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Three New Species of Small-eared Shrews, Genus *Cryptotis*, from El Salvador, Guatemala, and Honduras (Mammalia: Eulipotyphla: Soricidae)

Neal Woodman

Front cover: Dorsal view of the dried skins of three new species of small-eared shrews, as proposed herein. A, *C. eckerlini* sp. nov. (TTU 136187; image by N. Woodman); B, *C. matsoni* sp. nov. (USNM 275681; image by N. Woodman); and C, *C. montecristo* sp. nov. (SMF 14837; image courtesy of Irina Ruf and Katrin Krohmann, SMF).

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Three New Species of Small-eared Shrews, Genus *Cryptotis*, from El Salvador, Guatemala, and Honduras (Mammalia: Eulipotyphla: Soricidae)

Neal Woodman

Abstract

The *Cryptotis goldmani* group of small-eared shrews (Eulipotyphla: Soricidae: *Cryptotis* Pomel, 1848) is a clade of semifossorially adapted species discontinuously distributed in moist highlands from central Mexico to western Panama. Inspection of a recent collection of small mammals resulting from field work in Guatemala provided the impetus for a re-evaluation of one member of that group, Goodwin's small-eared shrew, *Cryptotis goodwini* Jackson, 1933. On the basis of the results of that study, three new species of small-eared shrews are described from (1) disturbed cloud forest on Cerro Cucurucho, Sacatepéquez Department, Guatemala; (2) highlands east of Mataquescuintla, Jalapa Department, Guatemala; and (3) Cerro Montecristo, a massif at the mutual borders of northern El Salvador, eastern Guatemala, and western Honduras. The new species are most similar morphologically to the Guatemalan endemic species *C. goodwini* and *C. mam* Woodman, 2010, from which they are distinguished by a variety of external and cranial characters. Recognition of the three new species more narrowly defines the distribution of *C. goodwini* (*sensu stricto*), which is now known only from portions of the western Sierra Madre of Guatemala.

Key words: biodiversity, Central America, cloud forest, conservation, locomotor adaptation, morphology, Neotropics

Resumen

Las musarañas de orejas pequeñas (Eulipotyphla: Soricidae: *Cryptotis* Pomel, 1848) del grupo *Cryptotis goldmani* es un clado de especies semifosoriales distribuidas de manera discontinua en las tierras altas húmedas desde el centro de México hasta el oeste de Panamá. La inspección de una colección reciente de pequeños mamíferos que resultó del trabajo de campo en Guatemala proporcionó el ímpetu para una reevaluación de un miembro de ese grupo, la musaraña de orejas pequeñas de Goodwin, *Cryptotis goodwini* Jackson, 1933. Sobre la base de los resultados de ese estudio, se describen tres nuevas especies de musarañas a partir de (1) bosque nuboso perturbado de Cerro Cucurucho, Departamento de Sacatepéquez, Guatemala; (2) tierras altas al este de Mataquescuintla, Departamento de Jalapa, Guatemala; y (3) Cerro Montecristo, un macizo en las fronteras mutuas de El Salvador, Guatemala, y Honduras. Las nuevas especies son más similares morfológicamente a las endémicas guatemaltecas *C. goodwini* y *C. mam* Woodman, 2010, de las cuales se distinguen por una variedad de caracteres externos y craneales. El reconocimiento de las tres nuevas especies define más estrechamente la distribución de *C. goodwini* (*sensu stricto*), que ahora se conoce solo en partes de la Sierra Madre occidental de Guatemala.

Palabras clave: biodiversidad, América Central, bosque nublado, conservación, adaptación locomotora, morfología, Neotrópico

Introduction

Small-eared shrews of the genus *Cryptotis* have a wide distribution that extends from eastern North America through Central America to the northern Andean highlands of South America, with isolated species in the Sierra de Aroa and Serranía Litoral of northern Venezuela (Quiroga-Carmona and Molinari 2012; Quiroga-Carmona 2013). The genus attains its greatest diversity in the northern tropics of southern Mexico and northern Central America, although overlap in the local distributions of species appears to be limited (Woodman et al. 2012).

The northern Central American nations of El Salvador, Guatemala, and Honduras currently are home to 14 recognized species of small-eared shrews. These species are partitioned among three of the five traditional, morphologically-defined species groups within the genus (Choate 1970; Woodman and Timm 1993, 1999) that have proven to be distinct clades (Guevara and Cervantes 2014; He et al. 2015; Baird et al. 2017): *Cryptotis cavatorculus* Woodman, 2015, *C. celaque* Woodman, 2015, *C. goodwini* Jackson, 1933, *C. lacertosus* Woodman, 2010, *C. magnimanus* Woodman and Timm, 1999, *C. mam* Woodman, 2010, *C. mccarthyi* Woodman, 2015, and *C. oreoryctes* Woodman, 2011 are members of the Middle American *Cryptotis goldmani* group. *Cryptotis hondurensis* Woodman and Timm, 1992, *C. lacandonensis* Guevara et al., 2014, *C. mayensis* (Merriam, 1901), and *C. merriami* Choate, 1970 are part of the Central American and Colombian *Cryptotis nigrescens* group. *Cryptotis orophilus* (J. A. Allen, 1895) and *C. tropicalis* (Merriam, 1895) are part of the North American *Cryptotis parvus* group. Lacking from Guatemala are any species of the Mexican *C. mexicanus* group or of the southern Central American and South American *C. thomasi* group (Woodman and Timm 2016).

A small series of *C. goldmani*-group shrews recently were obtained from Cerro Cucurucho in the central Sierra Madre range of southern Guatemala. These specimens were expected to represent a new population of *C. goodwini*, but an attempt to confirm that identity instead revealed the presence of a distinct, previously undescribed form. This stimulated a closer review of individuals from two other isolated populations considered to be *C. goodwini* in southern Guatemala, northern El Salvador, and western Honduras. Based on the results of these analyses, three new species of semifossorial small-eared shrews are described herein from Cerro Cucurucho, Sacatepéquez Department, Guatemala; from highlands east of Mataquescuintla, Jalapa Department, Guatemala; and from Cerro Montecristo at the junction of the borders of El Salvador, Guatemala, and Honduras (Fig. 1). Recognition of these three new species increases the combined diversity of small-eared shrews in El Salvador, Guatemala, and Honduras to 17 species. It also more narrowly defines the distribution of *C. goodwini* (*sensu stricto*), which is now known only from portions of the western Sierra Madre of Guatemala.

Materials and Methods

In evaluating morphological variation among populations of *Cryptotis*, qualitative characters and quantitative variables from the skin, skull, and, where available, the postcranial skeleton, were utilized. Specimens from the following institutions were used in this study (Appendix; abbreviations follow Dunnum et al. 2018:SD4): American Museum of Natural History, New York (AMNH); Angelo State University Natural History Collection, San Angelo (ASNHC); The Natural History Museum, London (BMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México, Mexico City (CNMA); Escuela Nacional de Ciencias Biológicas, Mexico City (ENCB); Field Museum of Natural History, Chicago (FMNH); University of Kansas Natural History Museum, Lawrence (KU); Museum of Natural Science, Louisiana State University, Baton Rouge (LSUMZ); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museo Nacional de Costa Rica, San José (MNCR); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum of Vertebrate Zoology, University of Califor-

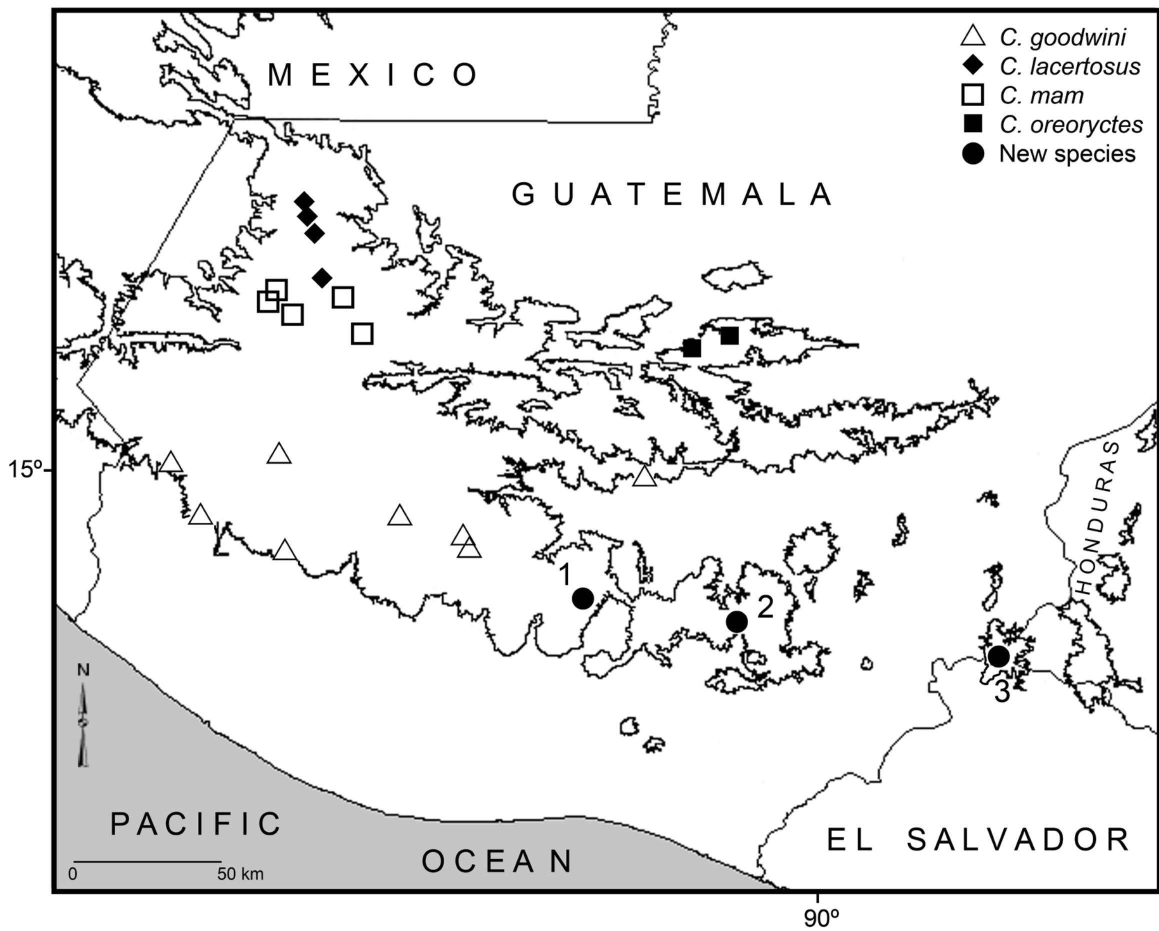

Figure 1. Map of northern El Salvador, southern Guatemala, and western Honduras, illustrating the distributions of species of large-footed shrews of the *Cryptotis goldmani* group in the region. The contour marks 1,500 m. Key to localities: 1, Cerro Cucurucho; 2, highlands east of Mataquescuintla; 3, Cerro Montecristo.

nia, Berkeley (MVZ); Museum of Wildlife and Fish Biology, University of California, Davis (MWFB); Universidad de Costa Rica, San Pedro de Montes de Oca (MZUCR); Naturhistorisches Museum, Vienna (NMW); Royal Ontario Museum, Toronto (ROM); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (SMF); University of Iowa Museum of Natural History, Iowa City (SUI); Museum of Texas Tech University, Lubbock (TTU); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Universidad Nacional Autónoma de Honduras, Tegucigalpa (UNAH); Universidad de San Carlos de Guatemala, Guatemala City (USAC); and National Museum of Natural History, Washington (USNM).

Terminology of dentition and dental characteristics follows Choate (1970), whereas postcranial anatomical and capitalized color terminology follow Reed (1951) and Ridgway (1912), respectively. Capitalized life zone terminology follows Holdridge (1947), with determinations made from a life zone map published by the Laboratorio de Información Geográfica, Guatemala (LIG 2002). Elevations are given in meters above mean sea level (mamsl). All measurements are in millimeters and all masses are in grams. Tabular summary statistics include mean ± *SD* and range. A measured character for a given species is considered "small" if its mean is ≥ 1 *SD* below the mean for the genus, "medium" if within ± 1 *SD* of the genus mean, or "large" if greater than the genus mean by ≥ 1 *SD*. The mean for the genus is based on measurements from up to 60 species and distinctive populations of *Cryptotis*.

External measurements (Tables 1 and 2) are those recorded by the collector, except for head-and-body length (HB), which was calculated by subtracting tail length (TL) from total length (TOT). Skull measurements (Fig. 2; Tables 1 and 2) follow Woodman and Timm (1993) and were recorded to the nearest 0.1 mm using either hand-held dial calipers or an ocular micrometer in a binocular microscope. Following procedures detailed in Woodman and Gaffney (2014), Woodman and Morgan (2005), and Woodman and Stabile (2015a, 2015b), images of the skeletons of the manus and pes were obtained by digitally x-raying the hands and feet of dried skins, and selected postcranial bones (scapula, humerus, ulna, radius, femur, and tibiofibula) were photographed digitally. From these images, 21 measurements of the postcranial skeleton (Fig. 3; Table 3), 10 measurements of ray III of the manus, and 10 measurements of ray III of the pes (Fig. 4; Table 4) were obtained using the measuring tool in the program ImageJ 1.51 (Image Processing and Analysis in Java: Schneider et al. 2012). Univariate statistics were calculated in Excel 97-2003 (Microsoft Corp., Redmond, Washington) and multivariate statistics in Systat 11.00.01 (Systat Software, Inc., Chicago, Illinois). All relative characters and indices calculated from measurements are expressed as percentages (Tables 5 and 6).

To examine the morphometrical distinctiveness of the three populations from Cerro Cucurucho (hereafter, Cucurucho), highlands near Mataquescuintla (hereafter, Mataquescuintla), and Cerro Montecristo (hereafter, Montecristo), two complete discriminant function analyses (DFAs) were conducted using 17 log-transformed skull variables (CBL, ZP, IO, U1B, U3B, M2B, PL, TR, UTR, MTR, HCP, HCV, HAC, AC3, TRD, M13, and M1L). The first analysis included measurements from the three populations and from four Guatemalan species: *C. goodwini*, *C. lacertosus, C. mam*, and *C. oreoryctes*. The second analysis included measurements from Cucurucho, Mataquescuintla, and Montecristo, and from *C. goodwini*, the species that is geographically and morphologically closest to the three populations.

Functional anatomy and locomotor mode were assessed for the Cucurucho and Mataquescuintla populations, for which specimens with postcranial skeletons were available. Postcranial, manual, and pedal measurements (Tables 3 and 4) were used to calculate 23 functional morphological indices (Table 6) that have been shown to help characterize locomotor mode and adaptations for substrate use among soricids and other small mammals (Samuels and Van Valkenburgh 2008; Woodman and Gaffney 2014; Woodman and Stabile 2015a, 2015b). These indices were compared to those previously calculated for 20 species of small-eared shrews by Woodman and Gaffney (2014) and Woodman and Timm (2016). Populations designated as "Celaque," "Cusuco," and "Las Minas" in Woodman and Gaffney (2014) are now recognized respectively as *C. celaque*, *C. mccarthyi*, and *C. oreoryctes*. The 23 indices used herein are a reduced set of the most relevant of 33 indices whose individual performances were assessed in Woodman and Gaffney (2014) and Woodman and Stabile (2015b). Overall locomotor function was evaluated by computing percentile ranks for each of the 23 morphological indices for each of 22 species. Percentile ranks were then averaged to obtain a mean percentile rank (MPR) for each species that represents its relative locomotor adaptation on a possible scale from 0 (most ambulatory) to 100 (most fossorial). The osteological indices and percentile ranks additionally serve as postcranial characters that aid in distinguishing the species.

Table 1. External and skull measurements of Guatemalan species of the *C. goodwini* group. Statistics are mean ± SD and range. Sample sizes are in parentheses. Lengths are in mm; weights are in g.

Cucurucho	*C. goodwini*	*C. lacertosus*	*C. mam*	Mataquescuintla	Montecristo	*C. oreoryctes*
			External Measurements			
(*n* = 8)	(*n* = 32)	(*n* = 8)	(*n* = 31)	(*n* = 1)	(*n* = 3)	(*n* = 18)
Total length (TOT)						
103 ± 3	113 ± 6	110 ± 4	103 ± 5	113	123 ± 5	112 ± 5
98–107	103–128	105–116	86–111		118–127	101–119
Head-and-body length (HB)						
75 ± 2	84 ± 5	82 ± 4	75 ± 4	86	92 ± 4	82 ± 6
71–77	75–94	75–87	64–81		88–96	71–90
Length of tail (TL)						
28 ± 1	29 ± 2	28 ± 2	29 ± 2	27	31 ± 1	30 ± 2
26–30	25–34	24–30	22–32		30–31	27–32
Length of hind foot (HF)						
14 ± 1	15 ± 1	14 ± 1	14 ± 1	14	15 ± 1	14 ± 1
12–15	14–17	12–15	11–16		14–15	11–16
Weight (WT)						
9 ± 1	17 ± 1	15 ± 3	8 ± 1	—	16 ± 1	14 ± 2
8–10	16–19	10–17	7–11		15–17	10–17
	(*n* = 9)	(*n* = 7)	(*n* = 12)			
			Skull Measurements			
(*n* = 8)	(*n* = 24)	(*n* = 8)	(*n* = 26)	(*n* = 1)	(*n* = 1)	(*n* = 13)
Condylobasal length (CBL)						
20.0 ± 0.3	21.0 ± 0.5	21.5 ± 0.6	19.9 ± 0.4	20.4	20.8	21.1 ± 0.4
19.6–20.4	20.0–21.8	20.8–22.8	18.8–20.4			20.2–21.6
	(*n* = 19)		(*n* = 22)			
Breadth of braincase (BB)						
10.7 ± 0.2	11.2 ± 0.3	11.0 ± 0.3	10.2 ± 0.2	10.6	10.8	10.9 ± 0.2
10.5–11.0	10.8–11.6	10.8–11.6	10.0–10.7			10.5–11.3
	(*n* = 18)	(*n* = 7)	(*n* = 21)			
Breadth of zygomatic plate (ZP)						
1.9 ± 0.1	1.9 ± 0.1	2.1 ± 0.2	2.0 ± 0.1	2.1	1.8	2.0 ± 0.1
1.7–2.1	1.6–2.2	1.8–2.5	1.6–2.1			1.8–2.3

Table 1. (cont.)

