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A new small-eared shrew of the *Cryptotis nigrescens*-group from Colombia (Mammalia: Soricomorpha: Soricidae)

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Abstract.—*Cryptotis colombiana* Woodman & Timm, 1993 previously was known from few specimens from two isolated regions in the Cordillera Central and Cordillera Oriental of Colombia. Recent collecting in the northern Cordillera Central and review of older collections from the central Cordillera Oriental in the vicinity of Bogotá yielded additional specimens that permit reevaluation of the two geographic populations of these small-eared shrews. Morphological and morphometrical studies indicate that the population inhabiting the Cordillera Oriental represents a distinct, previously unrecognized species that I describe herein as *Cryptotis brachyonyx*. Study of 54 specimens of shrews from the Cordillera Oriental in systematic collections in North America, South America, and Europe yielded only four specimens of the new species, all collected before 1926. The paucity of modern specimens suggests that *C. brachyonyx* may be extremely restricted in distribution, or possibly extinct.

Small-eared shrews of the genus *Cryptotis* occur from eastern North America south through Central America to the Andes Mountains of South America. Recent systematic studies on these shrews generally partition the species among four informal, groupings originally defined by Choate (1970) and modified by Woodman & Timm (1993, 1999, 2000). Only two of these groups have members that occur in South America. The *C. nigrescens*-group is primarily a Central American group, but with two species occurring in South America: *Cryptotis mera,* along the Panama/Colombia border (Woodman & Timm 1993), and *Cryptotis colombiana,* reported from the Cordillera Central and Cordillera Oriental of Colombia (Woodman 1996). The *C. thomasi*-group is comprised entirely of Andean species. The *C. nigrescens*-group and the *C. thomasi*-group can be distinguished using a combination of external, cranial, and postcranial characters. Two of the more reliable external characters are the relative size of the forefeet and length of the foreclaws: members of the *C. thomasi*-group tend to have large forepaws with notably elongate foreclaws, whereas species in the *C. nigrescens*-group have smaller forefeet and foreclaws.

Cryptotis colombiana Woodman & Timm, 1993 originally was described from a single specimen collected in 1950 from Río Negrito on the Cordillera Central of Colombia and now housed in the Field Museum, Chicago. A second specimen, collected in 1925 from San Juán de Ríoseco on the Cordillera Oriental of Colombia, subsequently was identified in the collection of the American Museum of Natural History, New York. At that time, I (Woodman 1996) noted differences between the two specimens, but indicated that the taxonomic significance of this variation was difficult to interpret based on only two specimens. Field work during the past few years in the Cordillera Central by Colombian colleagues has added a number of important new specimens of *C. colombiana* that permit more comprehensive evaluation

of the characteristics of this species (Woodman et al. 2003). However, its presence in the Cordillera Oriental has continued to be based on the single American Museum specimen. Recently, I studied available collections of Colombian shrews from the Cordillera Oriental, among them a series of ten specimens in The Natural History Museum, London, and the National Museum of Natural History, Washington, that were collected from April to November 1895 at or near La Selva. These specimens include at least five of the individuals Merriam (1897) used when he described *C. thomasi,* the first valid species of shrew identified from South America. The pelage of each of the skins is faded, and most are irregularly and somewhat overly stuffed, obscuring external differences. However, among the ten are three specimens that possess small forepaws, short claws, and distinctive cranial features that mark them as members of the *C. nigrescens*-group, rather than *C. thomasi.* This conclusion is supported by morphological and morphometrical characters of the skull. Additional morphological and morphometrical analyses of the four specimens from the Cordillera Oriental show them to be distinct from the population of *C. colombiana* on the Cordillera Central. Herein, I describe the population from the Cordillera Oriental as a new species and report on variation within and between the two species based on the available specimens from the two Colombian cordilleras.

Materials and Methods

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 my review of published localities, maps, and gazetteers of Colombia (Paynter & Traylor 1981, USBGN 1988). Capitalized lifezone names follow Espinal and Montenegro (1963) and IGAC (1988). The species synonomy lists only the first use of published names.

Information from personal correspondence is based on my inspection of original letters from George O. Child to Oldfield Thomas [# Df 232/1/55–56] and photocopies of correspondence from Clinton Hart Merriam to Thomas [# Df 232/1/252–257] in the Official Archives of The Natural History Museum, London, and from microfilm of correspondence from Thomas to Merriam in The Bancroft Library, University of California, Berkeley [BANC Film 1958].

Terminology of dentition and dental characteristics follows Choate (1970). Capitalized color names for pelage hues are from Ridgway (1912). Pelage coloration was determined only from museum specimens. All four specimens of the new species were collected more than 80 years ago, and their pelages are faded and do not accurately represent those of live or newly-captured specimens.

Measurements used in my analyses follow Woodman & Timm (1993, 1999) and are in mm, weights in g. Abbreviations are explained in Table 1. External measurements were recorded from skin tags or original field notes, 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 $\pm$ *SD* and total range. Ratios of measurements were multiplied by 100 to calculate percentages (Table 2). In describing species of *Cryptotis,* I compare them primarily with other members of the genus, unless stated otherwise. Comparative terms used for measurements and ratios reflect this context. A feature of "moderate" length or width is one whose mean value for the species falls within the range of plus or minus one standard deviation (*SD*) of the mean value for the genus. A "long" or "wide" feature is one greater than the mean plus one *SD*; a "short" or "narrow" feature is less than the mean minus one *SD*.

Principal components analysis (PCA) of a correlation matrix of 16 log-transformed craniomandibular variables (ZP, IO, M2B, PL, TR, UTR, MTR, M1W, ML, HCP, HCV, HAC, AC3, TRM, Lm1, BAC—Table 3) was used to investigate relationships in overall shape of the skull among 6 *C. colombiana* from the Cordillera Central, 6 *C. mera,* 32 *C. thomasi,* and 4 individuals of the new species. I carried out a second PCA to determine morphometrical relationships between just *C. colombiana* and the new species using a correlation matrix of 8 log-transformed cranial variables (ZP, IO, U3B, PL, TR, UTR, MTR, M1W—Table 4). Values of the variable M2B do not overlap between the two species (Table 1), and it was excluded from the second PCA to determine whether the two samples would continue to be separated using combinations of other variables.

In my investigations of *Cryptotis,* I operate under a systematic framework for the genus outlined previously (Woodman 2002). My comprehension of the biological species is under the philosophical influence of the evolutionary species concept as redefined by Wiley (1978) and characterized by Wiley & Mayden (2000). In application, a species represents the largest monophyletic entity whose constituent parts interact, that maintains its own identity, and that has an independent evolutionary trajectory (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 application provides testable hypotheses for additional studies.

Specimens from the following institutions were used in this study: American Museum of Natural History, New York (AMNH); Natural History Museum [formerly British Museum (Natural History)], 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 Biology

Cryptotis brachyonyx, new species
Figs. 1A, 1B, 2, 4A, 5A, 6A

Blarina thomasi Merriam, 1897:227 (in part).

[*Blarina* (*Cryptotis*)] *thomasi*: Trouessart, 1904:138 (in part; name combination).

Cryptotis thomasi: O. Thomas, 1921:354 (in part; name combination).

Cryptotis avia: Tate, 1932:226 (in part; not *Cryptotis avia* G. M. Allen, 1923).

Cryptotis thomasi thomasi: Cabrera, 1958: 48 (in part; name combination).

Cryptotis colombiana: Woodman, 1996:417 (in part; not *Cryptotis colombiana* Woodman & Timm, 1993).

Holotype.—Dried skin (Fig. 1) and skull (Fig. 2) of adult male, BM number 99.10.3.2, collected by an unnamed worker for George O. Child of Bogotá, Colombia, on 19 October 1895; purchased from G. O. Child and presented to the British Museum (Natural History) by Oldfield Thomas. Skin in fair to good condition: all fur present, faded; 2 small holes near right cheek; left hind foot sewn on; other feet loosely attached. Skull in good condition: slight damage to orbital areas; small crack running dorsally from foramen magnum; mandibles separate; both angular processes intact. Of standard external field measurements, only length of hind foot (= 12 mm) was recorded on the skin tag, and this measurement probably was taken from the dried skin.

