FIELDIANA

Geology
NEW SERIES, NO. 51

Fossil Shrews from Honduras and Their Significance for Late Glacial Evolution in Body Size (Mammalia: Soricidae: *Cryptotis*)

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PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

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Neal Woodman   Darin A. Croft

Abstract

Our study of mammalian remains excavated in the 1940s from McGrew Cave, north of Copán, Honduras, yielded an assemblage of 29 taxa that probably accumulated predominantly as the result of predation by owls. Among the taxa present are three species of small-eared shrews, genus *Cryptotis*. One species, *Cryptotis merriami*, is relatively rare among the fossil remains. The other two shrews, *Cryptotis goodwini* and *Cryptotis orophila*, are abundant and exhibit morphometrical variation distinguishing them from modern populations. Fossils of *C. goodwini* are distinctly and consistently smaller than modern members of the species. To quantify the size differences, we derived common measures of body size for fossil *C. goodwini* using regression models based on modern samples of shrews in the *Cryptotis mexicana*-group. Estimated mean length of head and body for the fossil sample is 72–79 mm, and estimated mean mass is 7.6–9.6 g. These numbers indicate that the fossil sample averaged 6–14% smaller in head and body length and 39–52% less in mass than the modern sample and that increases of 6–17% in head and body length and 65–108% in mass occurred to achieve the mean body size of the modern sample. Conservative estimates of fresh (wet) food intake based on mass indicate that such a size increase would require a 37–58% increase in daily food consumption. In contrast to *C. goodwini*, fossil *C. orophila* from the cave is not different in mean body size from modern samples. The fossil sample does, however, show slightly greater variation in size than is currently present throughout the modern geographical distribution of the taxon. Moreover, variation in some other dental and mandibular characters is more constrained, exhibiting a more direct relationship to overall size. Our study of these species indicates that North American shrews have not all been static in size through time, as suggested by some previous work with fossil soricids.

Lack of stratigraphic control within the site and our failure to obtain reliable radiometric dates on remains restrict our opportunities to place the site in a firm temporal context. However, the morphometrical differences we document for fossil *C. orophila* and *C. goodwini* show them to be distinct from modern populations of these shrews. Some other species of fossil mammals from McGrew Cave exhibit distinct size changes of the magnitudes experienced by many northern North American and some Mexican mammals during the transition from late glacial to Holocene environmental conditions, and it is likely that at least some of the remains from the cave are late Pleistocene in age. One curious factor is that, whereas most mainland mammals that exhibit large-scale size shifts during the late glacial/postglacial transition experienced dwarfing, *C. goodwini* increased in size. The lack of clinal variation in modern *C. goodwini* supports the hypothesis that size evolution can result from local selection rather than from cline translocation. Models of size change in mammals indicate that increased size, such as that observed for *C. goodwini*, are a likely consequence of increased availability of resources and, thereby, a relaxation of selection during critical times of the year.

Resumen

Estudiamos restos de mamíferos excavados en los años 1940s de la Cueva de McGrew, al norte de Copán, Honduras. La colección de 29 taxones probablemente fue acumulada probablemente como resultado de la depredación por lechuzas. Entre los taxones colectados, se encontraron tres especies de musarañas de orejas pequeñas del género *Cryptotis*. Una especie, *Cryptotis merriami*, fue relativamente escasa; las otras dos especies de musarañas, *Cryptotis goodwini* y *Cryptotis orophila* fueron abundantes y mostraron variación morfométrica, diferenciándose de poblaciones actuales. Los fósiles de *C. goodwini* son distintivamente más pequeños que individuos actuales. Para cuantificar las diferencias en tamaño, se tomaron medidas convencionales del tamaño de cuerpo para fósil *C. goodwini* por medio de modelos de regresión, basándose en muestras actuales del grupo de especies de *C. mexicana*. El promedio estimado de la longitud de la cabeza y cuerpo para la muestra fósil fue de 72–79 mm, y el promedio estimado de peso fue de 7.6–9.6 g. Estos valores indican que la muestra fósil es más corto, por un promedio de 6–14% y que pesaba 39–52% menos que individuos actuales de la especie. Un aumento de 6–17% en largo de cabeza y cuerpo y 65–108% en peso se requieren para alcanzar el tamaño de la muestra de individuos actuales. Estimaciones conservadoras del consumo de alimentos frescos (húmidos) en base a su peso indican que el incremento en tamaño exige 37–58% más consumo de alimento diario. En contraste a *C. goodwini*, fósiles de *C. orophila* no fueron diferentes en tamaño al de la muestra de individuos actuales. Sin embargo, la muestra fósil exhibe un poco mas de variación en tamaño, a lo largo de su distribución geográfica. Además, las variaciones de algunos caracteres dentales y mandibulares son más constreñidos, y muestran una relación directa con respecto al tamaño del cuerpo. Este estudio sugiere que las musarañas norteamericanas no han estado estables por largos periodos de tiempo, como se indicaba en algunos estudios previos.

La falta de información de la estratigrafía en el sitio, y la inhabilidad de obtener fechas radiométricas confiables por los restos faunísticos, limitan la oportunidad a ubicar el sitio en un contexto temporal bien definido. Sin embargo, las diferencias morfométricas que documentamos para los fósiles de *C. orophila* y *C. goodwini* indican que fueron diferentes de poblaciones modernas. Otras especies de mamíferos fósiles de la Cueva de McGrew muestran cambios de tamaño de la magnitud de los cambios documentados por algunos mamíferos norteamericanos y mexicanos, durante la transición de ambientes del glacial tardío hasta ambientes del Holoceno. Por este razón, es probable que por lo menos algunos restos de la caverna pertenecen al Pleistoceno tardío. Un hecho curioso es, que aunque la mayoría de los mamíferos terrestres que cambiaron en tamaño durante las transición glacial tardía/post-glacial mostraron una disminución de tamaño, *C. goodwini* aumentó su tamaño. La falta de variación clinal en *C. goodwini* actual apoya la hipótesis que la evolución de tamaño puede resultar de selección local, en vez de una transubicación clinal. Modelos de cambio en tamaño de mamíferos indica que el aumento de tamaño, como se observa en *C. goodwini*, probablemente es una consecuencia de un aumento en la disponibilidad de recursos y, por este medio, una disminución de selección natural durante épocas críticas del año.

Introduction

From November 1941 through April 1942, Paul McGrew, Field Museum of Natural History, Chicago (now the Field Museum), and Albert A. Potter, Nebraska State Teachers College, Chadron, prospected for fossil mammals in Honduras with the objective of collecting specimens that would shed light on the timing of the emergence of the Panamanian land bridge (McGrew, 1942a). This expedition was McGrew's second fossil-collecting trip to Honduras (Webb & Perrigo, 1984), and his team succeeded in excavating remains of late Miocene mammals from the Gracias Formation in the Department of Gracias and late Pleistocene large mammals from a bog near Yeroconte in the Department of Copán (McGrew, 1942a,b, 1944; Webb & Perrigo, 1984). In addition to their reported collections, McGrew and Potter bulk-excavated sediments from an unnamed cave approximately 6–8 km north of Copán (14°50′N, 89°09′W), Copán Department (Fig. 1). Fossils re-
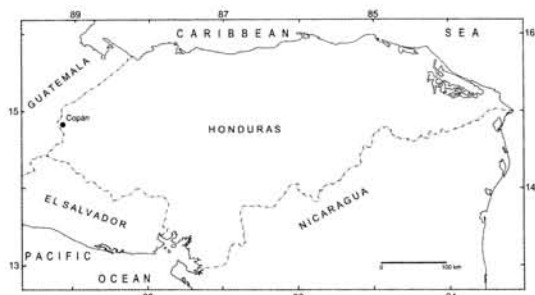
FIG. 1. Location of Copán in western Honduras, near the Guatemalan border.

covered from the cave remained unstudied until 1994, when one of us (Croft, 1998) began working with the material as part of a master's degree project at the University of Chicago.

The cave near Copán, which we refer to herein as McGrew Cave, represents the first site in Honduras that includes abundant, well-preserved remains of Quaternary small mammals (i.e., marsupials, shrews, bats, rodents, lagomorphs). Among the fossils recovered from the cave, we identified three species of small-eared shrews of the New World genus *Cryptotis*. Recent small-eared shrews occur from southernmost Canada through the eastern half of the United States, Mexico, and Central America to the Andean highlands of northwestern South America. *Cryptotis* shares much of its northern range with other soricid genera, but south of Honduras it is the only shrew present. Only one species, *Cryptotis parva*, inhabits the eastern United States and Canada, and it is known from at least 59 Quaternary fossil sites in North America (Faunmap Working Group, 1994; Harris, 1998). The genus reaches its greatest modern diversity in the tropics of Mexico and Central America, where 19 species currently are recognized (Hutterer, 1993; Woodman & Timm, 1993, 1999, 2000). Only three species of *Cryptotis* previously have been reported as Pleistocene fossils from this region, all from Mexico: *Cryptotis mayensis* from Loltún and Actun Spukil caves, Yucatán (Hatt, 1953; Alvarez, 1982; Woodman, 1995); *Cryptotis obscura* from San Josecito Cave, Nuevo León (Findley, 1953; Choate, 1970; Arroyo-Cabrales & Johnson, 1995); and *C. parva* from Cueva de Abra, Tamaulipas (Dalquest & Roth, 1970), and Jiménez Cave, Chihuahua (Messing, 1986).

In this paper, we describe the fossil *Cryptotis* from McGrew Cave, characterize the morphological and morphometrical differences between fos-

sil and modern populations of their respective species, and explain the potential significance of the fossil material for understanding Quaternary size evolution in mammals.

Materials and Methods

Remains of fossil shrews were hand-picked from the original matrix and identified by comparison with modern specimens from Mexico and northern Central America. For this study, we used only mandibles and humeri because they were the most abundant and most complete skeletal elements recovered that are readily identifiable in modern small-eared shrews. We identified fossil material using known suites of characters (e.g., Repenning, 1967; Woodman & Timm, 1992, 1993, 1999, 2000; Carraway, 1995) and direct comparisons with modern specimens of shrews.

Modern small-eared shrews have been partitioned among as many as five informal groupings. The *C. mexicana*-group (Choate, 1970; redefined by Woodman & Timm, 1999, 2000) includes 10 species (*C. alticola, C. goldmani, C. goodwini, C. griseoventris, C. magna, C. mexicana, C. nelsoni, C. obscura, C. peregrina, C. phillipsii*). The *C. nigrescens*-group (Choate, 1970; Woodman & Timm, 1993, 1999; Woodman 2003) includes seven species: *C. brachyonyx, C. colombiana, C. hondurensis, C. mayensis, C. mera, C. merriami, C. nigrescens*. The *C. parva*-group (Choate, 1970; Woodman & Timm, 1999) includes those taxa considered subspecies of *C. parva* by Choate (1970): *C. orophila, C. pueblensis, C. tropicalis, C. parva berlandieri, C. p. floridana, C. p. parva, C. p. soricina*. In addition, most South American species are members of the *C. thomasi*-group (e.g., Choate, 1970; Woodman, 2003), and a number of southern Central American species have been assigned to a group that Choate (1970) termed "relict" species. In the systematic accounts for each species, modern geographic and habitat distributions (from Woodman & Timm, 1992, 1993, 1999, 2000) are provided as context for understanding the environmental conditions under which the fossils may have accumulated.

Taxonomy, phylogenetic systematics, and character polarities follow Woodman and Timm (1992, 1993, 1999, 2000). Terminology of dentition and dental characteristics follows Choate (1970). Anatomical terminology of the mandible (Fig. 2) and humerus (Fig. 3) follows Woodman
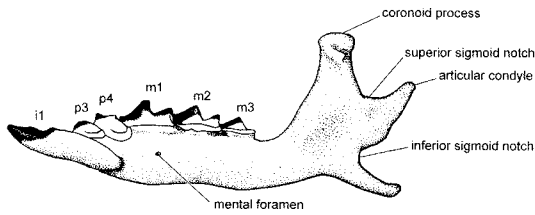
FIG. 2. Lateral aspect of left mandible, illustrating dental and anatomical features. Abbreviations: i1 = first lower incisor; p3 = third lower premolar; p4 = fourth lower premolar; m1 = first lower molar; m2 = second lower molar; m3 = third lower molar.

and Timm (1993, 1999) and Reed (1951), respectively. The nine measurements used in our analyses (Fig. 4; Table 1) follow Woodman (1995) and Woodman and Timm (1993, 1999). All linear measurements are in millimeters (mm), weights in grams (g). Univariate statistics include mean ± standard deviation and observed range. Mensural characters (and corresponding abbreviations) are as follows: length of head and body (HB); body weight (WT); length of mandible (ML), measured from the lower sigmoid notch to the posterior edge of the mental foramen; height of coronoid process (HCP), from base to superior tip; height of coronoid valley (HCV), from base of coronoid process to upper sigmoid notch; height of articular condyle (HAC), from base of coronoid process to superior tip of articular condyle; superior tip of articular condyle to posterior edge of m3 (AC3); occlusal length of toothrow (TRD), from anterior edge of p3 to posterior edge of m3; length of molar row (M13), from anterior edge of m1 to posterior edge of m3; length of m1 (M1L); breadth of articular condyle (BAC), from superior tip to medio-inferior tip. These variables were measured to the nearest 0.1 mm using an ocular micrometer in a binocular microscope. We used only right mandibles for fossil *C. goodwini* and *C. merriami* and only left mandibles of fossil *C. orophila* because these provided the largest independent sample sizes. Measured fossil specimens used in statistical analyses are given in **bold type** in the list of referred specimens accompanying each species account. Minimum number of individuals (MNI) represented by the recovered remains was determined by the largest number of any single element from one side of the body.

