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**Taxonomic status of the enigmatic *Cryptotis avia*
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distribution of the Colombian small-eared shrew,
*Cryptotis colombiana***

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Abstract.—*Cryptotis avia* G. M. Allen 1923, from the Eastern Andean Cordillera of Colombia, is a small-eared shrew previously known from, at most, five specimens. Review of the holotype, consisting of an understuffed skin and a partial skull, and three potential topotypes indicates that they are referable to *Cryptotis thomasi* Merriam, 1897, and *C. avia* should be considered a junior synonym of that name. *Cryptotis thomasi* is restricted to highlands around Bogotá in the Eastern Cordillera. Another specimen previously referred to *C. avia* is the second known specimen of *Cryptotis colombiana* Woodman & Timm 1993. This second record expands the known distribution of *C. colombiana* to include both the Central and Eastern Cordilleras of Colombia, and emphasizes a previous hypothesis that *C. colombiana* also will be found in the Western Cordillera, geographically closer to its sister species (*Cryptotis mera*, *Cryptotis nigrescens*) in southern Central America.

Resumen.—*Cryptotis avia* G. M. Allen 1923, de la Cordillera Oriental de Colombia, es una musaraña conocida anteriormente de, a lo más, cinco especímenes. Estudio del holotipo, que consta de una piel poca rellenada y un cráneo parcial, y tres posibles topotipos indica que todos son iguales a *Cryptotis thomasi* Merriam 1897, y *C. avia* es un sinónimo menor de *C. thomasi*. *Cryptotis thomasi* ocurre solamente en las montañas alrededores de Bogotá en la Cordillera Oriental. Otra espécimen referida anteriormente a *C. avia* es en realidad la segunda espécimen identificada de *Cryptotis colombiana* Woodman & Timm 1993. Este segundo registro amplía la distribución de *C. colombiana* a las Cordilleras Central y Oriental de Colombia. Esta especie también debe ser encontrada en la Cordillera Occidental, la cual está más cerca geográficamente de las especies más relacionadas (*Cryptotis mera*, *Cryptotis nigrescens*) en el sur de Centroamérica.

Small-eared shrews of the genus *Cryptotis* are a relatively poorly studied group, notwithstanding their wide distribution in North America, Central America, and the Andean highlands of South America. *Cryptotis* reaches its greatest species diversity in southern Mexico and Central America, and

most taxonomic studies of the genus have been carried out on species in this region (Choate 1970; Woodman & Timm 1992, 1993). The most recent, comprehensive compendium of mammalian species recognized 14 species of *Cryptotis* (Hutterer 1993), and subsequent studies have re-

vealed additional species, mostly in Mexico and Central America (Woodman & Timm 1993). Little work has focused on South American taxa (Tate 1932, Hutterer 1986), and these are in need of taxonomic and systematic reevaluation (Hutterer 1993).

Most species of *Cryptotis* in South America are members of the *Cryptotis thomasi* group (sensu Choate 1970). Recently, however, Woodman & Timm (1993) described a new species of the *Cryptotis nigrescens* group (sensu Woodman & Timm 1993), *Cryptotis colombiana*, based on a specimen from the Central Cordillera of Colombia. Most other members of this latter group of shrews are found in southern Mexico and Central America, although *Cryptotis mera* is known to occur on two isolated highland areas along the border between Panama and Colombia.

One of the least known species of the *Cryptotis thomasi* group is *Cryptotis avia* from the eastern Andean cordillera of Colombia. As part of a comprehensive revision of South American members of the genus, I reviewed the holotype and other possible specimens of this species. This paper presents my conclusions concerning the taxonomic status and relationships of *C. avia* and new data on the content and distribution of *Cryptotis colombiana* and *C. thomasi*.

Taxonomic Status of *Cryptotis avia* Allen 1923

Cryptotis avia was described by G. M. Allen (1923) based on a specimen collected by Nicéforo María in October 1922 from "El Verjón" (Fig. 1); the Páramo el Verjón is at an elevation of 3400 to 3600 m in the Andean highlands east of Bogotá, Colombia (Paynter & Traylor 1981). Aside from the holotype [MCZ 20091] in the Museum of Comparative Zoology, Harvard University, few records of this species exist. Tate (1932:226) noted two individuals in the American Museum of Natural History [AMNH], "both of them from the type lo-