Type locality.—COLOMBIA: *Department of Cundinamarca*: "La Selva, near Bogotá." La Selva was the name of George O. Child's estate on the Plains of Bogotá, the altitude of which he estimated as approximately 8900 feet (G. O. Child, in litt.

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

C. mera	*C. colombiana*	*C. brachyonyx*	*C. thomasi*
External measurements:			
$n = 7$	$n = 4$	$n = 0$	$n = 12$
Head-and-body length (HB)			
69 ± 2	65 ± 7	—	87 ± 6
66–73	60–76		74–96
Tail length (TL)			
27 ± 2	30 ± 3	—	24 ± 2
24–31	27–34		20–27
Skull measurements:			
$n = 6$[a]	$n = 6$[a]	$n = 4$[a]	$n = 17$[a]
Condylobasal length (CBL)			
18.3 ± 0.4	19.6 ± 0.3	20.4 ± 0.1	21.7 ± 0.5
17.7–18.7	19.4–20.1	20.3–20.4	20.7–22.6
($n = 5$)		($n = 3$)	
Cranial breadth (CB)			
9.4 ± 0.3	9.7 ± 0.4	9.7	10.5 ± 0.2
9.1–9.8	9.2–10.0		10.2–10.9
		($n = 1$)	($n = 13$)
Breath of zygomatic plate (ZP)			
2.0 ± 0.1	2.0 ± 0.1	1.9 ± 0.1	2.0 ± 0.2
1.9–2.2	1.8–2.1	1.7–2.0	1.7–2.4
Interorbital breadth (IO)			
4.5 ± 0.2	4.8 ± 0.1	4.9 ± 0.2	5.0 ± 0.2
4.3–4.7	4.7–4.9	4.6–5.0	4.6–5.2
Breadth across first unicuspids (U1B)			
2.5 ± 0.1	2.7 ± 0.05	2.6 ± 0.1	2.7 ± 0.1
2.4–2.6	2.6–2.7	2.5–2.6	2.6–2.9
		($n = 3$)	
Breadth across third unicuspids (U3B)			
2.9 ± 0.1	3.1 ± 0.1	3.0 ± 0.05	3.1 ± 0.1
2.7–3.0	2.9–3.2	2.9–3.0	2.9–3.2
Breadth across second molars (M2B)			
5.6 ± 0.1	6.2 ± 0.2	5.8 ± 0.1	6.2 ± 0.2
5.5–5.8	6.0–6.4	5.7–5.9	5.8–6.5
Palatal length (PL)			
7.8 ± 0.1	8.7 ± 0.3	8.6 ± 0.2	9.4 ± 0.2
7.6–7.8	8.1–9.0	8.3–8.8	8.8–9.8
Length of upper toothrow (TR)			
7.1 ± 0.1	7.6 ± 0.2	7.6 ± 0.3	8.2 ± 0.3
6.9–7.2	7.3–7.8	7.3–7.9	7.7–8.7
Length of unicuspid toothrow (UTR)			
2.4 ± 0.1	2.5 ± 0.1	2.5 ± 0.1	2.8 ± 0.2
2.3–2.5	2.4–2.6	2.4–2.5	2.4–3.0
Length of molariform toothrow (MTR)			
5.1 ± 0.1	5.5 ± 0.2	5.5 ± 0.2	5.8 ± 0.1
5.1–5.2	5.3–5.8	5.3–5.7	5.5–6.0

Table 1.—Continued.

C. mera	*C. colombiana*	*C. brachyonyx*	*C. thomasi*
Posterior width of first upper molar (M1W)			
1.8 ± 0.05	2.0 ± 0.1	1.8 ± 0.5	1.9 ± 0.1
1.8–1.9	1.9–2.0	1.8–1.9	1.8–2.1
Length of mandible (ML)			
5.9 ± 0.4	6.7 ± 0.2	6.8 ± 0.3	7.0 ± 0.2
5.2–6.2	6.3–7.0	6.4–7.0	6.6–7.4
Height of coronoid process (HCP)			
4.5 ± 0.1	4.6 ± 0.2	4.6 ± 0.1	4.7 ± 0.1
4.3–4.6	4.3–4.7	4.5–4.7	4.5–4.9
Height of coronoid valley (HCV)			
2.7 ± 0.1	2.8 ± 0.2	2.8 ± 0.05	3.1 ± 0.1
2.6–2.8	2.5–3.0	2.8–2.9	2.9–3.3
Height of articular condyle (HAC)			
3.8 ± 0.1	3.8 ± 0.2	3.9 ± 0.1	4.3 ± 0.1
3.6–3.8	3.6–4.2	3.8–4.1	4.1–4.6
Breadth of articular condyle (BAC)			
3.0 ± 0.1	3.2 ± 0.2	3.1 ± 0.2	3.6 ± 0.2
2.9–3.1	3.0–3.4	3.0–3.4	3.4–4.1
Articular condyle to m3 (AC3)			
4.4 ± 0.1	4.9 ± 0.1	5.0 ± 0.1	5.7 ± 0.3
4.3–4.6	4.6–5.0	4.9–5.1	5.0–6.0
Length of lower toothrow (TRM)			
5.5 ± 0.1	5.9 ± 0.2	6.0 ± 0.2	6.4 ± 0.2
5.4–5.7	5.6–6.3	5.7–6.2	6.1–6.7
Length of lower toothrow (M13)			
4.3 ± 0.1	4.6 ± 0.1	4.5 ± 0.1	4.7 ± 0.2
4.1–4.4	4.5–4.8	4.3–4.5	4.2–5.1
	(n = 4)		(n = 17)
Length of first lower molar (Lm1)			
1.8 ± 0.1	1.9 ± 0.1	1.8 ± 0.1	1.9 ± 0.1
1.7–1.8	1.8–1.9	1.7–1.8	1.7–2.0
Weight (g):			
—	—	—	10, 10
			(n = 2)

[a] Except as noted.

13 July 1895). Merriam (1897) gave the elevation of La Selva as 9000 ft. This slightly higher elevation probably was based on information in a letter to him from Thomas (quoted below).

Paratypes (2).—COLOMBIA: *Cundinamarca*: Plains of Bogotá (USNM 80905; "topotype" [of *C. thomasi*] written on tag); La Selva, near Bogotá (BMNH 99.10.3.3).

Referred specimen (1).—COLOMBIA: *Cundinamarca*: San Juan de Ríoseco (AMNH 70597).

Etymology.—Greek: *brachys* (short) + *onyx* (claw), hence "short claw;" a noun in apposition.

