

A new species of small-eared shrew (Mammalia, Eulipotyphla, *Cryptotis*) from the Lacandona rain forest, Mexico

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The diversity and distribution of mammals in the American tropics remain incompletely known. We describe a new species of small-eared shrew (Soricidae, *Cryptotis*) from the Lacandona rain forest, Chiapas, southern Mexico. The new species is distinguished from other species of *Cryptotis* on the basis of a unique combination of pelage coloration, size, dental, cranial, postcranial, and external characters, and genetic distances. It appears most closely related to species in the *Cryptotis nigrescens* species group, which occurs from southern Mexico to montane regions of Colombia. This discovery is particularly remarkable because the new species is from a low-elevation habitat (approximately 90 m), whereas most shrews in the region are restricted to higher elevations, typically > 1,000 m. The only known locality for the new shrew is in one of the last areas in southern Mexico where relatively undisturbed tropical vegetation is still found. The type locality is protected by the Mexican government as part of the Yaxchilán Archaeological Site on the border between Mexico and Guatemala.

Key words: Chiapas, *Cryptotis nigrescens* species group, North America, protected area, Soricidae, tropical forests

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Small-eared shrews (Eulipotyphla, Soricidae) of the genus *Cryptotis* Pomel, 1848 comprise a group of small- to medium-sized soricids that are endemic to the New World (Choate 1970). Species of the genus occur from southeastern Canada to montane regions of northern South America (Quiroga-Carmona 2013). With 37 described species (Woodman 2010; Quiroga-Carmona 2013), *Cryptotis* is one of the most diverse genera of small mammals in the Americas. On the basis of their morphological characteristics, species have been separated into 4 informal groups (Choate 1970; Woodman 2011; Guevara and Cervantes 2013). The *C. mexicanus* species group includes 14 taxa that occur from northeastern Mexico to Honduras; the *C. nigrescens* species group has 7 species distributed from southeastern Mexico to northern Andes; the *C. parvus* species group contains at least 4 species from southern Canada to Costa Rica; and the *C. thomasi* species group has 10 species in northern South America. In addition, 2 southern Central American species have uncertain relationships to other members of the genus.

Most species of *Cryptotis* are restricted to middle- and high-elevation habitats above 1,000 m. Until now, only 3 species of small-eared shrews have been known to occur below approximately 500 m: *C. mayensis* has an elevational distribution from 0 to 600 m (Woodman and Timm 1993; Engilis et al. 2012), *C. pueblensis* from 60 to 2,745 m, and *C. parvus* from 0 to 2,750 m, respectively. During an inventory in the Lacandona rain forest (Selva Lacandona), Chiapas, Mexico, in 1998–1999, 2 shrews were collected at an elevation of 90 m and identified as *C. griseoventris* (Escobedo-Morales et al. 2005; Carraway 2007). Previous records for *C. griseoventris* were restricted to pine–oak and cloud forests above 2,100 m (Woodman 2011), so these specimens represented a remarkable record that extended the geographical and elevational distribution of this species (Escobedo-Morales



et al. 2006). We recently re-evaluated the specimens and determined that neither individual has the morphological characteristics typical for *C. griseoventris* (Guevara et al. in press), and that they are distinct from every other known species of the genus. Herein, we describe the 2 specimens collected in the Lacandona rain forest as a new species, on the basis of qualitative characters; univariate, bivariate, and multivariate morphometrical characters; and molecular characters. In addition, we use species distribution models to understand the potential ecological relationships of the new species with other *Cryptotis* in the region.

MATERIALS AND METHODS

We follow the evolutionary species concept characterized by Wiley and Mayden (2000). In practice, we use evidence from morphology, mitochondrial deoxyribonucleic acid (DNA), and potential distribution to discover those lineages representing evolutionary species.

Morphology.—Morphological analyses were based on comparison of our 2 specimens from the Lacandona rain forest, with specimens belonging to the 6 known species of the genus *Cryptotis* geographically closest to the Lacandona rain forest and most likely to occur in that region. These species represent 3 species groups: *C. mexicanus* group (*C. griseoventris* and *C. mexicanus*), *C. parvus* group (*C. pueblensis* and *C. tropicalis*), and *C. nigrescens* group (*C. mayensis* and *C. merriami*). We examined and compared qualitative characters of skins, skulls, and postcranial skeletons to gauge intraspecific and interspecific morphological variation. Anatomical, cranial, dental, and postcranial terminology follows Choate (1970), Reed (1951), and Woodman and Timm (1999). Formal color names for pelage coloration are capitalized and come from Ridgway (1912). External measurements were recorded from specimen tags. Length of the head and body (HB) was obtained by subtracting tail length (TL) from total length. Tail as percentage of HB was determined by $(TL/HB) \times 100$. All comparative statements in the description of the new shrew are relative to other members of the genus *Cryptotis*, unless otherwise stated.

The following craniomandibular measurements were recorded for morphometric analysis (Woodman and Timm 1999; Ramírez-Pulido et al. 2004): condylobasal length (CBL), cranial breadth (CB), interorbital breadth (IO), zygomatic plate breadth (ZP), breadth of palate across second molars (M2B), breadth across 1st unicuspid (U1B), breadth across 3rd unicuspid (U3B), length of the upper tooth row (TR), length of molariform tooth row (MTR), palatal length (PL), height of coronoid process (HCP), height of coronoid valley (HCV), height of articular condyle (HAC), lower tooth-row length (TRD), and length from the upper border of the articular condyle to the posterior border of the m3 (LAM). Measurements were taken with a Mitutoyo electronic caliper, 500-171-20 model at 0.1 mm precision under a stereomicroscope from 12 *C. griseoventris*, 36 *C. mexicanus*, 38 *C. mayensis*, 18 *C. merriami*, 26 *C. tropicalis*, and 111 *C. pueblensis*. Missing values were not estimated. All measurements are in millime-

ters. Tabular univariate statistics include mean \pm SD and total range for each species (Appendix I). Multivariate analyses were focused on the comparison with members of *C. nigrescens* group and *C. griseoventris* because of their greater similarity in body size to the Lacandona specimens. To describe and evaluate the degree of craniomandibular differentiation among the species, a principal component analysis (PCA) was performed on 6 variables after log transformation. We also attempted to distinguish the samples within the *C. nigrescens* group using a discriminant function analysis (DFA) on all variables. All statistical analyses were performed using Statistica software (StatSoft Inc., 2005).

Specimens examined are housed in the following collections (followed by their abbreviations, Appendix II): American Museum of Natural History, New York, New York (AMNH); Angelo State Natural History collections, Angelo State University, San Angelo, Texas (ASNHC); The Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco, California (CAS); Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CMNH); Colección Nacional de Mamíferos, Mexico City, Distrito Federal (CNMA); Colección Mastozoológica El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas (ECO-SC-M); Escuela Nacional de Ciencias Biológicas, Mexico City, Distrito Federal (ENCB); Field Museum of Natural History, Chicago, Illinois (FMNH); The University of Kansas Natural History Museum, Lawrence, Kansas (KU); Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ); James Ford Bell Museum, University of Minnesota, Minneapolis, Minnesota (MMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Museo de Zoología 'Alfonso L. Herrera', Mexico City, Distrito Federal (MZFC); Naturhistorisches Museum Wien, Vienna (NMW); Royal Ontario Museum, Toronto, Ontario (ROM); Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt (SMF); University of Iowa Museum of Natural History, Iowa City, Iowa (SUI); Universidad Autónoma Metropolitana Unidad Iztapalapa, Mexico City, Distrito Federal (UAMI); Universidad Autónoma de Yucatán, Mérida, Yucatan (UADY); University of Michigan, Museum of Zoology, Ann Arbor, Michigan (UMMZ); Museo de Historia Natural, Universidad de San Carlos de Guatemala, Guatemala City (USAC); National Museum of Natural History, Washington, District of Columbia (USNM); Museum of Wildlife and Fish Biology, University of California, Davis, California (WFB).

Mitochondrial DNA.—To minimize damage, genomic DNA was extracted from skin and phalanges of only 1 of the 2 Lacandona specimens (MZFC 7168) using the DNeasy tissue kit (QIAGEN Inc., Valencia, California). We amplified the mitochondrial cytochrome *b* gene (*Cytb*; 1,140 base pairs) because it has proven useful in discriminating among species of *Cryptotis* and relevant sequences are available for comparison (Ohdachi et al. 2006; Guevara and Cervantes 2013). Owing to DNA degradation, we used 3 primer pairs for amplification: MVZ05 (5'-CGA AGC TTG ATA TGA AAA ACC ATC GTT G—Smith and Patton 1993) with MVZ04 (5'-GCA GCC CCT CAG AAT GAT ATT TGT CCT C—Smith

and Patton 1993); MVZ045 (5'-ACJ ACH ATA GCJ ACA GCA TTC GTAGG—Smith and Patton 1993) with MVZ16 (5'-AAA TAG GAA RTA TCA YTC TGG TTT RAT—Smith and Patton 1993), and MVZ17 (5'-AAC TCC TAG GAG AYC CAG AHA AYT—Smith and Patton 1999) with H15915 (5'-AAC TGC AGT CAT CTC CGG TTT ACA AGA C—Irwin et al. 1991). Polymerase chain reactions (PCRs) were performed using a reaction mix consisting of 2.0 μ l of DNA, 0.5 μ l of deoxynucleotide triphosphates (1.25 mM), 2.5 μ l of 10 \times *Taq* buffer, 1.0 μ l of each primer (100 mM), 1.5 μ l of MgCl₂ (25 mM), 16.4 μ l of water, and 0.125 μ l of *Taq* DNA polymerase. Cycles for the PCR were 1 cycle at 94°C for 1 min; 27 cycles for 1 min at 45°C (alignment); and 2 min at 72°C, plus a final 7-min cycle at 72°C. Sequence electropherograms were visually examined using Geneious software (Geneious Trial 6.1.6 2013) and sequence identities were evaluated by the BLAST process (Altschul et al. 1990). We included in our final data set *Cytb* for all sequences of the genus *Cryptotis* available from GenBank for comparison (i.e., *C. alticola*, *C. goldmani*, *C. magnus*, *C. mayensis*, *C. mexicanus*, *C. obscurus*, *C. nelsoni*, *C. parvus*, *C. peregrinus*, and *C. phillipsii*; Appendix III (Supplemental Data S1, DOI: 10.1644/14-MAMM-A-018.S1). We used the short-tailed shrew, *Blarina brevicauda*, as the outgroup because *Blarina* is the sister genus to *Cryptotis* (Ohdachi et al. 2006; Guevara and Cervantes 2013). A neighbor-joining tree based on uncorrected genetic distances (*p*-distance) was created using MEGA 5 (Tamura et al. 2011) and was bootstrapped with 1,000 replicates to provide percent bootstrap values for each branch.

