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42. EVOLUTION AND BIOGEOGRAPHY OF MEXICAN SMALL-EARED SHREWS OF THE *CRYPTOTIS MEXICANA*-GROUP (INSECTIVORA: SORICIDAE)

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Abstract

The *Cryptotis mexicana*-group of small-eared shrews is distributed from southern Tamaulipas, México, to western Honduras. Species in this group are distinguished by unique modifications of the fore limb that include enlargement of the fore paws and fore claws and notable changes in the structure of the humerus. Phylogenetic analysis supports the monophyly of the *C. mexicana*-group, as well as that of the *C. goldmani*-group, which consists of the five species with the most derived states of fore arm modifications. *Cryptotis magna* appears to be closely related to the base of the *C. mexicana*-group. On the basis of branch supports for the phylogeny, I hypothesize three primary divergence events that resulted in the modern diversity seen within the group. Fossils of *Cryptotis goodwini*, one of the most derived species in the *C. mexicana*-group, suggest that major morphological modifications of the fore limb had occurred prior to the late Pleistocene. Late Pleistocene records of *C. goodwini* and *Cryptotis obscura* indicate that the *C. mexicana*-group already occupied most of its modern distribution by that time.

Key words: shrews, *Cryptotis mexicana*, *Cryptotis goldmani*, *Cryptotis goodwini*, *Cryptotis obscura* morphology, phylogenetic analysis, diversity, Tamaulipas, México, Honduras.

Resumen

El grupo *Cryptotis mexicana* de las musarañas de orejas pequeñas se distribuye desde Tamaulipas, México, hasta Honduras occidental. Especies de este grupo se caracterizan por modificaciones únicas de los miembros delanteros que incluyen la agrandación de las patas y las uñas, y cambios notables en la estructura del húmero. Análisis filogenético apoya el monofilio del grupo *C. mexicana*, y también el monofilio del grupo *C. goldmani*, lo cual consta de cinco especies con los estados los más derivados de las modificaciones del miembro delantero. *Cryptotis magna* probablemente está muy relacionada con la base del grupo *C. mexicana*. Por la fuerza de los apoyos de rama en el filogenio, parece que hubieron tres acontecimientos de divergencia los que resultaron en la diversidad actual de este grupo de musarañas. Fósiles de Honduras de *Cryptotis goodwini*, una de las especies más derivadas del grupo *C. mexicana*, sugieren que las principales modificaciones del miembro delantero hubieran ocurridas antes del Pleistoceno tardío. Registros del Pleistoceno tardío de *C. goodwini* y *Cryptotis obscura* indican que el grupo *C. mexicana* ya ocupaba la mayoría de su distribución moderna en esa época.

Palabras clave: musarañas, *Cryptotis mexicana*, *Cryptotis goldmani*, *Cryptotis goodwini*, *Cryptotis obscura* morfología, análisis filogenético, diversidad, Tamaulipas, México, Honduras.

Small-eared shrews of the Pan-American genus *Cryptotis* are found from eastern United States of America and southernmost Canada through México and Central America to the Andes of northern Peru. The species with the widest geographical and elevational distribution is *Cryptotis parva*, which, as currently understood, has a discontinuous range from the northeastern United States to the Valle de México. The genus includes at least 27 other species distributed from northeastern México to Peru. *Cryptotis* reaches its greatest diversity in the state of Oaxaca, where six species occur, although three or fewer species typically are present at any given locality. In northern portions of their range, small-eared shrews are sympatric, often syntopic, with other genera of soricids. South of Guatemala, however, *Cryptotis* is the only genus of soricid—indeed, the only member of the Order Soricomorpha—present. With the notable exceptions of some species of the *Cryptotis parva*-group and the exclusively lowland *Cryptotis mayensis* (Woodman and Timm, 1993), members of the genus in México and southwards are montane species, occurring at elevations greater than 800 m.

One significant subset of the genus is the *Cryptotis mexicana*-group (Choate 1970) comprised of nine species (*C. alticola*, *C. goldmani*, *C. goodwini*, *C. griseoventris*, *C. mexicana*, *C. nelsoni*, *C. obscura*, *C. peregrina*, and *C. phillipsii*—Woodman and Timm 1999, 2000) distributed discontinuously from southern Tamaulipas to western Honduras (Fig. 1). All species within this group appear to be restricted to moist vegetational associations above at least 800 m in elevation, and several are not known from elevations below 2000 m. Members of the *C. mexicana*-group are distinct cranially from other members of the genus, and they possess unique external and osteological modifications of the fore limb that include lengthening and broadening of the claws, broadening of the fore feet, and expansion of a number of processes of the humerus (Woodman and Timm 1999, 2000). Five members of the *C. mexicana*-group (*C. alticola*, *C. goldmani*, *C. goodwini*, *C. griseoventris*, *C. peregrina*) exhibiting the most derived states of the fore limb form a well-defined clade, termed the *C. goldmani*-group (Woodman and Timm 2000). Recently, late Pleistocene remains of *C. goodwini*, a member of

