Taxonomy and evolutionary relationships of Phillips' small-eared shrew, *Cryptotis phillipsii* (Schaldach, 1966), from Oaxaca, Mexico (Mammalia: Insectivora: Soricidae)

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Abstract.—The name *Cryptotis peregrina* (Merriam, 1895) previously encompassed two separate populations of a small-eared shrew of the *Cryptotis mexicana*-group inhabiting the Sierra de Cuatro Venados and the Sierra de Miahuatlán in Oaxaca, Mexico. Analysis of museum specimens from these two populations, including the type series of *C. peregrina*, indicates that they are neither conspecific nor even sister taxa. We taxonomically restrict the name *C. peregrina* to populations in the Sierra de Cuatro Venados and adjoining Sierra Yucuyacua, whereas the name *Cryptotis phillipsii* (Schaldach, 1966) is available for the population in the Sierra de Miahuatlán. Moreover, we demonstrate that *C. phillipsii* is the most primitive member of the *C. mexicana*-group, whereas, *C. peregrina* is one of the more derived members of the group.

Choate's (1970) comprehensive revision of the small-eared shrews of the genus *Cryptotis* divided the Mexican and Central American species into three informal groupings: the "*Cryptotis mexicana*-group," the "*Cryptotis parva*-group," and a group of three "relict species." At that time, *C. mexicana* (with four subspecies), *Cryptotis goldmani* (with two subspecies), and the monotypic *Cryptotis goodwini* comprised the *C. mexicana*-group. Based on cranial and postcranial morphology (in particular, unique modifications of the forelimb) and biogeographic patterns, we (Woodman & Timm 1999) recently revised the *C. mexicana*-group, providing evidence that it may represent a natural grouping distinct from other members of the genus. Our revision recognized eight species in the *C. mexicana*-group, many of which were treated previously as subspecies (Choate 1970, Hall 1981): *C. alticola, C. goldmani, C.*

goodwini, C. griseoventris, C. mexicana, C. nelsoni, C. obscura, and *C. peregrina.*

Cryptotis peregrina, which is endemic to Oaxaca, Mexico, was first described by Merriam (1895) as a subspecies of *C. mexicana* based on a series of 24 specimens collected by E. W. Nelson and E. A. Goldman in 1894 "from mountains 15 miles [south] west of city of Oaxaca" (Merriam 1895:24). Binford (1989) identified this range of mountains as the Sierra de Cuatro Venados. In addition to the type series, Choate (1970) referred specimens from the Sierra de Miahuatlán in southern Oaxaca, including the holotype and two paratypes of *Notiosorex phillipsii,* to *C. mexicana peregrina.* We initially agreed with Choate's assessment, referring material from the Sierra de Cuatro Venados and the Sierra de Miahuatlán to the species *Cryptotis peregrina* (Woodman & Timm 1999). Cranially, the shrews previously considered by Choate (1970) and subsequent authors (e.g., Hall

1981) to be subspecies of *C. mexicana* (*C. mexicana, C. nelsoni, C. obscura, C. peregrina*) are quite similar and can be difficult to distinguish. However, the foreclaws vary noticably in length and breadth among members of the *C. mexicana*-group (Choate 1970, Woodman & Timm 1999), and we showed that other aspects of the forelimb, in particular the morphology of the humerus, are distinct as well (Woodman & Timm 1999). Our phylogenetic analysis indicated that *C. peregrina* was the most plesiomorphic member of the *C. mexicana*-group.

Our study (Woodman & Timm 1999) focused mainly on the larger, broad-clawed shrews that we termed the *Cryptotis goldmani*-group, which are a subset of the *C. mexicana*-group. Initially, we were interested in the former subspecies of *C. mexicana* primarily as outgroups to aid in polarizing characters for phylogenetic analysis. In studying *Cryptotis peregrina*, we depended heavily on specimens from the Sierra de Miahuatlán in the University of Kansas Natural History Museum collection, because they were readily available to us and included the only postcranial material then known for the species. One inconsistency we noted between our study and Choate's revision was that he referred to *C.* [*m.*] *mexicana* as "having less highly developed front feet and claws" (Choate 1970:232) than *C.* [*m.*] *peregrina*. However, the specimens from the Sierra de Miahuatlán had distinctly shorter and narrower claws than *C. mexicana*. We also observed that their humeri were less modified that those of *C. mexicana*, adding to our view of their being more plesiomorphic.

Recently, we re-studied the holotype and type series of *Cryptotis peregrina* at the National Museum of Natural History and discovered that Choate's (1970) observations were correct—specimens in the type series from Sierra de Cuatro Venados all possess longer, broader claws than *C. mexicana*. In addition, we were graciously granted permission by the American Museum of Natural History to remove the humerus from the only known fluid-preserved specimen of *C. peregrina* from the Sierra Yucuyacua, a mountain range in western Oaxaca that adjoins the Sierra de Cuatro Venados. Study of these specimens indicates that the two populations of *Cryptotis* inhabiting the Sierra de Cuatro Venados\Sierra Yucuyacua complex and the Sierra de Miahuatlán, respectively, are not conspecific. Herein, we taxonomically restrict the name *Cryptotis peregrina* to shrews inhabiting the former region. The name *Cryptotis phillipsii* (Schaldach, 1966) is available for the population in the Sierra de Miahuatlán. Much of what we reported earlier in regard to *C. peregrina* (Woodman & Timm 1999) actually refers to a combination of *C. peregrina* and *C. phillipsii*. It is our purpose here to redescribe *C. peregrina* and *C. phillipsii* in light of this new information and to clarify the distinctions among the species in the *Cryptotis mexicana*-group. In addition, we present a refined hypothesis of phylogenetic relationships among the species in this group of shrews.

Methods

Our current work used the techniques and methods of our previous studies of shrews (Woodman & Timm 1992, 1993, 1999), and more detailed accounts of methodology are presented there. Species and subspecies synonymies list only published uses of names. Regional names, place names, and coordinates in Oaxaca derive from Binford (1989), Choate (1970), and our review of maps and gazetteers of the region. Terminology of dentition and dental characteristics follows Choate (1970). Anatomical terminology of the humerus and other aspects of the postcranial skeleton follows Reed (1951). Measurements used in our analyses follow Woodman & Timm (1993, 1999); abbreviations of measurements are explained in Table 1. Measurements of the skull were taken to the nearest 0.1 mm using either an ocular micrometer in a binocular microscope or a hand-held

dial caliper (for condylobasal-length and cranial-breadth). Univariate statistics include mean ± standard deviation.

Multivariate analysis was carried out using Minitab 8.0. Our principle components analysis (PCA; Fig. 1, Table 2) used ten logarithm-transformed cranial measurements (condylobasal-length, breadth-of-zygomatic-plate, interorbital-breadth, breadth-across-U^1s, breadth-across-U^3s, breadth-across-M^2s, palatal-length, length-of-upper-toothrow, length-of-unicuspid-toothrow, length-of-upper-molariform-toothrow) from 12 *Cryptotis peregrina* and 14 *C. phillipsii* with complete crania.

Phylogeny and character evolution were analyzed using PAUP 4.0b2 (see Swofford 1998) and MCCLADE 3.0 (see Maddison & Maddison 1992). Phylogenetic analysis (Fig. 2) was carried out using an exhaustive search of 32 unordered and equally-weighted transition series (Table 3, Appendix I), with *Cryptotis parva parva* and *C. nigrescens* serving as outgroups for polarizing characters.

