

TAXONOMIC STATUS OF WHITE-BACKED HOG-NOSED SKUNKS, GENUS *CONEPATUS* (CARNIVORA: MEPHITIDAE)

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The taxonomic status of white-backed hog-nosed skunks (genus *Conepatus*, subgenus *Oryctogale*) was examined using external and cranial morphology as well as mitochondrial deoxyribonucleic acid sequence. Two species, *Conepatus leuconotus* and *C. mesoleucus*, and their subspecies were determined to represent only a single species, *C. leuconotus*. Within this species there are 3 management units, or subspecies, recognized conservatively. These subspecies are *C. l. leuconotus* (including *C. l. texensis*, *C. m. mearnsi*, *C. m. mesoleucus*, *C. m. nelsoni*, *C. m. venaticus*, *C. m. nicaraguae*, *C. m. sonoriensis*, and *C. m. filipensis*); *C. l. figginsi* (= *C. m. figginsi* and including *C. m. fremonti*); and *C. l. telmalestes* (= *C. m. telmalestes*). In the case of *C. l. figginsi* and *C. l. telmalestes*, further genetic research may indicate that these taxa are not valid, but the populations that they represent (if not extinct) will require different management strategies from the wide-ranging *C. l. leuconotus*.

Key words: *Conepatus*, conservation, hog-nosed skunks, Mephitidae, taxonomy

Many species of mammalian carnivore are provided protection under the Endangered Species Act of 1973, yet the actual number of threatened or endangered carnivores probably is much higher. The primary reason for some species of carnivores not being provided special protection is the absence of biological information pertaining to the systematics, distribution, relative abundance, and ecology of taxa of uncertain status. The unfortunate problem is that many carnivore populations have reached the point of no return prior to the collection of such biological data. As an example of a species that had almost reached that point, in 1920 an estimated 500,000 black-footed ferrets existed. That number had been reduced to a total of 18 individuals by 1987

(Dobson and Lyles 2000). Between 1851 and 1981, only 1 population of black-footed ferret had been studied (Clark 1987).

The real problems faced by those interested in the conservation of biodiversity are identifying species at risk prior to their extirpation and devising proper management schemes for the conservation of populations and species. The first step toward answering these questions is to identify unique populations through an examination of geographic variation defined by morphology or genetics or both. The uniqueness of particular stocks provides a rational basis for the identification of taxa that need special protection (Moritz 1994).

Biological information (much in the form of reports to both state and federal agencies) from surveys and research in Texas provides strong evidence of a drastic de-

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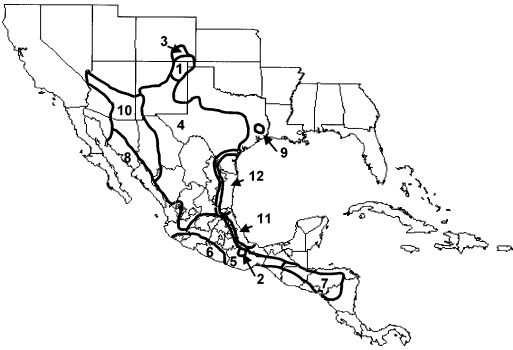


FIG. 1.—Distribution of white-backed hog-nosed skunks in North and Central America. Subspecies shown are: 1) *Conepatus mesoleucus figginsi*, 2) *C. m. filipensis*, 3) *C. m. fremonti*, 4) *C. m. mearnsi*, 5) *C. m. mesoleucus*, 6) *C. m. nelsoni*, 7) *C. m. nicaraguae*, 8) *C. m. sonoriensis*, 9) *C. m. telmalestes*, 10) *C. m. venaticus*, 11) *C. leuconotus leuconotus*, and 12) *C. l. texensis*.

cline of populations of hog-nosed skunks (genus *Conepatus*) in the eastern region and the Gulf Coast region of Texas (J. Drago et al., in litt.; J. Rappole and A. Tipton, in litt.; Schmidly 1983). Taxonomically these populations are considered as 2 species (Davis and Schmidly 1994; Jones et al. 1997; Wozencraft 1993).

There are currently 5 recognized species in this genus that occur from southern Colorado to Argentina (Wozencraft 1993). Two species, *Conepatus chinga* and *C. humboldtii*, occur only in South America. *C. semistriatus* occurs from Central America to South America. *C. mesoleucus*, with 10 subspecies (Hall 1981), ranges from southwestern United States through most of Mexico and into Central America (Fig. 1). *C. leuconotus* is represented by 2 subspecies occurring along the coastal plain of the Gulf of Mexico from Veracruz to the southern tip of Texas (Fig. 1). *C. leuconotus* is likely parapatric with the closely related and widely distributed western hog-nosed skunk, *C. mesoleucus* (Dragoo et al. 1989).

Since the designation of *C. leuconotus* and *C. mesoleucus* as distinct species (Audubon and Bachman 1851; Lichtenstein

1832), the systematics of named taxa within the genus has been controversial. Based on the descriptions of the different species, Coues (1877) could find no justification for more than a single species in the United States and Mexico. In support of Coues' contention, Hall and Kelson (1952) reported that the only significant difference between *C. leuconotus* and *C. mesoleucus* was size, with color pattern differences between these 2 taxa being at most an indicator of geographic variation rather than a consistent character for the recognition of distinct species. They further stated that proof of intergradation, or lack of it, could best be sought by obtaining specimens from areas between the distributions of these 2 taxa. Raun and Wilks (1961) subsequently reported a specimen from Atascosa County, Texas that, based on size and color pattern, was intermediate between *C. mesoleucus* and *C. leuconotus*. Raun and Wilks (1961: 205) stated "Although the majority of the published checklists treat *mesoleucus* and *leuconotus* as separate species, most workers agree that the 2 should be conspecific."

Part of the current controversy over the number of species and uniqueness of geographic variation within the genus can be related to taxonomic characters and techniques used in these early systematic studies. For instance, the taxonomy of hog-nosed skunks is based on cranial morphology, body size, and color patterns, all of which are quantitative traits that may be strongly influenced by environmental factors. In spite of this fact, with the exception of Van Gelder's (1968) study of nongeographic variation of cranial measurements and color patterns within hog-nosed skunks from Uruguay, no detailed analysis of nongeographic variation of taxonomic characters used to describe hog-nosed skunk taxa has been conducted. This is important, because subspecies in Texas and Colorado that are either endangered or extinct have been described based on these characters that are potentially influenced by environment.

A detailed systematics study of hog-nosed skunk taxa from Texas and adjacent geographic regions is required if one is to make informed decisions concerning the uniqueness of declining genetic stocks of hog-nosed skunks in the United States. In an effort to assess taxonomic status of currently recognized species and subspecies in the United States (Hall 1981), 2 experimental approaches were employed. First, specimens of hog-nosed skunks were measured for color patterns and 24 cranial measurements. Second, the degree of genetic differentiation was examined by sequencing selected regions of the mitochondrial control region (D-loop).

MATERIALS AND METHODS

We examined 976 specimens from 29 museum collections (Appendixes I and II) for color pattern analyses, cranial measurements, or deoxyribonucleic acid (DNA) sequence analyses.

Morphological analyses.—Photographs were taken of 85 museum skins to observe variation in color pattern. These skins included 21 *C. l. texensis*, 11 *C. m. telmalestes*, and 53 *C. m. mearnsi*. Specimens were assigned subspecies names based on geographic locality (Hall 1981) and grouped into 1 of 6 color pattern categories (Fig. 2A). These specimens also were grouped into categories based on whether the terminal white stripe of the head was wedge-shaped, curved, or truncated (Fig. 2B).

Twenty-four cranial characters were measured to the nearest 0.1 mm with dial calipers from a total of 614 specimens. These measurements, described by Van Gelder (1968), were used to examine patterns of morphological variation. Tooth wear and suture lines were used to determine age of specimens. Descriptive statistics (mean, range, and *SE*), and multivariate analyses were all performed using the Statistical Analysis System 84.2 (SAS Institute Inc. 1982a, 1982b).

