A new species of small-eared shrew from Colombia and Venezuela (Mammalia: Soricomorpha: Soricidae: Genus *Cryptotis*)

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Abstract.—Populations of small-eared shrews inhabiting the northern Cordillera Oriental of Colombia and adjoining Venezuelan highlands in the vicinity of Páramo de Tamá have been referred alternatively to *Cryptotis thomasi* or *Cryptotis meridensis*. Morphological and morphometrical study of this population indicates that it belongs to neither taxon, but represents a distinct, previously unrecognized species. I describe this new species as *Cryptotis tamensis* and redescribe *C. meridensis*. Recognition of the population at Páramo de Tamá as a separate taxon calls into question the identities of populations of shrews currently represented only by single specimens from Cerro Pintado in the Sierra de Perijá, Colombia, and near El Junquito in the coastal highlands of Venezuela.

All South American shrews (Family Soricidae) are members of the genus *Cryptotis,* a taxon that is widespread in eastern and central North America, Central America, and northwestern South America. Soricids inhabit exclusively montane regions in South America, being restricted to highlands above at least 1200 m in the Andes north of the Huancabamba Depression, Peru. Shrews were first reported from South America near the end of the 19th century, when *Cryptotis thomasi* (Merriam, 1897) was described from near Bogotá in the Cordillera Oriental of Colombia. Since then, several additional taxa of shrews have been named from the continent (e.g., Thomas 1898, 1912, 1921; Allen 1912; Anthony 1921; Woodman & Timm 1993; Vivar et al. 1997), although the number of recognized species has varied from one (Hershkovitz 1969, 1972) to as many as ten (Tate 1932). The taxonomy of North American and Central American species of *Cryptotis* has been studied in some detail, but a comprehensive revision of South American taxa has not been attempted since Tate (1932) summarized their distributions. The taxonomy, systematics, and geographic distributions of South American soricids remain poorly understood.

The first species of shrew recorded from Venezuela was *Cryptotis meridensis* (Thomas, 1898), which was described based on specimens from Venezuela's Cordillera de los Andes, near Mérida. Although the taxonomic status of *C. meridensis* has fluctuated between that of a subspecies of a widespread, poorly-defined *C. thomasi* (Cabrera 1958; Handley 1976; Corbet & Hill 1980, 1986, 1991; Honacki et al. 1982; Durant & Pefaur 1984; Eisenberg 1989) and that of a distinct species (Cabrera 1925; Tate 1932; Cabrera & Yepes 1940, 1960; Hutterer 1986, 1993; Linares 1998), its position as a definable taxon has appeared to remain relatively stable. In reality, its perceived membership has varied considerably.

The geographic range of *C. meridensis* traditionally has included both the Cordillera de los Andes (including Sierra de Mérida and Sierra del Norte [= Sierra de La Culata]) in Venezuela and the Páramo de Tamá (= Macizo de El Tamá) on the Co-

lombia-Venezuela border along Colombia's Cordillera Oriental (Osgood 1912, Tate 1932, Cabrera 1958, Durant & Pefaur 1984, Linares 1998). The first individuals from the latter locality were collected for the Field Museum by W. H. Osgood and S. G. Jewett in 1911. These specimens were identified as *Blarina meridensis* with assistance from Oldfield Thomas (Osgood 1912), who first described the species. Páramo de Tamá is physiographically separated from the Cordillera de los Andes by the Táchira Depression, an arid valley that, according to Durant & Pefaur (1984), drops to ca. 800 m elevation. (Most large-scale maps of the region show this feature as above 1000 m.) Possibly owing to this disjunct distribution and the location of Páramo de Tamá in the Cordillera Oriental, some authors more recently have referred shrews from Páramo de Tamá to *C. thomasi,* restricting *C. meridensis* mainly to populations in the Cordillera de los Andes and the coastal highlands near Caracas (Hutterer 1986, 1993; Soriano et al. 1999).

Recent redefinition of *C. thomasi* (Woodman 1996, Vivar et al. 1997) has made it much easier to compare this species with other South American shrews. My morphometrical and character analyses of *Cryptotis* from Páramo de Tamá and the Cordillera de los Andes indicate that neither population is referable to *C. thomasi.* These studies also indicate, however, that *C. meridensis* s. l. is polytypic. The purpose of this paper is to describe a previously unrecognized species of small-eared shrew from Páramo de Tamá and to redescribe *Cryptotis meridensis* (Thomas, 1898) in the context of our greater understanding of variation within and among species of *Cryptotis.*

Materials and Methods

The current work relied on the techniques and methods of previous studies of *Cryptotis* (Woodman & Timm 1992, 1993, 1999). Additional information regarding methodology is presented there. Species synonomies list only first use of published names. Regional names, place names, and map coordinates derive from original collector tags, field notes, and field catalogs supplemented with additions, corrections, and alternative readings based on review of published localities, maps, and gazetteers of the region (Paynter & Traylor 1981; Paynter 1982; USBGN 1988, 1993). Localities for specimens from the Smithsonian Venezuelan Project (SVP) are based on original field tags supported by information from Norman E. Peterson's unpublished field catalog and journal for 1968, reposited at the National Museum of Natural History. SVP localities had been recalculated prior to being published by Handley (1976), and I note his equivalent localities in brackets. Capitalized lifezone names follow Holdridge (1947), Ewel et al. (1965), and Ewel & Madriz (1968).

In the descriptions of the new species of *Cryptotis* and *C. meridensis,* I compare characteristics of the species primarily with other members of the genus *Cryptotis,* unless stated otherwise. This context is reflected in the comparative terms used for measurements and ratios. A feature referred to as of "moderate" length, for example, is one whose mean value for the species falls within the range of plus or minus one standard deviation of the mean for the genus. The mean for *Cryptotis* was established by averaging the means of all known species. A "long" or "wide" feature is one greater than the mean plus one standard deviation; a "short" or "narrow" feature is less than the mean minus one standard deviation.

Terminology of dentition and dental characteristics follows Choate (1970). Anatomical terminology of the humerus and other aspects of the postcranial skeleton follows Reed (1951). Formal color names for pelage hues are from Ridgway (1912). Pelage coloration was determined only from museum specimens. Because such specimens may exhibit varying degrees of foxing, colors may not accurately represent those of live or newly-captured specimens.

Measurements used in my analyses follow Woodman & Timm (1993, 1999); abbreviations are explained in Table 1. In addition, crown-to-rump length (CR) is reported for embryos. External measurements are those taken by the original collector, except for head-and-body length, which was calculated by subtracting length of tail from total length. Measurements of the skull were taken to the nearest 0.1 mm using either an ocular micrometer in a binocular microscope or a hand-held dial caliper (for CBL and CB). Univariate statistics include mean ± *SD* and total range. Ratios of measurements were multiplied by 100 to calculate percentages. Orthogonal principal components were calculated from matrices of 18 untransformed craniomandibular variables (CBL, ZP, IO, U1B, M2B, PL, TR, UTR, MTR, LM1, ML HCP, HCV, HAC, BAC, AC3, TRM, Lm1) to understand the relationships in overall shape of the skull among 36 *Cryptotis meridensis,* 16 *C. thomasi,* and 13 individuals of the new species with complete crania.

Male and female *Cryptotis* are difficult to distinguish externally, and many museum specimens either lack sexual identification or may have been sexed incorrectly in the field. Previous tests for sexual dimorphism in *Cryptotis,* including *C. meridensis* (Durant & Pefaur 1984), indicate that males and females generally are not significantly different in size or shape (Choate 1970, Woodman 1992, Woodman & Timm 1993). For these reasons, both sexes were grouped together for all statistical analyses.

In my investigations of *Cryptotis,* I operate under the philosophical influence of the evolutionary species concept as redefined by Wiley (1978, 1981), which requires that the species category (and taxonomy in general) be logically consistent with reconstructed phylogenetic history. In application, I consider a species to be the largest monophyletic entity whose constituent parts interact and are not on different evolutionary trajectories (Alternative 2 of Frost & Hillis 1990). In practice, I use unique distributional patterns of morphological characters among populations to distinguish individual, presumably genetically-cohesive groups from other genetically-cohesive groups. This results in a clear, supportable, and testable framework for additional studies.

Specimens from the following institutions were used in this study: American Museum of Natural History, New York (AMNH); Natural History Museum, London (BM); Field Museum, Chicago (FMNH); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN); University of Kansas Natural History Museum, Lawrence (KU); Museum of Comparative Zoology, Cambridge (MCZ); Museo de la Universidad de Antioquia, Medellín (MUA); Royal Ontario Museum, Toronto (ROM); National Museum of Natural History, Washington (USNM).

Systematic Framework

Ongoing studies of morphological variation, species diversity, evolutionary relationships, and biogeography of *Cryptotis* (Choate 1970; Hutterer 1986; Vivar et al. 1997; Woodman 1992, 1996; Woodman & Timm 1992, 1993, 1999, 2000) have added to our knowledge of Central American and South American members of the genus. Within *Cryptotis,* I recognize four informal, but definable, groups of species that correspond closely to groupings originally delineated by Choate (1970): *Cryptotis mexicana*-group, containing nine species occurring from northeastern Mexico to central Honduras (Woodman & Timm 1999, 2000); *C. nigrescens*-group, consisting of six species distributed from southern Mexico to Colombia (Woodman & Timm 1993; 1999); *C. parva*-group, comprising at least two diagnosable species (*C. orophila* and *C. parva*) and having a discontinuous distribution from southeasternmost Canada and the eastern United States to the Central Valley of Costa Rica; *C. thomasi*-group, comprised entirely of Andean spe-

Table 1.—Measurements of selected *Cryptotis* from Colombia and Venezuela. Statistics are mean ± *SD*, and range. Measurements follow Woodman & Timm (1993).