Cucurucho	*C. goodwini*	*C. lacertosus*	*C. mam*	Mataquescuintla	Montecristo	*C. oreoryctes*
Interorbital Breadth (IO)						
5.3 ± 0.1	5.6 ± 0.2	5.3 ± 0.2	5.2 ± 0.2	5.3	5.6	5.5 ± 0.2
5.2–5.5	5.3–5.8	5.1–5.7	4.8–5.4			5.3–6.0
Breadth across U1s (U1B)						
2.6 ± 0.1	2.7 ± 0.1	2.7 ± 0.1	2.5 ± 0.1	2.7	2.8	2.7 ± 0.1
2.5–2.8	2.6–2.9	2.6–2.9	2.3–2.6			2.6–2.9
	(*n* = 23)		(*n* = 25)			
Breadth across U3s (U3B)						
3.1 ± 0.1	3.3 ± 0.1	3.3 ± 0.1	3.0 ± 0.1	3.1	3.3	3.3 ± 0.1
3.0–3.3	3.0–3.4	3.2–3.5	2.9–3.2			3.1–3.5
			(*n* = 25)			
Breadth across M2s (M2B)						
6.0 ± 0.1	6.2 ± 0.2	5.9 ± 0.2	5.7 ± 0.1	6.0	6.2	6.2 ± 0.2
5.9–6.1	6.0–6.7	5.7–6.3	5.4–5.9			5.9–6.4
Palatal Length (PL)						
8.6 ± 0.2	9.2 ± 0.2	9.3 ± 0.3	8.7 ± 0.2	8.8	9.1	9.4 ± 0.2
8.4–9.0	8.8–9.5	9.0–10.1	8.1–9.1			9.1–9.8
Length of upper toothrow (TR)						
7.5 ± 0.3	7.9 ± 0.2	8.0 ± 0.3	7.6 ± 0.2	7.6	7.8	8.3 ± 0.3
7.1–7.8	7.5–8.3	7.7–8.6	7.2–8.0			7.7–8.8
Length of unicuspid toothrow (UTR)						
2.7 ± 0.1	2.7 ± 0.1	2.8 ± 0.1	2.7 ± 0.1	2.6	2.5	2.9 ± 0.1
2.4–2.8	2.5–2.9	2.7–2.9	2.5–2.8			2.6–3.1
Length of upper molariform toothrow (MTR)						
5.3 ± 0.2	5.6 ± 0.2	5.6 ± 0.2	5.3 ± 0.1	5.3	5.7	5.7 ± 0.2
5.0–5.6	5.3–5.9	5.4–5.8	5.0–5.5			5.3–6.0
Mandible length (ML)						
6.3 ± 0.3	6.6 ± 0.2	6.4 ± 0.2	6.2 ± 0.2	6.5	—	6.9 ± 0.2
5.6–6.5	6.2–7.0	6.2–6.8	5.7–6.5			6.7–7.3
	(*n* = 25)		(*n* = 28)			

Table 1. (cont.)

Cucurucho	*C. goodwini*	*C. lacertosus*	*C. mam*	Mataquescuintla	Montecristo	*C. oreoryctes*
Height of coronoid process (HCP)						
4.6 ± 0.2	4.8 ± 0.1	4.6 ± 0.1	4.4 ± 0.2	4.7	4.8	4.8 ± 0.1
4.5–4.9	4.6–5.2	4.5–4.8	4.1–4.8			4.6–4.9
	(*n* = 25)		(*n* = 28)			
Height of coronoid valley (HCV)						
2.9 ± 0.1	3.0 ± 0.1	2.9 ± 0.1	2.8 ± 0.1	3.0	2.8	3.1 ± 0.1
2.8–3.1	2.8–3.4	2.8–3.1	2.6–3.0			2.9–3.2
	(*n* = 25)					
Height of articular condyle (HAC)						
4.1 ± 0.1	4.2 ± 0.1	4.1 ± 0.2	3.9 ± 0.1	4.1	4.1	4.2 ± 0.1
4.0–4.3	3.8–4.6	3.9–4.5	3.7–4.1			4.1–4.3
	(*n* = 25)		(*n* = 28)			(*n* = 12)
Articular condyle to M_3 (AC3)						
5.2 ± 0.2	5.5 ± 0.2	5.4 ± 0.3	5.2 ± 0.2	5.3	5.6	5.7 ± 0.1
5.1–5.6	5.2–5.9	5.1–5.8	4.8–5.5			5.5–6.0
	(*n* = 25)		(*n* = 28)			(*n* = 12)
Length of lower toothrow (TRD)						
6.0 ± 0.2	6.4 ± 0.2	6.4 ± 0.2	6.1 ± 0.2	6.2	6.5	6.5 ± 0.2
5.8–6.3	6.1–6.7	6.2–6.8	5.8–6.3			6.1–6.8
			(*n* = 28)			
Length of lower molar row (M13)						
4.4 ± 0.2	4.7 ± 0.1	4.6 ± 0.1	4.3 ± 0.1	4.6	4.8	4.8 ± 0.2
4.2–4.7	4.4–4.9	4.5–4.9	4.1–4.5			4.5–5.0
			(*n* = 28)			
Length of M_1 (M1L)						
1.8 ± 0.1	1.9 ± 0.1	1.9 ± 0.1	1.7 ± 0.1	1.9	2.0	1.8 ± 0.1
1.7–1.9	1.8–2.1	1.8–2.0	1.6–1.8			1.7–1.9
			(*n* = 28)			
Breadth of articular condyle (BAC)						
3.2 ± 0.1	3.3 ± 0.1	3.3 ± 0.1	3.0 ± 0.1	3.2	3.3	3.2 ± 0.1
3.1–3.4	3.0–3.6	3.2–3.6	2.8–3.2			3.2–3.3
	(*n* = 25)		(*n* = 28)			(*n* = 5)

Table 2. External and skull measurements for species of the *C. parvus* group (*C. orophila*, *C. tropicalis*) and *C. nigrescens* group (*C. mayensis*, *C. merriami*) known to occur in El Salvador, Guatemala, and Honduras. These are compared with the range of means ([a]) and the range of measurements ([b]) for seven El Salvadoran and Guatemalan species of the *C. goldmani* group (Table 1). Statistics are mean ± *SD* and range. Sample sizes are in parentheses. Lengths are in mm; weights are in g.

C. orophila	*C. tropicalis*	*C. mayensis*	*C. merriami*	*C. goldmani* group (ranges)
External Measurements				
(*n* = 29)	(*n* = 19)	(*n* = 17)	(*n* = 44)	(*n* = 7 spp.)
Total length (TOT)				
88 ± 8	92 ± 7	97 ± 8	97 ± 7	103–123[a]
68–99	73–103	87–118	83–108	86–128[b]
Head-and-body length (HB)				
62 ± 7	69 ± 6	68 ± 7	69 ± 5	75–92
48–77	53–78	60–90	59–77	64–96
Length of tail (TL)				
21 ± 2	23 ± 3	29 ± 2	28 ± 3	27–31
17–24	18–29	24–33	21–34	22–34
Relative length of tail (%TL)				
34 ± 4	33 ± 4	42 ± 5	41 ± 5	31–38
27–42	25–41	31–49	30–50	28–45
Length of hind foot (HF)				
11 ± 1	12 ± 1	12 ± 1	12 ± 1	14–15
6–13	11–13	10–13	8–14	11–17
	(*n* = 15)	(*n* = 13)	(*n* = 42)	
Weight (WT)				
6 ± 2	7 ± 1	6 ± 1	7 ± 1	8–17
3–10	5–8	4–8	5–9	7–19
(*n* = 16)	(*n* = 5)	(*n* = 11)	(*n* = 26)	
Skull Measurements				
(*n* = 27)	(*n* = 19)	(*n* = 20)	(*n* = 34)	
Condylobasal length (CBL)				
16.9 ± 0.4	17.7 ± 0.6	19.2 ± 0.5	19.5 ± 0.5	19.9–21.5
16.1–17.7	16.8–18.6	18.2–20.0	18.7–20.9	18.8–22.8
(*n* = 17)	(*n* = 14)	(*n* = 16)		

Table 2. (cont.)

C. orophila	*C. tropicalis*	*C. mayensis*	*C. merriami*	*C. goldmani* group (ranges)
Breadth of braincase (BB)				
8.3 ± 0.3	8.7 ± 0.4	9.2 ± 0.3	9.5 ± 0.2	10.2–11.2
7.8–8.8	7.9–9.3	8.8–9.8	8.7–10.0	10.0–11.6
(*n* = 16)	(*n* = 14)	(*n* = 14)		
Breadth of zygomatic plate (ZP)				
1.6 ± 0.2	1.7 ± 0.1	2.3 ± 0.1	2.3 ± 0.2	1.8–2.1
1.3–2.0	1.5–1.9	2.1–2.5	2.0–2.7	1.6–2.3
Interorbital Breadth (IO)				
4.0 ± 0.1	4.2 ± 0.2	4.4 ± 0.2	4.7 ± 0.2	5.2–5.6
3.7–4.3	4.0–4.5	4.1–4.8	4.2–4.9	4.8–6.0
	(*n* = 18)			
Breadth across U^1s (U1B)				
2.4 ± 0.1	2.4 ± 0.1	2.5 ± 0.1	2.6 ± 0.1	2.5–2.8
2.2–2.5	2.3–2.6	2.2–2.7	2.1–2.8	2.3–2.9
Breadth across U^3s (U3B)				
2.7 ± 0.1	2.8 ± 0.1	3.0 ± 0.1	3.0 ± 0.1	3.0–3.3
2.4–2.8	2.6–3.0	2.8–3.3	2.7–3.3	2.9–3.5
Breadth across M^2s (M2B)				
5.2 ± 0.2	5.5 ± 0.2	5.5 ± 0.1	5.8 ± 0.2	5.7–6.2
4.9–5.9	5.2–5.9	5.3–5.7	5.2–6.3	5.4–6.7
Palatal Length (PL)				
7.2 ± 0.3	7.5 ± 0.3	8.4 ± 0.4	8.5 ± 0.3	8.6–9.4
6.8–7.8	7.1–8.1	7.8–9.1	7.9–9.5	8.1–10.1
Length of upper toothrow (TR)				
6.3 ± 0.2	6.6 ± 0.2	7.4 ± 0.3	7.4 ± 0.3	7.5–8.3
5.9–6.7	6.3–7.3	6.9–8.0	6.8–8.4	7.1–8.8
Length of unicuspid toothrow (UTR)				
2.1 ± 0.1	2.2 ± 0.1	2.6 ± 0.2	2.5 ± 0.1	2.5–2.9
1.8–2.3	2.1–2.5	2.1–3.1	2.2–2.8	2.4–3.1
Length of upper molariform toothrow (MTR)				
4.5 ± 0.1	4.8 ± 0.2	5.1 ± 0.2	5.4 ± 0.2	5.3–5.7
4.2–4.7	4.5–5.2	4.8–5.5	5.0–6.0	5.0–6.0

Table 2. (cont.)

C. orophila	*C. tropicalis*	*C. mayensis*	*C. merriami*	*C. goldmani* group (ranges)
Mandible length (ML)				
5.4 ± 0.2	5.8 ± 0.2	6.3 ± 0.3	6.6 ± 0.3	6.2–6.9
4.8–5.9	5.3–6.1	5.8–7.0	5.8–7.2	5.6–7.3
Height of coronoid process (HCP)				
4.1 ± 0.1	4.4 ± 0.2	5.2 ± 0.3	5.0 ± 0.2	4.4–4.8
3.9–4.3	4.1–4.7	4.8–5.7	4.5–5.4	4.1–5.2
Height of coronoid valley (HCV)				
2.4 ± 0.2	2.6 ± 0.2	2.9 ± 0.1	2.9 ± 0.2	2.8–3.1
2.1–2.8	2.3–2.9	2.7–3.2	2.4–3.3	2.6–3.4
Height of articular condyle (HAC)				
3.3 ± 0.2	3.5 ± 0.2	3.9 ± 0.2	3.8 ± 0.2	3.9–4.2
2.8–3.7	3.3–4.0	3.5–4.4	3.3–4.3	3.7–4.6
Articular condyle to M_3 (AC3)				
4.1 ± 0.2	4.4 ± 0.2	4.7 ± 0.2	4.7 ± 0.2	5.2–5.7
3.7–4.4	4.2–4.9	4.4–5.2	4.3–5.2	4.8–6.0
Length of lower toothrow (TRD)				
4.9 ± 0.2	5.2 ± 0.2	5.6 ± 0.2	5.7 ± 0.2	6.0–6.5
4.6–5.3	4.9–5.6	5.3–6.0	5.3–6.4	5.8–6.8
Length of lower molar row (M13)				
3.7 ± 0.1	3.9 ± 0.1	4.2 ± 0.2	4.4 ± 0.2	4.3–4.8
3.4–3.9	3.7–4.2	3.9–4.5	4.1–4.9	4.1–5.0
Length of M_1 (M1L)				
1.5 ± 0.1	1.5 ± 0.1	1.7 ± 0.1	1.8 ± 0.1	1.7–2.0
1.3–1.6	1.4–1.7	1.6–1.9	1.6–1.9	1.6–2.1
Breadth of articular condyle (BAC)				
2.6 ± 0.1	2.8 ± 0.2	3.0 ± 0.1	3.0 ± 0.2	3.0–3.3
2.4–2.7	2.5–3.2	2.8–3.3	2.6–3.3	2.8–3.6

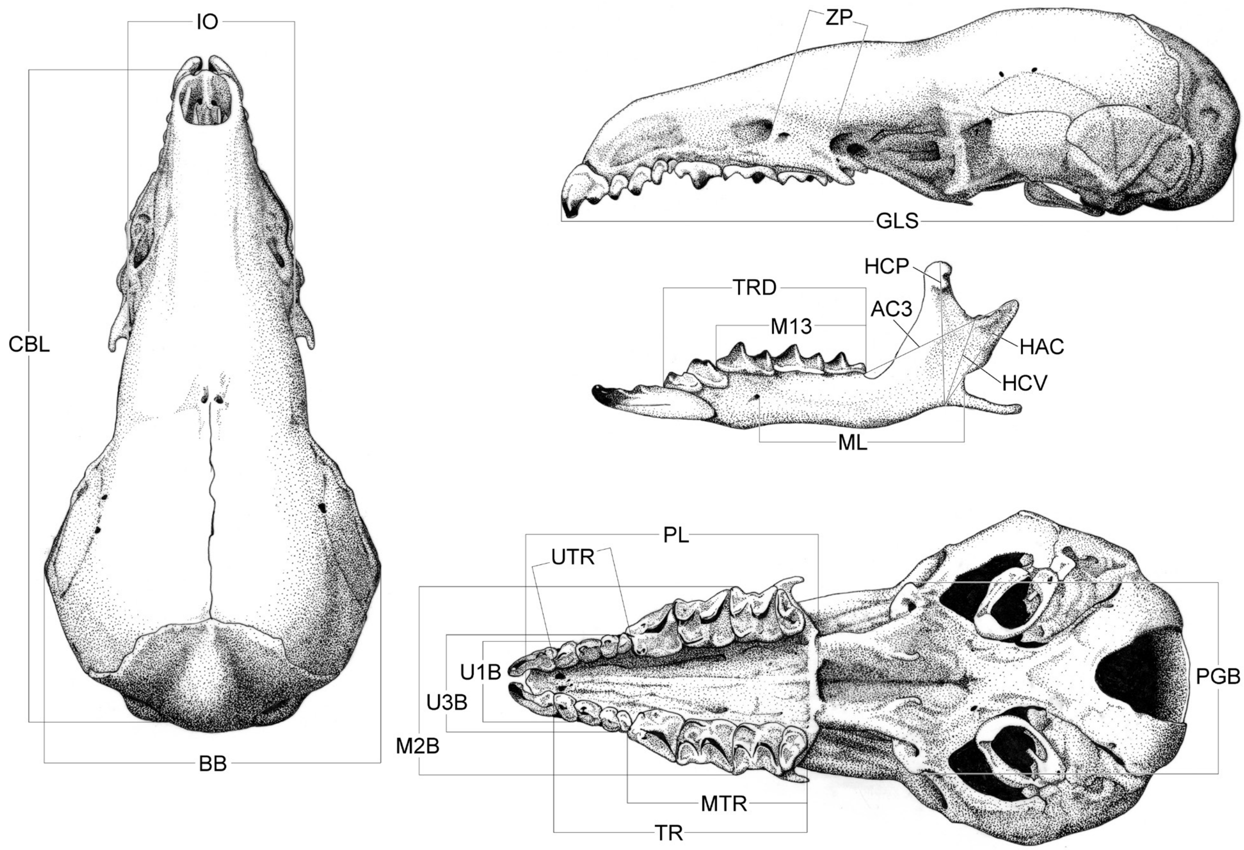

Figure 2. Skull measurements. Cranial abbreviations: breadth of braincase, BB; condylobasal length, CBL; greatest length of skull, GLS; interorbital breadth, IO; palatal breadth across M^2s, M2B; length of upper molariform toothrow, P^4 to M^3, MTR; postglenoid breadth, PGB; palatal length, PL; length of upper toothrow, U^1 to M^3, TR; breadth across 1st unicuspids, U1B; breadth across 3rd unicuspids, U3B; length of unicuspid toothrow, U^1 to U^4, UTR; zygomatic plate breadth, ZP. Dentary abbreviations: articular condyle to posterior edge of M_3, AC3; height of coronoid process, HCP; height of coronoid valley, HCV; height of articular condyle, HAC; length of lower molar row, M_1 to M_3, M13; mandible length, from inferior sigmoid notch to posterior edge of mental foramen, ML; length of lower toothrow, P_3 to M_3, TRD.