Species distribution models (SDM).—Historical records for species were collected from the National Information System on Biodiversity (CONABIO), the Global Biodiversity Information Facility, and the Mammal Networked Information System. The records were matched with specimens we examined and literature records (Appendix IV, Supplemental Data S2, DOI: 10.1644/14-MAMM-A-018.S2—Choate 1970; Woodman and Timm 1993, 1999; Carraway 2007; Woodman 2010, 2011; Woodman et al. 2012; Guevara et al., in press). Initially, 19 bioclimatic data layers derived from the WorldClim database (Hijmans et al., 2005) and 3 topographic layers obtained from Hydro1k (Verdin 2011) were used at a resolution of \sim 1 km. To define the spatial extent of the study area, we intersected each species record in shapefile format with Terrestrial Ecoregions of Mexico (INEGI, CONABIO, and INE 2008) and, for species distributed farther south, we included countries where records exist. Ecological information was extracted for each environmental and topographic variable. Extracted values were log transformed and used in a PCA using a correlation matrix. From the results of the PCA, we chose factors with eigenvalues $>$ 1.0 that explained most of the variance for each species for use in the species distribution models (Appendix V, Supplemental Data S1, DOI: 10.1644/14-MAMM-A-018.S1). This process was performed in ArcMap software (ESRI 1999–2010) and statistical analyses were performed Statistica software (StatSoft Inc. 2005).

SDM were constructed with Maxent v3.3 software, which uses the principle of maximum entropy to calculate the probable distribution of a species in environmental space to be projected to a geographic space as its potential distribution (Phillips et al. 2006). Maxent provides useful SDM to explore and predict the distribution of multiple taxa, even in instances where there are a small number of records (Wisz et al. 2008). SDM were estimated for each species, excluding the records from the Lacandona rain forest, as our aim was to test the ability of models to specifically predict this locality. The prediction of interest refers to areas where unknown populations of known species could potentially occur (e.g., in the Lacandona rain forest). We generated 10 models per species using bootstrap resampling, and each model was validated with 20% of the original records. Each model was evaluated using the value of area under the curve (AUC) generated by the technique receiver operating characteristic. For each species, we calculated an average AUC value \pm *SD*. To obtain the potential distribution, we reclassified the average value for each species using the 10th percentile training presence. The result is a binary map indicating suitable conditions for each taxon (1 = suitable, 0 = unsuitable).

RESULTS

Principal component analysis.—Principal components 1 and 2 explained 89.2% of the variation in the data (PC 1 = 57.5% and PC 2 = 31.7%) and were correlated with breadth of palate across second molars and lower tooth-row length, respectively (Table 1). In a plot of 1st PCs from the PCA, the Lacandona specimens tended to plot among the larger *C. merriami* (Fig. 1a). In general, these results indicate that the new species from the Lacandona rain forest is morphometrically distinct from its congeners, but more similar to *C. merriami* and *C. mayensis* than to *C. griseoventris*.

Discriminant function analysis.—The 1st function accounts for over 87% of the explained variance (Table 2), which is weighted most heavily by the HCP contrasted with CB, MTR, and HCV. A plot of the 2 canonical axes demonstrated that all examined specimens formed 3 well-defined groups (Fig. 1b). This 1st axis separates *C. merriami* and the Lacandona shrews from *C. mayensis*, whereas the 2nd axis distinguishes the Lacandona shrews from the other 2 species. This 2nd function is most greatly influenced by MTR, TR, and CBL, which are all variables related to length of the cranium. The classification function classified 100% of specimens into their a priori species. DFA results indicate that the new species is morphometrically distinct from its congeners within the *C. nigrescens* group.

Comparison of molecular data.—Because of the degraded state of DNA extracted from dried skin, we were able to obtain only 651 base pairs (bp) with reliable readings. These are located at positions 1 to 422 and 912 to 1,140; therefore, we reduced all sequences to the same length. Despite the short segments, mitochondrial DNA discriminated the Lacandona shrew from 10 other species of *Cryptotis* (Fig. 2). Specimens of each species clustered together, and the resulting genetic

TABLE 1.—Factor loadings of the first 2 principal components (PC) axes based on 6 log-transformed craniomandibular variables from *Cryptotis mayensis*, *C. merriami*, *C. griseoventris*, and the new species, *C. lacandonensis*. See text for character abbreviations.

	PC 1	PC 2
CBL	0.776119	-0.529984
CB	0.884835	-0.185063
M2B	-0.908824	-0.363467
TR	0.596288	-0.685085
HAC	-0.877519	-0.395847
TRD	-0.336293	-0.909617
Eigenvalue	3.449946	1.900678
Explained variance (%)	57.5	31.68

relationships resemble to some degree phylogenetic relationships hypothesized on the basis of morphology and mitochondrial DNA (see Woodman 2005; Guevara and Cervantes 2013). The new species is genetically closest to *C. mayensis*, averaging a genetic distance of 5.7% with nodal support value of 100. The average genetic distances between other sister species of *Cryptotis* (sensu Guevara and Cervantes 2013) range from 2.0% to 6.8% (Table 3; e.g., *C. magnus* and *C. phillipsii*, 6.8%; *C. mexicanus* and *C. obscurus*, 5.1%; *C. goldmani* and *C. peregrinus*, 2.0%). Small (< 5%) genetic distances are known for other closely related species of mammals that had been recognized on the basis of morphology before use of molecular approaches (see Baker and Bradley 2006). The genetic distances support our morphological result in allying the Lacandona shrew most closely with the *C.*