cality and apparently collected at the same time as the type". Although he did not provide catalog numbers, Tate almost certainly was referring to two skins lacking skulls [AMNH 62789 and 62790], collected at El Verjón in October 1922 by Nicéforo María. A fourth specimen from near the type locality, and hence, potentially referable to *C. avia*, is MCZ 19995, a skin with skull collected at "Laguna del Verjón" by Nicéforo María in March 1922. MCZ 19995 was available to Allen (1923) when he described *C. avia* (note the catalog number is lower than that of the holotype), but he did not refer this specimen to the new species or use it for comparison. [The two specimens of *C. thomasi* that Allen (1923:37) mentions in his report as "lately received by the Museum of Comparative Zoölogy from the Instituto de la Salle" with the holotype of *C. avia* probably are MCZ 20090 and 20092, from the Páramo de Choachi.] The three specimens [MCZ 19995, AMNH 62789, 62790] from the type locality of *C. avia* are identified (correctly) as *Cryptotis thomasi* in their respective collections. In my searches of North American and Colombian systematic collections, I encountered only one specimen other than the holotype that clearly was referred to *C. avia*; this is AMNH 70597, from San Juan de Río seco (but see below). The lack of well identified specimens of *C. avia* in itself is not surprising given the generally poor representation of South American shrews in systematic collections. However, the holotype of *C. avia* is from the vicinity of Bogotá, a region that, as far as South American shrews are concerned, is relatively well collected.

The holotype of *Cryptotis avia* consists of a skin and skull of an adult animal of unknown sex. Allen (1923) described *C. avia* as being about the size of *Cryptotis nigrescens* [a small member of the genus] and suggested a possible close phylogenetic relationship between *C. avia* and both *C. nigrescens* and *Cryptotis mexicana nelsoni*. The skin is in poor condition and is under-