Specimens from the following institutions were used in this study: American Museum of Natural History, New York (AMNH); Natural History Museum, London (BM); California Academy of Sciences, San Francisco (CAS); Escuela Nacional de Ciencias Biológicas, Mexico City (ENCB); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (UNAM); University of Kansas Natural History Museum, Lawrence (KU); Natural History Museum of Los Angeles County, Los Angeles (LACM); Museum of Comparative Zoology, Cambridge (MCZ); James Ford Bell Museum of Natural History, St. Paul (MMNH); Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City (MZFC); Texas Cooperative Wildlife Collection, College Station (TCWC); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); National Museum of Natural History, Washington (USNM).

Results of Multivariate Analysis

Principle components analysis (PCA) of cranial variables supports the separation of *Cryptotis peregrina* and *Cryptotis phillipsii*. A plot of factor scores on factor axes 1 and 2 shows a clear distinction between these two species with minimal overlap (Fig. 1). This plot emphasizes the generally larger cranial size (factor axis 1—Table 2) of *C. phillipsii*, despite the generally similar external measurements of the two species (Table 1). In the region of size overlap between the two species on the plot, *C. peregrina* and *C. phillipsii* are separated by the combined effects of the two axes, suggesting a common, but offset trend of decreasing unicuspid-toothrow-length and palatal-length and increasing interorbital-breadth and palatal-breadth (M2B) with increasing size (Table 2).

Revised Phylogeny of the *Cryptotis mexicana*-group

Our re-analysis of phylogenetic relationships within the *Cryptotis mexicana*-group, based on 32 transition series (Table 3), resulted in a single most parsimonious tree of 67 steps (Fig. 2). Discounting differences such as the exclusion of *Cryptotis goodwini magnimana* and the inclusion of *Cryptotis phillipsii* as a species separate from *Cryptotis peregrina*, the new tree essentially matches three of the nine most parsimonious trees from our previous phylogenetic analysis of this group of shrews (Woodman & Timm 1999, fig. 13, central column of trees). The four species that comprised the *Cryptotis goldmani*-group (*C. alticola, C. goldmani, C. goodwini, C. griseoventris*) form the crown clade of the *C. mexicana*-group, whereas the species previously subsumed under the name *C. mexicana* (*C. mexicana, C. nelsoni, C. obscura, C. peregrina, C. phillipsii*) appear as individual branches at different levels of the tree. This supports our previous view that *C. mexicana* (*sensu latu*) was paraphyletic with respect to the *C. goldmani*-group.

Table 1.—Measurements of *Cryptotis mexicana*-group shrews used in this study. Statistics presented are mean ± standard deviation of the mean, and observed extremes.

C. mexicana (Oaxaca)	C. nelsoni	C. obscura	C. peregrina	C. phillipsii
Skin measurements				
$n = 118$	$n = 9$	$n = 55$	$n = 24$	$n = 27$
Head and body length (HB)				
69 ± 4	76 ± 3	66 ± 4	72 ± 3	68 ± 6
55–88	72–79	56–75	66–78	58–78
Tail length (TL)				
27 ± 3	29 ± 3	26 ± 2	30 ± 2	31 ± 3
20–34	22–33	20–32	24–33	23–36
Craniomandibular measurements				
$n = 30$	$n = 6$	$n = 32$	$n = 12$	$n = 14$
Condylobasal-length (CBL)				
18.7 ± 0.4	19.5 ± 0.3	18.4 ± 0.4	19.1 ± 0.4	19.5 ± 0.5
17.5–19.3	19.1–20.0	17.4–19.1	18.3–19.8	18.8–20.2
Breadth-of-braincase (BB)				
9.8 ± 0.3	10.4 ± 0.3	9.6 ± 0.2	9.9 ± 0.1	10.3 ± 0.3
9.3–10.7	9.9–10.7	9.2–10.2	9.7–10.1	9.8–10.7
($n = 28$)		($n = 30$)	($n = 11$)	($n = 13$)
Breadth-of-zygomatic-plate (ZP)				
1.8 ± 0.1	2.0 ± 0.1	2.0 ± 0.1	1.6 ± 0.1	2.0 ± 0.1
1.4–2.0	1.0–2.2	1.8–2.1	1.5–1.8	1.8–2.3
Interorbital-breadth(IO)				
4.7 ± 0.2	5.1 ± 0.1	4.7 ± 0.1	4.7 ± 0.1	4.9 ± 0.1
4.3–5.0	4.8–5.2	4.4–4.9	4.6–4.9	4.7–5.1
Breadth-across-first-unicuspids (U1B)				
2.4 ± 0.1	2.8 ± 0.1	2.5 ± 0.1	2.5 ± 0.1	2.6 ± 0.1
2.3–2.5	2.6–2.9	2.3–2.6	2.1–2.6	2.5–2.8
Breadth-across-third-unicuspids (U3B)				
2.8 ± 0.1	3.3 ± 0.2	2.9 ± 0.1	2.8 ± 0.1	3.1 ± 0.1
2.7–3.0	3.0–3.4	2.6–3.2	2.6–3.0	2.9–3.4
Breadth-across-second-molars (M2B)				
5.4 ± 0.2	6.1 ± 0.2	5.3 ± 0.1	5.5 ± 0.2	5.8 ± 0.1
5.1–5.8	5.9–6.3	5.1–5.5	5.3–5.8	5.6–6.0
Palatal-length (PL)				
8.2 ± 0.2	8.4 ± 0.2	7.9 ± 0.2	8.5 ± 0.2	8.5 ± 0.2
7.3–8.5	8.1–8.7	7.5–8.5	8.2–8.9	8.0–8.7
Length-of-upper-toothrow (TR)				
7.2 ± 0.2	7.6 ± 0.2	7.1 ± 0.2	7.3 ± 0.1	7.5 ± 0.3
6.6–7.5	7.4–7.8	6.8–7.4	7.2–7.5	7.2–8.0
Length-of-unicuspid-toothrow (UTR)				
2.4 ± 0.1	2.4 ± 0.1	2.4 ± 0.1	2.5 ± 0.1	2.5 ± 0.1
2.1–2.5	2.4–2.6	2.1–2.6	2.4–2.6	2.3–2.7
Length-of-upper-molariform-toothrow (MTR)				
5.2 ± 0.1	5.6 ± 0.2	5.2 ± 0.1	5.3 ± 0.1	5.4 ± 0.2
4.9–5.5	5.4–5.8	4.9–5.4	5.1–5.4	5.3–5.8

Table 1.—Continued.