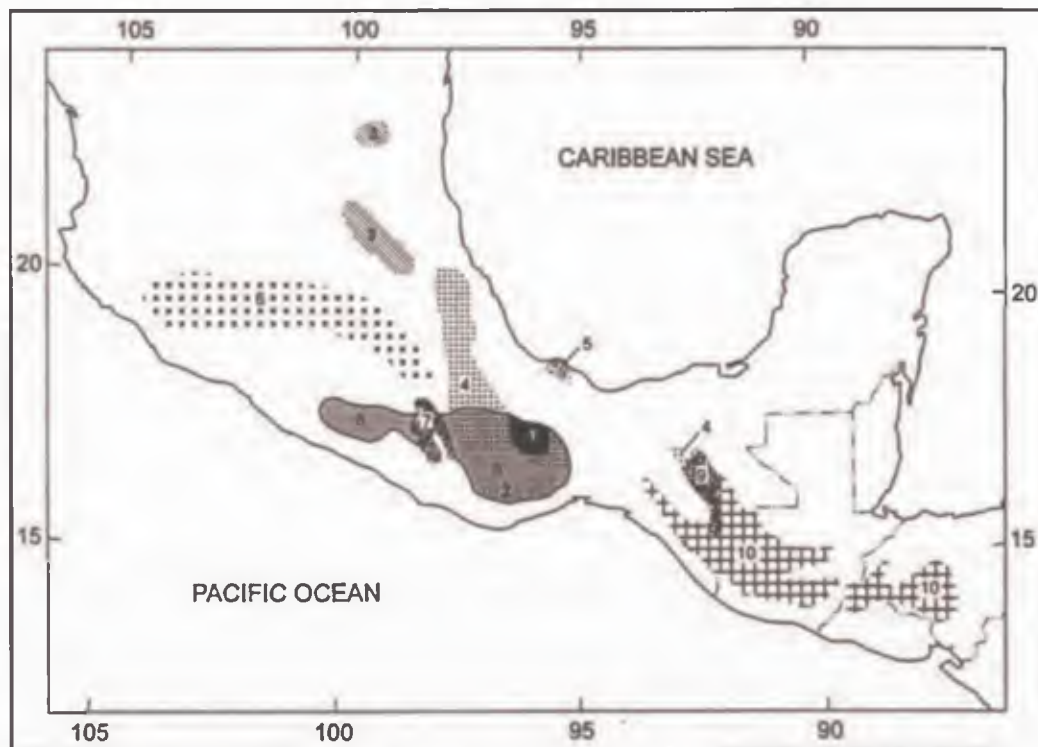


Fig. 1. Map of the distributions of *C. magna* (1) and the *C. mexicana*-group (*C. phillipsii*, 2; *C. obscura*, 3; *C. mexicana*, 4; *C. nelsoni*, 5; *C. alticola*, 6; *C. peregrina*, 7; *C. goldmani*, 8; *C. griseoventris*, 9; *C. goodwini*, 10).

the *C. goldmani*-group, were identified from Honduras (N. Woodman and D. A. Croft, unpublished data). These fossils, together with late Pleistocene remains of *C. obscura* from Nuevo León (Choate 1970; Findley 1953), provide constraints on the latest date at which members of the *C. mexicana*-group evolved. They also provide information on the biogeographic history of the group and the evolution of the forelimb structures.

One Mexican species, *Cryptotis magna*, has long had a cryptic relationship with other members of the genus. This species is endemic to northern Oaxaca, where it occurs in moist habitats above ca. 1350 m. It bears the distinction as being the largest *Cryptotis* in Mexico and northern Central America, almost as large in head-and-body length (and approximately equivalent in weight) as *C. meridensis* from South America (Woodman 2002). Choate (1970) treated *C. magna* as one of his "relic species," a polyphyletic group of taxa sharing primitive cranial characters, and he suggested that *C. magna* is only distantly related to other extant *Cryptotis*. Woodman and Timm (1993) thought that *C. magna* might be imbedded within the *C. nigrescens*-group. More comprehensive study of external characters and the craniomandibular and postcranial skeleton suggests that a basal relationship within or near the *C. mexicana*-group may be more accurate. For this reason, it was considered in the current analysis.

In this paper, I review current understanding of the taxonomy and distribution of the *Cryptotis mexicana*-group, and I present a revised phylogeny of the group that tests previously hypothesized relationships among its member species and examines the phylogenetic position of *C. magna* in relation to the group. I also interpret the biogeography of the *C. mexicana*-group in light of both this new phylogeny and the fossil shrews from Honduras.

Materials and Methods

This paper relies upon the techniques, methods, and results of previous studies of Mexican and Central American shrews (Choate 1970; Woodman and Timm 1992, 1993, 1999, 2000). Taxonomy follows Woodman and Timm (1999, 2000). Distributions of species are from Choate (1970) and Woodman and Timm (1999, 2000). Terminology of dentition and dental characteristics follows Choate (1970). Anatomical terminology of the postcranial skeleton fol-

lows Reed (1951). Many comparative terms used in taxonomic descriptions, such as "small," "medium," and "large," are defined in the list of characters (see Appendix). Otherwise, they represent comparisons with the average value for all species in the genus *Cryptotis*. In this sense, "medium" or "moderate" is a mean value that falls within the mean \pm *SD* for the genus; "small" $<$ (mean $-$ *SD*); "large" $>$ (mean $+$ *SD*).

