

# Geographic Variation and Evolutionary Relationships Among Broad-Clawed Shrews of the *Cryptotis goldmani*-Group (Mammalia: Insectivora: Soricidae)

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## Abstract

The *Cryptotis goldmani*-group of small-eared shrews consists of species that occupy high-elevation (>1000 m) habitats in Mexico and northern Central America. Previously, this group was viewed as consisting of only two species (*C. goldmani* and *Cryptotis goodwini*) that were characterized by extreme enlargement of the forefeet and foreclaws. Phylogenetically, *C. goldmani* and *C. goodwini* were placed in Choate's (1970) *Cryptotis mexicana*-group, which otherwise consisted of the four subspecies of *C. mexicana*. Our reevaluation of these shrews indicates that the subspecies of *C. mexicana* are well-differentiated taxa that we recognize as separate species (*C. mexicana*, *Cryptotis nelsoni*, *Cryptotis obscura*, and *Cryptotis peregrina*). The *C. goldmani*-group consists of at least four distinct species: *Cryptotis alticola*, in Colima, Jalisco, México, Michoacán, Puebla, and the Distrito Federal of Mexico; *C. goldmani*, in the Sierra Madre del Sur of Guerrero and Oaxaca; *C. goodwini*, in Chiapas, Guatemala, El Salvador, and Honduras; and *Cryptotis griseoventris*, in the northern highlands of Chiapas and Guatemala. A single new specimen of *C. goodwini* indicates the presence of this species in Honduras, which is outside of the previously recognized geographic range of the *C. mexicana*-group. This new specimen possesses characters suggesting that the Honduran population is phylogenetically distinct from other *C. goodwini*, and we herein describe a new subspecies for *C. goodwini*.

Our morphological analysis indicates that enlargement of the forefeet and foreclaws is a trend found throughout the *C. mexicana*-group, reaching its xenith in members of the *C. goldmani*-group. This trend is accompanied by functional modifications of the forelimb skeleton. Our phylogenetic analysis, based on 29 transition series, indicates that the *C. mexicana*-group forms a well-supported clade and justifies nesting of the *C. goldmani*-group within the *C. mexicana*-group. Topology of each of the shortest trees shows that the species previously recognized as subspecies of *C. mexicana* are paraphyletic with respect to the *C. goldmani*-group.

## Resumen

Las musarañas de orejas pequeñas del grupo de especies *Cryptotis goldmani* ocurren en hábitats de altas elevaciones (> 1000 msnm) en México y el norte de Centroamérica. Anteriormente, se consideraba que este grupo se constaba de solamente dos especies (*C. goldmani* y *Cryptotis goodwini*) que se caracterizaban por la agrandación excesiva de las patas y las uñas delanteras. Filogenéticamente *C. goldmani* y *C. goodwini* se encontraban en el grupo de especies *Cryptotis mexicana* sensu Choate (1970), un grupo que además incluía solamente *C. mexicana* con cuatro subspecies. Nuestra revisión de estas musarañas indica que las subspecies de *C. mexicana* son taxones bien diferenciados que reconocemos como especies distintas (*C. mexicana*, *Cryptotis nelsoni*, *Cryptotis obscura*, y *Cryptotis peregrina*). El grupo de especies

*C. goldmani* consta de por lo menos cuatro especies distintas: *Cryptotis alticola*, en Colima, Jalisco, México, Michoacán, Puebla y el Distrito Federal de México; *C. goldmani*, en la Sierra Madre del Sur en Guerrero y Oaxaca; *C. goodwini*, en Chiapas, Guatemala, El Salvador, y Honduras; y *Cryptotis griseoventris*, en las montañas del norte de Chiapas y Guatemala. Un ejemplar único de *C. goodwini* muestra la presencia de tal en Honduras, fuera de la distribución anteriormente conocida para el grupo de especies *C. mexicana*. Este espécimen nuevo tiene características que sugieren que la población hondureña es filogenéticamente distinta a los demás *C. goodwini*; por lo tanto, se lo describe aquí como una nueva subespecie de *C. goodwini*.

Nuestro análisis morfológico muestra que la agrandación de las patas y las uñas delanteras es una tendencia presente en todo el grupo *C. mexicana*, y que alcanza su desarrollo máximo en las especies del grupo *C. goldmani*. Tal tendencia se relaciona con modificaciones funcionales del esqueleto del miembro delantero. Nuestro análisis filogenético, basado en 29 caracteres, indica que el grupo *C. mexicana* es un clado bien definido y justifica la posición del grupo *C. goldmani* dentro del grupo anterior. La topología de cada uno de los arboles filogenéticos más cortos demuestra que las especies anteriormente tratadas como subespecies de *C. mexicana* son parafiléticas con respecto al grupo de especies *C. goldmani*.

## Introduction

Small-eared shrews of the New World genus *Cryptotis* range geographically from southernmost Canada, through the eastern half of the United States, Mexico, and Central America, to the Andean highlands of northwestern South America. A large array of names has been proposed for the Mexican and Central American members of the genus; however, the paucity of specimens available has hindered assessment of geographic and nongeographic variation. Choate (1970), in his monograph on the Middle American members of this group, recognized eight species that he arranged into three informal groupings: the "*Cryptotis mexicana*-group" (containing three species: *Cryptotis goldmani*, *Cryptotis goodwini*, and *C. mexicana*), the "*Cryptotis parva*-group" (two species: *C. parva* and *Cryptotis nigrescens*), and "relict species" (three species: *Cryptotis endersi*, *Cryptotis gracilis*, and *Cryptotis magna*). Recently, we (Woodman & Timm, 1992) described a ninth species for the region, *Cryptotis hondurensis*, from high-elevation pine forest and pine-oak forest of south-central Honduras. In addition, we (Woodman & Timm, 1993) recognized *C. nigrescens*, a member of Choate's *C. parva*-group, to be a complex of at least five species distributed from southern Mexico to Colombia. Thus, the genus *Cryptotis* is considerably more diverse in Central America than previously thought.

The three species recognized by Choate (1970) as comprising his *C. mexicana*-group (*C. goldmani*, *C. goodwini*, and *C. mexicana*) occur in

middle- to high-elevation habitats distributed from the Mexican state of Tamaulipas to El Salvador. Among these species, *C. goldmani* and *C. goodwini* can be distinguished most readily from *C. mexicana* by their greatly enlarged front feet and foreclaws, characters unique among members of the genus. Under Choate's (1970) taxonomy, *C. goldmani* included two subspecies, *C. goldmani alticola* and *C. goldmani goldmani*, that were known to occur from the Mexican state of Jalisco southeast into Guatemala. The monotypic *C. goodwini* was known from Guatemala, El Salvador, and Chiapas, Mexico.

We recently obtained a new specimen of the *C. goldmani*-group from Honduras, which is outside of the previously known geographic range for these broad-clawed shrews. Our attempts to identify this specimen and adequately document its phylogenetic and biogeographic relationships to other members of the *C. goldmani*-group led us to reevaluate the taxonomic status of these poorly known shrews.

It is the purpose of this paper to review published knowledge of the broad-clawed shrews of the *C. goldmani*-group and analyze their phylogenetic relationships. We redescribe four species described previously (*Cryptotis alticola*, *C. goldmani*, *C. goodwini*, and *Cryptotis griseoventris*) and describe a new subspecies for *C. goodwini*. Our accounts for these species include a review of all available information on reproduction, elevational and geographic distributions, and habitat, and we provide a key for their identification. We present diagnostic characteristics of the postcranial skeleton of *Cryptotis* for the first time.

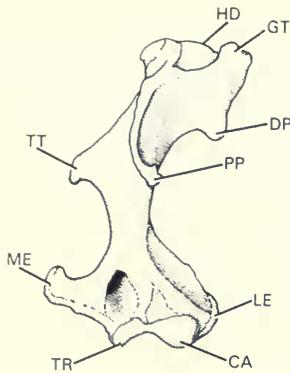


FIG. 1. Left humerus of *Cryptotis goldmani*, indicating anatomical features mentioned in the text. Abbreviations: CA, capitulum; DP, deltoid process; GT, greater tuberosity; HD, head; LE, lateral epicondyle; ME, medial epicondyle; PP, pectoral process; TR, trochlea; and TT, teres tubercle. Anatomical terminology follows Reed (1951).

## Methods

For the purposes of this paper, we use *Cryptotis mexicana*-group to refer informally to the set of taxa that includes *C. mexicana*, *Cryptotis nelsoni*, *Cryptotis obscura*, *Cryptotis peregrina*, *Cryptotis laticola*, *Cryptotis goldmani*, *Cryptotis goodwini*, and *Cryptotis griseoventris*. The *Cryptotis goldmani*-group, or broad-clawed shrews, refers to the subset of the *C. mexicana*-group that includes *C. laticola*, *C. goldmani*, *C. goodwini*, and *C. griseoventris*. The *Cryptotis nigrescens*-group includes *Cryptotis colombiana*, *Cryptotis hondurensis*, *Cryptotis mayensis*, *Cryptotis mera*, *Cryptotis merriami*, and *Cryptotis nigrescens* (Woodman & Timm, 1993). In the *Cryptotis parva*-group, we include all taxa currently included as subspecies of *C. parva* (*C. parva berlandieri*, *C. p. elasson*, *C. p. floridana*, *C. p. orophila*, *C. p. parva*, *C. p. ueblensis*, *soricina*, and *tropicalis*). The *C. mexicana*-group and the *C. goldmani*-group appear to be natural groupings of species. The *C. nigrescens*-group and the *C. parva*-group may represent nonphylogenetic groupings of species, but they remain informal, awaiting a comprehensive phylogenetic study of the genus.

Terminology of dentition and dental characteristics follows Choate (1970). Anatomical terminology of the humerus (Fig. 1) and other parts of the postcranial skeleton follows Reed (1951). Measurements used in our analyses follow Woodman and Timm (1993). Measurements of the skull (Fig. 2) were taken to the nearest 0.1 mm using

either an ocular micrometer in a binocular microscope or a handheld dial caliper. Standard external measurements are those recorded by the collector, except for head-and-body length (HB), which we calculated by subtracting the recorded tail length (TL) from the total length. Other abbreviations of measurements found in the text include distance from articular condyle to posterior edge of  $M_1$  (AC3); breadth of articular condyle (BAC); cranial breadth (CB); condylobasal length, not including the upper incisors (CBL); height of articular condyle (HAC); height of coronoid process (HCP); height of coronoid valley (HCV); interorbital breadth (IO); length of lower first molar ( $M_1L$ ); breadth of palate across second molars ( $M^2B$ ); length of molariform toothrow,  $P^1$  through  $M^3$  (MTR); mandibular length, from inferior sigmoid notch to mental foramen (ML); palatal length (PL); upper toothrow length,  $U^1$  through  $M^3$  (TR); lower toothrow length,  $P_3$  through  $M_3$  (TRD); breadth of palate across first unicuspid ( $U^1B$ ); breadth of palate across third unicuspid ( $U^3B$ ); length of unicuspid toothrow (UTR); and breadth of zygomatic plate (ZP). All measurements are in millimeters. Univariate statistics include mean  $\pm$  standard deviation. Multivariate analyses and analyses of variance (ANOVA) were carried out using BMDP on the University of Kansas Academic Computing Service IBM VM/CMS computer system and Minitab release 8.0 for DOS-based personal computers. *F*-values and *P*-values for ANOVAs (Table 1) were calculated using a Brown-Forsythe equality of means test that does not assume equality of the variances. Localities and elevations that we report are taken directly from specimen tags and represent the descriptions provided by the original collectors. We provide corrections and additions in brackets. Latitudinal and longitudinal coordinates for specimens used in the analysis of geographic variation of *C. goodwini* and *C. griseoventris* are from the U.S. Board on Geographic Names (1956a,b, 1965). Species and subspecies synonymies list only published uses of names.

We attempted to accurately characterize variation in pelage coloration in our descriptions of species; all capitalized color names follow Ridgway (1912). However, foxing is likely to have occurred, especially in older specimens, and minor variations in pelage color should not be misconstrued as real differences among species without further testing. In general, pelage in living members of the *C. mexicana*-group is dark chocolate-brown or darker in coloration, and it is not pos-

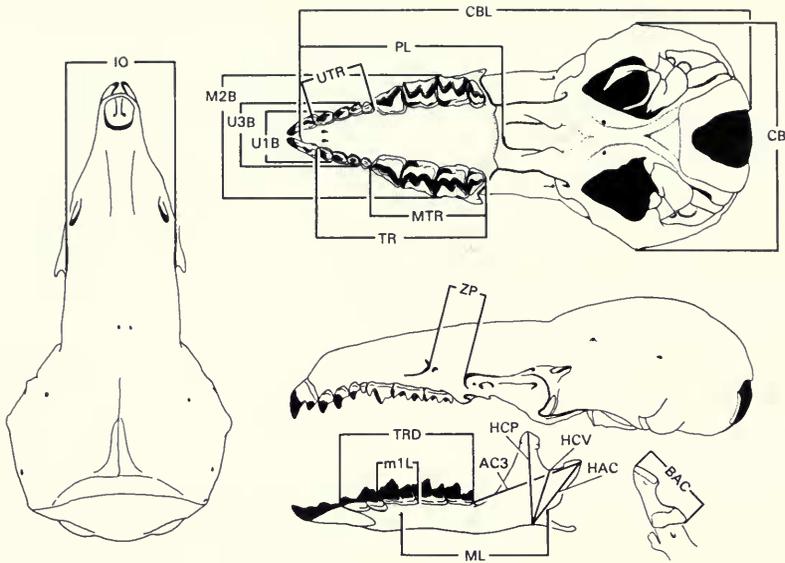


FIG. 2. Measurements of the skull used in this study (see Table 1). The lines represent the orientation of the measurements. Abbreviations: **AC3**, distance from articular condyle to posterior edge of  $M_3$ ; **BAC**, breadth of articular condyle; **CB**, cranial breadth; **CBL**, condylobasal length, not including the upper incisors; **HAC**, height of articular condyle; **HCP**, height of coronoid process; **HCV**, height of coronoid valley; **IO**, interorbital breadth; **m1L**, length of lower first molar; **M2B**, breadth of palate across second molars; **MTR**, length of molariform tooththrow,  $P^1$  through  $M^3$ ; **ML**, mandibular length, from inferior sigmoid notch to mental foramen; **PL**, palatal length; **TR**, upper tooththrow length,  $U^1$  through  $M^3$ ; **TRD**, lower tooththrow length,  $P_1$  through  $M_3$ ; **U1B**, breadth of palate across first unicuspid; **U3B**, breadth of palate across third unicuspid; **UTR**, length of unicuspid tooththrow; **ZP**, breadth of zygomatic plate. Measurements follow those of Woodman and Timm (1993).

sible to distinguish them on the basis of pelage alone.

Previous investigations of sexual dimorphism in *Cryptotis* (Choate, 1970—*C. mexicana*; Woodman, 1992—*Cryptotis gracilis*; Woodman & Timm, 1993—*C. nigrescens*) revealed no clear pattern of morphological differences between males and females. We had insufficient sample sizes of complete individuals of both sexes to carry out adequate analyses of secondary sexual variation for any one species. Based on the lack of obvious sexual variation in these or other members of the genus, we assumed that there was no confounding sexual variation in our analyses. Therefore, males, females, and specimens of unknown sex were combined.

In our investigations of the *C. goldmani*-group, we operated under the philosophical influence of the evolutionary species concept as redefined by Wiley (1978, 1981). This concept requires that the species category (and taxonomy in general) be logically consistent with reconstructed phylogenetic history. In application, we considered a species as the largest monophyletic entity whose constituent parts interact and are not on different evo-

lutionary trajectories (Alternative 2 of Frost & Hillis, 1990). Operationally, we used unique distributional patterns of morphological characters among populations to distinguish presumably genetically cohesive groups from other genetically cohesive groups. This results in a clear, supportable, testable framework for further phylogenetic, biogeographic, and ecological studies. Similarly, we consider the subspecies category to represent a phylogenetically distinct entity; in practice, we use it to separate poorly defined taxa that require further taxonomic study.

Phylogeny and character evolution in the *C. goldmani*-group were analyzed using PAUP 3.1.1 (see Swofford, 1993) and MacClade 3.0 (see Maddison & Maddison, 1992). Phylogenetic analysis was carried out using an exhaustive search of 29 unordered transition series (TS; see Appendix 1). In addition to the four species in the *C. goldmani*-group, we included the four taxa previously treated as subspecies of *Cryptotis mexicana* (*C. mexicana*, *C. nelsoni*, *C. obscura*, and *C. peregrina*). One or more of these taxa should represent the first outgroup to the *C. goldmani*-group, and we thought that the *C. goldmani*-group might

prove to be paraphyletic with respect to one or more of these taxa. As outgroups, we chose *C. parva parva* from Kansas and *C. nigrescens* from Costa Rica because they were considered previously to be phylogenetically distinct from the *C. mexicana*-group (Choate, 1970), and large series of specimens of those taxa were readily available to us.

Specimens from the following institutions were used in this study: American Museum of Natural History, New York (AMNH); Angelo State University Natural History Collection, San Angelo (ASNBC); California Academy of Sciences, San Francisco (CAS); Escuela Nacional de Ciencias Biológicas, Mexico City (ENCB); Field Museum, Chicago (FMNH); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (IBUNAM); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBio); 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 Nacional de Costa Rica, San José (MNCR); Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City (MZFC); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF); Texas Cooperative Wildlife Collection, College Station (TCWC); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); and National Museum of Natural History, Washington (USNM).

## Systematic Biology

Based on elevational and geographic distributions of specimens and the correlation of character states to these elevational and geographic distributions, we recognize four distinct species within the *C. goldmani*-group. These are *C. goodwini*, *C. goldmani*, and two species previously synonymized with *C. goldmani* (*C. alticola* and *C. griseoventris*). In addition, we recognize *C. goodwini* as a polymorphic species consisting of *C. g. goodwini* and a new subspecies that we describe below.