	C. meridensis	C. tamensis	C. thomasi	C. medellinia
External measurements:				
$n = 65$		$n = 21$	$n = 22$	$n = 13$
head-and-body length (HB)				
	89 ± 5	86 ± 4	86 ± 6	85 ± 7
	76–102	80–91	69–96	77–98
tail length (TL)				
	34 ± 3	36 ± 2	24 ± 2	37 ± 6
	25–41	32–39	20–27	29–46
Skull measurements:				
$n = 35$		$n = 13$	$n = 28$	$n = 12$
condylobasal length (CBL)				
	21.5 ± 0.7	21.5 ± 0.5	21.7 ± 0.5	22.0 ± 1.0
	20.5–23.5	20.8–22.9	20.4–22.6	20.0–23.2
			($n = 23$)	($n = 11$)
cranial breadth (CB)				
	10.4 ± 0.3	10.5 ± 0.2	10.6 ± 0.2	10.9 ± 0.4
	10.0–11.0	10.1–10.8	10.2–11.0	10.3–11.4
		($n = 11$)	($n = 18$)	($n = 10$)
breadth of zygomatic plate (ZP)				
	2.0 ± 0.2	2.1 ± 0.1	2.0 ± 0.2	2.1 ± 0.2
	1.6–2.4	1.9–2.3	1.7–2.4	1.7–2.4
interorbital breadth (IO)				
	5.0 ± 0.2	5.0 ± 0.2	5.0 ± 0.2	5.4 ± 0.2
	4.7–5.4	4.8–5.3	4.6–5.4	5.0–5.8
breadth across first unicuspids (UIB)				
	2.9 ± 0.1	3.0 ± 0.1	2.7 ± 0.1	3.0 ± 0.2
	2.6–3.1	2.7–3.1	2.5–2.9	2.7–3.2
breadth across second molars (M2B)				
	6.4 ± 0.2	6.4 ± 0.1	6.2 ± 0.2	6.7 ± 0.4
	6.0–7.0	6.1 –6.6	5.9–6.5	6.0–7.2
palatal length (PL)				
	9.5 ± 0.4	9.5 ± 0.2	9.3 ± 0.3	9.8 ± 0.4
	8.8–10.2	9.1–9.8	8.6–9.7	9.2–10.4
length of upper toothrow (TR)				
	8.2 ± 0.3	8.3 ± 0.3	8.2 ± 0.2	8.7 ± 0.4
	7.3–8.8	7.9–8.7	7.7–8.5	8.1–9.2
length of unicuspid toothrow (UTR)				
	2.8 ± 0.1	2.8 ± 0.1	2.8 ± 0.1	3.0 ± 0.1
	2.6–3.0	2.6–3.0	2.4–3.0	2.8–3.2
length of molariform toothrow (MTR)				
	5.8 ± 0.2	5.9 ± 0.2	5.8 ± 0.1	6.2 ± 0.3
	5.5–6.3	5.6–6.1	5.5–6.0	5.7–6.5
posterior width of first upper molar (M1W)				
	2.0 ± 0.1	2.0 ± 0.1	1.9 ± 0.1	2.1 ± 0.1
	2.0–2.2	1.9–2.1	1.8–2.1	2.0–2.3

Table 1.—Continued.

C. meridensis	C. tamensis	C. thomasi	C. medellinia
length of mandible (ML)			
6.9 ± 0.3	7.0 ± 0.2	7.0 ± 0.2	7.5 ± 0.3
6.3–7.6	6.9–7.4	6.6–7.4	7.0–8.0
height of coronoid process (HCP)			
4.8 ± 0.2	4.6 ± 0.2	4.6 ± 0.1	5.1 ± 0.3
4.5–5.2	4.3–4.8	4.3–4.9	4.5–5.5
height of coronoid valley (HCV)			
3.3 ± 0.1	3.1 ± 0.1	3.1 ± 0.1	3.3 ± 0.2
3.1–3.5	3.0–3.2	2.8–3.4	2.9–3.6
height of articular condyle (HAC)			
4.4 ± 0.2	4.4 ± 0.1	4.3 ± 0.1	4.5 ± 0.3
4.0–4.8	4.2–4.6	4.1–4.6	4.0–4.9
breadth of articular condyle (BAC)			
3.6 ± 0.2	3.5 ± 0.1	3.6 ± 0.1	3.7 ± 0.1
3.2–4.0	3.3–3.6	3.4–3.8	3.4–3.8
articular condyle to m3 (AC3)			
5.6 ± 0.3	5.4 ± 0.1	5.7 ± 0.2	5.5 ± 0.2
5.1–6.3	5.2–5.7	5.0–6.0	5.1–5.8
length of lower toothrow (TRM)			
6.5 ± 0.2	6.6 ± 0.2	6.4 ± 0.2	6.8 ± 0.3
6.1–6.9	6.3–6.9	6.1–6.7	6.4–7.2
length of first lower molar (Lm1)			
2.0 ± 0.1	1.9 ± 0.1	1.9 ± 0.1	2.0 ± 0.1
1.8–2.1	1.8–2.1	1.7–2.0	1.9–2.2
Weight (g):			
12.3 ± 2.0	13.9 ± 2.2	10, 10	15.5, 16, 17
8.5–18.0	10.8–16.1		
($n = 48$)	($n = 6$)	($n = 2$)	($n = 3$)

cies (Hutterer 1993, Woodman 1996, Vivar et al. 1997). All South American shrews are members of either the *C. thomasi*-group or the *C. nigrescens*-group. Eisenberg (1989) incorrectly suggested that *C. parva* might occur in northern Colombia. In fact, the southernmost taxon of the *C. parva*-group, *C. orophila*, is not known from south of central Costa Rica, and there is no evidence that it ever extended into South America. Specimens of *C. parva* previously reported from Panama were shown to be misidentified *C. nigrescens* (Woodman & Timm 1993).

With the exceptions of *C. mera* and *C. colombiana*, which are members of the mostly Central American *C. nigrescens*-group (Woodman & Timm 1993, Woodman 1996), South American taxa of shrews are members of the *C. thomasi*-group. The *C. thomasi*-group currently includes only South American taxa, but the membership of the group may change as additional South American and southern Central American taxa are analyzed and phylogenetic relationships are understood more completely. This group appears to share a number of apomorphies with the *C. mexicana*-group (Woodman & Timm 1999, 2000) and may prove to be a subset of that

group. Within this framework, all of the species considered in this study (*C. medellinia, C. meridensis, C. thomasi,* and the new species from Páramo de Tamá) are members of the *Cryptotis thomasi*-group of shrews.

Some portions of this view of relationships of South American shrews were challenged by Vivar et al. (1997), who restricted membership of the *C. thomasi*-group to *C. thomasi* and possibly *C. medellinia.* They suggested that *C. colombiana* be removed from the *C. nigrescens*-group, but provided no guidance as to its possible alternative relationships.

The *C. thomasi*-group and the *C. nigrescens*-group can be distinguished using a combination of characters. Members of the *C. thomasi*-group all have longer, more luxuriant fur than members of the *C. nigrescens*-group. Unlike other New World soricids, males of the *C. thomasi*-group lack obvious bare patches marking the location of the lateral glands. The forefeet of these shrews are somewhat enlarged, and the foreclaws are elongate (but not broadened, as in the *C. mexicana*-group), unlike the *C. nigrescens*-group in which neither forefeet nor foreclaws are enlarged. U1–3 typically are relatively narrow and concave to very concave on the posteroventral margin, rather than cone-shaped with a straight or convex posteroventral margin. The anterior element of ectoloph of M1 is reduced relative to the posterior element, rather than being of approximately equal size. The anterior border of the coronoid process of the mandible joins the horizontal ramus at a relatively low angle, rather than at a high angle. The articular process is relatively high and narrow, rather than low and broad. The humerus in the *C. thomasi*-group is moderately long, quite robust, and slightly curved with a prominent medial epicondyle and a well-defined teres tubercle that is more centrally located. The humerus in the *C. nigrescens*-group is similar to that of the *C. parva*-group: it is

long, straight, and narrow, with the teres tubercle more proximally located.

I consider *Cryptotis thomasi* s. s. to be restricted entirely to the central portion of the Eastern Cordillera of Colombia around Bogotá, where it is known only from elevations above 2700 m (Woodman 1996). This region has a long history of scientific collection, and, for shrews, it is one of the better represented parts of the Andes. The southern limit of *C. thomasi's* distribution probably is north of the Paso de las Cruces (3°17'N, 74°37'W), which drops below 1900 m. There are no specimens known from between the northern border of Cundinamarca Department and northern Santander Department, and the northern limit of the species may be associated with headwater valleys and tributaries of the Río Chicamocha and Río Upía.

Cryptotis medellinia is distinct from *C. thomasi* and is known mainly from the northern portion of the Central Cordillera of Colombia. More recently, I identified specimens of this species from the northern part of the Western Cordillera of Colombia as well. Its elevational range is from about 2000 to 3800 m. The southern limits of its distribution in each of the cordilleras is uncertain, but no specimens are known from south of Paso de Quindío (= Boquerón de Quindío, 4°38'N, 75°32'W) in the Central Cordillera, nor south of Páramo Frontino (6°28'N, 76°04'W) in the Western Cordillera.

Cryptotis tamensis, new species
Figs. 1, 3–7

Blarina meridensis: Osgood, 1912:62.
C[*ryptotis*] *meridensis*: Thomas, 1921:354 (in part).
Cryptotis thomasi meridensis: Cabrera, 1958:48 (in part).
Cryptotis meridensis meridensis: Linares, 1998:106 (in part).