Two preliminary analyses were performed in an effort to determine if individuals from different age and sex classes could be pooled for between-group comparisons. Data were log transformed and any character with a coefficient of variation (*CV*) >5% after transformation were excluded from further analysis. In the 1st analysis, individuals from all 4 classes (adult males,

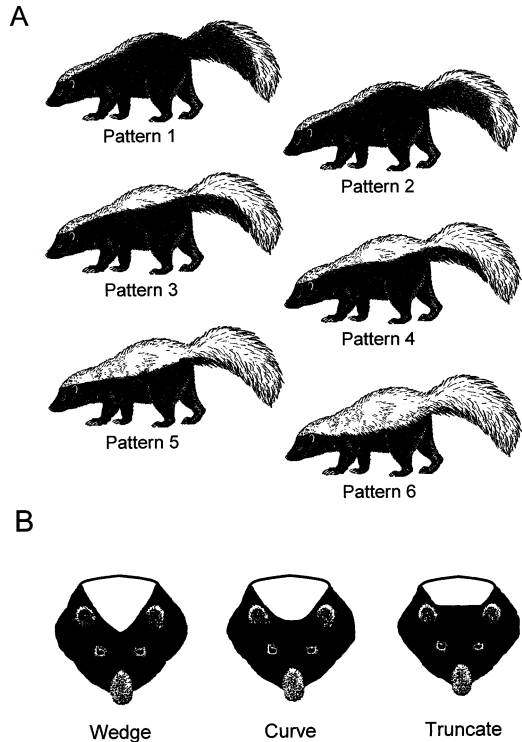


FIG. 2.—A) Six categories of dorsal stripe patterns in hog-nosed skunks. These categories are pattern 1, the median dorsal stripe terminates leaving no white on the rump, and >50% of tail is white to the tip (the width of the stripe near the shoulders varies from narrow to wide); pattern 2, median dorsal stripe and white on tail are connected by a narrow stripe of white, basal 3rd of tail black on the sides (width of stripe between shoulders ranges from narrow to wide); pattern 3, median dorsal stripe is narrow between shoulders and the hips, with only a slight constriction at hips; pattern 4, median dorsal stripe narrow at neck and expanded in midregion of back; pattern 5, median dorsal stripe wide from neck to hips; pattern 6, median dorsal stripe completely covers back. B) Three head-stripe patterns in hog-nosed skunks: wedged, curved, and truncated.

subadult males, adult females, and subadult females) were examined for variation using principal components analysis (PCA). Second, Tukey's Student range test was used to compare the 4 classes for significant differences related to size. Both PCA and discriminant function analyses were used to evaluate degree of differ-

entiation among populations of hog-nosed skunks.

Genetic analyses.—Twenty-six specimens were examined by mitochondrial DNA (mtDNA) sequence analyses of the cytochrome-*b* gene. DNA from frozen tissue (heart, liver, or kidney) was isolated using either a direct purification of mtDNA by cesium chloride:propidium iodide gradient centrifugation (Brown 1980) or phenol:chloroform extraction of total DNA (Hillis et al. 1996). Total genomic and mtDNA from museum specimens was isolated using a modified technique described by Pääbo et al. (1988).

The entire mitochondrial control region (D-loop) from 3 species (*C. leuconotus*, *C. mesoleucus*, and *C. chinga*) was amplified using polymerase chain reaction (PCR). Double-stranded DNA products of the D-loop were amplified with primers L16272 (5'-TACACTGGTCTTGTAAC-3') and H1008 (5'-AAGGCTAGGACAAACCT-3'). The names of the oligonucleotides indicate the heavy (H) or light (L) strand and the position of the 3' end of the oligonucleotide according to the numbering of *Phoca vitulina* (Arnason and Johnsson 1992). Double-stranded DNA products were obtained with PCR amplification using *Taq* DNA polymerase (Saiki et al. 1986, 1988), following similar procedures used by Dragoo et al. (1993). As suggested by Pääbo (1990), all PCR reactions had amplification controls, in which water was added to the reaction in the place of DNA extract. PCR products were sequenced as described by Dragoo et al. (1993).

The Clustal V program (Higgins et al. 1992) and visual inspection were used to align the entire D-loop sequences. These aligned sequences were used to identify regions within the D-loop that might be suitable for the design of primers bracketing regions that were both variable and small in size (≤ 250 base pairs [bp]). Smaller regions of the D-loop were used for more extensive comparisons of variation among taxa of *C. mesoleucus* and *C. leuconotus*. This approach was used because DNA isolated from museum specimens was degraded, reducing the ability to isolate larger fragments of D-loop via PCR amplification.

After comparing D-loop variation, 2 regions were selected for detailed comparisons of nucleotide sequence variation within and among several subspecies of hog-nosed skunks. These 2 regions included 1) approximately 170-bp region bracketed by primers L398 (5'-CCTCTCA-

AATGGGACATCTCG-3') and H601 (5'-GGTTGTATGATGCGGGTAAATG-3'); and 2) approximately 230-bp region bracketed by primers L724 (5'-CCGCCAAACCCCAAAAA-3') and H1008. These 2 regions were examined for detailed phylogenetic analyses of specimens of mephitids including the outgroup taxon *Mydaus* (Dragoo and Honeycutt 1997), 2 striped skunks (*Mephitis mephitis* and *M. macroura*), eastern spotted skunk (*Spilogale gracilis*), *C. chinga*, 4 representatives of *C. leuconotus*, 7 individuals of *C. m. mearnsi* from several geographic localities, and subspecies *C. m. sonoriensis*, *C. m. figginsi*, and *C. m. venaticus*, which represent more peripherally isolated races. Many of these sequences were obtained from DNA extracted and amplified from museum specimens. The eastern Texas hog-nosed skunk (*C. m. telmalestes*) and *C. m. fremonti* were not examined, because we were unable to obtain PCR amplification products from museum skin samples. All sequences have been deposited in GenBank with accession numbers AY159816–AY159836.

Parsimony analyses of the aligned D-loop sequences were conducted with PAUP 3.1.1 (Swofford 1993). Variable nucleotide positions were treated as unordered discrete characters, and insertion or deletion or both characters were coded as a new state. A phylogenetic tree was obtained using 1,000 heuristic searches (tree bisection and reconnection algorithm) in which input order of taxa was randomized. This phylogenetic analysis was used to evaluate the uniqueness of any recognized subspecies and species of *Conepatus* relative to other taxa of skunks.

RESULTS

Variation in color pattern.—Relative to 6 categories of stripe pattern, *C. m. mearnsi* was represented in 5 of 6 categories, with 1.9% of the specimens in category 2, 18.9% in category 3, 13.2% in category 4, 41.5% in category 5, and 24.5% in category 6 (Fig. 3A). The terminal white stripe on the head was wedge-shaped in 26.4%, curved in 54.7%, and truncated in 18.9% (Fig. 3B). *C. m. telmalestes* was represented in 4 of 6 categories, ranging from 9.1% in category 4 to 45.5% in category 3, and subsets of these specimens grouped in all 3 categories of stripe pattern on the head region (Figs.

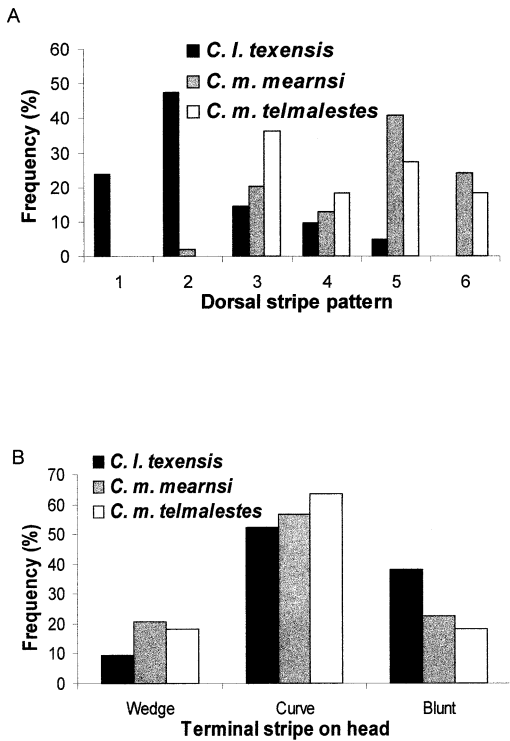


FIG. 3.—Observed frequency for hog-nosed skunks (*Conepatus leuconotus texensis*, *C. mesoleucus mearnsi*, and *C. m. telmalestes*) in Texas and adjacent states for A) dorsal-stripe patterns and B) head-stripe patterns.

3A and 3B). The Gulf Coast hog-nosed skunk, *C. l. texensis*, also was represented in 5 of 6 color-pattern categories (Fig. 3A), with 23.8% in category 1, 47.6% in category 2, 14.3% in category 3, 9.5% in category 4, and 4.8% in category 5. Again, there were representative specimens for all 3 head patterns (Fig. 3B). Also in Fig. 3A, there was a trend for *C. l. texensis* specimens to have a stripe pattern more like categories 1 and 2, whereas more of the *C. m. mearnsi* individuals were like categories 4 and 5. Nevertheless, considerable overlap in color pattern on both the back and head was observed among all specimens.

Morphological variation.—Descriptive statistics of cranial measurements for each nominal taxon examined are available, either electronically or as hard copy, and ar-

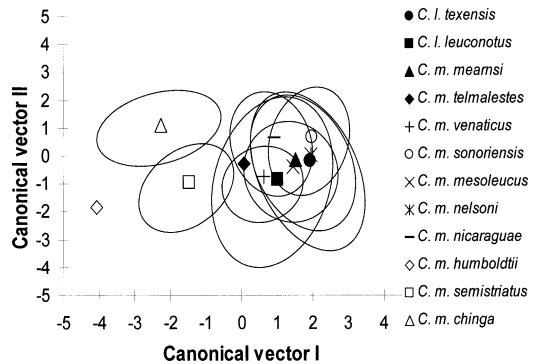


FIG. 4.—Plot of the first 2 canonical vectors obtained from discriminant function analyses of cranial measurements showing the mean centroids and 95% confidence ellipses for *Conepatus chinga*, *C. humboldtii*, *C. semistriatus*, *C. leuconotus leuconotus*, *C. l. texensis*, *C. mesoleucus mesoleucus*, *C. m. mearnsi*, *C. m. nelsoni*, *C. m. nicaraguae*, *C. m. sonoriensis*, *C. m. telmalestes*, and *C. m. venaticus*.

chived at the Museum of Southwestern Biology. Nongeographic variation in *C. m. mearnsi* indicated that males are larger than females for the measurements recorded in this study, and a Tukey's Student range test demonstrated a significant difference between males and females for most of the measurements. Therefore, all further analyses were conducted separately for males and females.