### Family Soricidae von Waldheim, 1817 Subfamily Soricinae von Waldheim, 1817 Genus *Cryptotis* Pomel, 1848

#### “*Cryptotis mexicana*-group” Choate, 1970

DESCRIPTION—These shrews are small to medium-sized members of the genus with long, dark dorsal pelage. They are characterized by variably broadened forefeet; moderately elongate and moderately broad to greatly elongate and very broad foreclaws; posterior border of the zygomatic plate usually positioned equal to, or slightly posterior to, the posterior base of the maxillary process (Fig. 3C); upper tooththrow 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; and deeply pocketed posterior edge of the falciform process of the tibia.

INCLUDED TAXA—*Cryptotis alticola*, *C. goldmani*, *C. goodwini*, *C. griseoventris*, *C. mexicana*, *C. nelsoni*, *C. obscura*, and *C. peregrina*.

#### “*Cryptotis goldmani*-group”

DESCRIPTION—A subset of the *C. mexicana*-group, the *C. goldmani*-group consists of medium-sized members of the genus with relatively short tails (mean TL < 39% of HB—Tables 1 and 2); greatly broadened forefeet; extremely long, broad foreclaws; fourth upper unicuspid usually aligned with the unicuspid tooththrow and partially visible in labial view; protoconal basin of  $M^1$  reduced relative to hypoconal basin;  $M^3$  simple, hypocone absent or poorly developed and lacking metacone; relatively low coronoid process of the mandible; entoconid of  $M_3$  vestigial or absent; and extremely broad humerus, with greatly elongated processes.

INCLUDED TAXA—*Cryptotis alticola*, *C. goldmani*, *C. goodwini*, and *C. griseoventris*.

TABLE 1. Measurements of *Cryptotis* used in this study. Statistics presented are mean  $\pm$  standard deviation of the mean and observed extremes. Sample sizes (n) are different for skin measurements, skull measurements, and weight; sample sizes for cranial breadth are different than those for other variables of the skull. The *F*-value and *P*-value for each variable are from an analysis of variance (ANOVA) of the variables from *C. goldmani* and the two species previously considered conspecific with it (*C. alticola* and *C. griseoventris*).

	<i>C. alticola</i>	<i>C. goldmani</i>	<i>C. g. goodwini</i>	<i>C. g. goodwini</i> (El Salvador)	<i>C. g. magnimana</i> (holotype)	<i>C. griseoventris</i>
External measurements						
	n = 22	n = 28	n = 34	n = 1	n = 1	n = 27
Head-and-body length	79 $\pm$ 5 69-87	76 $\pm$ 5 62-84	84 $\pm$ 5 75-94	—	80	77 $\pm$ 3 73-85
Tail length	26 $\pm$ 2 23-30	29 $\pm$ 3 24-36	29 $\pm$ 2 25-34	—	25	29 $\pm$ 1 27-32
Skull measurements						
	n = 16	n = 16	n = 20	n = 1	n = 1	n = 20
Condylobasal length ( <i>F</i> = 6.53, <i>P</i> = 0.003)	20.2 $\pm$ 0.5 19.3-21.1	19.6 $\pm$ 0.5 18.9-20.5	21.1 $\pm$ 0.7 20.0-22.8	20.8	20.3	19.9 $\pm$ 0.4 18.8-20.4
Cranial breadth	10.4 $\pm$ 0.2 9.9-10.8 (n = 15)	10.2 $\pm$ 0.2 9.8-10.5 (n = 18)	11.1 $\pm$ 0.3 10.6-11.6 (n = 15)	10.8	10.8	10.2 $\pm$ 0.2 9.8-10.7 (n = 19)
Breadth of zygomatic plate ( <i>F</i> = 1.91, <i>P</i> = 0.164)	1.9 $\pm$ 0.1 1.7-2.1	1.8 $\pm$ 0.2 1.4-2.2	1.9 $\pm$ 0.1 1.6-2.2	1.8	2.2	1.9 $\pm$ 0.1 1.6-2.1
Interorbital breadth ( <i>F</i> = 4.92, <i>P</i> = 0.012)	4.9 $\pm$ 0.2 4.7-5.3	5.0 $\pm$ 0.2 4.7-5.3	5.6 $\pm$ 0.2 5.3-5.8	5.6	5.3	5.1 $\pm$ 0.2 4.8-5.3
Breadth across first unicuspid ( <i>F</i> = 31.53, <i>P</i> = 0.0000)	2.7 $\pm$ 0.1 2.5-2.8	2.6 $\pm$ 0.1 2.4-2.7	2.7 $\pm$ 0.1 2.6-2.9	2.8	2.6	2.5 $\pm$ 0.1 2.3-2.6
Breadth across third unicuspid ( <i>F</i> = 19.51, <i>P</i> = 0.0000)	3.2 $\pm$ 0.1 3.0-3.2	3.0 $\pm$ 0.1 2.8-3.2	3.3 $\pm$ 0.1 3.0-3.5	3.3	3.0	3.0 $\pm$ 0.1 2.8-3.2
Breadth across second molars ( <i>F</i> = 95.12, <i>P</i> = 0.0000)	6.2 $\pm$ 0.2 5.8-6.4	5.8 $\pm$ 0.1 5.6-5.8	6.2 $\pm$ 0.2 6.0-6.6	6.2	5.9	5.6 $\pm$ 0.1 5.4-5.9
Palatal length ( <i>F</i> = 0.20, <i>P</i> = 0.816)	8.7 $\pm$ 0.3 8.1-9.2	8.7 $\pm$ 0.3 8.0-9.2	9.2 $\pm$ 0.3 8.8-10.1	9.1	8.8	8.7 $\pm$ 0.2 8.1-9.0
Length of upper toothrow ( <i>F</i> = 4.72, <i>P</i> = 0.014)	7.6 $\pm$ 0.2 7.1-7.9	7.4 $\pm$ 0.2 7.0-7.8	7.9 $\pm$ 0.3 7.5-8.6	7.8	7.5	7.6 $\pm$ 0.2 7.3-7.8
Length of unicuspid toothrow ( <i>F</i> = 55.19, <i>P</i> = 0.0000)	2.5 $\pm$ 0.1 2.3-2.7	2.3 $\pm$ 0.1 2.0-2.5	2.7 $\pm$ 0.1 2.5-2.9	2.5	2.4	2.7 $\pm$ 0.1 2.5-2.9
Length of molariform toothrow ( <i>F</i> = 17.71, <i>P</i> = 0.0000)	5.5 $\pm$ 0.2 5.1-5.7	5.4 $\pm$ 0.1 5.3-5.7	5.6 $\pm$ 0.2 5.3-5.9	5.7	5.5	5.2 $\pm$ 0.1 5.0-5.4
Length of mandible ( <i>F</i> = 14.35, <i>P</i> = 0.0000)	6.6 $\pm$ 0.2 5.9-6.8	6.3 $\pm$ 0.3 5.8-6.8	6.6 $\pm$ 0.2 6.2-6.8	—	6.5	6.2 $\pm$ 0.2 5.7-6.4
Height of coronoid process ( <i>F</i> = 16.35, <i>P</i> = 0.0000)	4.6 $\pm$ 0.2 4.3-4.9	4.6 $\pm$ 0.2 4.3-4.9	4.8 $\pm$ 0.1 4.6-5.2	4.8	4.7	4.4 $\pm$ 0.1 4.2-4.6

TABLE 1. Continued.

<i>C. alticola</i>	<i>C. goldmani</i>	<i>C. g. goodwini</i>	<i>C. g. goodwini</i> (El Salvador)	<i>C. g. magnimana</i> (holotype)	<i>C. griseiventris</i>
Height of coronoid valley ( $F = 10.75, P = 0.0001$ )					
2.9 ± 0.1	2.8 ± 0.1	3.0 ± 0.1	2.8	2.9	2.8 ± 0.1
2.8-3.1	2.7-3.0	2.8-3.4			2.6-3.0
Height of articular condyle ( $F = 9.22, P = 0.0005$ )					
4.1 ± 0.2	3.9 ± 0.2	4.2 ± 0.2	4.1	4.1	3.9 ± 0.1
3.7-4.3	3.8-4.2	3.8-4.6			3.7-4.1
Breadth of articular condyle ( $F = 31.46, P = 0.0000$ )					
3.3 ± 0.1	3.1 ± 0.1	3.3 ± 0.2	3.3	3.1	3.0 ± 0.1
3.0-3.5	2.9-3.2	3.0-3.6			2.8-3.1
Articular condyle to M <sub>1</sub> ( $F = 3.64, P = 0.035$ )					
5.2 ± 0.2	5.1 ± 0.2	5.6 ± 0.2	5.6	5.3	5.1 ± 0.1
4.8-5.6	4.8-5.3	5.2-5.9			4.8-5.3
Length of lower toothrow ( $F = 1.11, P = 0.341$ )					
6.2 ± 0.2	6.1 ± 0.2	6.4 ± 0.2	6.5	5.9	6.1 ± 0.1
5.8-6.5	5.4-6.4	6.1-6.8			5.8-6.3
Length of M <sub>1</sub>					
1.8 ± 0.1	1.8 ± 0.1	1.9 ± 0.1	2.0	1.8	1.8 ± 0.1
1.7-2.0	1.7-2.0	1.8-2.0			1.7-1.9
Weight (g):					
11 ± 3	8 ± 1	16 ± 2	—	—	—
8-16	6-10	12-19			
(n = 10)	(n = 15)	(n = 10)			

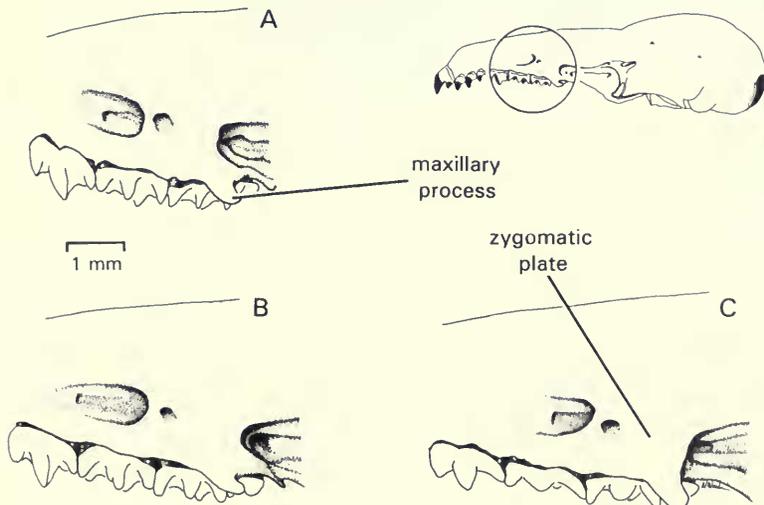


FIG. 3. Lateral views of the left zygomatic plates of A, *Cryptotis parva orophila*; B, *C. nigrescens*; and C, *C. mexicana*. The arrangement of the zygomatic plate in *C. mexicana*, in which the posterior border is even with and confluent with the posterior root of the maxillary process, is representative of the *C. mexicana*-group. Among members of the *C. nigrescens*-group, the posterior border of the zygomatic plate and the posterior root of the maxillary process are separated by the posterior edge of the palate. Scale bar = 1 mm.

TABLE 2. Comparisons of characters among taxa in the *Cryptotis goldmani*-group. Relative measurements are percentages. Sample sizes are presented in accounts for each species. Abbreviations as in Methods section of the text.

	<i>C. alticola</i>	<i>C. goldmani</i>	<i>C. g. goodwini</i>	<i>C. g. magnimana</i>	<i>C. griseiventris</i>
Foramen of sinus canal	vestigial	well developed	absent	absent	absent
Foramen dorsal to dorsal articular facet	present	present	present	present	present
	39%	16%	90%	81%	81%
Two dorsal foramina present	54%	61%	82%	92%	92%
Posteroventral border of unicuspid	straight	concave	concave	concave	concave
to convex					
Vestigial entoconid of M <sub>3</sub> present	64%	52%	14%	?	0%
Humerus	derived	most derived	derived	derived	?
	(Fig. 15E)	(Fig. 15H)	(Fig. 15G)	(Fig. 15F)	
Tail length as % of head-and-body length (TL/HB × 100)	33 ± 4	38 ± 5	35 ± 3	31	38 ± 2
	27-41	31-48	30-41		34-42
Relative length of rostrum (PL/CBL × 100)	43.2 ± 1.2	44.2 ± 1.0	43.6 ± 0.7	43.3	43.8 ± 0.8
	40.1-45.5	41.9-45.6	42.5-44.8		42.1-45.0
Relative breadth of zygomatic plate (ZP/PL × 100)	21.8 ± 1.2	21.1 ± 2.4	21.1 ± 1.9	25.0	22.3 ± 1.7
	19.6-24.1	15.7-23.4	17.2-24.4		18.2-24.7
Relative length of unicuspid tooththrow (UTR/CBL × 100)	12.3 ± 0.4	11.9 ± 0.6	13.0 ± 0.5	11.8	13.7 ± 0.5
	11.6-13.0	10.5-13.0	12.0-14.0		12.9-14.5
Relative palatal breadth (M2B/PL × 100)	70.9 ± 3.0	66.4 ± 2.3	67.6 ± 2.4	67.1	64.3 ± 2.1
	64.1-77.8	63.0-71.2	62.4-71.6		60.7-68.2
Relative height of coronoid process (HCP/ML × 100)	70.5 ± 3.3	73.6 ± 4.4	72.7 ± 2.2	72.3	70.5 ± 1.8
	64.2-80.0	66.2-81.0	68.7-76.5		67.2-73.7
Relative length of posterior portion of the mandible (AC3/ML × 100)	79.3 ± 2.0	80.5 ± 2.6	84.2 ± 2.8	81.5	82.9 ± 2.3
	76.2-83.6	76.1-84.5	79.1-90.5		79.7-86.9

***Cryptotis goodwini* Jackson, 1933**

***Cryptotis goodwini goodwini* Jackson, 1933**

*Cryptotis goodwini* Jackson, 1933:81; Goodwin, 1934:6; Felten, 1958:218; Hall and Kelson, 1959:61; Genoways and Choate, 1967:204; Choate, 1970:249; Hall, 1981:60; Medellín, 1988:84.

*Cryptotis nigrescens*: Burt and Stirton, 1961:21 (in part).

*C[ryptotis]. goodwini*: Musser, 1964:7.

HOLOTYPE—Skin and skull of adult male, USNM 77074; taken 13 January 1896 by E. W. Nelson

(collector number 9073); from "Cale" (Jackson, 1933:81), Quezaltenango, Guatemala, 10,200 ft.

DISTRIBUTION—Contiguous highland regions above 1100 m in the Mexican state of Chiapas and Guatemala, and in a separate highland area in northern El Salvador. The population in El Salvador probably extends northward along the Merendón Cordillera into western Honduras (Fig. 4).

DESCRIPTION—Size large for the genus (Table 1); tail short, averaging 29 mm, or ca. 35% (Table 2) of HB; the dorsal guard hairs 6-8 mm long; dorsal pelage Saccardo's Umber/Prout's Brown/Mummy Brown; ventral pelage somewhat paler than dorsum, Light Drab/Drab to almost Wood Brown; dorsal fur three-banded: basal five-sixths

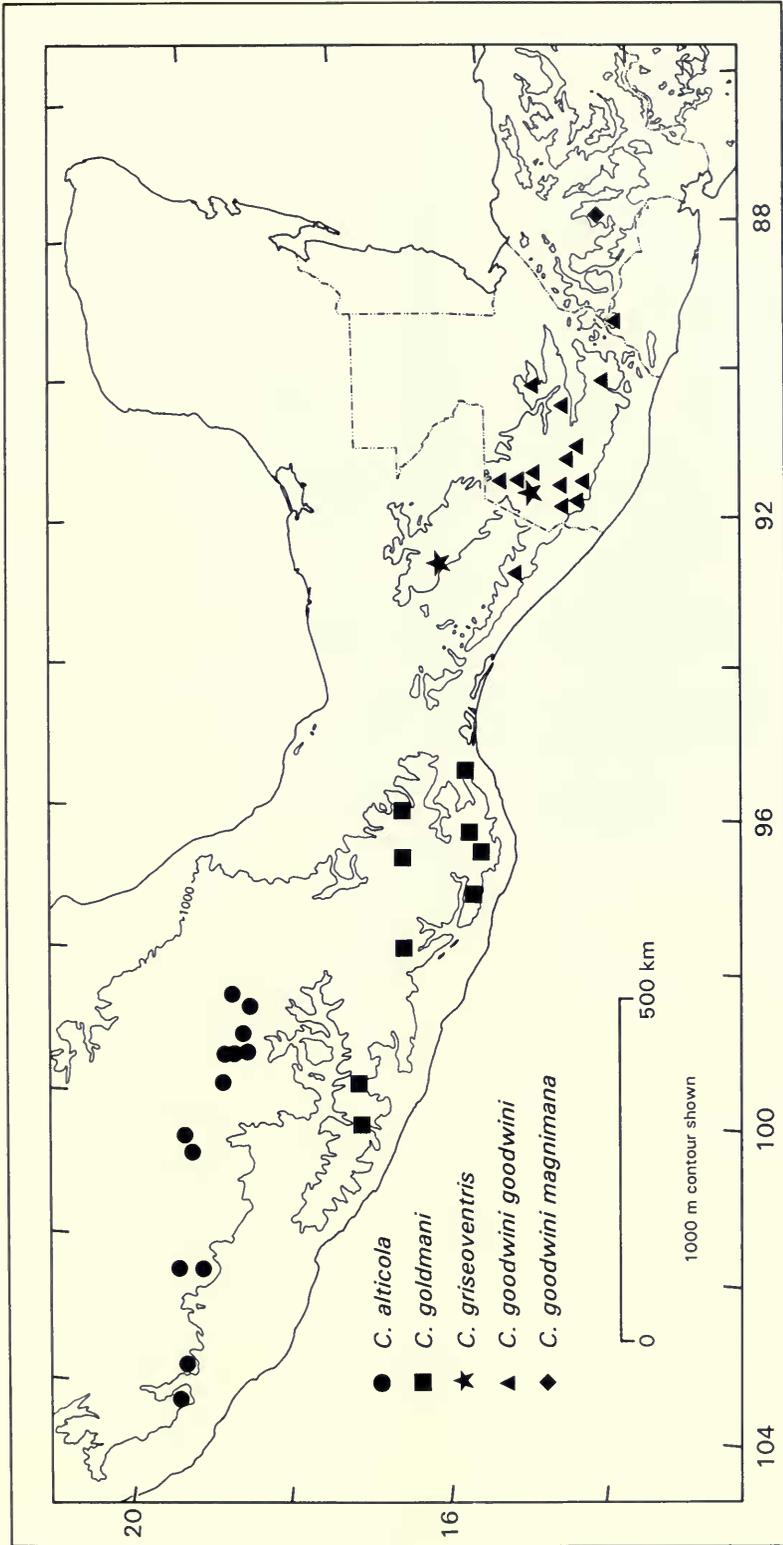


Fig. 4. Map of southern Mexico and northwestern Central America showing the geographic distribution of the *Cryptotis goldmani*-group. Contour represents 1000 m elevation. Scale bar = 500 km.

of hairs silvery gray, followed by a thin, very pale brown band grading into dark brown tip. Rostrum of moderate length (PL/CBL =  $43.6\% \pm 0.7$ ,  $n = 20$ ); usually two well-developed dorsal foramina (82%,  $n = 28$ ); no ventral extension of the sinus canal or associated foramen posterior to dorsal articular facet (see account for *C. goldmani*, below); a foramen dorsal to the dorsal articular facet usually present on one or both sides of the skull (90%,  $n = 20$ ); zygomatic plate of moderate breadth (ZP/PL =  $21.1\% \pm 1.9$ ,  $n = 20$ ), anterior border usually aligned with mesostyle–metastyle valley or metastyle of  $M^1$ ;  $P^4$ ,  $M^1$ , and  $M^2$  slightly to moderately recessed on posterior border;  $M^3$  usually with paracrista, paracone, precentrocrista, mesostyle, very short postcentrocrista (all pigmented), and a well-developed, pigmented protocone. Mandible relatively long and of moderate breadth for the genus; articular process generally moderately tall and wide, with a moderately broad lower articular facet; entoconid usually absent (86%,  $n = 29$ ), but when present, poorly developed.