Distribution.—Presumably Premontane Moist Forest, Premontane Wet Forest, Lower Montane Moist Forest, Montane Moist

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

C. mera (n = 7)[a]	*C. colombiana* (n = 7)[a]	*C. brachyonyx* (n = 4)	*C. thomasi* (n = 39)[a]
Foramen of sinus canal present			
0%	0% (n = 5)	0%	8% (minute) (n = 38)
Foramen dorsal to dorsal articular facet present			
71% two	43% two	25% two	3% two
14% one	14% one	50% one	15% one
14% none	43% none	25% none	82% none
Two dorsal foramina present			
71%	86%	100%	79%
Petromastoid foramen present one or both petromastoids			
14% (med–lg)	100% (n = 5)	100%	100% (n = 35)
Postero-lingual cuspules on cingulae of U1–3			
17% absent			16% absent
83% minute		100% minute	62% minute
	100% obvious		22% obvious
(n = 6)	(n = 4)		(n = 32)
Size of U4 (% of U3)			
54 ± 10.0%	42 ± 13%	40 ± 7%	48 ± 9%
40–66	32–61	31–48	22–64
(n = 6)	(n = 5)		(n = 35)
Emargination of posterior borders of P4, M1			
v. slight to slight	v. slight to slight	v. slight to slight	v. slight to mod. deep
Complexity of M3			
100% simple	86% simple		50% simple
	14% complex	100% complex	50% complex (n = 28)
Lower sigmoid notch			
v. shallow to shallow	shallow	v. shallow to mod. deep	v. shallow to mod. deep
Entoconid of m3 present			
			11% obvious
29% minute		100% minute	32% minute
71% absent	100% absent		57% absent (n = 28)
Mensural characters:			
n = 6[a]	n = 6[a]	n = 4[a]	n = 17[a]
Relative tail length (TL/HB × 100)			
39 ± 4	47 ± 9	—	28 ± 3
34–46	36–57		21–36
(n = 7)	(n = 4)		(n = 22)
Relative length of rostrum (PL/CBL × 100)			
42.2 ± 1.1	43.8 ± 1.5	42.9 ± 0.6	43.2 ± 0.5
41.3–44.1)	41.8–46.2	42.2–43.4	42.4–44.0
(n = 5)		(n = 3)	
Relative breadth of zygomatic plate (ZP/PL × 100)			
26.0 ± 1.3	22.7 ± 0.8	21.7 ± 1.1	21.2 ± 1.5
24.7–28.2	22.1–24.1	20.5–23.3	18.7–24.7

Table 2.—Continued.

C. mera (*n* = 7)[a]	*C. colombiana* (*n* = 7)[a]	*C. brachyonyx* (*n* = 4)	*C. thomasi* (*n* = 39)[a]
Relative breadth of zygomatic plate (ZP/CBL × 100)			
11.0 ± 0.7	9.9 ± 0.5	9.5 ± 0.3	9.2 ± 0.6
10.3–12.1	9.3–10.5	9.3–9.8	7.8–10.6
(*n* = 5)		(*n* = 3)	
Breadth of interorbital area (IO/CBL)			
24.8 ± 0.6	24.5 ± 0.4	24.4 ± 0.3	23.1 ± 0.8
24.3–25.8	23.9–25.1	24.0–24.6	21.0–24.6
(*n* = 5)		(*n* = 3)	
Relative length of unicuspid toothrow (UTR/CBL × 100)			
13.3 ± 0.4	12.7 ± 0.4	12.1 ± 0.3	13.0 ± 0.6
12.6–13.6	12.0–13.2	11.8–12.3	11.6–14.0
(*n* = 5)		(*n* = 3)	
Relative palatal breadth (M2B/PL × 100)			
72.7 ± 2.2	71.2 ± 2.2	67.0 ± 2.0	66.6 ± 2.6
70.5–76.3	69.0–75.3	64.8–68.7	60.8–70.5
Relative height of coronoid process (HCP/ML × 100)			
76.3 ± 4.8	68.3 ± 1.9	67.8 ± 2.6	66.1 ± 1.9
71.0–82.7	65.7–71.2	64.3–70.3	63.4–70.6
Relative length of posterior portion of the mandible (AC3/ML × 100)			
75.5 ± 5.7	73.1 ± 2.0	74.1 ± 2.2	81.0 ± 3.4
68.4–82.7	70.0–75.8	71.4–76.6	71.4–86.8
Relative length of posterior portion of the mandible (AC3/HCP × 100)			
98.9 ± 2.3	107.0 ± 2.7	109.3 ± 1.2	122.5 ± 4.7
95.7–102.2	104.3–111.4	108.5–111.1	111.1–128.9

[a] Except as noted.

Forest, and Montane Wet Forest life zones on the Cordillera Oriental in central and eastern Cundinamarca Dept., Colombia (Fig. 3); known elevational distribution, ca. 1300–2715 m.

Diagnosis.—A small- to medium-sized *Cryptotis* with a moderately long tail, long dorsal pelage, small forepaws, and short foreclaws. Typically two large dorsal foramina; no lateral branch of the sinus canal or associated foramen; a large foramen on postero-medial edge of tympanic process of each petromastoid. Interorbital area broad; rostrum, zygomatic plate, and palate of moderate breadth. Dentition bulbous; U4 large, but not visible in lateral view; teeth moderately pigmented, with distinct color in protoconal basins (and occasionally pale pigmentation in hypoconal basin) of P4 and M1–2; posterior borders of P4 and M1–2 only slightly recessed; anterior and posterior elements of ectoloph of M1 about equal; M3 complex. Coronoid process moderately high, joins horizontal ramus at a high angle; posterior mandible short; articular process low and broad; inferior sigmoid notch variably shallow; p3 short and high; minute entoconid on m3.

Description.—A small- to medium-sized *Cryptotis.* Tail moderately long (Fig. 1; there are no external measurements, except length of hind foot, recorded for any of the four specimens). Forepaws and foreclaws small (Fig. 4), similar in proportions to those of *C. nigrescens* and other members of the *C. nigrescens*-group. Dorsal fur typically 5–6 mm long, individual hairs up to 7 mm. Dorsal pelage of the four available

Table 3.—Factor loadings for the first three factor axes from principal components analysis (PCA) of 18 cranial measurements from *Cryptotis colombiana, C. mera, C. brachyonyx,* 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
ZP	−0.060	0.210	−0.610
IO	−0.238	0.202	−0.081
M2B	−0.245	0.406	0.079
PL	−0.298	−0.088	0.058
TR	−0.298	−0.077	0.082
UTR	−0.264	−0.133	0.070
MTR	−0.293	0.128	0.073
M1W	−0.136	0.647	−0.107
LM	−0.277	−0.015	−0.037
HCP	−0.197	−0.068	−0.057
HCV	−0.276	−0.174	−0.156
HAC	−0.265	−0.288	−0.022
AC3	−0.291	−0.224	−0.014
TRM	−0.291	−0.009	0.158
Lml	−0.161	0.303	0.443
BAC	−0.265	−0.153	0.106
Eigenvalue:	10.183	1.308	1.143
Proportion of variation explained:	0.636	0.082	0.071

specimens Chestnut Brown to Prout's Brown to Mummy Brown; venter Olive Brown to Buffy Brown to Hair Brown; dorsal and ventral hairs 2-banded, with gray base and mid-section and ca. 1 mm brownish distal tip. [Pelage of these skins is faded; live *C. brachyonyx* probably have a darker pelage, possibly similar to that of *C. colombiana* (see *Comparisons,* below).]

Two obvious dorsal foramina present along the suture between the frontals (100%; Table 2); generally about equal in size (75%). Typically lacking lateral branch of sinus canal and associated foramen (see Woodman & Timm 1999) posterior to the dorsal articular facet (100%). A minute foramen often present dorsal to one (50%) or both (25%) dorsal articular facets. Large, obvious foramen on the postero-medial edge of the tympanic process of both petro-

Table 4.—Factor loadings for the first three factor axes from principal components analysis (PCA) of 8 cranial measurements from *Cryptotis colombiana* and *C. brachyonyx.* 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
U3B	−0.246	0.533	0.075
UTR	−0.140	0.506	−0.695
M1W	−0.231	0.478	0.526
ZP	−0.404	−0.006	0.347
PL	−0.449	−0.034	−0.1.08
MTR	−0.429	−0.093	−0.059
TR	−0.417	−0.242	−0.310
IO	−0.379	−0.404	0.054
Eigenvalue:	4.1890	1.3537	0.9006
Proportion of variation explained:	0.524	0.169	0.113

Fig. 1. Dried skins of *C. brachyonyx* (A: BM 99.10.3.2—holotype; B: USNM 80905) and *C. thomasi* (C: USNM 80904; D: USNM 80903). The smaller body size and shorter length of tail in *C. brachyonyx* are perceptible despite the irregular preparation.

mastoids (100%); foramen not as large as in *C. thomasi* or *C. colombiana*; positioned more medially than in either of those species. Rostrum of moderate length (PL/CBL = 42.9%). Interorbital area broad (IO/CBL = 24.4%). Zygomatic plate of moderate breadth in proportion to CBL (9.5%) and PL (21.7%); anterior border of zygomatic plate at posterior mesostyle-metastyle valley to metastyle of M1; posterior border from parastyle to posterior half of M3, and from posterior one-half to posterior edge of maxillary process. Palate of moderate breadth for the genus (M2B/PL = 67.0%). Anterior process of petromastoid variable in size.