In our multivariate statistical analyses, we compared the fossil specimens with modern members of their respective species as well as with neighboring sister taxa to aid in determining whether any temporal variation between fossil and modern
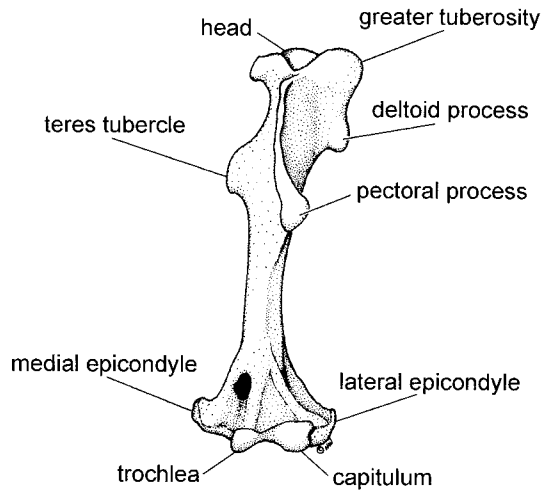
FIG. 3. Anterior aspect of left humerus, illustrating anatomical features.

populations might correspond to modern geographic variation. Sample sizes of modern comparative specimens included 27 *C. griseoventris*, 29 *C. goodwini*, 3 *C. hondurensis*, 32 *C. merriami*, 29 *C. orophila*, and 17 *C. tropicalis* (see Appendix). We are aware that important additional specimens of *C. goodwini*, *C. merriami*, and *C. orophila* from Guatemala and Honduras are now cataloged into the Carnegie Museum of Natural History, Pittsburgh, but these specimens were still under study by their collectors and were not made available to us. Orthogonal principal components were calculated from matrices of up to eight log-transformed mandibular variables (ML, HCP, HCV, HAC, AC3, M13, M1L, BAC) to determine the overall similarity of identified fossils to modern taxa. Our choices of mensural characters used in individual multivariate analyses represented compromises between the incompleteness of many fossil specimens and our desire to retain larger sample sizes.
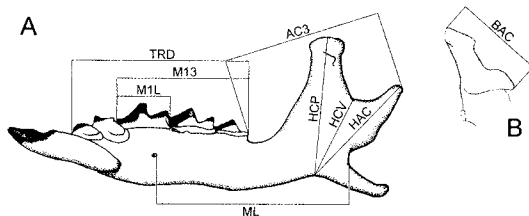
FIG. 4. Lateral aspect of left mandible (**A**) and proximal view of articular process of left mandible (**B**), illustrating measurements used in this study. Abbreviations are explained in *Materials and Methods*.

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We determined the magnitude of size increase between the fossil and modern samples of *C. goodwini* by calculating a percentage change in the mean value using the following expression:

$$[(\text{modern}) \times 100/(\text{fossil})] - 100$$

A positive value represents an increase in size and a negative value a decrease in size through time. This expression was used to calculate magnitude of size change in reverse chronological order (from modern to fossil) by placing the value of the fossil sample in the dividend and that of the modern sample in the divisor. Size change was calculated individually for each of the mandibular variables and for each of our estimates of body size. We also used this expression for calculating magnitudes of size change from data in the literature on Pleistocene mammals.

Valuable discussions regarding estimating body size from fossil materials are presented in Damuth and MacFadden (1990). Martin (1990) was particularly pertinent to our work. We estimated body size of the individuals represented by fossil mandibles of *C. goodwini* by comparing them with up to nine modern species in the *C. mexicana*-group (*C. alticola, C. goldmani, C. goodwini, C. griseoventris, C. mexicana, C. nelsoni, C. obscura, C. peregrina, C. phillipsii*). The *C. mexicana*-group shares a common evolutionary history with *C. goodwini* (Woodman & Timm, 1999), and therefore it should most closely represent the different size morphs of that species. A commonly used measure of size for small mammals is mass, as represented by WT. This measure generally correlates strongly with linear body measures as well as with important life history characteristics (Iskjaer et al., 1989; Brown, 1995). Weights generally are not available, however, for most modern Central American specimens (and many taxa) of *Cryptotis,* so our modern reference samples for this variable were relatively low and incompletely representative of the species group. A reasonable alternative measure of overall body size within the genus is external HB, determined by subtracting length of tail from total length. For the *C. mexicana*-group, the correlation coefficient between WT and HB is 0.725. Sample size for estimating WT was 75 specimens of six species (Table 2); for HB, we used 248 specimens of 10 groups representing nine species (*C. mexicana* provided two independent samples, from Oaxaca and from Veracruz). We derived a procedure based on that in Iskjaer et al. (1989) to calculate regression equations for estimating WT and HB

from mandible size (Martin, 1990). Our method involved carrying out principal component analyses (PCAs) on correlation matrices of six log-transformed mandibular variables (ML, MCP, HCV, HAC, M1L, BAC) measured from species in the *C. mexicana*-group. The first principal components axes (PC 1) from these analyses represent size, as indicated by the nearly equal weightings of all variables on these axes (Table 3). Because the loadings on PC 1 are negative, the largest individuals have the lowest scores. We corrected for the negative weights by reversing the X axis in the subsequent plots. To obtain regression equations for estimating WT for the fossil specimens, we regressed log WT on PC 1 score, and we regressed log HB on PC 1 score to get equations for estimating HB. To obtain estimates of WT and HB for individual specimens, the corresponding regression equations were solved for individual PC 1 scores. Resulting individual estimates subsequently were used to calculate estimated mean values of the size measures for individual populations. The potential predictive values of the regressions were assessed by visual inspection of the plots relative to the regression lines.

Food requirements for modern and fossil *C. goodwini* were estimated using the equations for grams of dry matter intake per day (g DMI/d) and grams of fresh matter intake per day (g FMI/d) determined for Insectivora by Nagy (2001). The data used to calculate these equations did not include any soricids, however, and they tend to underestimate food consumption for shrews. Based on data compiled by Whitaker (1974) for individual least shrews (*C. parva*), which reportedly eat 77–110% of their body weight per day, the equation for g FMI/d underestimated food intake by 17–44%. It must be emphasized that food consumption was estimated for fossil *C. goodwini* from *estimates* of mass—hence it has the overall stability of a house of cards.

In our test for geographic variation among modern *C. orophila,* we used a single numeral, termed "locality," to represent the locality of collection for each of the modern reference specimens. This term is the PC 1 score from a PCA on pairs of coordinates (latitude and longitude) representing each collection locality (Woodman, 2000).

Fossil specimens are cataloged in the Geology Collection, Field Museum, Chicago (FMNH-PM). Recent comparative specimens from the following institutions were used in this study: American Museum of Natural History, New York (AMNH);

TABLE 1. Mandibular measurements of modern and fossil *Cryptotis*. Statistics presented are mean ± standard deviation of the mean and observed extremes.

	C. orophila (modern) (n = 37)[1]	C. orophila (fossil) (n = 31)[1]	C. tropicalis (modern) (n = 17)[1]	C. hondurensis (modern) (n = 3)	C. merriami (fossil) (n = 1)[1]	C. merriami (modern) (n = 32)	C. griseoventris (modern) (n = 27)	C. goodwini (fossil) (n = 7)[1]	C. goodwini (modern) (n = 31)
ML	5.4 ± 0.2 4.8–5.9	5.4 ± 0.2 4.8–5.8	5.7 ± 0.2 5.3–6.1	5.8, 6.1, 6.3	6.1	6.5 ± 0.23 5.8–7.2	6.2 ± 0.2 5.7–6.6	6.0 ± 0.2 5.7–6.3	6.6 ± 0.2 6.2–7.2
HCP	4.1 ± 0.2 3.7–4.5	4.1 ± 0.2 3.8–4.4	4.3 ± 0.1 4.1–4.7	4.4, 4.8, 4.6	4.5	5.0 ± 0.2 4.5–5.3	4.4 ± 0.1 4.1–4.6	4.6 ± 0.1 4.3–4.7	4.8 ± 0.2 4.6–5.3
HCV	2.4 ± 0.1 2.1–2.8	2.4 ± 0.1 2.2–2.7	2.6 ± 0.2 2.3–2.9	2.7, 2.7, 2.7	2.7	2.9 ± 0.2 2.4–3.3	2.8 ± 0.1 2.5–3.0	2.8 ± 0.1 2.7–3.0	3.0 ± 0.1 2.8–3.4
HAC	3.3 ± 0.2 2.8–3.7	3.2 ± 0.2 2.9–3.5	3.5 ± 0.1 3.3–3.7	3.6, 3.6, 3.4	3.5	3.8 ± 0.2 3.3–4.3	3.9 ± 0.1 3.7–4.1	3.8 ± 0.1 3.6–3.9	4.2 ± 0.2 3.8–4.8
AC3	4.1 ± 0.2 3.7–4.4 (n = 33)	4.0 ± 0.1 3.8–4.2 (n = 16)	4.4 ± 0.1 4.2–4.7	4.3, 4.3, 4.4	—	4.7 ± 0.2 4.3–5.0	5.1 ± 0.2 4.8–5.5	4.8 ± 0.1 4.7–5.0 (n = 5)	5.5 ± 0.2 5.0–5.9
TRD	4.9 ± 0.2 4.6–5.3 (n = 31)	5.0 ± 0.2 4.9–5.3 (n = 5)	5.1 ± 0.2 4.8–5.4 (n = 16)	5.3, 5.5, 5.2	—	5.7 ± 0.2 5.3–5.9	6.1 ± 0.1 5.8–6.3	5.8, 5.9 (n = 2)	6.4 ± 0.2 6.1–6.8
M13	3.7 ± 0.1 3.4–3.9 (n = 33)	3.8 ± 0.2 3.5–4.1 (n = 17)	3.9 ± 0.1 3.7–4.1	4.1, 4.2, 3.9	—	4.4 ± 0.2 4.1–4.7	4.3 ± 0.1 4.1–4.6	4.4 ± 0.1 4.4–4.6 (n = 5)	4.7 ± 0.1 4.4–4.9
M1L	1.5 ± 0.1 1.3–1.6	1.6 ± 0.1 1.4–1.8 (n = 28)	1.5 ± 0.1 1.4–1.7	1.7, 1.7, 1.6	1.8	1.8 ± 0.1 1.7–2.0	1.8 ± 0.1 1.6–1.9	1.9 ± 0.1 1.8–1.9	1.9 ± 0.1 1.8–2.1

TABLE 1. Continued

	C. orophila (modern) (n = 37)[1]	C. orophila (fossil) (n = 31)[1]	C. tropicalis (modern) (n = 17)[1]	C. hondurensis (modern) (n = 3)	C. merriami (fossil) (n = 1)	C. merriami (modern) (n = 32)	C. griseoventris (modern) (n = 27)	C. goodwini (fossil) (n = 7)[1]	C. goodwini (modern) (n = 31)
BAC	2.6 ± 0.1 2.4–2.7	2.6 ± 0.2 2.2–2.8	2.8 ± 0.1 2.5–3.0	2.8, 3.0, 2.7	2.9	3.0 ± 0.1 2.6–3.2	3.0 ± 0.1 2.8–3.1	2.9 ± 0.1 2.8–3.0	3.3 ± 0.2 3.0–3.7
HCP/ML × 100	75.9 ± 3.9 67.3–86.5	76.6 ± 2.5 71.7–81.1	75.7 ± 2.8 70.0–81.0	75.9, 78.7, 73.0	73.8	76.4 ± 2.8 69.4–81.3	70.1 ± 2.0 65.6–73.7	75.8 ± 3.9 68.3–79.0	72.6 ± 2.4 68.7–76.5
AC3/ML × 100	76.4 ± 3.3 70.7–85.4 (n = 33)	75.1 ± 2.0 70.7–79.2 (n = 15)	77.7 ± 3.0 71.7–83.9	77.9, 78.7, 73.0	—	71.7 ± 2.4 67.6–75.0	82.9 ± 2.5 79.7–87.3	81.5 ± 3.8 75.8–84.2 (n = 4)	83.2 ± 3.3 76.1–90.5

[1] Except as noted.

Natural History Museum, London (BM); Escuela Nacional de Ciencias Biológicas, Mexico City (ENCB); Field Museum, Chicago (FMNH); University of Kansas Natural History Museum, Lawrence (KU); Louisiana State University, Baton Rouge (LSU); Museum of Comparative Zoology, Cambridge (MCZ); Sternberg Museum of Natural History, Hays (MHP); Museum National d'Histoire Naturelle, Paris (MNHM); Museum of Vertebrate Zoology, Berkeley (MVZ); Naturhistorisches Museum, Vienna (NMW); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Universidad Nacional Autónoma de Honduras, Tegucigalpa (UNAH); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (UNAM); National Museum of Natural History, Washington (USNM); Zoologisches Forschungsinstitut und Museum Alexander Köenig, Bonn (ZMFK).

Study Site

The primary result of the McGrew–Potter expedition to Honduras was the recovery of late Miocene mammals from the Gracias Formation and Pleistocene megafauna at Yeroconte (McGrew, 1942a,b). Both sites are described in detail in McGrew's field notes, which are preserved in the Department of Geology, Field Museum. The McGrew Cave deposit and its associated fossil remains, including the shrews that are the subject of this paper, are not mentioned in his field notes. The only written record regarding this material consists of a few lines inscribed by McGrew on a 5 × 7-inch index card that was included with the remains in the Geology Collection of the Field Museum:

> These specimens are part of a great quantity taken from a cave roughly five miles north of Copan, Honduras. The top two feet of debris in the third room of the cave was made up almost entirely of bone. There is a considerable quantity of this material waiting shipment with our other things from Guatemala City. McGrew.