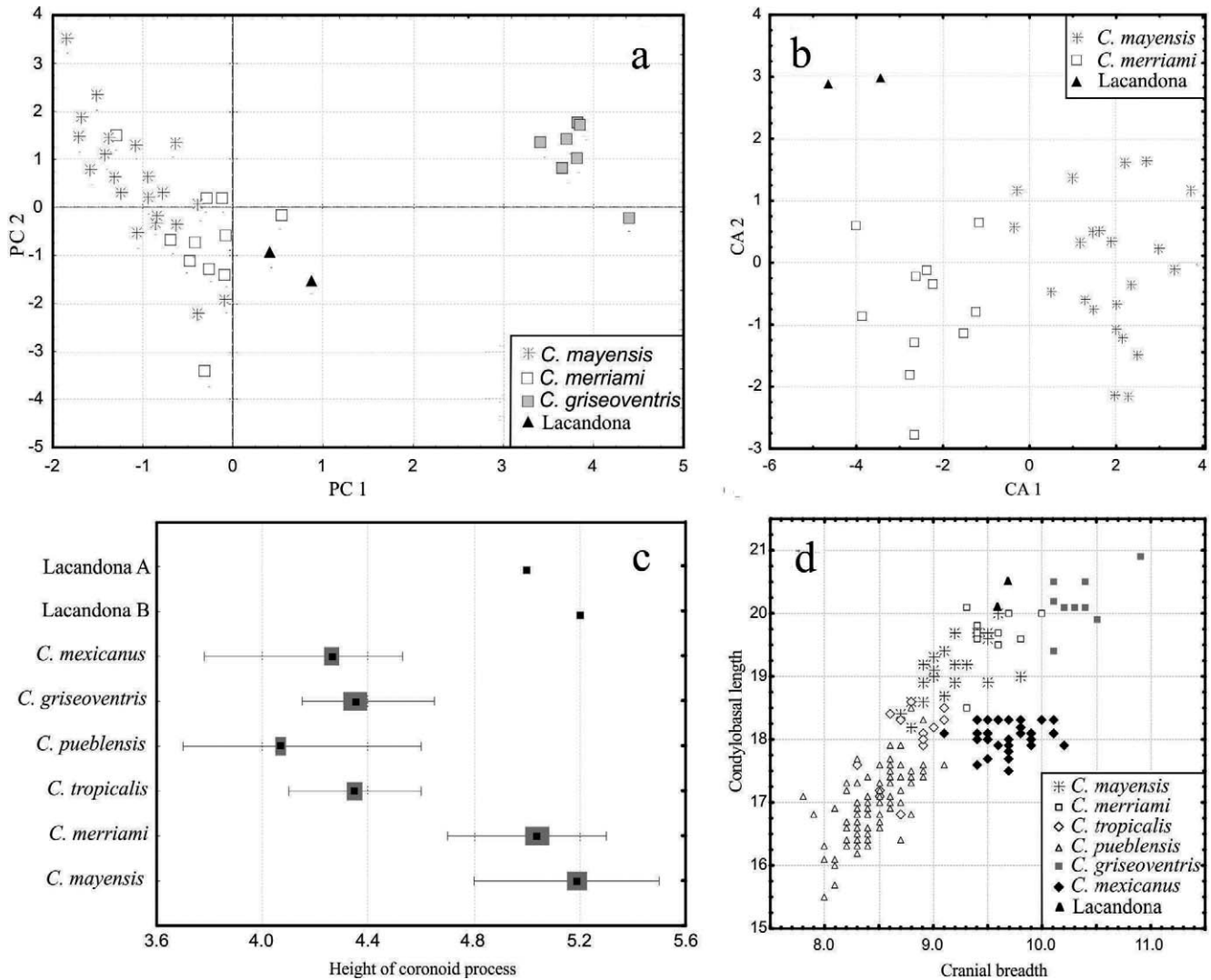


Fig. 1.—Univariate, bivariate, and multivariate analyses among species of *Cryptotis*. a) Plot of the first 2 principal components from a principal component analysis (PCA) of 6 craniomandibular measurements from *C. mayensis*, *C. merriami*, *C. griseoventris*, and the Lacandona shrew. b) Plot of the first 2 canonical axes from a discriminant function analysis (DFA) of 15 craniomandibular measurements from *C. mayensis*, *C. merriami*, *C. lacandonensis*. c) Box-and-whisker plot of height of coronoid process for 7 species of *Cryptotis*, including the 2 specimens from the Lacandona rain forest, Mexico (Lacandona A = MZFC 7168, Lacandona B = MZFC 7107). d) Bivariate plots of cranial variables among 7 species of *Cryptotis* from Central America.

TABLE 2.—Standardized coefficients of canonical variables based on 15 log-transformed craniomandibular variables from *Cryptotis mayensis*, *C. merriami*, and *C. lacandonensis*. DF, discriminant function.

	DF 1	DF 2
CBL	−0.28716	1.21662
CB	−1.27396	−0.15305
ZP	0.18796	0.03209
IO	−0.26248	−0.32075
U1B	−0.17394	0.27095
U3B	−0.06691	−0.05892
M2B	0.47518	0.22693
PL	−0.44087	0.53412
TR	0.13389	1.22674
MTR	−1.25993	−1.33314
HCP	1.47188	−0.54612
HCV	−0.89435	0.27373
HAC	1.23293	−0.34397
LAM	−0.38411	−0.53479
TRD	1.29689	−0.95100
Eigenvalues	5.39190	0.77658
Cumulative proportion of explained variance	0.87410	1.00000

nigrescens species group rather than either the *C. mexicanus* or *C. parvus* groups. Unfortunately, sequences from other species in the *C. nigrescens* group are not yet available.

Estimating potential distributions.—SDM projections (Fig. 3) of *C. pueblensis* ($n = 84$, AUC = 0.88; Fig. 3a) and *C. tropicalis* ($n = 8$, AUC = 0.68; Fig. 3b) predicted potential occurrences in the Lacandona rain forest. In the SDM for the latter species, however, the validation value was low; therefore the SDM should be regarded with caution. SDM for *C. griseoventris* ($n = 6$, AUC = 0.97; Fig. 3c) and *C. mexicanus* ($n = 98$, AUC = 0.95; Fig. 3d) predicted the distributions of closely related species, such as *C. mam*, *C. nelsoni*, and *C. goodwini*, suggesting conservatism of their measurable ecological niche (Peterson et al. 1999), but SDM for these 2 species did not predict the Lacandona rain forest. In the instance of the *C. nigrescens* group, the SDM of *C. mayensis* ($n = 20$, AUC = 0.94; Fig. 3e) predicted suitable conditions only in the Yucatan Peninsula province, including Cerro Cahuí, Guatemala, from which 1 specimen from *C. mayensis* was recently reported (Woodman et al. 2012; pentagon in Fig. 4). Additionally, a fragmented region in the lowlands of Honduras was predicted, and we suspect that *C. mayensis* or a related species is likely to inhabit that region. Unfortunately, that part of the country remains poorly studied (Woodman et al. 2012). All confirmed records of *C. mayensis* are within the Yucatán Peninsula, including a collection of skeletal remains discovered in a vase in the Mayan ruins at Uaxactún, Guatemala (Murie 1935), and Pleistocene fossils (Woodman 1995). *C. mayensis* also was reported from owl pellets collected in Guerrero, western Mexico. That fragmented and incomplete sample, however, might prove to be misidentified or an undescribed species (Choate 1970; Woodman and Timm 1993).

The potential distribution of *C. merriami* ($n = 20$, AUC = 0.95; Fig. 3f) includes the highlands of Central America, and it coincides with distributions of other montane species, such as

C. goodwini, *C. griseoventris*, *C. hondurensis*, *C. lacertosus*, and *C. mam*. None of the 10 SDM of *C. merriami* predicted the record from the Lacandona rain forest. At present, *C. merriami* is represented in Mexico only by skeletal remains from owl pellets collected at 1,500 m of elevation, near Comitán, Chiapas (Choate 1970; Woodman and Timm 1993). Despite this, our SDM predicted the Maya Mountains of Belize, where *C. mayensis* recently was captured, as a region with suitable habitat for *C. merriami* (Engilis et al. 2012; triangle in Fig. 4). In contrast, this same region was not predicted by *C. mayensis* distribution models. Our results suggest that environmental conditions in the lowland Lacandona rain forest are most similar to the tropical habitat of the *C. parvus* species group. Not surprisingly, these are different from habitats inhabited by the more typically montane species in the *C. nigrescens* and *C. mexicanus* species groups.

Family Soricidae Fischer, 1814

Subfamily Soricinae Fischer, 1814

Tribe Blarinini Kretzoi, 1965

Genus *Cryptotis* Pomel, 1848

Cryptotis lacandonensis, new species

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Holotype.—Skin, skull, and postcranial skeleton of an adult female (Museo de Zoología ‘Alfonso L. Herrera,’ Universidad Nacional Autónoma de México [UNAM], MZFC 7168; Fig. 5), collected 3 February 1999 by Luis Arturo Escobedo Morales (collector number, 265). The sex of the holotype was determined to be female on the basis of the width of the pubis (see Carraway 2009).

Type locality.—Yaxchilán Archaeological Site, 90-m elevation, municipality of Ocosingo, Chiapas, Mexico (star in Fig. 4; 16°54'N, 90°58'W). The type locality of the Lacandona shrew is in lowland tropical rain forest dominated by trees > 40 m in height on the floodplain of the Lacantún–Usumacinta rivers (Domínguez-Vázquez et al. 2004). At the time of collection, the immediate locality was described as having numerous seedlings and a thick layer of fallen leaves (Escobedo-Morales et al. 2006).

Paratype (1).—Skin, skull, and postcranial skeleton of an adult female from the type locality collected 28 August 1998 by L. A. Escobedo Morales; MZFC 7107 (collector number, 177).

Distribution.—*Cryptotis lacandonensis* is known only from the Lacandona rain forest, Chiapas, Mexico (Fig. 4). On the basis of the habitat at the type locality, the species could occur throughout the Usumacinta–Lacantún River plain in the Lacandona rain forest. Because this drainage and its associated vegetation also occur in the Petén of Guatemala (Rzedowski 2006), *C. lacandonensis* potentially inhabits this area. Until more specimens are found in neighboring countries, we consider this species as endemic to Mexico.

Etymology.—The specific epithet *lacandonensis* refers to the Lacandona rain forest, a tropical evergreen forest in southern