Phylogeny and character evolution in the *Cryptotis mexicana*-group were analyzed using PAUP* 4.0b4a (Swofford 2002) and MCCLEDE 4.0 (Maddison & Maddison 2000). Phylogenetic analyses were carried out using an exhaustive search of 34 unordered and weighted transition series (TS) based on morphological characters (Table 1; Appendix). *Cryptotis parva parva* and *C. nigrescens* served as outgroups for polarizing characters, and *Cryptotis magna* was included to determine its relationship to the *C. mexicana*-group. Weighting of transition series was based on amount of variation within and among species, with less variable characters weighted higher. Transition series 23, "body size," was given no weight pending an independent study of the evolution of this trait in the *C. mexicana*-group. The strength of branch support was measured by both bootstrap and jackknife analyses using a branch-and-bound search option with 10,000 replicates each. The current analysis differs from phylogenetic analyses carried out by Woodman and Timm (2000) in use of some different transition series, more conservative scoring of transition series (*i.e.*, fewer states), differential weighting of transition series, and the inclusion of *Cryptotis magna*.

Information regarding fossil shrews from near Copán, western Honduras, derive from unpublished data in a report prepared by Darin A. Croft and me, which has been submitted for publication elsewhere. Among the fossil remains, we were able to identify complete and partial mandibles, maxillae, and postcranial bones referable to three modern species of small-eared shrews: *Cryptotis orophila*, *C. merriami*, and *C. goodwini*.

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 (ASNH); California Academy of Sciences, San Francisco (CAS); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City

(CNMA); Escuela Nacional de Ciencias Biológicas, Mexico City (ENCB); Field Museum, Chicago (FMNH); Department of Geology, Field Museum, Chicago (FMNH-PM); University of Kansas Natural History Museum, Lawrence (KU); Natural History Museum of Los Angeles County, Los Angeles (LACM); Museum of Comparative Zoology, Cambridge (MCZ); James Ford Bell Museum of Natural History, St. Paul (MMNH); Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City (MZFC); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF); Texas Cooperative Wildlife Collection, College Station (TCWC); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Universidad Nacional Autónoma de Honduras, Tegucigalpa (UNAH); National Museum of Natural History, Washington (USNM).

Results

Parsimony analysis of the *Cryptotis mexicana*-group found nine shortest trees with a length of 124. The strict consensus tree computed from these nine most parsimonious trees is shown in Fig. 2, with bootstrap and jackknife values >50 on the respective branches. In general, there is strong support (ten apomorphies) for the grouping of *Cryptotis magna* with the *C. mexicana*-group rather than grouping with either *C. parva* or *C. nigrescens*, and for considering the five species of the *Cryptotis goldmani*-group a clade within the *C. mexicana*-group (ten apomorphies). Bootstrap and jackknife values of 70 or above support recognition of the nine species of the *C. mexicana*-group. There also is support for a subgroup of eight species within the *C. mexicana*-group to the exclusion of *C. phillipsii*, indicating that this latter taxon is the most plesiomorphic member of the group. Two regions among the nine most parsimonious trees exhibit variation in branching patterns. These regions appear on the strict consensus tree as trichotomous nodes. The first variable region involves the positions of *C. obscura* and *C. mexicana* relative to a clade including *C. nelsoni* and the *C. goldmani*-group. Three alternative scenarios are presented: *C. obscura* as a sister group to a clade including *C. mexicana* and the clade of *C. nelsoni* and the *C. goldmani*-group; *C. mexicana* as a sister group to a clade including *C. obscura* and the *C. nelsoni*-*C. goldmani*-group clade; *C. mexicana* and

C. obscura together forming a sister group to the clade of *C. nelsoni* and the *C. goldmani*-group. The second region of instability is within the *C. goldmani*-group and involves the position of *C. alticola* relative to two clades consisting of *C. goldmani* and *C. peregrina* on the one hand and *C. goodwini* and *C. griseoventris* on the other. The three alternative arrangements here are: *C. alticola* as a sister group to a clade comprised of the other four species; *C. alticola* as a sister group to the *C. goodwini*-*C. griseoventris* clade; *C. alticola* as a sister group to the *C. goldmani*-*C. peregrina* clade. None of the alternative topologies within the two variable regions of the tree is supported either by