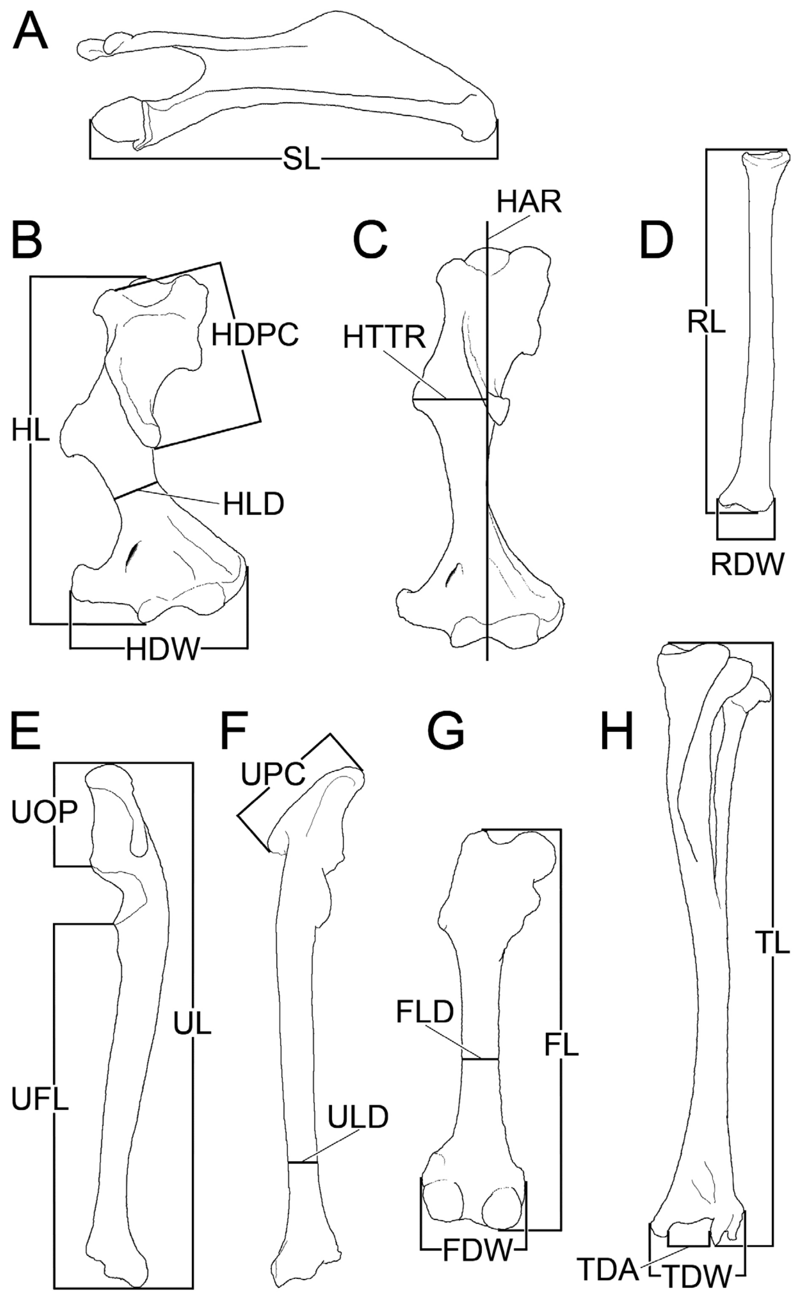

Figure 3. Postcranial measurements. Abbreviations—A, scapula: greatest length of scapula, SL. B, humerus: length of humerus, HL; distal width of humerus, HDW; length of deltopectoral crest, HDPC. C, humerus: axis of rotation of the humerus, HAR; least mediolateral diameter of humerus, HLD; length from head of humerus to distal edge of teres tubercle, HTT; teres tubercle input lever for rotation, HTTR. D, radius: length of radius, RL; distal width of radius, RDW. E, ulna: total length, UL; functional length, UFL; length of olecranon process, UOP. F, ulna: width of proximal crest, UPC; least mediolateral diameter, ULD. G, femur: length, FL; distal width, FDW; least mediolateral diameter, FLD. H, tibiofibula: length, TL; width of distal articular surface, TDA; distal width, TDW.

Table 3. Mean postcranial measurements for 23 species of *Cryptotis*. Abbreviations are explained in Figure 3. Species are listed in order by increasing mean percentile rank (see Table 9:MPR).

Species	SL	HL	HDW	HDPC	HLD	HTTR	HAR	HTT	RL	RDW	UL	UFL	UOP	UPC	ULD	FL	FDW	FLD	TL	TDA	TDW
C. merus	7.09	7.56	2.71	3.48	0.66	0.90	7.30	2.70	–	–	–	–	–	–	–	8.55	1.88	0.78	11.86	0.75	1.83
C. parvus	6.21	6.20	2.23	2.63	0.54	1.00	5.95	2.39	6.36	0.82	8.26	6.16	1.10	1.45	0.35	7.22	1.64	0.59	10.48	0.58	1.41
C. tropicalis	6.87	6.83	2.31	3.09	0.67	1.16	6.61	2.77	7.00	0.88	9.23	7.06	1.23	1.69	0.42	7.84	1.64	0.62	11.57	0.68	1.57
C. nigrescens	7.38	7.89	2.76	3.37	0.71	1.39	7.59	2.96	6.89	0.87	9.23	6.78	1.37	1.93	0.48	8.59	1.90	0.81	11.72	0.74	1.60
C. merriami	7.33	7.77	2.69	3.44	0.74	1.24	7.43	2.80	7.24	0.87	9.63	7.04	1.41	1.89	0.47	8.47	1.85	0.83	12.08	0.71	1.64
C. meridensis	8.22	8.44	3.38	3.70	0.86	1.49	8.04	3.58	8.73	1.21	11.83	8.56	1.81	2.23	0.54	9.38	2.34	0.84	15.52	0.92	2.08
C. phillipsii	–	7.77	3.25	3.27	0.83	1.68	7.38	3.13	–	–	–	–	–	–	–	–	–	–	–	–	–
C. monteverdensis	–	8.33	3.58	3.61	0.82	1.45	7.95	3.63	–	–	–	–	–	–	–	–	–	–	–	–	–
C. endersi	8.22	8.59	3.57	3.61	0.77	1.67	8.33	3.42	–	–	–	–	1.76	2.30	0.56	9.53	2.59	0.89	–	–	–
C. thomasi	8.93	8.83	–	3.85	0.95	1.92	8.04	3.57	–	–	–	–	–	–	–	9.84	2.31	0.95	–	–	–
C. mexicanus	8.06	7.29	3.32	3.19	0.79	1.69	6.82	3.35	–	–	–	–	–	–	–	–	–	–	–	–	–
C. gracilis	7.52	7.07	3.10	3.23	0.77	1.40	6.73	3.06	–	–	–	–	–	–	–	7.74	2.10	0.81	13.57	0.84	1.95
C. celaque	8.84	7.89	3.99	3.54	0.99	2.29	7.38	3.61	8.42	1.18	12.16	8.33	2.17	2.75	0.66	9.00	2.51	0.83	–	–	–
Mataquescuintla	9.25	8.14	4.28	3.38	1.02	2.40	7.59	3.84	–	–	–	–	2.44	2.92	0.74	9.92	2.51	0.95	–	–	–
C. mccarthyi	–	8.04	4.08	3.48	1.04	2.25	7.55	3.45	–	–	–	–	–	–	–	–	–	–	–	–	–
C. mam	8.83	7.81	4.02	3.60	1.02	2.37	7.37	3.78	8.32	1.32	11.80	8.16	2.01	2.70	0.58	8.89	2.33	0.79	13.59	0.88	1.99
C. magnimanus	–	8.27	4.50	3.55	1.07	2.32	7.86	3.92	–	–	–	–	–	–	–	–	–	–	–	–	–
C. oreoryctes	9.63	8.29	4.46	3.66	1.11	2.63	7.78	3.96	8.60	1.31	12.34	8.23	2.39	3.01	0.61	9.91	2.66	0.93	15.40	1.07	2.16
Cucurucho	8.76	7.77	4.25	3.85	0.97	2.22	7.52	3.67	8.06	1.27	9.03	5.83	2.43	2.80	0.67	9.14	2.53	0.90	–	–	–
C. cavatorculus	–	8.35	4.34	4.18	1.04	2.50	7.88	3.79	8.08	1.24	11.63	8.17	2.32	2.77	0.55	–	–	–	–	–	–
C. lacertosus	10.87	8.83	5.09	3.87	1.32	2.70	8.17	4.15	9.01	1.54	13.31	8.83	2.46	3.57	0.80	9.58	2.73	0.94	14.08	1.07	2.22
C. goodwini	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

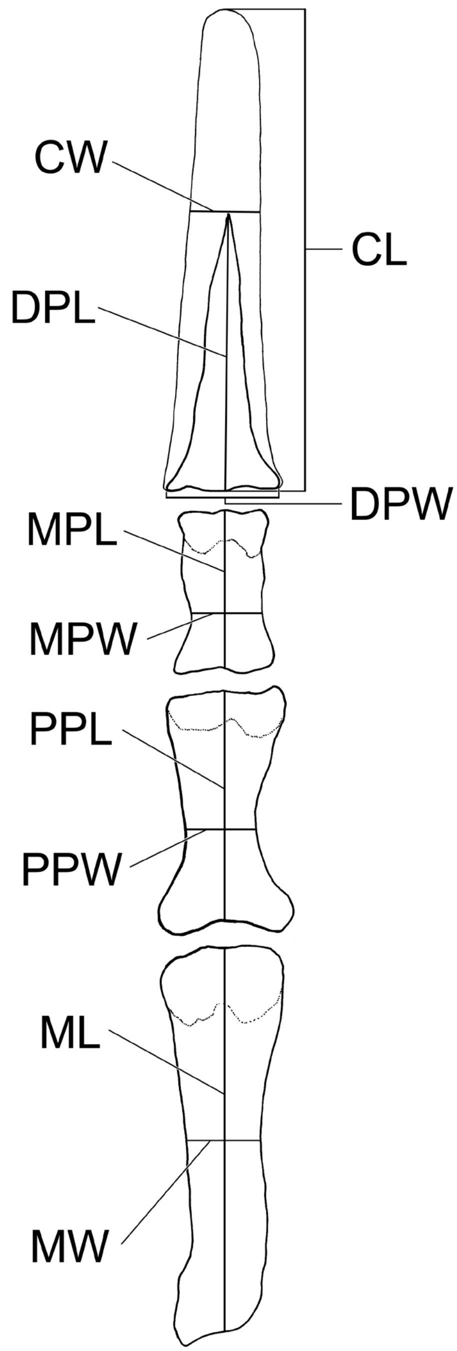

Figure 4. Ray III of the manus illustrating variables measured on the manus and pes. Abbreviations—length of claw, CL; width of claw, CW; length of metacarpal, ML; length of proximal phalanx, PPL; length of middle phalanx, MPL; length of distal phalanx, DPL; width of metacarpal, MW; width of proximal phalanx, PPW; width of middle phalanx, MPW; width of distal phalanx, DPW. Pes measurements are preceded by an "h" (e.g., hML represents the length of the metatarsal).

Table 4. Mean measurements of bones of the manus and pes for 23 species of *Cryptotis*. Abbreviations are explained in Figure 4. Species are listed in order by increasing mean percentile rank (see Table 9:MPR).

Manus measurements

Species	3MW	3ML	3PPW	3PPL	3MPW	3MPL	3DPW	3DPL	3CW	3CL
C. merus	0.27	2.75	0.27	1.57	0.24	0.96	0.22	0.71	0.26	1.57
C. parvus	0.21	2.25	0.21	1.21	0.20	0.85	0.31	0.67	0.17	1.51
C. tropicalis	0.25	2.48	0.24	1.48	0.21	0.95	0.26	0.63	0.17	1.48
C. nigrescens	0.31	2.70	0.27	1.60	0.27	0.94	0.40	0.82	0.21	1.62
C. merriami	0.24	2.50	0.28	1.54	0.26	0.92	0.35	0.75	0.26	1.43
C. meridensis	0.36	3.30	0.36	1.54	0.34	1.05	–	1.09	–	2.17
C. phillipsii	–	–	–	–	–	–	–	–	–	–
C. monteverdensis	–	–	–	–	–	–	–	–	–	–
C. endersi	–	–	–	–	0.31	0.97	0.42	1.08	0.28	2.40
C. thomasi	0.38	3.11	0.38	1.61	0.36	0.97	0.52	1.10	0.31	2.26
C. mexicanus	0.37	2.57	0.35	1.47	0.35	0.83	0.25	1.28	–	2.32
C. gracilis	0.30	2.56	0.29	1.49	0.28	0.84	0.41	1.01	0.27	2.01
C. celaque	0.45	2.70	0.44	1.49	0.45	0.78	0.56	1.66	0.43	2.90
Mataquescuintla	0.51	2.63	0.47	1.35	0.51	1.12	0.64	1.72	0.49	3.04
C. mccarthyi	0.47	2.44	0.46	1.43	0.49	0.79	0.61	1.64	0.44	2.88
C. mam	0.42	2.56	0.43	1.54	0.44	0.93	0.61	1.74	0.46	3.13
C. magnimanus	–	–	–	–	–	–	–	–	–	–
C. oreoryctes	0.47	2.72	0.50	1.56	0.50	0.95	0.66	1.91	0.49	3.35
Cucurucho	0.47	2.53	0.47	1.53	0.45	1.11	0.60	1.78	0.45	3.25
C. cavatorculus	0.52	2.74	0.49	1.63	0.53	0.91	0.74	1.93	0.52	3.18
C. lacertosus	0.53	2.63	0.55	1.54	0.52	1.02	0.70	1.87	0.50	3.25
C. goodwini	0.54	2.65	0.56	1.62	0.55	1.02	0.76	2.02	0.58	3.36

Table 4. (cont.)

Pes measurements

Species	3hMW	3hML	3hPPW	3hPPL	3hMPW	3hMPL	3hDPW	3hDPL	3hCW	3hCL
C. merus	0.42	3.88	0.26	1.71	0.28	0.90	0.39	0.76	0.27	1.60
C. parvus	0.23	3.35	0.21	1.43	0.18	0.82	0.27	0.71	0.20	1.44
C. tropicalis	0.29	3.74	0.23	1.58	0.20	0.77	0.29	0.78	0.26	1.42
C. nigrescens	0.40	3.70	0.27	1.78	0.27	0.96	0.38	0.93	0.23	1.69
C. merriami	0.39	3.70	0.29	1.78	0.25	0.97	0.34	0.75	0.25	1.49
C. meridensis	–	–	–	1.81	0.33	1.08	0.49	1.27	0.28	1.96
C. phillipsii	–	–	–	–	–	–	–	–	–	–
C. monteverdensis	–	–	–	–	–	–	–	–	–	–
C. endersi	0.43	4.53	0.32	2.04	0.33	1.17	0.48	0.92	0.24	1.66
C. thomasi	0.45	4.43	0.34	1.77	0.32	1.02	0.47	1.11	0.31	2.00
C. mexicanus	–	–	–	–	–	–	–	–	–	–
C. gracilis	0.41	4.06	0.30	1.80	0.30	1.01	0.42	1.09	0.29	1.91
C. celaque	0.46	3.98	0.34	1.79	0.36	0.82	0.48	1.35	0.31	2.05
Mataquescuintla	0.41	4.42	–	1.71	0.31	1.00	0.50	1.43	–	2.19
C. mccarthyi	0.49	3.78	0.34	1.70	0.37	0.85	0.50	1.41	0.30	2.33
C. mam	0.45	3.97	0.31	1.66	0.33	0.90	0.47	1.31	0.31	2.33
C. magnimanus	–	–	–	–	–	–	–	–	–	–
C. oreoryctes	0.50	4.35	0.36	1.75	0.38	0.94	0.54	1.50	0.33	2.42
Cucurucho	0.48	4.13	0.31	1.67	0.33	0.99	0.47	1.27	0.32	2.26
C. cavatorculus	0.53	3.98	0.35	1.74	0.36	–	0.53	1.44	0.41	2.08
C. lacertosus	0.49	3.95	0.37	1.66	0.37	0.96	0.53	1.49	0.35	2.48
C. goodwini	–	–	–	–	–	–	–	–	–	–

Table 5. External and skull characters of Guatemalan species of the *C. goodwini* group. Statistics are mean ± *SD* and range. Sample sizes are in parentheses.