Holotype.—Skin, skull (Fig. 1), and fluid-preserved body of adult female (lactating, gravid: 2 fetuses, CR = 19), USNM
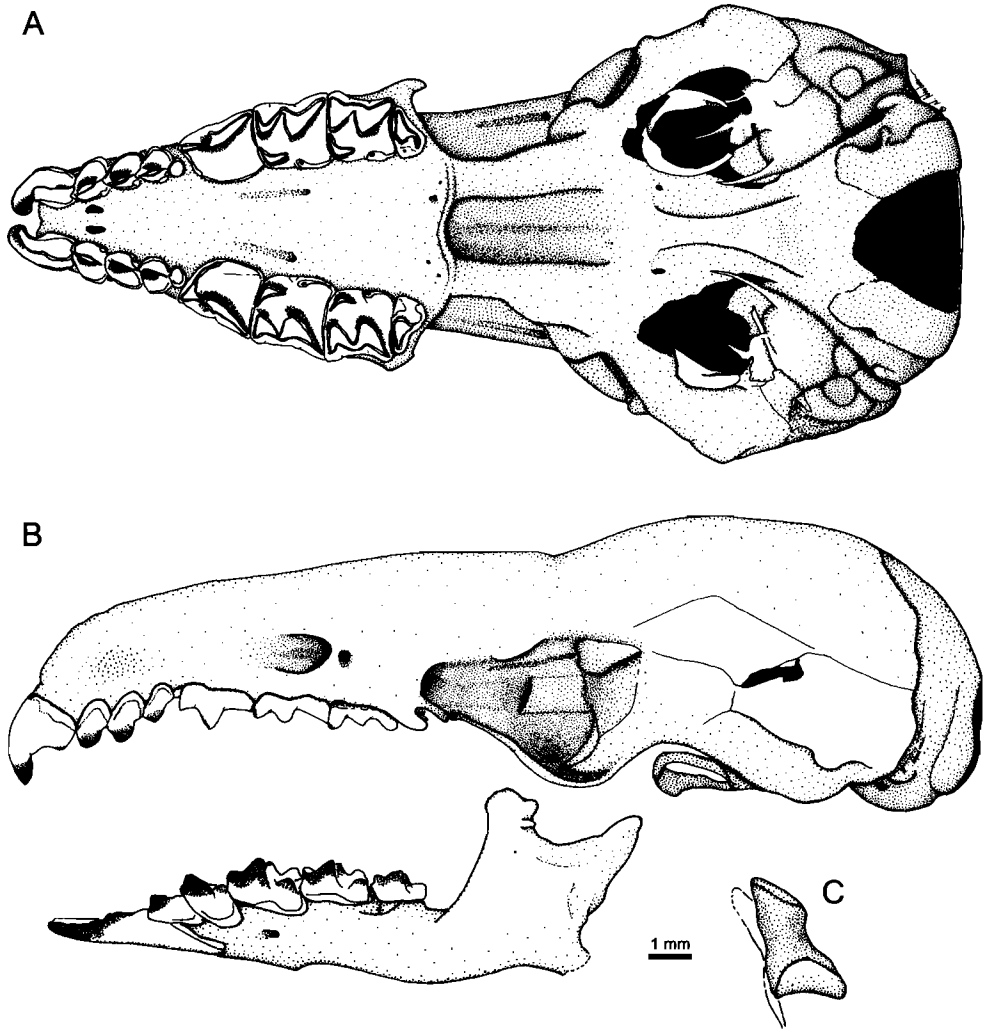
A

B

C

1 mm

Fig. 1. Holotype of *Cryptotis tamensis* (USNM 418567): (A) palatal view of cranium; (B) lateral view of the cranium and mandible; and (C) posterior view of articular process of the mandible.

418567, taken in a snap trap baited with sardines, rolled oats, and raisins on 8 March 1968 by a Smithsonian Venezuelan Project (SVP) team led by Norman E. Peterson, field number SVP 21863. Skin in good condition, some matting of fur; skull has well worn dentition, lacking left tympanic, some damage to right pterygoid; mandible lacks both angular processes. Standard field measurements: total length = 118; length of tail = 35; length of hind foot = 17; length of ear slit = 8; weight = 15.9 g.

Type locality.—VENEZUELA: *State of*

Táchira: Buena Vista, 7°27′N, 72°26′W, 2415 m; near Páramo de Tamá; 35 km S, 22 km W of San Cristóbal [reported as "41 km SW San Cristóbal and 12 km SSE Las Delicias" by Handley 1976:64].

Referred specimens (21).—COLOMBIA: *Norte de Santander*: Páramo de Tamá, head of Río Táchira [7°25′N, 72°26′W, 2450 m—Paynter & Traylor 1981] (FMNH 18571, 18614, 18615); Páramo de Tamá [7°25′N, 72°26′W, 3329 m—Paynter & Traylor 1981] (FMNH 18572, 18608–18611, 18613, 18621; MCZ 21004 [=
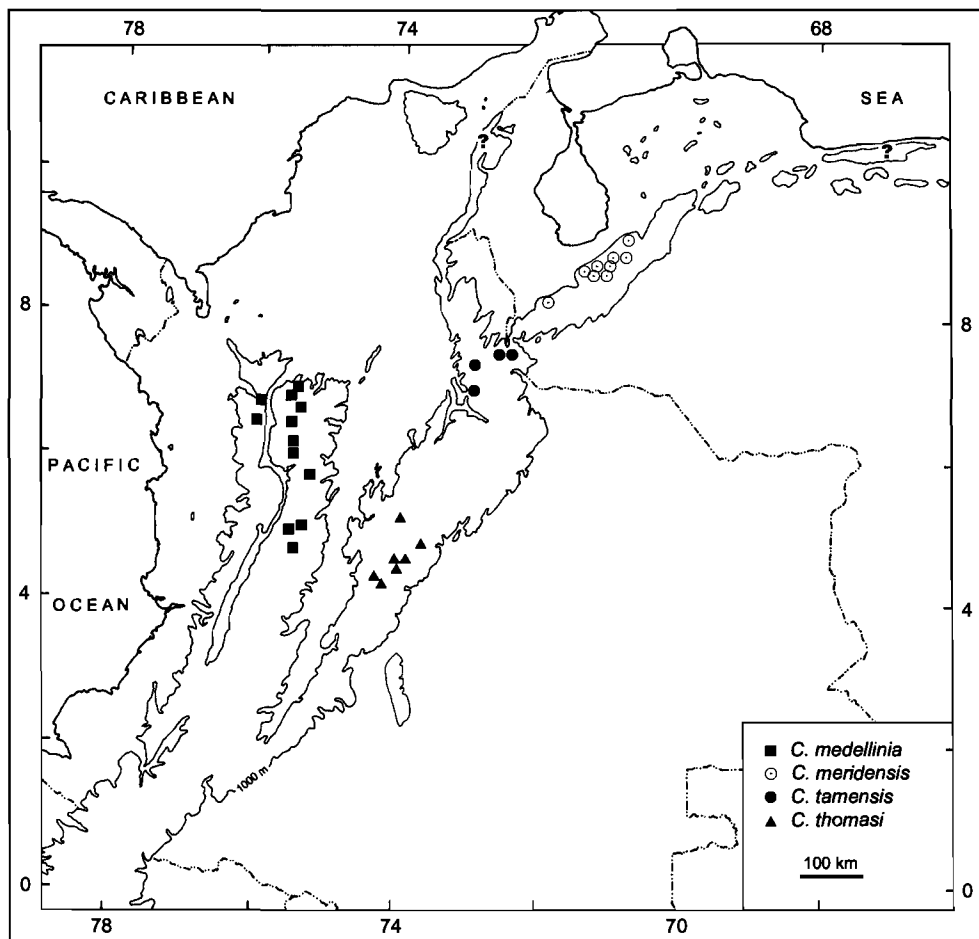
Fig. 2. Map of the northern Andes showing the distributions of four species of *Cryptotis* in Colombia and Venezuela: *C. medellinia* (closed squares); *C. meridensis* (dotted open circles); *C. tamensis* (closed circles); *C. thomasi* (closed triangles). Question marks indicate the locations of two reported collections of *Cryptotis* whose specific identities are unknown (see text). The 1000 m contour is shown.

FMNH 18616]; USNM 260747 [= FMNH 18612]). *Santander*: above Suratá [7°22'N, 73°00'W—USBGN 1988], 2750 m (LACM 56101). VENEZUELA: *Táchira*: Buena Vista, 7°27'N, 72°26'W, 2380–2415 m [type locality] (USNM 418566, 418569, 418570, 490534); Páramo de Tamá [7°25'N, 72°26'W—USBGN 1988] (FMNH 18617–18620).

Additional record.—COLOMBIA: *Santander*: Finca El Rasgón, 6°55'30"N, 73°02'40"W, 2350 m, Vereda La Cristalina, Municipio de Piedecuesta (MUA no number).

Etymology.—*Tam*(á) + *ensis* [Latin ending denoting place], "from Tamá."

Distribution.—Montane Rain Forest, Montane Wet Forest, Lower Montane Wet Forest, disturbed "cloud forest," and pasture margins, from the Tamá highlands of western Táchira, Venezuela, and southeastern Norte de Santander Dept., Colombia, to northeastern Santander Dept., Colombia (Fig. 2); known elevational distribution, 2385–3329 m. Also may occur in Lower Montane Rain Forest and Lower Montane Moist Forest life zones.

Diagnosis.—A large *Cryptotis* with long,

chocolate-brown dorsal pelage that contrasts subtly with paler, olive-brown venter; moderately long tail, averaging 42% of head-and-body length; enlarged forepaws and elongate foreclaws; indistinct lateral glands. Distinguished within *C. thomasi*-group by possessing bulbous dentition; reduced U4 (averaging 29% of U3), but having four unicuspids visible in lateral view of cranium; slender U1–3 with concave posteroventral margins; low coronoid process; short posterior mandible behind m3; simple M3; often an obvious foramen on posterior edge of tympanic process of one or both petromastoids; distinct pigmentation in protoconal basin (occasionally pale pigmentation in hypoconal basin) of P3, M1–2; shallow inferior sigmoid notch; no obvious entoconid on m3.

Description.—A large *Cryptotis*, head-and-body length averaging 86 mm (Table 1). Tail moderately long, averaging 42% of head-and-body length (Table 2). Dorsal hairs about 6–7 mm long. Dorsal pelage Mummy Brown to Clove Brown; venter Olive Brown to Buffy Brown; dorsal hairs 2-banded, with grey base and mid-section, and 1–1.5 mm brown distal tip. Forepaws somewhat enlarged (Fig. 3). Foreclaws similar to those of *C. thomasi*: elongate, but not broadened; similar in length to those of *C. phillipsii* and *C. obscura*, but relatively narrower. Lateral glands of males indistinct.

Usually two obvious dorsal foramina along the suture between the frontals (95%, *n* = 19); generally unequal in size (67%). Typically lacking lateral branch of sinus canal and associated foramen (see Woodman & Timm 1999) posterior to the dorsal articular facet (94%, *n* = 18); this foramen was found on only one specimen (USNM 418566), in which it is well developed, but present only on one side of the cranium. A foramen often present dorsal to one or both dorsal articular facets (44%, *n* = 18); sometimes only on one side (18%, *n* = 18) of the cranium; typically minute, but can be well developed. Typically a foramen on the posterior edge of the tympanic process of

one or both petromastoids (88%, *n* = 16 individuals; Fig. 4); typically on both tympanic processes (73%, *n* = 15 individuals); foramen usually small (71%, *n* = 24 foramina), but can be medium-sized and obvious (29%); often varies in size between left and right sides of a single individual (46%, *n* = 13; 38% of all individuals have at least one foramen that is medium-sized or larger, *n* = 16; Fig. 4); foramen never as large as in *C. thomasi* or *C. medellinia*. Rostrum of moderate length (PL/CBL = 44.0%). Interorbital area moderately broad (IO/CBL = 23.2%). Zygomatic plate of moderate breadth in proportion to CBL (9.6%) and PL (21.9%); anterior border of zygomatic plate at mesostyle-metastyle valley to metastyle of M1; posterior border from metastyle of M2 to parastyle-mesostyle valley of M3, and from about middle to posterior edge of maxillary process. Palate of moderate breadth for the genus (M2B/PL = 68.0%). Anterior process of petromastoid low and narrow.