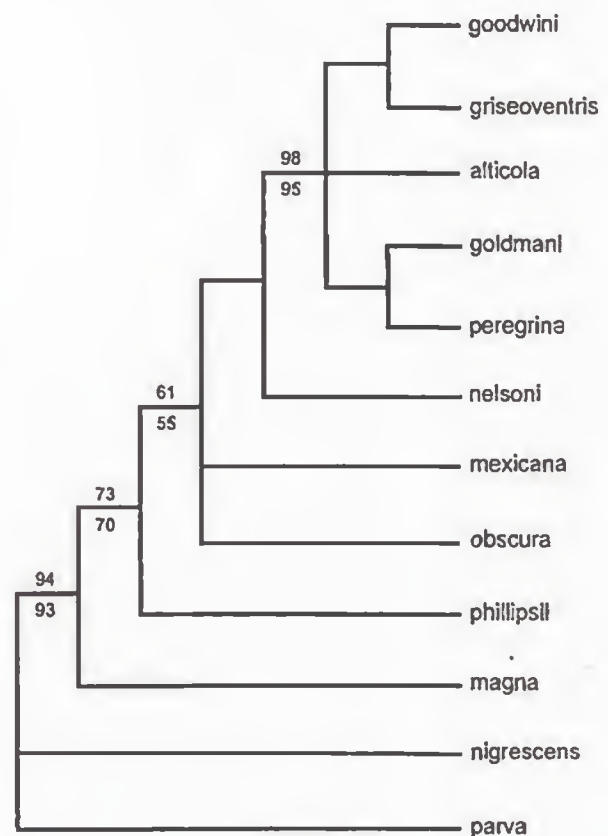


Fig. 2. Strict consensus tree of nine most parsimonious trees resulting from phylogenetic analysis of the *Cryptotis mexicana*-group of shrews. Bootstrap and jackknife values >50 are placed above and below each branch, respectively. Statistics for each of the most parsimonious trees: tree length = 124 (minimum possible length = 98; maximum possible length = 256); consistency index = 0.790; rescaled consistency index = 0.660; retention index = 0.835; homoplasy Index = 0.210.

bootstrap or jackknife values >50 (Fig. 2). Bootstrap and jackknife analyses also fail to strongly support three other clades that appear in the strict consensus tree: (1) *C. nelsoni* with the *C. goldmani*-group (supported by one apomorphy); (2) *C. peregrina* with *C. goldmani* (supported by two apomorphies); and (3) *C. goodwini* with *C. griseoventris* (supported by two apomorphies).

The present phylogenetic analysis supports critical portions of previous phylogenies inferred by Choate (1970) and substantiated by Woodman and Timm (2000). Most significant are support for the *C. mexicana*-group as a natural grouping and for the *C. goldmani*-group as a clade within the *C. mexicana*-group. Also supported were Woodman and Timm's (2000) hypothesis that *C. phillipsii* is the sister taxon to all other members of the *C. mexicana*-group.

Other branches of their phylogeny both outside and within the *C. goldmani*-group were weakly supported or unsupported, resulting in a less well resolved tree overall.

Comparison of the phylogeny of the species of the *C. mexicana*-group with the map of their modern geographic ranges provides a sense of the complex biogeographical history of this group in the montane areas of Mexico and northern Central America (Fig. 3). The greatest concentration of species occurs in Oaxaca (Fig. 1), where *C. magna*, *C. phillipsii* (the most plesiomorphic species in the *C. mexicana*-group), *C. mexicana*, and two of the more derived members of the group (*C. goldmani*, *C. peregrina*) are found. Two species, *C. alticola* and *C. obscura*, have allopatric distributions in central and northern Mexico, respectively, and *C. nelsoni* occurs