Cucurucho (*n* = 8)	*C. goodwini* (*n* = 20)	*C. lacertosus* (*n* = 8)	*C. mam* (*n* = 22)	Mataquescuintla (*n* = 1)	Montecristo (*n* = 1)	*C. oreoryctes* (*n* = 13)
			Relative length of tail (TL/HB x 100)			
38 ± 2	35 ± 3	34 ± 4	38 ± 3	31	33 ± 1	38 ± 4
34–40	30–41	28–40	33–44		32–34	31–45
	(*n* = 33)		(*n* = 28)		(*n* = 3)	
			Relative breadth of interorbital area (IO/CBL x 100)			
26.6 ± 0.5	26.6 ± 0.9	24.6 ± 0.2	25.9 ± 0.8	26.0	26.9	26.3 ± 0.9
25.9–27.2	25.2–28.4	24.3–25.0	24.3–27.6			25.1–28.0
			Relative breadth of braincase (BB/CBL x 100)			
53.5 ± 1.1	52.6 ± 0.9	51.5 ± 0.9	51.4 ± 1.3	52.0	51.9	51.6 ± 1.3
51.3–54.6	50.5–53.7	50.9–53.4	49.0–54.3			49.7–53.8
	(*n* = 16)	(*n* = 7)	(*n* = 21)			
			Relative length of rostrum (PL/CBL x 100)			
43.0 ± 0.6	43.6 ± 0.7	43.5 ± 0.8	43.5 ± 0.9	43.1	43.8	44.9 ± 0.8
42.3–43.9	42.5–44.8	42.1–44.7	42.1–45.0			43.6–46.4
			Relative breadth of zygomatic plate (ZP/CBL x 100)			
9.5 ± 0.6	9.3 ± 0.8	9.7 ± 1.2	9.8 ± 0.6	10.3	8.7	9.7 ± 0.7
8.7–10.4	7.4–10.8	7.9–11.8	8.0–10.4			8.3–10.9
			Relative breadth of zygomatic plate (ZP/PL x 100)			
22.1 ± 1.2	21.3 ± 1.8	22.4 ± 3.0	22.6 ± 1.4	23.9	19.8	21.7 ± 1.5
20.3–23.6	17.2–24.4	17.8–27.2	18.2–24.7			18.9–23.8
			Relative length of unicuspid row (UTR/CBL x 100)			
13.3 ± 0.5	13.0 ± 0.5	13.0 ± 0.3	13.5 ± 0.3	12.7	12.0	13.6 ± 0.5
12.1–13.9	12.0–14.0	12.6–13.6	12.9–14.1			12.4–14.5
			Relative breadth of palate (M2B/PL x 100)			
69.2 ± 2.1	68.1 ± 2.0	63.6 ± 1.5	65.5 ± 1.4	68.2	68.1	65.6 ± 1.6
65.6–72.2	64.2–71.6	62.4–66.7	63.2–68.2			63.3–68.2

Table 5. (cont.)

Cucurucho (n = 8)	*C. goodwini* (n = 20)	*C. lacertosus* (n = 8)	*C. mam* (n = 22)	Mataquescuintla (n = 1)	Montecristo (n = 1)	*C. oreoryctes* (n = 13)
Relative height of coronoid process (HCP/ML x 100)						
74.4 ± 5.0	72.5 ± 2.0	71.2 ± 2.2	71.9 ± 2.1	72.3	–	69.9 ± 2.2
68.0–84.2	68.7–76.5	69.2–76.2	67.2–76.3			66.7–73.7
Relative height of coronoid process (HCP/CBL x 100)						
23.2 ± 0.8	22.9 ± 0.6	21.3 ± 0.4	22.2 ± 0.7	23.0	23.1	22.8 ± 0.6
21.9–24.2	21.9–23.9	21.0–22.1	21.8–23.8			21.6–23.7
Relative posterior length of mandible (AC3/ML x 100)						
83.9 ± 5.1	83.8 ± 2.5	84.1 ± 3.7	83.8 ± 2.2	81.5	–	82.6 ± 1.9
78.7–92.8	79.1–87.3	79.7–90.5	78.1–86.9			78.7–85.6
						(n = 12)
Relative extension of articular condyle (AC3/HCP x 100)						
112.8 ± 2.1	115.7 ± 4.0	118.0 ± 3.5	116.6 ± 4.2	112.8	116.7	118.1 ± 3.5
110.2–115.7	110.2–125.5	113.3–124.4	104.2–123.3			114.3–125.8
						(n = 12)
Size of U^4 as % of U^3						
50 ± 6%	46 ± 10%	44 ± 3%	44 ± 8%	71%	48%	56 ± 7%
41–61	33–71	41–48	26–62			47–65
	(n = 16)	(n = 5)	(n = 27)			(n = 5)
Foramen of sinus canal (present)						
0%	17% tiny	0%	0%	no	no	0%
	(n = 12)	(n = 6)	(n = 25)			(n = 3)
Foramen dorsal to dorsal articular facet (present)						
50% tiny	100%	50%	96%	yes (tiny)	–	100%
	(n = 14)	(n = 6)	(n = 25)			(n = 3)
Two obvious dorsal foramina (present)						
25%	80%	100%	88%	yes	yes	66%
	(n = 15)	(n = 6)	(n = 25)			(n = 3)

Table 5. (cont.)

Cucurucho ($n = 8$)	*C. goodwini* ($n = 20$)	*C. lacertosus* ($n = 8$)	*C. mam* ($n = 22$)	Mataquescuintla ($n = 1$)	Montecristo ($n = 1$)	*C. oreoryctes* ($n = 13$)
Distinct foramen on tympanic process of one or both petromastoids						
0%	25% tiny to small ($n = 12$)	0% ($n = 6$)	21% tiny to small ($n = 24$)	no	–	100% small to large ($n = 3$)
Posteroventral border of unicuspids						
convex	concave to convex	concave	concave	convex	convex	concave to convex
Vestigial entoconid of M_3 (present)						
0%	8% ($n = 12$)	0% ($n = 5$)	0% ($n = 25$)	no	?	50% ($n = 2$)

Table 6. Locomotor indices calculated from mean postcranial measurements of 22 species of *Cryptotis* (Tables 3 and 4; Figs. 3 and 4). Abbreviations—intermembral index, **IM** (= [HL + RL]/[FL + TL]); humerofemoral index, **HFI** (= HL/FL); metapodial index, **FOOT** (= 3ML/3hML); distal phalanx length index, **CLAW** (= 3DPL/3hDPL); claw length index, **CLI** (= 3CL/3hCL); scapulohumeral index, **SHI** (= SL/HL); brachial index, **BI** (= RL/HL); shoulder moment index, **SMI** (= HDPC/HL); humeral robustness index, **HRI** (= HLD/HL); humeral rotation lever index, **HTI** (= HTTR/HAL); teres tubercle position index, **TTP** (= HTT/HAL); humeral epicondylar index, **HEB** (= HDW/HL); radial distal width index, **RDW** (= RDW/RL); olecranon length index, **OLI** (= UOP/UFL); triceps metacarpal outforce index, **TMO** (= UOP/[UFL + 3ML]); triceps claw outforce index, **TCO** (= UOP/[UFL + 3ML + 3PPL + 3MPL +3CL]); olecranon crest index, **OCI** (= UPC/UFL); ulnar robustness index, **URI** (= ULD/UFL); relative length of the manual distal phalanx, **%DPL** (= 3DPL/(3ML + 3PPL + 3MPL); relative length of the manual claw, **%CL** (= 3CL/(3ML + 3PPL + 3MPL)]; relative support for the claw, **%CLS** (= 3DPL/3CL); metacarpal width index, **MW3** (= 3MW/3ML); phalangeal index (PI (= (PPL + MPL)/ML); manus proportions index, **MANUS** (= 3PPL/3ML); crural index, **CI** (= TL/FL); pes length index, **PES** (= 3hML/FL); femoral robustness index, **FRI** (= FLD/FL); femoral epicondylar index, **FEB** (= FDW/FL); distal tibiofibular articulation index, **DTA** (= TDA/TDW); relative length of the pedal distal phalanx, **%hDPL** (= 3hDPL/(3hML + 3hPPL + 3hMPL)]; relative length of the pedal claw, **%hCL** (= 3hCL/(3hML + 3hPPL + 3hMPL)]; relative support for the pedal claw, **%hCLS** (= 3hDPL/3hCL). See Woodman and Gaffney (2014) and Woodman and Stabile (2015b) for additional information on the significance and performance of these indices. Species are listed in order by increasing mean percentile rank (Table 9:MPR).

Species	CLAW	CLI	SHI	SMI	HRI	HTI	TTP	HEB	RDW	OLI	OCI	URI
C. merus	93	98	94	46	9	12	37	36	–	–	–	–
C. parvus	94	105	100	42	9	17	40	36	13	18	24	6
C. tropicalis	81	105	101	45	10	18	42	34	13	17	24	6
C. nigrescens	89	96	94	43	9	18	39	35	13	20	29	7
C. merriami	99	96	94	44	9	17	38	35	12	20	27	7
C. meridensis	86	111	97	44	10	18	45	40	14	21	26	6
C. phillipsii	–	–	–	42	11	23	42	42	–	–	–	–
C. monteverdensis	–	–	–	43	10	18	46	43	–	–	–	–
C. endersi	117	145	96	42	9	20	41	42	–	–	–	–
C. thomasi	99	113	101	44	11	24	44		–	–	–	–
C. mexicanus	–	–	110	44	11	25	49	46	–	–	–	–
C. gracilis	93	105	106	46	11	21	46	44	–	–	–	–
C. celaque	123	142	112	45	13	31	49	51	14	26	33	8
Mataquescuintla	120	139	114	41	12	32	51	53	–	–	–	–
C. mccarthyi	117	124	–	43	13	30	46	51	–	–	–	–
C. mam	133	134	113	46	13	32	51	52	16	25	33	7
C. magnimanus	–	–	–	43	13	30	50	54	–	–	–	–
C. oreoryctes	127	138	116	44	13	34	51	54	15	29	37	7
Cucurucho	140	144	113	50	12	29	49	55	16	42	48	11
C. cavatorculus	134	153	–	50	12	32	48	52	15	28	34	7
C. lacertosus	125	131	123	44	15	33	51	58	17	28	40	9
C. goodwini	–	–	–	–	–	–	–	–	–	–	–	–

Table 6. (cont.)

Species	%DPL	%CL	%CLS	MW3	MANUS	PES	FRI	FEB	%hDPL	%hCL	%hCLS
C. merus	13	30	45	10	57	45	9	22	12	25	48
C. parvus	16	35	44	9	54	46	8	23	13	26	49
C. tropicalis	13	30	43	10	60	48	8	21	13	23	55
C. nigrescens	16	31	51	12	59	43	9	22	14	26	55
C. merriami	15	29	52	10	62	44	10	22	12	23	50
C. meridensis	19	37	50	11	47		9	25	–	–	65
C. phillipsii	–	–	–	–	–	–	–	–	–	–	–
C. monteverdensis	–	–	–	–	–	–	–	–	–	–	–
C. endersi	–	–	45	–	–	48	9	27	12	21	56
C. thomasi	19	40	49	12	52	45	10	24	15	28	55
C. mexicanus	26	48	55	15	57	–	–	–	–	–	–
C. gracilis	21	41	50	12	58	53	10	27	16	28	57
C. celaque	33	58	57	17	55	44	9	28	20	31	66
Mataquescuintla	34	59	56	19	51	45	10	25	20	31	65
C. mccarthyi	35	62	57	19	59	–	–	–	22	37	60
C. mam	35	62	56	17	60	45	9	26	20	36	56
C. magnimanus	–	–	–	–	–	–	–	–	–	–	–
C. oreoryctes	36	64	57	17	58	44	9	27	21	34	62
Cucurucho	34	63	55	19	61	45	10	28	19	33	56
C. cavatorculus	37	60	61	19	60	–	–	–	25	36	69
C. lacertosus	36	63	58	20	58	41	10	28	23	38	60
C. goodwini	38	63	60	20	61	–	–	–	–	–	–

RESULTS

Multivariate analyses of skull variables and locomotor analysis of the postcranium revealed the morphometrical and morphological distinctiveness of the three *C. goldmani*-group populations from Cerro Cucurucho, from near Mataquescuintla, and from Cerro Montecristo, and they confirmed each population's distinctiveness from described species of *Cryptotis* known from the region.

Multivariate analyses.—Discriminant function analysis (DFA) of 17 log-transformed skull variables from the three distinctive populations and four species yielded a correct classification rate of 97% (jackknifed classification = 65%; Table 7). The only misclassifications were two *C. goodwini* misidentified as *C. oreoryctes*. A plot of individuals on the first two canonical variates (CV) shows the seven samples as distinct, cohesive clusters, although there is considerable overlap between most adjacent clusters (Fig. 5). The variables all loaded heavily and negatively on the first canonical variate (CV1), which differentiates the species on the basis of overall skull size: the smallest species on CV1 is *C. mam*; the Cucurucho population and *C. lacertosus* are intermediate in size; and *C. goodwini*, the Mataquescuintla population, the Montecristo population, and *C. oreoryctes* generally are larger species. The second canonical variate (CV2) was influenced by various length measures of the skull. This axis distinguishes the longer skulls of *C. lacertosus* and *C. oreoryctes* from the intermediate-length skulls of *C. goodwini*, the Montecristo population, and *C. mam*, and from the shorter skulls of the Cucurucho population and the Mataquescuintla population. Together, the plot on these two axes shows the three samples from Cerro Cucurucho, Mataquescuintla, and Cerro Montecristo as distinct from most other species, except *C. goodwini*. The single specimens in the analysis representing the Mataquescuintla and Montecristo populations fall within the distribution of *C. goodwini*, which occurs along the lower half of CV1 and in the lower left quadrant of the plot. The smaller-sized Cucurucho individuals cluster around the lower half of CV2, where they are separated from most other species, but grade into *C. goodwini* toward the lower left corner.

The second DFA of skull variables focused on the three focal populations and *C. goodwini*, which was most closely associated morphometrically with them in the first analysis. The correct classification rate of the second analysis was 100% (jackknifed classification = 50%; Table 8). A plot of individuals on the first two CVs shows each of the four samples completely separated into distinct regions of the graph (Fig. 6). All variables load heavily and negatively on CV1, which clearly differentiates the larger skulls of *C. goodwini* and of the Montecristo populations from the smaller skulls of the Cucurucho and Mataquescuintla populations. CV2 is most heavily influenced by the length of the unicuspid toothrow (UTR), which clearly separates the Cucurucho population and *C. goodwini* from the Mataquescuintla and Montecristo populations.

Locomotor mode and function.—Among the 22 species analyzed, only nine have complete data for the calculation of all 23 morphological indices (Table 6), preventing comprehensive analysis of the relative locomotor mode for each species. Fifteen or more indices could be calculated for 17 species, providing an adequate level of analysis. Unfortunately, only five indices could be calculated for four species and 11 for one other. The lack of data mostly resulted from the paucity of available skeletons, which, unfortunately, is common for species of small mammals (Bell and Mead 2014). A complete set of 23 indices was obtained for the Cucurucho population and 19 indices for the Mataquescuintla population, providing adequate analysis of the locomotor morphology of both samples.

Percentile rank analysis of functional limb anatomy and locomotor mode among the 22 species resulted in a range of values on the mean percentile rank scale from 20 (most ambulatory: *C. merus*) to 92 (most fossorial: *C. goodwini* [*sensu stricto*]; Table 9). Both the Cucurucho population and the Mataquescuintla population are grouped with other strongly fossorial species of the *C. goldmani* group (Fig. 7) and distant from more ambulatory members of the *C. nigrescens*, *C. parvus*, and *C. thomasi* groups. Within the *C. goldmani* group, the Mataquescuintla population (MPR = 63) ranks lower on the scale, near *C. celaque* (62), whereas, the Cucurucho population (76) is positioned near the more fossorial end of the scale, close to *C. cavatorculus* (78) and *C. lacertosus* (79). Lack of information on the postcranial skeleton of the

Table 7. Discriminant function analysis of all crania. Results from complete DFA of 17 variables from seven species of shrews: (A) Pearson correlations (loadings) of log-transformed input variables with the first three canonical variates (CV); (B) corresponding post hoc classification matrix; and (C) jackknifed classification matrix. Variable abbreviations are explained in Figure 2 and Table 1. Significant correlations are based on Bonferroni probabilities: *, <0.05; **, <0.01; ***, <0.001.

A. Correlation Matrix

Variable	CV1	CV2	CV3
CBL	-0.624***	0.563***	0.357
ZP	-0.024	0.396	0.002
IO	-0.779***	0.082	-0.063
U1B	-0.784***	0.239	0.206
U3B	-0.701***	0.345	0.194
M2B	-0.908***	0.102	0.003
PL	-0.636***	0.703***	0.085
TR	-0.528***	0.676***	-0.116
UTR	-0.192	0.596***	-0.199
MTR	-0.658***	0.537***	0.022
HCP	-0.856***	0.060	-0.059
HCV	-0.782***	0.121	-0.229
HAC	-0.809***	0.023	0.025
AC3	-0.757***	0.370	-0.065
TRD	-0.593***	0.628***	0.003
M13	-0.768***	0.434*	0.053
M1L	-0.632***	0.057	0.520***
Eigenvalues	5.484	2.340	1.870
Canonical correlations	0.920	0.837	0.807
Cumulative proportion of total dispersion (%)	50.9	72.6	90.0

Table 7. (cont.)