Dentition bulbous. Teeth moderately pigmented: medium red to dark red on tips of cones, styles, and cristae; pale to medium pigment typically extends into protoconal basins of M1 and M2; very pale pigment only occasionally in hypoconal basins. Short, somewhat crowded unicuspid toothrow (UTR/CBL = 12.1%); U4 mostly obscured by U3 and P4 in lateral view of skull (100%; Fig. 5). U1–3 broad in lateral view and straight to convex on posteroventral margin. Cuspules on posterolingual cingulum of U1–3 typically absent to minute; this region of these unicuspids typically pigmented. U4 large, averaging ca. 40% of the surface area of U3 (Fig. 6). Posterior borders

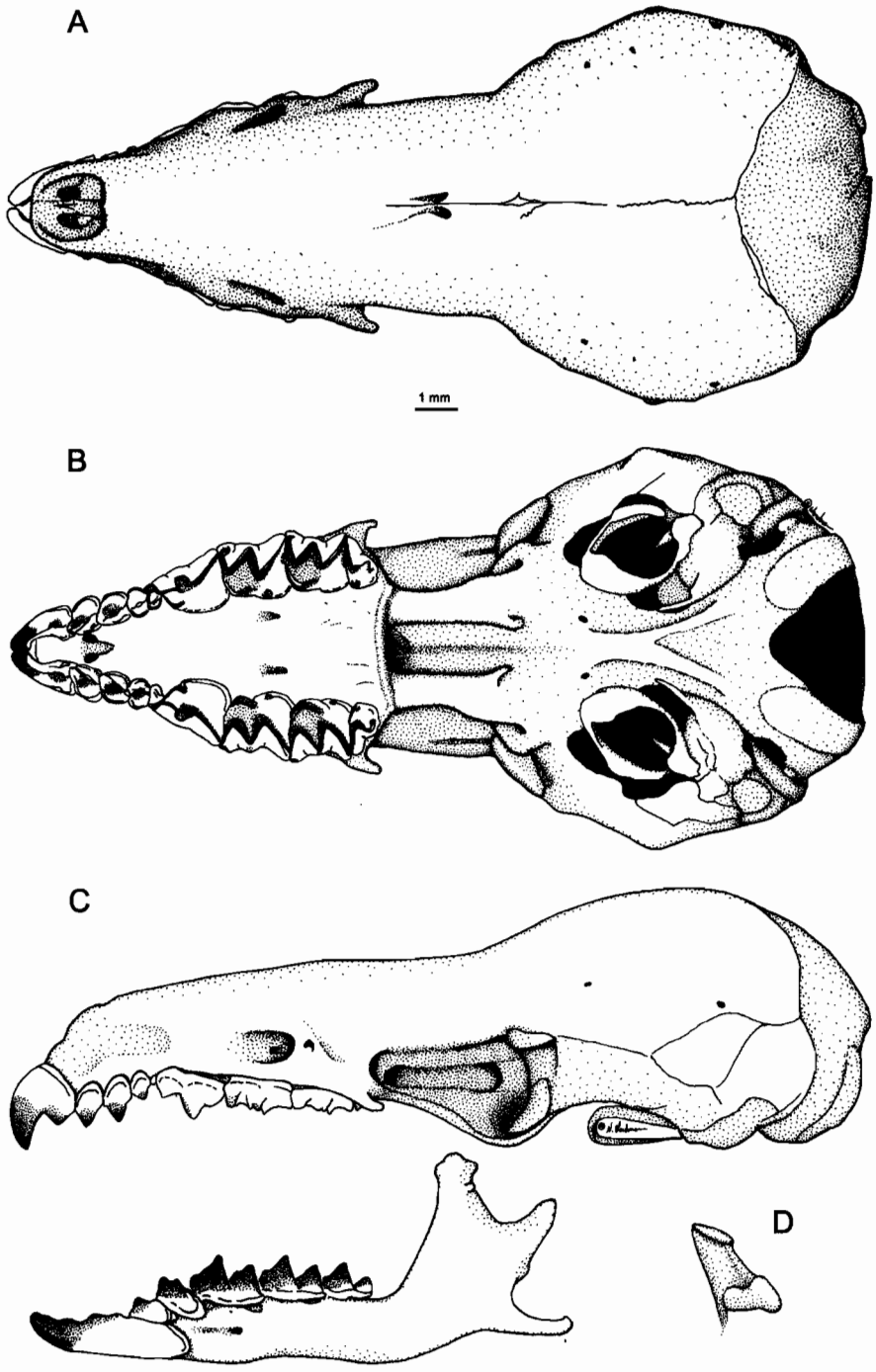

Fig. 2. Skull of the holotype of *Cryptotis brachyonyx* (BM 99.10.3.2): (A) dorsal view of cranium; (B) ventral view of cranium; (C) lateral view of cranium and mandible; and (D) posterior view of articular process of the mandible.