COMPARISONS—*Cryptotis goodwini goodwini* is the largest of the broad-clawed shrews in overall body size.

*Cryptotis alticola*—*Cryptotis g. goodwini* has somewhat shorter, narrower foreclaws; lacks ventral extension of sinus canal and associated foramen posterior to dorsal articular facet; has a foramen dorsal to dorsal articular facet; has a relatively narrower palate; and has a shorter mandible.

*Cryptotis goldmani*—*Cryptotis g. goodwini* has a relatively shorter tail; lacks ventral extension of sinus canal and associated foramen posterior to dorsal articular facet; has a foramen developed dorsal to the dorsal articular facet; usually lacks an entoconid on  $M_3$ ; and has a longer, narrower humerus with less enlarged bony processes.

*Cryptotis griseoventris*—*Cryptotis g. goodwini* is larger overall.

REMARKS—The known biology of *Cryptotis goodwini goodwini* was summarized previously by Choate (1970) and Choate and Fleharty (1974). *Cryptotis goodwini goodwini* has been found in high-elevation pine forests, sometimes mixed with firs, oaks, and other trees. Severe frosts are associated with at least some of their habitats (Goldman, 1951). Most specimens are from localities of 1200 m or more in elevation. Although Choate (1970:251) reported a specimen from Finca Xicacao, Guatemala, as from ca. 3000 ft, no elevation is given on the specimen tag for this specimen,

and Xicacao is located in a region higher than 1000 m. James W. Bee (KU unpublished field catalog, 1954, 1955) recorded taking *Sorex veraepacis*, *Microtus guatemalensis*, *Peromyscus guatemalensis*, *Reithrodontomys microdon*, *Reithrodontomys sumichrasti*, and *Reithrodontomys tenuirostris* along with *C. g. goodwini* 3.5 mi SW of San Juan Ixcay, Guatemala, at 10,120 ft, on 27 December 1954. At 6000 ft, 5 mi N and 1 mi W of El Chol, Guatemala, on 30 January 1955, he captured *C. g. goodwini* with *Oligoryzomys fulvescens*, *Peromyscus aztecus*, *Peromyscus levipes*, *Reithrodontomys fulvescens*, *Reithrodontomys mexicanus*, *R. sumichrasti*, and *Scotinomy teguina*.

Reproductive data for *Cryptotis goodwini goodwini* are lacking. Our inspection of study skins of males taken from 4 to 15 January ( $n = 6$ ), 5–22 May ( $n = 2$ ), 20 August ( $n = 3$ ), and 27 December ( $n = 1$ ) yielded none with well-developed lateral glands. On study skins, lateral glands typically appear as paired, oval regions approximately 6–9 mm in length and 5–6 mm in width. These glandular areas lack long guard hairs and normal underfur, but they have a sparse covering of short, fine, pale hairs. Among most genera of Soricidae, both males and females possess lateral glands, but those of females are smaller and more difficult to see (Murariu, 1976; Bee et al., 1980). Eadie (1938) found that the lateral glands of *Blarina* showed increased activity with enlargement of the testes, and they may serve a function in sexual and social communication. The occurrence of enlarged lateral glands on study skins has been used to infer timing of sexual activity in adult male *Cryptotis* (Woodman & Timm, 1993).

The occurrence of *Cryptotis goodwini goodwini* in El Salvador is documented by a single specimen from Hacienda Montecristo on Cerro Montecristo (Felten, 1958; Choate, 1970). Cerro Montecristo is an isolated mountain, separated from the Guatemalan Highlands by a deep, wide valley occupied by tributaries of the Río Motagua. This lowland valley supports xeric vegetation (Stuart, 1954), unlike that found in cool, moist highlands generally inhabited by *C. g. goodwini*, and it probably provides an effective barrier to gene flow. Because of this, we hypothesized that the specimen from El Salvador might prove to represent a distinct species. This individual has less emarginate upper dentition than *C. g. goodwini*, but otherwise it cannot be separated from them on qualitative characteristics. To test the overall similarity of the specimen from El Salvador to

those from Guatemala, we carried out a principal components analysis using seven uncorrelated variables (CBL, ZP, IO, M<sup>2</sup>B, UTR, MTR, and HCP) from 20 Guatemalan *C. g. goodwini*, plus the specimen from El Salvador. A plot of the first three factor axes from this analysis is shown in Figure 5. The specimen from El Salvador shows up in the centers of factor axis 1 (size; see Table 6) and factor axis 2 (UTR and HCP), but it represents the lower extreme of variation for factor 3 (ZP and UTR). This is due to the individual's relatively narrow zygomatic plate and its relatively short unicuspid tooththrow (Table 1). The specimen from El Salvador falls within the overall range of variation for *C. g. goodwini*, and, lacking any definitive characters that would set it off from that species, we consider it most appropriate to continue to refer it to *C. g. goodwini*.

**SPECIMENS EXAMINED (36)—EL SALVADOR:** SANTA ANA: Hacienda [Finca] Montecristo [13°40'N, 89°29'W] (SMF 14837). **GUATEMALA:** ALTA VERAPAZ: Finca Xicacao (UMMZ 87869). BAJA VERAPAZ: 5 mi N, 1 mi W El Chol, 6000 ft (KU 64611). CHIMALTENANGO: Santa Elena [14°48'N, 91°01'W], 9900–10,000 ft (FMNH 41791–41794). HUEHUETENANGO: 3.5 mi SW San Juan Ixcay [15°36'N, 91°27'W], 10,120 ft (KU 64610); San Mateo Ixtatán, ca. 4 km NW Santa Eulalia [15°45'N, 91°29'W], Yayquich, 2950 m (UMMZ 117843); Hacienda Chanco, 9500–11,000 ft (USNM 77069). JALAPA: Mataquesuintla [14°32'N, 90°11'W], 8400 ft (USNM 275681). QUEZALTENANGO: Calel [15°04'N, 91°34'W], 10,200 ft (USNM 77070, 77072–77073, 77075–77084, includes holotype); Volcán Santa María [14°45'N, 91°33'W], 9000–11,000 ft (USNM 77086–77087). SAN MARCOS: S slope Volcán Tajumulco, 10,000 ft (UMMZ 99541). TOTONICAPÁN: Cumbre María Tecún [14°52'N, 91°13'W], 3000 m (UMMZ 112004–112011). **MEXICO:** CHIAPAS: 17 km SE Finca Prusia, Reserva Ecológica El Triunfo, 2000 m (IBUNAM 22784).

**ADDITIONAL RECORDS—GUATEMALA:** CHIMALTENANGO: Tecpam [= Tecpán], 9700 ft (Goodwin, 1934); SAN MARCOS: Finca La Paz, 1200 m (Choate, 1970:251).

*Cryptotis goodwini magnimana*, new subspecies  
Honduran Broad-clawed Shrew  
(Fig. 6)

**HOLOTYPE**—Fluid-preserved pregnant adult female with skull and humerus removed and

cleaned, KU 144611; collected 21 November 1991 by Peter Holm and Gustavo Cruz (no field number). Fluid-preserved body intact; skull nearly complete, but with a hole in braincase dorsally and lacking left tympanic.

**TYPE LOCALITY**—2.5 km N, 1.6 km E Cerro San Juanillo [14°30'N, 87°53'W], Reserva Biológica Cordillera de Montecillos, Comayagua Department, Honduras, 1730 m (see Fig. 4). The only known specimen was found dead in mixed pine and broadleaf forest.

**DISTRIBUTION**—Known only from the type locality; probably occurs throughout the Cordillera de Montecillos and adjoining highland areas in high-elevation (> 1000 m) pine forest and mixed pine and broadleaf forest (Fig. 4).

**MEASUREMENTS OF HOLOTYPE**—HB, 80; TL, 25; hindfoot, 14; ear, 6; CBL, 20.3; PL, 8.8; M<sup>2</sup>B, 5.9; IO, 5.3; TR, 7.5; CB, 10.8; TRD, 5.9 (see Table 1). Because no external measurements were recorded by the collectors, we measured the fluid-preserved body prior to removal of the skull.

**DIAGNOSIS**—A taxon possessing all of the common characteristics of the *Cryptotis goldmani*-group (see above). Within this group, the holotype is characterized by its relatively short tail; relatively broad zygomatic plate; lack of a ventral extension of the sinus canal; a well-developed foramen dorsal to the dorsal articular facet; two well-developed dorsal foramina (= foramina orbitalia of Bühler, 1964); relatively short upper unicuspid tooththrow; unicuspid teeth with concave posteroventral border; P<sup>1</sup>, M<sup>1</sup>, and M<sup>2</sup> very slightly recessed on posterior border; and a short, broad humerus similar in grade to that of *Cryptotis g. goodwini*.

**DESCRIPTION**—Size medium for the genus (Table 1); tail short, 25 mm (31% of HB—see Table 2); dorsal guard hairs about 5–7 mm long; dorsal pelage of fluid-preserved holotype Mummy Brown to Fuscous when air-dried; Brownish Olive venter appears to be somewhat paler than dorsum; dorsal fur two-banded, basal three-fourths silvery gray, distal one-fourth grading from pale brown to brown at the tip. Rostrum of moderate length (PL/CBL = 43.3%); two well-developed dorsal foramina; no ventral extension of the sinus canal or associated foramen posterior to the dorsal articular facet (see account for *C. goldmani*, below); well-developed foramina dorsal to the dorsal articular facet on both sides of the skull; zygomatic plate broad (ZP/PL = 25%), anterior border aligned with metastyle of M<sup>1</sup>; posterior border of P<sup>1</sup>, M<sup>1</sup>, and M<sup>2</sup> only very slightly recessed; M<sup>1</sup>

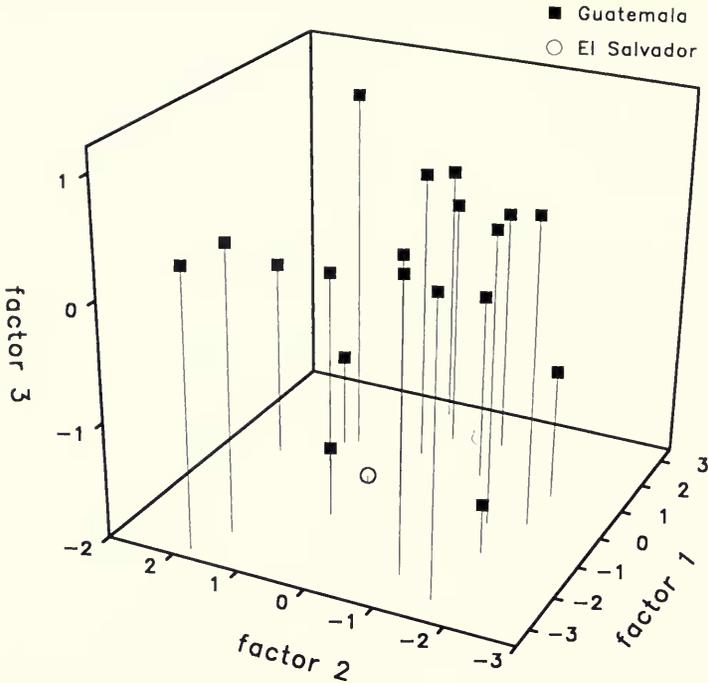


FIG. 5. Three-dimensional plot showing similarities and differences among specimens of *Cryptotis goodwini* from Guatemala (solid squares) and El Salvador (open circle) based on the first three factors from principal components analysis of seven skull variables. Factor 1 represents size, factor 2 contrasts length of unicuspid tooththrow with height of coronoid process, and factor 3 represents length of zygomatic plate and length of unicuspid tooththrow (Table 6).

has paracrista, paracone, precentrocrista, mesostyle, very short postcentrocrista, and well-developed protocone (because of wear, it cannot be determined whether protocone was pigmented). Mandible relatively long and of moderate breadth; articular process generally tall and wide, with a broad lower articular facet and a relatively shallow lingual notch between articular facets; because of wear, it cannot be determined whether an entoconid was present in talonid of  $M_3$ . Humerus similar to *C. g. goodwini* (see below).

COMPARISONS—*Cryptotis goodwini magnimana* has a relatively broader zygomatic plate and a relatively shorter unicuspid tooththrow compared to those of the other four taxa of broad-clawed shrews.

*Cryptotis goodwini goodwini*—*Cryptotis g. magnimana* is smaller overall (see Remarks, below); has a relatively and absolutely shorter unicuspid tooththrow; and has less deeply recessed posterior borders of  $P^4$ ,  $M^1$ , and  $M^2$ .

*Cryptotis alticola*—*Cryptotis g. magnimana* has somewhat shorter, narrower foreclaws; lacks ventral extension of sinus canal and associated foramen posterior to dorsal articular facet; possesses

a foramen dorsal to posterior dorsal articular facet and two well-developed dorsal foramina; has a relatively and absolutely narrower palate; has concave posteroventral borders of unicuspid; and has less deeply recessed posterior edges of  $P^4$ ,  $M^1$ , and  $M^2$ .

*Cryptotis goldmani*—*Cryptotis g. magnimana* is larger overall and has a relatively shorter tail; lacks ventral extension of sinus canal and associated foramen posterior to dorsal articular facet; possesses a foramen dorsal to dorsal articular facet and two well-developed dorsal foramina; and has a relatively longer, narrower humerus with less enlarged bony processes (see below).

*Cryptotis griseoventris*—*Cryptotis g. magnimana* is larger overall (see Remarks, below); has a relatively and absolutely shorter tail; has a relatively and absolutely broader zygomatic plate; and has a relatively and absolutely shorter unicuspid tooththrow.

REMARKS—The only known specimen of this subspecies is an adult female that was pregnant when collected on 21 November 1991. She carried four embryos, three in the right horn of the

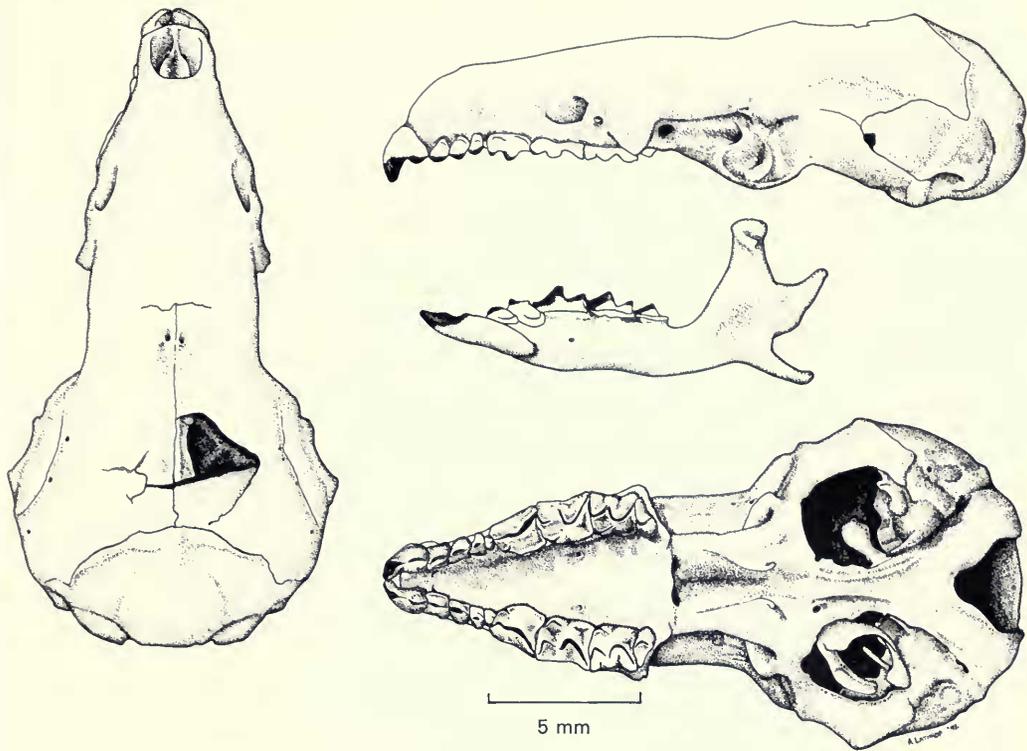


FIG. 6. Dorsal and ventral views of the cranium and lateral view of the skull of the holotype of *Cryptotis goodwini magnimana*. Scale bar = 1 mm.

uterus and one in the left (crown to rump length = 8 mm).