B. Classification matrix

Species	Cucurucho	*C. goodwini*	*C. lacertosus*	*C. mam*	Mataques-cuintla	Montecristo	*C. oreoryctes*	% correct
Cucurucho	8	0	0	0	0	0	0	100
C. goodwini	0	16	0	0	0	0	2	89
C. lacertosus	0	0	8	0	0	0	0	100
C. mam	0	0	0	21	0	0	0	100
Mataquescuintla	0	0	0	0	1	0	0	100
Montecristo	0	0	0	0	0	1	0	100
C. oreoryctes	0	0	0	0	0	0	12	100
Total	8	16	8	21	1	1	14	97

C. Jackknifed classification matrix

Species	Cucurucho	*C. goodwini*	*C. lacertosus*	*C. mam*	Mataques-cuintla	Montecristo	*C. oreoryctes*	% correct
Cucurucho	6	2	0	0	0	0	0	75
C. goodwini	3	8	1	0	3	0	3	44
C. lacertosus	0	2	6	0	0	0	0	75
C. mam	1	0	2	17	0	0	1	81
Mataquescuintla	0	1	0	0	0	0	0	0
Montecristo	0	1	0	0	0	0	0	0
C. oreoryctes	0	1	1	1	1	0	8	67
Total	10	15	10	18	4	0	12	65

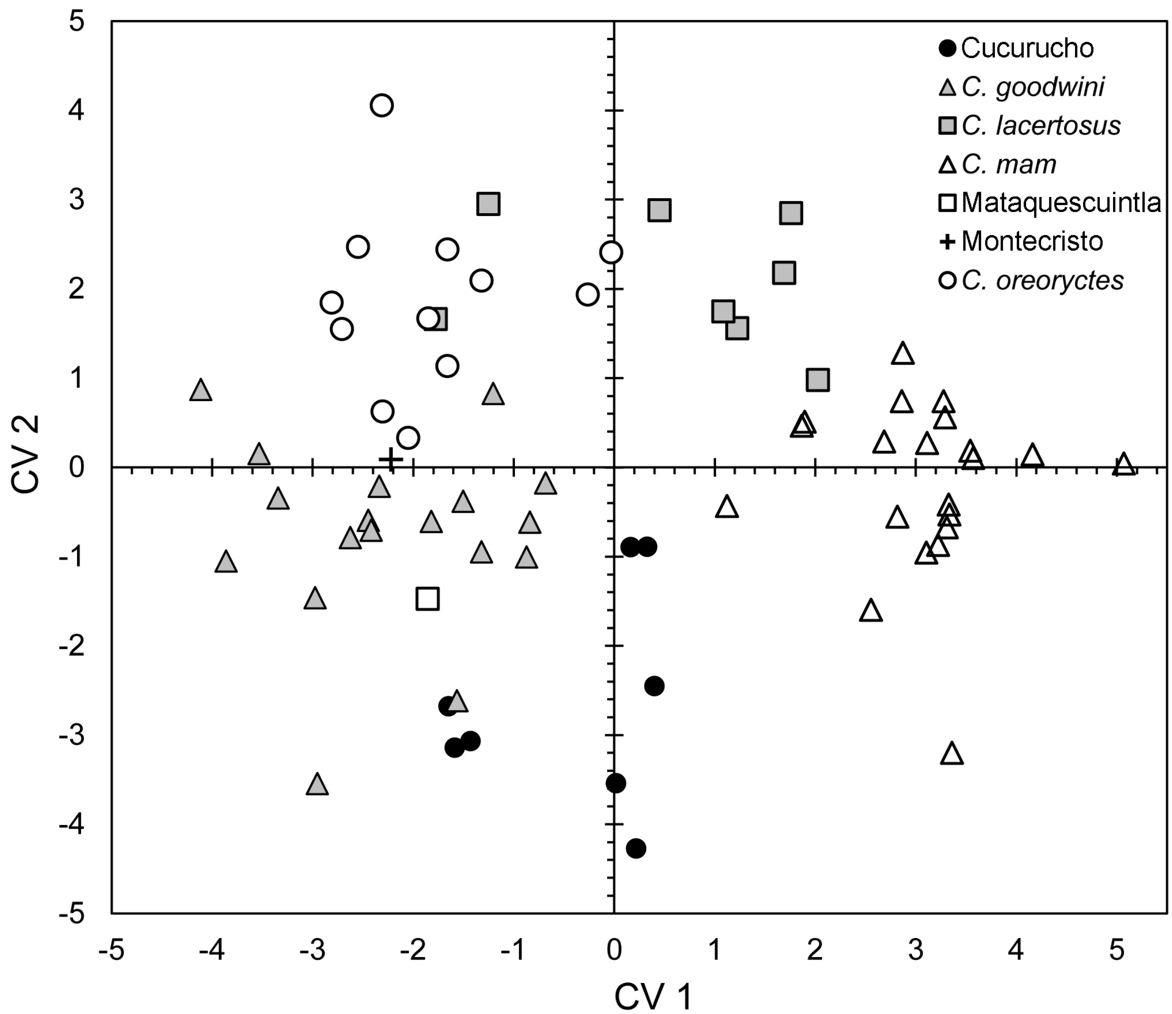

Figure 5. Plot of scores on the first two axes (CV) from DFA of seven species of large-footed shrews from El Salvador and Guatemala.

Table 8. Discriminant function analysis of crania of four species of *Cryptotis*. Results from complete DFA of 17 variables from four species of shrews: (A) Correlations (loadings) of log-transformed input variables with the first two canonical variates (CV); (B) corresponding post hoc classification matrix; and (C) jack-knifed classification matrix. Variable abbreviations are explained in Figure 2 and Table 1. Significant correlations are based on Bonferroni probabilites: *, <0.05; **, 0.01; ***, <0.001.

A. Correlation Matrix

Variable	CV1	CV2	CV3
CBL	-0.746***	-0.046	0.075
ZP	-0.047	0.013	0.450
IO	-0.730**	-0.093	-0.142
U1B	-0.427	0.21	-0.034
U3B	-0.503	-0.055	-0.183
M2B	-0.663**	-0.088	-0.012
PL	-0.839***	-0.038	0.038
TR	-0.704**	-0.097	0.051
UTR	-0.246	-0.467	0.211
MTR	-0.592*	0.039	-0.175
HCP	-0.512	-0.015	0.018
HCV	-0.311	-0.296	0.386
HAC	-0.369	-0.229	0.082
AC3	-0.667**	-0.005	-0.062
TRD	-0.754***	0.129	-0.031
M13	-0.615*	0.190	-0.016
M1L	-0.715**	0.261	0.032
Eigenvalues	8.035	1.759	0.889
Canonical correlations	0.943	0.798	0.686
Cumulative proportion of total dispersion (%)	75.2	91.7	100.0

B. Classification matrix

Species	Cucurucho	*C. goodwini*	Mataquescuintla	Montecristo	% correct
Cucurucho	8	0	0	0	100
C. goodwini	0	18	0	0	100
Mataquescuintla	0	0	1	0	100
Montecristo	0	0	0	1	100
Total	8	18	1	1	100

Table 8. (cont.)

C. Jackknifed classification matrix

Species	Cucurucho	*C. goodwini*	Mataquescuintla	Montecristo	% correct
Cucurucho	5	1	2	0	63
C. goodwini	2	9	2	5	50
Mataquescuintla	1	0	0	0	0
Montecristo	0	1	0	0	0
Total	8	11	4	5	50

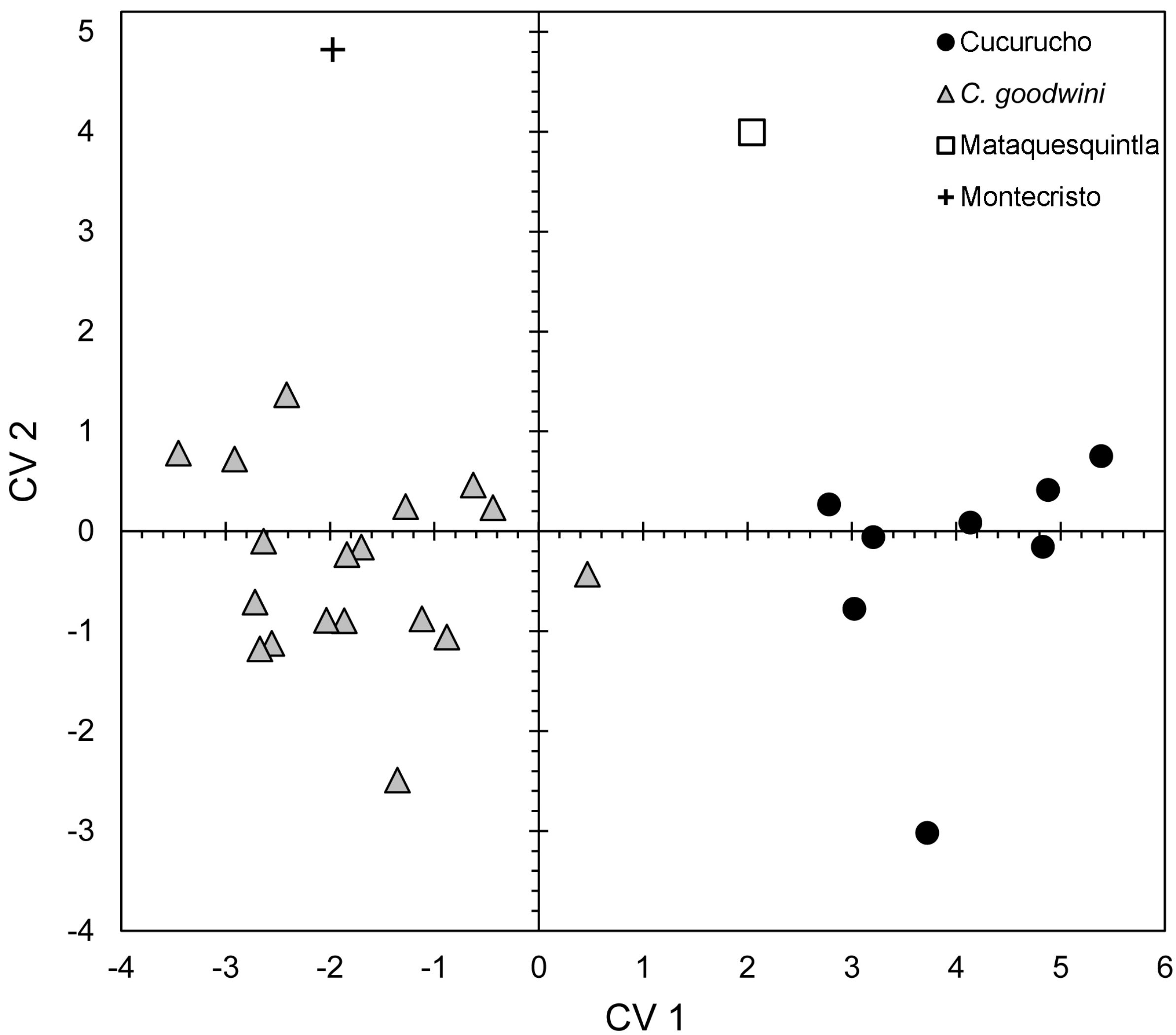

Figure 6. Plot of scores on the first two axes (CV) from DFA of four species of large-footed shrews from El Salvador and Guatemala.

Table 9. Percentile ranks calculated for the 23 locomotor indices in Table 6. The Mean Percentile Rank (MPR) in the last column serves as a general measure of relative locomotor function, from more ambulatory (lower values) to more fossorial (higher values). Species are listed in order by increasing mean percentile rank.

Species	CLAW	CLI	SHI	SMI	HRI	HTI	TTP	HEB	RDW	OLI
C. merus	24	15	9	83	12	2	2	20	–	–
C. parvus	32	26	34	12	12	10	17	20	23	14
C. tropicalis	3	26	44	71	31	24	29	3	23	5
C. nigrescens	15	6	9	29	12	24	12	10	23	27
C. merriami	41	6	9	52	12	10	7	10	5	27
C. meridensis	9	38	28	52	31	24	40	28	45	41
C. phillipsii	–	–	–	12	48	45	29	35	–	–
C. monteverdensis	–	–	–	29	31	24	50	43	–	–
C. endersi	53	91	22	12	12	36	21	35	–	–
C. thomasi	41	44	44	52	48	50	36	–	–	–
C. mexicanus	–	–	59	52	48	55	69	53	–	–
C. gracilis	24	26	53	83	48	40	50	48	–	–
C. celaque	68	79	66	71	83	74	69	60	45	59
Mataquescuintla	62	74	84	2	64	83	90	78	–	–
C. mccarthyi	53	50	–	29	83	67	50	60	–	–
C. mam	85	62	75	83	83	83	90	70	82	50
C. magnimanus	–	–	–	29	83	67	79	85	–	–
C. oreoryctes	79	68	91	52	83	98	90	85	64	86
Cucurucho	97	85	75	95	64	60	69	93	82	95
C. cavatorculus	91	97		95	64	83	60	70	64	73
C. lacertosus	74	56	97	52	98	93	90	98	95	73
C. goodwini	–	–	–	–	–	–	–	–	–	–

Table 9 (cont.)

Species	OCI	URI	%DPL	%CL	%CLS	MW3	MANUS	PES	FRI	FEB
C. merus	–	–	6	11	16	14	33	54	37	17
C. parvus	9	14	22	25	8	3	19	75	7	30
C. tropicalis	9	14	6	11	3	14	75	86	7	3
C. nigrescens	41	50	22	19	39	36	61	11	37	17
C. merriami	32	50	14	3	45	14	97	25	80	17
C. meridensis	23	14	33	31	32	25	3		37	47
C. phillipsii	–	–	–	–	–	–	–	–	–	–
C. monteverdensis	–	–	–	–	–	–	–	–	–	–
C. endersi	–	–	–	–	16	–	–	86	37	70
C. thomasi	–	–	33	36	24	36	14	54	80	37
C. mexicanus	–	–	47	47	53	47	33	–	–	–
C. gracilis	–	–	42	42	32	36	47	96	80	70
C. celaque	55	77	53	53	76	58	25	25	37	90
Mataquescuintla	–	–	61	58	63	78	8	54	80	47
C. mccarthyi	–	–	72	72	76	78	61	–	–	–
C. mam	55	50	72	72	63	58	75	54	37	57
C. magnimanus	–	–	–	–	–	–	–	–	–	–
C. oreoryctes	77	50	83	97	76	58	47	25	37	70
Cucurucho	95	95	61	86	53	78	89	54	80	90
C. cavatorculus	68	50	92	64	97	78	75	–	–	–
C. lacertosus	86	86	83	86	87	94	47	4	80	90
C. goodwini	–	–	97	86	92	94	89	–	–	–

Table 9 (cont.)

Species	%hDPL	%hCL	%hCLS	sum	n	MPR
C. merus	9	21	3	387	19	20
C. parvus	25	29	9	475	23	21
C. tropicalis	25	12	26	548	23	24
C. nigrescens	34	29	26	590	23	26
C. merriami	9	12	15	591	23	26
C. meridensis	–	–	82	662	20	33
C. phillipsii	–	–	–	168	5	34
C. monteverdensis	–	–	–	176	5	35
C. endersi	9	3	44	547	15	36
C. thomasi	41	41	26	736	18	41
C. mexicanus	–	–	–	563	11	51
C. gracilis	47	41	56	961	19	51
C. celaque	66	53	91	1433	23	62
Mataquescuintla	66	53	82	1188	19	63
C. mccarthyi	84	85	65	986	15	66
C. mam	66	76	44	1543	23	67
C. magnimanus	–	–	–	342	5	68
C. oreoryctes	78	68	74	1637	23	71
Cucurucho	53	62	44	1755	23	76
C. cavatorculus	97	76	97	1491	19	78
C. lacertosus	91	91	65	1816	23	79
C. goodwini	–	–	–	459	5	92

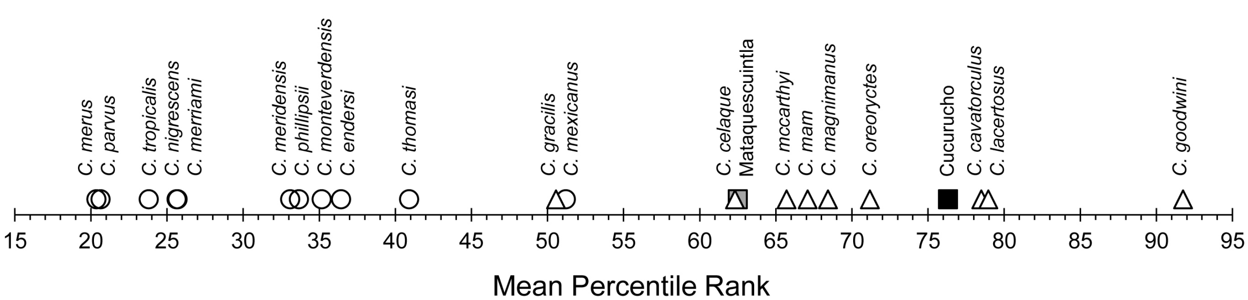

Figure 7. Plot of mean percentile ranks (MPR) illustrating relative locomotor function among 22 species of small-eared shrews. Lower scores represent greater ambulatory adaptation; higher scores, more fossorial adaptation.

Montecristo population precluded evaluation of the locomotor adaptations of that group, but qualitative evaluation of its external characteristics, particularly the forefeet, suggest that it should rank among other members of the *C. goldmani* group.

Systematic biology.—The assessment of the qualitative characters of the three *C. goldmani* group populations of small-eared shrews from Cerro Cucurucho, from highlands near Mataquescuintla, and from Cerro Montecristo, reinforced by the preceding multivariate analysis of their skull morphometry and locomotor analysis of their postcrania, indicates that these populations warrant recognition as distinct species.

Family Soricidae G. Fischer, 1814
Subamily Soricinae G. Fischer, 1814
Tribe Blarinini Kretzoi, 1965
Genus *Cryptotis* Pomel, 1848 (Small-eared Shrews)
Cryptotis goldmani **group Woodman and Timm, 1999 (Broad-clawed Shrews)**

Relative to other species in the genus *Cryptotis*, broad-clawed shrews of the *C. goldmani* group are medium- to large-bodied species (as measured by HB) with a broad manus and long, broad fore claws. Cranially, these shrews typically have an uncrowded upper unicuspid row in which U^4 is aligned with the other three unicuspids and may be partly visible (rather than obstructed by P^4) in labial view of the rostrum; the protoconal basin of M^1 is reduced relative to the hypoconal basin; the entoconid of M_3 is vestigial or absent. Post-cranially, the humerus is robust and possesses enlarged processes; the manus has short, wide metacarpals and proximal and middle phalanges, and the distal phalanges are elongate and broad.