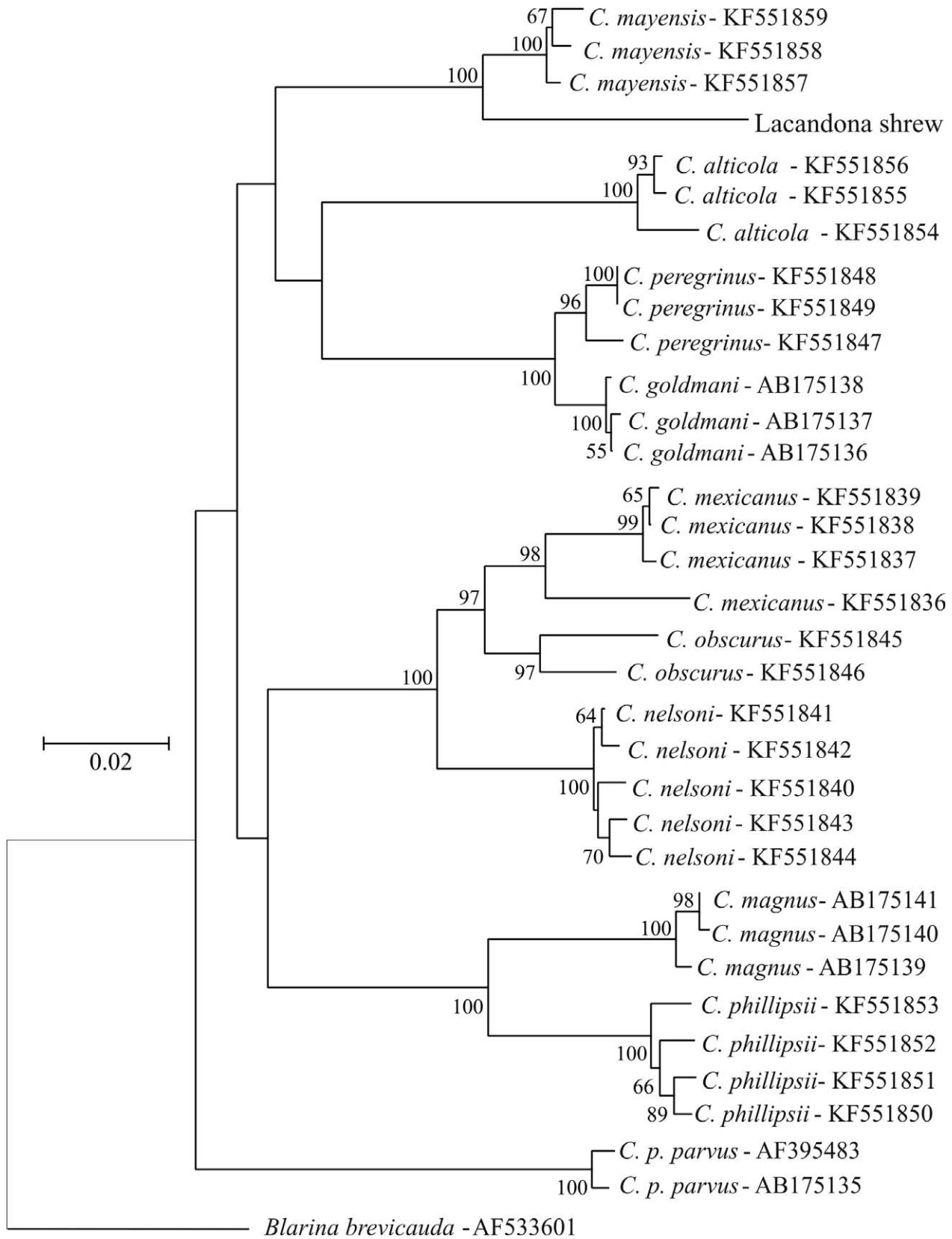


Fig. 2.—Neighbor-joining tree for 651 base pairs of cytochrome *b* gene sequences from specimens of *Cryptotis* with *Blarina brevicauda* as an outgroup. Numbers supporting groups are bootstrap values; only bootstraps > 60 are given.

TABLE 3.—Genetic distances based on analysis of 651 base pairs of cytochrome *b* sequences among *Blarina brevicauda*, 10 species of *Cryptotis*, and the new species from the Lacandona rain forest, Mexico.

	1	2	3	4	5	6	7	8	9	10	11	
1	<i>B. brevicauda</i>											
2	<i>C. alticola</i>	13.8										
3	<i>C. goldmani</i>	15.4	10.8									
4	<i>C. magnus</i>	15.9	13.3	13.6								
5	<i>C. mayensis</i>	15.1	11.3	10.9	12.8							
6	<i>C. mexicanus</i>	15.2	14.2	12.6	13.9	11.7						
7	<i>C. nelsoni</i>	14.0	13.7	12.4	12.4	11.8	6.7					
8	<i>C. obscurus</i>	14.9	13.4	12.3	12.5	11.6	5.1	6.1				
9	<i>C. parvus</i>	15.7	13.8	13.7	15.8	13.5	14.7	12.8	14.1			
10	<i>C. peregrinus</i>	15.4	10.3	2.0	13.7	10.8	13.0	12.6	12.5	13.2		
11	<i>C. phillipsii</i>	15.6	13.4	13.6	6.8	11.9	12.9	13.1	12.3	15.7	13.4	
12	<i>C. lacandonensis</i>	17.4	13.6	13.4	15.0	5.7	15.4	14.4	14.9	15.4	13.2	15.0

Mexico and the only known locality for the new species. The name Lacandona is the Spanish rendering of the Chortís-Mayan word Lacantún (“large rock”), which refers to the Lacantún River.

Common name.—Lacandona Shrew; Musaraña Lacandona.

Diagnosis.—*Cryptotis lacandonensis* is distinguished from most other species in the genus in having a tail that is proportionally longer than among members of the *C. mexicanus* and *C. parvus* species groups (Appendix I); small forepaws and short foreclaws typical of the *C. nigrescens* and *C. parvus* groups (in the *C. mexicanus* and *C. thomasi* groups the forepaws are broader and the foreclaws are longer and broader); pale gray dorsal pelage (darker pelage in the *C. mexicanus* and *C. thomasi* species groups and Central American members of the *C. parvus* species group); relatively long and broad skull for the genus (Fig. 1d); broad zygomatic plate, the anterior border of which is located more posteriorly than in any species of the *C. mexicanus* group; moderately steeply angled anterior border of the coronoid process where it joins the horizontal ramus of the mandible (as in all members of *C. nigrescens* group; in the *C. parvus* group, this angle is slightly less steep; in the *C. mexicanus* group, the angle is relatively low); substantially higher coronoid process than in the *C. mexicanus* and *C. parvus* groups (Fig. 1c); humerus long and narrow (similar morphologically to that in the *C. nigrescens* and *C. parvus* groups, but longer than in any member of the 2nd group).

Within the *C. nigrescens* group, the Lacandona shrew has a grayish pelage, more closely resembling the pale gray pelage of *C. mayensis* (darker in *C. merriami*, *C. merus*, *C. brachyonyx*, *C. colombianus*, *C. nigrescens*, and *C. hondurensis*). *C. lacandonensis* is distinguished by its large body size (HB = 78, 81 mm; Appendix I) and long skull (CBL = 20.1, 20.5). Although large-sized individuals of *C. mayensis* have been documented from Maya Mountains, Belize (triangle in Fig. 4; Engilis et al. 2012), they are distinguished by a massive cranium, much larger unicuspid teeth, U4 lingually displaced by U3, and U4 not visible in lateral view of the cranium (Engilis et al. 2012). The Lacandona shrew has “slender” dentition, as in *C.*

hondurensis (not bulbous, as is characteristic of *C. mayensis*, *C. colombianus*, *C. merriami*, *C. merus*, and *C. brachyonyx*; Choate, 1970); U4 aligned with the tooth row and completely visible in labial view of the rostrum. Complex M3 with well-developed and pigmented protocone, paracrista, and conspicuous paracone; as well as well-developed mesostyle, postcentrocrista, and metacone (Fig. 6C; similar to *C. hondurensis* and *C. brachyonyx* Woodman and Timm 1992); M3 simpler in *C. mayensis*, *C. merriami*, *C. colombianus*, *C. merus*, *C. nigrescens*. Only a hypoconid is present in talonid of m3 (in contrast to *C. brachyonyx* and *C. nigrescens*). The humerus of the Lacandona shrew (8.3 for holotype and 8.1 for paratype) is longer than is typical for *C. mayensis* (7.5 ± 0.3 , 7.2–8.0, $n = 10$) or *C. merriami* (7.7 ± 0.2 , 7.5–7.8, $n = 4$).

Description.—Medium-sized species within the genus *Cryptotis* (HB averaging 79.5 mm and CBL 20.3 mm) with a relatively medium-length tail averaging 42.5% of head–body length (Appendix I). Dorsal pelage is Deep Vinaceous-Gray to Dark Plumbago Gray. Ventrums only slightly paler than dorsum: Clear Green-Blue Gray (Fig. 5A). Rostrum long (Figs. 1d and 5B; PL/CBL = 44.7%); postorbital area of medium breadth (IO/CBL = 23.3%); 2 obvious dorsal foramina present; 1 well-developed foramen leading to a ventral extension of the sinus canal is present to the dorsal articular facet on both sides of the skull (see Woodman and Timm 1999); no foramen on the posteromedial edge of tympanic process of the petromastoids; palate long (PL averaging 9.1 mm); zygomatic plate quite broad (ZP averaging 2.6 mm; 12.6% of CBL); in lateral view, the anterior border of the ZP is aligned with the mesostyle of M1 and the posterior border is aligned with the middle of M3; in ventral view, the zygomatic process projects to the midpoint of M3. Dentition not bulbous; upper and lower dentition moderately pigmented from medium red to dark red on tips of the cones, cristae, and styles; U1–U3 cone-shaped, with a straight or slightly convex posteroventral margin; U4 aligned with the unicuspid tooth row and completely visible in labial view of the skull (Fig. 6); U4 large, averaging approximately 55% of the surface area of U3; U3 and P4 are not in contact; M3 medium-sized and complex