A PCA for females was conducted using the 21 cranial characters with $CV < 5$. Because the 1st principal component primarily is related to size, it was eliminated, and principal components 2–21 were used in a discriminant function analyses (Owen 1987).

We used 228 females in this discriminant function analyses. Because males had a pattern similar to that of females, results are not reported for males. The first 2 canonical vectors accounted for 72% of the variation in the 21 cranial characters entered into the model (Fig. 4). Small sample sizes for *C. m. telmalestes*, *C. l. leuconotus*, and *C. humboldtii* precluded derivation of a 95% confidence limit for these taxa. Also, *C. m. figginsi*, *C. m. fremonti*, and *C. m. filipensis*

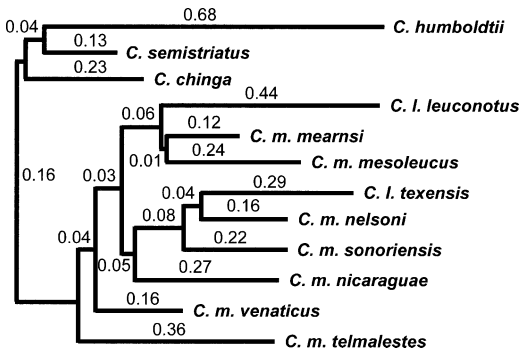


FIG. 5.—Neighbor-joining distance phenogram derived using Manhattan distances (calculated from canonical vectors derived from principal components 2–21 of cranial measurements) for *Conepatus chinga*, *C. humboldtii*, *C. semistriatus*, *C. leuconotus leuconotus*, *C. l. texensis*, *C. mesoleucus mesoleucus*, *C. m. mearnsi*, *C. m. nelsoni*, *C. m. nicaraguae*, *C. m. sonoriensis*, *C. m. telmalestes*, and *C. m. venaticus*. Tree rooted using midpoint method. Minimum evolution score = 3.80728, and numbers above branches represent branch lengths.

could not be included in analyses because of missing values for specimens, unknown sex, or existence of only a single specimen.

Three of the 4 groups represented South American and Central American species, *C. chinga*, *C. humboldtii*, and *C. semistriatus* (Fig. 4). The 4th group represented a series of overlapping clusters depicting subspecies of both *C. mesoleucus* and *C. leuconotus*. There was no distinctive break among taxa represented in this 4th group.

Canonical vectors obtained from this analysis were used to produce taxonomic distances (Manhattan distances). Phenetic variation was evaluated using distance values and neighbor-joining procedure (Saitou and Nei 1987). As seen in the discriminant function analyses (Fig. 4), Central and South American species were grouped separately from representative taxa of *C. leuconotus* and *C. mesoleucus*. The 2 subspecies of *C. leuconotus* were intermixed with the subspecies of *C. mesoleucus* (Fig. 5).

Genetic variation in mitochondrial D-loop.—Twelve equally most parsimonious

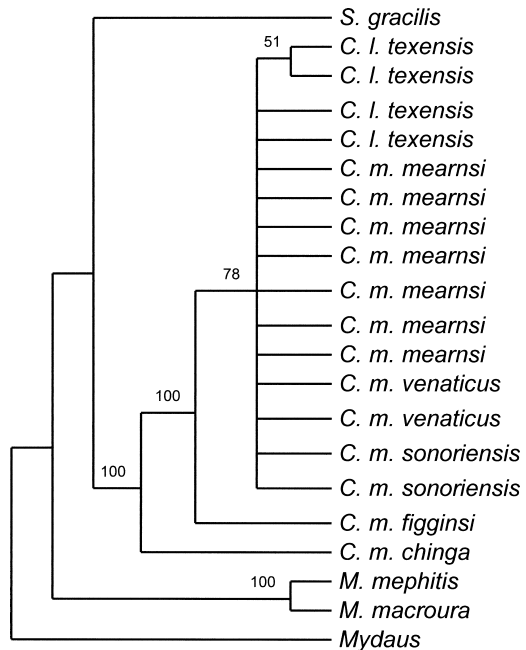


FIG. 6.—A 50% majority rule consensus tree derived from 12 equally parsimonious trees, resulting from a parsimony analysis of 427 base pairs of the D-loop using heuristic search in PAUP. Numbers along branches denote bootstrap values or support for selected nodes on the tree. Tree length = 166, consistency index = 0.843, and retention index = 0.832.

trees (derived using a heuristic search in PAUP) of length 166, consistency index (CI) of 0.843, and retention index (RI) of 0.832 were generated from the analyses (Fig. 6). Of the 427 characters used in this analysis, 98 were informative. Two specimens of *C. leuconotus* from the same locality in Tamaulipas, Mexico, formed a monophyletic group. The only major separation among the various North American hog-nosed skunks involved *C. m. figginsi*, which grouped separately from the other individuals examined. A South American species, *C. chinga*, was the most divergent taxon, differing from the others by approximately 6.28% (Kimura 2-parameter sequence divergence—Kimura 1980). *C. m. figginsi* differed from the other major clade by 2.5%, and skunks within the clade con-

taining the remaining individuals averaged 0.65% sequence divergence. The 2 species of *Mephitis* differed by approximately 12%.

DISCUSSION

Current status of hog-nosed skunks.—Hog-nosed skunk populations are declining in number throughout a major portion of their historical range in the United States. The eastern Texas subspecies, *C. m. telmalestes*, is presumed extinct throughout its range in the Big Thicket region (Schmidly 1983). To quote Bailey (1905:205), “the white-backed skunk is said to be the commonest species, and under a trapper’s shed at a ranch on Tarkington Prairie in November 1904, I saw eight or ten of their skins hanging up to dry with a small number of skins of *M. mesomelas* [striped skunk].” No new specimens of this subspecies have been collected in the Big Thicket area of Texas since Bailey’s report in 1905. Although Raun and Wilks (1961) found a road-killed *Conepatus* in Waller County, 30 miles SW of the range of *C. m. telmalestes*, they were unable to identify the specimen to species but suggested (Raun and Wilks 1961:204) it was “geographically *C. mesoleucus* (possibly *C. m. telmalestes*).” The disappearance of *C. m. telmalestes* is even more apparent when one considers that in 7 years of concentrated research within the range of this subspecies, no direct evidence of the hog-nosed skunk was obtained (D. Schmidly et al., in litt.).

A likely cause for the decline of populations of hog-nosed skunks may be the increase in the number of trappers or possibly the increase of feral hogs that have been introduced into the area. Feral hogs eat a variety of items, including fruits, roots, mushrooms, and invertebrates, depending on the season. Their rooting behavior is competitive with the rooting behavior of hog-nosed skunks. Feral hogs can have detectable influences on wildlife and plant communities as well as on domestic crops and livestock. Extensive disturbance of vegetation and soil occurs as a result of

their rooting habits. Feral hogs compete, to some degree, with several species of wildlife for some foods (Davis and Schmidly 1994).

Another population in southern Texas is potentially threatened or endangered as well. J. Rappole and A. Tipton (in litt.) presented a report to the United States Fish and Wildlife Service, Office of Endangered Species, that briefly summarized information on terrestrial mammals that might be declining, threatened, or endangered in Texas. While not currently assigned to special protective status under federal law, they recommended that *C. l. texensis* be considered as “threatened.” Research efforts by D. Schmidly et al. (in litt.) and J. Dragoo et al. (in litt.) agreed with J. Rappole and A. Tipton (in litt.).

In the case of *C. l. texensis* (Gulf Coast hog-nosed skunk), 80% of all museum specimens from Texas were collected before the turn of the century (mid-1800 to 1900), 13% between 1901 and 1950, and only 7% after 1950 (J. Dragoo et al., in litt.). One additional specimen was salvaged in 2000 (M. Tewes, pers. comm.). Recent surveys and detailed scent-station studies in southern Texas also verify reduction of this subspecies’ range and numbers in the lower Rio Grande Valley, possibly as a result of habitat loss (J. Dragoo et al., in litt.; Stapper 1989). The question as to whether or not this population has experienced a similar reduction of numbers throughout its range in Mexico is more difficult to answer.

