus	NK 34578	AF294571	AF294506	CO: Las Animas Co.
M. occultus	NK 34579	AF294572	AF294507	CO: Las Animas Co.
M. occultus	NK 34560	AF294567	AF294502	NM: Cibola Co.
M. occultus	NK 34540	AF294568	AF294503	NM: Grant Co.
M. occultus	NK 34508	AF294570	AF294505	NM: Socorro Co.
M. occultus	NK 34544	AF294566	AF294501	NM: Catron Co.
M. occultus	NK 34526	AF294569	AF294504	NM: Otero Co.
M. l. carissima	NK 34610	AF294573	AF294508	WY: Sweetwater Co.
M. l. carissima	NK 3413	AF294574	AF294509	WY: YNP
M. l. carissima	NK 3428	AF294575	AF294510	WY: YNP
M. l. carissima	NK 3410	AF294576	AF294511	WY: YNP
M. l. carissima	NK 3380	AF294577	AF294512	CA: Modoc Co.
M. velifer	NK 3623	AF294578	AF294513	NM: Hildalgo Co.
M. yumanensis	NK 36150	AF294579	AF294514	UT: E. bank Lake Powell, Ribbon Canyon, San Juan Co.