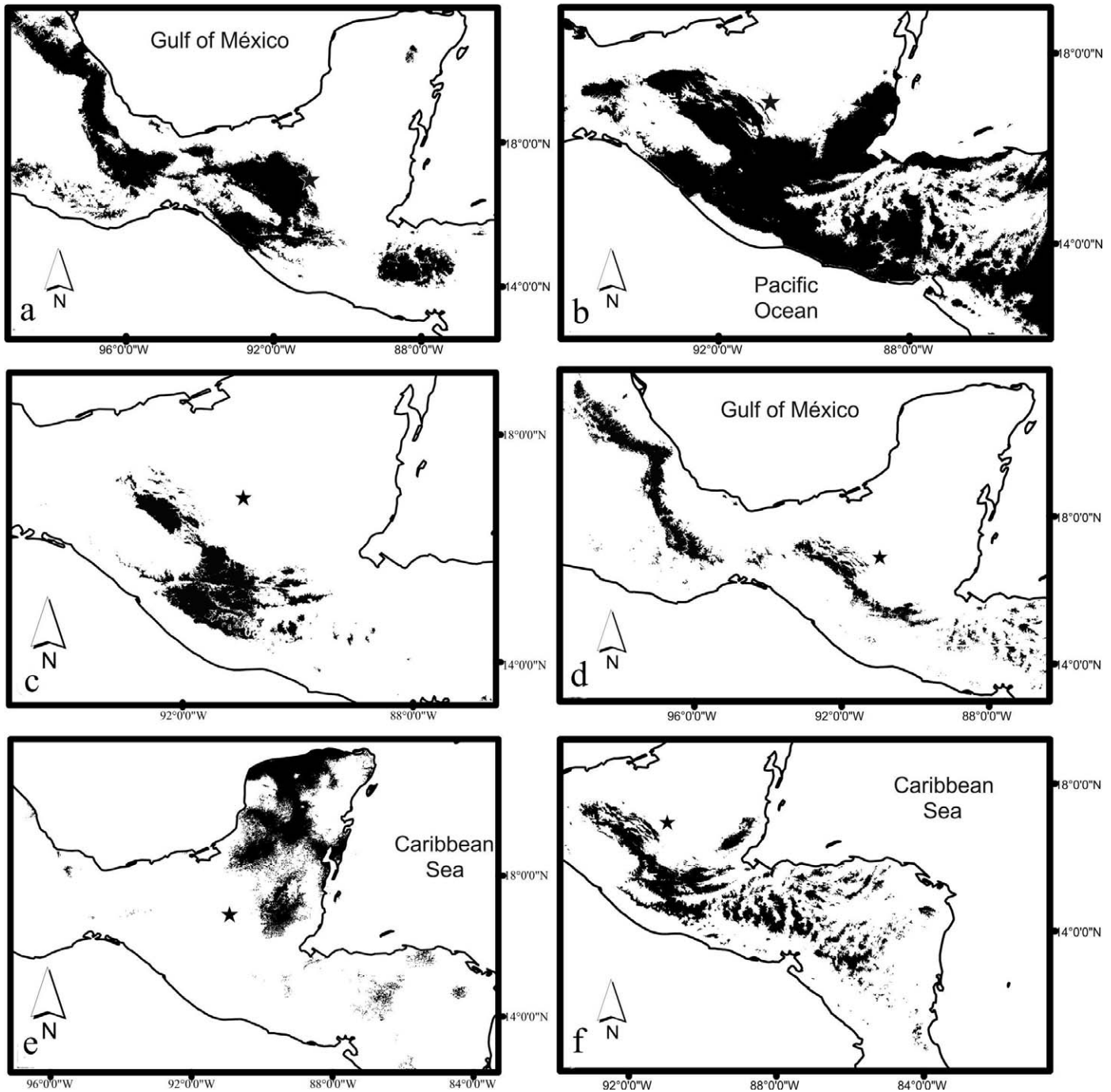


Fig. 3.—Species distribution models projected as potential distribution of a) *Cryptotis pueblensis*, b) *C. tropicalis*, c) *C. griseiventris*, d) *C. mexicanus*, e) *C. mayensis*, and f) *C. merriami*. Star indicates the type locality of the Lacandona shrew, *C. lacandonensis*.

(Fig. 6): well-developed protocone, paracrista, and paracone; mesostyle, postcentrocrista, and metacone are conspicuous. Posterior borders of P4, M1, and M2 only very slightly recessed; P4, M1, and M2 have well-developed and moderately pigmented protocones; anterior element of ectoloph of M1 nearly equal in length to posterior element; protoconal and hypoconal basins of M1 are approximately equal in size. Mandible moderately long and coronoid process of mandible high; anterior border of the coronoid process of the mandible

joins horizontal ramus at approximately a right angle; the articular condyle is broad and short; the inferior sigmoid notch is very shallow; m1 and m2 with well-developed and pigmented entoconids and hypoconids; and only a hypoconid in talonid of m3. Forefeet relatively small; foreclaws neither broadened nor elongated, similar in proportion to other members of the *C. nigrescens* and *C. parvus* species groups (Woodman et al. 2003); the length of 3rd claw averages 1.8 mm (± 0.08); humerus considerably long (8.1–8.3 mm) and

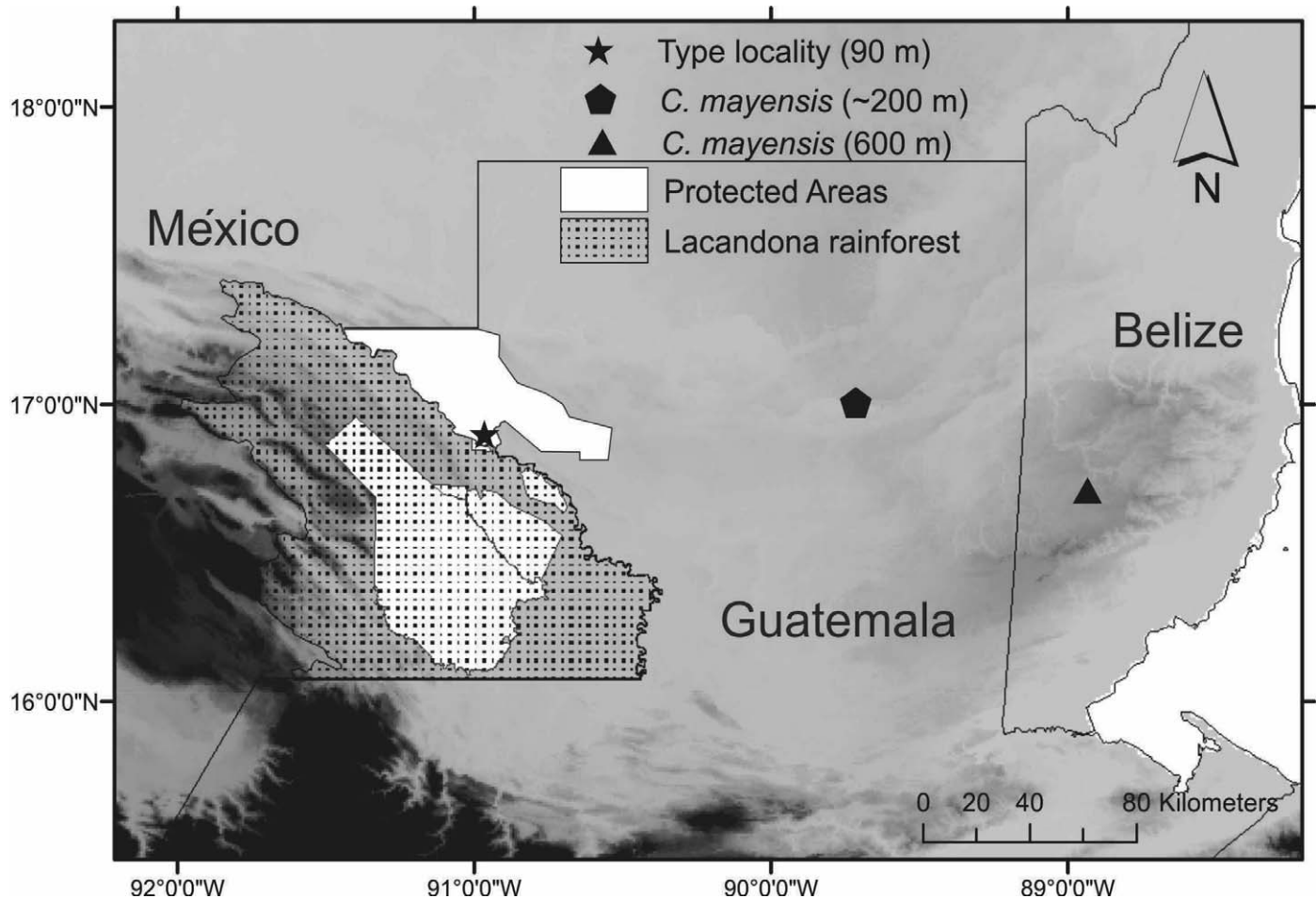


Fig. 4.—Map showing the type locality of Lacandona shrew, *C. lacandonensis* (star near the edge of the Lacandona rain forest and the decreed protected area). The pentagon is a record of *C. mayensis* from Cerro Cahui, Guatemala, and the triangle is the record of *C. mayensis* from the Maya Mountains of Belize. Areas shaded in light gray indicate lower elevations.

narrow, without elongated processes; teres tubercle located proximal to the pectoral process; medial epicondyle short for the genus.

Remarks.—To the north of the Lacandona rain forest is the Yucatan Peninsula biogeographic province that includes parts of southeastern Mexico, Guatemala, and Belize. A strong vegetational gradient is recognized as beginning within the province and extending outward to adjacent regions; scrub forest in the northern Yucatan grades to tropical rain forest in the south, and to pine–oak forests in the highlands of southern Mexico in the west and Guatemala in the east (Rzedowski 2006). With very few exceptions, mammal faunas of northern Yucatan, including bats and rodents, are closely related to the fauna in the southern Yucatan Peninsula, such as the Petén in Guatemala, where more humid habitats occur (Arita 1997; Vázquez-Domínguez and Arita 2010; Gutiérrez-García and Vázquez-Domínguez 2012). A biogeographic regionalization of the mammals of tropical evergreen forests from southern Mexico also indicates that mammalian faunas from the Lacandona rain forest are associated with the lowlands of the Yucatan Peninsula, the Petén region, and the highlands in

Guatemala (Olguín-Monroy et al. 2013), where other species of the *C. nigrescens* group (*C. mayensis* and *C. merriami*) are present. Our analysis of genetic distances suggests that *C. mayensis*, the only known shrew in the Yucatan Peninsula, is closely related to *C. lacandonensis* from the Lacandona rain forest. To test the relationships of the *C. lacandonensis* will require a comprehensive phylogenetic framework including an exhaustive sampling of all species groups.