What has caused the demise of hog-nosed skunk populations in southern Texas? As reported by Tewes and Schmidly (1987), in the past 60 years, 95% of native vegetation in the Rio Grande Valley has been transformed from subtropical plant communities to cotton, sorghum, sugar cane, vegetable crops, and citrus orchards. Because hog-nosed skunks generally are associated with rough rocky areas (Patton 1974) and brushy habitat (Schmidly and Hendricks 1984), the conversion of native vegetation to row-crop agriculture may be

partially responsible for the decline of hog-nosed skunks. However, habitat modification may not be the primary cause of the observed decline, because specimens of *C. l. leuconotus* have been collected in cultivated areas near Veracruz, Mexico (Hall and Dalquest 1963). A more direct cause of population decreases may be associated with use of pesticides in agriculture. Hog-nosed skunks are primarily insectivorous (Bailey 1905; Davis 1951; Hall and Dalquest 1963; Patton 1974; Seton 1926), and use of pesticides has increased throughout their range in conjunction with row-crop agriculture. However, no data are available to support or refute this hypothesis.

Finally, no new specimens of hog-nosed skunks in Colorado, referred to as *C. m. figginsi* and *C. m. fremonti*, have been collected since 1920 and 1933, respectively (Armstrong 1972; Miller 1925, 1933; Warren 1921). Armstrong (1972) examined these specimens and suggested that rather than distinct subspecies they may represent sex and age variants of the more widely distributed *C. m. mearnsi*.

Color pattern as an indicator of taxonomic distinction.—Individual variation in color is quite common within the family Mephitidae. Davis (1974) and Hall (1946) found stripe patterns to be highly variable in the striped skunk. Hall (1946) found 1 litter of striped skunk in Kansas that contained 3 of 4 distinct color patterns recognized by fur traders, and Hall and Villa-R. (1949) found 6 hooded skunks, collected within a 3-mile radius, that ranged from having a single white spot on the head to a white stripe down the back and tail, as well as a stripe down each side. Van Gelder (1968) made a similar observation for a population of *Conepatus* from Uruguay, and Patton (1974) found a specimen of *C. m. mearnsi* from Terrell County, Texas, that had the "typical" *C. leuconotus* pattern.

When Lichtenstein (1832) originally described *C. leuconotus* and *C. mesoleucus*, he relied heavily on color patterns to distinguish the 2 species. He felt that characters

such as dentition were arbitrary and not of much use to taxonomists, but that color pattern was more reliable. Merriam (1902) and Bailey (1905) relied on Lichtenstein's (1832) description of the species when they described the subspecies in Texas, and most recent keys of hog-nosed skunks have emphasized color pattern as a major distinguishing characteristic for the identification of taxa (Davis 1974; Hall 1981; Schmidly 1984).

Although color pattern has been used in the past as a taxonomic character to diagnose unique populations and taxa of hog-nosed skunks, a closer examination of color-pattern variation suggests that the degree of variation associated with this character is too large for any meaningful use as a diagnostic character. For instance, Goldman (1922) realized that color pattern in hog-nosed skunks is not a valid taxonomic character. Under the remarks section of his description of *C. m. venaticus* (Arizona hog-nosed skunk) he states (Goldman 1922:40), "The extension of white of upper parts is variable as usual in the species." Our study of color pattern supports Goldman's (1922) statement. In Lichtenstein's (1832) description, the terminal shape of the stripe on the head was used as a diagnostic feature. Nevertheless, in our examination of this characteristic, considerable overlap among recognized taxa was found, with all 3 categories (sharp, wedge-shaped, and truncated) observed for different species and subspecies. The same can be said for stripe pattern on the back and tail. Although there is a trend for hog-nosed skunks from the northwestern part of their range to have more white on the back, there is still considerable variation with respect to stripe pattern, making it difficult to identify either species or subspecies on the basis of color pattern. Therefore, if color pattern were used as the sole characteristic for the identification of distinct groups of hog-nosed skunks, all populations of white-backed hog-nosed skunks would belong to the same taxonomic group.

Morphometric variation.—Although the 3 Central American and South American species are distinct from species seen in Mexico and the United States, the evidence for recognition of currently named species and subspecies of North American *Conepatus* is not convincing. There is a trend toward *C. leuconotus* being somewhat larger than *C. mesoleucus*, yet the phenetic analyses performed for representative subspecies of these 2 taxa did not reveal any apparent difference that would merit recognition of these 2 forms as distinct species. In addition, morphological distinction among most of the currently recognized subspecies of *C. mesoleucus* also is not apparent.

Mitochondrial gene tree.—Mitochondrial DNA has proven useful for examining patterns of phylogeographic variation in many species of vertebrates (Avisé et al. 1987), and in many cases, patterns of mtDNA variation have been much more effective than traditional taxonomy in defining units of conservation (Avisé 1989, 1992; Avisé and Nelson 1989; Bowen et al. 1991, 1993; Morin et al. 1994).

In terms of the patterns of mtDNA variation in hog-nosed skunks, the phylogenetic relationships derived from the D-loop sequence data are not congruent with traditional taxonomic designations. As mentioned above, most species and subspecies of hog-nosed skunks were named originally on the basis of limited phenotypic information that reflected either differences in color pattern or size. As seen in Fig. 6, there is no difference between *C. leuconotus* and *C. mesoleucus*, with only *C. chinga* and possibly *C. m. figginsi* representing unique lineages relative to the larger clade containing the remaining taxa from North America.

Moritz (1994) has provided a discussion regarding the use of genetics and phylogenetics to identify “evolutionary significant units” and “management units” in conservation biology. In terms of such units, he suggested that evolutionary significant units

represent historically isolated and distinct populations. As pointed out by Moritz, the identification of such units is important to long-term management of biodiversity. The criterion set for the identification of evolutionary significant units is that members of such units should reflect reciprocal monophyly with regard to mtDNA haplotype relationships as well as significant divergence in terms of allelic variation at nuclear loci. In most respects an evolutionary significant unit is equivalent to a phylogenetic species (Cracraft 1989). No mention was made regarding morphological divergence. With respect to this criterion, an evolutionary significant unit should be unique from other such units in terms of its mtDNA phylogeny. Based on our data, at most 3 major lineages could be recognized as evolutionary significant units.

Taxonomy of white-backed hog-nosed skunks.—Morphologically, there is no clear separation among named subspecies and species of *Conepatus* in the United States and Mexico, whereas South American taxa consistently are distinct on the basis of cranial measurements, overall color pattern, and genetics. The patterns of mtDNA variation among North American populations are congruent with detailed morphological assessment, except that *C. m. figginsi* groups separately from the other taxa examined. Although the small sample sizes and quality of existing specimens precluded a detailed analysis of a few subspecies from Mexico and Colorado, we suggest that, on the basis of the overall patterns seen in the taxa that were examined, it is unlikely that these subspecies are morphologically distinct. However, we do withhold a decision on *C. m. telmalestes* and *C. m. fremonti* until genetic data can be obtained. In all likelihood, the 2 Colorado subspecies, *C. m. figginsi* and *C. m. fremonti*, are genetically similar. It may be possible to verify this if mtDNA fragments could be amplified from the 1 skin that exists for *C. m. fremonti*.

As a result of these findings, we make the following recommendations regarding

taxonomy of hog-nosed skunks. First, based on morphology, genetics, or both, the 3 taxa *C. chinga*, *C. semistriatus*, and *C. humboldtii* from Central and South America should each be recognized as a distinct species. These are the striped hog-nosed skunks of the subgenus *Marputius* (Merriam 1902). Second, based on results from the combined morphological and genetic analyses, we recommend that only 1 species of white-backed hog-nosed skunk (subgenus *Oryctogale*; Merriam 1902) be recognized in North America. According to Lichtenstein (1832) *C. leuconotus* has page priority. Third, an examination of morphological and genetic variation throughout most of the range of the inclusive species *C. leuconotus* suggests that many of the currently recognized subspecies should be synonymized. White-backed hog-nosed skunks for the most part can be treated as a distinct taxonomic unit. However, there are 2 populations (*C. l. telmalestes* and *C. l. figginsi*) on the periphery of the range that could warrant unique management strategies. In this regard, we conservatively recommend that only 3 subspecies (*C. l. leuconotus*, *C. l. telmalestes*, and *C. l. figginsi*) be maintained. All other nominal taxa of white-backed hog-nosed skunks are synonymized under one or another of these subspecies.

Conepatus leuconotus leuconotus
(Lichtenstein 1832)

Mephitis leuconata Lichtenstein 1832. Darstellung neuer oder wenig bekannter Säugethiere in Abbildungen und Beschreibungen von fünf und sechzig Arten auf funfzig colorirten Steindrucktafeln nach den Originalen des zoologischen Museums der Universität zu Berlin, Pl. 44, Fig. 1, type from Río Alvarado, Veracruz.

Mephitis mesoleuca Lichtenstein 1832. Darstellung neuer oder wenig bekannter Säugethiere in Abbildungen und Beschreibungen von fünf und sechzig Arten auf funfzig colorirten Steindrucktafeln

nach den Originalen des zoologischen Museums der Universität zu Berlin, Pl. 44, Fig. 2, type from near Chico, Hidalgo, Mexico.

Conepatus leuconotus Merriam 1902. Proceedings of the Biological Society of Washington 15:161

Conepatus leuconotus texensis Merriam 1902. Proceedings of the Biological Society of Washington 15:162, type from Brownsville, Lower Rio Grande, Texas.