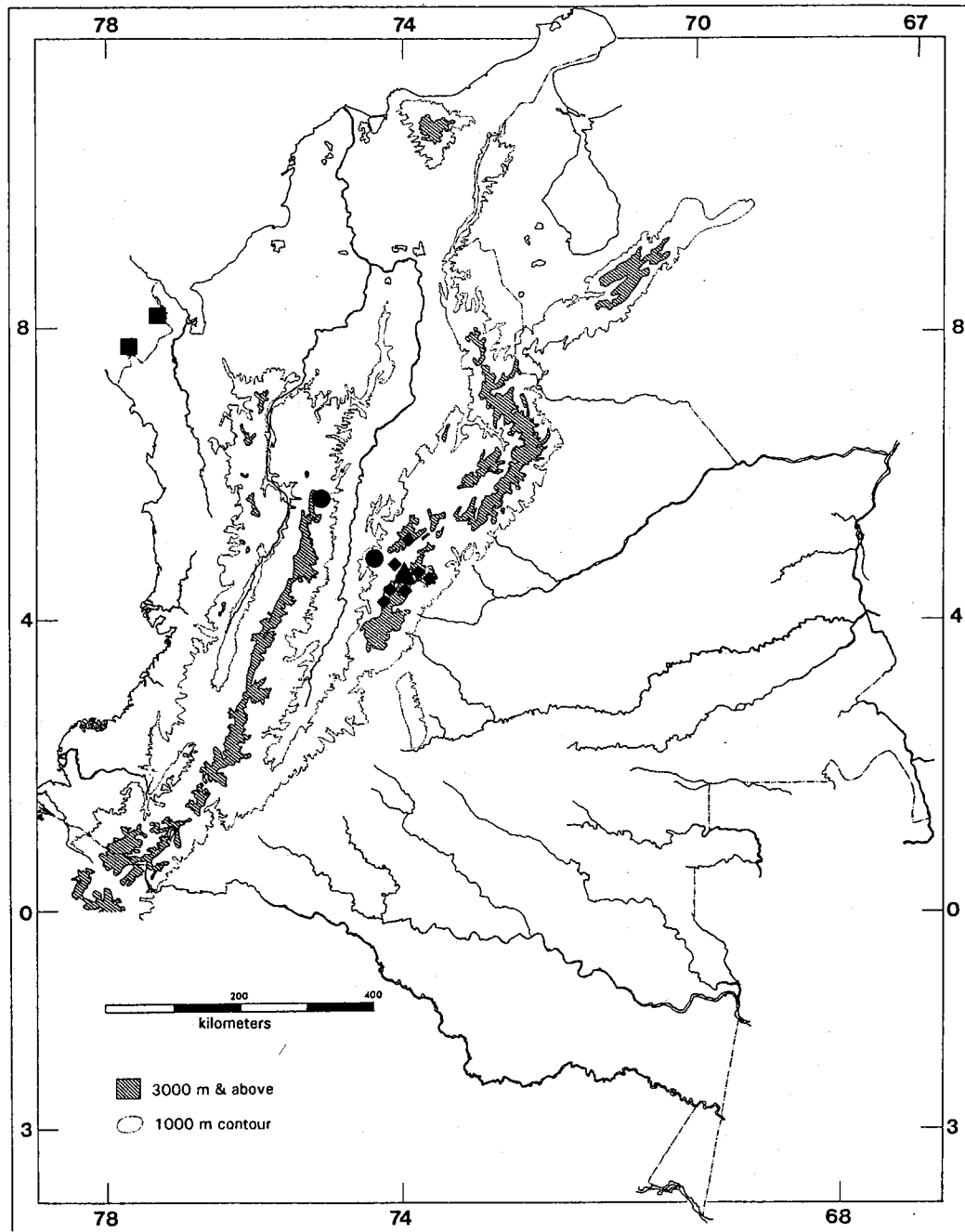


Fig. 1. Distributions of *Cryptotis mera* (solid squares) in western Panama and *Cryptotis colombiana* (filled circles) and *Cryptotis thomasi* (small, solid diamonds) in Colombia. *Cryptotis thomasi* also is known from the type locality of *Cryptotis avia* (solid triangle).

stuffed, giving the impression that it is indeed from a small animal. Unfortunately, total-length and tail-length measurements were not recorded at the time the animal was prepared, and Allen (1923) reported measurements obtained from the prepared skin. Subsequent treatments of *C. avia* have used its small size as the primary criterion for distinguishing it from *Cryptotis thomasi* and other Colombian members of the genus. Cabrera & Yepes (1960) indicated a head-and-body-length for *C. avia* of ca. 7 cm, compared to ca. 8 cm for *C. thomasi*. Choate & Fleharty (1974) distinguished *C. avia* from other South American taxa based on its shorter palatal-length and narrower maxillary-breadth, as well as its supposedly more homogeneous dorsal and ventral pelage coloration. Eisenberg (1989) gave total length of the *C. avia* as <100 mm.

In light of current knowledge of the taxonomic and morphological diversity in *Cryptotis*, Allen's (1923) description of *Cryptotis avia* no longer suffices to distinguish the species. In order to define this species more completely, I inspected the holotype and all potential topotypes of *C. avia*, reviewing the characteristics used by Allen and subsequent authors, as well as a suite of characters used to distinguish other species (Choate 1970; Woodman 1992; Woodman & Timm 1992, 1993).

Because *Cryptotis thomasi* occurs in the same region of the Eastern Cordillera as *Cryptotis avia*, it is logical to make comparisons between the two species. In order to adequately characterize *C. thomasi*, I inspected every specimen of this species readily available to me. On the basis of this study, I herein use the name *C. thomasi* only for shrews from highlands in the vicinity of Bogotá in the Eastern Cordillera of Colombia (Fig. 1); these sometimes are referred to *C. thomasi thomasi* (Cabrera 1958). *Cryptotis thomasi* (sensu stricto) is restricted to elevations above 2700 m, and the highland region around Bogotá almost certainly represents the true distributional limits of the species. Along the Eastern

Cordillera, there are no specimens of *Cryptotis* from south of Paso de las Cruces, a valley that drops to below 2000 m. Similarly, there are no specimens known from the region between the northern border of Cundinamarca Dept. and the Páramo de Tama along the Venezuelan border, where *Cryptotis meridensis* occurs.

The skull of the holotype of *Cryptotis avia* is broken behind the dorsal foramina, and all of the posterior braincase is missing. This is unfortunate because several important characters can not be evaluated and because this makes the skull appear shorter than it originally was. Although the remaining rostrum and central portion of the skull and the mandible are small in comparison with many other specimens from South America, they are within the range of morphological variation for specimens of *Cryptotis thomasi*, and most craniomandibular measurements from the holotype of *C. avia* fall well within the range of size variation for that species (Table 1). To test this further, I carried out a principle components analysis of nine cranial measurements (breadth of zygomatic plate, postorbital-breadth, breadth across U1s, breadth across M2s, palatal-length, maxillary-toothrow-length, unicuspid-toothrow-length, molariform-toothrow-length, posterior width of M1) from the holotype of *C. avia* and 24 specimens of *C. thomasi*. The holotype of *C. avia* plots among the smallest specimens on the factor axis 1 (Fig. 2), which represents a combination of palatal-length and maxillary-toothrow-length (Table 2), but principle components analysis failed to identify any mensural characters or combinations of characters that clearly separate it from *C. thomasi*.