Because of the dangers of overwater transportation associated with World War II, fossils excavated during McGrew and Potter's Honduran expedition were moved to Guatemala and stored there temporarily (McGrew, 1942a,b). Whether the specimens now in the Field Museum represent

TABLE 2. Comparative body size measures for species in the *C. mexicana*-group. Species are listed in ascending order by mean length of head and body. Statistics presented are mean ± standard deviation of the mean, observed extremes, and sample size in parentheses.

	HB	ML	WT
C. obscura	66 ± 4	5.9 ± 0.2	6.9 ± 1.1
	56–75	5.3–6.4	5.0–10.0
	(n = 53)	(n = 53)	(n = 21)
C. phillipsii	67 ± 5	6.4 ± 0.3	8.3 ± 2.0
	59–77	5.8–7.1	6.5–14.0
	(n = 16)	(n = 16)	(n = 14)
C. mexicana (Oaxaca)	69 ± 5	6.0 ± 0.3	7.7 ± 0.9
	62–88	5.4–6.3	6.4–9.5
	(n = 32)	(n = 32)	(n = 21)
C. peregrina	72 ± 3	6.2 ± 0.2	—
	66–77	5.8–6.4	
	(n = 13)	(n = 13)	
C. mexicana (Veracruz)	75 ± 3	6.0 ± 0.3	—
	67–78	5.5–6.5	
	(n = 25)	(n = 25)	
C. goldmani	75 ± 5	6.3 ± 0.3	8.4 ± 1.2
	62–84	5.8–6.8	6.5–10.2
	(n = 23)	(n = 23)	(n = 10)
C. nelsoni	76 ± 2	6.4 ± 0.1	—
	72–79	6.2–6.6	
	(n = 10)	(n = 10)	
C. griseoventris	77 ± 3	6.2 ± 0.2	—
	73–85	5.7–6.6	
	(n = 27)	(n = 27)	
C. alticola	79 ± 5	6.6 ± 0.2	10.0
	69–86	5.9–6.9	10.0–10.0
	(n = 19)	(n = 19)	(n = 2)
C. goodwini	84 ± 5	6.6 ± 0.2	15.8 ± 2.0
	75–94	6.2–7.2	12.0–18.7
	(n = 30)	(n = 31)	(n = 7)
Totals	248	249	75

TABLE 3. Factor loadings for the first axis from two PCAs of six log-transformed mandibular variables measured from species in the *C. mexicana*-group. Scores from the PCAs were used to represent mandibular size in regression analyses for estimating HB and WT of the fossil sample of *C. goodwini* (Figs. 9–14). See Table 1 for definitions of abbreviations.

	Correlations	
Variable	HB PC 1	WT PC 1
HAC	−0.444	−0.452
HCV	−0.428	−0.432
BAC	−0.425	−0.423
ML	−0.406	−0.393
HCP	−0.396	−0.400
M1L	−0.342	−0.340
Eigenvalue	4.4892	4.1919
Proportion of variation	74.8%	69.9%
Number of species or groups (a)	10	6
Number of specimens (n)	248	75

the bulk of the McGrew Cave material or only some portion is unknown. Many of the specimens from this cave remained uncataloged until autumn 1994 (Croft, 1998).

Preserved matrix from McGrew Cave consists mostly of light tan, carbonate rock fragments, and the cave probably was one of a number of solution caverns developed in a limestone cliff where the stream Quebrada Sesesmiles intersects Cerro María, a ridge about 6.4 km north of Copán. According to Gordon (1898), these caverns contained deposits as deep as 4.5 m. Further downstream toward Copán, the cliffs along the stream are of volcanic origin and lack caves.

Elevations around Copán range from <600 m in the main river valley to >1200 m in nearby highlands. Copán is in a region originally dominated in the late Holocene by Subtropical Moist

Forest in the Holdridge Life Zone system (Holdridge, 1947); mean annual rainfall is from 1000–2000 mm, and mean annual temperature is 18–24°C (Wilson & Meyer, 1985).

Vertebrate Fauna

Skeletal elements representing a minimum of 396 individual mammals belonging to 29 identifiable taxa (Table 4), plus uncounted remains of birds, reptiles, and amphibians, were recovered from the stored matrix from McGrew Cave. All the identified mammal remains can be referred to species living in Honduras today, and the list of mammals includes species typical of a variety of modern habitats, including tropical evergreen and semideciduous forest (e.g., *Peromyscus mexicanus*), tropical deciduous forest (e.g., *Liomys salvini*), grasslands (e.g., *Sigmodon hispidus*), marsh (e.g., *Oryzomys couesi*), and cool, moist montane regions (e.g., *Reithrodontomys sumichrasti*). With the exception of a few specimens of bats that may have roosted in the cave, remains from the deposit are overwhelmingly of small, nocturnal and crepuscular terrestrial mammals. Diurnal rodents, such as squirrels and gophers, are mostly absent. Notably scarce are remains of medium- to large-bodied mammals, which are represented by only two large, burned tooth fragments, possibly from *Tayassu*, and a single distal human phalanx that could have resulted from an intrusive burial. Additional information regarding specific members of the fauna was provided by Croft (1998).

Remains of small mammals from McGrew Cave include abundant postcranial elements as well as crania, mandibles, and teeth. Most of these remains are superficially well preserved, with little evidence of gastric dissolution and relatively little fragmentation. Overall, the situation of the cave, the taxa represented, the large numbers and variety of skeletal elements, and the high degree of preservation of the remains are consistent with materials derived from owl pellets and are not what would be expected in an accumulation resulting from carnivore scats, pellets of diurnal raptors, or fluvial sedimentary processes (Dodson & Wexlar, 1979; Korth, 1979; Andrews & Evans, 1983; Hoffman, 1988; Andrews, 1990; Kusmer, 1990). Gordon (1898) noted the presence of an abandoned raptor nest in one of the caves near Copán, indicating that the caves provided favorable nesting sites for birds of prey.

TABLE 4. Mammals recovered from McGrew Cave, Honduras (after Croft, 1998).

Didelphimorphia
  Didelphidae
    Marmosa cf. *M. mexicana*
    Philander opossum

Eulypotyphla
  Soricidae
    Cryptotis orophila
    Cryptotis merriami
    Cryptotis goodwini

Chiroptera
  Molossidae
    Molossus ater

  Mormoopidae
    Pteronotus parnellii

  Phyllostomidae
    Artibeus indet. A (large)
    Artibeus indet. B (small)
    Sturnira indet.

  Vespertilionidae
    Myotis cf. *M. velifer*

Rodentia
  Heteromyidae
    Heteromys desmarestianus
    Liomys salvini

  Muridae
    Baiomys musculus
    Neotoma mexicana
    Nyctomys sumichrasti
    Oligoryzomys fulvescens
    Oligoryzomys couesi
    Oryzomys saturatior
    Oryzomys sp. A (large)
    Ototylomys phyllotis
    Peromyscus aztecus
    Peromyscus levipes
    Peromyscus mexicanus
    Reithrodontomys mexicanus
    Reithrodontomys fulvescens
    Reithrodontomys sumichrasti
    Sigmodon hispidus

Lagomorpha
  Leporidae
    Sylvilagus indet.

Artiodactyla
  Tayassuidae
    cf. *Tayassu*

Primates
  Hominidae
    Homo sapiens

Age of the Deposit

Because of the lack of adequate field documentation and the manner in which the sediments from McGrew Cave originally were excavated and stored, the stratigraphic context of the recovered remains from the cave was lost. This fact has hindered our attempts to understand absolute or even relative ages of individuals and taxa within the fauna. Radiometric dating of fecal pellets from rodents (and possibly chiropterans) recovered from the cave residue yielded a date of 10 ± 40 yr B.P. (TX-9344), indicating that the pellets are modern. Charcoal from the sediments was dated at 2940 ± 110 yr B.P. (TX-9345), hence late Holocene. Samples of bone submitted for accelerator mass-spectrometer (AMS) dating (AA34630) yielded insufficient carbon to obtain a date. Although owls vary in the extent to which they digest bone (Raczyński & Ruprecht, 1974; Dodson & Wexlar, 1979; Andrews, 1990), fossil bone accumulations from North American owls have been radiocarbon-dated successfully (Klippel & Parmalee, 1982; Semken, 1984; Stafford et al., 1999), indicating that the digestive processes of owls do not completely leach carbon from the bones of their prey. The presence of datable late Holocene pellets and charcoal together with bone samples that contain too little carbon for AMS dating suggests both mixing of the deposit and an older age for the vertebrate remains. There are no ceramic fragments or other human artifacts among the sediments. The presence of a single human phalanx could be the result of a subsequent, intrusive burial, but it also suggests that some of the fauna may be Holocene in age.

The mammal fauna includes elements that are suggestive of an older assemblage. A number of mammal species from the deposit differ substantially in size from their respective modern populations. Similar size variation characterizes Pleistocene samples of mammals from temperate North America (Hoojier, 1950; Guilday et al., 1964, 1977, 1978; Lundelius et al., 1983; Semken, 1984; Martin & Barnosky, 1993). Remains of a rice rat (*Oryzomys* sp. A in Table 4) from McGrew Cave represent individuals larger than any species of *Oryzomys* presently living in Honduras (Croft, 1998). These remains may be from a species now extirpated from the country or from an extinct or extirpated size morph of an extant species. Similarly, fossils of the big-eared climbing rat, *Ototylomys phyllotis,* are substantially larger than those of modern individuals from the region

(Croft, 1998). Large *O. phyllotis* also are known from sediments dated at more than 28,400 yr B.P. at Loltún, on the Yucatan Peninsula, Mexico (Alvarez, 1982), and are associated with the extinct ground sloth *Paramylodon harlani* at Actun Spukil, Mexico (Hatt, 1953; McDonald, 2002). In addition, two species of *Cryptotis* described later exhibit patterns of variation distinct from those seen in modern representatives of their respective species. One species, *C. goodwini,* is distinctly smaller than modern samples. The other, *C. orophila,* exhibits a larger overall size range than modern samples from throughout the distribution of the species. The lack of size intergrades between the fossil and modern samples suggests that the fossils could represent exclusively late Pleistocene forms.

A Pleistocene age for part of the McGrew Cave fauna also appears to be supported by the composition of the small mammal fauna, which represents a variety of distinct modern ecological associations. Such a nonanalog fauna is similar to the late glacial faunas described from northern North America that have been interpreted as resulting from the unique ecological habitats then extant (Lundelius et al., 1983; Graham & Lundelius, 1984; Semken, 1988; Faunmap Working Group, 1996; Stafford et al., 1999; Bell et al., 2004). Pollen sequences from Central America lend credence to the possibility of nonanalog mammal faunas in that region as well because they indicate both depression of montane forest zones and the occurrence of plant communities without modern analog during the late Pleistocene (Markgraf, 1989; Bush & Colinvaux, 1990; Bush et al., 1992; Leyden et al., 1993; Islebe & Hooghiemstra, 1997). As noted previously, however, the taphonomy of the cave deposit strongly suggests that it derived from the work of avian predators, most likely owls. A sequence of different species of owls occupying various parts of McGrew Cave (or nesting in the cave at different times) and hunting in different habitats conceivably could result in an ecologically mixed sample of the small mammal fauna.

Without firm radiocarbon dates to support the age and lacking a stratigraphic record to provide relative ages, we must assume that the fauna from McGrew Cave may be a mixed temporal assemblage that could include individuals from both late glacial and postglacial environments. Despite the drawbacks associated with this site, it provides the first fauna available from Central America in which abundant soricids are preserved. The pat-

terns of variation exhibited by these small mammals are sufficiently distinct from modern variation of their respective species to warrant documentation.

Systematic Paleontology

Genus *Cryptotis* Pomel, 1848

DESCRIPTION—Mandibles identified as belonging to *Cryptotis* have conspicuously pigmented teeth, a large internal temporal fossa, a strong lingual emargination of the articular condyle, and a posterolingual basin on p4 (characteristics of Soricinae—Repenning, 1967). The interarticular area of the articular condyle is relatively broad (Blarinini—Repenning, 1967). Characteristics specific to *Cryptotis* include the shape of the articular condyle, which is generally tall and broad with a strong, somewhat squared lingual emargination (see Carraway, 1995: fig. 5) and the broad angle (>90°) formed by the anterior edge of the coronoid process and the superior margin of the horizontal ramus. In addition, mandibles of *Cryptotis* do not have the very deep inferior sigmoid notch present in *Sorex* or the large coronoid spicule characteristic of *Blarina*.

Humeri of species of *Cryptotis* have relatively longer and broader processes than other species of North American soricids, and the teres tubercle is more distally located on the shaft.

Cryptotis goodwini Jackson, 1933

REFERRED SPECIMENS—Right mandibles (9): FMNH-PM 17053, **17068**, 17071, **17075, 17081, 17083**, **17098, 17100**, 57551. Left mandibles (3): FMNH-PM 17065, 17138, 17154. Right humeri (7): FMNH-PM 59380–59385, 59395. Left humeri (9): FMNH-PM 59423–59431.

MODERN DISTRIBUTION—*C. goodwini* inhabits pine-dominated cloud forests above 1100 m from eastern Chiapas, Mexico, to western Honduras.

SYSTEMATIC CONTEXT—*C. goodwini* is the largest species of the *C. mexicana*-group, a cohesive clade of shrews whose members are uniquely characterized within the genus by their derived forelimbs with enlarged paws and claws and modified humeri (Choate, 1970; Woodman & Timm, 1999, 2000).