Conepatus sonoriensis Merriam 1902. Proceedings of the Biological Society of Washington 15:162, type from Camoa, Rio Mayo, Sonora, Mexico.

Conepatus mesoleucus Merriam 1902. Proceedings of the Biological Society of Washington 15:163.

Conepatus mesoleucus mearnsi Merriam 1902. Proceedings of the Biological Society of Washington 15:163, type from Mason, Mason County, Texas.

Conepatus filipensis Merriam 1902. Proceedings of the Biological Society of Washington 15:163, type from Cerro San Felipe, Oaxaca, Mexico.

Conepatus pediculus Merriam 1902. Proceedings of the Biological Society of Washington 15:164, type from Sierra Guadalupe, Coahuila, Mexico.

Conepatus nicaraguae Allen 1910. Bulletin of the American Museum of Natural History 28:106, type from San Rafael del Norte, Nicaragua.

Conepatus mesoleucus venaticus Goldman 1922. Journal of Mammalogy 3:40, type from Blue River (Cosper Ranch), 12 miles S of Blue, Arizona.

Conepatus mesoleucus nelsoni Goldman 1922. Journal of Mammalogy 3:41, type from Armeria (near Manzanillo), Colima, Mexico.

Conepatus mesoleucus nicaraguus Goodwin 1946. Bulletin of the American Museum of Natural History 87:437.

Conepatus mesoleucus filipensis Hall and Kelson 1952. University of Kansas Publications, Museum of Natural History 5: 335.

Conepatus mesoleucus pediculus Hall and Kelson 1952. University of Kansas Publications, Museum of Natural History 5: 335.

Conepatus mesoleucus sonoriensis Hall and Kelson 1952. University of Kansas Publications, Museum of Natural History 5: 335.

Conepatus leuconotus telmalestes
(Bailey 1905)

Conepatus mesoleucus telmalestes Bailey 1905. North American Fauna 25:203, type from Big Thicket, 7 miles northeast of Sour Lake, Texas.

Conepatus leuconotus figginsi
(Miller 1925)

Conepatus mesoleucus figginsi Miller 1925. Journal of Mammalogy 6:50, type from Furnace Canyon, western Baca County, Colorado.

Conepatus mesoleucus fremonti Miller 1933. Proceedings of the Colorado Museum of Natural History 12:1, type from Garden Park, near Canon City, Fremont County, Colorado.

RESUMEN

Se revisó el estado taxonómico del zorrillo cadeno (género *Conepatus*, subgénero *Oryctogale*) usando morfología cranial y externa así como la secuencia de DNA mitocondrial. Se determinó que las dos especies, *Conepatus leuconotus* y *C. mesoleucus* así como sus respectivas subespecies representan sólo una especie, *C. leuconotus*. Dentro de esta especie existen al menos tres unidades o subespecies reconocidas. Estas subespecies son: *C. l. leuconotus* (incluye *C. l. texensis*, *C. m. mearnsi*, *C. m. mesoleucus*, *C. m. nelsoni*, *C. m. venaticus*, *C. m. nicaraguae*, *C. m. sonorensis* y *C. m. filipensis*); *C. l. figginsi* (= *C. m. figginsi* e incluye *C. m. fremonti*); y *C. l. telmalestes* (= *C. m. telmalestes*). En el caso de *C. l.*

figginsi y *C. l. telmalestes* investigaciones futuras podrán indicar que este taxa no es válido, pero sus poblaciones (probablemente extintas) requerirán diferentes estrategias de manejo que las de amplia distribución como *C. l. leuconotus*.

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- 172187); Cordova (AMNH 30526); Patrero Llano (KU 29995); Rio Blanco, 20 km WNW Piedras Negras (KU 17898, 17899).
- Conepatus leuconotus texensis*.—MEXICO: San Luis Potosi: 12 km SE El Salto (MSUMZ 59); El Salto Falls (MSUMZ 58). Tamaulipas: 19 mi W Victoria (KU 100726); La Pesca (KU 57000); Mier (USNM 39655); Mulato (UMMZ 61391); San Carlos Mountains Rancho Carricitos (TCWC 30653, 33329, 48374); 7 mi W La Pesca (MSUM 5683). UNITED STATES: Texas: Aransas County: Rockport (AMNH 5130, 5883). Brooks County: 20 mi S Falfurrias (TCWC 4963). Cameron County: Brownsville (KU 1269, 1273–1276; USNM 29792, 32689, 32690, 33128, 33129, 33865; 34353, 34354, 34856–34858, 36353, 45131, 46687). Kleberg County: 6 mi W Kingsville (TCWC 21348–21350); Kingsville (AMNH 70341). Webb County: Laredo (USNM 24839, 24840, 24842).
- Conepatus mesoleucus figginsi*.—UNITED STATES: Colorado: Baca County: Furnace Canon (DMNH 1961, 1964, 2246, 2332, 2337, 2338, 2372, 2373, 2376). Oklahoma: Cimarron County: 3 mi N Black Mesa (OUM uncataloged); 2 mi NE base of Black Mesa (ECOSU 416); Kenton (USNM 248214).
- Conepatus mesoleucus filipensis*.—MEXICO: Oaxaca: Cerro San Felipe (USNM 68172).
- Conepatus mesoleucus fremonti*.—UNITED STATES: Colorado: Fremont County: Garden Park near Canon City (DMNH 2506).
- Conepatus mesoleucus mearnsi*.—MEXICO: Chihuahua: 18 mi SW Gallego (ANSP 19992); Arroyo del Nudo 30 mi SW Chihuahua (MVZ 121824); Saucedo 27 mi W Parral (MVZ 76291). Coahuila: (USNM 80191); Escantada (KU 34560); 12 mi N, 12 mi W Jimenez (KU 49628); 2 mi W Jimenez (KU 49629); 3 mi SE Torreon (KU 40773); 5 mi NW Piedra Blanca Sierra del Carmen (MVZ 117020, 117021, 124190); 8 mi W Nadadores (MSUM 4109); Don Martin (KU 34559); Sierra Guadalupe (USNM 116953); Sierra Guadalupe 10 mi S, 5 mi W General Cepedo (KU 56999). Durango: 3.5 km SE Atotonilco (MSUM 13856); 4 mi SW La Pila (MSUM 876); 7 mi NW La Resolana (MSUM 10253); Rio Nazas (USNM 3377, 20898). Guadalajara: (AMNH 16651, 16652). Guerrero: (UMMZ 81032); Rancho Los Margaritas 28 mi S, 17 mi W Vicente (MSUM 877). Jalisco: 2 mi SW Ameia (KU 30975); 7 mi SSW Tequila (KU 105877); 8 mi NW Guadalajara

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APPENDIX I

Specimens examined.—The 976 specimens examined for morphology are listed here by museum acronym (Hafner et al. 1997).

Conepatus leuconotus leuconotus.—MEXICO: Veracruz: 24 mi S Veracruz (AMNH 204288, 204289); 7 mi N Alverado (AMNH