*Cryptotis goodwini magnimana*, *C. goodwini goodwini*, and *C. griseoventris* are similar in many respects, and the three taxa share several synapomorphies (see below) that distinguish them from *C. alticola* and *C. goldmani*. Many of the differences among *C. g. magnimana*, *C. g. goodwini*, and *C. griseoventris* are related to variation in body size or proportions of certain features (Table 2). To help evaluate the distinctiveness of these three populations, we examined their overall similarity using principal components analysis on eight variables (CBL, ZP, IO, UTR, MTR, HCP, BAC, and M<sub>1</sub>L) measured on 20 *C. griseoventris*, 22 *C. g. goodwini*, and the holotype of *C. g. magnimana*. The specimens of *C. griseoventris* included seven from Chiapas and 13 from Guatemala; those of *C. g. goodwini* included 21 from Guatemala and one from El Salvador. Each of these subsets was plotted separately to facilitate recognition of geographic variation within and among taxa. A plot of the first two factor axes from the principal components analysis (Fig. 7)

shows all three named taxa to be distinct. Six of the eight variables are weighted relatively evenly on the first factor axis (Table 3), suggesting that this axis represents overall size of the individuals. Breadth of zygomatic plate (ZP) and length of unicuspid tooththrow (UTR) are weakly weighted on the first axis, indicating that they do not correlate strongly with size. Correlation coefficients of ZP and UTR with each of the other variables in the analysis fall below 0.24, and many are negative (Table 4). The first factor axis clearly separates the larger *C. g. goodwini* from the smaller *C. griseoventris*, with the holotype of *C. g. magnimana* between them. The difference in size between *C. g. goodwini* and *C. griseoventris* indicated by the first factor axis is supported by *t*-tests between means of each of the individual variables; of 21 variables tested, only three—length of tail (TL), breadth of zygomatic plate (ZP), and length of unicuspid tooththrow (UTR)—did not show statistical differences between means for the two taxa. Means of each of the other 18 variables were significantly different ( $P < 0.001$ ). On the second factor axis, ZP and UTR weigh out heavily, in-

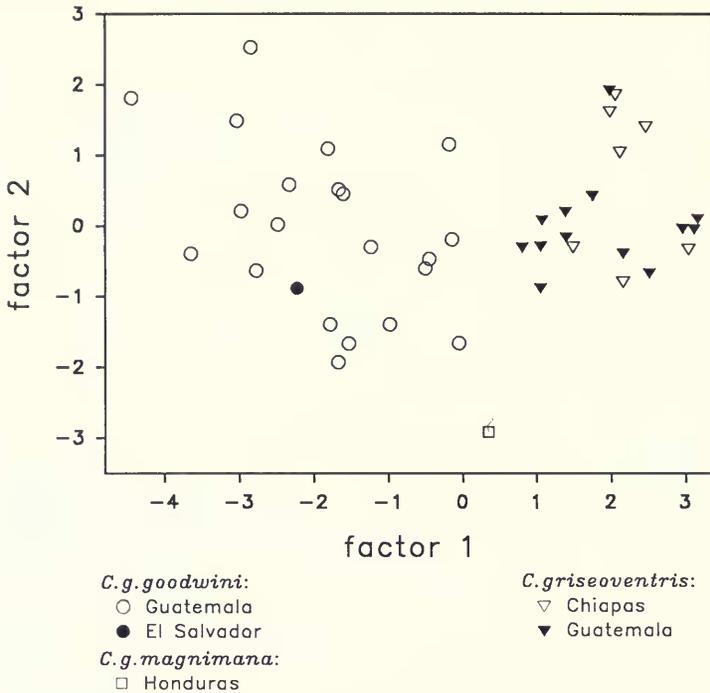


FIG. 7. Plot of the first two factors from principal components analysis of specimens of *Cryptotis griseoventris*, *C. goodwini goodwini*, and *Cryptotis g. magnimana*. Factor 1 represents size; factor 2 contrasts length of zygomatic plate and length of unicuspid toothrow (Table 3).

indicating that the axis represents a contrast between these two variables (Table 3). The second factor axis separates the holotype of *C. g. magnimana* from *C. g. goodwini* and *C. griseoventris*, reflecting the relatively shorter unicuspid toothrow and relatively broader zygomatic plate of *C. g. magnimana*.

We subsequently investigated size variation

TABLE 3. Factor loadings for the first two factor axes from principal components analysis of *Cryptotis griseoventris*, *C. goodwini goodwini*, and *C. goodwini magnimana*. These two axes (PC1, PC2) together accounted for 74% of the variation. Variables are listed in descending order by their loadings on the first factor axis. Abbreviations as in the Methods section.

Variable	PC1	PC2
ZP	0.052	-0.666
UTR	-0.048	0.638
mIL	-0.349	-0.263
IO	-0.408	-0.075
MTR	-0.410	0.145
BAC	-0.419	0.056
HCP	-0.424	-0.185
CBL	-0.427	0.123

among *Cryptotis goodwini magnimana*, *C. g. goodwini*, and *C. griseoventris* in relation to their geographic distributions to determine whether differences among them might be attributable to clinal variation. *Cryptotis g. goodwini* and *C. griseoventris* appear to be parapatric; their distributions may overlap on a regional scale, but the two taxa have never been reported from the same site (Fig. 4). The distance between the closest known occurrences of *C. g. goodwini* and *C. griseoventris* is much less than the dimensions of either of their geographic ranges. If the two populations were members of a single species, we would expect them to grade into each other where their distributions are in closest proximity. To examine this, we determined the approximate latitude and longitude of the collecting locality for each of the 43 specimens used in the principal components analysis of morphology (above) and carried out a second principal components analysis on these pairs of geographic coordinates. Latitude and longitude were evenly weighted (0.707) on the first factor axis; hence each score on that first factor axis represented the coordinates of one collecting locality (Table 5). Plotting the factor scores from

TABLE 4. Correlation matrix for the eight variables used in principal components analysis of *Cryptotis griseoventris*, *C. goodwini goodwini*, and *C. goodwini magnimana*. Abbreviations as in Methods section.

	CBL	ZP	IO	UTR	MTR	HCP	BAC
ZP	-0.128						
IO	0.715	-0.109					
UTR	0.234	-0.173	-0.004				
MTR	0.824	-0.187	0.641	0.184			
HCP	0.798	0.053	0.830	-0.054	0.738		
BAC	0.813	-0.169	0.784	0.055	0.772	0.774	
mIL	0.612	0.132	0.623	-0.025	0.602	0.652	0.536

the first factor axis ("size") of the initial analysis of morphological variation against the factor scores from the first factor axis of the analysis of latitude and longitude ("geographic locality") provides a graphical representation of geographic variation in size among the three taxa (Fig. 8). We calculated regressions of size on geographic locality for *C. g. goodwini* and *C. griseoventris* to aid in the identification of geographic trends in size. The slope of the regression line was not significantly different from zero (horizontal) for either *C. g. goodwini* ( $y = -1.83 - 0.024x$ ;  $F = 0.00$ ,  $P = 0.956$ ) or *C. griseoventris* ( $y = 1.72 + 0.208x$ ;  $F = 0.80$ ,  $P = 0.383$ ), indicating that no clear trends in size variation occur within either taxon. Therefore, the difference in body size between these two parapatric populations is not a gradual transition but represents a sharp change. One possible explanation might be that some local

selective factor maintains this size difference between the two populations. We believe that it is much more likely that the difference in body size has a genetic basis, and *C. g. goodwini* and *C. griseoventris* represent two closely related taxa that differentiated in isolation and subsequently expanded their ranges so that they are now in contact or near contact. Competition may prevent them from coexisting in the same sites.

Variation in *Cryptotis goodwini magnimana* is impossible to ascertain given a single specimen. The holotype of *C. g. magnimana* is intermediate in size between *C. g. goodwini* and *C. griseoventris*, and the population of *C. g. magnimana* probably partially overlaps one or both of the latter two taxa in this factor. *Cryptotis g. magnimana* is distinguished morphologically from both *C. g. goodwini* and *C. griseoventris* by the combination of its broader zygomatic plate and its shorter unicuspid tooththrow. It is additionally separated from *C. g. goodwini* by the less deeply recessed  $P^4$ ,  $M^1$ , and  $M^2$  (but see below), and from *C. griseoventris* by its absolutely and relatively shorter tail. We believe that the morphological distinctiveness of the holotype of *C. g. magnimana* from *C. g. goodwini* probably represents a phylogenetic distinctiveness as well. Unfortunately, the extremely small sample size by which *C. g. magnimana* is currently represented prevents us from adequately testing this hypothesis. Future study of this problem, based on larger sample sizes of the new taxon, will show that it is (1) a species distinct from *C. goodwini*; (2) an individual of *C. goodwini* that shows greater than normal variation for the species and does not warrant a separate name; or (3) one extreme of a morphological (not size) cline that does not merit a separate name. In support of the last hypothesis is the less deeply recessed upper dentition and the short unicuspid tooththrow (Fig. 9, Tables 1 and 2), two characters that *C. g. magnimana* shares with the specimen of *C. g.*

TABLE 5. Latitude and longitude for collecting sites of *Cryptotis griseoventris*, *C. goodwini goodwini*, and *C. goodwini magnimana*. "Geographic locality" is a single factor score derived from the first factor axis of a principal components analysis of sets of coordinates for collecting sites of the three species. Because latitude and longitude loaded equally (0.707) on this first factor axis, each factor score represents latitude and longitude evenly at a given site.

Latitude	Longitude	Geographic locality (factor score)
16°45'	92°38'	2.29730
15°36'	91°37'	0.80463
14°48'	91°01'	-0.15638
15°36'	91°27'	0.75103
14°52'	91°13'	-0.05716
15°45'	91°29'	0.84030
15°04'	91°34'	0.50925
14°45'	91°33'	-0.01106
14°32'	90°11'	-0.77840
13°40'	89°29'	-2.02087
14°30'	87°53'	-2.17865

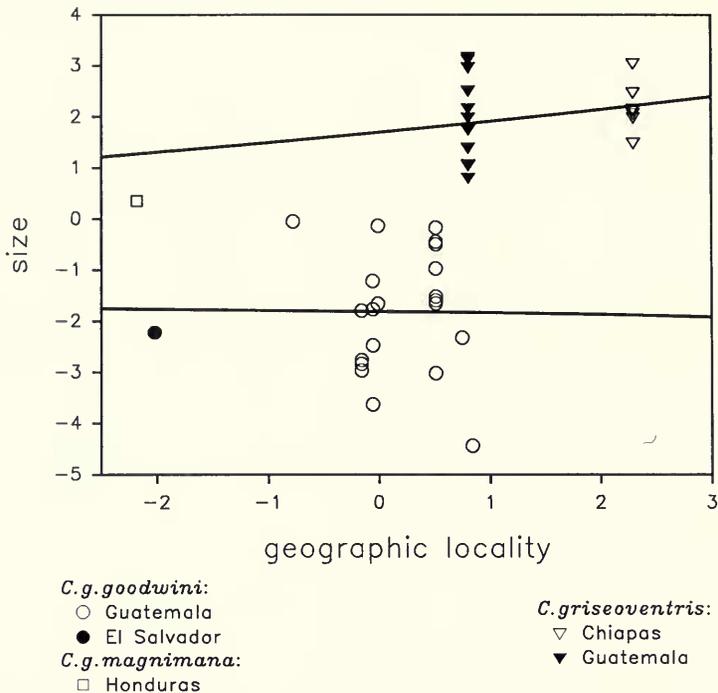


FIG. 8. Plot of size against geographic locality for specimens of *Cryptotis griseoventris*, *C. goodwini goodwini*, and *Cryptotis g. magnimana*. Size is represented by the scores from the first factor axis of a principal components analysis of morphological variation among the three species. Because variables were negatively weighted on the first factor axis (Table 3), larger animals are more negative on the y axis, smaller animals more positive. Geographic locality is represented by scores from the first factor axis of a principal components analysis of latitude and longitude of collecting localities. Localities more to the northwest are more positive on the x axis, those to the southeast are more negative. The regression lines for *C. g. goodwini* ( $y = -1.83 - 0.024x$ ;  $F = 0.00$ ,  $P = 0.956$ ) and *C. griseoventris* ( $y = 1.72 + 0.208x$ ;  $F = 0.80$ ,  $P = 0.383$ ) are not significantly different from zero.

*goodwini* from El Salvador. In contrast to *C. g. magnimana*, however, the individual from El Salvador has an extremely narrow zygomatic plate (Fig. 10, Tables 1 and 2).

ETYMOLOGY—The subspecific epithet *magnimana* is an adjectival construction (Latin *magnus* “large” + *-i-* a connective vowel + *manus*

TABLE 6. Factor loadings for the first three factor axes from principal components analysis of *Cryptotis goodwini* from Guatemala and El Salvador. These three axes (PC1, PC2, and PC3) together accounted for 77% of the variation. Abbreviations as in Methods section.

Variable	PC1	PC2	PC3
ZP	0.272	0.388	0.754
UTR	-0.204	-0.493	0.613
IO	-0.324	0.327	-0.131
HCP	-0.401	0.463	0.168
MTR	-0.434	-0.350	0.014
M2B	-0.460	0.349	0.003
CBL	-0.467	-0.202	0.101

“hand”) meaning “large-handed.” This is in reference to the enlarged forefeet and foreclaws that distinguish this taxon from other shrews in Honduras. The subspecific name takes a feminine termination to agree in gender with the feminine generic name, *Cryptotis* (Woodman, 1993).

SPECIMEN EXAMINED (1)—**HONDURAS: CO-MAYAGUA:** Reserva Biológica Cordillera de Montecillos; 2.5 km N, 1.6 km E Cerro San Juanillo [14°30'N, 87°53'W], 1730 m (KU 144611—holotype).

### *Cryptotis griseoventris* Jackson, 1933

*Cryptotis griseoventris* Jackson, 1933:80; Hall and Kelson, 1959:60.

*Cryptotis goldmani goldmani*: Choate, 1970:247 (in part); Hall, 1981:59 (in part).

HOLOTYPE—Skin and skull of adult male, USNM

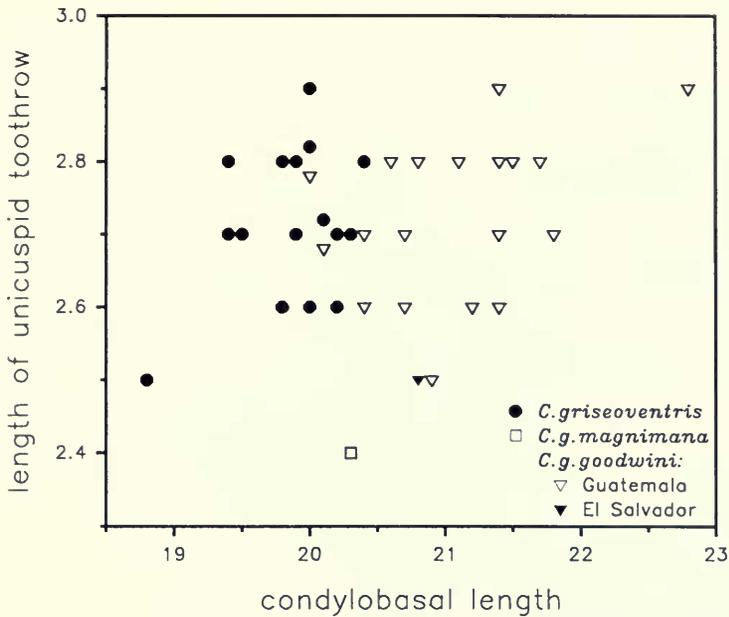


FIG. 9. Plot of length of unicuspid tooththrow (UTR) against condylobasal length (CBL) for *Cryptotis goodwini goodwini*, *C. g. magnimana*, and *C. griseoventris*. Both *C. g. magnimana* and *C. g. goodwini* from El Salvador have relatively short unicuspid tooththrows.

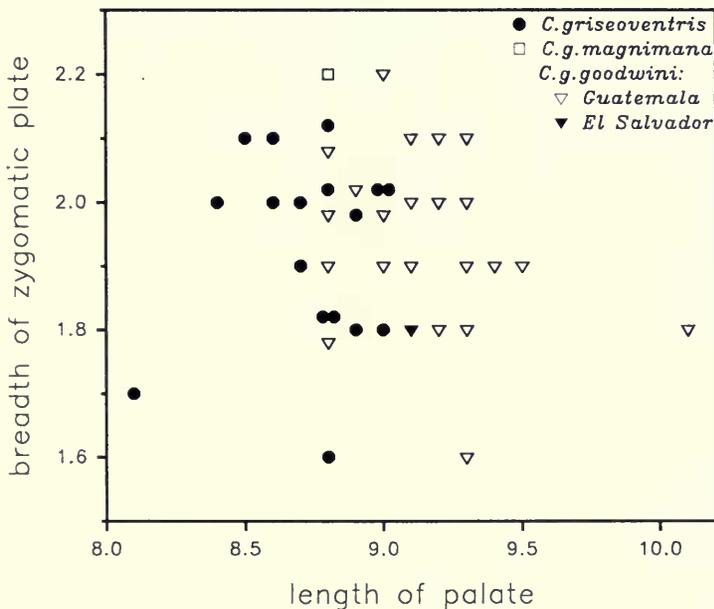


FIG. 10. Plot of breadth of zygomatic plate (ZP) against length of palate (PL) for *Cryptotis goodwini goodwini*, *C. g. magnimana*, and *C. griseoventris*. *Cryptotis g. magnimana* has a broad zygomatic plate, whereas *C. g. goodwini* from El Salvador has a relatively narrow zygomatic plate.