In the vicinity of the type locality Escobedo-Morales et al. (2005) registered 70 native mammals. Among the small mammal community are *Ototylomys phyllotis*, *Heteromys desmarestianus*, *Oryzomys rostratus*, *Marmosa mexicana*, *Nyctomys sumichrasti*, and *Sigmodon hispidus*. To our knowledge, no other shrews have been reported from the Lacandona rain forest, although Medellín (1994) predicted the presence of a species of the *C. parvus* or *C. nigrescens* species groups. The Lacandona rain forest is one of the last areas where relatively undisturbed tropical vegetation is found in southern Mexico (Delgadillo and Cárdenas 2002), and it supports viable populations of such endangered mammals as *Panthera onca* and *Tapirus bairdii*. It is also home for the only Mexican

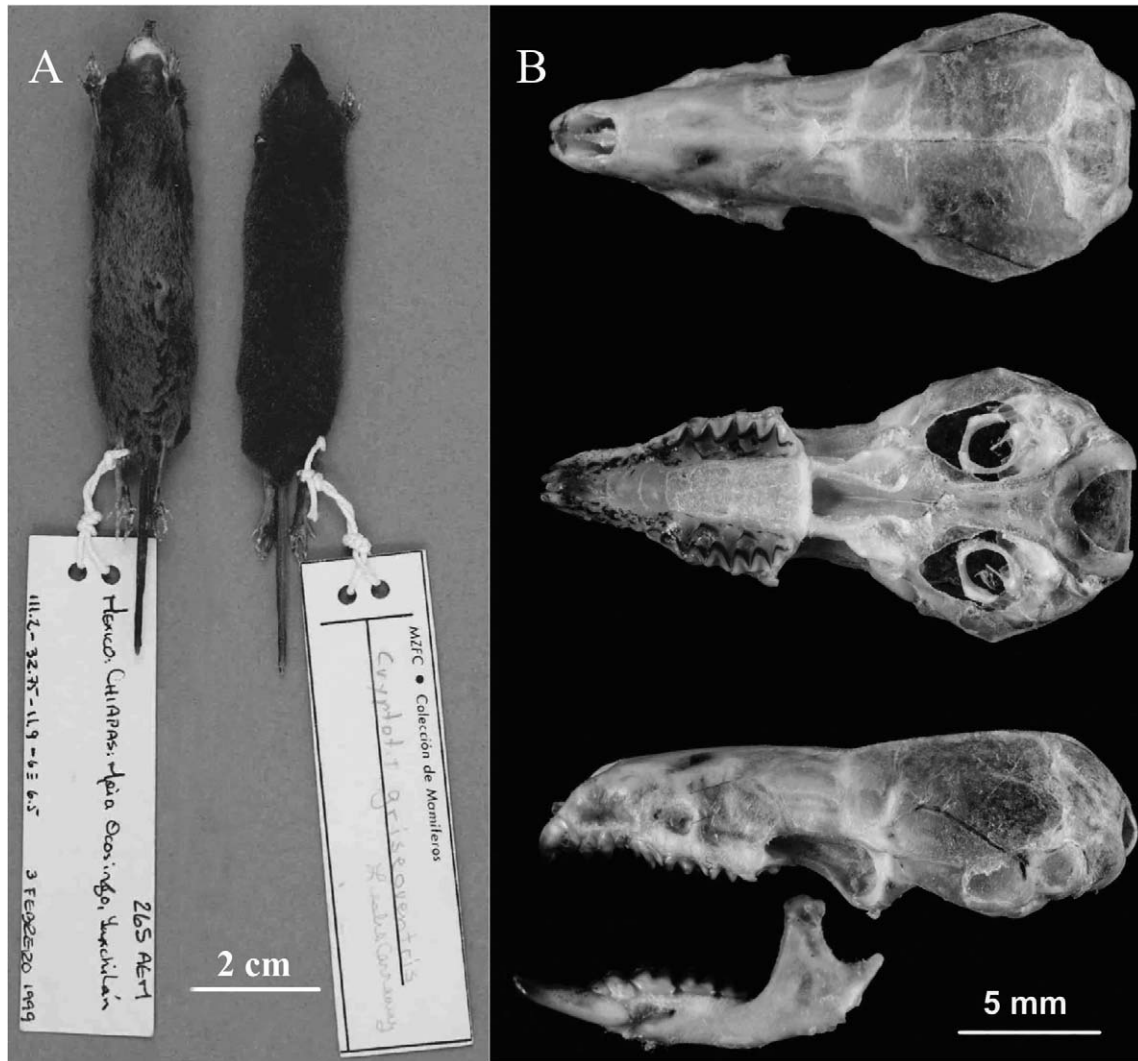


Fig. 5.—Skin, cranium, and mandible of holotype of the Lacandona shrew, *Cryptotis lacandonensis* (MZFC 7168). A) Dorsal and ventral views of skin. B) From top to bottom, dorsal, ventral, and lateral views of the cranium and lateral view of the mandible (see Appendix I for measurements).

populations of *Metachirus nudicaudatus*, *Cabassous centralis*, and *Trinychteris nicefori* (Medellín 1994; Escobedo-Morales et al. 2006). Other species restricted to this area are *Zamia lacandona* (Schutzman and Vovides 1998), *Lacandonia schismatica* (Martínez and Ramos 1989), and *Diplocentrus chol* (Francke 2007).

RESUMEN

La diversidad y distribución de las musarañas en el trópico americano son, aún, parcialmente conocidas. Aquí presentamos la descripción de una nueva especie de musaraña de orejas cortas (Soricidae, *Cryptotis*) con base en dos ejemplares de museo colectados en la selva Lacandona, Chiapas, en el sur de México. La nueva especie se puede distinguir de otras especies del género por una combinación de características que incluye la coloración del pelaje, el tamaño, caracteres dentales, craneales, postcraneales y distancias genéticas. El nuevo taxón

podría estar relacionado al grupo de especies *Cryptotis nigrescens*, cuyas especies habitan desde el sur de México hasta las montañas de Colombia. El descubrimiento es particularmente notable ya que la especie nueva habita en tierras bajas (cerca de los 90 m), mientras que la mayoría de las especies en la región están restringidas a elevaciones mayores a los 1000 m. La única localidad para la nueva especie descrita se ubica en la selva Lacandona, una de las últimas áreas al sur de México con vegetación tropical que permanecen sin alterar. La localidad tipo se encuentra en una zona protegida por el gobierno federal mexicano, ya que es parte de la Zona Arqueológica Yaxchilán, ubicada en la frontera entre México y Guatemala.

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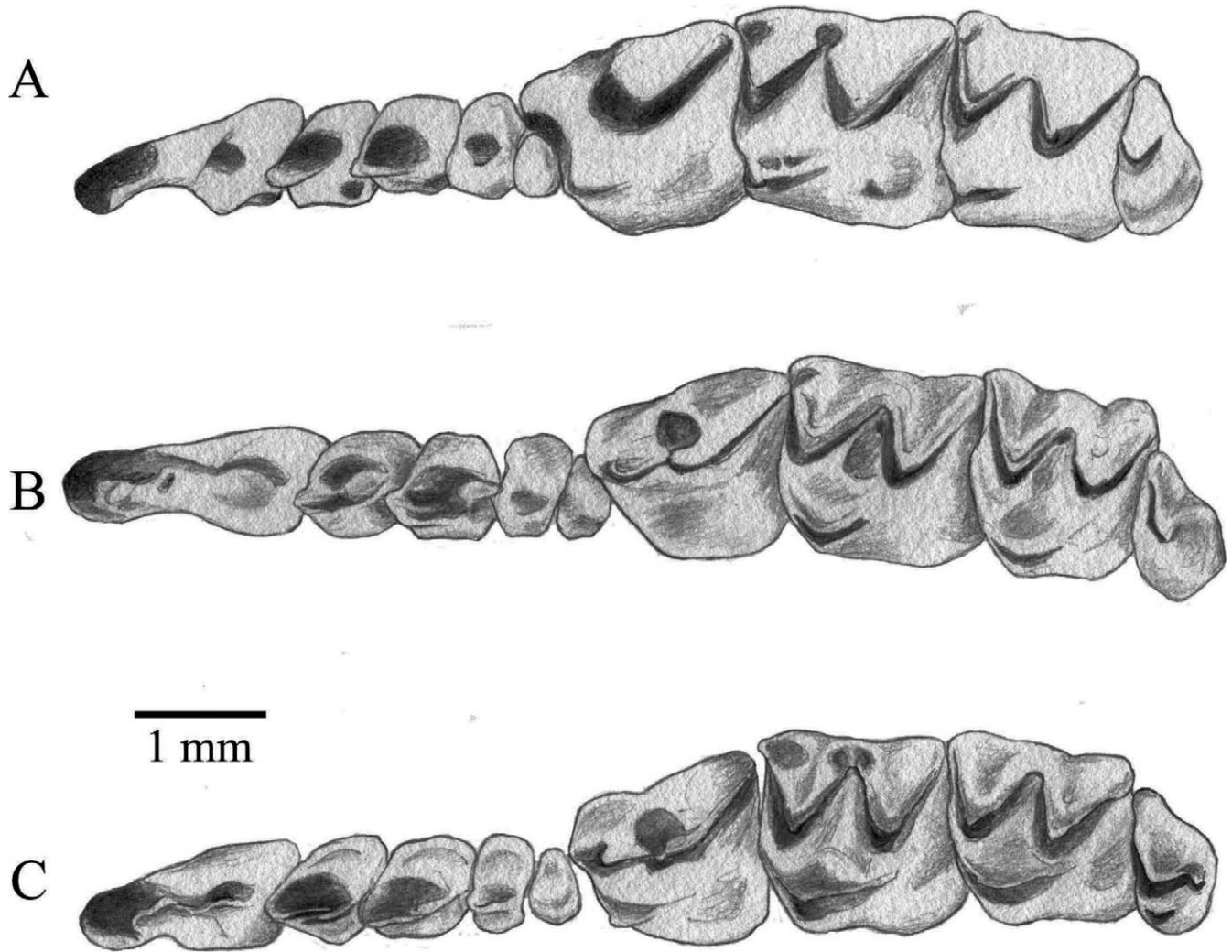