(KU 40177); Toliman (KU 109463, 109464); Zapotlan (USNM 34336). Nuevo Leon: Zaragoza (KU 98710); Ibarra 35 mi S Linares (KU 89154); Monterey (USNM 25555); Pablillo 38 km W, 28 km S Cinaras (KU 89010). San Luis Potosi: 16 mi S Matahuala (KU 68062); Hacienda La Pasada (USNM 35519–35521); Jesus Maria (USNM 50833). Tamaulipas: 2 mi W Ocampo (KU 100656); Nicolas 56 km NW Tula (KU 89011, 89012). Zacatecas: 2 mi E Villa Insurgentes (MSUM 878); 2.7 mi N Santa Rosa (OUM 8454); Monte Escobado (LACM 34941); 10 mi W Jalpa (LACM 35466); 8 mi NW Nochistlan (LACM 35465). UNITED STATES: New Mexico: (USNM 130670); Pinon (USNM 248368). Bernalillo County: Sandia Mountains Dominae Boca Canyon (MCZ 10513). Chaves County: Hagerman on Felix River (MVZ 84577, 84578). Dona Ana County: (UTEP 7574, 7575); 1 mi S, 0.3 mi E Mesquite (NMSU 15576); Soledad Canon Oregon Mountains 17 mi E Las (MVZ 52002). Eddy County: Carlsbad Cave (USNM 244450, 530904); Lincoln National Forest 2 mi E Sitting Bull Falls (UTEP 7161). Harding County: 2.5 mi S, 8.5 mi W Roy (ENMU 651). Lincoln County: 2 mi W San Patricio (ENMU 701); Capitan Mountains (USNM 130092). Otero County: 18.2 mi S Pinon (NMSU 13890). Sierra County: San Andres Sheep Mountains near Salines Peak (USNM 119857, 120050). Socorro County: 1 mi W, 5 mi N San Antonio (MSB 6466); Big Rosa Canyon (MSB 3514, 3515); Ladrons Mountains (MSB 37680). Texas: (TCWC 28370; USNM 790); 18 mi W Lampazos (USNM 25691); N of base of Rosillas Mountains (UMMZ 103343); near Jonestown (FMNH 129312, 129313). Atascosa County: (FMNH 129311); 8 mi NW Jourdanton (WWF 157). Bexar County: Ebbtide Drive SW San Antonio (TCWC 49679); San Antonio Camp Bullis (CUM 13239). Brewster County: 11 mi E Alpine (SRSU JMC83); 11.2 mi W Alpine (SRSU 1312); 11.5 mi N, 2 mi W Marathon (TTU 29030); 18.6 mi N, 1.2 mi E Marathon (TTU 22983); 5 mi W Alpine (TCWC 28367); Big Bend National Park (USNM 274475, 274476); Boquillas (USNM 108764, 108765); Calamity Creed 26 mi S Alpine (UTEP 141, 1986); Chisos Mountains (USNM 116178); Chisos Mountains Juniper Canyon (AMNH 136415); E base Burro Mesa Chisos Mountains (MVZ 74355, 80336); Grape Vine Spring, Big Bend National Park (UF 5715); McKinney Spring, Big Bend National Park (TCWC 3600); Mouth Santa Elena Canyon, Big Bend National Park (TCWC 3602, 3603); N base Rosillas Mountains (UMMZ 103343); Neuil Ranch Calamity Creek 26 mi S Alpine (MSUM 15883); Santa Elena Canyon (USNM 274477); The Basin Chisos Mountains (FMNH 46952, 46953; TCWC 3604, 4474, 4475). Brown County: 5 mi N Brownwood (MWSU 12641). Coke County: 17 mi W Ballinger near Bronto (TTU 47); 2.2 mi N Robert Lee (ASNHC 238). Crockett County: 3 mi NW Ozona (TCWC 22785); Devil's River 13 mi below Juno (USNM 119013, 119014). Culberson County: "Bowl," Guadalupe Mountains (TCWC 1299, 1300); 1 mi N Kent (TCWC 48379); McKittrick Canyon Guadalupe Mountains (TCWC 1278–1281, 1298); The Bowl Guadalupe Mountains National Park (TTU 20686). Dawson County: N of city limits of Lamesa (TTU 11974). Hudspeth County: (UTEP 3113). Jeff Davis County: 14 mi NW Fort Davis (TCWC 2519); 15 mi SW Labo White Tank Evans Ranch (TTU 11764); 25.5 mi NW jct 17 and 118 (TCWC 28366); 5 mi E Mount Livermore (UMMZ 79401); 5.6 mi N, 6.4 mi E Fort Davis (TTU 32462); 9 mi NE Fort Davis (TTU 14057); Davis Mountains 15 mi E Valentine (USNM 25487, 108934, 117648, 349998, 349999). Kerr County: (MCZ 15487, 15726); Felix Real Ranch 6 mi S Kerrville (TCWC 1882); 25 mi W Mountain Home (TCWC 268, 270, 273); 35 mi SW Kerrville (TCWC 2672). Kimble County: 10 mi E Junction (MWSU 3711); 12 mi E Junction (MWSU 11092); 6 mi E Junction (MWSU 1245); 7 mi E Junction (MWSU 1755); 8 mi E Junction (MWSU 6378, 6487, 15361). Mason County: 12 mi S Mason (TCWC 3706, 3707); 20 mi S Mason (TCWC 3708); Mason (USNM 186455). McCulloch County: 13 mi S Brady (MWSU 7509); 8 mi W Brady (MWSU 6379). Menard County: 3 mi S Hext (MWSU 15396). Pecos County: 13 mi N, 19.7 mi E Marathon (CM 48894); 17.1 mi E Bakersfield (MSB 57640); 8 mi N Fort Stockton (MWSU 6424). Presidio County: 8 mi NE Candeloria (TCWC 22863–22865, 28368); 80 mi SW Marfa (TCWC 23519); 9 mi NE Candeloria (TCWC 22862). Reagan County: 25 mi N Big Lake (ASNHC 275). Runnels County: 2 mi SE Wingate (TTU 34775). Terrell County: 10 mi S Sheffield (TCWC 28369). Tom Green County: (ASNHC 613); San Angelo (USNM 244474). Uvalde

County: Montell (KU 54344). Val Verde County: 20 mi N, 0.25 E del Rio Devil's River (OSU 9476); 7 mi S, 2 mi W Langtry (TTU 51930); Langtry (USNM 126241); Osman Canyon near Langtry (USNM 31165). Webb County: 50 mi SE Eagle Pass Blocker Ranch (USNM 24575).

Conepatus mesoleucus mesoleucus.—(UMMZ 83346). MEXICO: Chiapas: (AMNH 175087); 3 mi E Cintalapa (TCWC 8641). Guanajuato: Santa Rosa (USNM 81721). Mexico: Salazar (USNM 36172, 36173). Michoacan: Patzeuaro (USNM 35518). Morelos: 24 mi W Huitzilac (TCWC 4691). Oaxaca: 4 mi E Tapan Tepec (TCWC 16299); Huilatepec (USNM 73480); Juchitan San Dionisio Buena Vista (AMNH 145968, 145969); Llans Grande (USNM 74685); Santa Domingo (USNM 73481); Tahuantepec (USNM 94224); Tapanatepec (AMNH 172188, 176665–176668); Tehuantepec La Concepcion (AMNH 145973); Tehuantepec (AMNH 171717); Zanatepec (FMNH 14049). Puebla: 4.5 mi E Izucar de Matamoros (UIMNH 15462, 15463).

Conepatus mesoleucus nelsoni.—MEXICO: Colima: 1 km NE San Antonio (OUM 6359); 12.5 mi SE Los Tempames (LACM 29320); 3 km S Santiago (KU 87664); 5 mi NE Laco Fradia (LACM 59423, 59424); 7 mi NE Laco Fradia (LACM 59425, 59426); Armeria (USNM 33252); Colima (USNM 33253); El Charco (LACM 59420, 59421); Hacienda Magdalena (USNM 33254); Laco Fradia (LACM 59427); Pueblo Juarez 20 mi SW Colima (AMNH 171901). Guerrero: Chilpancingo (MCZ 39592); 1 mi SW Tierra Calorado (TCWC 5016); Acahuizotla (TCWC 6378, 5571); Acapulco (USNM 70621); Ometepec (USNM 74678). Jalisco: 20 mi S, 5 mi W Pihuamo (KU 111977). Michoacan: Mountain Tancitaro (USNM 126714, 126145); Tamcitaro Mountain (FMNH 52217). Oaxaca: Llano Grande (USNM 74685).

Conepatus mesoleucus nicaraguae.—EL SALVADOR: Chalatenango: Los Esesmles (MVZ 98297, 132159, 132160, UMMZ 110954, 110955). Morazan: 12.5 mi N Divisa Oero (MVZ 132161); N Slope Mount Cacaguatigue (MVZ 98295). San Miguel: Lake Olomega (MVZ 132162); Mount Cacquatigue (MVZ 132163); Mount Cacquatigue (MVZ 132164); SW edge Calre Alomega (MVZ 98298). Usulután: Puerto del Tricenfo (MVZ 132165–132167); Puerto del Triunfo (MVZ 132168–132170). GUATEMALA: (USNM 61272–

61274); Sierra Santa Elena (FMNH 15130, 15954–15956). Huchuelenango: Guezaltenango, 130.5 km N Sierra de Los (LACM 53551, 53556). Jutiapa: Taxisco (FMNH 73660, 74020). San Marcos: Tajumulco (FMNH 74121)2. Zacapa: 3 km S, 30 km W Zacapa (TCWC 7840). HONDURAS: Archaga (AMNH 127568); Catcamas (AMNH 128125, 128470–128474); Cerro Pucco Gracias (AMNH 130030); Cimenteva Gracias (AMNH 129710); El Caliche Cedros (AMNH 127569); La Cueva Archaga (AMNH 128123); La Flor Archaga (AMNH 128996, 129712); La Paz El Zahote (AMNH 126759); Las Flores Gracias (AMNH 128997, 129709). NICARAGUA: (AMNH 41245); Matagalpa (AMNH 33190); San Rafeal Rio del Norte (AMNH 29281, 29283, 29284). Boaco: Santa Azucena, 9 km S, 5.5 km W Boaco (KU 115622). Choutales: Hato Grande 13 km S, 8 km W Juigalpa (KU 115623). Leon: HDA Las Colinas (USNM 337831). Matagalpa: 5 mi NE Sebaca (TCWC 10649).