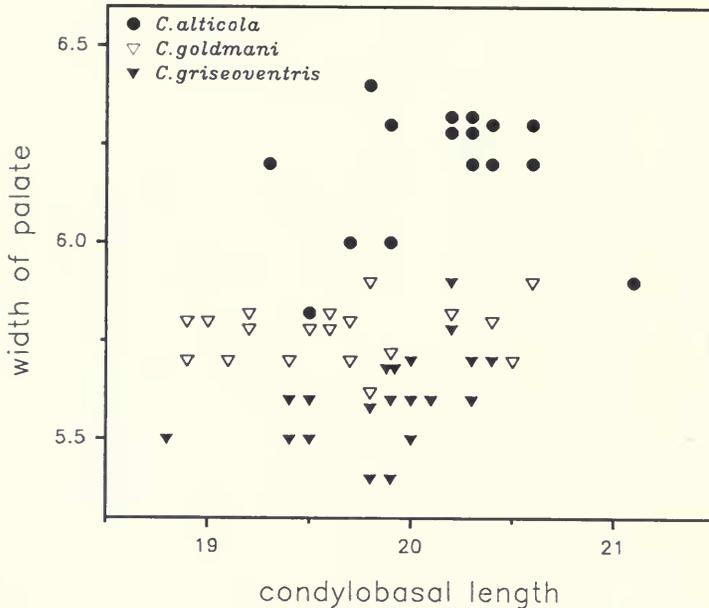


FIG. 11. Plot of width of palate (M2B) against condylobasal length (CBL) for *Cryptotis alticola*, *C. goldmani*, and *C. griseoventris*, all of which were considered previously as conspecific.

75894; taken 4 October 1895 by E. W. Nelson and E. A. Goldman (collector number 8545); from "San Cristobal" (Jackson, 1933:80) [San Cristóbal de las Casas], Chiapas, Mexico, 9500 ft.

**DISTRIBUTION**—Above at least 2000 m in continuous highland areas of Guatemala and Chiapas (Fig. 4).

**DESCRIPTION**—Size medium for the genus (Table 1); tail moderately long, averaging 29 mm, or ca. 38% of HB (Table 2); the dorsal guard hairs about 6–8 mm long; dorsal pelage Mummy Brown to Bister; ventral fur Light Drab to Drab, somewhat paler than dorsum; dorsal fur three-banded: basal five-sixths of hairs silvery gray, followed by a thin, lightly colored band grading into dark brown at the tip. Rostrum of moderate length (PL/CBL =  $43.8\% \pm 0.8$ ,  $n = 20$ ); usually two well-developed dorsal foramina (92%,  $n = 25$ ); no ventral extension of the sinus canal or associated foramen (see account for *C. goldmani*, below); a foramen dorsal to the dorsal articular facet usually present on one or both sides of the skull (81%,  $n = 27$ ); zygomatic plate of moderate breadth (ZP/PL =  $22.3\% \pm 1.7$ ,  $n = 20$ ), anterior border usually aligned with mesostyle–metastyle valley, metastyle of  $M^1$ , or parastyle of  $M^2$ ; upper toothrow uncrowded,  $U^4$  aligned with toothrow and partially visible in labial view;  $P^4$ ,  $M^1$ , and  $M^2$  only very slightly recessed on posterior bor-

der;  $M^3$  usually with paracrista, paracone, precentrocrista, mesostyle, very short postcentrocrista; (all pigmented), and a well-developed, lightly pigmented protocone. Mandible relatively long and of moderate breadth for the genus; articular process tall and wide, with a broad lower articular facet and a relatively shallow lingual notch between articular facets; entoconid absent (100%,  $n = 23$ ).

**COMPARISONS**—*Cryptotis griseoventris* has a relatively longer unicuspid tooththrow than any of the other species except *C. g. goodwini*.

***Cryptotis alticola***—*Cryptotis griseoventris* has a somewhat shorter, narrower foreclaws; a relatively longer tail; lacks any vestige of the ventral extension of the sinus canal or the associated foramen; possesses a foramen dorsal to posterior dorsal articular facet and two well-developed dorsal foramina; has a relatively and absolutely narrower palate (Fig. 11); has a relatively and absolutely longer unicuspid tooththrow; and relatively shorter mandible.

***Cryptotis goldmani***—*Cryptotis griseoventris* lacks the ventral extension of the sinus canal and associated foramen; possesses a foramen dorsal to posterior dorsal articular facet and two well-developed dorsal foramina; has a relatively and absolutely narrower palate (Fig. 11), relatively an absolutely longer unicuspid tooththrow, and a lon-

ger, narrower humerus with less enlarged bony processes.

REMARKS—*Cryptotis griseoventris* was originally described by Jackson (1933) based on a specimen from Chiapas. This was one of many names that Choate (1970) synonymized under the subspecies *C. goldmani goldmani*—an understandable move, given the confused taxonomic state of the genus and lack of adequate sample sizes at that time. However, a major discontinuity existed in the range of Choate's *C. goldmani goldmani* at the Isthmus of Tehuantepec, and populations on either side of the isthmus are completely isolated from each other. These two populations are easily distinguishable based on a number of cranial and postcranial characters (see Comparisons, above), and it is now clear that they represent distinct species.

Specimens of *Cryptotis griseoventris* have been captured above at least 2100 m in forests dominated by pines and firs and in oak-dominated cloud forest. Some areas inhabited by this small-eared shrew undergo nightly winter frosts and occasional snow (Goldman, 1951).

No reproductive data are available for *Cryptotis griseoventris*. None of the skins we inspected of adult males collected 25–30 September (n = 4), 2–6 October (n = 2), and 25–31 December (n = 10) had obvious lateral glands.

SPECIMENS EXAMINED (28)—**GUATEMALA:** HUEHUETENANGO: Todos Santos Cuchumatán (15°36'N, 91°37'W), 10,000 ft (USNM 77051–77068). **MEXICO:** CHIAPAS: San Cristóbal de las Casas [16°45'N, 92°38'W], 8000–9500 ft (USNM 75886–75894, includes holotype); 6 mi SE San Cristóbal de las Casas (MCZ 48061).

### *Cryptotis goldmani* (Merriam, 1895)

*Blarina mexicana goldmani*: Merriam, 1895:25; Elliot, 1904:560.

*Blarina mexicana machetes*: Merriam, 1895:26; Elliot, 1904:561.

*Blarina fossor*: Merriam, 1895:28; Elliot, 1904:562.

*Cryptotis frontalis*: Miller, 1911:222; Hall and Kelson, 1959:60; Goodwin, 1969:40.

*Cryptotis mexicana goldmani*: Miller, 1912:27; Davis and Lukens, 1958:350; Hall and Kelson, 1959:59; Genoways and Choate, 1967:204.

*Cryptotis mexicana machetes*: Miller, 1912:27; Hall and Kelson, 1959:60; Schaldach, 1966:288; Goodwin, 1969:40 (in part).

*Cryptotis fossor*: Miller, 1912:28; Hall and Kelson, 1959:62; Goodwin, 1969:41.

*Cryptotis guerrerensis*: Jackson, 1933:80; Hall and Kelson, 1959:60.

*Notiosorex phillipsii*: Goodwin, 1969:43 (in part).

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

*Cryptotis goldmani goldmani*: Choate, 1970:247 (in part); Hall, 1981:59 (in part).

HOLOTYPE—Skin and skull of adult male, USNM 70244; taken 23 December 1894 by E. W. Nelson and E. A. Goldman (collector number 7231); “from mountains near Chilpancingo, Guerrero, Mexico” (Merriam, 1895:25), 10,000 ft.

DISTRIBUTION—Conterminous high mountain areas in the Sierra Madre del Sur and Sierra Madre de Oaxaca (Fig. 4); known from above 1500 m in the Mexican state of Guerrero and above 2000 m in Oaxaca.

DESCRIPTION—Size medium for the genus (Table 1); tail moderately long, averaging 29 mm, or ca. 38% of HB (Table 2); dorsal guard hairs about 6–8 mm long; dorsal pelage Mummy Brown; ventral pelage somewhat paler than that on dorsum, between Light Drab and Drab; dorsal fur three-banded: basal five-sixths of hairs silvery gray, followed by a thin, lightly colored band grading into brown tip. Rostrum of moderate length (PL/CBL = 44.2% ± 1.0, n = 16); usually two well-developed dorsal foramina (61%, n = 41); an obvious, well-developed foramen (that opens into a ventral extension of the sinus canal) typically is present posterior to the dorsal articular facet on one or both sides of the skull (97%, n = 38; see Remarks, below); a foramen dorsal to the dorsal articular facet only occasionally present on one or both sides of the skull (16%, n = 38); zygomatic plate of moderate breadth (ZP/PL = 21.2% ± 2.4, n = 16), anterior border usually aligned with mesostyle–metastyle valley of M<sup>1</sup>, but may extend as far posteriorly as the parastyle of M<sup>2</sup>; upper tooth-row uncrowded, U<sup>4</sup> aligned with tooththrow and usually partly visible in labial view; P<sup>4</sup>, M<sup>1</sup>, and M<sup>2</sup> only very slightly recessed on posterior border; M<sup>3</sup> with paracrista, paracone, precentrocrista, and a small, lightly pigmented or unpigmented protocone; mesostyle of M<sup>3</sup> is usually small and uncolored, and occasionally has a short, uncolored postcentrocrista. Mandible of moderate length and breadth; articular process tends to be tall and wide, with a narrow ventral articular facet and a shallow lingual notch between articular facets (Oaxaca), or tall and moderately wide, with a

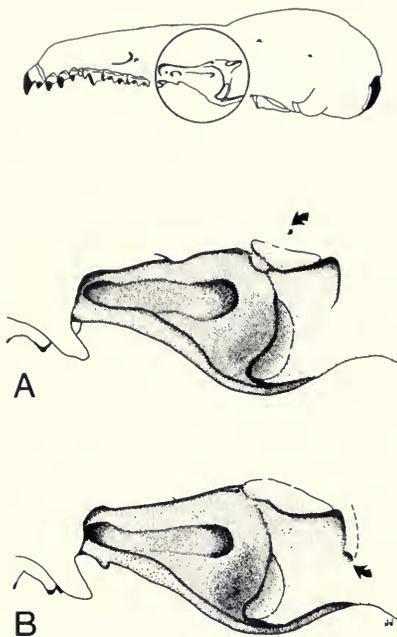


FIG. 12. Lateral views of the orbital areas of the skulls of **A**, *Cryptotis griseoventris* (USNM 75887); and **B**, *Cryptotis goldmani* (KU 98727). **Arrows** indicate approximate locations of foramen dorsal to (**A**) and foramen posterior to (**B**) the dorsal articular facet and associated with the ventral extension of the sinus canal. **Dashed line** on **B** indicates the path of the ventral branch of the sinus canal.

broad ventral articular facet and a deep notch between articular facets (Guerrero); entoconid of  $M_3$  often present, but usually poorly developed (48%,  $n = 23$ ), occasionally well developed (4%).

**COMPARISONS**—*Cryptotis goldmani* is the only member of the *C. mexicana*-group with an obvious, well-developed foramen posterior to the dorsal articular facet. The humerus in this species is the shortest and broadest in the genus, and it has the most elongate and enlarged bony processes.

***Cryptotis alticola***—*Cryptotis goldmani* averages smaller in HB, CBL, and weight (Table 1); has a relatively longer tail; has smaller forefeet and foreclaws; averages narrower in relative palatal breadth; and has less recessed posterior borders of  $P^4$ ,  $M^1$ , and  $M^2$ .

**REMARKS**—*Cryptotis goldmani* is unique among the broad-clawed *Cryptotis* in its possession of a well-developed foramen associated with a ventral branch of the sinus canal (Fig. 12B). This ventral branch canal exits through a foramen that usually is located posterior to the dorsal articular facet and is approximately the size of the

anterior orifice of the sinus canal. The foramen associated with the ventral branch of the sinus canal is a convenient character for distinguishing crania of *C. goldmani* from those of other members of the *C. mexicana*-group. This foramen is absent from the holotype of *C. g. magnimana* and all specimens of *C. g. goodwini*, *C. griseoventris*, and *C. nelsoni* that we inspected. A minute foramen associated with an equally diminutive ventral branch canal is present in many *C. alticola* (54%,  $n = 22$ ), *C. mexicana* (22%,  $n = 92$ ), *C. obscura* (21%,  $n = 34$ ), and *C. peregrina* (85%,  $n = 20$ ); however, the foramina in these species never approach the size of the well-developed foramen of the ventral branch canal present in *C. goldmani*. Another foramen, dorsal to the dorsal articular facet, often is present among members of the *C. mexicana*-group, but this foramen is much less prevalent in species (and individuals) that possess a ventral branch of the sinus canal, regardless of size.

*Cryptotis goldmani*, *C. mexicana*, and *C. peregrina* all occur in Oaxaca, and they can be difficult to tell apart, as attested by the number of misidentified specimens we have encountered. *Cryptotis goldmani* tends to be larger (HB =  $71 \pm 5$ ; CBL =  $19.6 \pm 0.5$ ; see Table 1) than Oaxacan *C. mexicana* (HB =  $67 \pm 3$ ,  $n = 16$ ; CBL =  $18.6 \pm 0.4$ ,  $n = 13$ ; *C. mexicana* from other Mexican states are larger) and *C. peregrina* (HB =  $66 \pm 4$ ,  $n = 17$ ; CBL =  $19.7 \pm 0.4$ ,  $n = 17$ ); but there is sufficient overlap in size to make this an undesirable character for identifying individuals with any certainty. *Cryptotis goldmani* can be identified most easily by its much longer and broader foreclaws and, cranially, by its very well-developed ventral sinus canal. From *C. mexicana*, *C. goldmani* usually can be distinguished by its vestigial or absent entoconid on  $M_3$ . *Cryptotis mexicana* can be distinguished most conclusively from *C. peregrina* by its wider foreclaws and forefeet and its relatively shorter tail ( $34\% \pm 3$  of HB vs.  $48\% \pm 5$ ). *Cryptotis mexicana* is also much more likely (72%) to have a distinct entoconid on  $M_3$  than is *C. peregrina* (6%).

Specimens of *Cryptotis goldmani* have been taken in high-elevation pine forest in Oaxaca at Guerrero. The climates of some localities where the species has been found include severe winter frosts and heavy summer rains (Goldman, 1951). Percy L. Clifton (KU field notes and catalog, 1966) took *C. goldmani* in snap traps set under rocks and logs in pine forest with scattered oak trees 7300 ft at Omiltemi, Guerrero, on 15 July 1966.

Other species taken in the same habitat included *Neotoma mexicana*, *Peromyscus aztecus*, *Peromyscus megalops*, and *Reithrodontomys* sp. Paul B. Robertson (KU field notes and catalog, 1970) captured two *C. goldmani* while trapping along a small rivulet and a larger stream lined with hardwood trees at 2300 m at Campamento Río Molino, Oaxaca, from 14 to 16 April 1970. The nearby slopes were covered with pines. Musser (1964) reported that the canyon bottom at Río Molino contained relatively moist, open forest with bromeliad-covered oaks and a dense understory of shrubs, ferns, and herbaceous vegetation. The higher slopes of the canyon were drier and covered with a mixed secondary growth of oaks and pines. In the same trapline, Robertson (KU field notes and catalog, 1970) took *Cryptotis peregrina*, *Sorex saussurei*, *Microtus mexicanus*, *Oryzomys chapmani*, *Peromyscus megalops*, *Reithrodontomys mexicanus*, and *Rattus* sp. In a nearby overgrown field, he captured *Cryptotis peregrina*, *Reithrodontomys megalotis*, *R. sumichrasti*, and *Sigmodon alleni*.

Reproductive data for *Cryptotis goldmani* are lacking. Lateral glands were well developed on three males collected 21–25 March, three of four males from 18–28 April, three males from 11–15 June, six males from 25–31 July, and one male from 5 August. A male taken on 26 December had lateral glands that were visible, but not particularly well developed. Lateral glands were not developed on single specimens taken during the months of January, February, and October. The timing of gland development that we ascertained for *C. goldmani* suggests that adult males may be reproductively active from March through June. However, data are lacking entirely for five months of the year, and there are no large series of males from any single month.

**SPECIMENS EXAMINED (58)—MEXICO: GUERRERO:** S slope of Cerro Teotepec, 3150 m (UMMZ 14710); mountains near [N and NW of] Chilpancingo, 9500–9800 ft (USNM 70243–70245 [including holotype], 70247); Los Retrocesos, 1550 m (MZFC 3485–3486); El Iris (MZFC 3481–3482); Omiltemi, 5700–8700 ft, 2450 m (ASNHC 3493–494; IBUNAM 29471, 32006; KU 98725–98727; ACM 74156–74161; MZFC 3480, 3483–3484; USNM 126895–126897 [including holotype of *Cryptotis guerrerensis*], 126947, 127500, 127506); 2 mi NW Omiltemi, 2300 m (USNM 329427); 2 mi W Omiltemi, 7800–7900 ft (TCWC 5573–5575, 665); 3 mi W Omiltemi, 8200 ft (MVZ 113491); 2 mi SW Filo de Caballo, 8200 ft (TCWC 41948–

41949). OAXACA: Campamento Río Molino, 2300 m (KU 124278, 124301); Vista Hermosa (KU 143749); Cerro Zempoaltepec, 8000–10,500 ft (USNM 68531, 68542, 68545 [holotype of *Cryptotis fossor*], 68547); Cerro Zempoaltepec, 4.5 km N of Santa María Yacochí, Mpio. Tlahuitoltepec, 2450 m (IBUNAM 33601–33602); Puerto Ángel Road, lumber camp, km 158, 8375 ft (CAS 15477); 2 km NE San Andrés Chichuaxtla, 2300 m (UMMZ 113888); Santa María Ozolotepec [mountains near La Cieneguilla], 10,000 ft (USNM 71454–71460, includes holotype of *Cryptotis mexicana machetes*); “near the City of Tehuantepec” (USNM 123429, holotype of *Cryptotis frontalis*).

**ADDITIONAL RECORDS—MEXICO: OAXACA:** Lachao; San Miguel Suchixtepec; San Juan Ozolotepec; Mixteguilla (Choate, 1970:249).

### *Cryptotis alticola* (Merriam, 1895)

*Blarina alticola* Merriam 1895:27, Elliot, 1904:561.

*Cryptotis alticola* Miller: 1912:27; Davis, 1944:376; Hooper, 1957:3; Hall and Kelson, 1959:60; Genoways and Choate, 1967:204.

*Cryptotis euryrhynchis*: Genoways and Choate, 1967:203.

*Cryptotis goldmani alticola*: Choate, 1970:245; Hall, 1981:59.