Fig. 6.—Comparison of the left upper tooth row among A) *Cryptotis merriami* (KU 84365), B) *C. mayensis* (ECO-SC-M 2358), and C) *C. lacandonensis* (MZFC 7107).

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descriptive purposes only and does not imply endorsement by the United States government.

SUPPORTING INFORMATION

SUPPLEMENTAL DATA 1. Appendix III—Specimens used in molecular analyses. Available from GenBank (Benson et al. 2013); codes are in parentheses. Appendix V—List of environmental and topographical variables used to estimate the potential distribution. For each species the variables selected on the basis of the PCA are listed.

Found at DOI: <http://dx.doi.org/10.1644/14-MAMM-A-018.S1> (16 KB DOC)

SUPPLEMENTAL DATA 2. Appendix IV—Localities used to generate the species distribution models.

Found at DOI: [10.1644/14-MAMM-A-018.S2](http://dx.doi.org/10.1644/14-MAMM-A-018.S2) (43 KB XLS)

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APPENDIX I

Craniomandibular variables from 7 species of *Cryptotis*. For the Lacandona shrew, the measurements from the holotype precede those of the paratype. Abbreviations of variables are described in “Materials and Methods.”

	<i>C. griseiventris</i>	<i>C. mexicanus</i>	<i>C. pueblensis</i>	<i>C. tropicalis</i>	<i>C. mayensis</i>	<i>C. merriami</i>	<i>C. lacandonensis</i>
HB							
Mean ± SD	78.3 ± 4.4	64.5 ± 4.8	65 ± 5	69 ± 7	65 ± 5	73 ± 9	78, 81
Range	71–85	54–74	53–74	53–78	55–76	60–101	
n	15	36	55	18	29	15	
TL							
Mean ± SD	28.6 ± 2.1	25.1 ± 2	22 ± 3	23 ± 2	28 ± 3	29.0 ± 3	33, 35
Range	24–31	21–29	14–27	18–29	21–33	24–34	
n	15	36	54	18	29	15	
TL/HB × 100							
Mean ± SD	37 ± 33	39 ± 3.5	34 ± 4	34 ± 4	43 ± 4	40 ± 5	43, 42
Range	31–42	32–50.0	26–43	25–41	30–49	29–48	
n	15	36	54	18	22	15	
CBL							
Mean ± SD	20.2 ± 0.4	18.1 ± 0.2	17.0 ± 0.5	17.9 ± 0.6	19.1 ± 0.5	19.6 ± 0.4	20.1, 20.5
Range	19.4–20.9	17.5–18.3	15.5–18.5	16.8–18.6	18.2–20.0	18.5–20.1	
n	11	36	98	16	24	12	
CB							
Mean ± SD	10.3 ± 0.3	8.5 ± 0.3	8.4 ± 0.2	8.8 ± 0.3	9.2 ± 0.3	9.5 ± 0.2	9.6, 9.7
Range	10.1–10.9	7.8–9.1	7.8–9.1	8.3–9.4	8.7–9.8	9.3–10.0	
n	9	33	92	16	22	12	
IO							
Mean ± SD	5.1 ± 0.2	4.1 ± 0.2	4.0 ± 0.2	4.2 ± 0.2	4.5 ± 0.2	4.7 ± 0.2	4.7, 4.8
Range	4.9–5.4	3.7–4.6	3.4–4.6	4.0–4.5	4.1–4.9	4.2–4.9	
n	12	34	110	7	34	16	

APPENDIX I.—Continued

	<i>C. griseoventris</i>	<i>C. mexicanus</i>	<i>C. pueblensis</i>	<i>C. tropicalis</i>	<i>C. mayensis</i>	<i>C. merriami</i>	<i>C. lacandonensis</i>
ZP							
Mean ± SD	2.1 ± 0.1	1.7 ± 0.2	1.6 ± 0.2	1.7 ± 0.1	2.3 ± 0.2	2.3 ± 0.2	2.7, 2.4
Range	1.9–2.4	1.4–2.0	1.1–2.0	1.4–2.0	1.7–2.7	2.0–2.6	
<i>n</i>	12	34	111	26	38	16	
M2B							
Mean ± SD	5.5 ± 0.2	5.0 ± 0.2	5.0 ± 0.3	5.4 ± 0.2	5.3 ± 0.3	5.7 ± 0.3	5.5, 5.4
Range	5.3–5.9	4.4–5.3	4.4–5.6	4.9–5.7	4.5–5.7	5.3–6.3	
<i>n</i>	12	34	110	26	36	16	
U3B							
Mean ± SD	3.0 ± 0.1	2.7 ± 0.2	2.6 ± 0.2	2.8 ± 0.1	3.0 ± 0.1	3.1 ± 0.1	3.1, 3.0
Range	2.8–3.1	2.1–3.1	2.2–3.1	2.6–2.9	2.8–3.3	3.0–3.3	
<i>n</i>	10	34	106	23	34	15	
U1B							
Mean ± SD	2.4 ± 0.1	2.3 ± 0.1	2.2 ± 0.1	2.4 ± 0.1	2.6 ± 0.1	2.7 ± 0.1	2.6, 2.6
Range	2.3–2.5	1.9–2.4	1.9–2.4	2.3–2.6	2.4–2.8	2.5–2.8	
<i>n</i>	10	32	106	23	32	15	
MTR							
Mean ± SD	5.2 ± 0.1	4.5 ± 0.1	4.4 ± 0.2	4.7 ± 0.1	5.0 ± 0.2	5.4 ± 0.2	5.3, 5.2
Range	4.9–5.5	4.1–4.8	3.8–4.8	4.5–5.0	4.6–5.5	5.1–5.6	
<i>n</i>	12	34	111	26	37	16	
TR							
Mean ± SD	7.7 ± 0.2	6.3 ± 0.2	6.2 ± 0.2	6.6 ± 0.2	7.3 ± 0.3	7.5 ± 0.2	7.7, 7.7
Range	7.3–8.2	5.8–6.8	5.3–6.8	6.3–6.9	6.8–8.0	7.1–7.9	
<i>n</i>	11	34	108	24	34	15	
PL							
Mean ± SD	8.9 ± 0.1	7.2 ± 0.2	7.0 ± 0.3	7.5 ± 0.2	8.5 ± 0.4	8.6 ± 0.3	9.1, 9.1
Range	8.6–9.1	6.6–7.6	6.1–7.6	6.9–7.8	7.8–9.1	8.1–9.1	
<i>n</i>	10	33	109	25	31	16	
HCP							
Mean ± SD	4.4 ± 0.1	4.2 ± 0.3	4.1 ± 0.3	4.3 ± 0.1	5.2 ± 0.2	5.0 ± 0.2	5.0, 5.2
Range	4.2–4.7	3.8–5.7	3.7–5.7	4.1–4.6	4.8–5.5	4.7–5.3	
<i>n</i>	11	34	108	25	38	18	
HAC							
Mean ± SD	3.7 ± 0.1	3.2 ± 0.1	3.2 ± 0.1	3.5 ± 0.1	3.8 ± 0.2	3.7 ± 0.2	3.7, 3.5
Range	3.5–4.0	2.9–3.4	2.9–3.7	3.3–3.7	3.4–4.1	3.4–4.2	
<i>n</i>	11	34	108	25	38	18	
HCV							
Mean ± SD	2.7 ± 0.1	2.4 ± 0.1	2.4 ± 0.1	2.6 ± 0.1	2.8 ± 0.2	2.8 ± 0.2	2.8, 2.7
Range	2.6–2.8	2.1–2.7	2.1–2.7	2.3–2.9	2.3–3.1	2.6–3.3	
<i>n</i>	11	34	108	25	38	18	
TRD							
Mean ± SD	6.1 ± 0.2	4.9 ± 0.2	4.8 ± 0.2	5.1 ± 0.2	5.5 ± 0.2	5.7 ± 0.3	5.6, 5.8
Range	5.8–6.3	4.3–5.2	4.3–5.2	4.8–5.4	5.0–6.0	5.5–6.6	
<i>n</i>	11	33	107	24	37	18	
LAM							
Mean ± SD	5.2 ± 0.2	4.3 ± 0.2	4.1 ± 0.2	4.4 ± 0.2	4.8 ± 0.2	4.8 ± 0.2	5.0, 5.0
Range	4.9–5.5	3.8–4.6	3.5–4.6	4.2–4.7	4.2–5.2	4.5–5.3	
<i>n</i>	10	32	108	25	38	18	

APPENDIX II

Specimens examined

Cryptotis griseoventris (12).—MEXICO: **Chiapas**; 0.95 km W Bazóm, Huixtán, 2,370 m, (ECO-SC-M 1023); San Cristóbal [= San Cristóbal de Las Casas], 2,400–2,900 m (USNM 75886–75894); Reserva Ecológica Huitepec, 5.5 km NW San Cristóbal de Las Casas, 2,400 m (ECO-SC-M 142); Cerro Tzontehuitz, 11 km NE San Cristóbal de Las Casas, San Juan Chamula, 2,890 m (ECO-SC-M 2051).