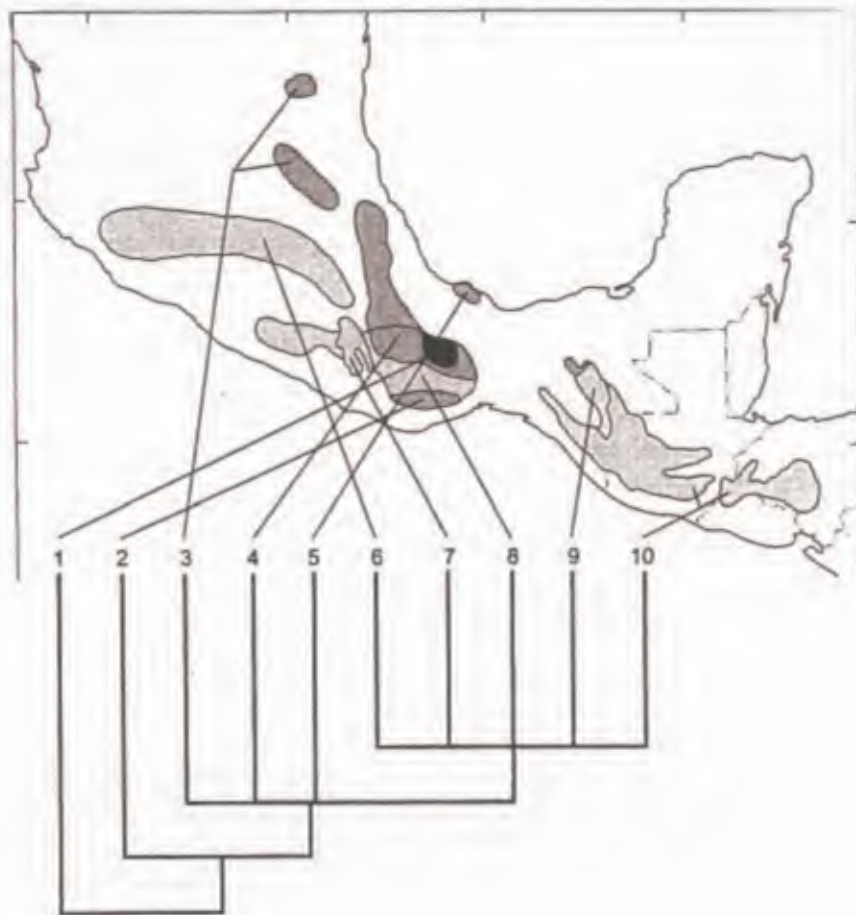


Fig. 3. Area cladogram for *Cryptotis magna* (1) and the *C. mexicana*-group (*C. phillipsii*, 2; *C. obscura*, 3; *C. mexicana*, 4; *C. nelsoni*, 5; *C. alticola*, 6; *C. peregrina*, 7; *C. goldmani*, 8; *C. griseoventris*, 9; *C. goodwini*, 10). Nodes with bootstrap values <50 are collapsed and shown as polytomies.

in the isolated Sierra de los Tuxtlas along the Caribbean coast of Mexico. The Isthmus of Tehuantepec stands out as a distinct gap in the modern distributions. The isthmus currently is a dry lowland that acts as an effective barrier to dispersal for montane shrews, just as it does for montane amphibians (Duellman, 1960, 1966), and probably has done so since the end of the last Glacial. The isthmus probably has played an important role contributing to modern diversity of shrews in southern Mexico and Central America (Choate, 1970). In general, all of the more plesiomorphic species in the *C. mexicana*-group (i.e., *C. phillipsii*, *C. obscura*, *C. mexicana*, *C. nelsoni*), as well as *C. magna*, are distributed to the north of the Isthmus of Tehuantepec, as are three members of the more derived *C. goldmani*-group (*C. alticola*, *C. peregrina*, *C. goldmani*). Two species of the *C. goldmani*-group (*C. goodwini*, *C. griseoventris*) occur to the south of the isthmus. Disjunct modern distributions are exhibited by three species: *C. obscura* in northeastern Mexico, *C. goodwini* in northern Central America, and *C. mexicana*, which occurs mainly to the north of the Isthmus of Tehuantepec, but also is known from two localities in Chiapas, just south of the isthmus.

Discussion

Based on the present analysis, a more complete description of the characteristics of the *Cryptotis mexicana*-group can be provided. Members are generally medium-sized species of *Cryptotis* (except *C. goodwini*, which is large-bodied), with long, dark dorsal pelage and a moderately long tail (except *C. alticola*, which has a short tail). As with many groups of mammals, cranial features have provided the traditional, primary database for understanding systematics of the genus *Cryptotis*. Within the *C. mexicana*-group, overall cranial morphology tends to be relatively conservative. Three derived craniomandibular characters that define the group are: the low angle of the junction of the anterior border of the coronoid process with the horizontal ramus of the mandible (TS 6); the shape of the articular face of the articular process (TS 7); and the shape of the unicuspid (TS 9) [except for *C. obscura* and *C. alticola*, which appear to be reversals]. In addition, a number of primitive or unpolarized characters describe the group: zygomatic plate of moderate breadth [except *C. peregrina*, which has

a short zygomatic plate]; posterior border of the zygomatic plate typically posterior to the middle of the maxillary process (TS 5) [however, four species—*C. mexicana*, *C. obscura*, *C. nelsoni*, *C. phillipsii*—have the posterior border aligned with, or posterior to, the posterior base of the maxillary process, a derived condition; three of these species also have longer zygomatic plates than other species in the *C. mexicana*-group.]; lower sigmoid notch deep (TS 8); third lower premolar relatively long and low (TS 12); anterior element of the ectoloph of M1 is reduced (TS 27); dentition uncrowded and not bulbous (TS 30); coronoid process of moderate height (TS 33); length of posterior mandible medium to long.

Characteristics of the fore limbs are particularly useful for identifying the *C. mexicana*-group. Externally, the fore claws generally are longer and broader and the fore paws expanded relative to other species of *Cryptotis* (TS 1–3). Variability in these characters has long been used to help distinguish taxa within the group as well (e.g., Choate, 1970), and more recently, it has been linked to corresponding variation in the skeleton of the fore arm (Woodman and Timm 1999, 2000). Most notable are the podials and metapodials (TS 4, 28), which exhibit shortening and broadening, and the humerus (TS 13–18), which exhibits a seemingly graded series of modifications that includes elongation and more distal positioning of the teres tubercle, expansion of the medial and lateral epicondyles, and enlargement of the pectoral process (Woodman and Timm 1999, 2000). Overall, the humerus becomes broader and the shaft more curved. The humerus also becomes relatively and absolutely shorter as it is increasingly modified, whereas the animals themselves tend to increase in body size.