Conepatus mesoleucus sonoriensis.—MEXICO: Jalisco: 10 mi NE Huejuquilla (KU 109465); Ameca (USNM 82262); Arroyo de Plantonar (AMNH 25177); Estancia (AMNH 25168, 25174, 25175, 25178); Etzatlan (USNM 34407); Garabatos (AMNH 25169, 25171–25173, 25176, 25179); Jalisco (AMNH 25180); La Cienaga (AMNH 25878); La Laja (AMNH 25874–25877, 25879–25887); Las Canoas (AMNH 26159–26164, 26166, 26167); Los Masos (AMNH 27257). Sinaloa: 1 mi E Sinaloa (KU 90529); 1.5 km N Bodiraquata (KU 96723); 10 km S, 38 km E Sinaloa (KU 90530, 90531); 15 km N, 65 km E Sinaloa (KU 90527, 90528); 16 km NNE Choix (KU 89905–89908); 19.2 km NE Santa Lucia (KU 94620, 94621); 2 mi N San Blas (KU 89910); 3 mi NE El Fuerte (KU 89909); 3 mi NE San Miguel (KU 85407); 4 mi S Villa Union (KU 85900); 44 km ENE Sinaloa (KU 90525, 90526); 5 km NE Santa Lucia (KU 96189, 96190); 5 mi N Carrizalejo (KU 95604); 8 km N Villa Union (KU 96191–96194); Capala (LACM 9819, 9820); El Batel 70 km NE Mazatlan (MVZ 106116); Escuinapa (AMNH 24070, 24071, 24703–24714, 25018); Matatan (KU 90984); Rancho Rosalita 26 mi NE Choix (KU 75388, 75389); Rogario (USNM 90985); San Benito (KU 99208); San Ignacio (KU 90983); Santa Cruz de Alaya (USNM 91357). Sonora: Camoa Rio Mayo (MVZ 85318–85320; USNM 95915, 95916). Zacate-

cus: Platendo (USNM 90983, 90984); Valparaiso Mountains (USNM 92117).

Conepatus mesoleucus telmalestes.—UNITED STATES: Texas: Hardin County: Sour Lake (USNM 136989, 136990, 136549–136551, 136533). Liberty County: Cleveland (USNM 136771, 136772, 140358–140360); Tarkington Prairie (USNM 135098).

Conepatus mesoleucus venaticus.—MEXICO: San Jose Mountains (USNM 58926). Chihuahua: 3 mi S 10 mi E Pacheco (KU 64366); Colonia Garcia (USNM 98334, 136196); Rio Gavila 7 mi SW Pacheco (MVZ 109606–109609). Sonora: Nogales (USNM 46058); Santa Cruz (USNM 58867). UNITED STATES: Arizona: Cochise County: (AMNH 1924); Huachuca Mountains (UMMZ 78555, MCZ 18951, KU 51973, 51974); McMillenville (USNM 214351); Nahtan Plateau (USNM 222830); Coronado National Forest South Fork Campground (TTU 30422); 0.5 mi SW Portal Ranger Station (AMNH 180010); 10 mi E Douglas (UIMNH 15165); 13 mi S Fort Huachuca (UIMNH 4082); Cave Creek Canyon 2 mi S, 2 mi W Portal (AMNH 185358); Chiricahua Mountains (MVZ 32491–32497); Chiricahua Mountains Portal (OSUMNH FW6076, FW6211); Chiricahua Mountains SW Research Station (UIMNH 15164); Fort Huachuca (UIMNH 4085; USNM 61878); Huachuca Mountains (FMNH 15044, 18536; MCZ 10600, 10601, 17955, 17956; UIMNH 4083, 4084; USNM 21889); Miller Canyon (KU uncataloged); Nicksville Huachuca Mountains (UIMNH 22602); Pinery Canyon Chiricahua Mountains (MVZ 31331); SW Research Station Chiricahua Mountains (AMNH 185357; MVZ 121106); SW Research Station Rattle Snake Hill (AMNH 184915). Gila County: Black River (USNM 209149). Graham County: Ash Creek Graham Mountains (USNM 203906, 203907); Graham Mountains Cluff Farm (UIMNH 5827–5831); Stanley (MVZ 47653). Greenlee County: Beaver Creek (MVZ 62707); Blue River (Cospers Ranch) (USNM 205377, 205378, 205382, 205828); Blue River (Cospers Ranch); 12 mi S Blue (USNM 205376); Raspberr Creek Prieto Plateau (USNM 205829). Mohave County: Huahpai Mountains (UIMNH 13368). Pima County: (MVZ 24672; UMMZ 63993–63995, 107963); 2.5 mi S, 0.75 mi W Arivaca (UIMNH 17252); 23.5 mi N Sasabe (UIMNH 17251); 36 mi SE Tucson (USNM 272467); 40 mi S Tucson Madera Canyon

(UMMZ 63993–63997); Fort Lowell (UCLA D22, D23, D34, 6830, 6844, 6962); Fort Lowell near Tucson (MVZ 24622); Mouth of Sabino Canyon 10 mi E, 6 mi N Tucson (KU 22636); Sabino Canyon Babuq. Mountains (UIMNH 13614); Sabino Canyon Santa Catalina Mountains (OSU 5909); Santa Catalina Mountains (UMMZ 107961–107963); Tucson (USNM 167890); Upper Sabino Canyon Tucson (MWSU 1973). Pinal County: (AMNH 605, 1362; FMNH 5437); La Osa (USNM 37285). Santa Cruz County: Oro Blanca Mountains (MCZ 17956); 1 mi S Patagonia (UIMNH 26980); 11 mi ENE Nogales (UIMNH 15163); Santa Rita Mountains Madera Canyon (LACM 10205). Yavapai County: Fort Whipple (USNM 214352); near Fort Verde (AMNH 1918–1922). New Mexico: Dry Creek (USNM 158890); Hillsboro (USNM 167688); Lake Valley (USNM 167689). Catron County: East Diamond Creek Gila National Forest (USNM 159331); Gila National Forest (USNM 151219). Grant County: 1 mi S Cliff (AMNH 127111); 13 mi N Gila (AMNH 127110); 13 mi S Cliff (AMNH 127112); Head of Mimbres River (USNM 147417, 147418). Hidalgo County: 6 mi NW Cloverdale (AMNH 127252); Animas Mountains Black Bill Canyon (MSB 46327); Animas Valley (USNM 167999); Cloverdale (UIMNH 50819); Granite Gap (MSB 27016); Indian Creek (MSB 2765, 10560, 10561); Indian Creek Canyon (MSB 11094). Otero County: Sacramento Mountains near Mescalero (ANSP 14844).

Conepatus chinga.—ARGENTINA: Buenos Aires near Henderson (FMNH 24354); Cordoba (AMNH 36933); Lavalle S of de Estero (AMNH 41530–41534); Los Angeles Estancia (USNM 331066). Mendoza: Nacuan (OUM 15157). San Juan: Sarmiento, Pederal (OUM 466). BOLIVIA: Tujma (AMNH 39011). Chuquisaca: 6 km W Carandayti (MSB 56102). Cochabamba: 20 mi S Tiraque (USNM 271410). LaPaz: 4 km E Villa Ulla (AMNH 247712). SantaCruz: 5 km SE Tita (AMNH 260327). BRAZIL: (AMNH 235995, 235997). Matto Grosso Maracaju (AMNH 133946); Onnapolis Goyaz (AMNH 133948); Urugucyana (AMNH 235994). Quinta: Rio Grande de Sul (AMNH 235512–235514). CHILE: (AMNH 93324); Perinacota Tarapaca (USNM 391850, 391851); Santiago (USNM 391848); Tarapaca Tucna (FMNH 24352, 24353); Valdivia Lago Rinihue (FMNH 24349, 24350). Maquehue: Temuco (AMNH 33290,

33291). PARAGUAY: Chaco; 50 km WNW Fortin Madrejon (AMNH 248467–248470). PERU: (AMNH 238425; MCZ 5257–5259; MVZ 135873, 141630); Ancach Macate (FMNH 21060); Arequipa Cailloma (FMNH 49722, 49723); Arequipa near Cailloma (FMNH 49721); Arequipa Salinas (FMNH 49732–49734); Arequipa Sumbay (FMNH 49720); Arequipa Yura (FMNH 106007); Cajamarca Taulis (AMNH 73123); Chaspoc Huarcocondo River (USNM 194322); Huanuco Acomayo (FMNH 106495); Matchu Picchu (USNM 194323); near Huarochiri (USNM 176320); Oacabamba Valley (USNM 194319, 194320); Pumo Hacienda Col-laeachi (FMNH 49724–49731); Puno Huacul-lani (FMNH 52486); San Pedro (AMNH 73220); Urca Calea (USNM 194324); Valley of Chicama (USNM 172857). Huanuco: 5 km NE Acomayo Tinyahuayin (MSB 50008). Lalibertad: 15 mi S Pacasmayo (MVZ 138150). Puno: 10 mi S Mazocruz (MVZ 114940); Hacienda Calacala 7 mi SW Putima (MVZ 114775); Hacienda Pairumani 24 mi S Kave (MVZ 114776, 114941). URUGUAY: Rio Negro Paso Correntino (FMNH 29301). Artigas: 6 km NNW Balen (AMNH, 205833–205836, 205841). Bocha: 15 mi N San Vicenta de Castillos (FMNH 29304); 22 km SE Lascano (AMNH 205870–205878, 205884, 205890). Carro Largo: 6 km SE Metro Estancia Las Marias (AMNH 205838); 20 km NW del Paso del Dragon (AMNH 205839); 20 km SE Metro Estancia Las Marias Sierra de Vas (AMNH 205840); 6 km SE Metro Estancia Las Marias (AMNH 205837); Sierra de Vas Rio Tacijari (AMNH 205846). Colonia: 10 km S La Lata (FMNH 29291–29294). Lavalleja: 12 km WSW Zapican (AMNH 205842, 205843, 205845, 205869). Maldonado: N of San Carlos (FMNH 29280). Rio Negro: Arroyo Negro 15 km S Paysandu (AMNH 205844, 205847–205859, 205861–205867). Rocha: 15 mi N San Vicenta de Castillos (FMNH 29282); 15 mi N San Vicente de Castillos (USNM 259436). Soriano: 15 mi SW Dolores (FMNH 27673, 29295–29300); 3 km E Cardona (AMNH 205889). Tacucirembo: (AMNH 205886); 40 km N Tacucirembo (AMNH 205879–205883, 205885–205888). Treinta Tres: Quebiada de los Cueruos (FMNH 29283, 29285, 29286–29289, 106002); 13 km WSW Vergara (AMNH 205901); 15 km NW Baca del Rio Tacuari (AMNH 205899); 16 km SSW Boca del Rio Tacuari (AMNH 205891–205898); 80 km NE

Trenta Tres (AMNH 205900); Quebiada de los Cueruos (FMNH 29284).