Cryptotis eckerlini **sp. nov.**
Ralph's Broad-clawed Shrew or Cucurucho Broad-clawed Shrew
(Figs. 8A, 9A, 10D)

Cryptotis goodwini: Ordóñez-Garza et al. (2014:1), part.

Holotype.—Skin, skull, and skeleton of adult female, Texas Tech University Museum (TTU) number 136186; collected on 9 January 2015 and prepared by John O. Matson (Nicté Ordóñez-Garza field number 1699).

Type locality.—Guatemala: Sacatepéquez Department: Cerro Cucurucho; 11 km by road SE of Antigua Guatemala; Finca El Pilar (14º 31.112′ N, 90º 41.472′ W); 2,640 m elevation (Fig. 1: locality 1). Ordóñez-Garza et al. (2014:5) reported the habitat of Cerro Cucurucho to be "severely disturbed" cloud forest. This area is mapped as Subtropical Lower Montane Moist Forest (LIG 2002).

Paratypes.—Four adult females, 3 adult males (TTU 136183–136185, 136187–136189, and 136192) from the type locality.

Referred specimens.—Six shrews (3 adult females, 3 adult males) identified as *C. goodwini* collected on Cerro Cucurucho in January 2013 and deposited in the Museo de Historia Natural de la Universidad de San Carlos de Guatemala (Ordóñez-Garza et al. 2014).

Distribution.—Known only from the type locality at 2,640 m on Cerro Cucurucho in the eastern Sierra Madre de Guatemala. Distribution of the species may extend north to highlands near San Mateo Milpas Altas and south to Volcán de Agua.

Etymology.—The species name is in honor of Ralph P. Eckerlin, a wellspring of natural history information whose contributions to mammalogy as a collector, parasitologist, and tireless field companion are insufficiently acknowledged.

Nomenclatural statement.—The Life Sciences Identifier (LSID) number for *Cryptotis eckerlini* is urn:lsid:zoobank.org:act:09DAEB4D-836C-42A2-ACCE-A6E044516061.

Diagnosis.—A broad-clawed shrew of the *Cryptotis goldmani* group, *C. eckerlini* can be distinguished from most other species in the genus by a combination of its large body size, short tail, broad manus and long, broad foreclaws; generally uncrowded upper unicuspid row; protoconal basin of M^1 reduced relative to hypoconal basin; entoconid of M_3 vestigial or absent;

Figure 8. Dorsal view of the dried skins of A, *C. eckerlini* (TTU 136187); B, *C. matsoni* (USNM 275681); and C, *C. montecristo* (SMF 14837; image courtesy of Irina Ruf and Katrin Krohmann, SMF).

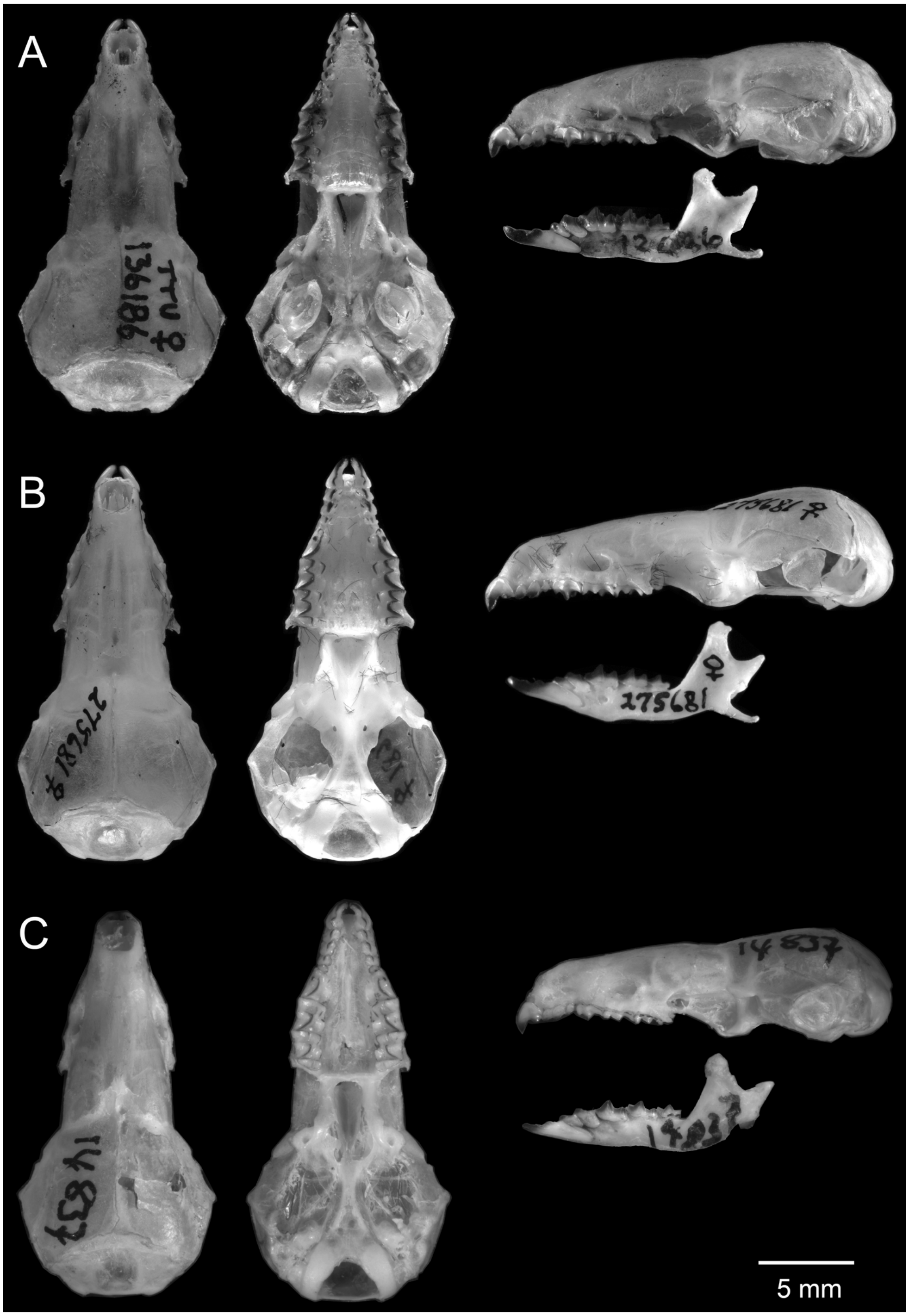

Figure 9. Dorsal and ventral views of the cranium, and lateral views of the cranium and left dentary of the holotypes of A, *C. eckerlini* (TTU 136186); B, *C. matsoni* (USNM 275681); and C, *C. montecristo* (SMF 14837; image courtesy of Irina Ruf and Katrin Krohmann, SMF).

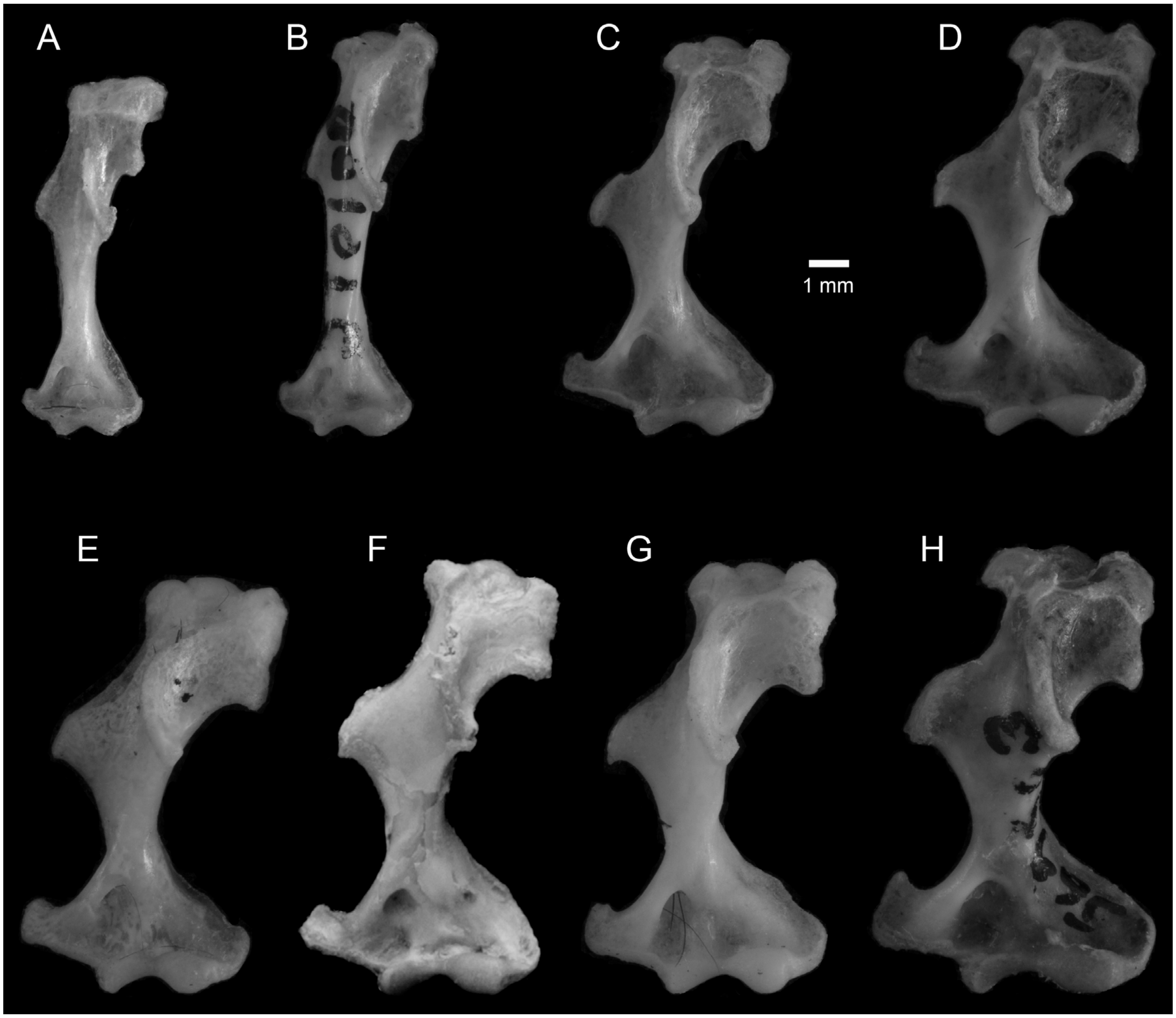

Figure 10. Anterior aspect of left humeri of A, *C. tropicalis* (USNM 570435); B, *C. merriami* (USNM 570108); C, *C. mam* (USNM 569555); D, *C. eckerlini* (TTU 136186); E, *C. matsoni* (USNM 275681); F, *C. goodwini* (UMMZ 103416), G, *C. oreoryctes* (USNM 569878), and H, *C. lacertosus* (USNM 569503).

broad humerus with elongated processes; short, wide metacarpals and proximal and middle phalanges; and elongate and broad distal phalanges. Among El Salvadoran, Guatemalan, and Honduran species in the *C. goldmani* group, *C. eckerlini* is distinguished by its medium external body size (smaller than *C. goodwini* and *C. oreoryctes*); medium-length tail (relatively longer than in *C. lacerosus*, *C. maccarthyi*, and *C. magnimanus*); medium-length skull (shorter than in *C. goodwini, C. lacertosus*, and *C. oreoryctes*) with a relatively broad braincase (relatively broader than in *C. griseoventris*, *C. lacertosus*, *C. mam*, and *C. oreoryctes*); medium-breadth interorbital region (relatively broader than in *C. griseoventris* and *C. lacertosus*; but relatively narrower than in *C. mccarthyi*); medium-breadth zygomatic plate (relatively narrower than in *C. cavatorculus*, *C. celaque*, *C. magnimanus*, and *C. mccarthyi*); relatively short palate (relatively shorter than in *C. celaque*, *C. griseoventris*, *C. mccarthyi*, and *C. oreoryctes*) of medium breadth (relatively broader than in *C. griseoventris*, *C. lacertosus*, *C. mam*, and *C. oreoryctes*); medium-length upper toothrow (U^1–M^3; relatively shorter than in *C. cavatorculus*, *C. celaque*, *C. griseoventris*, *C. mccarthyi*, and *C. oreoryctes*); medium-length unicuspid row (relatively longer than in *C. cavatorculus* and *C. magnimanus*); relatively high coronoid process of the dentary (relatively higher than in *C. celaque*, *C. goodwini*, *C. griseoventris*, *C. lacertosus*, *C. magnimanus*, *C. mam*, *C. mccarthyi*, and *C. oreoryctes*); long posterior dentary, from articular process to posterior of M_3 (relatively longer than in *C. cavatorculus*, *C. celaque*, *C. griseoventris*, *C. magnimanus*, and *C. mccarthyi*); and lack of entoconid of M_3 (vestigial entoconid present in about half of *C. oreoryctes*).

Description.—A medium-sized *Cryptotis* as measured by HB (75 ± 2 mm; compared to 74 ± 8 mm for the genus; Table 1, Fig. 8A), or somewhat larger as measured by CBL (20.7 ± 0.4 mm; 19.6 ± 1.7 mm for the genus); tail of medium length, 38% ± 2 of HB (40% ± 7 for the genus; Table 5). Dorsal guard hairs typically 5–7 mm long and indistinctly two-banded: basal 5/6ths of hairs silver-gray, grading to a dark brown tip; dorsum appears generally Mummy Brown to Clove Brown in color. Ventrum somewhat paler than dorsum; tips of hairs Buffy Brown to Hair Brown. Forefeet broad; fore claws elongate and broad.

Rostrum of moderate length (PL/CBL = 43.0% ± 0.6; 43.4% ± 1.1 for the genus; Table 5, Fig. 9A); interorbital region proportionally broad (IO/CBL = 26.6% ± 0.5; 24.4% ± 1.3 for the genus); a medium- to large-size, widely-rounded foramen (*foramen orbitalium* of Bühler 1964) opens medially along the sagittal suture on one (63%) or both (37%) frontals; typically no foramen dorsal to external capitular facet (*sensu* McDowell 1958), minute when present; no foramen (associated with sinus canal) present posterior to either external capitular facet; no foramen on posteromedial edge of caudal tympanic process of petrosal; zygomatic plate of medium breadth (ZP/CBL = 9.5% ± 0.6; 9.8% ± 1.0 for the genus), anterior border aligned with posterior of mesostyle/metastyle valley or anterior edge of metastyle of M^1; posterior border of zygomatic plate straight to roundly concave, aligned with, or just posterior to, M^3 parastyle and generally confluent with the posterior border of the maxillary process; palate of medium bread (M2B/CBL = 29.8% ± 0.6; 29.3% ± 1.2 for the genus); upper toothrow uncrowded, of medium length (TR/CBL = 37.4% ± 1.0; 38.2% ± 1.0 for the genus); dentition not bulbous; teeth moderately pigmented: tips of first three unicuspids pigmented; medium red to dark red on tips of cones (except hypocone), styles, and cristae of P^4 and M^{1-3}, pale coloration only occasionally extending into protoconal (but not hypoconal) basins of M^{1-2}; unicuspid toothrow proportionally long (UTR/CBL = 13.3% ± 0.5; 12.8% ± 0.6 for the genus); in labial view of the cranium, posteroventral borders of unicuspids convex; U^4 aligned with the unicuspid toothrow in occlusal view, but typically not visible, or only partly visible, in labial view of the skull; occlusal area of U^4 about 50% ± 6 that of U^3; P^4, M^1, and M^2 only slightly recessed on their posterior borders; protoconal basin of M^1 reduced relative to hypoconal basin; occlusal surface of M^3 simple, with prominent, pigmented parastyle, paracrista, and paracone, reduced precentrocrista and mesostyle; protocone of M^3 small, sometimes lightly pigmented; and hypocone poorly developed or absent.

Mandible of moderate length and breadth for the genus; coronoid process somewhat high (HCP/LM = 74.4% ± 5.0; 71.2% ± 5.5 for the genus); anterior border of coronoid process joins the horizontal ramus of the mandible at a relatively low angle; long distance from the superior tip of the articular process to the posterior border of M_3 (AC3/ML = 83.9% ± 5.1; 78.2% ± 5.3 for the genus); articular process tall and broad; depth of inferior sigmoid notch variable, shallow to deep; posterior border of cingulum of lower incisor aligned with posterior paraconid of M_1; P_3 proportionally long and low; entoconid absent from M_3; and talonid of M_3 vestigial or, for one specimen, absent.

Humerus considerably shortened and broadened with enlarged processes and dorso-ventrally elongate head (Fig. 10D). Metacarpals and proximal and middle phalanges relatively short and broad; distal phalanges elongate and broad (Fig. 11; Table 4).

Comparisons.—Like most other members of the *C. goldmani* group, *C. eckerlini* can be distinguished from El Salvadoran and Guatemalan members of the *C. parvus* group (*C. orophilus* and *C. tropicalis*) and *C. nigrescens* group (*C. mayensis* and *C. merriami*) by a combination of its larger external body size (Table 2: HB); long pelage; longer skull (Table 2: CBL); broad, robust humerus with large processes (Fig. 10); and broad forefeet and long, broad foreclaws (Fig. 11; Table 4). For additional measurements and characters of those species, see Woodman and Timm (1992, 1993, 2016).