DESCRIPTION—The mandible of *C. goodwini*
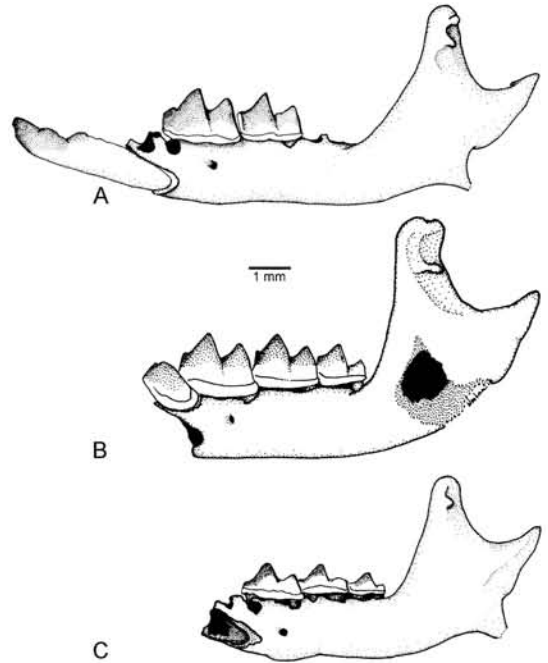
FIG. 5. Lateral (buccal) view of fossil left mandibles of (**A**) *C. goodwini* (FMNH-PM 17138), (**B**) *C. merriami* (FMNH-PM 17147), and (**C**) *C. orophila* (FMNH-PM 17137).

(Fig. 5A) possesses a number of derived and unpolarized characters for the genus (Woodman & Timm, 1999, 2000): low coronoid process, anterior border joining the horizontal ramus at a relatively low angle; posterior border of lower incisor anterior to posterior border of p4; long posterior portion of mandible (articular process to posterior border of m3); tall, wide articular process with a broad lower articular facet; deep lower sigmoid notch; long p3; entoconid usually absent from talonid of m3, although a minute entoconid occasionally is present; dentition not bulbous; very dark tooth pigmentation, with moderate to dark color extending most of the height of the entoconids and into talonid basins of m1 and m2. The humerus (Fig. 6A–B) is shortened, broadened, and curved with a dorsoventrally elongate head and elongated processes; the teres tubercle is more centrally located on the shaft (see Woodman & Timm, 1999: fig. 15, 2000: fig. 4).

COMPARISONS—The mandible of *C. goodwini* differs from those of both the *C. parva*-group (including *C. orophila*) and the *C. nigrescens*-group (including *C. merriami*) in having a broader angle between the anterior edge of the coronoid process and the horizontal ramus, relatively longer posterior mandible (Table 1), posterior edge of i1 an-

FIG. 6. Anterior views of **(A)** fossil (FMNH-PM 59430) and **(B)** modern (UNSM 275681) left humeri of *C. goodwini*; **(C)** fossil left humerus of *C. orophila* (FMNH-PM 59394) and **(D)** fossil right humerus of *C. merriami* (FMNH-PM 59375).

terior to posterior border of p4 and not generally underlying m1, relatively higher and narrower articular process, and longer p3 (Fig. 5). It further differs from the mandible of *C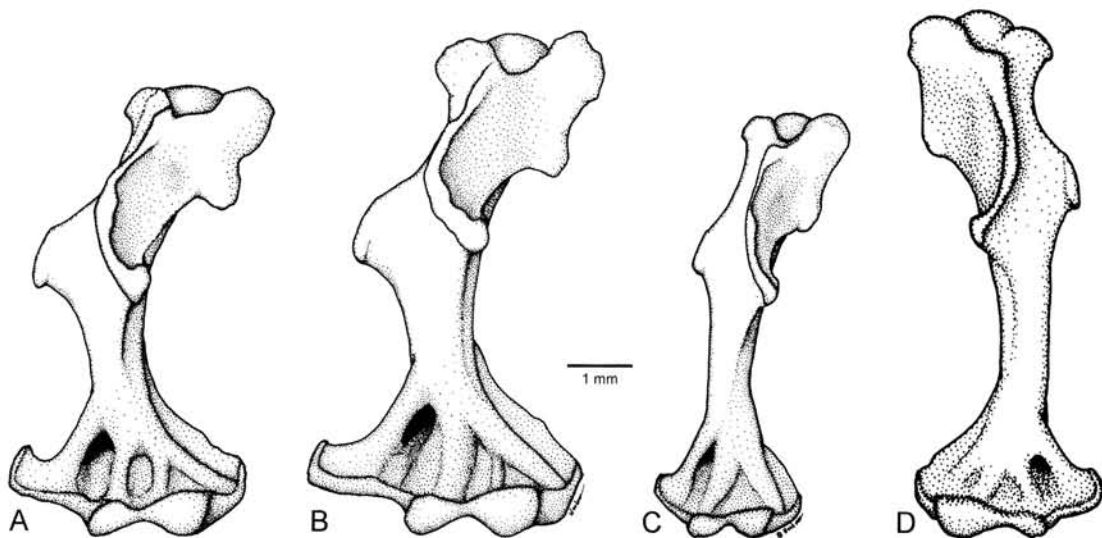. merriami* in lacking bulbous dentition. The humerus of *C. goodwini* is distinctive, being relatively broader with greatly enlarged processes and more centrally located teres tubercle (Fig. 6).

Within the *C. mexicana*-group, the mandible of *C. goodwini* differs from those of *C. mexicana, C. nelsoni, C. obscura,* and *C. phillipsii* by lacking the strongly developed, darkly pigmented entoconid on m3. The relative height of coronoid process averages higher than for *C. alticola* and

C. griseoventris. The humerus of *C. goodwini* exhibits one of the most derived states for the genus, with processes more greatly enlarged than any members of the *C. mexicana*-group except *C. goldmani.* The humerus of *C. goodwini* differs from that of *C. goldmani,* however, by being relatively longer, being less broadened, and having less elongated processes (Woodman & Timm, 1999, 2000).

Both fossil mandibles and humeri differ from those of modern *C. goodwini* in averaging smaller for nearly all mensural variables (Table 1). Relative height of the coronoid process averages slightly higher and relative posterior length of mandible averages slightly lower than for modern samples of *C. goodwini*.

STATISTICAL ANALYSES—To understand the relationships of fossil *C. goodwini* to modern *C. goodwini* and *C. griseoventris,* we carried out a six-variable PCA and plotted the resulting scores along the first three factor axes, which together account for more than 93% of the variation in this model (Table 5). PC 1 represents overall size. PC 2 is a contrast of M1L with BAC and ML. PC 3 is a contrast of HCV and HCP with BAC, M1L, and ML. In the trivariate plot from this analysis, the three samples form three cohesive, if somewhat overlapping, groups (Fig. 7A). To more concisely illustrate relationships along the three axes, we plotted factor scores along pairs of axes. The plot of the first two factor axes (Fig. 7B) shows

TABLE 5. Factor loadings for the first three axes from PCA of six mandibular variables from modern *C. goodwini,* modern *C. griseoventris,* and fossil *C. goodwini* (Fig. 7). See Table 1 for definitions of abbreviations.

Variable	Correlations		
	PC 1	PC 2	PC 3
M1L	−0.321	0.889	−0.308
ML	−0.403	−0.293	−0.508
HCV	−0.419	−0.007	0.613
BAC	−0.421	−0.303	−0.281
HCP	−0.427	0.083	0.436
HAC	−0.447	−0.161	−0.049
Eigenvalue	4.6047	0.6217	0.3571
Proportion of variation	76.7%	10.4%	6.0%
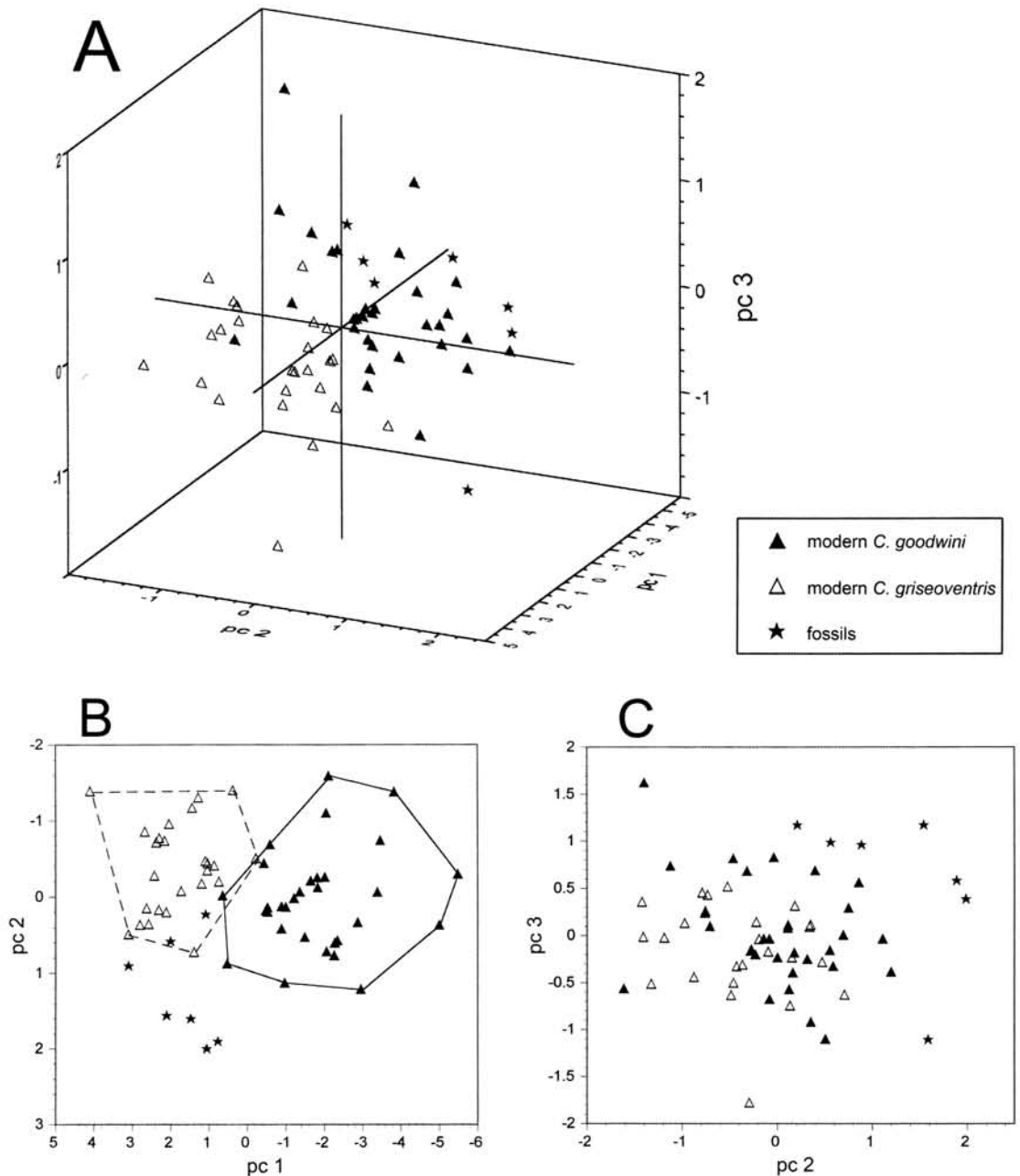
FIG. 7. Plots of scores from PCA of six mandibular variables from modern *C. goodwini,* modern *C. griseoventris,* and fossil *C. goodwini:* **(A)** trivariate plot on first three factor axes; **(B)** bivariate plot on PC 1 and PC 2; **(C)** bivariate plot on PC 2 and PC 3. Axis scales on PC 1 and PC 2 in Figure 7B are reversed to match the trivariate plot. Factor loadings on PC 1 (size) are negative (Table 5), so the most negative scores represent the largest individuals.

the differences in size among the samples. Modern *C. goodwini* and *C. griseoventris* plot as distinct clusters along PC 1. The fossil mandibles overlap completely with modern *C. griseoventris* on this axis, and they are distinct from *C. good-*

wini, emphasizing the fossil mandibles' smaller size. The plot of the second and third factor axes illustrates variation in shape (Fig. 7C). Modern *C. goodwini* and *C. griseoventris* overlap broadly long both PC 2 and PC 3. On each of these axes,
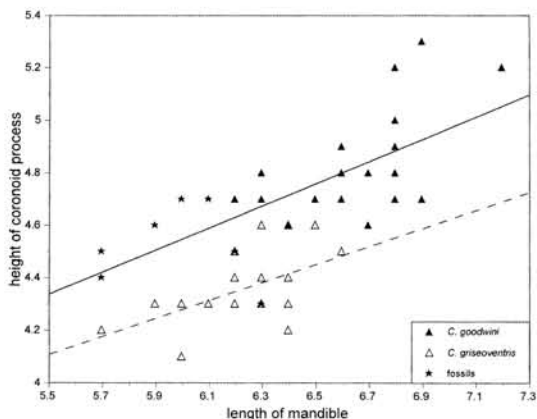
FIG. 8. Plot of HCP on length of mandible for modern *C. goodwini*, modern *C. griseoventris*, and fossil *C. goodwini*. Regressions calculated individually for modern *C. goodwini* (solid line: $HCP = 2.021175 + 0.4212133 ML$; $F = 14.95$, $p = 0.001$, adjusted $R^2 = 31.7\%$) and *C. griseoventris* (dashed line: $HCP = 2.224451 + 0.3427198 ML$; $F = 12.15$, $p = 0.002$, adjusted $R^2 = 30.0\%$) have significantly positive slopes that are approximately parallel (see text). A regression calculated using both modern and fossil *C. goodwini* as a single sample is similar to that calculated for modern *C. goodwini* alone (not shown: $HCP = 2.171703 + 0.3977192 ML$; $F = 31.50$, $p < 0.001$, adjusted $R^2 = 45.2\%$).