How variation in body size and in the fore limb structure among modern members of the *C. mexicana*-group may be reflected in their individual ecologies and behaviors is unknown. The enlargement of forefeet and fore claws, and the modifications of the humerus appear to be obvious adaptations, possibly to enhance actual digging, or for pushing aside surface litter while foraging. Unfortunately, there are no direct ecological studies or even anecdotal evidence of the behavior of live animals that might substantiate this impression. There is a general tendency for members of the more derived *C. goldmani*-group to have higher minimum

and maximum elevational limits to their geographic distributions than less derived members of the *C. mexicana*-group, implying some form of elevation-related ecological differences between species with different grades of fore arm modifications. What factors may influence such responses are unknown. Also not known is how variation in fore arm structures contributes to interspecific interactions within the group. Species with similar grades of fore arm modification (i.e., *C. phillipsii*; *C. mexicana*, *C. nelsoni*, *C. obscura*; *C. goldmani*-group) tend to have allopatric or parapatric distributions with respect to one another, whereas some species with different grades of fore arm modification can be sympatric (Figs. 1, 3). For example, the possible sister species *C. goodwini* and *C. griseoventris* appear to be parapatric in Guatemala, each likely excluding the other. In contrast, the geographic range of *C. goldmani* overlaps parts of the distributions of *C. mexicana*, *C. peregrina*, and *C. phillipsii*. Collection records indicate sympatry of some species in Oaxaca and at least narrow syntopy in a few cases. *Cryptotis goodmani* has been captured in the same trap line with *C. phillipsii* at Campamento Río Molino (Woodman and Timm, 1999). *Cryptotis goldmani* and *C. mexicana* have been taken at least in the general vicinity of each other at Cerro Zempoaltepec (USNM specimens) and at different times at Vista Hermosa (KU specimens). Morphological differences between syntopic *C. goldmani* and *C. mexicana* may provide clues as to the minimum morphological divergence necessary to permit two members of the *C. mexicana*-group to coexist.

My phylogenetic analysis indicates that *Cryptotis magna* has a close relationship with the base of *C. mexicana*-group (Fig. 2). Because it shares a number of apomorphic states with this group, particularly in regard to modification of the fore limb (TS 1–4, 12–14, 16–18, 26), it is tempting to suggest that *C. magna* merits membership within the *C. mexicana*-group as its earliest branch. In possible support of this arrangement, *C. magna* shares the derived state of the posterior border of the zygomatic plate (TS 5), and a long zygomatic plate, with four species in the group (*C. mexicana*, *C. obscura*, *C. nelsoni*, *C. phillipsii*). However, some of the other characteristics that *C. magna* shares with the *C. mexicana*-group also are present among members of the *C. thomasi*-group from the Andes of South America (e.g., Woodman 1996, 2002). Additional

southern Central American and South American species will need to be sampled and incorporated into the phylogenetic data set in order to accurately determine the status of *C. magna*—whether it represents the sister taxon to both the *C. mexicana*-group and the *C. thomasi*-group; is imbedded within one of those groups; or has some other, as yet undefined, relationship to these and other species in the genus. At this time, it seems least problematic to consider *C. magna* separate from the *C. mexicana*-group.

Among the branching patterns described by the phylogeny of the *C. mexicana*-group, several branches show moderate to strong support, whereas others are weakly supported (Fig. 2). One way to interpret this tree is to assume that, regardless of support for individual branches, there is an underlying pattern of sequential branching that can be revealed with the analysis of additional characters. An alternative explanation is that the strongly supported branches represent well-defined ancestral populations, whereas poorly supported branches are actually polytomies representing simultaneous, or near-simultaneous, divergence of a number of lineages. This pattern could result from vicariance if, for example, a large, continuous ancestral range at lower elevations were fragmented into a number of isolated populations restricted to higher elevations as a result of climatic change and associated sea level rise. This scenario is particularly plausible for the *C. mexicana*-group, which is comprised of high-elevation species restricted to moister vegetational associations in a topographically and climatically diverse region. If we assume that the weak branches are collapsible into a series of polytomies, evolution within the *C. mexicana*-group can be interpreted to reveal three primary vicariance events resulting in: (1) divergence of the ancestors of *C. phillipsii* and the remaining eight species of the *C. mexicana*-group; (2) differentiation of lineages leading to *C. mexicana*, *C. obscura*, *C. nelsoni*, and the *C. goldmani*-group; (3) and differentiation among the species in the *C. goldmani*-group. The groups of species that arose as a result of the three hypothesized vicariance events correspond to those representative of different grades of fore limb evolution, outlined above.

Species whose lineages are hypothesized to have differentiated within a single vicariance event tend to have distributions that are allopatric (e.g., *C. mexicana*, *C. nelsoni*, and *C. obscura*) or parapatric (e.g., *C. goldmani* and *C. peregrina*; *C. goodwini* and *C.*

griseoventris) with respect to one another (Fig. 1). In the case of those with allopatric ranges, subsequent range expansion may not have been sufficient for the species to come back into contact with one another. For species with parapatric distributions, it seems likely that these taxa are sufficiently similar in habits and habitat requirements that they exclude one another (see below). In contrast, some species whose lineages date to different vicariance events have geographic ranges that are at least partly sympatric or syntopic (e.g., *C. goldmani* and *C. mexicana*; *C. goldmani* and *C. phillipsii*).