**HOLOTYPE**—Skin and skull of adult male, USNM 52047; collected 25 February 1893 by E. W. Nelson (collector number 4396); “from Mount Popocatepetl” (Merriam, 1895:27) [Volcán Popocatepetl], México, Mexico, 11,500 ft.

**DISTRIBUTION**—Highland areas above 2000 m in the Mexican states of Colima, Jalisco, Michoacán, México, and Puebla, and the Distrito Federal (Fig. 4).

**DESCRIPTION**—Size medium for the genus (Table 1); tail short, averaging 26 mm, or ca. 33% of HB (Table 2); dorsal guard hairs about 6–8 mm long; dorsal pelage Olive Brown/Mummy Brown/Bister/Clove Brown; venter somewhat paler, Light Grayish Olive/Drab/Bufy Brown to Olive Brown; dorsal fur distinctly three-banded: basal five-sixths of hairs silvery gray, followed by a thin, lightly colored band grading abruptly to the brownish tip. Rostrum of moderate length (PL/CBL = 43.2% ± 1.2, n = 16); more than half of specimens examined (54%, n = 22) have two well-developed dorsal foramina; a minute foramen opening on an

equally minute, ventral extension of the sinus canal may be present posterior to the dorsal articular facet on one or both sides of the skull (52%,  $n = 23$ ; see account for *C. goldmani*, above); a foramen dorsal to the dorsal articular facet may be present on one or both sides of the skull (39%,  $n = 23$ ); zygomatic plate of moderate breadth ( $ZP/PL = 21.8\% \pm 1.2$ ,  $n = 16$ ), anterior border aligned with mesostyle–metastyle valley of  $M^1$ ; palate wide;  $P^4$ ,  $M^1$ , and  $M^2$  slightly to moderately recessed on posterior border, emargination reaching about halfway to hypocone;  $M^3$  with paracrista, paracone, and precentrocrista, as well as small, lightly colored or uncolored protocone; mesostyle of  $M^3$  usually small and uncolored, and sometimes having a short, uncolored postcentrocrista. Mandible relatively long and of moderate breadth; articular process generally tall and moderately wide, with a moderately broad lower articular facet; entoconid of  $M_3$  often present but very reduced (64%,  $n = 14$ ), or absent.

**COMPARISONS**—Comparisons of *Cryptotis alticola* with other broad-clawed shrews are presented in the above accounts for those species. Selected measurements are presented in Table 1.

**REMARKS**—Choate (1970) noted many of the differences between *Cryptotis alticola* and *C. goldmani* (*sensu stricto*). Although he considered the two taxa to be “incipient species,” he treated *C. alticola* formally as a subspecies of *C. goldmani*. We concur with Choate (1970) that it is unlikely that there is intergradation between *C. alticola* and *C. goldmani*. The large number of differences in external, cranial, and postcranial characters clearly indicates that they are distinct species.

*Cryptotis alticola* is known to occur in high-elevation forests dominated by pines and often mixed with firs, oaks, and other tree species. At least some of the areas inhabited by *C. alticola* are subjected to winter frosts and occasional snow (Goldman, 1951). Percy L. Clifton (KU field notes and catalog, 1967) noted that he captured three *C. alticola* along *Microtus* runways on the relatively dry east side of a hill in an area of bunch grass under scattered pine, oak, and fir at 9000 ft, 20 mi SE of Autlán, Jalisco, during 27–28 April 1967. The moister western slope of the hill supported denser forest. Other small mammals caught in this trapline included *Sorex saussurei*, *Microtus mexicanus*, *Peromyscus aztecus*, and *Reithrodontomys sumichrasti*. On 11 June 1967, at 10,000 ft, 12 mi SW of

Ciudad Guzmán, Jalisco, Clifton caught three *C. alticola* in Museum Special snap traps set along a rotten log in a grassy area along the edge of a fir, pine, and hemlock forest. Walter W. Dalquest (KU field notes, 1946) captured *C. alticola*, along with *Microtus mexicanus*, *Neotomodon alstoni*, *Peromyscus melanotis*, and *Reithrodontomys chrysopsis*, in a clearing dominated by 3-foot-high clumps of sacatón grass in coniferous forest at 11,500 ft, 12 km ESE of Amecameca, in the state of México, from 14 to 15 June 1946. At Monte Río Frio, México, Davis (1944) captured a *C. alticola* in an unbaite snap trap set along a *Microtus mexicanus* runway in short grass meadow bordered by pines at 10,500 ft. In a thick forest of pines, firs, and oaks at 9150 ft, ca. 12 mi W of Ciudad Hidalgo, Michoacán, Robert W. Dickerman (KU field notes and catalog, 1955) took *C. alticola* with *Neotomodon alstoni* and *Reithrodontomys megalotis*.

Few reproductive data are available for *Cryptotis alticola*. A female (KU 17691) from 12 km ESE of Amecameca, México, was lactating on 15 June, and a pregnant female (KU 62311) was found dead along a trail on Cerro Patamba, Michoacán, on 1 July. Our examination of lateral glands on preserved study skins reveals a pattern similar to that of *C. goldmani*: lateral glands were well developed on one of two males taken in January, three males captured 21–25 March, three of four males captured 27–28 April, and three males taken in June. Lateral glands were not visible on four males captured in February, July, October, and November, respectively.

**SPECIMENS EXAMINED (36)**—**MEXICO:** COLIMA: Volcán de Fuego [= Volcán de Colima], 8800 ft (LACM 29058). **DISTRITO FEDERAL:** Cerro de Santa Rosa, 3200 m (IBUNAM 951). Santa Rosa, 3000 m (UMMZ 93367); Canyon [Cañon] Contreras, 10,200 ft (UMMZ 94597). **JALISCO:** 20 mi SE Autlán [de Navarro], 9000 ft (KU 111385–111387); 12 mi SW Ciudad Guzmán, 10,000 ft (KU 112039–112041); Volcán de Fuego [= Volcán de Colima], 9800 ft (KU 107143, holotype of *Cryptotis euryrhynchus*). **MÉXICO:** 12 km ESE Amecameca, 11,500 ft (KU 17691); N edge Refugio San Cayetano, 8200 ft (UMMZ 102713); Llanuras de Zempoala [10 mi NNW Cuernavaca, Choate, 1970] 9100 ft (USNM 329424–329426); 45 km ESE Mexico City, Monte Río Frio (TCV 1927); Estación Experimental Forestal y de

TABLE 7. Complete character matrix for phylogenetic analysis of members of the *Cryptotis mexicana*-group and two outgroups, *Cryptotis parva parva* and *Cryptotis nigrescens*. Transition series are explained in Appendix II.

Taxon	Transition series																													
	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	
<i>parva</i>	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0
<i>nigrescens</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1
<i>mexicana</i>	1	1	1	1	2	1	1	1	1	0	1	1	1	1	1	1	2	2	1	1	1	1	0	0	0	1	0	0	2	
<i>nelsoni</i>	1	1	1	?	2	1	1	1	1	0	1	1	?	?	?	?	?	?	?	?	?	0	0	0	0	1	0	0	2	
<i>obscura</i>	0	0	1	?	2	1	1	1	0	0	1	1	1	1	1	2	2	1	1	1	1	0	0	0	0	1	0	1	2	
<i>regregrina</i>	0	0	1	1	2	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	0	1	0	2	
<i>niticola</i>	2	2	2	1	2	1	1	1	0	1	0	1	2	1	1	1	3	2	2	2	2	1	1	0	0	1	1	0	1	2
<i>goldmani</i>	2	2	2	1	2	1	1	1	1	1	0	1	2	1	1	3	3	2	2	3	1	2	0	0	1	1	0	1	2	
<i>goodwini</i>	2	2	2	?	2	1	1	1	1	1	0	1	2	1	1	2	3	2	2	2	1	0	1	1	2	1	0	1	2	
<i>griseoventris</i>	2	2	2	?	2	1	1	1	1	1	0	1	?	?	?	?	?	?	?	?	?	0	1	1	2	1	0	1	2	
<i>magnimana</i>	2	2	2	?	2	1	1	1	1	1	0	1	2	1	1	2	3	2	2	2	?	0	1	1	?	1	0	1	2	

lora "L. M. Arellano," 2500 m (IBUNAM 4779); Mount Popocatepetl [Volcán Popocatepetl], 11,500–13,500 ft (USNM 52043, 52045–2047, includes holotype); Salazár, 8800–10,000 ft (USNM 50757–50759); N slope Volcán Olcahuatl [= Nevado de Toluca; above San Juan de las Huertas], 11,500 ft (USNM 55896); 12 km S of San Juan de las Huertas (ENCB 22675); 15.5 km S, 7 km E Zinacantepec [= San Miguel Zinacantepec], 3470 m (ENCB 19357). MICHOACÁN: ca. 12 mi W Ciudad Hidalgo, 9150 ft (KU 6280); 17.5 km NW Ciudad Hidalgo, 2980 m (ENCB 26210); Sierra Patamba [Cerro Patamán], 9000 ft (KU 66311). PUEBLA: 10 km W of San Juan Tetla, 3300–3400 m (IBUNAM 26544–6548).

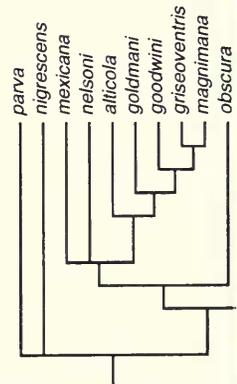
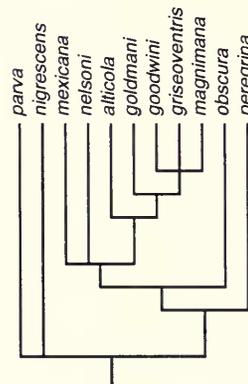
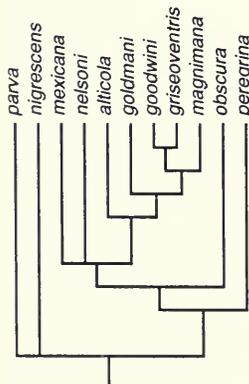
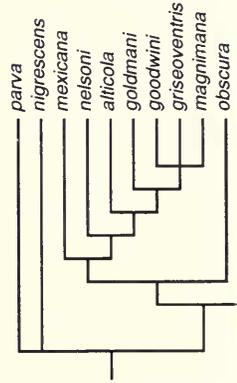
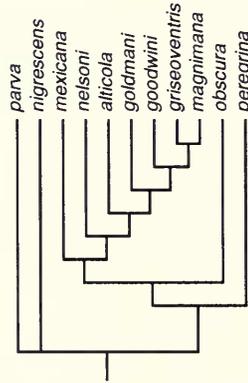
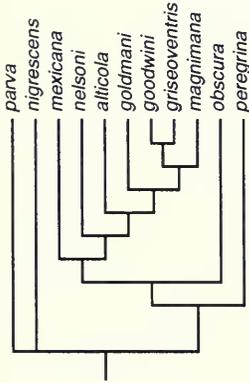
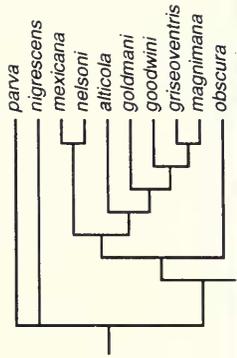
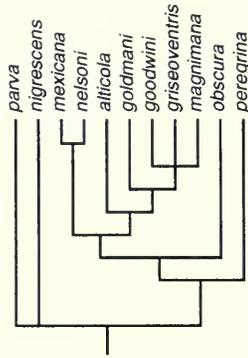
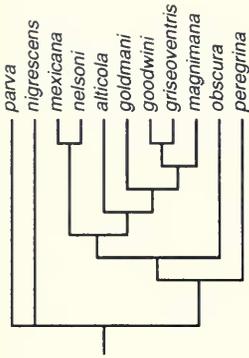
ADDITIONAL RECORDS—MEXICO: JALISCO: N slope Nevado de Colima [= Volcán de Colima], 8000–10,000 ft. MÉXICO: Cerro de San Juan, 11,000 ft. MICHOACÁN: Cerro de Tancítaro [= Pico de Tancítaro], 9000–12,000 ft (Choate, 1970:246).

### Phylogeny of the *Cryptotis goldmani*-Group

Our phylogenetic analysis of the *Cryptotis goldmani*-group and the subspecies of *Cryptotis mexicana*, based upon 29 morphological transition series (Table 7), provided nine shortest trees (length = 51 steps; Fig. 13). Strict consensus and Adams consensus trees constructed from the nine shortest trees are identical (Fig. 14) and represent the topology of one of the shortest trees. Areas of disagreement among the nine shortest-length trees center on two regions. The first contains the three

branches leading to *C. nelsoni*, to *C. mexicana*, and to the *Cryptotis goldmani*-group. These are presented alternatively (1) as an unresolved trichotomy; (2) with a clade consisting of *C. nelsoni* and *C. mexicana* representing the first outgroup to the *C. goldmani*-group; or (3) with *C. mexicana* as the second outgroup and *C. nelsoni* as the first outgroup to the *C. goldmani*-group (Fig. 13). The second region of disagreement consists of the branches leading to *C. g. goodwini*, *C. g. magnimana*, and *C. griseoventris*. This region is represented (1) as a trichotomy among the three taxa; (2) with *C. g. goodwini* and *C. griseoventris* as sister species; or (3) with *C. griseoventris* and *C. g. magnimana* as sister species. Further resolution of these two regions of the trees is hampered by the lack of complete skeletal material for *C. obscura* and *C. g. magnimana*, and the lack of any skeletons of *C. nelsoni* or *C. griseoventris*. Despite this, we have sufficient information to conclusively resolve the most basic relationships among these shrews.

Choate's (1970) *Cryptotis mexicana*-group is supported by as many as 16 synapomorphies. These species all have a similarly shaped skull, and they are most easily identified cranially by a suite of characters that includes the position of the zygomatic plate, the posterior border of which is even with (or slightly posterior to), and confluent with, the posterior root of the maxillary process (Fig. 3). In some North American species of *Cryptotis*, as well as in *Blarina* and *Sorex*, which commonly are considered to be sister groups of *Cryptotis* (George, 1986), the posterior border of the zygomatic plate is anterior to the posterior root of the maxillary process. Among members of the *C. nigrescens* complex, the posterior border of



the zygomatic plate is even with the posterior root of the maxillary process, as in the *C. mexicana*-group, but in the *C. nigrescens*-group the two structures are separated by the posterior edge of the palate (Woodman & Timm, 1993). Other craniomandibular characters that link members of the *C. mexicana*-group are the shape of the coronoid process as it joins the horizontal ramus; the relatively high and narrow articular condyle; and the long, low-cusped  $P_3$ . These three characters are similar to those of *Cryptotis gracilis* (see Woodman & Timm, 1992) and may link *C. gracilis* phylogenetically with the *C. goldmani*-group. We are in the process of studying *C. gracilis* and other southern Central American species, and we will address their relationship to the *C. mexicana*-group in the future. The members of the *Cryptotis mexicana*-group also show a number of synapomorphies associated with trends toward elongation of the foreclaws, broadening of the forefeet, and modification of the humerus. These are considered further below.

The four taxa previously considered to be subspecies of *Cryptotis mexicana* (*C. mexicana*, *C. nelsoni*, *C. obscura*, and *C. peregrina*) do not by themselves form a natural group. The *Cryptotis goldmani*-group is embedded within these taxa, indicating that *C. mexicana* (*sensu lato*) is paraphyletic. Among members of the *C. mexicana*-group, *C. peregrina* and *C. obscura* appear to be the most plesiomorphic species, based primarily upon the development of their foreclaws, their smaller body sizes, and their shorter tails relative to other members of the *C. mexicana*-group.

Monophyly of the *Cryptotis goldmani*-group is supported by at least seven synapomorphies (including one reversal). Most of the transition series supporting this clade concern the modification of structures of the forelimb. Among these species, the two most northern taxa, *C. alticola* and *C. goldmani*, appear to be the most plesiomorphic members (but see below). The three taxa from south of the Isthmus of Tehuantepec, *C. g. goodwini*, *C. g. magnimana*, and *C. griseoventris*, form a clade supported by three transition series, all based on cranial foramina.

## Evolution of the Forelimb

The most distinctive and intriguing characteristics of the *Cryptotis mexicana*-group occur in the forelimb. Our studies of these shrews indicate that modifications of the forelimb are not restricted to the *Cryptotis goldmani*-group, but represent common trends seen throughout the *C. mexicana*-group. Based on our phylogeny, the humerus shows a trend of becoming shorter relative to overall body size, and the shaft of the humerus broadens (Fig. 15). The articular regions become enlarged relative to the length of the humerus, and various bony processes (notably the teres tubercle, medial epicondyle, and pectoral process) elongate and enlarge. Due to widening of the base of the lateral epicondyle and a lateral shift in the position of the head of the humerus, the humerus appears more curved in the mediolateral plane. Nearly parallel trends are seen in the enlargement of the forefeet (Fig. 16), the shortening and broadening of the metacarpals and phalanges (Fig. 17), and the elongation and broadening of the foreclaws. The hindfeet show similar shortening and broadening of metatarsals and phalanges (Fig. 18), but this is not reflected to the same degree externally as it is in the forefeet. It is likely that some or all of these characters are linked, but we did not predict this *a priori*, and the lack of skeletal material for some taxa makes it impossible to confirm the extent of any linkages among these traits. For these reasons, we treated forelimb characters as separate transition series.

In general, five grades of evolutionary modification of the humerus and the rest of the forelimb are exhibited within the *Cryptotis mexicana*-group as compared to the plesiomorphic condition represented by the two operational outgroup species, *Cryptotis parva* and *Cryptotis nigrescens* (Fig. 15A). These grades are represented in order by (1) *C. peregrina* (Fig. 15B); (2) *C. obscura* (Fig. 15C); (3) *C. mexicana* (Fig. 15D); (4) *C. alticola* and *C. goodwini* (including *C. g. goodwini* and *C. g. magnimana*; Fig. 15E-G); and (5) *C. goldmani* (Fig. 15H). Within the *C. mexicana*-group, the humerus is least modified in *C. peregrina*; the bony

FIG. 13. Topologies of the nine shortest trees (length = 51 steps; consistency index = 0.82; resolution index = 0.86; rescaled consistency index = 0.71) from phylogenetic analysis of the *Cryptotis mexicana*-group using 29 morphological transition series. *Cryptotis parva parva* and *Cryptotis nigrescens* were used as outgroups. Differences among trees center on two regions: (1) branches leading to *C. mexicana*, *C. nelsoni*, and the *Cryptotis goldmani*-group; and (2) branches leading to *C. griseoventris*, *C. goodwini*, *C. g. goodwini*, and *Cryptotis g. magnimana*.