	C. mexicana (Oaxaca)	C. nelsoni	C. obscura	C. peregrina	C. phillipsii
Posterior-width-of-M¹ (WM1)					
	1.6 ± 0.1	1.9	1.7 ± 0.1	1.8 ± 0.1	1.8 ± 0.1
	1.5–1.8	—	1.6–1.8	1.6–2.0	1.6–2.0
	($n = 25$)	($n = 1$)			
Length-of-mandible (LM)					
	6.0 ± 0.2	6.4 ± 0.1	5.9 ± 0.2	6.2 ± 0.2	6.4 ± 0.3
	5.4–6.3	6.3–6.6	5.4–6.4	5.8–6.4	5.8–7.1
Height-of-coronoid-process (HCP)					
	4.3 ± 0.1	4.8 ± 0.1	4.4 ± 0.1	4.5 ± 0.1	4.8 ± 0.1
	4.1–4.6	4.7–4.8	4.0–4.6	4.3–4.7	4.7–5.1
Height-of-coronoid-valley (HCV)					
	2.6 ± 0.1	2.8 ± 0.1	2.6 ± 0.1	2.8 ± 0.1	2.8 ± 0.1
	2.3–2.8	2.8–2.9	2.4–2.8	2.7–3.0	2.7–2.9
Height-of-articular-condyle (HAC)					
	3.7 ± 0.2	3.9 ± 0.05	3.6 ± 0.2	3.8 ± 0.1	3.9 ± 0.2
	3.4–3.9	3.8–4.1	3.2–3.9	3.6–4.1	3.8–4.2
Breadth-of-articular-condyle (BAC)					
	2.9 ± 0.1	3.1 ± 0.1	2.9 ± 0.1	3.0 ± 0.1	3.1 ± 0.1
	2.7–3.2	3.0–3.2	2.6–3.0	2.8–3.2	3.0–3.3
Articular-condyle-to-M₃ (AC3)					
	4.9 ± 0.2	5.2 ± 0.1	4.6 ± 0.2	5.1 ± 0.2	5.0 ± 0.2
	4.4–5.2	5.0–5.3	4.3–5.0	4.8–5.3	4.8–5.3
Length-of-lower-toothrow					
	5.7 ± 0.1	6.0 ± 0.1	5.7 ± 0.1	5.9 ± 0.1	5.9 ± 0.2
	5.4–5.9	5.8–6.2	5.4–5.9	5.8–6.0	5.5–6.2
Length-of-lower-molar-row (m13)					
	4.3 ± 0.1	4.5 ± 0.1	4.2 ± 0.1	4.4 ± 0.1	4.4 ± 0.2
	4.1–4.5	4.4–4.6	4.0–4.4	4.2–4.5	4.0–4.8
		($n = 6$)			
Length-of-m1 (m1L)					
	1.7 ± 0.1	1.8 ± 0.05	1.7 ± 0.1	1.7 ± 0.1	1.9 ± 0.1
	1.6–1.9	1.8–1.9	1.6–1.8	1.6–1.8	1.6–2.0
Weight (g)					
	7.4 ± 1.0	—	6.9 ± 1.1	—	8.0 ± 1.1
	5.0–9.5		5.0–10.0		6.5–10.0
	($n = 37$)		($n = 23$)		($n = 19$)

Cryptotis phillipsii appears as the most primitive member of the *Cryptotis mexicana*-group, matching our supposition based on the morphology of its forelimb. In contrast, *Cryptotis peregrina* is much more derived and serves as a "link" between the *Cryptotis goldmani*-group of shrews and the more primitive members of the *C. mexicana*-group. Based on all but two characters (relative tail length and relative height of the coronoid process of the mandible) *C. peregrina* could, in fact, be considered a member of the *C. goldmani*-group. However, both characters are much more vari-

Table 2.—Factor loadings for the first two factor axes from principle components analysis of *Cryptotis peregrina* and *Cryptotis phillipsii* from Oaxaca. The two axes accounted for 72% of the variation. Abbreviations as in Table 1.

Variable	PC1	PC2
UTR	−0.170	0.378
PL	−0.195	0.523
IO	−0.208	−0.458
MTR	−0.334	−0.102
TR	−0.335	0.233
M2B	−0.337	−0.325
ZP	−0.371	0.221
CBL	−0.371	0.222
U1B	−0.372	−0.198
U3B	−0.373	−0.259

able among the more primitive members of the *C. mexicana*-group (Table 4) than we previously realized (Woodman & Timm 1999). For this reason, we redefine the *C. goldmani*-group below, excluding these two characters.

Systematic Biology

"*Cryptotis mexicana*-group" Choate, 1970

We (Woodman & Timm 1999) recently redescribed the *Cryptotis mexicana*-group as small to medium-sized members of the genus with long, dark dorsal pelage. All members possess variably broadened forefeet and variably broadened and elongated foreclaws; posterior border of the zygomatic plate usually positioned equal to, or
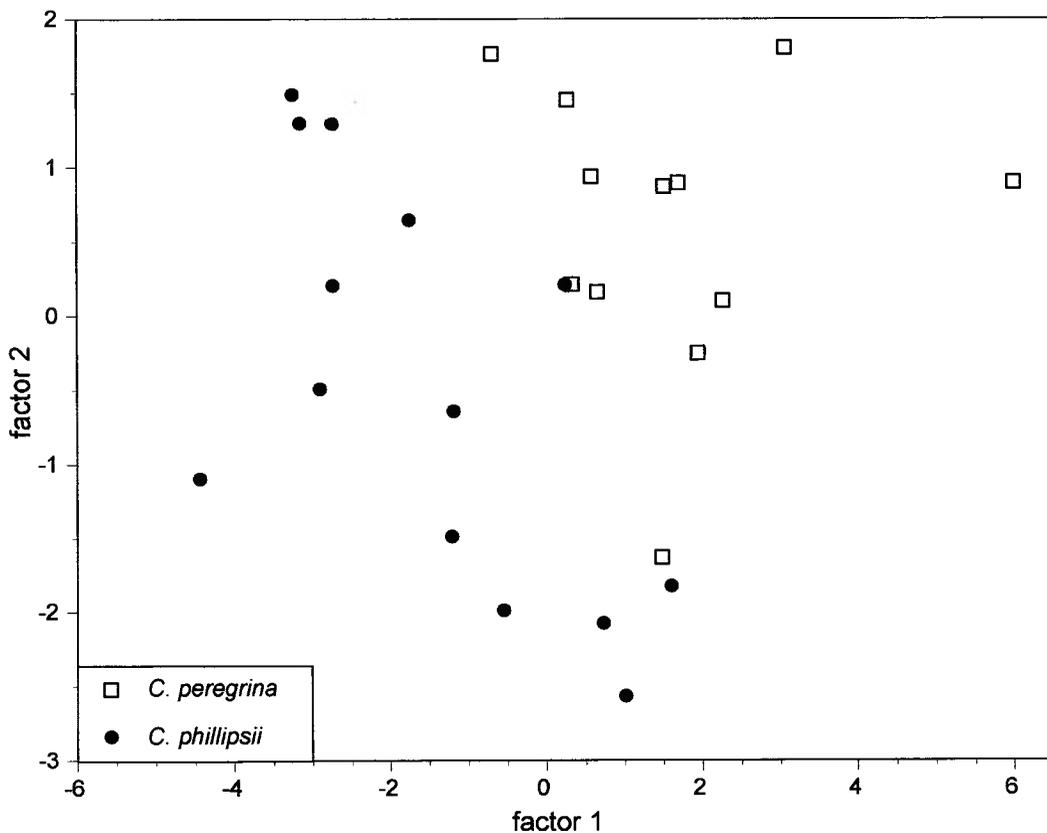