FIG. 9. Linear regression of log WT on PC 1 for modern members of the *C. mexicana*-group: log $WT = 0.911603 - 0.03937 PC1$; $F = 74.39$, $p < 0.001$, adjusted $R^2 = 49.8\%$. Factor loadings on PC 1 are negative (Table 3), so the most negative scores represent the largest mandibles. To account for the negative weighting, the PC 1 axis is reversed.

however, modern *C. goodwini* tends to have more positive scores, whereas *C. griseoventris* tends toward more negative scores. Although the fossils overlap both modern species along the two individual axes, they tend to have high positive scores. In the combined plot of PC 2 and PC 3, the fossils separate somewhat from both species but are very close to modern *C. goodwini*. Inspection of the three graphs together provides a good overview of the morphological relationships among the three samples. In general, the fossils tend to separate from modern *C. goodwini* on size but from modern *C. griseoventris* on shape.

To illustrate the size relationships among the three samples more clearly, we plotted HCP against ML. Regressions calculated separately for modern *C. goodwini* ($HCP = 2.02 + 0.421 ML$; adjusted $R^2 = 31.7\%$) and *C. griseoventris* ($HCP = 2.22 + 0.343 ML$; adjusted $R^2 = 30.0\%$) exhibit nearly parallel but offset positive trends of increasing HCP with ML (Fig. 8). A test for equality of slopes (Sokal & Rohlf, 1981) supported the null hypothesis that the two samples represented populations with equal slopes ($F_{[1,54]} = 0.280 \ll F_{\alpha=0.5[1,60]}$). The fossil mandibles are distributed mostly around the extended regression for modern

C. goodwini, and they appear to conform to the trend of this regression. In fact, a regression calculated using both modern and fossil *C. goodwini* as a single sample is similar to that calculated for modern *C. goodwini* alone, and it provides a better overall fit to the data ($HCP = 2.17 + 0.398 ML$; adjusted $R^2 = 45.6\%$). Because the data sets used to calculate these two regressions greatly overlap, however, they lack independence and cannot be compared statistically. The PCA and the regression analysis support the hypothesis based on qualitative morphological characters of the mandible and humerus that the two samples (modern *C. goodwini* and the fossils) represent nonoverlapping size morphs of the same species.

ESTIMATIONS OF BODY SIZE—Linear regressions calculated using all available members of the *C. mexicana*-group resulted in the following equations for estimating body size:

$$\log WT = 0.911603 - 0.03937(PC1)$$
$$[F = 74.39, p < 0.001,$$
$$\text{adjusted } R^2 = 49.8\%];$$

$$\log HB = 1.86277 - 0.012821(PC1)$$
$$[F = 162.04, p < 0.001,$$
$$\text{adjusted } R^2 = 39.5\%]$$

Despite our use of logarithmic transformations to straighten potential allometrical relationships (Sokal & Rohlf, 1981) between the body size variables and the mandibles (PC 1), visual inspection of the plots of these two regressions (Figs. 9, 10)

FIG. 10. Linear regression of log HB on PC 1 for modern members of the *C. mexicana*-group: log HB = $1.86277 - 0.012821$ *PC1*; $F = 162.04$, $p < 0.001$, adjusted $R^2 = 39.5\%$. Factor loadings on PC 1 are negative (Table 5), so the most negative scores represent the largest mandibles. To account for the negative weighting, the PC 1 axis is reversed.

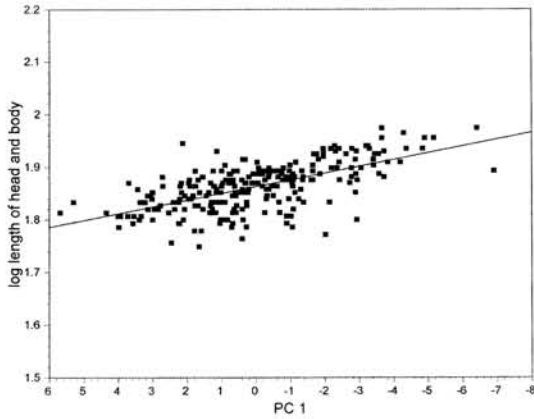FIG. 11. Third-degree polynomial regression of log WT on PC 1 for modern members of the *C. mexicana*-group: log $WT = 0.878905 - 0.02632823$ $(PC1)$ + 0.00476843 $(PC1)^2$ - 0.0008562133 $(PC1)^3$. Factor loadings on PC 1 are negative (Table 3), so the most negative scores represent the largest mandibles. To account for the negative weighting, the PC 1 axis is reversed.

showed that individuals with the largest mandibles tended to have disproportionately greater HB and WT. This impression was supported by calculating polynomial regressions for the same data sets. The resulting best-fit equations are a third-degree polynomial regression for WT and a second-degree polynomial regression for HB (Figs. 11, 12):

$$\log \mathrm{WT} = 0.878905 - 0.02632823(PC1)$$
$$+ 0.00476843(PC1)^2$$
$$- 0.0008562133(PC1)^3$$
$$[R0^2 = 58.9\%, R1^2 = 50.5\%,$$
$$R2^2 = 18.3\%, R3^2 = 49.2\%];$$

$$\log \mathrm{HB} = 1.860537 - 0.01249341(PC1)$$
$$+ 0.0004880436(PC1)^2$$
$$[R0^2 = 40.2\%, R1^2 = 39.7\%,$$
$$R2^2 = 4.3\%]$$

Plots by species (Figs. 13, 14) indicated that most of the larger individuals causing the disjuncture in the linear regression are modern *C. goodwini*—the species for which we wished to calculate body size. Because of its departure from the linear relationship with the remainder of the *C. mexicana*-group, we calculated an additional linear regression for each size variable using only *C. goodwini*. The resulting equations for estimating body size using *C. goodwini* alone are as follows:

$$\log \mathrm{WT} = 0.984 - 0.05516(PC1)$$
$$[F = 10.55, p = 0.023,$$
$$\text{adjusted } R^2 = 61.4\%];$$

$$\log \mathrm{HB} = 1.89817 - 0.008152(PC1)$$
$$[F = 6.34, p = 0.018,$$
$$\text{adjusted } R^2 = 15.5\%]$$

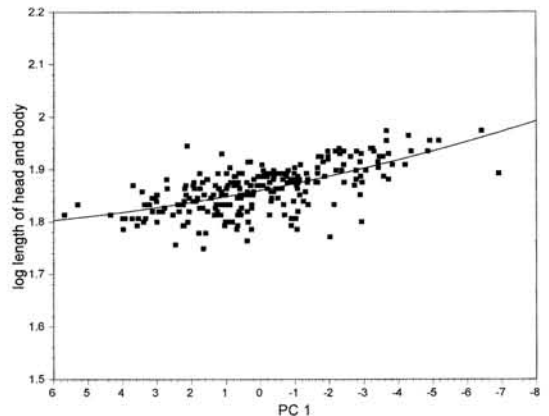These two sets of models—the polynomial re-

FIG. 12. Second-degree polynomial regression of log HB on PC 1 for modern specimens of the *C. mexicana*-group: log HB = $1.860537 - 0.01249341$ $(PC1)$ + 0.0004880436 $(PC1)^2$. Factor loadings on PC 1 are negative (Table 3), so the most negative scores represent the largest mandibles. To account for the negative weighting, the PC 1 axis is reversed.
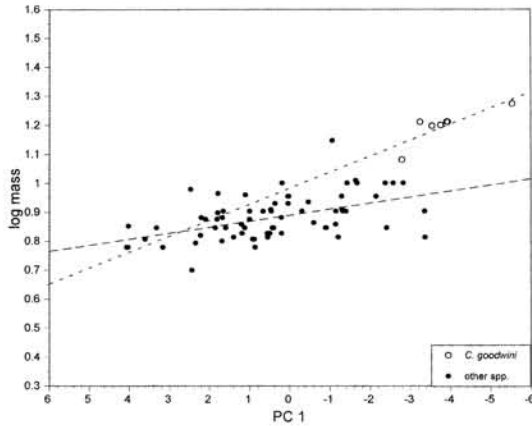
FIG. 13. Linear regressions of log WT on PC 1 for modern *C. goodwini* (dotted line: log WT = 0.984–0.05516 $PC1$; F = 10.55, p = 0.023, adjusted R^2 = 61.4%) and for the remaining modern members of the *C. mexicana*-group (dashed line: log WT = 0.891–0.0208 $PC1$; F = 21.26 p < 0.001, adjusted R^2 = 23.2%). Factor loadings on PC 1 are negative (Table 3), so the most negative scores represent the largest mandibles. To account for the negative weighting, the PC 1 axis is reversed.
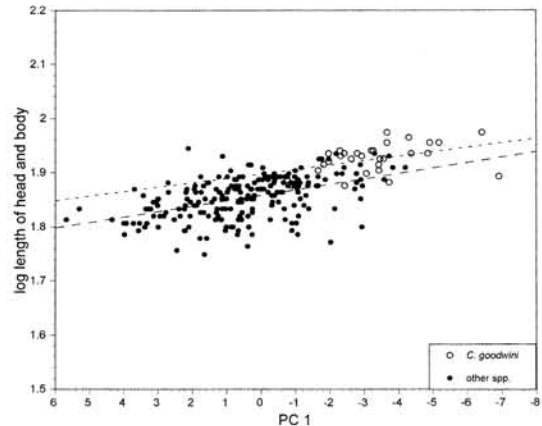
FIG. 14. Linear regression of log HB on PC 1 for modern *C. goodwini* (dotted line: log HB = 1.89817–0.008152 $PC1$; F = 6.34, p = 0.018, adjusted R^2 = 15.5%) and for the remaining modern members of the *C. mexicana*-group (dashed line: log HB = 1.858767–0.01001607 $PC1$; F = 62.01, p < 0.001, adjusted R^2 = 21.9%). Slopes of the two regressions are not significantly different ($F_{[1,248]}$ = 0.191 ≪ $F_{\alpha=0.5[1,120]}$), indicating that the two groups show offset but parallel trends. Factor loadings on PC 1 are negative (Table 3), so the most negative scores represent the largest mandibles. To account for the negative weighting, the PC 1 axis is reversed.

gressions for the inclusive *C. mexicana*-group (Figs. 11, 12) and the linear regressions for modern *C. goodwini* alone (Figs. 13, 14)—provide the best fit to their respective data sets and appear to have the greatest value for predicting body size for the fossils. The two models describe two different evolutionary scenarios. The polynomial regression for *C. mexicana*-group reflects a rapid, possibly punctuated increase in body size relative to mandible size. In contrast, the linear regression for modern *C. goodwini* models a more gradual increase in body size. Unfortunately, the lack of stratigraphic control or reliable dates from the site preclude our determining which of the two models best represents the evolutionary history of *C. goodwini* and hence provides the more accurate estimates of body size. When these two models are applied to the PC 1 scores for the fossils, the polynomial regressions provide estimates of mean HB = 72 ± 2 mm and mean WT = 7.6 ± 0.4 g for the sample (Table 6). The linear regressions estimate mean HB = 79 ± 1 mm and mean WT = 9.6 ± 1.0 g for the fossil sample.

MAGNITUDE OF SIZE CHANGE—Individual variables exhibited a range of size increase in *C. goodwini* from 0 to 15% (Table 7). Changes in size of single variables have been used in some studies as proxy values representing the magni-

tudes of body size change (e.g., Guilday et al., 1964; Marshall & Corruccini, 1978). Such variables are not comparable among taxa, however, and they do not all correlate well or equally with more standardized measures of body size, such as WT and HB. Our estimates of body size for the fossil sample of *C. goodwini* from McGrew Cave vary depending on the regression model used to calculate the statistics. These estimates indicate the fossil sample averaged 6–14% shorter in HB and 39–52% less in WT than the modern sample and required a 6–17% increase in mean HB and a 65–108% increase in WT to achieve the size of the modern sample (Table 6).

CHANGE IN USE OF RESOURCES—There are no reported data on food consumption or energy requirements for modern *C. goodwini*. We predicted mean food requirements for *C. goodwini* using recorded mean mass of modern specimens and estimated mean mass for the fossils using equations in Nagy (2001). Fossil shrews were estimated to have consumed 4.0–4.6 g FMI/d and 1.3–1.5 g DMI/d, whereas modern shrews were estimated to feed on 6.3 g FMI/d and 2.1 g DMI/d. These estimates suggest an increased intake of 37–58% in fresh (wet) matter and 40–62% in food by dry

TABLE 6. Estimates of mass and length of head and body for fossil *C. goodwini* based on various regression models. Statistics presented are mean ± standard deviation of the mean and observed extremes. Sample size for mass was 75 individuals representing five species. Sample size for length of head and body was 248 individuals from nine species (10 groups). Percentage increase refers to the difference between estimated smaller body size for the fossil sample and measured larger body size for the modern sample of *C. goodwini* (Table 2).

Estimation model	Size estimate for fossils	Percentage increase
WT		
Linear regression (Fig. 9)[1]	8.1 ± 0.6 7.1–8.8	95
Third-degree polynomial regression (Fig. 11)[1]	7.6 ± 0.4 7.0–8.0	108
Linear regression (Fig. 13)[2]	9.6 ± 1.0 7.9–10.7	65
HB		
Linear regression (Fig. 10)[1]	72 ± 2 69–74	17
Second-degree polynomial regression (Fig. 12)[1]	72 ± 2 69–74	17
Linear regression (Fig. 14)[2]	79 ± 1 77–80	6

[1] Regression based on all available modern members of the *C mexicana*-group.
[2] Regression based on modern *C. goodwini* only.

weight for the larger, modern *C. goodwini*. Because some small soricine shrews are known to consume quantities of fresh food daily that approach or exceed their own body weights (Morrison et al., 1957; Whitaker, 1974; Woodman & Díaz de Pascual, 2004), the numbers we calculated may represent underestimates. It is likely that fresh food intake may have increased by an

TABLE 7. Mean percentage changes in various univariate measures between smaller fossil and larger modern samples of *C. goodwini* (see Table 1). Percentage increase represents the magnitude of size change through time from the fossil sample to the modern sample (fossil sample is divisor in the equation in *Materials and Methods*). Percentage decrease is the amount the modern sample would have to decrease to reach the size of the fossil sample (modern sample is divisor). See Table 1 for definitions of abbreviations.