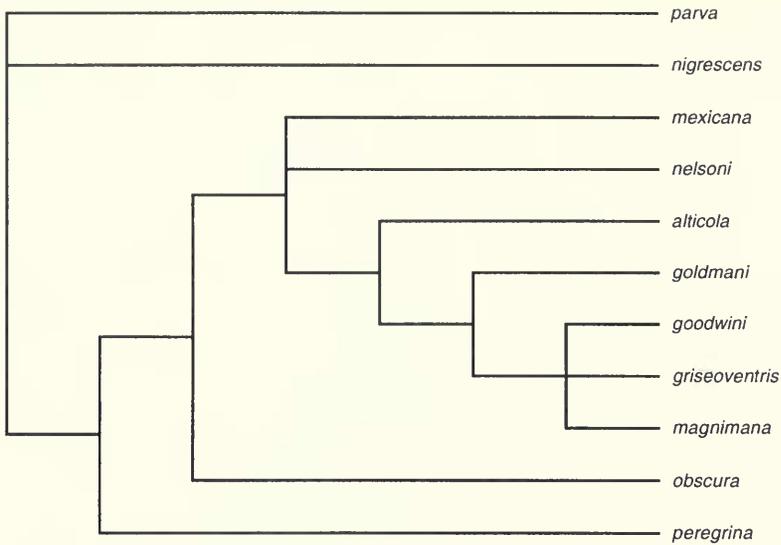


FIG. 14. Topology of strict consensus tree of the *Cryptotis mexicana*-group of species constructed from nine shortest length trees. This also is the topology of one of the nine shortest trees and the Adams consensus tree. See Figure 1 for additional explanation.

processes of the humerus are relatively small. Relative to the outgroups, however, the humerus of *C. peregrina* is shortened, broadened, and somewhat curved; the head of the humerus is dorsoventrally elongate; and the distal articular surfaces are enlarged (Fig. 15B). The metacarpals of *C. peregrina* (Fig. 17B) are relatively shorter and thicker than in *C. parva* and *C. nigrescens* (Fig. 17A). In the preceding grade, represented by *Cryptotis obscura* (Fig. 15C), the pectoral process, teres tubercle, and medial epicondyle of the humerus are enlarged relative to *C. peregrina*. The metacarpals of *C. obscura* are unknown. Both *C. peregrina* and *C. obscura* have elongate, but narrow, foreclaws and enlarged forefeet (Fig. 16B). The humerus of *Cryptotis mexicana* (Fig. 15D) shows a grade of development similar to that of *C. obscura*. No postcranial material is known for *Cryptotis nelsoni*; however, both *C. mexicana* and *C. nelsoni* have larger forefeet and broader foreclaws (Fig. 16C) than *C. obscura* and *C. peregrina*, and the metacarpals of *C. mexicana* (Fig. 17C) are broader than those of *C. peregrina*.

Members of the *Cryptotis goldmani*-group have the largest forefeet, the foreclaws are the most elongate and broadened (Fig. 16D), and the metacarpals and phalanges are the shortest and thickest (Fig. 17D). *Cryptotis alticola* and *Cryptotis g. goodwini* have the absolutely longest and broadest foreclaws, but this may be attributable in part to their larger overall body sizes (Table

1). Postcranial material is unknown for *Cryptotis griseoventris*, but *C. alticola*, *C. g. goodwini*, and *Cryptotis g. magnimana* have very similar humeri that are relatively shorter and much more curved than in *C. mexicana* (Fig. 15E-G). The bony processes are more elongate, and the teres tubercle and medial epicondyle are positioned much more closely to each other. The most derived condition of the humerus is observed in *Cryptotis goldmani* (Fig. 15H). The bony processes are the most pronounced in this species and the teres tubercle and medial epicondyle are most elongate and most closely situated to each other, their internal edges forming a symmetric reverse C-shape. *Cryptotis goldmani* was not identified as one of the most derived species in our phylogenetic analysis of the *C. mexicana* group because the characters that most distinguish its grade of forelimb development are autapomorphic. More interesting is the fact that although it has the most derived humerus, *C. goldmani* does not possess the most enlarged foreclaws or the broadest forefeet or metacarpals. This suggests that enlargement of forefeet and foreclaws and the change in the shape of the humerus are not entirely linked, although the difference in degree of development of the forefeet and foreclaws may be more closely associated with the body size of the animals involved.

Small-eared shrews in general have been considered to be semi-fossorial or semi-cursorial

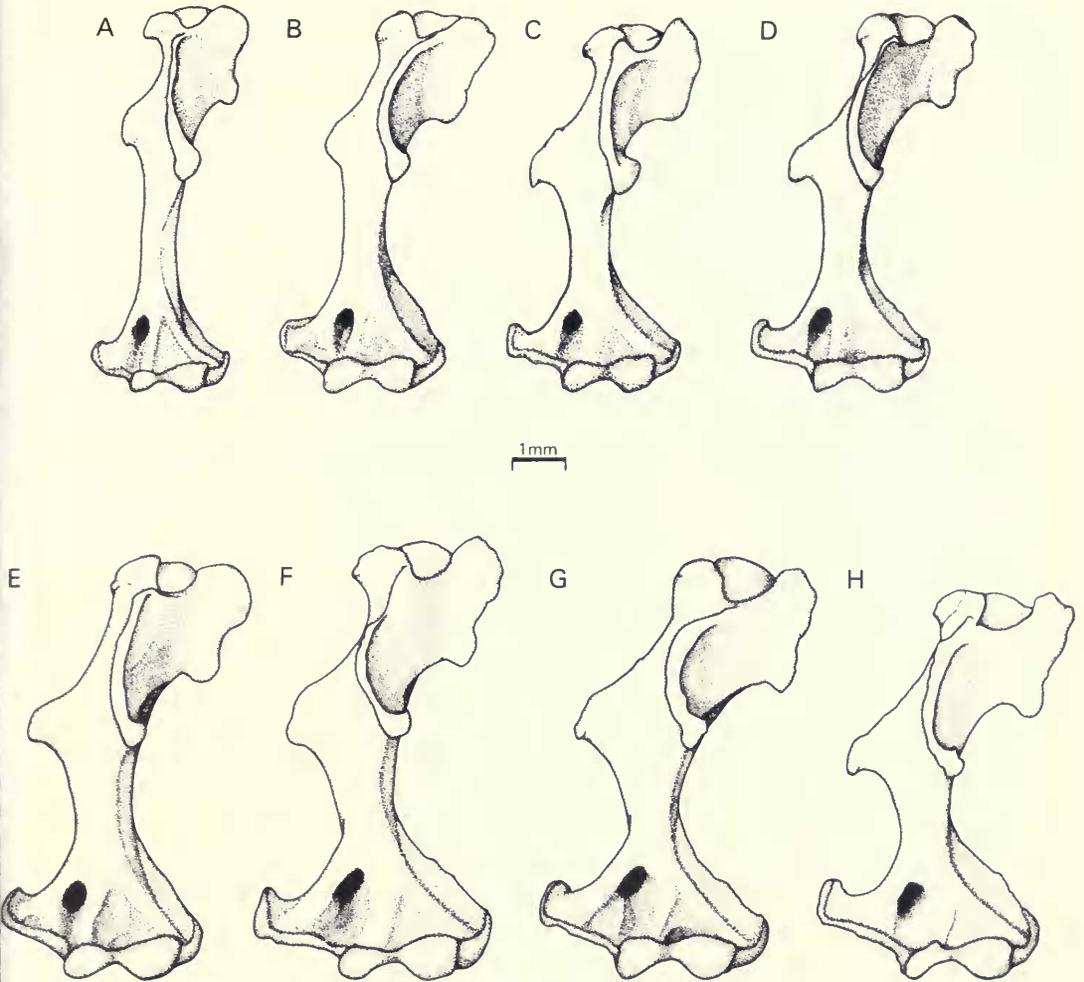


FIG. 15. Left humeri of selected *Cryptotis*: A, *C. nigrescens* (KU 142054, HB not recorded; however, KU 143384 as a slightly longer humerus and HB = 70 mm); B, *C. peregrina* (KU 124298, HB = 75 mm); C, *C. obscura* (MZFC 45, HB = 65 mm); D, *C. mexicana* (KU 29541, HB = 78 mm); E, *C. alticola* (IBUNAM 26544, HB = 85 mm); F, *C. g. magnimana* (KU 144611, HB = 80 mm); G, *C. g. goodwini* (USNM 275681, HB = 86 mm); and H, *C. goldmani* (IBUNAM 29471, HB = 84 mm). All humeri are drawn to the same scale. The humeri of *C. nelsoni* and *C. griseoventris* are unknown. Note the tendency of the humerus to shorten relative to head-and-body length (HB) as the humerus becomes more modified. Scale bar = 1 mm.

Reed, 1951), although most information about the habits of the genus is derived from studies of just one species, *Cryptotis parva*, in the United States. This shrew has been observed to be an active burrower in soft soil, and its nests are often located at or below ground level (see Whitaker, 1974, and references therein). However, the small feet and foreclaws with which *C. parva* excavates show no obviously specialized adaptations for digging relative to other small mammals. Changes in forelimb structure that we document for members of the *Cryptotis mexicana*-group (especially

the *Cryptotis goldmani*-group) are distinctive and suggest selected specialization, probably for excavating. It seems likely that these modifications permit this group of shrews to have a more fossorial niche than other members of the genus. Unfortunately, no behavioral or ecological studies are available that might support this hypothesis or help us understand the functional significance of these forelimb structures.

Many of the modifications of the humerus (shortening, dorsoventral elongation of the head, lengthening and enlargement of various processes,

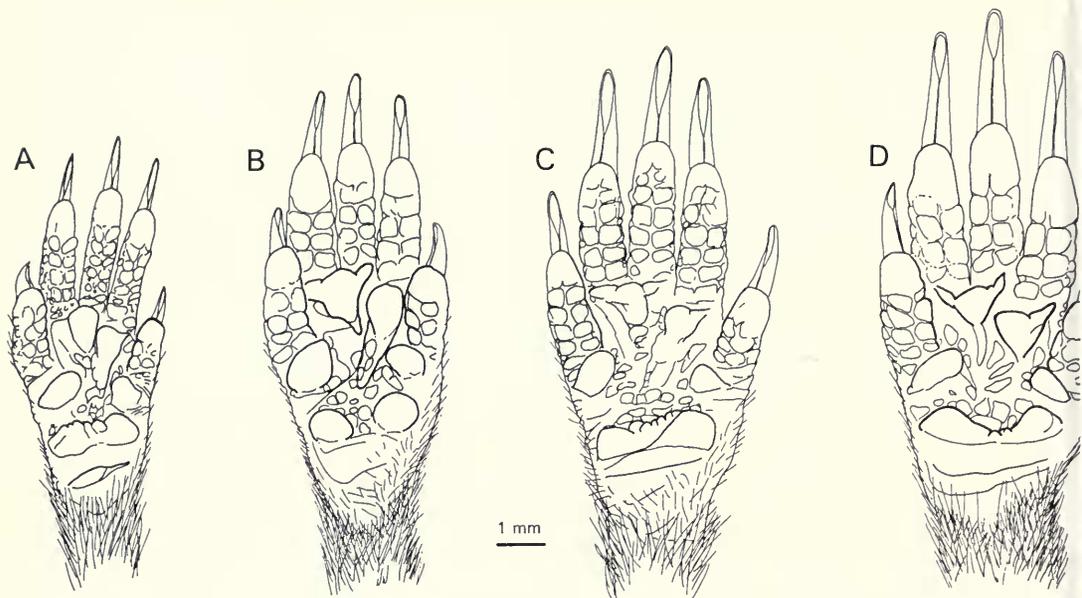


FIG. 16. Ventral views of the right forefoot of A, *Cryptotis parva orophila* (HB = 60 mm); B, *C. peregrina* (HB = 71 mm); C, *C. mexicana* (HB = 71 mm); and D, *C. goldmani* (HB = 68 mm). Scale bar = 1 mm.

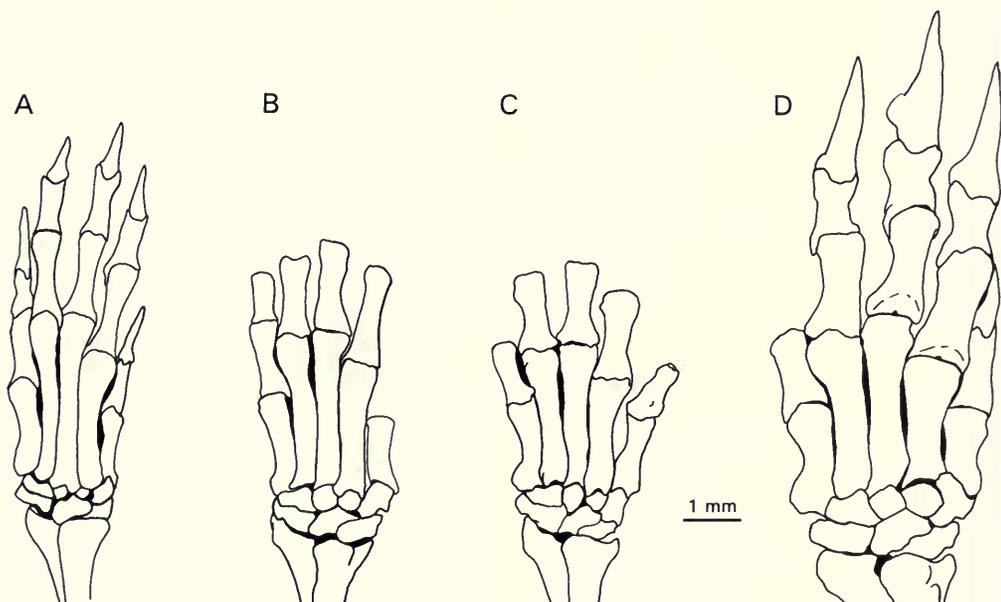


FIG. 17. Dorsal views of bones of the left manus of A, *Cryptotis parva orophila* (KU 142693, HB = 59 mm); B, *C. peregrina* (KU 124298, HB = 75 mm); C, *C. mexicana* (KU 29541, HB = 78 mm); and D, *C. goldmani* (IBUN 33602, HB = 76 mm). The metacarpals of *C. p. orophila* are nearly the same length as those of *C. goldmani*, despite the large difference in size between the two species. The metacarpals of *C. mexicana* are slightly shorter and broader than those of *C. peregrina*. Scale bar = 1 mm.

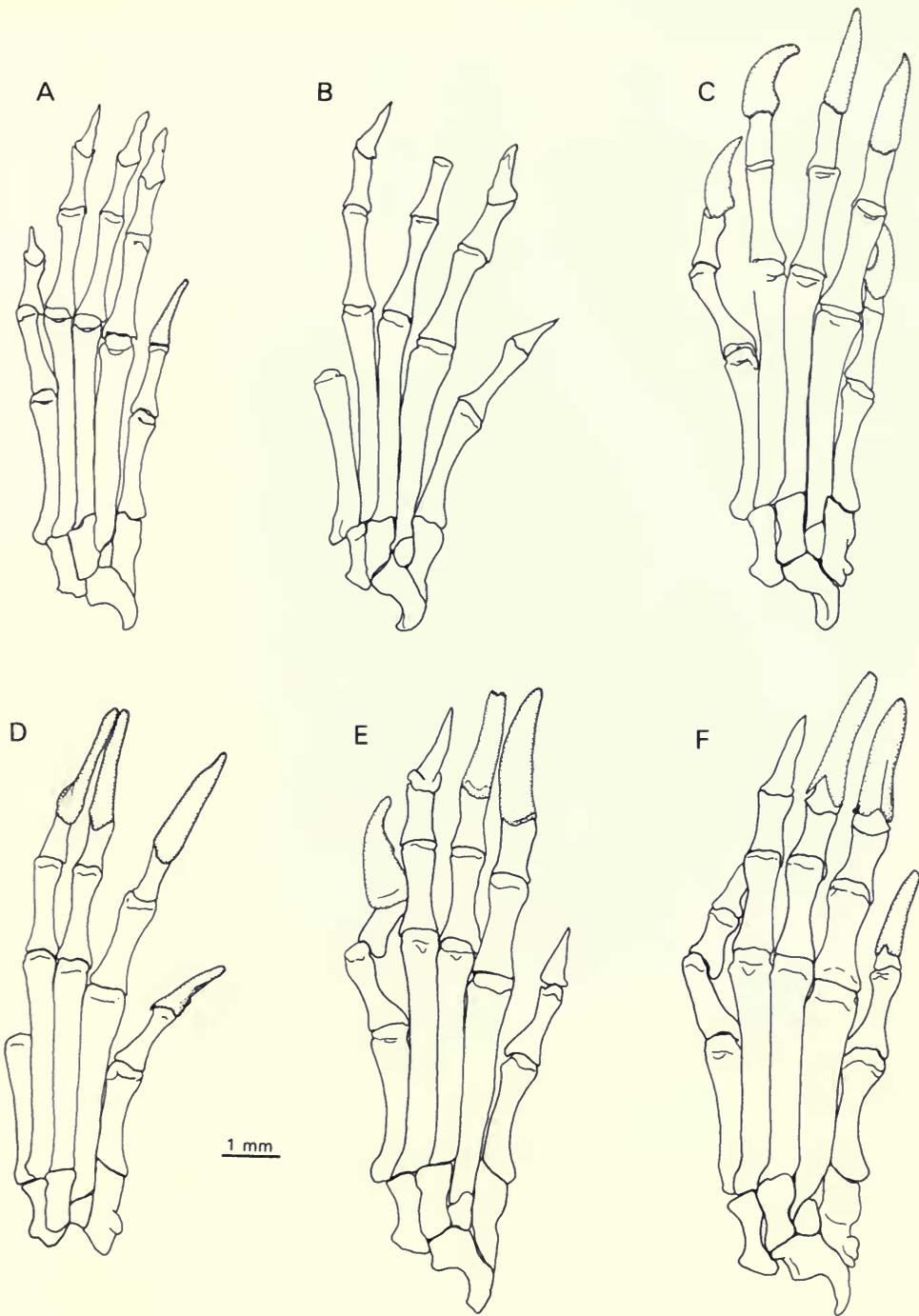


FIG. 18. Dorsal views of bones of the left pes of **A**, *Cryptotis parva orophila* (KU 142693, HB = 59 mm); **B**, *C. grescens* (KU 143385, HB = 67 mm); **C**, *C. peregrina* (KU 124298, HB = 75 mm); **D**, *C. mexicana* (KU 29541, HB = 78 mm); **E**, *C. alticola* (KU 62311, no measurements); and **F**, *C. goldmani* (IBUNAM 33602, HB = 76 mm). Elements with stippled borders are claws. Scale bar = 1 mm.

and close association of teres tubercle and medial epicondyle), metacarpals (shortening and broadening), and foreclaws (lengthening and broadening) are similar to characteristics seen in the forelimbs of talpids, and they even surpass the degree of modification of the humerus observable in some of the most primitive grades of moles (notably *Uropsilus*). The *C. mexicana*-group provides a living series of structural grades that may provide clues as to the early evolution of digging adaptations in talpids and possibly other strongly fossorial mammals.