Dentition bulbous. Teeth moderately pigmented: dark red to nearly black on tips of cones, styles, and cristae; pale to medium pigment typically extends into protoconal basin (and occasionally into hypoconal basin) of M1 and M2. Unicuspid toothrow of moderate length (UTR/CBL = 13.2%); uncrowded, U4 generally visible in lateral view of skull (74%, *n* = 19; Fig. 5). U1–3 relatively slender and concave on the posteroventral margin. Posterolingual cuspules typically minute (61%, *n* = 18) or obvious (39%) on cingulum of U1–3. U4 reduced, averaging 29% the surface area of U3 (Fig. 6). Posterior borders of P4, M1, M2 only slightly recessed. Anterior element of ectoloph of M1 reduced relative to posterior element; protoconal basin of M1 about equal in size to hypoconal basin. M3 generally appears simple: hypocone usually absent; postcentrocrista shortened; metacone minute (50%, *n* = 16) and often lightly pigmented, or absent (50%); reduced hypocone occasionally present, resulting in a larger, more squared M3 that appears complex.

Table 2.—Characters of selected Colombian and Venezuelan *Cryptotis.*

C. meridensis	C. tamensis	C. thomasi	C. medellinia
Petromastoid foramen present one or both petromastoids			
87%	88%	100%	100%
(n = 55)	(n = 16)	(n = 27)	(n = 14)
72% both	73% both	100% both	100% both
28% one	27% one		
(n = 46)	(n = 15)		
Postero-lingual cuspules on cingulae of U1-3			
78% absent	61% minute	30% absent	15% absent
22% minute	39% obvious	30% minute	70% minute
(n = 40)	(n = 18)	40% obvious	15% obvious
		(n = 10)	(n = 13)
U4 lacking			
25%	0%	0%	0%
(n = 51)	(n = 19)	(n = 13)	(n = 12)
Size of U4 (% of U3)			
19 ± 7%	29 ± 8%	50 ± 9%	40 ± 9%
(2–37)	(12–42)	(36–64)	(27–53)
(n = 48)	(n = 19)	(n = 13)	(n = 12)
Emargination of posterior borders of P4, M1			
v. slight	v. slight	slight to	v. slight
to slight	to slight	moderate	to slight
Complexity of M3			
98% simple	50% simple	8% simple	73% simple
2% minute	50% complex	92% complex	27% complex
(n = 45)	(n = 16)	(n = 13)	(n = 11)
Lower sigmoid notch			
shallow	shallow	shallow to	mod. deep
		v. shallow	
Entoconid of m3 present (absent, minute, obvious)			
15% minute	32% minute	30% obvious	53% minute
85% absent	68% absent	70 absent	47% absent
(n = 41)	(n = 19)	(n = 23)	(n = 15)
Relative tail length (TL/HB × 100)			
38 ± 4	42 ± 3	29 ± 4	43 ± 6
28–49	35–48	21–36	34–56
(n = 65)	(n = 21)	(n = 22)	(n = 13)
Relative length of rostrum (PL/CBL × 100)			
44.2 ± 0.9	44.0 ± 1.4	43.2 ± 0.6	44.3 ± 0.6
40.9–45.3	40.2–45.6	42.2–44.3	43.4–45.3
(n = 35)	(n = 13)	(n = 23)	(n = 10)
Relative breadth of zygomatic plate (ZP/PL × 100)			
21.2 ± 2.0	21.9 ± 1.4	21.3 ± 1.7	21.2 ± 2.1
15.8–25.0	19.6–25.0	18.5–25.3	17.7–24.0
(n = 50)	(n = 17)	(n = 27)	(n = 10)
Relative breadth of zygomatic plate (ZP/CBL × 100)			
9.5 ± 0.9	9.6 ± 0.6	9.3 ± 0.6	9.4 ± 1.0
7.1–10.9	8.7–10.8	7.8–10.6	7.7–10.6
(n = 35)	(n = 13)	(n = 23)	(n = 10)

Table 2.—Continued.

C. meridensis	C. tamensis	C. thomasi	C. medellinia
Breadth of interorbital area (IO/CBL)			
23.5 ± 0.8	23.2 ± 0.7	23.0 ± 1.0	24.3 ± 0.6
22.0–24.9	22.0–24.4	20.6–24.6	23.3–25.4
(n = 35)	(n = 13)	(n = 23)	(n = 10)
Relative length of unicuspid toothrow (UTR/CBL × 100)			
13.1 ± 0.5	13.2 ± 0.5	13.1 ± 0.5	13.5 ± 0.4
12.2–14.3	12.3–13.9	11.8–14.0	12.9–14.2
(n = 35)	(n = 13)	(n = 23)	(n = 10)
Relative palatal breadth (M2B/PL × 100)			
67.2 ± 2.1	68.0 ± 2.0	66.6 ± 2.5	68.3 ± 2.4
62.5–72.7	64.3–71.0	60.8–70.5	64.5–71.7
(n = 50)	(n = 17)	(n = 27)	(n = 10)
Relative height of coronoid process (HCP/ML × 100)			
69.8 ± 2.5	65.0 ± 2.0	66.0 ± 2.2	68.5 ± 2.5
63.4–76.2	62.3–68.1	60.6–70.6	64.3–72.6
(n = 50)	(n = 17)	(n = 27)	(n = 17)
Relative length of posterior portion of the mandible (AC3/ML × 100)			
81.0 ± 2.6	77.2 ± 1.8	80.9 ± 3.0	75.3 ± 3.0
73.7–86.6	75.0–80.9	71.4–86.8	71.3–78.1
(n = 50)	(n = 17)	(n = 27)	(n = 17)

Coronoid process low (HCP/LM = 65.0%); anterior border joins the horizontal ramus at a relatively low angle. Inferior sigmoid notch variable, but typically shallow; not as shallow as in *C. nigrescens,* in which the notch typically is absent. Posterior mandible behind m3 moderately long (AC3/ML = 77.2%). Articular process relatively high and narrow. Third lower premolar long and low. Entoconid minute (32%, n = 19) or absent (68%) from talonid of m3.

Humerus similar to that of *C. thomasi:* moderately long, robust, slightly curved; the narrowest portion of the shaft is broader in anterior aspect than in lateral aspect; head more or less rounded; proximal and distal ends broad; medial epicondyle and teres tubercle prominent (Fig. 7). Compared to members of the *C. nigrescens*-group and *C. parva*-group, the humerus is shorter relative to overall body size, more robust, and more curved, and teres tubercle more centrally located. Posterior edge of the falciform process of the tibia deeply pocketed.

Comparisons.—Cryptotis meridensis:

Cryptotis tamensis is most readily distinguished by having U4 present, much less reduced, and typically visible in lateral view of cranium; lower coronoid process relative to length of mandible (Table 2); and shorter posterior mandible (behind m3). In addition, *C. tamensis* averages smaller in head-and-body length (Table 1) and has a relatively longer tail; more commonly has an obvious foramen on the posterior edge of the tympanic process of the petromastoid (Fig. 4); dental pigmentation tends to be more extensive (pigment typically darker in hypoconal basin and more commonly found in protoconal basin); small posterolingual cuspule more commonly present (and more distinct) on cingulum of U1, U2, or U3; M3 occasionally complex.

Cryptotis thomasi: Cryptotis tamensis is most immediately and easily distinguished by its longer tail (Table 2); smaller, less evenly rounded foramen (when present) on the tympanic process of the petromastoid (Fig. 4); and more reduced U4. The new species also has a relatively longer rostrum
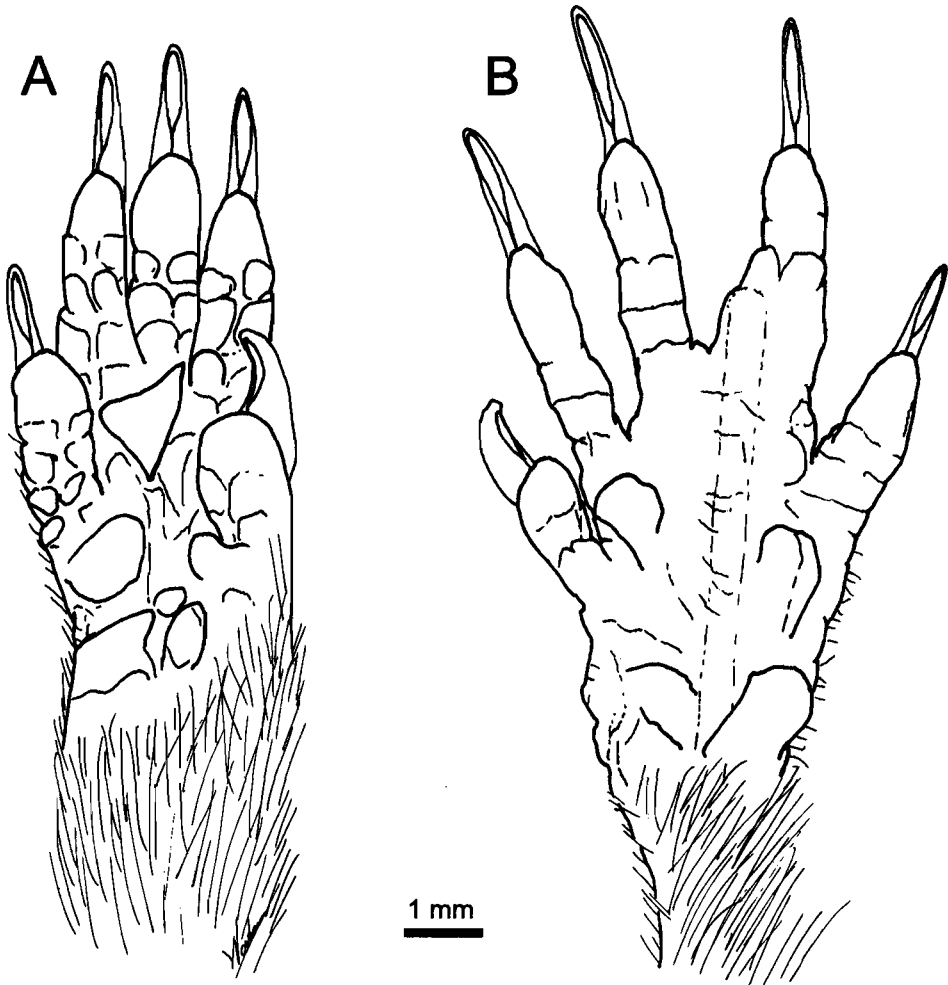
Fig. 3. Ventral views of forepaws of *C. tamensis*: (A) right forepaw of a fluid-preserved specimen (USNM 490534) showing plantar pads, but with atypically short claws; (B) left forepaw from dried skin (USNM 418570) showing typically long claws.

and broader palate (Table 2); less emarginate upper dentition; slightly deeper inferior sigmoid notch; shorter posterior mandible; less obviously complex M3.