Fig. 1. Plot of factor scores from PCA of ten log-transformed measurements from 12 *Cryptotis peregrina* and 14 *Cryptotis phillipsii*. Factor axis 1 represents size (Table 2); factor loadings are negatively weighted, so the largest individuals have the smallest scores. Factor axis 2 represents a combination of palatal-length, interorbital-breadth, unicuspid-toothrow-length, and breadth-across-M²s (Table 2).
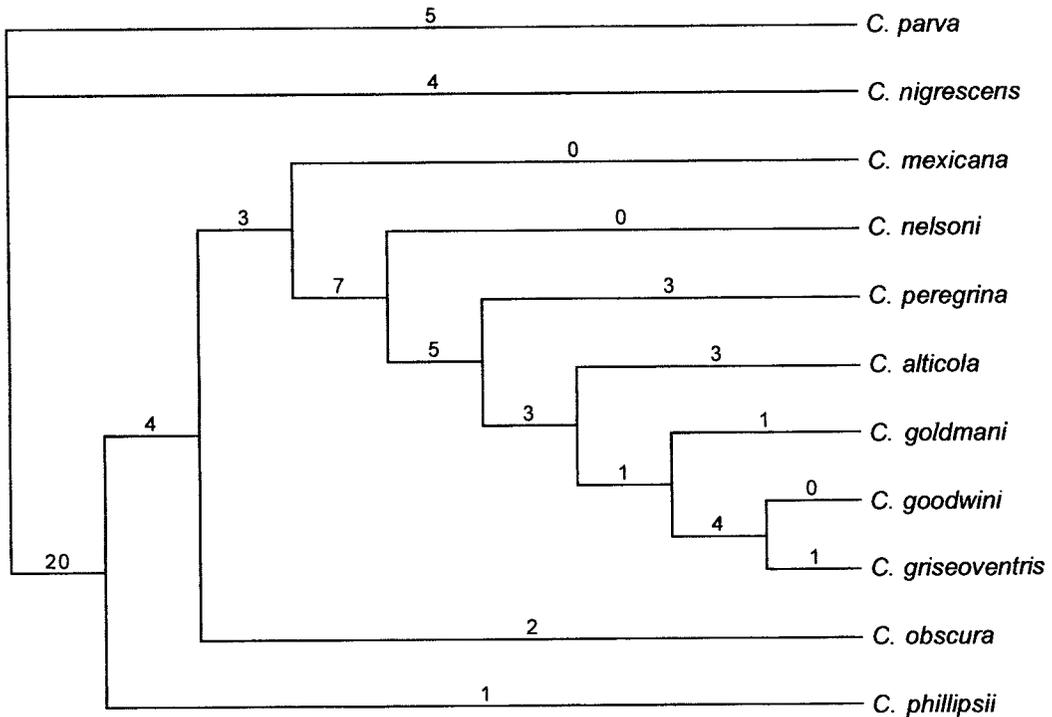
Fig. 2. Topology of the single most parsimonious tree resulting from phylogenetic analysis of the *Cryptotis mexicana*-group of shrews. *Cryptotis nigrescens* and *C. parva parva* served as the outgroups for polarizing characters. Number of transitions is shown for each branch. Tree length = 67 (minimum possible length = 49; maximum possible length = 122); consistency index = 0.731; rescaled consistency index = 0.551; retention index = 0.753; homoplasy index = 0.269.

slightly posterior to, the posterior base of the maxillary process; upper toothrow uncrowded; dentition not bulbous; anterior border of the coronoid process of the mandible joins the horizontal ramus at a relatively low angle; posterior border of lower incisor extends to posterior cingulum of P_4; relatively long distance from the coronoid process to the posterior border of M_3; tall, wide articular face of the articular process; deep lower sigmoid notch; relatively long, low P_3; relatively short, broad metacarpals; shortened and broadened humerus with elongated processes and a dorsoventrally elongate head; deeply pocketed posterior edge of the falciform process of the tibia.

Included species.—*Cryptotis alticola, C. goldmani, C. goodwini, C. griseoventris, C.* *mexicana, C. nelsoni, C. obscura, C. peregrina,* and *C. phillipsii.*

Cryptotis peregrina (Merriam, 1895)

Blarina mexicana peregrina Merriam, 1895:24.

C[ryptotis]. mexicana peregrina: Miller, 1911:222.

Cryptotis mexicana peregrina: Hall & Kelson, 1959:60; Goodwin, 1969:39 (in part); Choate, 1970:237 (in part); Hall, 1981:59 (in part).

Cryptotis mexicana mexicana: Goodwin, 1969:39 (in part).

Cryptotis peregrina: Woodman & Timm, 1999:35 (in part).

Holotype.—Skin and skull of male, USNM 68317; captured on 12 September

Table 3.—Complete character matrix for phylogenetic analysis of members of the *Cryptotis mexicana*-group and two outgroups. *Cryptotis parva parva*, and *Cryptotis nigrescens*. Transition series (TS) are explained in Appendix 1.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
																		Transition series														
parva	0	0	0	0	0	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	2
nigrescens	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	-	0	-	0	0	0
mexicana	2	2	-	-	2	-	-	-	-	0	-	-	-	-	-	0	-	-	-	-	-	-	0	0	0	-	0	0	2	-	-	0
nelsoni	2	2	-	?	2	-	-	-	-	0	-	-	?	?	?	?	?	?	?	?	?	0	0	0	0	-	0	0	2	?	?	-
obscura	-	-	-	?	2	-	-	-	0	0	-	-	-	-	-	0	-	-	-	-	-	-	0	0	0	0	-	0	2	-	?	0
peregrina	2	2	-	?	2	-	-	-	-	-	0	-	2	-	-	0	2	2	-	2	?	3	-	-	-	0	-	-	2	-	?	-
phillipsii	-	-	-	-	2	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	-	0	0	-	-	-	0	2	0	-	0
alticola	3	3	2	-	2	-	-	-	0	-	0	-	2	-	-	0	2	2	-	2	-	2	0	0	-	-	-	-	2	-	2	2
goldmani	3	3	2	-	2	-	-	-	-	-	0	-	2	-	-	-	2	2	-	3	-	3	0	0	-	-	0	-	2	-	2	-
goodwini	3	3	2	?	2	-	-	-	-	-	0	-	2	-	-	-	2	2	-	2	-	0	-	-	2	-	0	-	2	-	2	-
griseoventris	3	3	2	?	2	-	-	-	-	-	0	-	?	?	?	?	?	?	?	?	?	0	-	-	2	-	0	-	2	?	?	0

1894 by E. W. Nelson and E. A. Goldman (collector number 6748).

Type locality.—"mountains 15 miles [south]west of city of Oaxaca [de Juárez], Mexico (altitude, 9,500 feet)." According to Goldman (1951), the collectors spent September 10th to 19th, 1894, traveling to and from, and working at, this locality. This trip took them ca. 8 mi southwest of Oaxaca de Juárez to Cuilapan, then west into the mountains, passing Santa Inéz [Santa Inés del Monte, 16°54'30"N, 96°52'W] and climbing over the summit to a wet meadow called Nevería Herrera on the western slope.

> "These high mountains, which appeared to have no distinctive name, are somewhat isolated, the only connection with the high mountains to the east being through low hills north of Oaxaca. The upper slopes are well watered, and general conditions much as on Cerro San Felipe. Specimens were labeled 'Mountains 15 miles west of Oaxaca,' but as we later learned the direction was more nearly southwest." (Goldman, 1951:218).

Merriam (1895) reported that the specimens were obtained from a variety of elevations between 8800 [2680 m] and the summit at 9500 ft [2895 m], indicating that the type series of *Cryptotis peregrina* was collected at or near the top of the range. On topographic maps, the summit appears to be near a landmark called La Plazuela [16°56'52"N, 96°53'45"W]. Binford (1989) refers to these mountains as the Sierra de Cuatro Venados.

Distribution.—Known from 2680 to 3200 m in the Sierra de Cuatro Venados, central Oaxaca, and the Sierra Yucuyacua, western Oaxaca (Fig. 3).