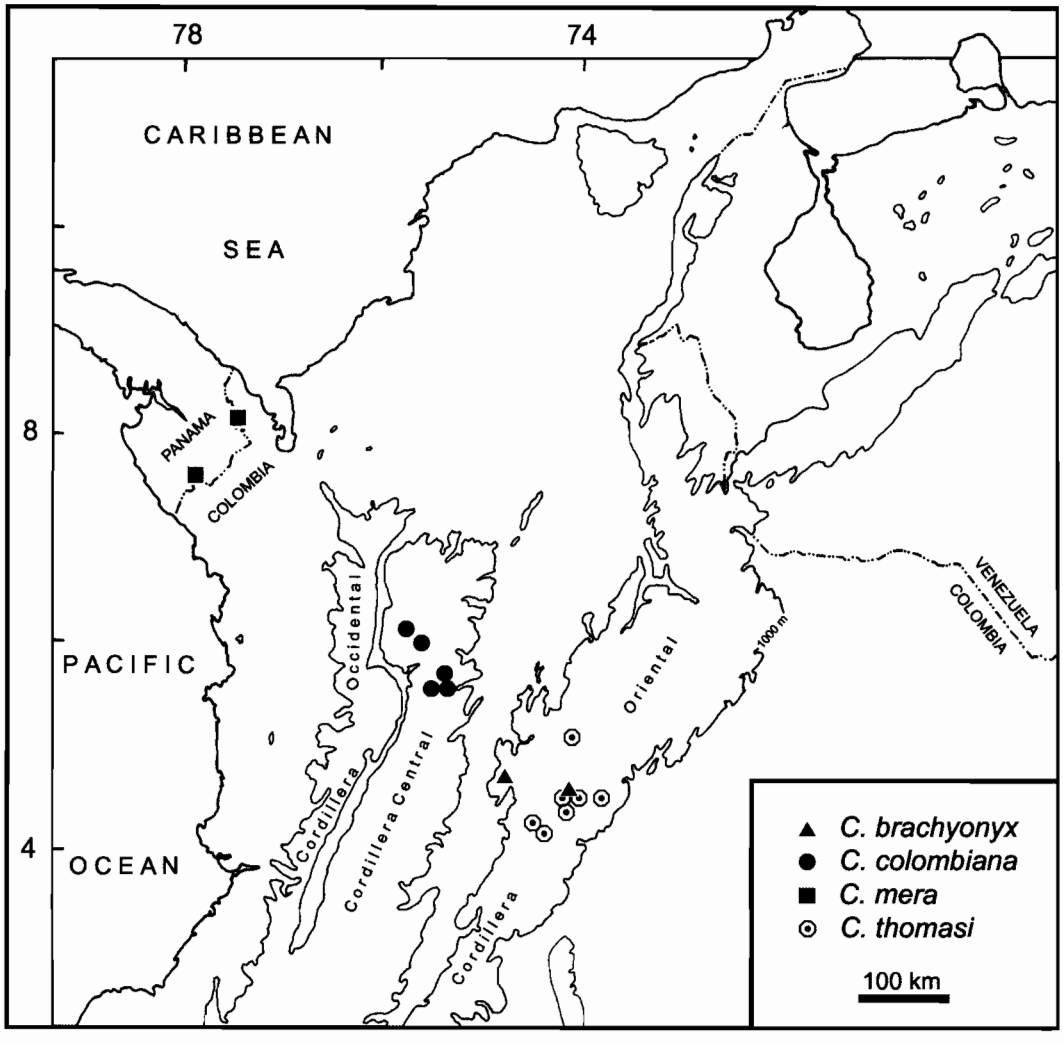

Fig. 3. Map of the northern Andes showing the distributions of *Cryptotis brachyonyx, C. colombiana, C. mera,* and *C. thomasi.* The 1000 m contour is shown.

of P4, M1, M2 only slightly recessed. Anterior element of ectoloph of M1 approximately equal in length to posterior element; protoconal basin of M1 about equal in size to hypoconal basin. M3 appears moderately complex, partly resulting from the presence of a small, but distinct hypocone that squares off the labial border of the tooth and from the relatively extensive pigmentation; parastyle, paracrista, paracone, and precentrocrista well-developed and pigmented; mesostyle, postcentrocrista, and metacone reduced, but pigmented and obvious; protocone pigmented and obvious; hypocone present, but reduced and unpigmented.

Anterior border of coronoid process of mandible joins horizontal ramus at a relatively high angle; coronoid process moderately high (HCP/LM = 67.8%). Inferior sigmoid notch variably shallow to moderately deep. Posterior mandible behind m3 short (AC3/ML = 74.1%). Articular process relatively low and broad. Third lower premolar nearly as high as it is long. Minute, uncolored, but distinct entoconid present (100%) on talonid of m3.

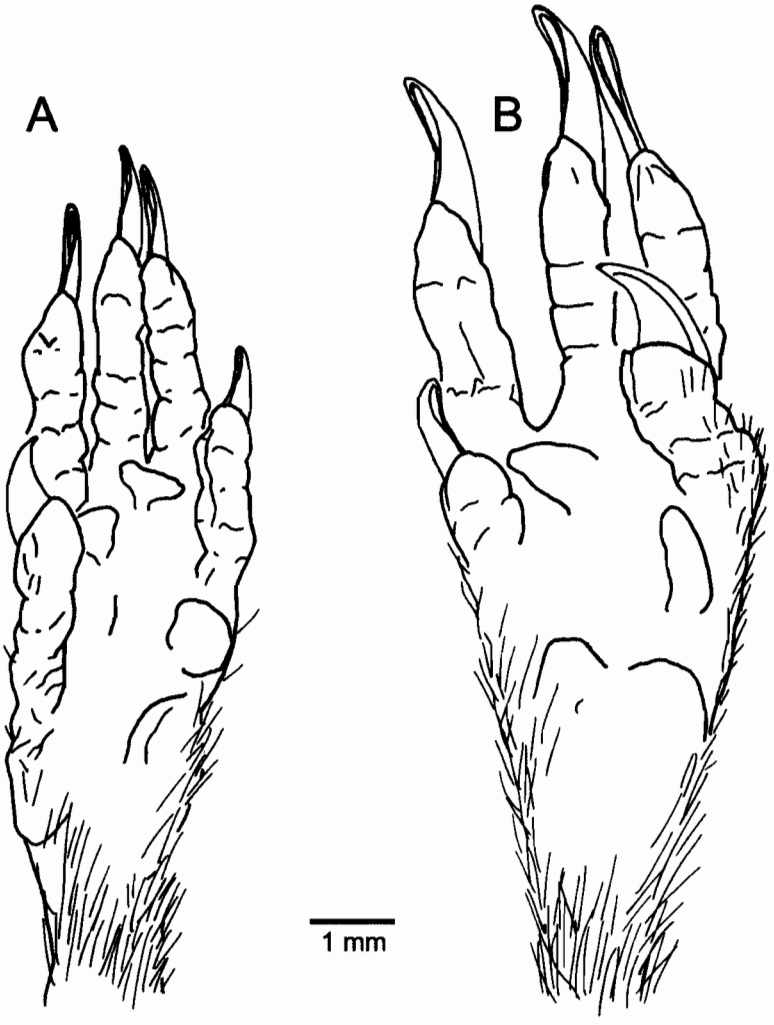

Fig. 4. Ventral views of left forepaws of (A) *Cryptotis brachyonyx* (BM 99.10.3.2) and (B) *C. thomasi* (BM 99.10.3.4), both from La Selva, Colombia.

Postcranial skeleton unknown.

Comparisons.—Cryptotis colombiana: Externally, *C. brachyonyx* and *C. colombiana* may be difficult to distinguish. Based on cranial dimensions, *C. brachyonyx* is generally close in size to *C. colombiana* (e.g., see *Multivariate Analyses,* below), both appear to have a moderately-long tail, and both may have dark pelage. The original description of the pelage of *C. colombiana* (dorsum Olive Brown to Fuscous; ventrum Buffy Brown to Hair Brown—Woodman & Timm 1993) was based solely on the faded holotype. Study of a more recently-collected specimen (MUA 62) indicates that the pelage is closer to Sooty Black to Chaetura Black dorsally, with a Dark Olive Gray to Chaetura Black venter. Dorsal and ventral hairs have a medium-gray base and middle, with a ca. 1 mm dark-brown to black tip. However, the two species are easily distinguished cranially: *C. brachyonyx* has a smaller and more medially located foramen on the tympanic process of the petromastoid; relatively and absolutely narrower palate; darker, more ex-

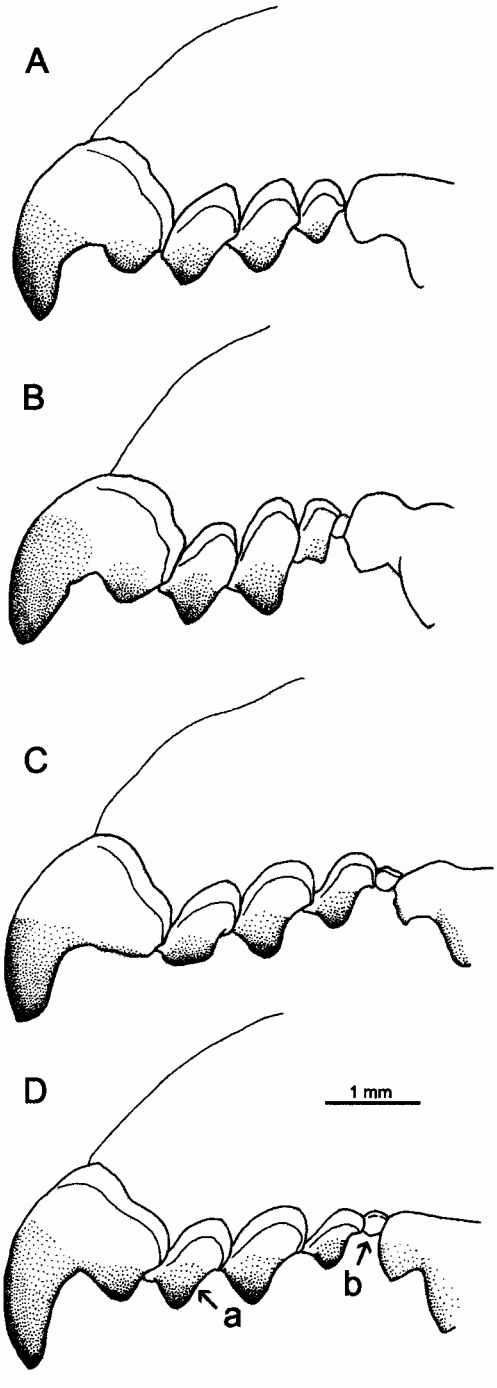

Fig. 5. Lateral view of upper first incisor and unicuspids: (A) *C. brachyonyx* (USNM 80905); (B) *C. colombiana* (MUA 62); (C, D) *Cryptotis thomasi* (KU 157765, FMNH 71030). Arrows point to (a) curvature of posteroventral margin of U1 and (b) visible U4.

tensively pigmented dentition, with pigment more completely coloring protoconal basins of M1–2 and hypocone of M1; narrower upper dentition; larger and more complex M3, resulting from more strongly pigmented protocone, better developed (but uncolored) hypocone, and better developed and pigmented postcentrocrista and metastyle; minute entoconid in talonid of m3.