Cryptotis lacandonensis (2).—MEXICO: **Chiapas**; Yaxchilán Archaeological Site, Ocosingo, 90 m (MZFC 7107, 7168).

Cryptotis mayensis (38).—BELIZE: **Cayo District**; Baking Pot (BM 65.3881, 66.2333; ROM 37651); 3.3 km E, 1.1 km N Las Cuevas Research Station (WFB 4243, 4271); GUATEMALA: **Petén**: Cerro Cahuí (USAC 89); MEXICO: **Campeche**; 60 km SE Dzibalchén (19°10'N, 89°20'W; ASNHC 6071, ROM 96535); 7.5 km W Escárcega (ASNHC 1286); La Tuxpana, Champotón [= La Tuxpeña; a small port located ~30 mi. SW Campeche] (USNM 170862); **Quintana Roo**; 6 km S, 1.5 km W Tres Garantías (ASNHC 6441); 2 km SE Laguna Chichancanab [= Chickannaab] (ENCB 1240); **Yucatán**; Chichen-Itzá, ~75 ft (USNM 108087); 6 km S

Mérida (KU 91463); 0.5 Km SW Dzilán de Bravo, Dzilán de Bravo, 500 m (CNMA 23796–23801); 13 km W Peto (KU 143892); Chichén Itzá, Tinum (AMNH 91191; FMNH 63928); Centro Agrícola Molas, 14.6 km N Mérida (ECO-SC-M 2354–2356, 2358); Colonia Espino, Mérida (UADY 833); Zona Arqueológica Maya Dzibilchaltún (UADY 834–840); 2.5 km NW Dzityá (SUI 34688); Loltun (ANSHC 3245, 3246).

Cryptotis merriami (18).—GUATEMALA: **Alta Verapaz**; Cobán (BM 43.6.13.6, 43.9.15.4, 43.9.15.3, 7.1.1.34); San Pedro Carchá (ENCB 35699); Hacienda Concepción, Tukurú, 1,100 m (UMMZ 117845); 3 km S Tukurú, Finca Concepción (USNM 570108, 570112); Finca Xicacao (UMMZ 87869); **Baja Verapaz**; 9 km S Pasmola, between km 166 and 167 on Ca-14, Hotel Country Delights (USNM 570122); **Huehuetenango**; Hacienda Santa Gregoria, Barillas (UMMZ 117844); Jacaltenango (USNM 77020, 77048–77050); **Izabal**; Río Bobos, 13.45 km S, 12.4 km E Morales (CM 118752); **Zacapa**; 9.5 km NW Gualan, El Limo, Sierra de las Minas (USNM 570049); no locality (MNHN 1962–2895).

Cryptotis mexicanus (36).—MEXICO: **Oaxaca**; Cerro Zempoaltepetl, 4.5 km N Santa María Yacochi, Totontepec Villa de Morelos (CNMA 29989); 1 km NE La Cumbre, Santa Catarina Ixtepeji (CNMA 43051, 43061); Llano de las Flores, San Juan Atepec (KU 121686); 6.5 km ESE Santa María Yavesía, Santa Catarina Lachatao (MZFC 8050); Puerto de la Soledad, Teotitlán de Flores Magón (MZFC 8353–8354); Cerro San Felipe (USNM 68310, 68314); Cerro Zempoaltepetl, Santa María Yacochi, Santa María Tlahuitoltepec (USNM 68549); Reyes, Santos Reyes Pápalo (USNM 69604, 69606–69608); **Puebla**; 15 km N Tlaxco, Chignahuapan (UAMI 2937, 2944, 2947, 2949); 2 km S Tlacuilotepec, Tlacuilotepec (UAMI 5679); Huauchinango, Huauchinango (USNM 92712); **Veracruz**; 0.5 km N Puerto del Aire, Acultzingo (CNMA 42746, 42749); 0.5 km S Puerto del Aire, Acultzingo (CNMA 42733, 42738, 42741, 42754); 0.625 km N Puerto del Aire, Acultzingo (CNMA 42731–42732); El Sumidero, Acultzingo (CNMA 41953); Las Vigas, Las Vigas de Ramírez (KU 29529, 29531, 29536, 29538, 29544–29545); Xico, Xico (USNM 55076).

Cryptotis pueblensis (111).—MEXICO: **Chiapas**; 8.6 mi SW San Cristóbal de las Casas, Zinacantán (CAS 13949–13950); Huixtla, Huixtla (CNMA 8010); 25 km S, 21 km W Comitán, Tzimol (ENCB 6861); 1 mi S Pueblo Nuevo Solistahuacán, Jilotol (KU 83943); Yajalón (USNM 75895); Valle de Comitán (USNM 77019); **Mexico**; Ex-Lago De Texcoco, 4 km S, 12 km W Texcoco (UAMI 9711–9715,

9721, 9724–9730, 9733–9737, 9739–9743, 9746, 9753–9754, 9768, 9775–9776, 9779–9780, 9782); **Oaxaca**; Las Cuevas, Santiago Lachiguiri (AMNH 145838); Juquila, San Gabriel Mixtepec (AMNH 189436); San Agustín Loxichia, Pochutla, San Agustín Loxichia (AMNH 213757); km 178 Puerto Ángel Road, Río Jalatengo Camp, 4275 ft (CAS 14070, 14074); km 123 (from Highway 110), Putla-Tlaxiaco Road (CAS 14073); 4 km W San Gabriel Mixtepec (CAS 14942–14943); 1.5 km NE Santa Rosa, Santiago Jamiltepec (CNMA 44691, 44693–44694, 44698, 44701); km 193 Oaxaca-Puerto Escondido Road, 2.25 km NE San Gabriel Mixtepec (CNMA 44704–44705, 44707–44709, 44711, 44713, 44715–44717); 20 mi S, 5 mi E Sola de Vega (KU 99547); 27 km (by road) S Juchatengo, 1850 m (KU 121662); 4.5 km N Santa María de Albarradas (KU 143596); Tuxtepec, San Juan Bautista Tuxtepec (USNM 65425); Choapam, San Juan Comaltepec (USNM 68555); Juquila (USNM 71265, 71447–71448, 71450, 71452–71453); **Puebla**; Villa Juárez, 3300 ft (ENCB 457); Huauchinango (USNM 92719–92721); Metlaltoyuca (USNM 93106); **Veracruz**; 3 mi SW Martínez de la Torre (MMNH 4378); Sihuapán, Sierra de Los Tuxtlas, 5 km E San Andrés Tuxtla, San Andrés Tuxtla (CNMA 13913); 3.25 km NE Calcahualco (CNMA 44719–44721); Potrero Viejo, 1700 ft (KU 12629); 5 km N Xalapa, 4500 ft (KU 19094); 7 km NNW Cerro Gordo, Emiliano Zapata (KU 23415–23417); 1 km E Mecayucan, Cotaxtla (KU 23418); Teocelo, Teocelo (KU 29521, 29523); Texolo (Teocelo) (MCZ B9895-B9902); 7 km W El Brinco, Papantla (KU 29522); 5 Km N Huatusco, Huatusco (UAMI 13236); Xico [=Jico] (USNM 55062, 55065, 55080–55081, 55085–55086); Orizaba (USNM 58274–58275, 58284); Catemaco (USNM 65426).

Cryptotis tropicalis (26).—BELIZE: **Cayo District**; Mountain Pine Ridge, 12 mi S Cayo (UMMZ 63008–63011). GUATEMALA: no locality (BMNH 71.11.28.1; NMW 12090); **Alta Verapaz**; Cobán (BMNH 43.6.13.5, 7.1.1.33); **Guatemala**; Guatemala City (USAC 4175); **Huehuetenango**; La Trinidad (USNM 570435); **Sololá**; Panajachel, 4900 ft (AMNH 74295–74301); **Santa Rosa**; 6 Km N La Avellana, Taxisco (AMNH 244327). MEXICO: “Mexico” (MNHN 1869-152); **Chiapas**; Finca Prusia, 1,110 m (UNAM 18, 170); Liquidambar (SMF 11477a); Barranca de Río Malá, Volcán Tacaná (UNAM 9063); Reserva de la Biosfera El Triunfo, 0.75 Km NNE Finca Prusia, Ángel Albino Corzo (CNMA 44751); Reserva de la Biosfera El Triunfo, Finca Prusia, Ángel Albino Corzo (CNMA 44752, 44756).