### Zoogeography of the *Cryptotis goldmani*-Group

Choate (1970:297) previously suggested that southern Mexico was "the center of origin and dispersal" for most modern members of the genus *Cryptotis* because of the large number of species there, the high degree of differentiation among subspecies, and the presence of what he considered to be the most derived species in the genus. We concur, based on our understanding of the modern biogeography and phylogeny of the *Cryptotis mexicana*-group, that a highland region of central or southern Mexico west of the Isthmus of Tehuantepec was the most likely location for the evolution of the common ancestor of this clade. Most of the eight species of shrews that make up the *C. mexicana*-group are restricted to the west of the isthmus, including the least specialized species, *Cryptotis peregrina* and *C. obscura*. In general, the members of the group inhabit high elevations; although *C. mexicana* has been found as low as ca. 500 m elevation in Veracruz, elsewhere this and all other species in the clade are known only from elevations above 1000 m (Choate, 1970; this paper).

The distribution of the more specialized *Cryptotis goldmani*-group is discontinuous from west central Mexico to western Honduras. In southern Mexico, the occurrence of these shrews corresponds roughly with the distribution of the tree genus *Pinus* (see Styles, 1993), an observation that seems to be supported by habitat descriptions in collectors' field notes (see comments on species, above). One of the major gaps in the distributions of both the *Cryptotis goldmani*-group and *Pinus* is at the Isthmus of Tehuantepec, where there is a break between the highlands of the Sierra Madre del Sur to the west and the Sierra Ma-

dre de Chiapas to the east. The continental divide at the isthmus drops to as low as 250 m, and montane plant communities give way to vegetation transitional between lowland rainforest and semi arid scrub (Duellman, 1960). Duellman (1960, 1966) recognized the break in the highlands at the Isthmus of Tehuantepec as a major barrier to the dispersal of montane amphibians. In general, the isthmus does not appear to have been regarded as a major barrier to most small mammals (Hershkovitz, 1958; Hall, 1981), although it may be implicated in the evolution of subspecies or species of montane *Peromyscus* (see Carleton, 1989). Many middle- to high-elevation mammal species including four taxa of soricids (*Cryptotis parva pueblensis*, *C. mexicana*, *Sorex saussurei*, and *Sorex veraepacis*), putatively occur on both sides of the isthmus (Choate, 1970; Hall, 1981). However, no species of shrews are known from the isthmus itself, and this dry lowland probably is now an effective barrier to the dispersal of all shrews. Clearly, the isthmus prevents contact between eastern and western members of the *C. goldmani* group; two species (*Cryptotis alticola* and *C. goldmani*) are found to the west of the isthmus and three taxa (*C. g. goodwini*, *C. g. magnimana* and *C. griseoventris*) occur on the eastern side.

Dispersal of the *Cryptotis goldmani*-group across the Isthmus of Tehuantepec probably took place during one of the Pleistocene glacial epochs as suggested by Duellman (1960, 1966) for montane amphibians. Climatic amelioration, combined with lowered sea level during one or more of the at least nine Pleistocene glacial maxima, would have resulted in a lowering or mixing of climatic and vegetational zones that permitted montane forest plants and animals to extend across the isthmus. The subsequent upward migration of climatic zones preceding a subsequent interglacial would have isolated populations on either side of the isthmus. The sparse paleofloral evidence available for southern Mexico and Central America provides support for fluctuation in elevational climatic zones in the past, although regional evidence for the timing of specific vegetational changes remains scant (Graham, 1993).

The topology of our phylogeny of the *Cryptotis goldmani*-group (Fig. 14) suggests that these shrews derived from a common ancestor that originated to the west of the Isthmus of Tehuantepec. The two species to the west of the isthmus, *C. alticola* and *C. goldmani*, are the two most primitive shrews in the *C. goldmani*-group in terms of numbers of shared-derived characters. Although

*C. goldmani* is clearly the most specialized member of the *C. goldmani*-group in terms of its forelimb structure, this degree of specialization is mostly autapomorphic. The three eastern taxa (*C. g. goodwini*, *C. g. magnimana*, and *C. griseoventris*) form a clade that is supported by up to four transition series (TS 22–25 in Appendix I). A single character of the humerus (TS 16 in Appendix I) links *C. goldmani* with the three eastern taxa, suggesting that they share a common ancestor. Based on our phylogeny and the modern distributions of the species in the *C. goldmani*-group, we speculate that the occurrence of members of this group on both sides of the Isthmus of Tehuantepec is the result of a single dispersal event from west to east; as habitat conditions on the isthmus became more favorable for shrews during a glacial maximum, the common ancestor (of *C. goldmani* and of the three western taxa) expanded its range from the west across the isthmus to east. As climatic conditions on the isthmus shifted with the onset of the succeeding interglacial, the geographic range of the ancestral population contracted into two smaller populations, isolated from each other by the isthmus. From the western population, *C. goldmani* ultimately evolved, whereas the eastern population gave rise to *C. goodwini* and *C. griseoventris*. (In this scenario, the lineage leading to modern *C. alticola* branched off prior to the dispersal across the isthmus.)

Two lines of evidence provide clues as to the timing of the dispersal of the *Cryptotis goldmani*-group across the isthmus. The modern occurrence of four species of shrews on both sides of the Isthmus of Tehuantepec (but absent from the isthmus itself; see above) suggests that these four species crossed the isthmus during the ultimate (Wisconsinan) glacial epoch, but that populations of these species on either side of the isthmus, isolated since the end of that epoch, have had insufficient time to differentiate (speciate). (Alternatively, these “species” may represent unresolved taxonomic problems.) Given similar rates of evolution among these species and the *C. goldmani*-group shrews, we can speculate that the eastern and western members of the *C. goldmani*-group separated earlier, possibly subsequent to the penultimate (Illinoian) glaciation at the latest. This is supported by the recent rediscovery of fossil remains of *C. goodwini*–*C. griseoventris*-grade shrews from a site in Honduras believed to be late Pleistocene in age (D. Croft, in lit.; Woodman, unpublished data). Given an Illinoian or earlier dispersal, migrations of the *C. goldmani*-group

across the isthmus either to the east or to the west during subsequent glacial epochs may have been blocked by the presence of sister species (and potential ecological competitors) in suitable habitat on both sides of the isthmus.

### Key to the *Cryptotis goldmani*-Group

1. West of the Isthmus of Tehuantepec: usually a foramen posterior to the dorsal articular facet (Fig. 12B); usually lacking a foramen dorsal to external capitular facet; vestigial entoconid may be present on  $M_3$  . . . . . 2
- 1'. East of the Isthmus of Tehuantepec: always lacking a foramen posterior to the dorsal articular facet (Fig. 12A); usually a foramen dorsal to dorsal articular facet; entoconid lacking from  $M_3$  . . . . . 3
2. Larger species (averaging  $11 \pm 3$  g) with shorter tail (23–30 mm, averaging 33% of HB); foramen posterior to dorsal articular facet is minute, if present . . . . . *C. alticola*
- 2'. Smaller species (averaging  $8 \pm 1$  g) with longer tail (24–36 mm, averaging 38% of HB); large foramen posterior to dorsal articular facet present . . . . . *C. goldmani*
3. Zygomatic plate broader (ca. 2.2 mm, 25.0% of PL); unicuspid toothrow shorter (ca. 2.4 mm, 11.8% of CBL) . . . . . *C. goodwini magnimana*
- 3'. Zygomatic plate narrower ( $\leq 2.2$  mm,  $\leq 24.7\%$  of PL); unicuspid toothrow longer ( $\geq 2.5$  mm, ca.  $\geq 12.0\%$  of CBL) . . . . . 4
4. Larger (CBL  $\geq 20.0$  mm; HB averaging  $84 \pm 5$  mm) . . . . . *C. goodwini goodwini*
- 4'. Smaller (CBL  $\leq 20.4$  mm; HB averaging  $77 \pm 3$  mm) . . . . . *C. griseoventris*

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## Appendix I: Transition Series Used in Phylogenetic Analysis

1. length of foreclaws (Fig. 16): short (0); elongate (1); greatly elongate (2).
2. breadth of foreclaws (Fig. 16): narrow (0); broadened (1); greatly broadened (2).
3. forefeet (Fig. 16): small (0); enlarged, broadened (1); greatly enlarged and broadened (2).
4. metacarpals (Fig. 17): long, narrow (0); short, broad (1).
5. posterior border of zygomatic plate (Fig. 3): 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 unicuspid (U<sup>1</sup>–U<sup>3</sup>): cone-shaped, posteroventral border straight-edged or convex (0); narrow, posteroventral border concave (1).
10. protoconal basin of M<sup>1</sup>: about equal in size to hypoconal basin (0); reduced relative to hypoconal basin (1).
11. M<sup>3</sup> morphology: simple, metacone absent (0); complex, metacone present (1).
12. shape of P<sub>3</sub>: short and high (0); long and low (1).
13. shape of humerus (Fig. 15): 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); very high (2); extremely high (3).
17. teres tubercle of humerus (Fig. 15): relatively short (0); elongate (1); moderately elongate (2); greatly elongate (3).
18. medial epicondyle of humerus (Fig. 15): short (0); elongate (1); greatly elongate (2).
19. lateral epicondyle of humerus (Fig. 15): small (0); expanded (1); greatly expanded (2).
20. teres tubercle and medial epicondyle of humerus (Fig. 15): 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 (Fig. 12): absent (0); present, but tiny (1); well developed (2).
23. dorsal foramina: two in < 75% of specimens (0); two in > 75% of specimens (1).
24. foramen dorsal to articular facet (Fig. 12): present in < 75% of specimens (0); present in > 75% of specimens (1).
25. entoconid of M<sub>3</sub>: well developed, present in > 75% of specimens (0); vestigial, but present in < 76% of specimens (1); absent (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 tooththrow: crowded, three unicuspid visible in lateral view (0); uncrowded, four unicuspid visible in lateral view (1).
29. dorsal guard hairs: short, < 4 mm (0); of intermediate length, 4–5 mm (1); long, > 5 mm (2).

## Appendix II: Additional Specimens Examined

*Cryptotis mexicana* (59)—MEXICO: CHIAPAS: 3 mi E Pueblo Nuevo Solistahuacán, 7000 ft (KU 83942); OAXACA: Vista Hermosa, 1500 m (KU 91464); 6.5 mi SSW Vista Hermosa, 7100 ft (KU 99546); 21.8 km S Vista Hermosa, 2100 m (KU 124274); 31.6 km S Vista Hermosa, N slope Cerro Pelón, 2650 m (KU 124275–124276); NE slope Cerro Pelón, 2620 m (KU 120302); Cerro San Felipe, 6 km W La Cumbre, 2670 m (KU 121658, 124293); 2 km W La Cumbre, 2900 m (KU 121414); 7 mi N Ixtlán de Juárez, 10,000 ft (CAS 12244–12245); Llano de las Flores, 2800–

3150 m (KU 91465, 120303, 121410–1214124277); 0.4 mi S Llano de las Flores, 9200 (TCWC 45106); 11 mi NE (Tuxtepec road) Llar de las Flores, 9100 ft (UMMZ 112571); 27.5 km NNE Llano de las Flores (LACM 74166–74173 Ixtlán, 16 mi WSW La Esperanza (TCWC 25076 PUEBLA: 7.5 mi NE Tezuitlán (MMNH 6875); mi NE Tezuitlán (MMNH 4710, 6939). VERACRUZ: Las Vigas, 8500 ft (KU 29525, 29528, 29540, 29542–29545, 29547–29549); 11 km N Las Vigas, 8500 ft (KU 29524); 5 mi E Las Vigas (TCWC 25077); 4 km W Tlapacoyan, 1700 ft (KU 23412–23414).

*Cryptotis nelsoni* (9)—MEXICO: VERACRUZ: Volcán Tuxtla, 4800 ft (MCZ 19747; USNM 65429–65433, 65435–65437, includes holotype).

*Cryptotis nigrescens* (62)—COSTA RICA: ALAJUELA: Cinchona, 1600 m (KU 106942 Monteverde Cloud Forest Reserve, 1580–1600 m (KU 143377–143380); Monteverde Cloud Forest Reserve, Peñas Blancas Valley, 870 m (KU 143371, 143381). CARTAGO: [Volcán] Irazú, 8000–9400 ft (AMNH 141200). GUANACASTE: PUNTARENAS border: Monteverde, Cerro Amigos, 1790 m (KU 143382, 143384). PUNTA ARENAS: Coto Brus [Canton], Sabalito District, L. Tablas, Río Cotón, 1700 m (MNCR no number; Monteverde, 1345–1600 m (FMNH 12410, 128415, 135224; INBio no number; KU 13489, 135008, 135083, 142053, 142689, 142788, 142789, 143295–143297, 143383, 143387, 143395, 143636, 143638, 144612; LACM 6484, 67443, 67453; MMNH 14095; UMMZ 115888, 115884, 117107–117110, 125632); Monteverde Cerro Amigos, 1760 m (KU 142054); Monteverde Cloud Forest Reserve, 1530–1660 m (KU 142786, 142787, 143386, 143396, 143496, 143637); S. Luis, 1200 m [ca. 2.5 km S Monteverde] (KU 143385); 1 mi SW of Finca Las Cruces, San Vito, 4000 ft (LACM 74351–74353). SAN JOSÉ: S. Isidro (AMNH 7952/9691, holotype); 9 mi N of S. Isidro del General (Pan American Highway), 4800 ft (UMMZ 111999).

*Cryptotis obscura* (42)—MEXICO: HIDALGO: Tlanchinol, 20°59'N, 98°39'W (IBUNA 4186); Tulancingo (USNM 55633); Encarnación (USNM 81125–81127, 81131–81134); 11 km E Acaxochitlán, Lago Tejocotal, 2250 m (KU 81770). QUERÉTARO: 1 km S Ahuacatlán (MZFC 637); Pinal de Amoles (USNM 81115–81117, 81123–81124, 81129, 81147); 1 km S Pinal de Amoles (MZFC 638–648); 4 km SW Pinal de Amoles, 2550 m (IBUNAM 29106, 29332). TAMALULPA: 5 mi NW of Gómez Farías, Rancho de

Cielo, 3500 ft (MMNH 4301-4305, 4570-4571, 4574). VERACRUZ: Zacualpan, 6000 ft (KU 58241).

*Cryptotis parva orophila* (25)—**COSTA RICA**: ALAJUELA: Santa Clara (MNCR no number). ALAJUELA: Zarcero, 6000 ft (FMNH 43974). CARTAGO: Cartago (KU 26932; UMMZ 66465, 67316); Coliblanco (KU 26930-26931); La Estrella (AMNH 14847); Estrella de Cartago, 4500 ft (UMMZ 64147); Guarco (KU 16563); Navarro (MCZ 21656); Irazu Range [Volcán de Irazú] (AMNH 9641/9841, holotype). HEREDIA: Barva Cantón, San José de la Montaña, Paso Llano, 1800 m (KU 142692-142694); Barva Cantón, San Miguel de la Montaña, 1690-1700 m (KU 143372-143374). SAN JOSÉ: 10 mi S of Cartago, El Muñeco, 3800 ft (UMMZ 67315); Cerro Tablazo, 1983 m (USNM 252525); San José (USNM 7224, 38477); San Pedro de Montes de Oca (AMNH 139282); San Rafael de Montes de Oca, 4300 ft (KU 147100); Santa Ana (LSU 15753).

*Cryptotis parva parva* (48)—**USA**: KANSAS: Douglas Co.: Lawrence (KU 22131-22142); 3.5 mi W of Lawrence (KU 125554-125568); 1.5 mi N, 1.7 mi E of Lawrence (courthouse), sandpits (KU 114236-114239, 114241-114247).

*Cryptotis peregrina* (18)—**MEXICO**: OAXACA: mountains 15 mi SW Oaxaca de Juárez, 9500 ft (USNM 68317, holotype); Río Molino, Puerto Ángel road, km 153, 2250-2300 m (CAS 14068; KU 121661; IBUNAM 8447); lumber camp, Puerto Ángel road, km 158, 8375 ft (CAS 15478); Río Jalatengo, Puerto Ángel road, km 178, 4275 ft (CAS 14069, 14071-14072, 15475; IBUNAM 27518); Puerto Ángel road, km 195, 3475 ft (IBUNAM 26551); La Cima, Puerto Escondido road, km 184.5, 5750 ft (CAS 15473); Puerto Escondido road, km 193, 4200 ft (CAS 15474); Río Guajalote, 2000 m (KU 114226); Sinai, 10 km E Nopala, 7200 ft (CAS 14940); 20 mi S, 5 mi E Sola de Vega, 4800 ft (KU 98728); 16 km SW Suchitpec, 2000 m (ENCB 3413-3414).