Conepatus humboldtii.—ARGENTINA: (MVZ 39875; UCLA 16618; USNM 12639); Gallegos (USNM 171957, 171958, 261479); Neuquen 3 km NW Confluencia (MVZ 159443); Neuquen Parque Nacional Laguna Blanca (MVZ 159444); Nuochea (USNM 172792); Patagonia (KU 2042, 2683); San Jose (USNM 172791); Tello (USNM 172793, 172794). Chubut: (AMNH 94329, 94330); 100 km NW Comentarn Rivadaira (AMNH 94317); Lago Col Huapi (AMNH 94328); Rawson (UCLA 16600). Huanuluan: (FMNH 34193; MCZ 19110–19114). Jujuy: Tres Cruces (UCLA 16542). Maquinchao: 20 mi S Maquinchao (MCZ 19115). Negro: Negro Estancia Condor 18 km SE Pariloche (MVZ 162288). Neuquen: Estacion Campo Grande 5 km N Los Colorados (MVZ 173707, 173708). Rio Chico: (AMNH 25669). Rio Negro: Pichi Mahuida (UCLA 16593–16596); 22 km ESE Bariloche Estancia el Condor (MVZ 172241). Santa Cruz: (AMNH 17446); Arroyo Pike (FMNH 124235). Tucuman: Burreyacu Garmendia (UCLA 16489, 16555). CHILE: (AMNH 130063); Chubibi (AMNH 36929); Llanguihue Balseo (FMNH 41361); Llanguihue Rio Niraguae (FMNH 23294, 23295, 24347, 24348); Magallanes Rio Ciaiike North Arm station (FMNH 50767, 50809, 53716, 53717); Punta Arenas (AMNH 130049–130067, 130069–130094, 130096–130100); Tierra del Fuego (AMNH 36928).

Conepatus semistriatus.—(MCZ 27218, 27219). BELIZE: 35.5 mi Northern Highway Melinda (FMNH 58560); Cayo district Red Creek Before Sant Elena (FMNH 121557); Stan Creek Valley (FMNH 63902). BRAZIL: Piatory: (MCZ 24828). COLOMBIA: (AMNH 14632; USNM 281460); Colonia Agric (USNM 281452); Cundinamarca Balcillas (AMNH 38423, 38424); El Orinoco (USNM 281456); El Orinoco (USNM 281455); Las Morimondas (USNM 281464, 281465); Magdalena (CM 665, 1028); Magdalena Bonda (AMNH 14632); Playa Brava (AMNH 15480); Rio Guaimaral (USNM 281453, 281454); Sierra Negra (USNM 281457–281459); Villanueva (USNM, 281461–281463). Cartage: 12 km SE de Turrialba (KU 32245). Cordoba: Bolivar Catival Rio San Jorge (FMNH 68904, 68905). COSTA RICA: (USNM 35641, 35642, 61205); Chiriqui Boqueron (AMNH 18700); Escazu (AMNH 135269–

135271, 137282, 137283); Pancho de R Simenez (AMNH 2794, 19206); Pozo Zul (AMNH 19205); Teresa Peralta (AMNH 141858). Puntarenas: (LACM 26686). ECUADOR: (AMNH 66244; MCZ 27341; MVZ 84332); 25 mi S Quito (AMNH 187838); Alao Calero Sangay (MCZ 52663); Alausi (AMNH 63577); Aloag (AMNH 66722–66724); Antisana (AMNH 66719, 66721); Hacienda Alao (MCZ 52661); Imbabura itad La Vega San Pablo del Lago 5 km ESE (FMNH 125113); Mi Pichincha (AMNH 36462, 36463); Occidente Balcon Pichincha (FMNH 44336); Quito (AMNH 36464–36466); Santa Rosa (AMNH 66720); Sinche (AMNH 67085). Carchi: 16 km SSE San Gabriel (TCWC 12944). Tunquraqua: Banos Runtun Hills (MCZ 38732). GUATEMALA: (USNM 61275); Petin Tikal (UF 6794). MEXICO: Merida (USNM 8610). Veracruz: 14 km SW Coatzacoalcos (KU 19274); 20 km ENE Vesus Carranza (KU 32224); 35 km SE Vesus Carranza (KU 24546); Achotol (FMNH 13825); Catemaco (USNM 65762, 65763); Lake Catemaco (AMNH 172190); Motzimrongo (USNM 63650); Pasa Nueva (AMNH 17201, 17202); Perez (USNM 132512). Yucatan: 6 km N Tizimin (KU 93830, 95112); La Vega (USNM 108502, 108503). NICARAGUA: Rio San Jaun Esperanza (USNM 361359). Managua: 6 mi WSW Managua (KU 71936). PANAMA: (AMNH 36932); 2 mi NE el Valcan (USNM 332037); Bocas del Toro Bibube (USNM 335773); Chiriqui Cerro Pinta Bandito (USNM 324236); Chiriqui Progreso (USNM 363346). Boquete: (MCZ 10115, 10116). Chirui: Casita (ANSP 18911–18913). PERU: Cajamarca Hacinda Limon (FMNH 19680); Libertad Trujillo Menocucho (FMNH 19976). Piura: Pariman 7 km N, 15 km E Talara (MVZ 135824). VENEZUELA: (CM 6353); 60 mi Zaraza (AMNH 135481); Caigara (USNM 296626); El Hocha Bolivar RR (AMNH 32073); Mercida (AMNH 21684, 21685); Monagas 10 km SE Araguade Matarin (UIMNH 18061); Neveri (AMNH 69609); Rancho Grande (AMNH 144821); Sucre Turumiquire Mountain (FMNH 38061); W of Merida (FMNH 22202); Zulia Rio Aurare (FMNH 18770). Falcon: 5.5 km NE Capatarida (USNM 443290, 443291); Capatarida (USNM, 443285, 443286, 443289, 443293–443296); Capatarida 49 km N, 34 km

W Coro (USNM 443414). Merida: W of Merida (FMNH 22203). Monagas: 47 km SE Maturin (USNM 388241, 388244). Portuguesa: Piritu San Jorge (UF 13302). Urunaco: Falon (MCZ 54383). Yaracuy: 40 km N, 19 km W Urama (USNM 372745). Zulia: 39 km WNW Encontrados (USNM 443576).

APPENDIX II

Specimens examined.—The 21 specimens examined for genetic analyses are listed here by museum acronym (Hafner et al. 1997), or by NK number (Museum of Southwestern Biology, Division of Genomic Resources), or JWD personal field catalog number (several skunk specimens did not survive the flood that occurred in 1994 at the Texas Cooperative Wildlife Collections). Additionally, ear punches were collected from 2 radiocollared animals in Tamaulipas, Mexico.

Conepatus chinga.—BOLIVIA: Chuquisaca NK12618 (MSB 56102).

Conepatus leuconotus texensis.—UNITED STATES: Texas: Brooks County (TCWC 4963). MEXICO: Tamaulipas (TCWC 30654), Ear punches from 2 radiocollared animals.

Conepatus mesoleucus figginsi.—UNITED STATES: Colorado: Baca County (DMNH 2373).

Conepatus mesoleucus mearnsi.—UNITED STATES: New Mexico: Eddy County (TCWC uncataloged—JWD 326). Texas: Bexar County (TCWC 49679); Crockett County (TCWC 22785); Kimble County (TCWC 55936); Mason County (TCWC uncataloged—JWD 331); Pecos County NK6832 (MSB 57640); Presidio County (TCWC 22863).

Conepatus mesoleucus sonoriensis.—MEXICO: Sinaloa (KU 89907; 89908).

Conepatus mesoleucus venaticus.—UNITED STATES: Arizona: Santa Cruz County (UIMNH 26980). New Mexico: Hidalgo County (MSB 11094).

Mephitis mephitis.—UNITED STATES: Texas: Wood County (TCWC uncataloged—JWD 389).

Mephitis macroura.—UNITED STATES: New Mexico: Hidalgo County (NK 8619).

Mydaus marchei.—PHILIPPINES: Palawan CMNH.

Spilogale gracilis.—MEXICO: Chihuahua: NK 17574 (MSB 60873).