Among members of the *C. goldmani* group in the immediate region (see below), *C. eckerlini* is distinguished by its small body size, which is closest to *C. mam* in external dimensions; its small cranium; broad braincase relative to cranial length (Table 5: BB/CBL); and high coronoid process relative to dentary length (HCP/ML). It can be distinguished from individual members of the *C. goldmani* group as follows: 1) Compared to *C. goodwini*, *C. eckerlini* has a relatively longer tail (Table 5: TL/HB) and averages smaller for most cranial variables; but averages a relatively broader braincase and relatively higher coronoid process (HCP/ML). The distribution of *C. goodwini* is now restricted to the western Sierra Madre of southern Guatemala. 2) Compared to *C. lacertosus*, which has the largest cranial dimensions of the *C. goldmani* group in El Salvador and Guatemala, *C. eckerlini* has a relatively longer tail, and it averages smaller for most cranial variables; yet, it averages a relatively broader braincase, interorbital area (IO/CBL), and palate (M2B/CBL), and relatively higher coronoid process. *Cryptotis lacertosus* is endemic to highlands in the northern extension of the Sierra de los Cuchumatanes near San Mateo Ixtatán, western Guatemala (Woodman 2010). 3) Compared to *C. mam*, *C. eckerlini* averages absolutely and relatively broader braincase and palate; absolutely and relatively higher coronoid process; higher articular valley; and broader articular process. *Cryptotis mam* is endemic to highlands in the Sierra de los Cuchumatanes, western Guatemala (Woodman 2010). 4) Compared to *C. oreoryctes*, *C. eckerlini* has somewhat paler pelage, with greater contrast between dorsum and venter, and it averages smaller externally and for most skull variables. It also has a relatively shorter maxillary toothrow (TR/CBL) and palate (PL/CBL), but a relatively broader braincase and palate and a higher coronoid process. *Cryptotis oreoryctes* is endemic to the Sierra de Yalijux, Guatemala (Woodman 2011).

Remarks.—Cerro Cucurucho is part of an isolated highland >2,000-mamsl between Guatemala City to the east and Antigua Guatemala to the west. The southern portion of this upland is dominated by Volcán de Agua, a currently inactive stratovolcano that rises to 3,760 m. The habitat at higher elevations on Cerro Cucurucho in 2013 was reported to be "severely disturbed" cloud forest (Ordóñez-Garza et al. 2014:5). Based on captures of small mammals over five nights in January 2013, *C. eckerlini* is the second most common species (13% of 46 total captures: Ordóñez-Garza et al. 2014) in a cloud forest community of at least 10 small mammals that is dominated numerically by *Peromyscus guatemalensis* (44% of captures). Other species comprising the known community include *Sorex veraepacis* (11%), *Reithrodontomys sumichrasti* (9%), *Handleyomys rhabdops* (7%), *Heteromys demarestianus* (4%), *P. beatae* (4%), *R. mexicanus* (4%), *Marmosa mexicana* (2%), and *Nyctomys sumichrasti* (2%). A second survey of Cerro Cucurucho over two nights in January 2015 yielded a smaller sample of five species: *P. guatemalensis* (56% of 25 total captures), *C. eckerlini* (34%), *S. veraepacis* (4%), *R. sumichrasti* (4%), and *H. demarestianus* (4%; Ralph Eckerlin, email communication, May 2018).

Nearly equal numbers of female and male *C. eckerlini* were collected during each survey (2013: 3 females, 3 males; 2015: 5 females, 3 males). Some individuals host an undescribed species of hymenolepid tapeworm (Ordóñez-Garza et al. 2014).

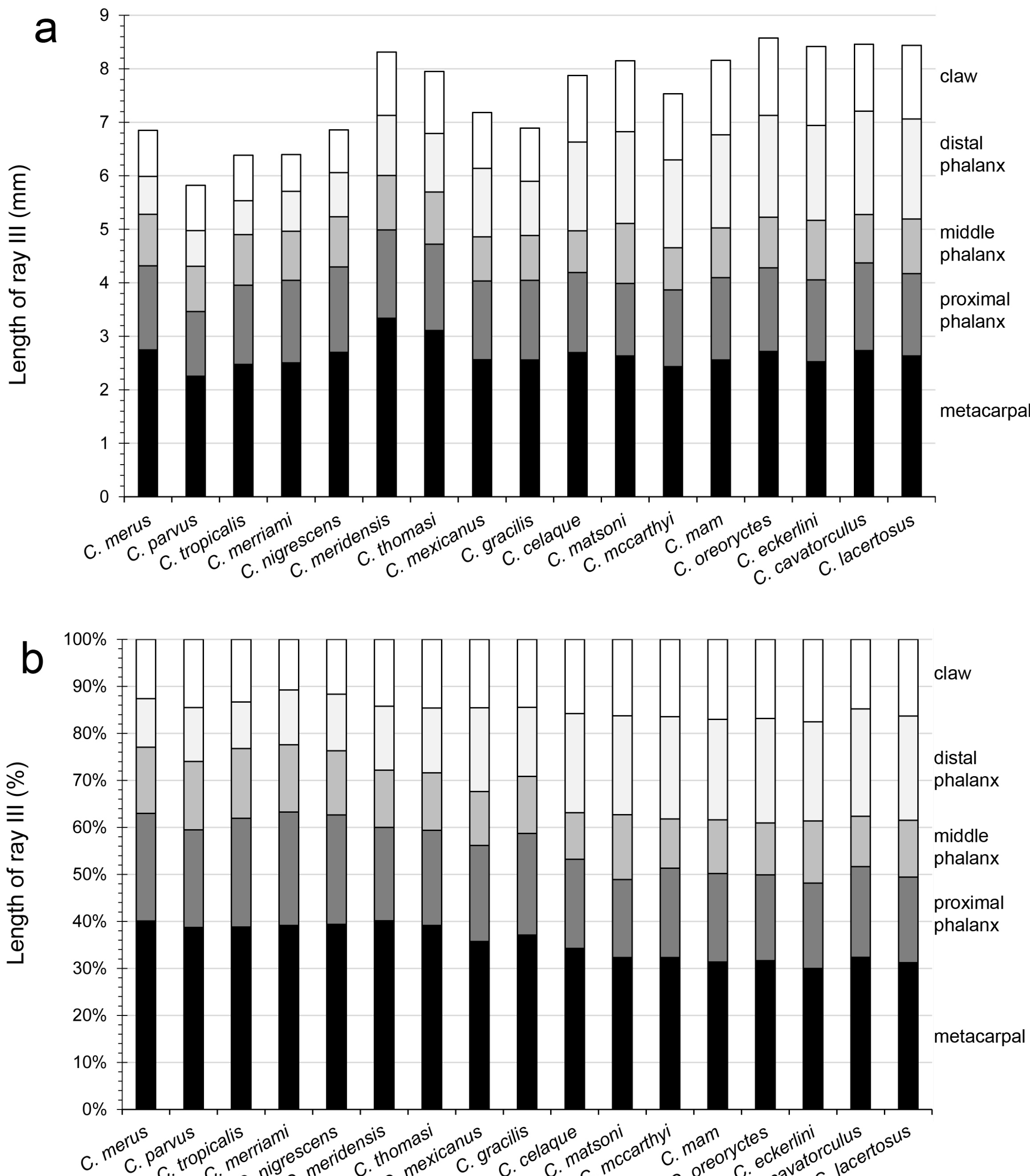

Figure 11. Diagrammatic comparison of bones contributing to ray III of the manus among 17 species of *Cryptotis*: (a) mean lengths (mm) of bones; (b) proportional lengths (%) of bones. "Claw" represents the length of the claw that extends beyond the tip of the distal phalanx. Note the increased lengths of the distal phalanx and claw and the decreased contribution of the metacarpal in species of the *C. goldmani* group (*C. gracilis*, *C. celaque*, *C. matsoni*, *C. mccarthyi*, *C. mam*, *C. oreoryctes*, *C. eckerlini*, *C. cavatorculus*, and *C. lacertosus*).

***Cryptotis matsoni* sp. nov.**
Jack's Broad-clawed Shrew or Mataquescuintla Broad-clawed Shrew
(Figs. 8B, 9B, 10E)

Cryptotis goodwini: Woodman (2010:1283; 2015:106, 119); Woodman and Gaffney (2014:746). Part, not *C. goodwini* Jackson, 1933.

Holotype.—Skin, skull, and skeleton of adult male, United States National Museum of Natural History (USNM) 275681; obtained 22 May 1947 by Charles Overton Handley, Jr. (field number COH 1148).

Type locality.—Guatemala: Jalapa Department: 11.6 km east of Mataquescuintla, 2,560 m [ca. 14º 32' N, 90º 08' W] (Fig. 1: locality 2).

Distribution.—Known only from the type locality at 2,560 m elevation in the eastern Sierra Madre de Guatemala. The species may be distributed through much of an isolated region of Subtropical Lower Montane Moist Forest, Subtropical Lower Montane Wet Forest, and Cool Temperate Wet Forest in western Jalapa and eastern Guatemala Departments.

Etymology.—The new species is named for John Orville ("Jack") Matson, who has been a driving force behind numerous productive research trips in Guatemala.

Nomenclatural statement.— The Life Sciences Identifier (LSID) number for *Cryptotis matsoni* is urn:lsid:zoobank.org:act:2C61897B-B693-4764-8359-EBF8F0FBD13B.

Diagnosis.—A broad-clawed shrew of the *Cryptotis goldmani* group, *C. matsoni* can be distinguished from most other species in the genus by a combination of its large body size, short tail, broad manus and long, broad foreclaws; generally uncrowded upper unicuspid row; protoconal basin of M^1 reduced relative to hypoconal basin; entoconid of M_3 vestigial or absent; broad humerus with elongated processes; short, wide metacarpals and proximal and middle phalanges; and elongate and broad distal phalanges. Among El Salvadoran, Guatemalan, and Honduran species in the *C. goldmani* group, *C. matsoni* is distinguished by its medium-to-large external body size (larger than *C. celaque*, *C. eckerlini*, *C. griseoventris*, *C. mam*, and *C. mccarthyi*); relatively short tail (relatively shorter than in *C. celaque*, *C. eckerlini*, *C. goodwini*, *C. griseoventris*, *C. mam*, and *C. oreoryctes*); medium-length skull (shorter than in *C. lacertosus* and *C. oreoryctes*) with medium-breadth braincase (relatively narrower than in *C. cavatorculus*, *C. eckerlini*, and *C. magnimanus*; but relatively broader than in *C. griseoventris*); medium-breadth interorbital region (relatively broader than in *C. griseoventris* and *C. lacertosus*); medium-breadth zygomatic plate (relatively broader than in *C. eckerlini*, *C. griseoventris*, and *C. goodwini*); short-to-medium-length palate (relatively shorter than in *C. celaque*, *C. griseoventris*, *C. mccarthyi,* and *C. oreoryctes*) of medium breadth (relatively broader than in *C. griseoventris*, *C. lacertosus*, *C. mam*, and *C. oreoryctes*; but relatively narrower than in *C. cavatorculus*); medium-length upper toothrow (U^1–M^3; relatively shorter than in *C. cavatorculus*, *C. celaque*, *C. griseoventris*, *C. mccarthyi*, and *C. oreoryctes*); medium-length unicuspid row (relatively longer than in *C. magnimanus*, but relatively shorter than in *C. celaque*, *C. griseoventris*, *C. mam*, and *C. oreoryctes*); medium-height coronoid process of dentary (relatively higher than in *C. griseoventris*, *C. lacertosus*, *C. mccarthyi*, and *C. oreoryctes*, but relatively shorter than in *C. cavatorculus* and *C. eckerlini*); and medium-length distance from articular process to posterior of M_3 (relatively longer than in *C. celaque* and *C. mccarthyi*, but relatively shorter than in *C. eckerlini*, *C. goodwini*, *C. lacertosus*, and *C. mam*).

Description.—A medium-to-large-sized *Cryptotis* as measured by HB (86 mm; compared to 74 ± 8 mm for the genus; Table 1, Fig. 8B), and by CBL (21.0 mm; 19.6 ± 1.7 mm for the genus); tail short, 31% of HB (40% ± 7 for the genus; Table 5). Dorsal guard hairs 5–6 mm long and indistinctly two-banded: basal 4/5ths of hairs silver-gray, grading to a dark brown tip; dorsum appears generally Bone Brown to Light Seal Brown in color. Ventrum somewhat paler than dorsum; tips of hairs Prouts Brown to Mummy Brown. Forefeet broad; fore claws elongate and broad.

Rostrum of moderate length (PL/CBL = 43.1%; 43.4% ± 1.1 for the genus; Table 5, Fig. 9B); interorbital region proportionally broad (IO/CBL = 26.0%; 24.4% ± 1.3 for the genus); a medium to large, widely-rounded foramen opens medially along the sagittal suture on each frontal; no obvious foramen dorsal to external capitular facet, minute when present; no foramen posterior to external capitular facet; no foramen on posteromedial edge of caudal tympanic process of petrosal; zygomatic plate of medium breadth (ZP/CBL = 10.3%; 9.8% ± 1.0 for the genus), anterior border aligned with middle of mesostyle/metastyle valley of M^1; posterior border of zygomatic plate broadly concave, aligned with M^3 parastyle and confluent with the posterior border of the maxillary process; palate of medium bread (M2B/CBL = 29.4%; 29.3% ± 1.2 for the genus); upper toothrow uncrowded, of medium length (TR/CBL = 37.3%; 38.2% ± 1.0 for the genus); dentition not bulbous; teeth moderately pigmented: tips of all four unicuspids bear pigment; medium red to dark red pigment is present on tips of cones (except hypocone), styles, and cristae of P^4 and M^{1-3}, extremely pale coloration present in protoconal basin of M^1; unicuspid toothrow of near average length (UTR/CBL = 12.7%; 12.8% ± 0.6 for the genus); posteroventral borders of unicuspids moderately convex in labial view of the cranium; U^4 aligned with the unicuspid toothrow in occlusal view and partly visible in labial view of the skull; occlusal area of U^4 about 71% that of U^3; P^4, M^1, and M^2 only slightly recessed on their posterior borders; protoconal basin of M^1 reduced relative to hypoconal basin; occlusal surface of M^3 simple, with prominent, pigmented parastyle, paracrista, and paracone, reduced precentrocrista and mesostyle; protocone of M^3 small, lightly pigmented; and hypocone absent.

Mandible of moderate length and breadth for the genus; coronoid process of medium height (HCP/LM = 72.3%; 71.2% ± 5.5 for the genus); anterior border of coronoid process joins the horizontal ramus of the mandible at a relatively low angle; somewhat long distance from the superior tip of the articular process to the posterior border of M_3 (AC3/ML = 81.5%; 78.2% ± 5.3 for the genus); articular process tall and broad; inferior sigmoid notch deep; posterior border of cingulum of lower incisor aligned with posterior paraconid of M_1; P_3 proportionally long and low; and entoconid lacking from vestigial talonid of M_3.

Humerus considerably shortened and broadened with enlarged processes (Fig. 10E) and dorsoventrally elongate head. Metacarpals and proximal and middle phalanges relatively short and broad, and distal phalanges elongate and broad (Fig. 11; Table 4).

Comparisons.—Like most other members of the *C. goldmani* group, *C. matsoni* can be distinguished most easily from El Salvadoran, Guatemalan, and Honduran members of the *C. parvus* group and *C. nigrescens* group by its much larger external and skull dimensions (Table 2); longer pelage; broader, more robust humerus with longer processes (Fig. 10); broader forefeet and longer, broader foreclaws (Fig. 11; Table 4).

Among members of the *C. goldmani* group in the region, *C. matsoni* is distinguished by its absolutely and relatively short tail; relatively broad zygomatic plate (Table 5: ZP/CBL); and relatively short unicuspid toothrow (UTR/CBL). It can be distinguished from individual members of the *C. goldmani* group as follows: 1) Compared to *C. eckerlini*, *C. matsoni* is larger in external body size, but has a relatively shorter tail. It has a relatively broader zygomatic plate; relatively shorter unicuspid toothrow; and relatively shorter posterior dentary (AC3/ML). 2) Compared to *C. goodwini*, *C. matsoni* is similar in external body size, but has a relatively shorter tail. It is smaller than average for *C. goodwini* in most cranial dimensions, and it has a relatively broader zygomatic plate and a relatively shorter posterior dentary and has a shorter cranium and narrower braincase. 3) Compared to *C. lacertosus*, *C. matsoni* is similar in external body size, but has a relatively shorter tail. Its cranium is shorter but relatively broader, particularly the braincase, interorbital region, and palate. It has a relatively broader zygomatic plate, a relatively higher coronoid process, and relatively shorter posterior dentary. 4) Compared to *C. mam*, *C. matsoni* is larger externally and has a longer, broader cranium with a relatively broader zygomatic plate, but relatively shorter maxillary toothrow and unicuspid toothrow; relatively shorter posterior dentary. 5) Compared to *C. oreoryctes*, *C. matsoni* has somewhat paler pelage, with greater contrast between dorsum and venter, and a relatively shorter tail. It has a shorter cranium with relatively shorter palate, maxillary toothrow, and unicuspid toothrow, but a broader zygomatic plate; relatively higher coronoid process; shorter posterior dentary.

***Cryptotis montecristo* sp. nov.**
Montecristo Broad-clawed Shrew
(Figs. 8C, 9C)

Cryptotis goodwini: Felten, 1958:218. Part, not *C. goodwini* Jackson, 1933.

Cryptotis nigrescens: Burt and Stirton, 1961:21. Part, not *C. nigrescens* (J. A. Allen, 1895).

Holotype.—Skin and skeleton of adult male, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany (SMF) 14837; obtained February 1954 by William Battles Heed. Pelage of dried skin bleached; patch of fur lacking from right laterum and ventrum; skin of both fore limbs cracked; parietal broken; both dentaries lack angular process.

Type locality.—El Salvador: Santa Ana Department; Hacienda Montecristo, north of Metapán; in cloud forest at 2,150 m [14º 25' N, 89º 22' W] (Felten 1958; Fig. 1: locality 3).