Cryptotis mera: *Cryptotis brachyonyx* is absolutely larger in many cranial dimensions, and it possesses a large, obvious foramen on the tympanic process of the petromastoid; relatively shorter zygomatic plate (Table 2); relatively narrower palate; more extensively pigmented dentition, with darker pigment more completely filling protoconal basins of M1–2 and coloring hypocone of M1; relatively shorter unicuspid toothrow; smaller average U4; more complex M3 possessing a small hypocone, strongly pigmented protocone, and more distinct postcentrocrista and metastyle; relatively lower coronoid process; minute entoconid more commonly present in talonid of m3.

Cryptotis thomasi-group: Like other members of the *C. nigrescens*-group, *C. brachyonyx* has noticeably smaller forefeet and shorter foreclaws; U1–3 typically are relatively broad and conical in lateral view of the skull, with a straight or convex posteroventral margin (Fig. 5); the anterior element of ectoloph of M1 is approximately equal in size to the posterior element; the anterior border of the coronoid process of the mandible joins the horizontal ramus at a relatively high angle; the articular process is relatively low and broad.

Cryptotis thomasi: This is the only species of shrew with which *C. brachyonyx* may be sympatric. In addition to the characters that separate it from members of the *C. thomasi*-group in general, *Cryptotis brachyonyx* can be separated by its smaller body size and longer tail. Cranially, *C. brachyonyx* has a smaller and more medially located foramen on the tympanic process of the petromastoid; smaller average

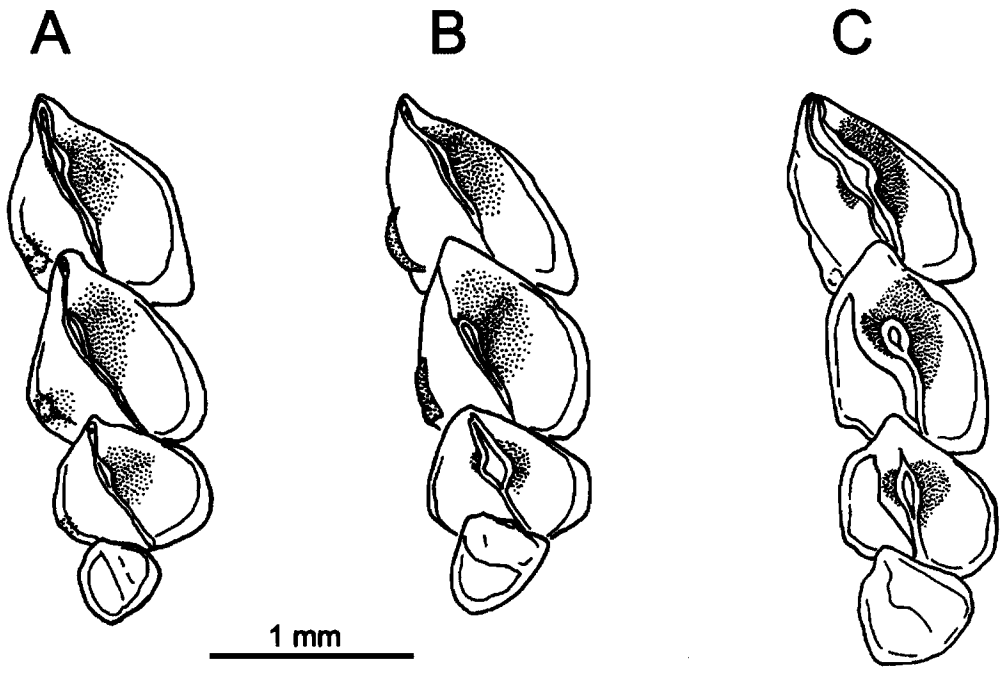

Fig. 6. Occlusal view of upper unicuspids: (A) *C. brachyonyx* (USNM 80905); (B) *C. colombiana* (MUA 62); and (C) *Cryptotis thomasi* (USNM 80906).

U4; less emarginate posterior borders of P4, M1, and M2; relatively shorter posterior portion of the mandible (AC3); minute entoconid more commonly present on talonid of m3.

Results of multivariate analysis.—Principal components analyses (PCA) of craniomandibular variables measured from *C. brachyonyx, C. colombiana, C. mera,* and *C. thomasi* strongly support the distinctiveness of *C. brachyonyx.* The first analysis, which incorporated all four species, showed greatest separation among groups on factor axes 1 and 2. When factor scores on these two axes are plotted, individuals of the four species form four distinct groups of points (Fig. 7). Along the first factor axis, interpreted as size (Table 3), the species separated into three size groupings with minimal overlap. Specimens of *C. thomasi* comprise the largest individuals, and those of *C. mera* the smallest. Individuals of *C. brachyonyx* and *C. colombiana,* which overlap nearly completely along this axis, form a single group of intermediate size. The largest *C. colombiana* and the smallest *C. thomasi* also overlap along this axis. Along the second factor axis, which is interpreted as representing width of palate (M2B) and width of dentition (WM1—see Table 3), the groupings of individuals of *C. colombiana* and *C. brachyonyx* separate without overlap.

A second PCA incorporating cranial variables from just *C. colombiana* and *C. brachyonyx* (Fig. 8) again shows nearly complete overlap along the first factor axis, interpreted as overall size of the cranium (Table 4). However, the two species segregate completely along the second factor axis, which represents the combined effects of variables that include IO, U3B, UTR, and WM1 (Table 4). The variable M2B was specifically excluded from this analysis to assess whether the two species could be separated using other variables. The lack of intersection between the scatters defined by the two samples is notable, because over-