Description.—Size medium to large for the genus (Table 1); tail long, averaging 30 mm, or ca. 42% (Table 4) of head-and-body length; dorsal guard hairs 6–7 mm long; forepaws enlarged; foreclaws noticeably elongate and broadened; rostrum of moderate length (PL/CBL = 44.5%, Table 4); often two well-developed dorsal foramina (44%, Table 4); foramen posterior to dorsal articular facet leading to ventral extension
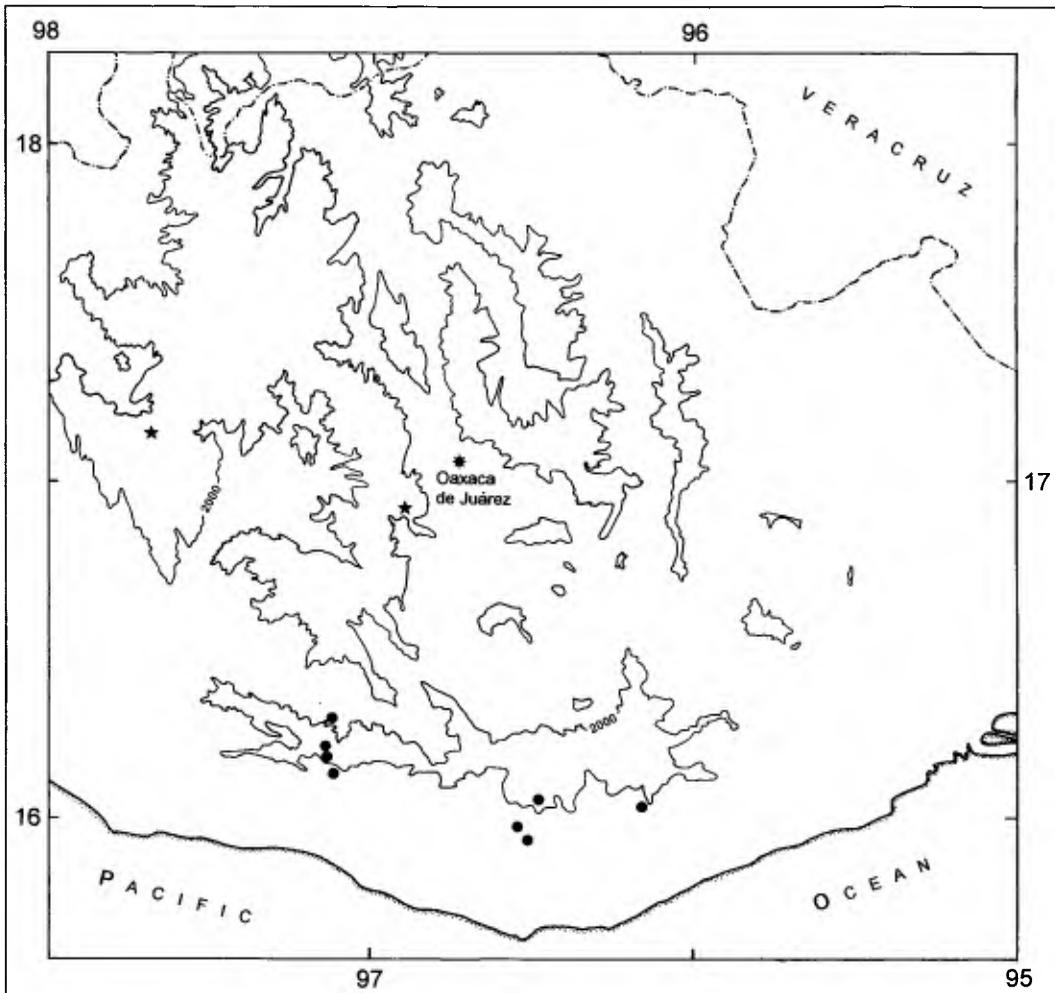
Fig. 3.   Map of part of Oaxaca, Mexico, illustrating the known distribution of *Cryptotis peregrina* (★) and *Cryptotis phillipsii* (●). The 2000 m contour is shown.

of the sinus canal typically present on one or both sides of the cranium (94%, Table 4); foramen dorsal to dorsal articular facet typically absent (87%, Table 4); zygomatic plate narrow (ZP/PL = 19.3%, Table 4), anterior border usually aligned with posterior ⅓ of mesostyle-metastyle valley or metastyle of M¹; U⁴ unreduced in size, surface area >½ that of U³; U⁴ usually aligned with the unicuspid toothrow and partially visible in lateral view of the skull; P⁴, M¹, and M² slightly to moderately recessed on posterior border; protoconal basin of M¹ reduced rel-

ative to hypoconal basin; M³ simple: usually possessing paracrista, paracone, precentrocrista (all pigmented), mesostyle, and very short postcentrocrista; M³ lacking metacone, hypocone absent or poorly-developed, and a reduced, typically unpigmented protocone occasionally present. Articular process of the mandible generally moderately tall and wide, with a moderately broad lower articular facet; moderately high coronoid process of the mandible (HCP/ML = 73.1%, Table 4); entoconid usually present on M₃ (73%, Table 4), typically vesti-

Table 4.—Characteristics among the five species previously synonomized with *Cryptotis mexicana*.

C. mexicana (Oaxaca)	C. nelsoni	C. obscura	C. peregrina	C. phillipsii
Foramen of sinus canal				
7%	0%	19%	94%	24%
n = 90	n = 8	n = 52	n = 16	n = 17
Foramen dorsal to dorsal articular facet present				
13%	38%	28%	13%	82%
n = 90	n = 8	n = 36	n = 15	n = 17
Two distinct dorsal foramina present				
54%	50%	22%	44%	47%
n = 95	n = 6	n = 58	n = 16	n = 19
Posteroventral border of unicuspids				
concave	concave	straight to convex	concave	concave
Entoconid of M_3 present				
100%	100%	96%	73%	93%
68% well-developed	100% well-developed	96% well-developed	100% vestigal	83% vestigal
n = 77	n = 7	n = 26	n = 22	n = 13
Humerus modified				
slightly	?	slightly	extremely	slightly
Relative tail length (TL/HB × 100)				
39 ± 5	38 ± 4	40 ± 6	42 ± 3	46 ± 6
26–52	28–44	29–55	36–47	30–59
n = 118	n = 9	n = 55	n = 24	n = 27
Relative rostrum length (PL/CBL × 100)				
43.7 ± 0.8	43.2 ± 0.8	43.1 ± 1.1	44.5 ± 0.7	43.3 ± 0.6
41.7–45.1	42.0–44.3	41.0–45.6	43.2–46.0	42.2–44.4
n = 30	n = 6	n = 32	n = 12	n = 14
Relative breadth of zygomatic plate (ZP/PL × 100)				
21.6 ± 1.6	23.8 ± 1.4	24.7 ± 1.1	19.3 ± 1.0	23.4 ± 1.6
17.9–24.4	21.8–25.6	22.2–26.9	18.1–21.2	21.4–26.4
n = 30	n = 7	n = 32	n = 12	n = 14
Relative breadth of zygomatic plate (ZP/CBL × 100)				
9.4 ± 0.7	10.2 ± 0.6	10.6 ± 0.5	8.6 ± 0.5	10.1 ± 0.6
7.9–10.4	9.5–11.2	9.7–11.5	7.8–9.4	9.2–11.4
n = 30	n = 6	n = 32	n = 12	n = 14
Relative length of unicuspid toothrow (UTR/CBL × 100)				
12.7 ± 0.4	12.5 ± 0.5	13.0 ± 0.4	12.9 ± 0.3	12.7 ± 0.6
11.4–13.3	12.0–13.4	11.6–13.9	12.1–13.4	11.4–13.7
n = 30	n = 6	n = 32	n = 12	n = 14
Relative palatal breadth (M2B/PL × 100)				
65.9 ± 2.5	72.3 ± 0.9	67.4 ± 2.2	65.2 ± 2.5	68.7 ± 2.1
60.0–72.6	70.9–73.3	62.4–70.7	60.9–68.7	65.1–72.5
n = 30	n = 7	n = 32	n = 12	n = 14
Relative height of coronoid process (HCP/ML × 100)				
70.8 ± 3.5	73.8 ± 1.3	74.3 ± 3.0	73.1 ± 1.6	75.7 ± 4.1
65.1–79.6	72.3–76.2	70.2–83.6	69.4–75.0	71.6–86.2
n = 30	n = 8	n = 32	n = 12	n = 16

Table 4.—Continued.

C. mexicana (Oaxaca)	C. nelsoni	C. obscura	C. peregrina	C. phillipsii
Relative posterior length of mandible (AC3/ML × 100)				
80.8 ± 2.6	80.2 ± 1.8	77.9 ± 3.0	82.1 ± 2.1	78.4 ± 3.6
77.4–86.2	77.8–82.5	72.6–85.5	77.8–85.0	73.2–86.2
n = 30	n = 8	n = 32	n = 12	n = 16
Relative extension of articular condyle (AC3/HCP × 100)				
114.3 ± 5.1	108.8 ± 1.7	105.0 ± 3.7	112.4 ± 2.0	103.7 ± 3.9
100.0–124.4	106.4–110.6	100.0–114.3	109.9–115.6	96.1–110.6
n = 30	n = 8	n = 32	n = 12	n = 16

gial and unpigmented when present. Broad, curved humerus, with elongated processes (Fig. 4B).