Cryptotis medellinia: Cryptotis tamensis is most easily distinguished by its shorter tail (Table 2); smaller, less evenly rounded foramen (when present) on the tympanic process of the petromastoid; and more reduced U4. It also has a relatively narrower interorbital area (Table 2); relatively shorter unicuspid toothrow; relatively lower coronoid process; shallower inferior sigmoid notch.

Results of multivariate analysis.—Principal components analysis (PCA) of craniomandibular variables from *C. meridensis, C. tamensis,* and *C. thomasi* yielded greatest separation on factors axes 2 and 3 (Fig. 8; Table 3). The three species overlap each other to a considerable and similar extent on both axes, despite the ease with which *C. thomasi* can be distinguished from the other two species using both external and craniomandibular characters (see comparisons). The broad intersections among the three groups reflect the generally conservative shape of the skull within the genus *Cryptotis*
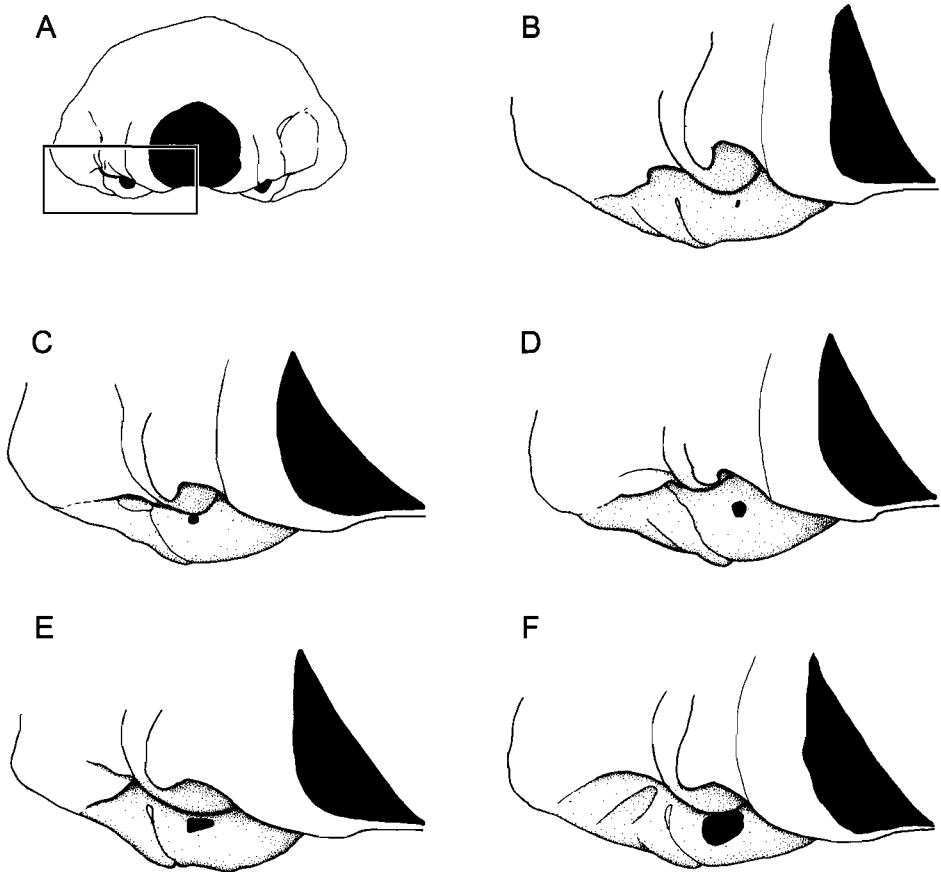
Fig. 4. Foramen on the posterior edge of the tympanic process of the petromastoid: (A) posterior view of cranium, illustrating the location and size of the foramen; (B) a minute foramen in *C. meridensis*; (C) a small foramen in *C. meridensis*; medium foramina in (D) *C. meridensis* and (E) *C. tamensis*; (F) a huge foramen typical of *C. thomasi*.

in general and among members of the *C. thomasi*-group in particular (note results of similar analyses for other species of *Cryptotis* in Woodman and Timm 1993, 1999, 2000).

A plot of scores on factor axes 1 and 2 from PCA of *C. meridensis* and *C. tamensis* supports the separation of the two species (Fig. 9). This plot shows the lack of difference in overall craniomandibular size (factor axis 1—Table 4) despite the larger head-and-body-length of *C. meridensis* (Table 1). Instead, the two species are separated by the combined effects of several, mostly mandibular, variables that include HCV, HCP, and AC3.

Remarks.—Based on the distribution of

unpolarized, shared characteristics (e.g., reduction of U4) and on overall similarity, *C. tamensis* and *C. meridensis* appear to be more closely related to each other than either is to any other species. This opinion contrasts with that of Hutterer (1986, 1993) and Soriano et al. (1999), who inferred that populations in the region of Páramo de Tamá were conspecific with (hence, more closely related to) *C. thomasi*. *Cryptotis thomasi* and *C. medellinia* nearly always have a very large, rounded foramen on the tympanic process of both petromastoids (an apomorphic character within the *C. thomasi*-group), and most likely, the two are sister species.
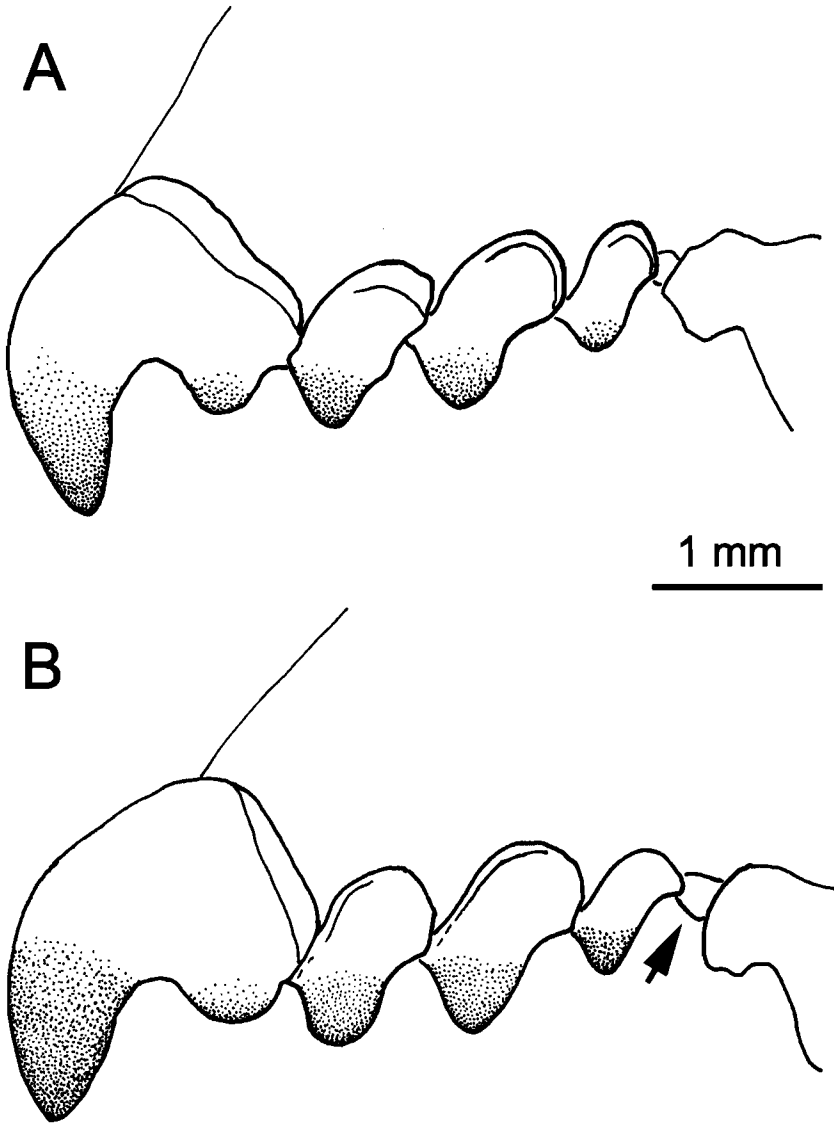
In commenting on Páramo de Tamá,

Fig. 5.   Lateral view of upper first incisor and unicuspids of *Cryptotis*: (A) fourth unicuspid not readily visible, typical for *C. meridensis*; (B) fourth unicuspid visible (arrow), typical for *C. tamensis*.

where he worked from 12 February to 6 March 1911, Osgood (1912) noted that the word "páramo" was used to designate the entire highland area (rather than the open, high-elevation vegetational formation with which it is more commonly associated today). In fact, there appears to be no true páramo vegetation present in this area, and most specimens were collected in dense cloud forest:

The large forest trees, all of unfamiliar species, lace their tops together at an average height of something over 100 feet. Mists and drizzling rains prevail a great part of the year and mosses, air plants, and climbing vines thrive, but the growth in general is not so profuse as that of the hot tropics. A beautiful climbing bamboo is exceedingly abundant, and graceful tree ferns raise their spreading tops at pleasing intervals (Osgood 1912:36).