Timing of events leading to the diversification of the *C. mexicana*-group and the evolution of fore limb modifications among these shrews are difficult to ascertain. There is only a scarce Quaternary fossil record of the *C. mexicana*-group, and no paleontological documentation of ancestral species. However, study of fossils from the late Pleistocene of Nuevo León (Choate 1970; Findley 1953) and Honduras (N. Woodman and D. A. Croft, unpublished data) indicate that *C. obscura* and *C. goodwini* both were extant by the late Glacial. Because the latter species is one of the most derived species in the group (particularly in the structure of the fore arm), its presence in the late Pleistocene suggests that the major evolutionary events marking the morphological diversity in this group had occurred by this time, and most, if not all, modern lineages had differentiated. This is not surprising, and it is very likely that morphological differentiation occurred much further back in time. Molecular clock studies of Amazonian small mammals suggest differentiation of species and even of some morphologically indistinguishable modern populations in the early Quaternary or earlier (Patton *et al.*, 2000). Late Quaternary fossils do communicate some information regarding what did *not* drive fore limb evolution. Modern *C. goodwini* average ca. 12% larger in body size than the late Pleistocene population from Honduras (N. Woodman and D. A. Croft, unpublished data), yet remains, including humeri, from the two time samples are otherwise indistinguishable in form. This fact indicates that the major evolutionary modifications of the fore arm (and, presumably, its function) in the *Cryptotis mexicana*-group probably were unrelated to changes in body size.

The lack of a well-documented fossil record also inhibits our ability to trace the historical biogeography of the *C. mexicana*-group in any detail. Late

Pleistocene fossils of *C. obscura* from Nuevo León (Choate, 1970; Findley, 1953) indicate that the species already occurred near the northern extent of the modern distribution of the *C. mexicana*-group. Similarly, fossils of *C. goodwini* from Honduras provide evidence of that species's presence near the southernmost extent of the modern distribution of the *C. mexicana*-group in the late Pleistocene. These two records are biogeographically significant if only because they indicate that the *C. mexicana*-group already occupied this broad portion of Mexico and northern Central America and that members of the *C. mexicana*-group had moved across the modern ecological barrier presented by the lowlands of the Isthmus of Tehuantepec before that time.

Summary

Phylogenetic analysis supports monophyly of both the *Cryptotis mexicana*-group, consisting of nine species of small-eared shrews, and the *Cryptotis goldmani*-group, comprised of a subset of five species imbedded within the *C. mexicana*-group. *Cryptotis magna* is more closely related to the *C. mexicana*-group than it is to either *Cryptotis parva* or *Cryptotis nigrescens*, however a definitive relationship with the *C. mexicana*-group awaits further analyses that include a larger sampling of species. Branch supports within the phylogeny suggest that three major divergence events contributed to modern species diversity within the *C. mexicana*-group. Modern distributional patterns in combination with the phylogeny suggest that the divergence events are consistent with near simultaneous vicariance of several lineages. Modern patterns of distribution of some species, together with late Pleistocene fossils of *Cryptotis goodwini* and *Cryptotis obscura*, suggest that the major morphological modifications of the fore limb in the *C. mexicana*-group took place before the late Pleistocene and that members of the group already occupied much of the group's current distributions both north and south of the Isthmus of Tehuantepec by that time.

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Appendix

Characters Used in Phylogenetic Analysis

1. fore claws: short (0); elongate (1); greatly elongate (2). [weight = 3]
2. fore claws: narrow (0); broadened (1); more broadened, base of the claw as broad as the digit and covering it entirely (2); greatly broadened (3). [weight = 3]
3. forefeet: small (0); enlarged, broadened (1); more enlarged, broadened (2); greatly enlarged and broadened (3). [weight = 3]
4. metacarpals: long, narrow (0); shortened, broadened (1); greatly shortened and broadened (2). [weight = 3]
5. posterior border of zygomatic plate: anterior to middle of maxillary process (0); posterior to middle of maxillary process (1); even with or posterior to posterior margin of maxillary process (2). [weight = 3]
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). [weight = 3]
7. articular condyle: low and broad (0); high and narrow (1). [weight = 2]
8. lower sigmoid notch: very shallow (0); shallow (1); moderately deep (2); deep (3). [weight = 2]
9. shape of unicuspid (U1– U 3): cone-shaped, posteroventral border straight-edged or convex (0); narrow, posteroventral border concave (1); very narrow, posteroventral border very concave (2). [weight = 2]
10. protoconal basin of M1 (Choate, 1970): subequal in size to hypoconal basin (0); much reduced relative to hypoconal basin (1). [weight = 1]
11. metacone of M3: typically present (0); reduced (1); absent (2). [weight = 1]
12. shape of p3: short and high (0); long and low (1). [weight = 2]
13. length and breadth of humerus shaft: long and narrow (0); shortened and thickened (1); very short and very thick (2). [weight = 2]
14. head of humerus: rounded (0); dorso-ventrally elongate (1). [weight = 2]
15. pectoral process of humerus: low (0); high (1). [weight = 2]
16. teres tubercle of humerus: short (0); elongate (1); greatly elongate (2). [weight = 2]
17. medial epicondyle of humerus: short (0); elongate (1); greatly elongate and typically hooked (2). [weight = 2]
18. teres tubercle of humerus: located along distal shaft [mean MT/HL x 100 > 44%] (0); near central shaft [mean MT/HL x 100 = 39–44%] (1); even more centrally located [mean MT/HL x 100 = 31–39%] (2); centrally located [mean MT/HL x 100 < 31%] (3). [weight = 2]
19. foramen of sinus canal: absent in 100% of individuals (0); typically absent (present in fewer than 25% of individuals) (1); typically present (>50% of individuals), usually tiny (2); typically present (>80% of individuals), usually large and obvious (3). [weight = 1]
20. dorsal foramina: two in < 75% of specimens (0); two in > 75% of specimens (1). [weight = 1]
21. foramen dorsal to articular facet: present in < 75% of specimens (0); present in > 75% of specimens (1). [weight = 1]
22. entoconid of m3: present in > 90% of individuals, typically well-developed (0); present in 45–75% of individuals, may be well developed or reduced (1); present in 10–35% of individuals, typically reduced (2); absent in > 90% of individuals (3). [weight = 1]
23. body size: small, mean head-and-body length < 64 mm (0); smaller medium-sized, 64–74 (1); larger medium-sized, 75–82 mm (2); large, > 83 mm (3). [weight = 0]
24. relative tail length (% of head-and-body length): short, averaging <36% (0); transitional, averaging 37–43% (1); medium length, 44–51% (2); long, >52% (3). [weight = 1]
25. upper unicuspid tooththrow: crowded, three unicuspid visible in lateral view (0); uncrowded, four unicuspid visible in lateral view (1). [weight = 1]
26. dorsal guard hairs: short, <4 mm (0); of intermediate length, 4–5 mm (1); long, >5mm (2). [weight = 1]
27. ectoloph of M1: anterior element reduced relative to posterior element (0); anterior and posterior elements equal in size (1). [weight = 2]
28. bones of hind paws: metatarsals and proximal phalanges long narrow (0); metatarsals and proximal phalanges broad (1); metatarsals and