Comparisons.—*Cryptotis peregrina* is distinctive among the species previously considered to be subspecies of *Cryptotis* *mexicana*. It has a narrow zygomatic plate, and it has the broadest forepaws and the longest and broadest foreclaws. The humerus is shorter, more curved, and generally more highly derived: the pectoral process is higher, lateral epicondyle more ex-
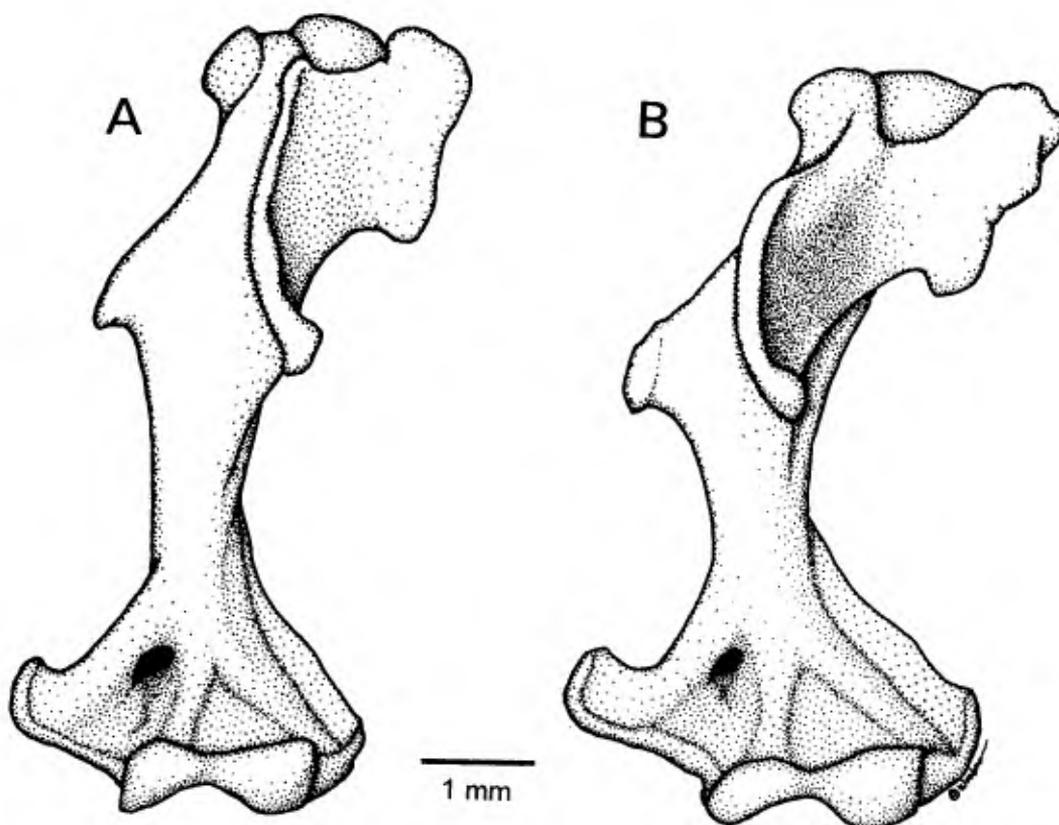
Fig. 4   Left humeri of (A) *Cryptotis phillipsii* (KU 124299) and (B) *Cryptotis peregrina* (AMNH 149965). The humerus labeled "*C. peregrina*" in Woodman and Timm (1999: Fig. 15B) is from a specimen (KU 124298) that we now recognize as *C. phillipsii*.

panded, and teres tubercle and medial epicondyle longer and more closely situated to each other. *Cryptotis peregrina* is the only species in the *C. mexicana*-group besides *Cryptotis goldmani* that usually has a well-developed foramen of the ventral branch of the sinus canal (Table 4; Woodman & Timm 1999).

Cryptotis mexicana: Cryptotis peregrina has slightly longer, broader claws and a much more derived humerus; M^3 simple, lacking metacone; entoconid of M_3 vestigial (rather than well-developed), when present.

Cryptotis nelsoni: Cryptotis peregrina has slightly longer, broader claws and a much more derived humerus; skull narrower overall; longer rostrum and much narrower palate (Table 4); M^3 simple, lacking metacone; entoconid of M_3 vestigial (rather than well-developed), when present.

Cryptotis obscura: Cryptotis peregrina has much longer, broader claws and a much more derived humerus; longer rostrum (Table 4); upper unicuspids concave on posterior surface (rather than straight or convex), appearing curved; M^3 simple, lacking metacone; more likely to have two well-developed dorsal foramina (44% vs. 22%, Table 4); entoconid of M_3 vestigial (rather than well-developed), when present.

Cryptotis phillipsii: Cryptotis peregrina has much longer and broader claws and a much more derived humerus; longer rostrum and much narrower palate (Table 4); absolutely and relatively broader zygomatic plate (Tables 1, 4); larger U^4 relative to U^3; slightly more recessed upper dentition; slightly less complex M^3; well-developed foramen of the ventral extension of sinus canal; usually no foramen dorsal to dorsal articular facet.

Cryptotis goldmani-group: *Cryptotis peregrina* is generally smaller in head-and-body-length and has a relatively longer tail (Table 1, 4); narrower zygomatic plate; more likely to possess a vestigial entoconid (rather than no entoconid) of M^3.

Remarks.—Nearly all known specimens of *Cryptotis peregrina* are part of the type series, collected in the Sierra de Cuatro Venados ca. 15 mi SW of Oaxaca de Juárez in 1894. Merriam (1895) stated that there were 25 specimens in the type series, but he did not list them individually. We were able to locate only 24 original specimens collected by Nelson and Goldman. The only other specimen of *C. peregrina* of which we are aware is a fluid-preserved individual (with the skull and left humerus removed) in poor condition, collected "N. La Muralla" in the Sierra Yucuyacua by Thomas B. MacDougall on 18 March 1952. Locality notes by MacDougall indicate this locality is at 10,500+ ft at the "top of Cerro Yucunino" (AMNH field notes, 1952). We believe (as apparently did Choate, 1970:239) that this peak is equivalent to Cerro Yucuyacua [= Piedra de Olla], based on its elevation and position relative to La Muralla and Santa María Asunción Tlaxiaco.

Goldman (1951:218) noted that the type locality was moist, with general conditions "much as on Cerro San Felipe." Areas above 8000 ft on Cerro San Felipe were covered in oak-dominated mixed forest with an herbaceous understory, and they experienced cold night-time temperatures, with frosts recorded in August. Meadows (neverías), such as the one in the vicinity of the type locality, were said to be employed by local people for making ice to be used at lower elevations. MacDougall (AMNH field notes, 1952) noted the presence of pine and oak where he captured *C. peregrina* north of La Muralla.

Specimens examined (25).—Mexico: Oaxaca: N[orth]. [of] La Muralla [16°58′N, 97°56′W], top of Cerro Yucuninó [= Cerro Yucuyacua, 17°06′N, 97°40′W], Tlaxiaco [Santa María Asunción Tlaxiaco, 17°16′N, 97°41′W], 10,500+ ft (AMNH 149965); mountains 15 mi [south] west Oaxaca de Juárez [16°30′N, 96°53′W], 9500 ft (BMNH 95.11.1.26 [= USNM 68337], USNM 68315–68336, 68338, including holotype).