Seven of the eight specimens of *C. tamensis* captured by the Smithsonian Vene-
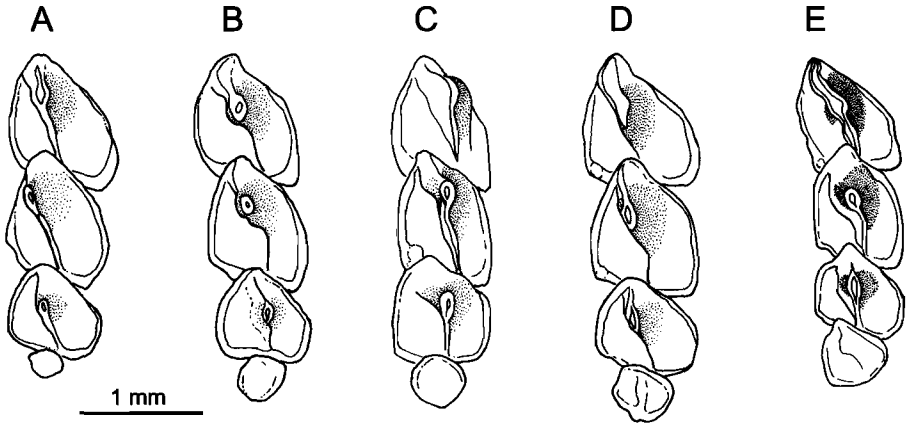
Fig. 6. Occusal view of unicuspid toothrows of *Cryptotis* illustrating size variation of U4. Percentages represent approximate surface area of U4 relative to U3. The U4 of *C. tamensis* (29 ± 8%) averages larger than that of *C. meridensis* (19 ± 7%) and smaller than that of *C. thomasi* (50 ± 9%): (A) U4 ca. 10% of U3 (*C. meridensis*, USNM 579288); (B) 20% (*C. meridensis*, USNM 579296); (C) 25% (*C. tamensis*, USNM 418570); (D) 38% (*C. tamensis*, FMNH 18621); (E) 49% (*C. thomasi*, USNM 80906).

zuelan Project at Buena Vista were taken in cloud forest and one in a cut and burned pasture bordered on all sides by cloud forest (N. E. Peterson 1968 field notes, USNM). Handley (1976:64–65) described Buena Vista as:

Hilly terrain on north facing slope at head of large, wide Andean valley. Numerous small (2–6 m wide), swift, rocky streams; Río Táchira nearby; occasional swampy and marshy areas. Mature cloud forest with discontinuous canopy of scattered trees 25–30

m high; subcanopy at 10–15 m, open or closed; many tree ferns, stilt palms, and thick clusters of tree bamboo; vines few and thin, or hanging from trees in abundance; shrub stratum 1.5 m high; moss and other epiphytes very abundant on trees and ground; abundant litter of logs, fallen trees, dead bamboo, and leaves. Virtually impenetrable clumps of vinelike bamboo dominant (choking out other vegetation), scattered throughout the forest, around fields, and forming thick canopies over streams. Clearings (formed by cutting and burning forest) with thick grass and clover, patches of neddlelike rushes, and clumps of ferns, herbs, low shrubs, and
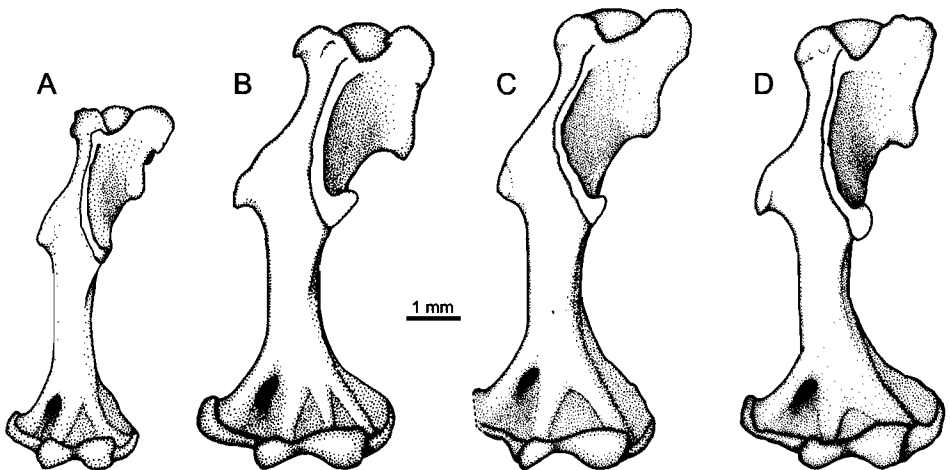

Fig. 7. Anterior aspect of left humeri of *Cryptotis*: (A) *C. orophila* (KU 142693), (B) *C. meridensis* (USNM 385102), (C) *C. tamensis* (FMNH 18621), and (D) *C. thomasi* (FMNH 71027).
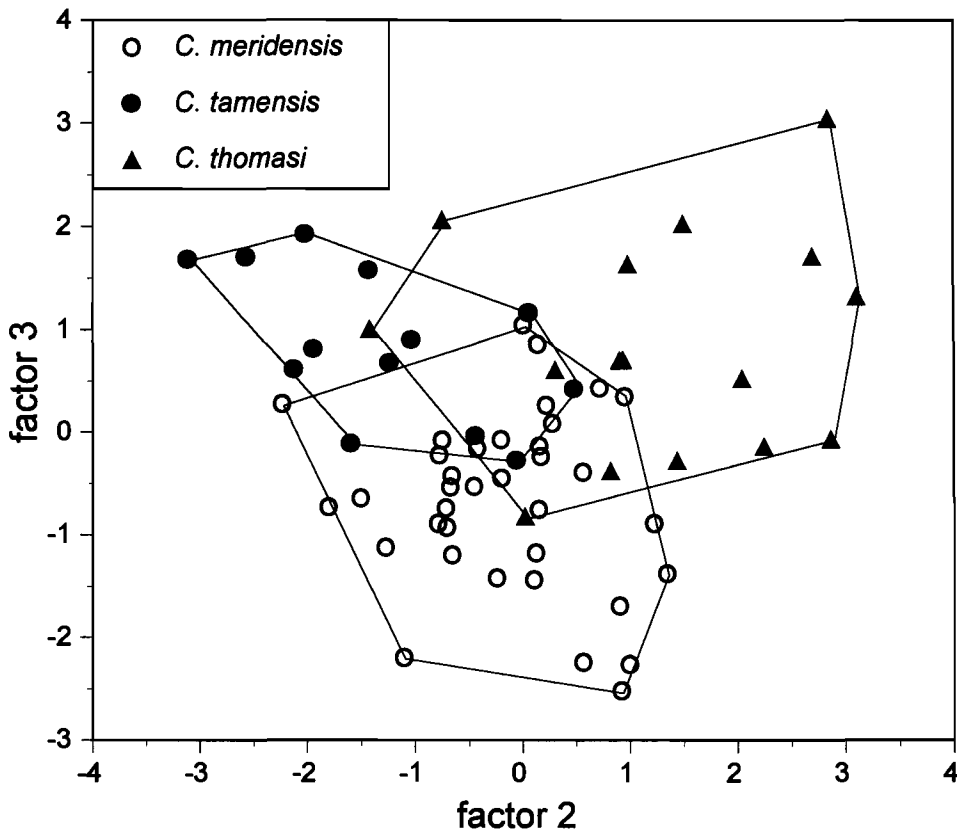
Fig. 8.   Plot of scores on factor axes 2 and 3 from principal components analysis (PCA) of 18 craniomandibular measurements (Table 3) from *C. meridensis, C. tamensis,* and *C. thomasi.*

blackberries. Collecting at upper edge of agricultural clearing (pasture and cropland); cloud forest continuous on steep slopes from this point up to ridgetop páramo, 5 hours' walk distant.

Reproductive data for *C. tamensis* are scarce. Gravid females were taken on 2 March (2 fetuses, no measurements, USNM 418565; 1 fetus, CR = 13 mm, USNM 418566) and 8 March (2 fetuses, CR = 19, USNM 418567). A lactating female was captured on 25 March (USNM 418570).

Cryptotis meridensis (Thomas, 1898)
Figs. 4–7

Blarina meridensis Thomas, 1898:457.
C[*ryptotis*]. *meridensis*: Thomas, 1921:354 (in part).
Cryptotis thomasi meridensis: Cabrera, 1958:48 (in part).

Cryptotis meridensis meridensis: Linares, 1998:106 (in part).

Holotype.—Skin and skull, British Museum no. 98.5.15.5.

Type locality.—"Montes del Valle Merida 2165 m," Mérida State, Venezuela. This locality is from the skin tag attached to the holotype. Thomas (1898:45) reported the type locality simply as "Merida, alt. 2165 m." Paynter (1982) equated Montes del Valle with "Valle" [ca. 8°40′N, 71°06′W]. See his discussion of possible locations; also may be "Valle Grande," a valley at 8°40′N, 71°08′W (USBGN 1993).

Distribution.—Cloud forest and páramo in the Cordillera de los Andes in Trujillo, Mérida, and eastern Táchira, Venezuela (Fig. 2); reported elevational range is 1640–3950 m. Durant & Pefaur (1984:7) gave the

Table 3.—Factor loadings for the first three factor axes from principal components analysis of (PCA) of 18 craniomandibular measurements from *Cryptotis meridensis, C. tamensis,* and *C. thomasi.* Variables are listed in descending order by their loadings on the second axis. Abbreviations of measurements are explained in Table 1.

Variable	Correlations		
	PC1	PC2	PC3
AC3	−0.213	0.500	0.028
BAC	−0.253	0.330	−0.028
HCP	−0.249	0.204	−0.350
ML	−0.249	0.187	0.247
CBL	−0.284	0.173	0.204
HAC	−0.262	0.158	−0.230
HCV	−0.212	0.101	−0.496
PL	−0.286	0.079	0.080
IO	−0.164	0.042	0.142
ZP	0.067	0.023	0.342
TR	−0.253	−0.085	0.312
UTR	−0.219	−0.103	0.232
MTR	−0.279	−0.173	0.158
Lm1	−0.205	−0.234	−0.034
TRM	−0.273	−0.252	0.163
M2B	−0.259	−0.299	−0.129
U1B	−0.217	−0.324	−0.010
M1W	−0.196	−0.361	−0.333
Eigenvalue:	9.0633	1.7975	1.3586
Proportion of variation explained:	50.4%	10.0%	7.5%

elevational limits as 1800–3600 m, although they also reported a specimen from 1640 m at Río Santo Domingo. Otherwise, the lowest reported records are at 1890 m at Río El Chama site E-II and Río Motatán site E-II (Durant & Díaz 1995). No subspecies are recognized.

Description.—Among the largest-bodied *Cryptotis,* head-and-body length averaging 89 mm (Table 1). Tail of moderate length for the genus, averaging 38% of head-and-body length (Table 2). Dorsal hairs about 4–6 mm long. Dorsal pelage Olive Brown, Mummy Brown to Clove Brown; venter Olive Brown to Buffy Brown; dorsal hairs 2-banded, with grey base and mid-section, and 1–1.5 mm brown distal tip. Forepaws somewhat enlarged, similar to those of *C. tamensis* (Fig. 3). Foreclaws elongate, but not broadened; similar overall to *C. thomasi* and *C. tamensis.* Lateral glands of males indistinct.