Variable	Percentage increase	Percentage decrease
ML	10.0	9.1
HCP	4.3	4.2
HCV	7.1	6.7
HAC	10.5	9.5
AC3	14.6	12.7
TRD	9.4	8.6
M13	6.8	6.4
M1L	0	0
BAC	13.8	12.1

amount closer in magnitude to the increase in body mass.

REMARKS—Fossil *C. goodwini* from McGrew Cave represents a population composed of individuals distinctly smaller than modern members of the species. None of the fossil individuals were the size of any modern *C. goodwini* in multivariate space (Fig. 7), although the ranges of individual variables for the fossils and the modern sample intersect (Table 1). Our estimates of the magnitude of the change in size of *C. goodwini* are similar to estimated size changes experienced by some other North American mammals between late glacial and early Holocene times (Table 8). The difference in size between the fossil and modern samples of *C. goodwini* suggests that the fossils represent a late glacial population, and it lends support to the hypothesis that McGrew Cave includes at least some late Pleistocene remains.

Of additional interest is the disproportionately large body size of modern *C. goodwini* relative to other modern members of the *C. mexicana*-group (Figs. 13, 14). This change in the relationship between body size and mandibular size may represent a phylogenetically linked trend independent of body size that is intrinsic to the lineage that includes both fossil and modern *C. goodwini*. Alternatively, it could be a strictly allometric phenomenon—such as a threshhold related to the ob-

TABLE 8. Quantified size changes in North American mammals during the late Pleistocene to the Holocene transition. Positive values of size change represent gigantism; negative values mark dwarfism through time; zero indicates no size change. Positive values for clinal variation (positive Bergmann's response) indicate that modern average size is larger with increasing latitude; negative values indicate smaller size to the north. Taxa are ordered approximately by magnitude of size change.[1]

Taxon	Percentage change in size	Modern clinal variation
Magnitude of change based on linear measures		
American marten (*Martes americana*)	−13	?
Northern flying squirrel (*Glaucomys sabrinus*)	−12 to 16	+
Red squirrel (*Tamiasciurus hudsonius*)	−10	+
Star-nosed mole (*Condylura cristata*)	−10	+
Jaguar (*Panthera onca*)	−9 to −20	?
Caribou (*Rangifer tarandus*)	−9 to −15	?
Bighorn sheep (*Ovis canadensis*)	−8 to −10	+
Woodland jumping mouse (*Napaeozapus insignis*)	−8	+
Dall sheep (*Ovis dalli*)	−7 to −10	+
Musk ox (*Ovibos moschatus*)	−7 to −14	?
Southern flying squirrel (*Glaucomys volans*)	−6	+
White-tailed prairie dog (*Cynomys leucurus*)	−6	?
Moose (*Alces alces*)	−6 to −11	?
Wolverine (*Gulo gulo*)	−5	?
Masked shrew (*Sorex cinereus*)	−5	+
Dall sheep (*Ovis dalli*)	−4 to −6	+
Chipmunk (*Tamias striatus*)	−2 to 5	−
Pronghorn (*Antilocapra americana*)	0	?
Short-tailed shrews (*Blarina* spp.)	0	?
Mayan small-eared shrew (*Cryptotis mayensis*)	0	0
Southern bog lemming (*Synaptomys cooperi*)	+5	−
Rock vole (*Microtus chrotorrhinus*)	+7	−
Snowshoe hare (*Lepus americanus*)	+11	−
Alaskan ground squirrel (*Spermophilus parryii*)	+12	+
Meadow vole (*Microtus pennsylvanicus*)	+13	−
Magnitude of change based on estimated mass		
Jaguar (*Panthera onca*)	−60	?
Muskrat (*Ondatra zibethica*)	−48	?
Bushy-tailed woodrat (*Neotoma cinerea*)	−20	+

[1] From Guilday et al. (1964, 1977, 1978); Brown and Lee (1969); Diersing (1980); Gilbert and Martin (1984); Guthrie (1984a); Jones et al. (1984); Bryant (1987); Chorn et al. (1988); Wang (1988); Youngman and Schueler (1991); Goodwin (1993); Martin (1993); Seymour (1993); Smith et al. (1995); Woodman (1995).

servation that larger mammals tend to have relatively smaller heads (Gould, 1966)—that is restricted to only the largest members of the species group. It is unfortunate that the lack of chronological control and intermediate forms (if intermediate forms existed) prevent us from investigating this question more completely.

Cryptotis merriami Choate, 1970

REFERRED SPECIMENS—Right mandible (1): FMNH-PM **17067**. Left mandible (1): FMNH-PM 17147. Right humerus (1): FMNH-PM 59375. Left humeri (4): FMNH-PM 59397, 59398, 59413, 59419.

MODERN DISTRIBUTION—Moist forests at ca. 975–1650-m elevation from Chiapas, Mexico, to northern Costa Rica.

SYSTEMATIC CONTEXT—*C. merriami* is a member of the *Cryptotis nigrescens*-group (Woodman & Timm, 1993).

DESCRIPTION—The mandible of *C. merriami* (Fig. 5B) has a high coronoid process, the anterior border of which joins the horizontal ramus at a high angle; posterior border of the lower incisor extends posterior to posterior border of p4; short posterior portion of mandible; short and broad

TABLE 9. Factor loadings for the first two axes from PCA of six mandibular variables from modern *C. merriami*, modern *C. hondurensis*, and fossil *C. merriami* (Fig. 15). See Table 1 for definitions of abbreviations.

Variable	Correlations	
	PC 1	PC 2
M1L	−0.323	0.339
BAC	−0.387	−0.405
HCV	−0.402	−0.254
HAC	−0.416	−0.553
ML	−0.452	0.422
HCP	−0.454	0.415
Eigenvalue	3.9481	0.6754
Proportion of variation	65.8%	11.3%

FIG. 15. Plot of scores on the first two axes from PCA of six mandibular variables measured on modern *C. merriami*, modern *C. hondurensis*, and one fossil *C. merriami*. Factor loadings on PC 1 (size) are negative (Table 9), so the most negative scores represent the largest mandibles. PC 2 is a contrast of ML and HCP with HAC and BAC.

vertical and horizontal branches of articular process; lower sigmoid notch essentially absent; short (in length) p3; no entoconid in talonid of m3; bulbous dentition; moderate to dark tooth pigmentation, moderately dark pigment extending to tips of entoconids but not into talonid basins of m1 and m2. The humerus is long and straight with unenlarged processes and a rounded head (Fig. 6D).

COMPARISONS—The mandible of *C. merriami* differs from those of the *C. parva*-group in having bulbous dentition and in lacking a lower sigmoid notch. From the mandible of *C. orophila*, it differs in having a less elongate internal temporal fossa. The humerus tends to have a more robust shaft.

Within the *C. nigrescens*-group, the mandible of *C. merriami* is most easily distinguished from *C. brachyonyx*, *C. colombiana*, and *C. mayensis* in having less extensive pigmentation that does not continue into the talonid basins of m1 and m2; from *C. brachyonyx*, *C. colombiana*, *C. mayensis*, and *C. mera* in having a relatively shorter posterior mandible; from *C. brachyonyx*, *C. colombiana*, and *C. nigrescens* in having a relatively higher coronoid process; from *C. hondurensis* and *C. nigrescens* by its robustness and its bulbous dentition; from *C. mayensis* by being less robust and having a narrower and relatively lower coronoid process. Within the *C. nigrescens*-group, the humerus tends to be similar in overall shape among species, differing mainly in size.

The fossil mandibles are within the limits of modern *C. merriami* for all variables. The HCP is at the lower extreme for modern members of the species (Table 1); however, the relative height of coronoid process for both left and right mandibles is well within the modern range of variation.

STATISTICAL ANALYSIS—We compared the fossil left mandible with modern specimens of *C. merriami* and *C. hondurensis* by carrying out a PCA with six variables (Table 9). The plot of scores for these specimens PC 1 and PC 2 shows that the fossil mandible lies within the overall pattern of variation for the species in multivariate space, corresponding well to a relatively small *C. merriami* (Fig. 15).

REMARKS—Modern *C. merriami* exhibit no identifiable clinal variation in size or shape (Woodman, 2000). Although our sample size is extremely low for this species (MNI, based on mandibles = 1), in general the fossils appear to fit within the range of modern pattern of variation within the species, matching most closely with smaller individuals.

Cryptotis orophila (J. A. Allen, 1895)

REFERRED SPECIMENS—Right mandibles (32): FMNH-PM 17051, 17054, 17055, 17057–17061, 17063, 17064, 17070, 17072–17074, 17076–17079, 17080, 17082, 17084–17088, 17093–17096, 17099, 57552, 60228. Left mandibles (50): FMNH-PM 17069, **17110–17112**, **17114**, 17115, **17116**, 17117, **17119**, 17121–17123, **17124**, 17125, **17126**, **17127**, 17128, **17129**, **17130**, 17131, **17132–17137**, 17139, 17141, **17142**, **17146**, **17148**, 17149–17151, **17152**, **17153**,

TABLE 10. Factor loadings for the first two axes from PCA of five mandibular variables from modern *C. orophila*, modern *C. tropicalis*, and fossil *C. orophila* (Fig. 16). See Table 1 for definitions of abbreviations.

Variable	Correlations	
	PC 1	PC 2
ML	−0.421	0.762
BAC	−0.441	0.213
HCP	−0.444	−0.385
HCV	−0.456	−0.471
HAC	−0.472	−0.062
Eigenvalue	3.5436	0.4658
Proportion of variation	70.9%	9.3%

TABLE 11. Factor loadings for the first two axes from PCA of eight mandibular variables from modern *C. orophila*, modern *C. tropicalis*, and fossil *C. orophila* (Fig. 17). See Table 1 for definitions of abbreviations.

Variable	Correlations	
	PC 1	PC 2
M1L	−0.238	−0.713
M13	−0.322	−0.529
ML	−0.362	0.076
HAC	−0.369	0.309
AC3	−0.374	0.304
BAC	−0.376	0.085
HCV	−0.376	0.090
HCP	−0.387	0.049
Eigenvalue	4.7440	1.2020
Proportion of variation	59.3%	15.0%

17155, **17156–17162**, 17163, 17164, **17165**, 17166, **59508**, 60229. Right humeri (27): FMNH-PM 59352–59374, 59376–59379. Left humeri (33): FMNH-PM 59386–59396, 59399–59412, 59414–59418, 59420–59422.

MODERN DISTRIBUTION—Secondary and open habitats from western Honduras and El Salvador to the Central Valley of Costa Rica; known elevational range is 1150–1990 m.

SYSTEMATIC CONTEXT—*C. orophila* is a member of the *C. parva*-group (Choate, 1970; Woodman & Timm, 1993, 1999).

DESCRIPTION—The mandible of *C. orophila* (Fig. 5C) has a high coronoid process, the anterior border of which joins the horizontal ramus at a high angle for the genus; posterior border of the lower incisor extends posterior to posterior border of p4; short posterior portion of mandible; relatively short and broad vertical and horizontal branches of articular process; shallow lower sigmoid notch; short p3; no entoconid in the reduced talonid of m3; dentition not bulbous; moderately dark tooth pigmentation, pigment absent from entoconids and trigonid and talonid basins of m1 and m2. The humerus is long, narrow, and straight with unenlarged processes and a rounded head (Fig. 6C).

COMPARISONS—Within the *C. parva*-group, the mandible of *C. orophila* differs from those of *C. parva berlandieri*, *C. p. floridana*, *C. p. parva*, and *C. p. soricina* in having a shallow lower sigmoid notch; from *C. pueblensis*, *C. parva berlandieri*, *C. p. floridana*, *C. p. parva*, and *C. p. soricina* in having internal temporal fossa obviously longer than wide, extending ≥⅔ width of base of coronoid process rather than ≤½ that width and differs from *C. tropicalis* by paler and less extensive dental pigmentation. Within the *C. parva*-

group, the humerus tends to be similar in shape among species, differing mainly in size.

The fossil mandibles exhibit pigmentation typical for *C. orophila* and average the same or nearly the same size as modern *C. orophila* for most individual measurements (Table 1). The fossils, however, average slightly longer (and have larger upper ranges of values) for measurements of the toothrow. Fossil humeri exhibit a broad range of sizes. Unfortunately, too few skeletons of modern *C. orophila* are available in systematic collections for adequate comparative study of variation in the humerus.