"Cryptotis goldmani-group" Woodman & Timm, 1999

Description.—The *C. goldmani*-group is a subset of the *C. mexicana*-group that is comprised of medium-sized members of the genus with greatly broadened forefeet; extremely long, broad foreclaws; fourth upper unicuspid usually aligned with the unicuspid toothrow and partially visible in labial view of the cranium; protoconal basin of M^1 reduced relative to hypoconal basin; M^3 simple, hypocone absent or poorly developed and lacking metacone; entoconid of M_3 vestigial or absent; and extremely broad humerus with greatly elongated processes.

Included species.—*Cryptotis alticola, C. goldmani, C. goodwini, C. griseoventris,* and *C. peregrina.*

Cryptotis phillipsii (Schaldach, 1966)

Notiosorex (Xenosorex) Phillipsii Schaldach, 1966:289; Goodwin, 1969:43.

Cryptotis mexicana machetes: Musser, 1964:6; Schaldach, 1966:288; Goodwin, 1969:40 (in part).

Cryptotis mexicana peregrina: Goodwin, 1969:40 (in part); Choate, 1970:237 (in part); Hall, 1981:59 (in part).

Cryptotis peregrina: Woodman & Timm, 1999:35 (in part).

Holotype.—Skin and skull of adult female, UNAM 8445; taken 18 Dec 1964 by W. J. Schaldach, Jr. (collector number 13278). Two paratypes, KU 114226 [= UNAM 8446] and UNAM 8447.

Type locality.—"the Río Molino, 3 kilometers S.W. San Miguel Suchixtepec, altitude 2250 meters, southern Oaxaca, México" (Schaldach, 1966:289).

Distribution.—Known from 1060 to 2745 m in the Sierra de Miahuatlán, southern Oaxaca, Mexico (Fig. 3).

Description.—Size medium to large for the genus (Table 1); tail long, averaging 31 mm, or ca. 46% (Table 4) of head-and-body length; dorsal guard hairs 6–7 mm long; forepaws somewhat enlarged; foreclaws among the narrowest for members of the *Cryptotis mexicana*-group, but elongate and somewhat broadened relative to other members of the genus; rostrum of moderate length (PL/CBL = 43.3%, Table 4); often two well-developed dorsal foramina (47%, Table 4); ventral extension of the sinus canal and associated foramen typically lacking (76%, Table 4), but well-developed when present; a foramen dorsal to the dorsal articular facet usually present on one or both sides of the skull (82%, Table 4); zygomatic plate broad (ZP/PL = 23.4%, Table 4), anterior border usually aligned with posterior ½ of mesostyle-metastyle valley or metastyle of M^1; P^4, M^1, and M^2 unrecessed to slightly recessed on posterior border; surface area of U^4 typically ≤½ that of U^3; U^4 usually aligned with the unicuspid toothrow, but not typically visible in lateral view of the skull; protoconal basin of M^1 same size as hypoconal basin; M^3 simple, lacking metacone, hypocone poorly-developed or absent; M^3 usually possessing paracrista, paracone, precentrocrista, and mesostyle (all pigmented), and occasionally a very short postcentrocrista and a well-developed, pigmented protocone. Articular process of the mandible generally moderately tall and wide, with a moderately broad lower articular facet; coronoid process of the mandible moderately high relative to mandibular length (HCP/ML = 75.7%, Table 4); entoconid usually present on M_3 (92%, Table 4), typically vestigial (83% of those possessing entoconids), but occasionally well-developed (17%). The tall, broad, slightly curved humerus has somewhat elongated processes, but it is among the least modified within the *C. mexicana*-group (Fig. 4).

Comparisons.—*Cryptotis phillipsii* has the least modified forelimbs of any member of the *Cryptotis mexicana*-group: it has the smallest forepaws and the shortest and narrowest foreclaws; the humerus is among the longest and least curved; teres tubercle is short, medial epicondyle is short and has a straight proximal edge, and teres tubercle and medial epicondyle are broadly separat-

ed. *Cryptotis phillipsii* also has the longest tail relative to head-and-body-length (Table 4). There *may* be a local tendency for some *C. phillipsii* to develop without U⁴s (12%, $n = 17$) in the region of the type locality, resulting in a reduced dentition.

Cryptotis mexicana: Cryptotis phillipsii has shorter, narrower foreclaws and a relatively longer tail; less modified humerus; broader palate (Table 4); simple M^3, lacking metacone; entoconid of M_3 usually vestigial (rather than well-developed) when present.

Cryptotis nelsoni: Cryptotis phillipsii has shorter, narrower foreclaws and a relatively longer tail; narrower palate (Table 4); simple M^3, lacking metacone; entoconid of M_3 usually vestigial (rather than well-developed) when present.

Cryptotis obscura: Cryptotis phillipsii has a relatively longer tail; upper unicuspids concave on posterior surface, appearing curved, rather than convex and cone-shaped; more likely to have two well-developed dorsal foramina (Table 4); simple M^3, lacking metacone; entoconid of M_3 usually vestigial (rather than well-developed) when present.

Cryptotis goldmani-group: *Cryptotis phillipsii* is smaller in head-and-body-length, and has much shorter, narrower foreclaws, a much less derived humerus, and a relatively longer tail; higher coronoid process (Table 4); shorter posterior portion of mandible (Table 4); much more likely to possess vestigial entoconid (rather than no entoconid) of M_3.

Remarks.—The type series of *Cryptotis phillipsii* was collected in 1964 by William J. Schaldach, Jr. and Allan R. Phillips during a trip to southern Oaxaca to obtain specimens of birds and mammals. Schaldach (1966) originally described a new species, *Notiosorex phillipsii,* on the basis of three specimens: a skin with skull and a skin without skull from Río Molino (UNAM 4445, 4447) and a skin with skull from Río Guajalote (KU 114226 = UNAM 8446). Originally identified as *Cryptotis mexicana,* the main consideration in sub-

sequently referring these three specimens to *Notiosorex* appears to have been the presence of only three unicuspids in the upper toothrow, rather than the four unicuspids typical of *Cryptotis.* A fourth specimen (UNAM 8444), collected at Río Molino and possessing four unicuspids, was reported as *Cryptotis mexicana* (Schaldach 1966). Noting strong differences in external, cranial, and dental characters between the type series of *N. phillipsii* and specimens of *Notiosorex crawfordi* and *Megasorex gigas* that he used for comparison, Schaldach (1966) erected a new subgenus, *Xenosorex,* to distinguish the new shrew. Choate (1969) reexamined the type series of *Notiosorex phillipsii* and reported a number of distinctive cranial, mandibular, and dental characters that clearly established *N. phillipsii* as a member of the genus *Cryptotis,* despite its reduced dentition. He justifiably placed Schaldach's *N. phillipsii* as a junior synonym of *Cryptotis* [*mexicana*] *peregrina,* where it has remained until now (Choate 1970, Hall 1981, Hutterer 1993, Woodman & Timm 1999).

Cryptotis phillipsii is known from higher elevation forest, including cloud forest, in the Sierra de Miahuatlán of southern Oaxaca. The species is syntopic with *Cryptotis goldmani* at some localities, but the geographic distribution of *C. phillipsii* is not nearly as broad as that of *C. goldmani,* despite an apparently lower elevational limit.