- proximal phalanges short and very broad (2).
[weight = 2]
29. posterior border of P⁴, M¹, and M²: slight to no emargination (0); noticeable emargination (1); strong emargination (2). [weight = 1]
30. bulbous dentition: dentition not bulbous (0); dentition bulbous (1). [weight = 1]
31. body of calcaneum: narrow (0); broad (1).
[weight = 2]
32. trochlear process of calcaneum: small (0); large (1). [weight = 2]
33. height of coronoid process: high (HCP/CBL x 100 > 77%) (0); of moderate height (67–77%) (1); low (< 67%) (3). [unpolarized, wt = 1]
34. hypocone of M³: typically reduced (0); absent (1). [weight = 1]

Table 1. Character matrix for phylogenetic analysis of the *Cryptotis mexicana*-group. Transition series are defined in the Appendix.

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	30	31	32	33	34	
<i>parva</i>	0	0	0	0	0	0	0	3	0	1	2	0	0	0	0	0	0	0	2	0	0	3	0	0	0	0	0	0	0	2	0	0	0	0	1
<i>nigrescens</i>	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	2	1	1	1	0	1	1	0	0	0	0	1	1	0
<i>magna</i>	1	2	2	1	2	0	0	2	0	0	2	1	1	1	0	0	1	1	1	1	1	0	3	3	0	2	0	?	0	1	1	1	0	0	
<i>phillipsii</i>	1	2	2	1	2	1	1	3	1	0	2	1	1	1	0	0	1	1	1	0	1	0	1	2	0	2	0	1	0	0	0	1	1	1	
<i>mexicana</i>	1	2	2	1	2	1	1	3	1	0	0	1	1	1	0	1	2	2	1	0	0	1	1	0	2	0	1	0	0	0	1	1	0	1	0
<i>nelsoni</i>	1	2	2	?	2	1	1	3	1	0	0	1	?	?	?	?	?	?	0	0	0	0	2	1	0	2	0	?	1	0	?	?	1	1	
<i>obscura</i>	1	2	2	?	2	1	1	3	0	0	0	1	1	1	0	1	2	2	1	0	0	1	1	0	2	0	?	0	0	?	?	?	1	0	
<i>alticola</i>	2	3	3	2	1	1	1	3	0	1	2	1	2	1	1	2	2	2	2	0	0	1	2	0	1	2	0	2	0	2	0	1	1	1	1
<i>goldmani</i>	2	3	3	2	1	1	1	3	1	1	2	1	2	1	1	2	2	3	3	0	0	1	2	1	1	2	0	2	1	0	1	1	1	1	1
<i>goodwini</i>	2	3	3	?	1	1	1	3	1	1	2	1	2	1	1	2	2	2	0	1	1	2	3	0	1	2	0	?	1	0	?	?	?	?	1
<i>griseoventris</i>	2	3	3	?	1	1	1	3	1	1	2	1	?	?	?	?	?	?	0	1	1	3	2	1	1	2	0	?	0	0	?	?	?	?	1
<i>peregrina</i>	2	3	3	?	1	1	1	3	1	1	2	1	2	1	0	2	2	3	3	1	0	1	1	1	1	2	0	?	1	0	?	?	?	?	1