STATISTICAL ANALYSES—In studying the fossils, we carried out two PCAs, one favoring a larger sample size ($n = 31$ fossil specimens) but containing only five variables (Table 10) and a second using eight variables (Table 11) measured from a smaller sample of fossils ($n = 12$). Plotted results from both analyses reflect the smaller average overall size (PC 1) of modern and fossil *C. orophila* compared to *C. tropicalis* and the generally similar distributions along PC 2 of the two modern samples. In the plot from the first analysis (Fig. 16), the fossils overlap broadly with modern *C. orophila*. The extent and distribution of their overlap with *C. tropicalis* is similar to that of modern *C. orophila* with *C. tropicalis*. In the plot from the second PCA (Fig. 17), which included three additional variables, the fossils also overlap to a large extent with modern *C. orophila*. In this analysis, however, the fossils exhibit a greater range of size variation along PC 1 than do modern *C. orophila*. In addition, the fossils show a clear, linear tendency to have longer molar toothrows
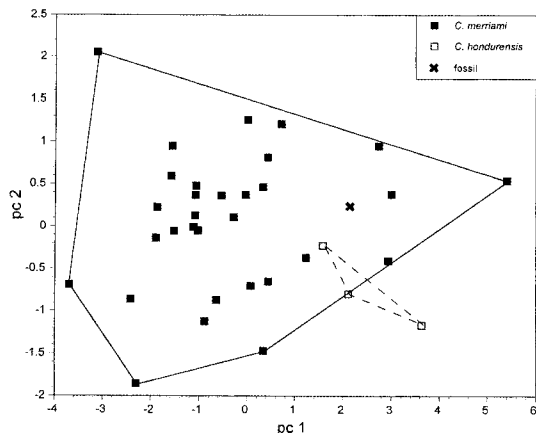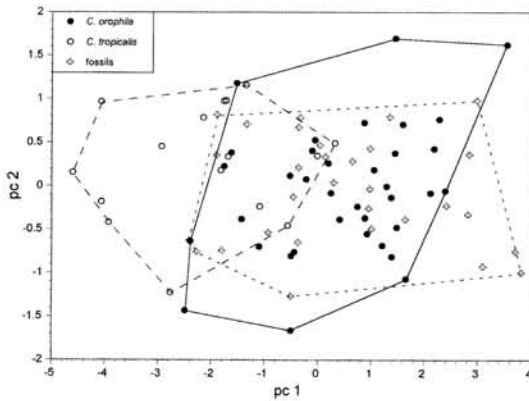
FIG. 16. Plot of scores on the first two axes from PCA of five mandibular variables measured on modern *C. orophila*, modern *C. tropicalis*, and fossil *C. orophila*. Factor loadings on PC 1 (size) are negative (Table 10), so the most negative scores represent the largest mandibles. PC 2 contrasts ML with BAC and HAC.
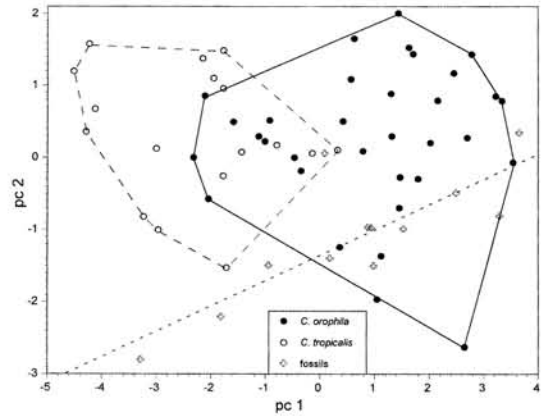

FIG. 17. Plot of scores on the first two axes from PCA of eight mandibular variables measured on modern *C. orophila*, modern *C. tropicalis*, and fossil *C. orophila*. Factor loadings on PC 1 (size) are negative (Table 11), so the most negative scores represent the largest mandibles. PC 2 contrasts HAC and AC3 with M13 and M1L. The dotted line marks the linear trend of longer toothrows and shorter articular condyles with increasing size exhibited by fossil *C. orophila* ($PC2 = -1.352251 + 0.3508869\ PC1$; $F = 19.03$, $p = 0.001$, adjusted $R^2 = 62.1\%$).

(M13, LM1) and shorter articular condyles (HAC, AC3) with increasing overall size. Regression statistics calculated for the fossils indicate that the slope of the trend is significant and that it explains a large share of the variation ($PC2 = -1.352251 + 0.3508869\ PC1$; $F = 19.03$, $p = 0.001$, adjusted $R^2 = 62.1\%$). This trend is not present in the samples of either modern *C. orophila* or modern *C. tropicalis*.

No previous studies of geographic variation within *C. orophila* or *C. tropicalis* have been carried out. To determine whether modern geographic variation might assist in understanding the variation observed among the fossil specimens, we plotted "size" (PC 1 from the five-variable PCA model—Table 10) against a score representing the combined latitude and longitude of the collecting locality ("locality"—Table 12) for each modern reference specimen of *C. orophila* and *C. tropicalis* (Fig. 18). In testing for clinal variation, we regressed size on locality for *C. orophila* and extended the regression line through the plots for the fossils and for neighboring *C. tropicalis*. The resulting plot emphasizes the similar ranges of size variation for modern and fossil *C. orophila* and the distinct, steplike change in mean size between (modern and fossil) samples of *C. orophila* and modern *C. tropicalis*. The slope of the regression, however, is not statistically different from zero, and it explains almost none of the variation among modern *C. orophila* ($PC1 = 0.5203365 + 0.005578872\ [locality]$; $F < 0.01$, $p = 0.980$, ad-

justed $R^2 = 0.002\%$), indicating that there is no obvious geographic component to mandibular size variation in this species.

REMARKS—In general, fossils of *C. orophila* from McGrew Cave tend to indicate that these shrews averaged about the same size as modern members of the species. In multivariate space, however, the fossils from this one locality slightly exceed the range of size variation (both larger and smaller) observed among modern members of the species from throughout its geographic distribution. Much of this size variation can be attributed to the *relatively* longer toothrows and shorter articular condyles of the fossils. At the same time, the relationship of those morphological attributes to overall mandibular size were more tightly constrained, possibly indicating the effects of local selection during that time.

The fossils may represent a single period of time when greater size variation was present within the species, or these specimens may reflect size variation through time, possibly spanning several thousand years during the late Pleistocene, during the Holocene, or spanning the late glacial into the postglacial. The lack of stratigraphic context in the fossil site hinders our interpretation of the morphological patterns present. Regardless of the magnitude of time represented, the differences ob-

TABLE 12. Approximate north latitude and west longitude of collection localities for *C. orophila* and *C. tropicalis*, with decimal and PC 1 equivalents. Factor score for each locality derives from the first axis of a PCA of all pairs of coordinates and represents the combined latitude and longitude of that locality (see text).

| Collecting locality	Degrees		Decimal		"Locality" (PC 1 score)
	Latitude	Longitude	Latitude	Longitude	
Mountain Pine Ridge	16°59'	88°48'	16.98	88.80	1.70404
Finca Prusia	15°45'	92°43'	15.75	92.72	2.19257
Liquidambar	15°44'	92°45'	15.73	92.75	2.29409
Texiguat	15°30'	87°28'	15.50	87.47	0.96978
Cobán	15°29'	90°22'	15.48	90.37	1.65592
Panajachel	14°44'	91°09'	14.73	91.15	1.63066
Copán	14°50'	89°09'	14.83	89.15	1.18175
Lago Yojoa	14°50'	88°00'	14.83	88.00	0.90743
Cantoral	14°20'	87°24'	14.33	87.40	0.62343
Yuscarán	13°55'	86°51'	13.92	86.85	0.37671
El Imposible	13°52'	89°59'	13.87	89.98	1.10926
Apaneca	13°52'	89°48'	13.87	89.80	1.06632
San Rafael del Norte	13°11'	86°06'	13.18	86.10	−0.01070
Jinotega	13°06'	86°00'	13.10	86.00	−0.05709
Sta. María de Ostuma	12°57'	85°58'	12.95	85.97	−0.10651
Paso Llano	10°04'	84°07'	10.07	84.12	−1.37965
Zarcero	10°11'	84°24'	10.18	84.40	−1.26149
Volcán Irazú	9°59'	83°51'	9.98	83.85	−1.44904
Coliblanco	9°57'	83°49'	9.95	83.82	−1.46464
Santa Ana	9°56'	84°11'	9.93	84.18	−1.38440
San Rafael	9°56'	84°08'	9.93	84.13	−1.39633
San Pedro	9°56'	84°03'	9.93	84.05	−1.41541
Cartago	9°52'	83°55'	9.87	83.92	−1.46333
Cerro Tablazo	9°50'	84°02'	9.83	84.03	−1.44836
Estrella	9°47'	83°57'	9.78	83.95	−1.48153
El Muñeco	9°47'	83°54'	9.78	83.90	−1.49346
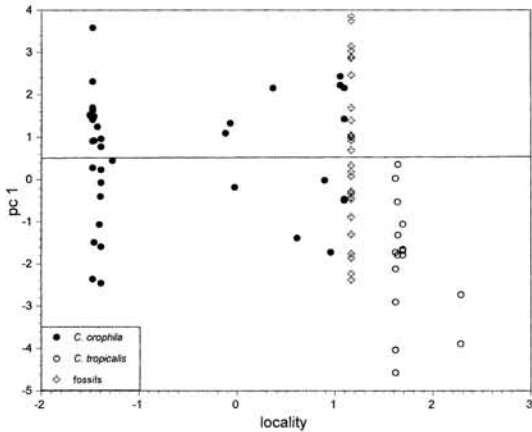
FIG. 18. Plot of size on geographic locality for modern *C. orophila*, modern *C. tropicalis*, and fossil *C. orophila*. The slope of the regression line, calculated only for modern *C. orophila*, is not statistically different from zero, indicating no clinal trend in size, and it explains only a small percentage of the variation in the species ($PC1 = 0.5203365 + 0.005578872$ [*locality*]; $F < 0.01$, $p = 0.980$, adjusted $R^2 = 0.002\%$). Size is represented by PC 1 scores from a five-variable PCA (Table 10) and geographic locality by PC 1 scores from a PCA of geographic coordinates (Table 12).

served between the modern and fossil samples suggest that the fossil specimens derive from a time (or span of time) well removed from the present.

Discussion

Two of the three species of fossil shrews from McGrew Cave exhibit patterns of morphological variation that are different from those present in modern members of their respective species. In the most obvious case, fossil *C. goodwini* averaged up to 13% smaller in various mandibular variables than its modern counterpart. From these numbers, we estimated that the fossil sample was 6–14% smaller in length of head and body and 39–52% smaller in mass. In contrast, fossil *C. orophila* averaged about the same size as modern *C. orophila* but showed a slightly greater range of size variation and much greater constraint of variation in some dental and mandibular variables relative to overall body size. The differences in

the two patterns probably represent individual responses of two species to changing environments, but whether these were responses to the same environmental changes is unknown. Uniform leaching of the fossils suggests that *C. goodwini* and *C. orophila* from McGrew Cave are of the same age, but the lack of stratigraphic information associated with the specimens prevents us from determining for certain whether the two populations were coeval or to what extent they may have overlapped in time. We can state that the two samples are morphologically distinct from modern populations.

Despite the changes each species underwent since the time the fossils were deposited in McGrew Cave, each retained its qualitative identity. For example, fossil humeri of *C. goodwini,* like the fossil mandibles, are much smaller than those of modern members of the species. Yet the derived morphology and evolutionary grade of the humerus, believed to be an adaptation for greater digging ability (Woodman & Timm, 1999), was conserved. Presumably, fossil and modern humeri functioned similarly despite the size differences, and the continued presence of the form of the humerus in northern Central America through time is indicative of the overall evolutionary stability of the species despite a large increase in body size. The implication is that the functional mode of life of this species is not size dependent, at least not at the scale of the size change that this species underwent.

With some exceptions, most lineages of North American Quaternary shrews previously have appeared to be fairly static in size through time (Jones et al., 1984). Guilday et al. (1964) reported two species of soricids from New Paris No. 4, Pennsylvania, that they described as being larger in the late Pleistocene than in the modern environment. *Sorex cinereus* at this site underwent a 5% decrease in size (based on length of p4–m3) at the end of the Wisconsinan (Table 8). *Blarina brevicauda* showed a gradual decrease in size from older to younger strata, but this seeming trend ultimately was determined to have resulted from increased contamination of larger, fossil *B. b. brevicauda* by smaller, modern *B. b. kirtlandi* (Guilday et al., 1964) or by varying mixtures of up to three contemporaneous taxa of *Blarina* (Graham & Semken, 1976; Lundelius et al., 1983). In a multivariate study of *Blarina,* Jones et al. (1984) found no substantial change in size in any species of the genus during the past 2 million years. Similarly, *C. mayensis* from the Yu-

catan Peninsula, Mexico, showed no change in size during the transition from late Pleistocene to Holocene conditions (Woodman, 1995). In contrast, our study indicates that *C. goodwini* recovered from McGrew Cave were distinctly smaller than modern populations, indicating that size fluctuations can occur and have occurred among individual species of soricids.

Change in body size of mammals at the end of the Pleistocene is a well-known but still inadequately studied and poorly understood phenomenon (Hoojier, 1950; Guthrie, 1984a; Marshall, 1984; Martin & Barnosky, 1993; Smith et al., 1995). Although some mammals are known to have fluctuated more or less gradually in size through the Pliocene and Pleistocene (Kurtén, 1968; Martin, 1993, 1996) and even during the Holocene (Purdue & Reitz, 1993), the size shift at the end of the Pleistocene was particularly rapid and of high magnitude (Guthrie, 1984a; Martin, 1993, 1996). It also has been typified as a dwarfing event (Gilbert & Martin, 1984; Guthrie, 1984a,b; McDonald, 1984). Table 8 provides a sample (neither exhaustive nor random) of mammals that have been investigated for change in size during the late Pleistocene to Holocene transition. Although most species listed experienced dwarfing, a few are known to have increased in size during that time. Guilday et al. (1964) noted that those that decreased in size tend to exhibit modern clinal variation in the form of a positive Bergmann's reponse (average body size increasing with latitude), whereas species that experienced gigantism show a negative Bergmann's response. Whether the fossil *C. goodwini* from McGrew Cave represents a late Pleistocene population is uncertain. Its change in body size, however, is opposite in direction from that experienced by the majority of mammals that experienced size change at the end of the last glacial. Moreover, *C. goodwini* is one of the few species exhibiting a substantial size change that does not exhibit modern clinal variation in size.