Usually two well-developed dorsal foramina (72%, $n = 39$), typically of similar size (64%). Usually lacking lateral branch of sinus canal and associated foramen posterior to the dorsal articular facet (94%, $n = 53$); this foramen minute when present, and may be on only one side of cranium. Usually no foramen dorsal to dorsal articular facet (81%, $n = 53$); when present this foramina can be well-developed, but is more typically minute and only on one side of the skull (70%, $n = 10$). Typically a foramen on the posterior edge of the tympanic process of one or both petromastoids (87%, $n = 55$ individuals; Fig. 4); typically on both petromastoids (72%, $n = 46$ individuals; foramina usually quite small (80%, $n = 80$ foramina), but can be of medium size and obvious (20%); often varies in size between left and right sides of a single individual (30%, $n = 33$; 20% of all individuals have at least one obvious foramen that is medium-sized or larger, $n = 55$; Fig. 4); foramen never as large as in *Cryptotis thomasi* or *C. medellinia.* Rostrum of moderate length (PL/CBL = 44.2%). Interorbital area
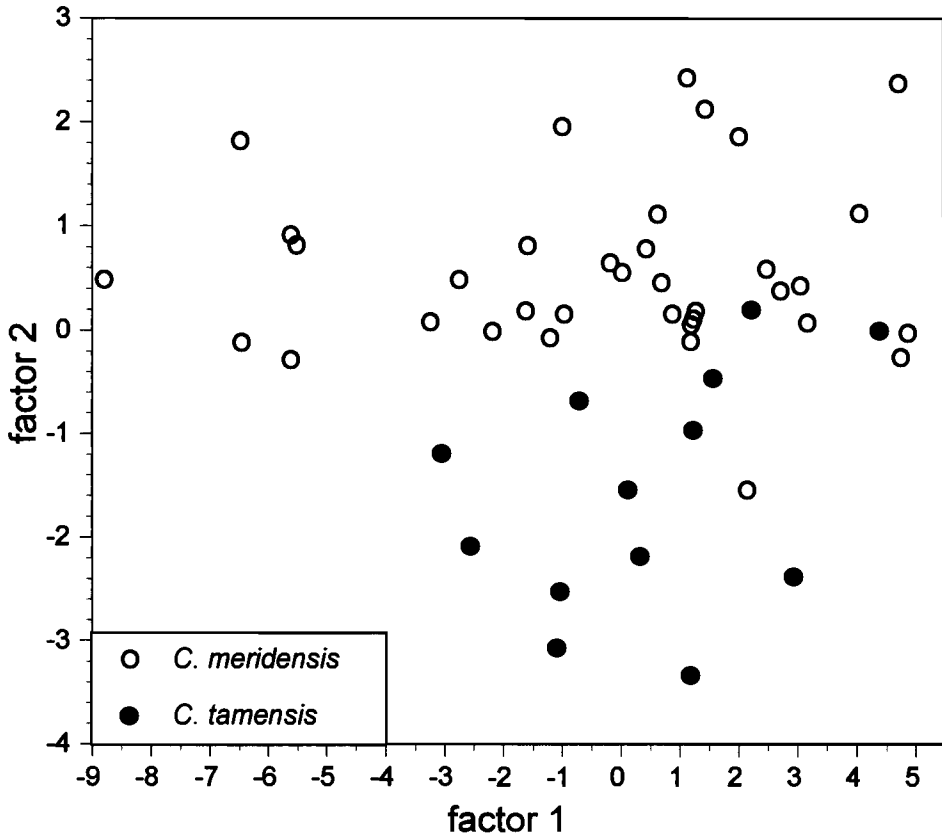
Fig. 9. Plot of scores on factor axes 1 and 2 from PCA of 18 craniomandibular measurements (Table 4) from *C. meridensis* and *C. tamensis*.

moderately broad (IO/CBL = 23.2). Zygomatic plate of moderate breadth in proportion to CBL (9.5%) and PL (21.2%); anterior border of zygomatic plate at mesostyle-metastyle valley to metastyle of M1; posterior border from mesostyle-metastyle valley of M2 to parastyle of M3, and from about middle to posterior one-half of maxillary process. Palate of moderate breadth (M2B/PL = 67.2%). Anterior process of petromastoid typically low and narrow.

Dentition bulbous. Teeth moderately pigmented: dark red to nearly black on tips of cones, styles, and cristae; pale to medium color often extending into protoconal basin (but not hypoconal basin) of M1 and M2. Unicuspid toothrow of moderate length (UTR/CBL = 13.1%) and uncrowded; however, U4 generally not visible in lateral view of skull (73%, n = 44; Fig. 5), obscured from view by U3 and P4. U4 often missing on one (19%; n = 51) or both (6%) sides of cranium; reduced when present, averaging 19% the surface area of U3 (Fig. 6); U4 often a simple, slender, rounded peg (38%, n = 48), occasionally smaller in diameter than the root of a neighboring unicuspid. The tendency to lose U4 is more prevalent than observed in *Cryptotis phillipsii* (12%—Woodman & Timm 2000). U1–3 relatively slender and concave on the posteroventral margin. Posterolingual cuspules typically absent (81%, n = 37) from cingulum of U1–3, or minute (19%). Posterior borders of P4, M1, M2 unrecessed or slightly recessed. M3 commonly appears simple: hypocone usually absent (84%, n = 45), postcentrocrista

Table 4.—Factor loadings for the first two factor axes from principal components analysis of (PCA) of *C. meridensis* and *C. tamensis*. Variables are listed in descending order by their loadings on the second axis. Abbreviations of measurements are explained in Table 1.

Variable	Correlations	
	PC1	PC2
HCV	−0.188	0.496
HCP	−0.232	0.422
AC3	−0.239	0.340
BAC	−0.267	0.199
HAC	−0.259	0.192
PL	−0.270	0.028
IO	−0.168	−0.002
Lm1	−0.208	−0.011
M1W	−0.226	−0.034
CBL	−0.288	−0.039
ZP	0.117	−0.053
ML	−0.267	−0.077
M2B	−0.261	−0.154
MTR	−0.270	−0.198
UTR	−0.211	−0.243
TR	−0.237	−0.245
TRM	−0.260	−0.305
U1B	−0.208	−0.310
Eigenvalue:	10.021	1.744
Proportion of variation explained:	55.7%	9.7%

shortened, metacone absent (76%, $n = 34$) or minute (24%).

Coronoid process of moderate height (HCP/LM = 69.8%). Inferior sigmoid notch variable, but typically shallow; similar to that of *C. tamensis*. Posterior portion of mandible (behind m3) quite long (AC3/ML = 81.0%). Articular process relatively high and narrow. Third lower premolar long and low. Entoconid of m3 absent (85%, $n = 41$) or minute (15%).

Humerus similar to those of *C. thomasi* and *C. tamensis*: moderately long, robust, slightly curved; the narrowest portion of the shaft is broader in anterior aspect than in lateral aspect; head more or less rounded; proximal and distal ends broad; medial epicondyle and teres tubercle prominent (Fig. 7). Posterior edge of the falciform process of the tibia deeply pocketed.

Comparisons.—*Cryptotis meridensis* is a large member of the genus with long, choc-olate-brown dorsal pelage contrasting subtly with paler, olive-brown venter; moderately long tail; enlarged forepaws and elongate foreclaws. Within the *C. thomasi*-group, *C. meridensis* is distinguished by having bulbous dentition; absent or reduced U4 (averaging 19% of U3); U4 not visible in lateral view of cranium; slender U1–3 with concave posteroventral margins; high coronoid process; long posterior mandible behind m3; simple M3; occasionally an obvious foramen on posterior edge of tympanic process of one or both petromastoids; distinct pigmentation in protoconal basin (but not hypoconal basin) of P3, M1–2; shallow inferior sigmoid notch; no entoconid on m3.

Cryptotis thomasi: Cryptotis meridensis is most readily distinguished by its longer tail (Table 2); and smaller foramen (when present) on the tympanic process of the petromastoid; absent or more reduced U4; and relatively higher coronoid process. *Cryptotis meridensis* averages larger in head-and-body length and has a relatively longer rostrum and broader palate; less extensive distribution of dental pigmentation (in *C. thomasi*, the protoconal basin and hypocone typically are darkly pigmented, and the hypoconal basin has pale- to medium-red pigmentation); slightly deeper lower sigmoid notch; less complex M3.

Cryptotis medellinia: Cryptotis meridensis is most easily distinguished by its shorter tail (Table 2); smaller foramen (when present) on the tympanic process of the petromastoid; more reduced or absent U4; and relatively shorter posterior portion of the mandible. It averages larger in head-and-body length; has a relatively narrower interobital area; relatively shorter unicuspid toothrow; shallower inferior sigmoid notch.

Remarks.—Durant & Péfaur (1984) noted differences in pelage color and texture between a series of *C. meridensis* from high elevation páramo (3300–3600 m) and those from cloud forest (1640–2500 m). They described the former as having longer, softer, paler, two-banded hairs on the dorsum and

a distinctly paler venter than dorsum. Shrews from cloud forest had shorter, coarser, unicolor dorsal hairs with more uniform dorsal and ventral coloration. Soriano et al. (1990) were unable to corroborate these differences. Among the dried skins I inspected, specimens from páramo and "Coloradito" (see below) vegetational associations typically had long (6–7 mm), pale dorsal hairs and a paler venter. Individuals from cloud forest and disturbed cloud forest included individuals with shorter (4–5 mm), darker dorsal hairs and less contrast between the dorsum and venter, but also included individuals indistinguishable from páramo and Coloradito specimens. I had insufficient specimens to determine whether the variation might be attributable to seasonal changes in the environment. Overall, the differences in pelage are subtle, and variation in coloration among museum specimens may be confounded by foxing and molt.