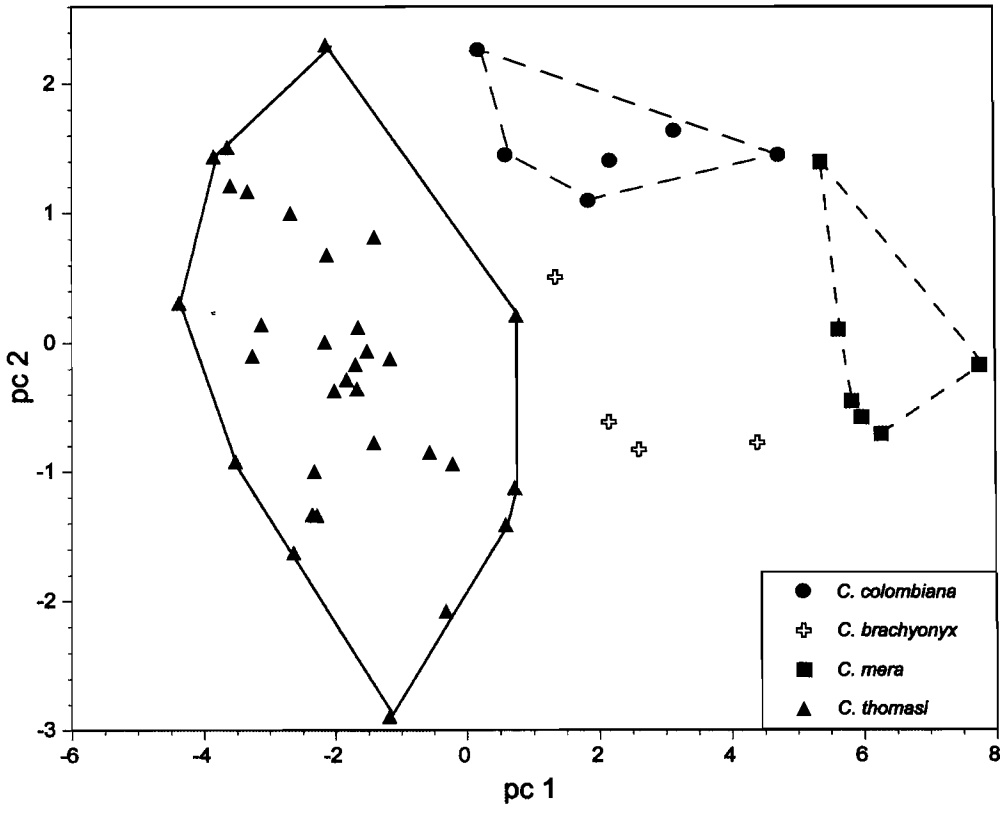

Fig. 7. Plot of scores on factor axes 1 and 2 from PCA of 18 craniomandibular measurements (Table 3) from *Cryptotis brachyonyx, C. colombiana, C. mera,* and *C. thomasi.*

laps in multivariate space are common among species within the *Cryptotis nigrescens*-group, even those that are geographical neighbors (Woodman & Timm 1993, Woodman 2000).

Discussion

The histories of the original specimens of *C. brachyonyx* and *C. thomasi* are closely associated. At least one of the specimens that Merriam (1897) used to name *C. thomasi* is now known to be of *C. brachyonyx,* indicating that since its original description, *C. thomasi* has been polytypic in content. This seeming oversight partly reflects an understandable ignorance at that time of the quality and extent of variation within and among species of small-eared shrews. It also can be attributed to the poor quality of preparation of the specimens, a point noted by Thomas in a letter to Merriam (see below).

In his paper naming *C. thomasi,* Merriam (1897:227) wrote: "For the opportunity to describe this very interesting shrew I am indebted to Mr. Oldfield Thomas, Curator of Mammals in the British Museum, who sent me seven specimens from the type locality. Heretofore the genus *Blarina* has not been recorded from any point south of Costa Rica; hence the discovery of the present species in South America is of unusual interest." The seven specimens sent to Merriam were from a collection of shrews that eventually numbered at least ten skins (eight with accompanying skulls) collected at or near La Selva for George O. Child in 1895 and purchased by Oldfield Thomas for the BM (Table 5). Six of these specimens, including the holotype of *C. thomasi,* cur-

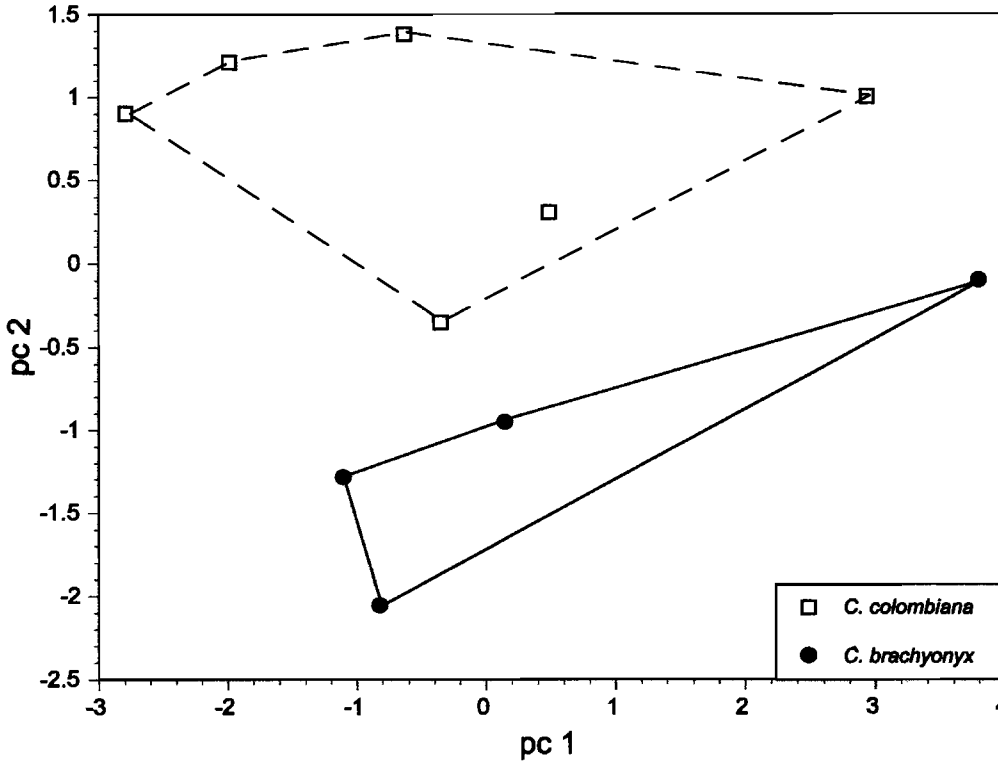

Fig. 8. Plot of scores on factor axes 1 and 2 from PCA of 8 craniomandibular measurements (Table 4) from *Cryptotis brachyonyx* and *C. colombiana.*

rently are in BM and four are in the USNM, the result of an ongoing exchange of specimens between Thomas and Merriam. In his letter to Merriam regarding these specimens, Thomas (in litt. 25 December 1895) wrote:

> I am sending you 6 or 7 Blarinas from Bogotá, a long way south of any locality that I expect you know of. We have had an odd specimen from there since about 1845 but it has never been named, & this lot have just come in to me personally. It is sad that they are such awful skins, but they are made by natives, & one must be thankful for the perfect

Table 5.—Specimens of shrews collected for G. O. Child from near the type locality of *C. brachyonyx* and *C. thomasi.* Specimens are listed in order by date. All specimens with dates were collected in the year 1895. Abbreviations and symbols: SS—skin and skull; SO—skin only; *—holotype.

Museum number	Species	Tag locality	Date	Preparation
USNM 80904	*C. thomasi*	Plains of Bogota	5 April	SO
USNM 80905	*C. brachyonyx*	Plains of Bogota	5 April	SS
USNM 80906	*C. thomasi*	La Selva	6 Aug.	SS
USNM 80903	*C. thomasi*	La Selva	9 Aug.	SS
BM 99.10.3.3	*C. brachyonyx*	Le Selva, near Bogota	10 Aug.	SS
BM 97.5.21.2*	*C. thomasi*	G. Child's Estate, Plains of Bogota	14 Sept.	SS
BM 99.10.31	*C. thomasi*	Boqueron, near Bogota	24 Sept.	SS
BM 99.10.3.2*	*C. brachyonyx*	La Selva, near Bogota	10 Oct.	SS
BM 99.10.3.4	*C. thomasi*	La Selva, near Bogota	1 Nov.	SS
BM no number (GDC #311)	*C. thomasi*	Bogota (Child)	no date	SO

> skulls & exact localities. A dozen more are likely to come to me, so I will give you all these except one, the best, which you shall select for me, & return with your determination upon it, of course if new, & you would kindly describe it I would ask you to make that one the type.
>
> "Plains of Bogota" means an estate some few miles out of the town, at an altitude of about 9000 feet. The other places are all about the Bogotá district.
>
> The material is so poor compared to what you are accustomed to that you may despise it, & not care to work it out. I have kept then back some here hoping to get your paper on the genus, but I am now going away for a long holiday on account of my health, & prefer to send them you before I go.