Schaldach (1966) reported the humid, shaded ravines along the slopes of the valley of the Río Molino at the type locality contained remnant, pine- and oak-dominated cloud forest, with a dense understory of ferns, mosses, vines, and shrubs. Musser (1964) described the canyon bottom as containing moist, open forest with bromeliad-covered oaks and a dense ground cover of shrubs, ferns, and herbaceous vegetation. The higher, drier slopes were covered with a mixed secondary growth of pines and oaks. Musser (1964:6) took one *C. phillipsii,* two *Sorex saussurei oaxacae,* and 29 *Peromyscus megalops* under a "lush her-

baceous ground cover" consisting largely of ferns along the steep banks of a "moist, densely vegetated streamside" with a "deep layer of wet humus and leaf litter" at 7300 ft [2225 m] near Río Molino. Paul B. Robertson (KU field notes and catalog, 1969, 1970) captured three *C. phillipsii* at Río Molino. In December 1969, he trapped one *C. phillipsii*, one *Microtus mexicanus*, two *Peromyscus aztecus*, two *P. levipes*, and four *P. megalops*. In April 1970 using a trapline "along a small rivulet," he took one *C. phillipsii* with two *Cryptotis goldmani*, one *Sorex saussurei oaxacae*, one *Microtus mexicanus*, one *Neotoma mexicana*, two *Oryzomys chapmani*, 12 *Peromyscus megalops*, and one *Reithrodontomys mexicanus*. Nearby, "among & under rocks in an overgrown field," he collected a *C. phillipsii* with two *Reithrodontomys megalotis*, three *R. sumichrasti*, and one *Sigmodon alleni*. He described the streamside vegetation at Río Molino as "hard wood" and the slopes as "almost pure pine." In addition, Schaldach (1966) reported capturing *Sorex mutabilis* (as *Sorex veraepacis*) and *Liomys pictus* at Río Molino. *Cryptotis phillipsii* and *C. goldmani* were collected in syntopy also at "lumber camp, km 158" along the Puerto Ángel Road in January 1970 by John R. Arnold and Craig Moe. *Cryptotis phillipsii* and *C. parva pueblensis* were captured syntopically 20 mi S, 5 mi E San Miguel Sola de Vega by Percy L. Clifton in June–July 1964. He described the habitat there as dense cloud forest, with *C. phillipsii* "caught under a rock in a low damp situation along a creek" (KU field notes, 1964). *Cryptotis phillipsii* also was taken in syntopy with *C. p. pueblensis* at San Miguel Suchixtepec by Thomas B. MacDougall in October 1967.

Specimens examined (36).—Mexico: Oaxaca: 20 mi S, 5 mi E Sola de Vega [San Miguel Sola de Vega, 16°31′N, 96°59′W], 4800 ft (KU 98728); 36 km (by road) N San Gabriel Mixtepec [16°06′N, 97°06′W], 1680 m (KU 124294); 27.8 km (by road) N San Gabriel Mixtepec, 1320 m (KU 124295, 124296); La Cima, Puerto Escondido road, km 184.5 [16°12′N, 97°07′W], 5750 ft (CAS 15473); Puerto Escondido road, km 193 [16°10′N, 97°07′W], 4200 ft (CAS 15474); Sinai [Finca Sinai, 16°07′N, 97°08′W], 10 km [by trail] E Nopala [Santo Reyes Nopala], 7200 ft (CAS 14940); Río Molino [16°04′N, 96°28′W], 2250–2745 m (AMNH 213758, 213759, 214152, 214803–214805; KU 121661, 124298, 124299; UNAM 8444, 8445, 8447—includes holotype); near campemento Río Molino (Hwy 175), 7300 ft (UMMZ 112572); Puerto Ángel road, km 153 [16°04′N, 96°28′W], 7100 ft (CAS 14068); San Miguel Suchixtepec [16°05′N, 96°28′W], Miahuatlán District (AMNH 214806–214808); 16 km SW [San Miguel] Suchixtepec, 2000 m (ENCB 3413, 3414); Lovene [16°02′N, 96°12′W], Miahuatlán (AMNH 178739); lumber camp, Puerto Ángel road, km 158, 8375 ft (CAS 15478); Río Guajalote [16°00′N, 96°28′W], 2000 m (KU 114226); Río Jalatengo [15°58′N, 96°27′W], Puerto Ángel road, km 178, 4275 ft (CAS 14069, 14071, 14072, 15475; UNAM 27518); Puerto Ángel road, km 195, 3475 ft (UNAM 26551); Puerto Ángel road (UNAM 27517).

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Appendix I: Transition Series Used in Phylogenetic Analysis

Transition series (TS) marked by an asterisk (*) were modified from Woodman & Timm (1999). TS 30–32 were added since that paper.

*1. length of foreclaws: short (0); elongate (1); more elongate (2); greatly elongate (3).

*2. breadth of foreclaws: narrow (0); broad (1); broader (2); extremely broad (3).

3. forefeet: small (0); enlarged, broadened (1); greatly enlarged and broadened (2).

4. metacarpals: long, narrow (0); short, broad (1).

5. posterior border of zygomatic plate: even with or anterior to anterior root of maxillary process (0); even with posterior root of zygomatic process, but separated from it by posterior border of palate (1); even with (or posterior to) and confluent with posterior root of zygomatic process (2).

6. anterior border of coronoid process: steep, forming a narrow angle with horizontal ramus of mandible (0); less steep, forming a wide angle with horizontal ramus of mandible (1).

7. articular condyle: low and broad (0); high and narrow (1).

8. lower sigmoid notch: very shallow (0); deep (1).

9. shape of unicuspids (U^1–U^3): cone-shaped, posteroventral border straight-edged or convex (0); narrow, posteroventral border concave (1).

10. protoconal basin of M^1: about equal in

size to hypoconal basin (0); reduced relative to hypoconal basin (1).

11. M³ morphology: simple, metacone absent (0); complex, metacone present (1).

12. shape of P₃: short and high (0); long and low (1).

13. shape of humerus: long, narrow, relatively straight (0); short, robust, curved (1); short, robust, and very curved (2).

14. head of humerus: rounded (0); dorsoventrally elongate (1).

15. ventral edge of proximal face of greater tuberosity of humerus: rounded (0); with broad, deep pocket (1).

*16. pectoral process of humerus: low (0); high (1).

*17. length of teres tubercle: relatively short (0); elongate (1); greatly elongate (2).

*18. medial epicondyle of humerus: short (0); elongate (1); greatly elongate (2).

19. lateral epicondyle of humerus: small (0); expanded (1).

20. teres tubercle and medial epicondyle of humerus: far apart (0); close together (1); very close (2); extremely close (3).

21. posterior edge of falciform process of tibia: not deeply pocketed (0); deeply pocketed (1).

*22. foramen of sinus canal: absent in 100% of specimens (0); absent in >75% of specimens (1); present in >50% of specimens, but vestigial (2); present in >90% of specimens, well-developed (3).

23. dorsal foramina: two in <75% of specimens (0); two in >75% of specimens (1).

24. foramen dorsal to articular facet: present in <75% of specimens (0); present in >75% of specimens (1).

*25. entoconid of M₃: present in >90% of specimens, typically well-developed (0); present in >50% of specimens, typically vestigial (1); absent in >80% of specimens (2).

26. body size (head-and-body length): smaller, mean <69 (0); larger, mean >72 (1).

27. relative tail length (% of head-and-body length): short, mean <39% (0); long, mean >40% (1).

28. upper unicuspid toothrow: crowded, three unicuspids visible in lateral view (0); uncrowded, four unicuspids visible in lateral view (1).

29. dorsal guard hairs: short, <4 mm (0); of intermediate length, 4–5 mm (1); long, >5 mm (2).

*30. distal edge of pectoral process of humerus relative to teres tubercle: extends well distal to teres tubercle (0); extends to proximity of distal edge of teres tubercle (1).

*31. bones of hind paws: metatarsals and proximal phalanges long narrow (0); metatarsals and proximal phalanges broad (1); metatarsals and proximal phalanges short and very broad (2).

*32. posterior border of P⁴, M¹, and M²: slight to no emargination (0); noticable emargination (1); strong emargination (2).