Referred specimens.—Three adult females identified as *C. goodwini* collected near the summit (ca. 2,418 m) of Cerro Montecristo, Esquipulas, Chiquimula Department, Guatemala, in July 2004 and deposited in the Museo de Historia Natural de la Universidad de San Carlos de Guatemala (Ralph Eckerlin, email communication, May 2018).

Distribution.—Known only from Cerro Montecristo, an isolated massif at the junction of the borders of northwestern El Salvador, eastern Guatemala, and western Honduras; elevational distribution 2,150–2,418 m. The species probably is restricted to higher parts of the mountain that support Subtropical Lower Montane Moist Forest and Subtropical Lower Montane Wet Forest. Cerro Montecristo is now part of an international protected zone, Área Protegida Trinacional Montecristo, which comprises Montecristo National Park in El Salvador, Trifinio Biosphere Reserve in Guatemala, and Montecristo Trifinio National Park in Honduras.

Etymology.—The name of the new species references the type locality and is used as a noun in apposition.

Nomenclatural statement.—The Life Sciences Identifier (LSID) number for *Cryptotis montecristo* is urn:lsid:zoobank.org:act:65480C0C-5F53-4A27-8002-67A6A5DBA7D1.

Diagnosis.—A broad-clawed shrew of the *C. goldmani* group, *C. montecristo* can be distinguished from most other species in the genus by a combination of its large body size, short tail, broad manus and long, broad foreclaws; generally uncrowded upper unicuspid row; protoconal basin of M^1 reduced relative to hypoconal basin; entoconid of M_3 vestigial or absent; broad humerus with elongated processes; short, wide metacarpals and proximal and middle phalanges; and elongate and broad distal phalanges. Among El Salvadoran, Guatemalan, and Honduran species in the *C. goldmani* group, *C. montecristo* is distinguished by its large external body size (larger than all other described species of the *Cryptotis goldmani* group in the region); medium-length tail (relatively shorter than in *C. eckerlini*, *C. griseoventris*, and *C. mam*); medium-length skull (shorter than in *C. lacertosus*) with medium-breadth braincase (relatively narrower than in *C. cavatorculus*, *C. eckerlini*, *C. magnimanus*, and *C. mccarthyi*); medium-breadth interorbital region (relatively broader than in *C. griseoventris*, *C. lacertosus*, *C. mam*, and *C. matsoni*); narrow zygomatic plate (relatively narrower than in *C. cavatorculus*, *C. celaque*, *C. eckerlini*, *C. griseoventris*, *C. lacertosus*, *C. magnimanus*, *C. mam*, *C. matsoni*, *C. mccarthyi*, and *C. oreoryctes*); medium-length palate (relatively shorter than in *C. celaque* and *C. oreoryctes*; but relatively longer than in *C. cavatorculus*) of medium breadth (broader than in *C. griseoventris*, *C. lacertosus*, *C. mam*, and *C. oreoryctes*; but relatively narrower than in *C. cavatorculus*); medium-length upper toothrow (U^1–M^3: relatively shorter than in *C. celaque*, *C. griseoventris*, *C. mccarthyi*, and *C. oreoryctes*); short unicuspid row (relatively shorter than in *C. celaque*, *C. eckerlini*, *C. goodwini*, *C. griseoventris*, *C. lacertosus*, *C. mam*, *C. matsoni*, *C. mccarthyi*, and *C. oreoryctes*); and medium-height coronoid process of dentary (higher than in *C. griseoventris*, *C. lacertosus*, and *C. mam*).

Description.—A large-sized *Cryptotis* as measured by HB (92 ± 4 mm; compared to 74 ± 8 mm for the genus; Table 1, Fig. 8C), but medium-sized as measured by CBL (20.8 mm; 19.6 ± 1.7 mm for the genus);

tail short, 33% of HB (40% ± 7 for the genus; Table 5). Original dorsal pelage slightly darker than Clove Brown in color; ventrum somewhat paler and grayer (Felten 1958). Forefeet broad; fore claws elongate and broad.

Rostrum of moderate length (PL/CBL = 43.8%; 43.4% ± 1.1 for the genus; Table 5; Fig. 9C); interorbital region proportionally broad (IO/CBL = 26.9%; 24.4% ± 1.3 for the genus); a large, widely-rounded foramen opens medially along the sagittal suture on each frontal; zygomatic plate narrow (ZP/CBL = 8.7%; 9.8% ± 1.0 for the genus), anterior border aligned with metastyle of M^1; posterior border of zygomatic plate aligned with posteror half of M^3 and and posterior half of the maxillary process; palate of medium bread (M2B/CBL = 29.8%; 29.3% ± 1.2 for the genus); upper toothrow uncrowded, of medium length (TR/CBL = 37.5%; 38.2% ± 1.0 for the genus); dentition not bulbous; teeth of the holotype are worn, making it difficult to determine the extent of pigmentation; unicuspid toothrow short (UTR/CBL = 12.0%; 12.8% ± 0.6 for the genus); U^4 aligned with the unicuspid toothrow in occlusal view, but not clearly visible in labial view of the skull; occlusal area of U^4 about 48% that of U^3; P^4, M^1, and M^2 only slightly recessed on their posterior borders; protoconal basin of M^1 reduced relative to hypoconal basin; occlusal surface of M^3 simple, with pigmented parastyle, paracrista, and paracone, reduced precentrocrista and mesostyle; and protocone of M^3 small.

Mandible of moderate length and breadth for the genus; coronoid process of about medium height; anterior border of coronoid process joins the horizontal ramus of the mandible at a relatively low angle; articular process tall and broad; inferior sigmoid notch deep; P_3 proportionally long and low; and entoconid lacking from vestigial talonid of M_3.

The postcranial skeleton of *C. montecristo* is unknown.

Comparisons.—Like most other members of the *C. goldmani* group, *C. montecristo* can be distinguished most easily from El Salvadoran, Guatemalan, and Honduran members of the *C. parvus* and *C. nigrescens* groups by its much larger external and skull dimensions (Table 2); longer pelage; broader forefeet and longer, broader foreclaws.

Among members of the *C. goldmani* group in El Salvador and Guatemala (see below), *C. montecristo* is distinguished by its absolutely and relatively short tail; relatively broad zygomatic plate (Table 5: ZP/CBL); and relatively short unicuspid toothrow (UTR/CBL). It can be distinguished from individual species of the *C. goldmani* group as follows: 1) Compared to *C. eckerlini*, *C. montecristo* is larger in external body size, but has a relatively shorter tail. It has a longer cranium with a relatively narrower braincase (BB/CBL); longer, but relatively narrow palate (M2B/PL); relatively shorter zygomatic plate; and relatively shorter unicuspid toothrow. 2) Compared to *C. goodwini*, *C. montecristo* is larger in external body size, but has a relatively shorter tail. It averages a shorter cranium with a narrower braincase; relatively shorter zygomatic plate; and shorter unicuspid toothrow. 3) Compared to *C. lacertosus*, *C. montecristo* is larger in external body size and has a shorter cranium with a relatively broader interorbital region (IO/CBL) and palate; relatively shorter zygomatic plate; shorter unicuspid toothrow; and higher coronoid process of the dentary. 4) Compared to *C. mam*, *C. montecristo* has larger external body size, but a relatively shorter tail. It has a longer cranium that is larger in most dimensions, but with a shorter zygomatic plate and shorter unicuspid toothrow; relatively broader interorbital area; and relatively broader palate. 5) Compared to *C. matsoni*, *C. montecristo* is larger in external body size and has a longer cranium with a relatively narrower interorbital region; relatively longer palate (PL/CBL); shorter zygomatic plate; and relatively shorter unicuspid toothrow. 6) Compared to *C. oreoryctes*, *C. montecristo* has paler pelage, with greater contrast between dorsum and venter. It is larger in external body size, but has a relatively shorter tail. It has a generally smaller cranium with a relatively shorter, but relatively broader palate; shorter zygomatic plate; relatively shorter unicuspid toothrow; and relatively higher coronoid process.

Remarks.—Woodman and Timm (1999) previously hypothesized that the population of *C. goodwini* on Montecristo might prove to be distinct from the rest of *C. goodwini* (*sensu lato*), which at that time was thought to occur throughout highlands in northern and southern Guatemala, as well as in Honduras and southern Chiapas, Mexico. They noted that *C. montecristo* had less emarginate upper dentition, a shorter zygomatic plate, and a shorter unicuspid toothrow than average *C. goodwini*, but considered these characters insufficient to distinguish the population on Cerro Montecristo from what was then a more geographically widespread and more morphologically diverse *C. goodwini*.

DISCUSSION

Recognition of the three populations of small-eared shrews from Cerro Cucurucho, from highlands near Mataquescuintla, and from Cerro Montecristo, as the distinct species *Cryptotis eckerlini*, *C. matsoni*, and *C. montecristo*, respectively, increases the number of recognized members of the *C. goldmani* group to 17 species. All of these shrews are high-elevation species that occur above 1,400 mamsl in Mexico and Central America. These species also possess modifications of the postcranial skeleton that are consistent with a more fossorial locomotor mode and are interpreted as adaptations that enhance their abilities to dig. These skeletal modifications are convergent on similar skeletal modifications documented for high-elevation species of myosoricine shrews in Africa (Woodman and Stabile 2015a, b).

Originally considered a clade within the *Cryptotis mexicanus* group (Woodman and Timm 1999; Woodman 2010, 2011), the *C. goldmani* group is now understood to be distinct (Guevara and Cervantes 2014; He et al. 2015; Baird et al. 2017). Within the *C. goldmani* group, molecular evidence supports the existence of two subclades that mostly represent species from north (*C. alticola*, *C. goldmani*, and *C. peregrinus*) and south (*C. cavatorculus*, *C. celaque*, *C. goodwini*, *C. gracilis*, *C. lacertosus*, *C. mam*, *C. maccarthyi*, and *C. oreoryctes*) of the Isthmus of Tehuantepec. One exception is an undescribed form from Chiapas that is sister to *C. mam* from Guatemala (Guevara and Cervantes 2014; He et al. 2015; Baird et al. 2017). Additional molecular studies will be required to fully determine the relationships of the new species within the *C. goldmani* group and whether they support the split between northern and southern subclades, or whether some new pattern of diversification emerges.

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Appendix

Specimens examined for this study. Institutional abbreviations follow Dunnum et al. (2018:supplementary data SD4) and are explained in Materials and Methods.

Cryptotis goodwini (*n* = 32): GUATEMALA: Quetzaltenango: Calel, 10,200 ft (USNM 77070, 77072–77084; includes holotype); Volcán Santa María, 9000–11,000 ft (USNM 77086, 77087). San Marcos: Finca La Paz, 1200 m (UMMZ 103416). San Marcos: S slope Volcán Tajumulco, 10,000 ft (UMMZ 99541). Baja Verapaz: 5 mi N, 1 mi W El Chol, 6000 ft (KU 64611). Chimaltenango: Santa Elena, 9900–10,000 ft (FMNH 41791–41794); Tecpán, 9700 ft (AMNH 74302). Totonicapan: Cumbre María Tecún, 3000 m (UMMZ 112004–112011).

Cryptotis mam (*n* = 27).—GUATEMALA: Huehuetenango: Todos Santos Cuchumatán, 10,000 ft (USNM 77051–77068); Hacienda Chancol, 9500–11,000 ft (USNM 77069); Laguna Magdalena, 2925 m (USNM 569554, 569555, 570337, 570340); Puerto al Cielo, 3350 m (USNM 570248); Aldea El Rancho, 3020 m (USNM 570256, 570257, 570313, 570314; 3 USAC [NOG 771, 804, 805]).

Cryptotis lacertosus (*n* = 8).—GUATEMALA: Huehuetenango: 5 km SW San Mateo Ixtatán, 3110 m (USNM 569420, 569431, 569442, 569443, 569503); Yaiquich [ca. 15º 45’ 44” N, 91º 30’ 10” W], 2680 m (USNM 569368); San Mateo Ixtatán, ca. 4 km NW Santa Eulalia, Yaiquich, 2950 m (UMMZ 117843); 3.5 mi SW San Juan Ixcoy, 10,120 ft (KU 64610).

Cryptotis mayensis (*n* = 23).—BELIZE: Cayo District: Baking Pot (BMNH 65.3881, 66.2333; ROM 37651); Belmopan, Las Cuevas Research Station, path off the Monkey Tail River (BMNH 2003.71); Cayo District, 3.3 km E, 1.1 km N Las Cuevas Research Station, 600 m (MWFB 4243, 4271). GUATEMALA: Petén; Flores; Cerro Cahui (USAC 89). MEXICO: Campeche: 60 km SE of Dzibalchen (ASNHC 6071, ROM 96535); 7.5 km W of Escárcega (ASNHC 1286); La Tuxpeña (USNM 107862). Quintana Roo: 6 km S, 1.5 km W of Tres Garantías (ASNHC 6441); Laguna Chichancanab (ENCB 1240). Yucatan: Chichén Itzá (AMNH 91191; FMNH 63928; USNM 108087—holotype); 500 m SW of Dzilam de Bravo (CNMA 23796–23799); 2.5 km NW Dzityá (SUI 34688); Loltún (ASNHC 3245); 6 km S Mérida (KU 91463).

Cryptotis merriami (*n* = 54).—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 (MNHN 1962-2895). Alta Verapaz: Cobán (BMNH 43.6.13.6, 7.1.1.34); Finca Xicacao (UMMZ 87869); San Pedro Carchá (ENCB 35699); Tucurú, Hacienda Concepción, 1100–1320 m (UMMZ 117845; USNM 570108, 570112). Baja Verapaz: Hotel Country Delights, 1640–1665 m (USNM 570122, 570132). Huehuetenango: Barillas, Hacienda Santa Gregoria (UMMZ 117844); Jacaltenango, 5400 ft (USNM 77020, 77048–77050, includes holotype). Izabal: Cerro Seja, 1020 m (CM 119079); Cerro Pozo de Agua, 1200 m (CM 119078). Zacapa: El Limo, 1475 m (USNM 570049, 570125). HONDURAS: Cortés: Cusuco, 1620 m (CM 119717–119731). El Paraiso: Yuscarán, Cerro de Moncerrato, cloud forest (MCZ 42992). Francisco Morazán: La Tigre National Park, San Juancito, La Rosario (UNAH no number). Lempira: Las Flores Gracias, 1850 ft (AMNH 129758); Celaque, 1430 m (CM 112883, 118520). Olancho: Sendero el Pizote, 1480 m (CM 118521. Santa Barbara: San José (AMNH 123567). NICARAGUA: Matagalpa: 9 mi N of Matagalpa, Santa María de Ostuma, 1400 m (UMMZ 117111).

Cryptotis oreoryctes (*n* = 22).—GUATEMALA: Alta Verapaz: Chelemhá, 2090 m (CM 120097–120102; USNM 569854, 569877, 569878); Chinaux, 2042 m (CM 120103–120108). El Progreso: Cerro Pinalón, Camino a las Torres, 2700 m (CM 113275). Zacapa: 6 km NNW of San Lorenzo, 2200 m, ca. 15.5 km NNW of Río Hondo (CM 113276; USAC no number [SGP 500]).

Cryptotis orophilus (*n* = 38).—COSTA RICA: ALAJUELA: 2 km oeste de Grecia (MZUCR 1298); Santa Clara (MNCR no number); Zarcero, 6000 ft (FMNH 43974). CARTAGO: Cartago (BMNH 7.5.30.4, 95.8.17.6; KU 26932; UMMZ 66465, 67316); Guarco (KU 16563); Coliblanco (KU 26930, 26931); La Estrella de Cartago, 4500 ft (AMNH 14847, UMMZ 64147); Volcán de Irazú (AMNH 9640/9558—holotype). 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 Luis de Santo Domingo de Heredia, 1400 m (KU 143375, 143376). SAN JOSÉ: Finca 2, Universidad de Costa Rica "Vargas Araya" campus (MZUCR 1500); El Muñeco, 10 mi S of Cartago, 3800 ft (UMMZ 67315); San Rafael de Montes de Oca, 4300 ft (KU 147100); Santa Ana (LSUMZ 15753). EL SALVADOR: AHUACHAPÁN: Peña Blanca, Bosque El Imposible, ca. 3 km from San Francisco Menéndez (KU 144613); 2 mi NW Apaneca, 5500 ft (MVZ 98179, 98180). HONDURAS: CORTÉZ: Rancho Azul, Lago Yojoa (MCZ 45608). EL PARAISO: Yuscaran, Cerro de Moncerrato (MCZ skin 42991); Refugio de Vida Silvestre Texiguat (UNAH 1054). OCOTEPEQUE: Belén Guacho (AMNH 124850). LEMPIRA: Celaque National Park Visitors Center, 1430 m (CM 118522). NICARAGUA: JINOTEGA: 12 km S. of Jinotega, 1400 m (KU 121591); San Rafael del Norte, 5000 ft (AMNH 28356). MATAGALPA: 9 mi N. of Matagalpa, Santa Maria de Ostuma, 1300 m (UMMZ 117112).

Cryptotis tropicalis (*n* = 23).—BELIZE: unknown locality (USNM 601301); Mountain Pine Ridge, 12 mi S Cayo (UMMZ 63008–63011). GUATEMALA: no locality (NMW 12090). ALTA VERAPAZ: Cobán (BMNH 43.6.13.5, 7.1.1.33); Finca La Primavera (AMNH 70485). GUATEMALA: Guatemala City (USAC 4175). HUEHUETENANGO: La Trinidad (USNM 570435). SOLOLÁ: Panajachel, 4900 ft (AMNH 74295–74301). MEXICO: Chiapas: no locality (ENCB 76); Liquidambar (SMF11477a); Finca Prusia, 1110m (CNMA 18, 170); Barranca de Río Malá,Volcán Tacaná (CNMA 9063).