There is a discrepancy between the numbers of specimens noted by both Thomas and Merriam and the current number of specimens available. Although Thomas clearly noted sending Merriam up to seven specimens (with permission to keep all but one), and, based on Merriam's (1897) report all seven arrived, only four specimens ever were catalogued in the collection of the USNM. The difference does not result from counting skins and skulls separately, because the four USNM specimens and the holotype in the BM include five skins and four skulls, which would yield nine specimens. There is no evidence that any specimens from Child were exchanged by either BM or USNM with any other collections in North America or Europe. One possibility is that Merriam returned to Thomas two specimens in addition to the holotype, in which case, the remaining specimens may be among those in the BM. Unfortunately, I have yet to find correspondence that mentions the return of the holotype to Thomas. Alternatively, some of specimens may have been lost or discarded prior to cataloging in either collection.

That there may at one time have been even more specimens is suggested by Thomas in his letter to Merriam, when he noted, "a dozen more are likely to come to me. . . ." This statement probably was based on a letter from Child to Thomas (in litt. 7 Nov. 1895), in which Child wrote, "I have got already some 12 shrews ready for you and some 20 bats." What happened to all of these specimens is not known. I have been able to trace only the 10 specimens now in the BM and USNM (Table 5).

The AMNH specimen of *C. brachyonyx* and one of the AMNH specimens of *C. thomasi* at one time were identified as the only other known specimens of *Cryptotis avia* G. M. Allen, 1923 (Tate 1932). *Cryptotis avia* originally was described on the basis of a single specimen, a dried skin with skull (MCZ 20091), collected by Nicéforo María at El Verjón on the Cordillera Oriental in 1922. Although the holotype is a small individual based on both the external measurements from the dried skin reported by G. M. Allen (1923) and my cranial measurements, in my opinion it is conspecific with specimens of *C. thomasi* (AMNH 62789, 62790; MCZ 19995) taken by the same collector from the type locality of *C. avia* in March and October 1922 and with specimens of *C. thomasi* from elsewhere (Woodman 1996). The name *C. avia* is therefore a junior synonym of *C. thomasi* and not applicable to *C. brachyonyx*. The previous confusion of the AMNH specimen of *C. brachyonyx* with *C. avia* is understandable, because the crania of both specimens are incomplete (Woodman 1996) and because, for some time, the mandibles of the two specimens had been interchanged. Both conditions served to obscure some of the characteristics important for distinguishing the two taxa.

As noted by Merriam (1897), *C. thomasi* was the first species of that genus (at that time a subgenus of *Blarina*) described from south of Costa Rica. It also represents the first valid species of the family Soricidae or of the order (Insectivora *or* Soricomorpha) from South America. Several species previously had been interpreted as South American shrews, although all were determined eventually to be otherwise. These erroneous soricids included *Mus araneus* Marggraf, 1648, and *Musaraneus brasiliensis* Brisson, 1762, both based on specimens of the didelphid marsupial *Monodelphis*

from Brazil [In any case, Marggraf's names are pre-Linnaean, and Brisson's names generally are considered unavailable (Hopwood 1947)]. Two species from Surinam, *Sorex surinamensis* Gmelin, 1789 and *Blarina pyrrhonota* Jentinck, 1910 (first mentioned, but not described, by Jentinck 1888), were based on specimens of European *Sorex araneus* mistakenly purported to hail from South America (Husson 1963, Hutterer 1993).

It is reasonable to presume that the specimens collected for George Child in 1895 may have been the first specimens of true shrews collected in South America. However, as noted by Thomas in his correspondence to Merriam, there is one other specimen in the BM (number 54.1.11.4)—a skull of *C. thomasi* without skin from "New Grenada" that had been "purchased of Mr. S. Stevens." Based on the catalog number, this specimen must have been collected in 1854 or earlier, and Thomas (in litt. 25 Dec. 1895) noted that it had been in the possession of the BM "since about 1845," making it the first verifiable specimen of a shrew from South America.

My inspection of 54 specimens of shrews from the Cordillera Oriental in Cundinamarca Department, Colombia, that are available in systematic collections has yielded only four specimens of *C. brachyonyx,* all of which were collected either in 1895 or in 1925. The remainder are all *C. thomasi. Cryptotis brachyonyx* represents 30% of the ten existing specimens collected from near La Selva in 1895. The four specimens of *C. brachyonyx* comprise 13% of 26 shrews collected in this region through 1931. Among 24 specimens collected since 1950, all are *C. thomasi*; there are no specimens of *C. brachyonyx.* The overall scarcity of *C. brachyonyx* and its absence in later collections may reflect a species restricted to habitats that have not been adequately sampled since the 1920s and that have shrunken dramatically in size or disappeared in the region surrounding the type locality as a result of agriculture and urban development. Alternatively, it is possible that the species may be extinct, but previous experience with the history of collecting *C. colombiana* (Woodman et al. 2003) suggests that this is unlikely and new specimens will begin to be collected. However, intensive surveys in the Cordillera Oriental using appropriate methods will be required to elucidate the modern geographic and ecological distributions of *C. brachyonyx.*

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Appendix: Specimens Examined

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

pellets. Specimens marked with an asterisk and in brackets are mandibles from owl pellets.

Cryptotis brachyonyx (4).—COLOMBIA: *Cundinamarca*: San Juan de Ríoseco (AMNH 70597); La Selva, near Bogotá (BM 99.10.3.2—holotype, 99.10.3.3); Plains of Bogotá (USNM 80905).

Cryptotis colombiana (14).—COLOMBIA: *Antioquia*: Corregimiento San Antonio de Prado, 2100–2800 m (MUA 060, 062); Finca Campiño, Alto de San Miguel, 2000 m (KU 157761); Reserva Ecológica Alto de San Miguel, 2150 m (MUA 12009, 12010*, 12011* [MUA 12012*, 12013*]); Vereda San Francisco, 2750 m (KU 157762*, MUA 12005* [MUA 12007*, 12008*]); Río Negrito, 15 km E of Sonsón, 1750 m (FMNH 69816—holotype); Finca Los Sauces, 2150 m (MUA 12001).

Cryptotis mera (7).—PANAMA: *Darien*: Cerro Tacarcuna, 4800 ft (USNM 337967–337969); Cerro Malí, 4700 ft (USNM 337966); Mount Pirri [Cerro Pirre], E slope near head of Río Limón, 4500–5000 ft (USNM 178974–178976—including holotype).

Cryptotis thomasi (50).—COLOMBIA: [no specific locality] (BM 54.1.11.4; MCZ 27596). *Cundinamarca*: Represa del Neusa (ICN 9659); Bogotá (AMNH 34605); Plains of Bogotá (USNM 80904); Páramo de Bogotá, 2900 m (AMNH 37381; MNHN 1962-1068); La Selva [G. O. Child's Estate], near Bogotá, (BM 97.5.21.2—holotype, 99.10.3.4, BM no number [GDC #311]; USNM 80903, 80906); Boquerón, near Bogotá (BM 99.10.3.1); Páramo de Monserrate, 3200–3300 m (ICN 9649, 9650, 9652, 9658; ROM 51870); San Francisco, 3000–3500 m (AMNH 71354, 71355; FMNH 71023, 71024, 71025, 71026, 71027, 71028, 71029, 71035); San Cristóbal, 2800–2900 m (FMNH 71030, 71031, 71032, 71033, 71034, 71036, 71037); Reserva Biológica Carpanta, 3000 m (ICN 10995, KU 157765); Páramo de Choachí, 3000 m, (AMNH 38405, MCZ 19885, 20090, 20092, 27597, 27598); Páramo el Verjón (AMNH 62789, 62790, MCZ 19995, 20091—holotype of *C. avia*); Chipaque (USNM 251960); Fusagasugá (MCZ 27599); Páramo de Chisacá, 3100 m (ICN 5223).