Cryptotis meridensis primarily occupies cloud forest and páramo vegetational assemblages, in which it is relatively abundant. Four of the 13 specimens of *C. meridensis* captured by the Smithsonian Venezuelan Project were taken in cloud forest, four in disturbed (previously burned) cloud forest, one in a thicket of bamboo and low trees bordering Quebrada Mucuy, one in previously burned cloud forest-páramo transition, and three in páramo (N. E. Peterson 1966 field notes, USNM). These records came from three Holdridge life zones: Lower Montane Moist Forest, Montane Rain Forest, and Subalpine Páramo (Handley 1976). Similarly, Durant & Díaz (1995) recorded *C. meridensis* at five sites in páramo, Montane Rain Forest, and Lower Montane Rain Forest. Aagaard (1982) found *C. meridensis* to be most abundant in Subalpine Páramo, Subalpine Rain Páramo, and a vegational assemblage he identified as "Coloradito," consisting of stands of arborescent *Polylepis sericea* and *Espeletia humertii* in sheltered areas surrounded by páramo vegetation. In these three assem-

blages, shrews were the most common or second most common species of small mammal captured using Museum Special mouse traps and Victor rat traps during a nine-month period. Individual shrews also were taken in Montane Wet Forest and Lower Montane Wet Forest, but not in Montane Rain Forest. Díaz de Pascual (1993, 1994) found *C. meridensis* to average second most common of eight species of small mammals taken in pitfall traps during the first four years of a study in cloud forest at Monte Zerpa.

Durant & Díaz (1995) showed two capture peaks during the year, in March–April and September–October, coinciding with the time periods leading up to biannual peaks in rainfall in many parts of the Venezuelan Andes (April–May and October; see Díaz de Pascual 1994, Durant & Díaz 1995:89, 90, table 5, fig. 3; Aagaard 1982: 7, fig. 1). The two peaks in abundance of *C. meridensis* suggest two periods of reproduction and/or two periods of increased activity during the two seasons of greatest rainfall. In contrast, Aagaard (1982) reported significantly more captures of *C. meridensis* in dry months [January ($n = 0$ captures), February (15), March (7), July (5), August (2)] than in wet months [April (6), May, (0), June (0), September (0)].

Little has been reported on reproduction in *C. meridensis*. A lactating female (USNM 385106) was captured on 15 April 1966 at Middle Refugio. Non-gravid females have been taken in February ($n = 5$), March ($n = 5$), April ($n = 4$), July ($n = 2$), and August ($n = 2$). Aagaard (1982) reported one gravid female from 16 July (4 fetuses, crown-to-rump-length = 11 mm). Based on testes sizes, he suggested that males were sexually active during both wet and dry months.

Specimens examined (62).—VENEZUELA: *Mérida:* near Laguna Mucubají [ca. 8°48′N, 70°48′W—Paynter 1982], 3600 m, 3.25 km ESE of Apartaderos (USNM 579287–579298); near Laguna Negra [ca. 8°48′N, 70°46′W—Paynter 1982], 3500 m,

5.75 km ESE of Apartaderos (USNM 579273–579286); Páramo de [La] Culata [ca. 8°45′N, 71°05′W—Paynter 1982], 9000 ft, Río Mucujún (FMNH 21837, 21838); Montes de La Culata [La Culata, ca. 8°45′N, 71°05′W—Paynter 1982], 2000 m, Mérida (BMNH 98.7.1.13); Río Mucujún [8°45′N, 71°04′W—from map], 9000–12,500 ft [Osgood & Conover 1922:23] (FMNH 21839, 21840, 21842, 21844; BMNH 29.11.7.16 [= FMNH 21841]; USNM 260756 [= FMNH 21843]); Montes del Valle [ca. 8°40′N, 71°06′W—Paynter 1982], 2125–2165 m, Mérida (BMNH 98.7.1.11, 98.7.1.12, 98.5.15.5—holotype); Páramo Tambor [at Hacienda La Carbonera (8°38′N, 71°32′W—Paynter 1982), near head of a western branch of Río Guachi (Osgood & Conover 1922:23)] (FMNH 21845); near Santa Rosa, 8°38′N, 71°09′30″W, 1980–1990 m, 1 km N, 2 km W of Mérida [reported as "1–2 km N Mérida" by Handley 1976:83; Handley (1976: 10) incorrectly reported USNM 385110 as from "La Carbonera, 12 km SE La Azulita, 1990 m"] (USNM 385110–385112); near La Mucuy [8°38′N, 71°02′30″W—from map], 2450 m, 2.9 km E of Tabay (USNM 579305); area 37, 8°37′00″N, 71°01′30″W, 2630 m, near Middle Refugio, 2 km S, 5.5 km E of Tabay [reported as "5 to 9 km SE and ESE Tabay," and "6 km ESE Tabay" by Handley 1976:10, 77] (USNM 385106); Mérida [8°36′N, 71°08W—Paynter 1982], 2165 m (USNM 94165—"paratype O[ldfield] T[homas]" written on skin tag); La Montaña, 2250 m, 3.1 km SE of Mérida (USNM 579307); La Aguada, near Laguna La Fría [Páramo La Fría, ca. 8°36′N, 71°02W—Paynter 1982], 3600 m, 7 km SE of Mérida (USNM 579299–579304); near Loma Redonda cable car station, 4100 m, 8.8 km SE of Mérida (USNM 579306); El Tambor [Páramo Tambor, 8°36′N, 71°24′W—Paynter 1982], 8800 ft (AMNH 96156–96158); Páramo de los Conejos [ca. 8°35′N, 71°14′W—from map], 9600 ft (AMNH 96159); La Coromoto, 8°35′45″N, 71°01′W, 3160–3175 m, 4 km S, 6.5 km E

of Tabay [reported as "5 to 9 km SE and ESE Tabay," and "7 km SE Tabay" by Handley 1976:10, 75] (USNM 385101, 385104); near Laguna Verde, 8°34′30″N, 71°00′30″W, 3533–3545 m, 7.5 km E, 6 km S of Tabay [reported as "5 to 9 km SE and ESE Tabay," and "9 km SE Tabay" by Handley 1976:10, 76] (USNM 385102, 385103, 385105).

Additional records.—VENEZUELA: *Merida*: Río Motatán site E-I, 8°49′N, 70°59′W, 3890 m (Durant & Díaz 1995); Páramo de Mucubají, 8°48′06″N, 70°48′57″W, 3420–3800 m, Distrito Rangel (Durant & Pefaur 1984); Río Chama site E-I, 8°48′N, 70°48′W, 3950 m (Durant & Díaz 1995); Monte Zerpa cloud forest, 8°37′N, 71°10′W, 2000–2800 m, Sierra del Norte de La Culata (Díaz de Pascual & de Ascençao 2000); area 51, 8°37′45″N, 71°01′30″W, 2640 m, near Middle Refugio, 1 km S, 5 km E of Tabay [reported as "5 to 9 km SE and ESE Tabay" and "6 km ESE Tabay" by Handley (1976:10, 77)]; Río Chama site E-II, 8°36′N, 71°10′W, 1890 m (Durant & Díaz 1995); Right bank of the Río Santo Domingo, 1640 m, near Quebrada de la Virgen, km 36 of the Apartadero-Barinas Highway, Distrito Rangel (Durant & Pefaur 1984). *Mérida-Tachira border*: Río Escalante site E-I [ca. 8°18′N, 71°55′W], 2600 m, Páramo de Mariño (Durant & Díaz 1995). *Trujillo*: Río Motatán site E-II, 9°05′N, 70°39′W, 1890 m (Durant & Díaz 1995); Parque Nacional General Cruz Carrillo (Guaramacal), ca. 2200–3100 m (Soriano et al. 1990).

Relevant Additional Records of Shrews from Venezuela and Colombia

Two records of *Cryptotis* from Venezuela and Colombia are noteworthy here because of their vicinity to the known distributions of *C. meridensis* and *C. tamensis*. Both records are based on individuals preserved as a skull without skin or skeleton. I have not had the opportunity to inspect either specimen. The two collection localities are rep-

resented on the map in Figure 2 by question marks. It is possible that these two records may provide geographic range extensions of known species as defined herein, or one or both may be undescribed taxa. Each population represented by these records will require study of a large series of complete specimens to adequately document local variation in characters and to correctly establish its relationship with other South American species.

Ojasti & Mondolfi (1968) reported a single specimen identified as "*Cryptotis thomasi meridensis*" from a forested area near El Junquito (10°28'N, 67°05') in the coastal highlands west of Caracas. This locality is separated from the main distribution of *C. meridensis* in the Cordillera de los Andes by an expanse of more than 300 km. In between are extensive lowlands below 500 m occupied by Tropical Dry Forest (Ewel et al. 1965, Ewel & Madriz 1968) that currently present a barrier to dispersal for Andean shrews. No description, photograph, or illustration of the specimen was provided, making it difficult to conjecture as to the identity of the population it represents. The specimen is reposited at the Museo de Biología, Universidad Central de Venezuela.

Duarte & Viloria (1992) reported a specimen of "*Cryptotis thomasi*" from the vicinity of Cerro Pintado (10°24'N, 72°53'W) in the Sierra de Perijá, northeastern Cordillera Oriental, Colombia. *Cryptotis tamensis, C. thomasi,* and *C. colombiana* are the only species known to occur in the Cordillera Oriental. The closest record of a shrew to this locality is that of *C. tamensis* from Páramo de Tamá, which is more than 300 km south of Duarte & Viloria's (1992) collection site. Photographs of the skull accompanying the report are unclear, and most characters are indistinct. However, the shape of the mandible, particularly at the junction of the coronoid process with the horizontal ramus, strongly suggests that it is a member of the *C. thomasi*-group rather than the *C. nigrescens*-group. This charac-

ter, together with the large size of the specimen, indicate that it is unlikely to be *C. colombiana.* The specimen appears to lack the very large foramen on the tympanic process of the petromastoid, an absence that would rule out both *C. colombiana* and *C. thomasi.* The low elevation (2100 m) at which the specimen was discovered, the depth of lower sigmoid notch, and the short posterior portion of the mandible also suggest that it is not *C. thomasi.* The specimen from Sierra de Perijá thus may represent *C. tamensis.* However, if measurements I obtained from the photographs are correct, the specimen has a relatively shorter zygomatic plate and a relatively broader palate and interorbital area than any measured specimen of either *C. tamensis* or *C. thomasi.* The specimen is in the collection of the Museo de Biología, Universidad del Zulia (MBLUZ M-105).

The two records from Sierra de Perijá and El Junquito exemplify the continued poor state of knowledge of South American shrews, and they communicate the need for more complete mammalian surveys even near well-populated areas. Regardless of whether the occurrence of shrews in the coastal highlands of Venezuela represents dispersal or vicariance, it testifies to their ability at some time in the past to negotiate, or even inhabit, lowlands that are currently inhospitable. It also hints at the probability that shrews may be found in suitable habitats elsewhere in the region, where they should be sought using appropriate methods. For example, the presence of *Cryptotis* in northernmost portion of the Cordillera Oriental, less than 100 km from the isolated Sierra Nevada de Santa Marta, suggests another place where shrews are likely to be discovered.

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