One of the major biogeographical questions related to the phenomenon of terminal Pleistocene size change is whether change in size represents a geographical displacement of a size cline ("cline translocation" of Koch, 1986) or natural selection acting directly on local populations (Smith et al., 1995). Although Smith et al. (1995) suspected local adaptation to be responsible, many modern representatives of species for which late Pleistocene size change has been identified exhibit clinal variation in size, making it difficult

to establish the cause with certainty. Because modern *C. goodwini* does not exhibit clinal size variation (Woodman & Timm, 1999), one explanation is removed. Immigration of individuals from other populations would have had no substantial impact on size; therefore, size change in the case of *C. goodwini* from McGrew Cave most likely resulted from selection acting directly on local populations. Koch (1986) similarly rejected cline translocation in favor of local selection to account for size evolution in three species of Eocene mammals from the Bighorn Basin, Wyoming.

The direction and magnitude of the size change in *C. goodwini* provide valuable clues regarding the causes of size shifts among Quaternary mammals and may assist our understanding of temporal variation in ecological pressures to which various species have been exposed. Explanations for why some mammals changed in size at the end of the last glacial generally have addressed dwarfing. Marshall (1984) divided these into four categories:

1. Culling of the largest individuals by human hunters. More typically applied to larger mammals, especially ungulates (Edwards, 1967; McDonald, 1984), this explanation also has been used to explain size reductions of muskrats (Martin, 1993) and prairie dogs (Goodwin, 1993). Although Clovis peoples once were thought to specialize exclusively on big game (Martin, 1973), it is now recognized that they relied on a broader variety of mammals and other vertebrates, including small mammals (Stanford, 1999). It is difficult to imagine an adequate scenario, however, that would explain how selection by Clovis hunters might be responsible for size changes in large populations of mice, voles, shrews, or moles or for the shift in the geographical patterns of size clines from the late glacial into the postglacial (Guilday et al., 1977, 1978).

2. Resource limitation. Reduction in energy resources can lead to reduced growth rates, and such limitation has been implicated in the dwarfing of species, particularly large insular species (Lomolino, 1985; Brown & Lomolino, 1998). Food availability also has been implicated in determining the maximum size limits of both endotherms and ectotherms on landmasses (Burnett et al., 2001). It has been hypothesized that size reduction of mammals at the end of the last glacial represents adaptation to a reduction in resources as a consequence of at least two related but distinct scenarios:

a. Reduction in habitat quality. The reorganization of vegetational habitats as species of plants responded individually to the changing climate at the end of the last glacial resulted in a reduction in overall habitat quality. Mammals adapted to foraging on particular assemblages of plants had to travel farther to obtain a sufficient variety of nutrients, or they may have had to change to lower quality or less abundant food resources (King & Saunders, 1984).

b. Shorter growing season. Some ungulates are capable of converting food into somatic growth (rather than, e.g., fat storage or reproduction) only during certain parts of the year (Guthrie, 1984a). Climatic change that resulted in a shorter growing season would reduce the time available for somatic growth, thereby limiting body size. Length of growing season also has been implicated as a cause for modern patterns of latitudinal size variation in some mammals (McNab, 1971; Geist, 1987).

3. Competition. Resource limitation can result from competitive exclusion or interference competion (Tchernov, 1984), and selection to avoid competition can result in character displacement, which often includes a change in body size. Body size affected by competition will respond to changes in community structure and competitive interactions (Brown & Wilson, 1956; Yom-Tov, 1991). For example, trophic guilds of sympatric species exhibiting more or less evenly spaced size distributions have been reported to result from competition for food resources (Maiorana, 1990; Yom-Tov, 1991; Dayan et al., 1993; Fox & Kirkland, 1992; Churchfield & Sheftel, 1994; Werdelin, 1996) following the ecological rule of limiting similarity (Hutchinson, 1959). Smaller members of such guilds typically are larger in regions where larger guild members are absent (McNab, 1971; Malmquist, 1985), and they exploit a broader array of food choice in the absence of such competition (Dickman, 1988). Selection to avoid competition may be strong enough to maintain a relative size distribution by means of parallel changes in size of members of a guild through time (Tchernov, 1984). The increased size of some species on islands has been attributed primarily to ecological release from competition (Lomolino, 1985; Brown & Lomolino, 1998), although immigrant selection and predation also may play important roles (Lomolino, 1984). The extinction of many potential competitors at the end of the last glacial, however, should have resulted in less competition for survivors, which

should then have exhibited a size increase rather than a size decrease (Guthrie, 1984a).

4. Temperature change. For many mammals, there appears to be a correlation between late Pleistocene size change and modern ecogeographical patterns, particularly latitudinal clinal variation (Guilday et al., 1964; Davis 1977). This phenomenon has been interpreted in the past in the context of a classical understanding of Bergmann's rule—that endotherms increase in size with latitude in order to save energy in cold environments by decreasing their surface-to-volume ratio (Mayr, 1963; McNab, 1971; Tchernov, 1984). Hence, larger size during the last glacial has been related directly to colder temperatures (Davis 1977; Gilbert & Martin, 1984; Marshall, 1984; Tchernov, 1984). Many late Pleistocene environments in North America, however, were less extreme and more equable rather than simply colder (Lundelius et al., 1983; Graham & Lundelius, 1984). Also, detailed studies of clinal variation have shown that the factors responsible for geographic variation in size are much more varied and complex than a response to either colder mean annual temperatures or greater extremes of cold (McNab, 1971; Boyce, 1978; Geist, 1987; Smith et al., 1995). One study of bushy-tailed woodrat (*Neotoma cinerea*) related size variation directly to the effects of temperature, but in that case the causal factor was heat stress rather than cold (Smith et al., 1995). Others attributed latitudinal size variation to size of prey, competition, and length of growing season (McNab, 1971; Geist, 1987).

Among these explanations for body size reduction of mammals, human culling seems inappropriate for small mammals, particularly shrews. Two of the others (competition, temperature change) contain independent components (e.g., heat stress in the case of temperature change) that may have explanatory power for individual species but also have components that relate directly back to the second explanation, namely, resource limitation.

Cryptotis goodwini presents the less common case for the late Pleistocene to Holocene transition, that of an increase in size through time rather than dwarfism. In general, soricine shrews exhibit patterns of size variation that may be considered atypical among small mammals. There are tendencies both for smaller species to occupy higher latitudes and for populations within a single species to have smaller mean body size in more northern regions (Mezhzherin, 1964; Rhymer et

al., 2004). Soricines are active throughout the year, even at the northernmost latitudes they inhabit. Species at high latitudes prepare for winter by losing body mass in autumn and early winter, so they are smaller during the coldest parts of the year—a trait known as Dehnel's phenomenon (Hyvärinen, 1984; Yaskin, 1984; Genoud, 1985; Merritt, 1995). The magnitude of this seasonal reduction in mass varies within species, with the greatest decrease in the coldest climates (Mezhzherin, 1964; Pucek, 1970; Hyvärinen, 1984). Dehnel's phenomenon is an adaptation to reduce overall energy demand by shrinking in size, thereby decreasing food requirements and foraging time during the period of the year when energy expenditures are at a maximum and food resources more difficult to locate (Mezhzherin, 1964; Hyvärinen, 1984; McNab, 1991). The primary concern is the limit to resources to fuel metabolism. Hence, an increase in size for a soricine shrew communicates an abundance of available resources.

Large body size conveys social, physiological, predatory, antipredatory, anticompetitory, and other ecological advantages to species of mammals. These advantages are offset primarily by costs associated with greater absolute food requirements (Guthrie, 1984a; Brown & Maurer, 1986), and modern species with abundant food resources tend to increase in size in the absence of competition (Lomolino, 1985; Brown & Lomolino, 1998). Increased size is considered a profitable strategy when the conditions limiting access to resources are moderated or removed. In other words, large size may represent a relaxation of selection. Larger size for *C. goodwini* is conservatively estimated to have increased its fresh food intake by as much as 58%. For this species, it appears that the environmental conditions of the Holocene represent an improvement in the availability and/or quality of resources relative to the time at which the fossils were deposited in McGrew Cave.

Acknowledgments

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Appendix: Modern Reference Specimens Examined

Specimens marked with an asterisk (*) in the following listings are cranial remains recovered from owl pellets.

Cryptotis goodwini (29)—**GUATEMALA**: ALTA VERAPAZ: Cobán (BM 43.9.15.5/43.10.28.7); Verapaz (BM 7.1.1.35). CHIMALTENANGO: Santa Elena, 9900–10,000 ft (FMNH 41791–41794). HUEHUETENANGO: San Mateo Ixtatlán, ca. 4 km NW Santa Eulalia, Yayquich, 2950 m (UMMZ 117843); 3.5 mi SW San Juan Ixcoy, 10,120 ft (KU 64610); Hacienda Chancol, 9500–11,000 ft (USNM 77069). JALAPA: Mataquescuintla, 8400 ft (USNM 275681). QUEZALTENANGO: Calel, 10,200 ft (USNM 77070, 77072, 77073, 77075–77082—includes holotype); Volcán Santa María, 9000–11,000 ft (USNM 77086, 77087). TOTONICAPAN: Cumbre María Tucum, 3000 m (UMMZ 112005–112007, 112009–112011). **MEXICO**: CHIAPAS: Reserva Ecológica El Triunfo, 17 km SE Finca Prusia, 2000 m (UNAM 22784); Catarina, 1300 m (ZMFK 63.484).

Cryptotis griseoventris (27)—**GUATEMALA**: HUEHUETENANGO: Todos Santos Cuchumatán, 10,000 ft (USNM 77051–77068). **MEXICO**: CHIAPAS: San Cristóbal de las Casas, 8000–9500 ft (USNM 75886–75893); 6 mi SE San Cristóbal de las Casas (MCZ B48061).

Cryptotis hondurensis (3)—**HONDURAS**: FRANCISCO MORAZAN: Cerro Oyuca, 12 km WNW El Zamorano, 1680 m (KU 106941—holotype); near San Juancito mines, 1700 m (FMNH 86886); La Rosario, San Juancito, La Tigra National Park (UNAH no number).

Cryptotis merriami (32)—**COSTA RICA**: GUANACASTE: 4.5 km NE of Tilarán (KU 84365). **EL SALVADOR**: MORAZAN: Mt. Cacaguatique, north slope, 3800–4000 ft (MVZ 98176–98178). SAN MIGUEL: Mt. Cacaguatique, 3500–4000 ft (MVZ 130328–130335; UMMZ 109892, 109893). **GUATEMALA**: no locality (MNHM 1962–2895). ALTA VERAPAZ: Cobán (BM 7.1.1.34, 43.6.13.6, 43.9.15.4, 43.10.28.6); San Pedro Carchá (ENCB 35699); Hacienda Concepción, Tucurú, 1100 m (UMMZ 117845). HUEHUETENANGO: Hacienda Santa Gregoria, Barillas (UMMZ 117844); Jacaltenango, 5400 ft (USNM 77020, 77048, 77050—holotype). **HONDURAS**:

EL PARAISO: Yuscarán, Cerro de Moncerrato, cloud forest (MCZ 42992). FRANCISCO MORAZAN: La Rosario, San Juancito, La Tigra National Park (UNAH no number). LEMPIRA: Las Flores Gracias (AMNH 129758). SANTA BARBARA: San José de las Colinas (AMNH 123567). **MEXICO**: CHIAPAS: Volcán Kagchiná, 3.5 km N Las Margaritas (MHP *8779—2 specimens). **NICARAGUA**: MATAGALPA: Santa María de Ostuma, 9 mi N of Matagalpa, 1400 m (UMMZ 117111).

Cryptotis orophila (37)—**COSTA RICA**: ALAJUELA: Zarcero, 6000 ft (FMNH 43974). CARTAGO: Irazu Range (AMNH 9640/9558—holotype, 9641/9841); Coliblanco (KU 26930, 26931); Cartago (UMMZ 66465, 67316; KU 26932); Guarco (KU 16563); Azabar de Cartago (BM 7.5.30.4, 95.8.17.6); La Estrella (AMNH 14847). HEREDIA: Paso Llano, San José de la Montaña, 1800 m (KU 142692–142694); 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 Pedro de Montes de Oca (AMNH 139282); San Rafael de Montes de Oca, 4300 ft (KU 147100); Santa Ana (LSU 15753). **EL SALVADOR**: AHUACHACAN: Peña Blanca, Bosque El Imposible, ca. 3 km from San Francisco Menéndez (KU *144620–144624); 2 mi NW Apaneca, 5500 ft (MVZ 98179, 98180). **HONDURAS**: COMAYAGUA: Cantoral (AMNH 123566). CORTEZ: Rancho Azul, Lago Yojoa (MCZ 45608). EL PARAISO: Yuscaran, Cerro de Moncerrato, cloud forest (MCZ skin number 42991); YORO: Refugio de Vida Silvestre Texiguat (UNAH 1054). **NICARAGUA**: JINOTEGA: San Rafael del Norte, 5000 ft (AMNH 28356—holotype of *Blarina olivaceous*); 12 km S of Jinotega, 1400 m (KU 121591). MATAGALPA: Santa María de Ostuma, 9 mi N of Matagalpa, 1300 m (UMMZ 117112).

Cryptotis tropicalis (17)—**BELIZE**: Mountain Pine Ridge, 12 mi S Cayo (UMMZ 63008–63011). **GUATEMALA**: no locality (BM 71.11.28.1; NMW 12090). ALTA VERAPAZ: Cobán (BM 7.1.1.33, 43.6.13.5). SOLOLÁ: Panajachel, 4900 ft (AMNH 74295–74301). **MEXICO**: CHIAPAS: Liquidambar (SMF 11477a); Finca Prusia, 1110 m (UNAM 18).