Characters preserved on the skin and skull of the holotype of *Cryptotis avia* are consistent with *Cryptotis thomasi*. As noted by Allen (1923), the foreclaws are elongate, although not particularly broad. In addition, the posterior border of the zygomatic plate is anterior to the posterior root of the maxillary process; U4 is mostly in line with the other upper unicuspid and is not obscured

Table 1.—Selected measurements of *Cryptotis* from Colombia. Measurements follow Woodman & Timm (1993).

<i>C. thomasi</i> (<i>n</i> = 24)	<i>C. avia</i> (MCZ 20091 [holotype])	<i>C. colombiana</i> (FMNH 69816 [holotype], AMNH 70597)
Breadth of zygomatic plate (ZP)		
2.0 + 0.2 1.7–2.4	1.9	2.0, 1.7
Postorbital-breadth (PO)		
5.0 + 0.2 4.6–5.4	5.0	4.9, 4.6
Breadth across U1s (U1B)		
2.7 + 0.1 2.5–2.9	2.7	2.6, x
Breadth across M2s (M2B)		
6.2 + 0.2 5.9–6.5	5.8	6.3, 5.7
Palatal-length (PL)		
9.3 + 0.3 8.6–9.7	8.7	8.8, 8.3
Maxillary-toothrow-length (TR)		
8.1 + 0.2 7.7–8.5	7.8	7.7, 7.3
Unicuspid-toothrow-length (UTR)		
2.8 + 0.1 2.4–3.0	2.6	2.5, 2.4
Molariform-toothrow-length (MTR)		
5.8 + 0.1 5.5–6.0	5.5	5.8, 5.3
Posterior width of M1 (WM1)		
1.9 + 0.1 1.8–2.1	1.8	1.8, 1.8
Length of mandible (ML)		
7.0 + 0.2 6.6–7.4	6.5	6.9, 6.4
Height of coronoid process (HCP)		
4.6 + 0.1 4.3–4.9	4.4	4.8, 4.5
Height of coronoid valley (HCV)		
3.1 + 0.1 2.8–3.4	2.9	2.9, 2.8
Height of articular condyle (HAC)		
4.3 + 0.1 4.1–4.6	4.0	4.1, 3.9
Breadth of articular condyle (BAC)		
3.6 + 0.1 3.4–3.8	3.4	3.1, 3.0

Table 1.—Continued.

<i>C. thomasi</i> (<i>n</i> = 24)	<i>C. avia</i> (MCZ 20091 [holotype])	<i>C. colombiana</i> (FMNH 69816 [holotype], AMNH 70597)
Articular condyle to m3 (AC3)		
5.7 + 0.2 5.5–5.8	5.6	4.9, 4.9
Length of lower toothrow (TRD)		
6.3 + 0.2 6.2–6.7	6.0	6.0, 5.7
Length of m1 (m1L)		
1.9 + 0.1 1.7–2.0	1.7	1.9, 1.8

in lateral view by P4; U1–U3 have narrow cusps with strongly concave posteroventral margins; dentition is bulbous; P4 and M1 are only slightly emarginated posteriorly; the anterior element of the ectoloph of M1 is reduced relative to the posterior element; the protoconal basin of M1 is reduced relative to the hypoconal basin; M3 is relatively complex and possesses a metacone; the coronoid process of the mandible is low and narrow, and its anterior border has a relatively shallow slope; the articular condyle is high and narrow; the lower sigmoid notch is shallow; p3 is long and low; m3 lacks an entoconid. Together, these characteristics serve to distinguish the holotype of *C. avia* from *Cryptotis parva*, *Cryptotis mexicana* (and its close relatives), members of the *Cryptotis nigrescens* group, and most other South American shrews.

The type locality of *Cryptotis avia* (Fig. 1) is within the established range of *Cryptotis thomasi*, and there are no characters, including size, that distinguish the holotype from that species. Similarly, the three other specimens [AMNH 62789, 62790, MCZ 19995] from El Verjón, including the two that Tate (1932) probably referred to *C. avia*, are indistinguishable from *C. thomasi*. For these reasons, *C. avia* should be considered conspecific with, and a junior synonym of, *C. thomasi*. Consequently, the synonymy of *C. thomasi* is amended as follows:

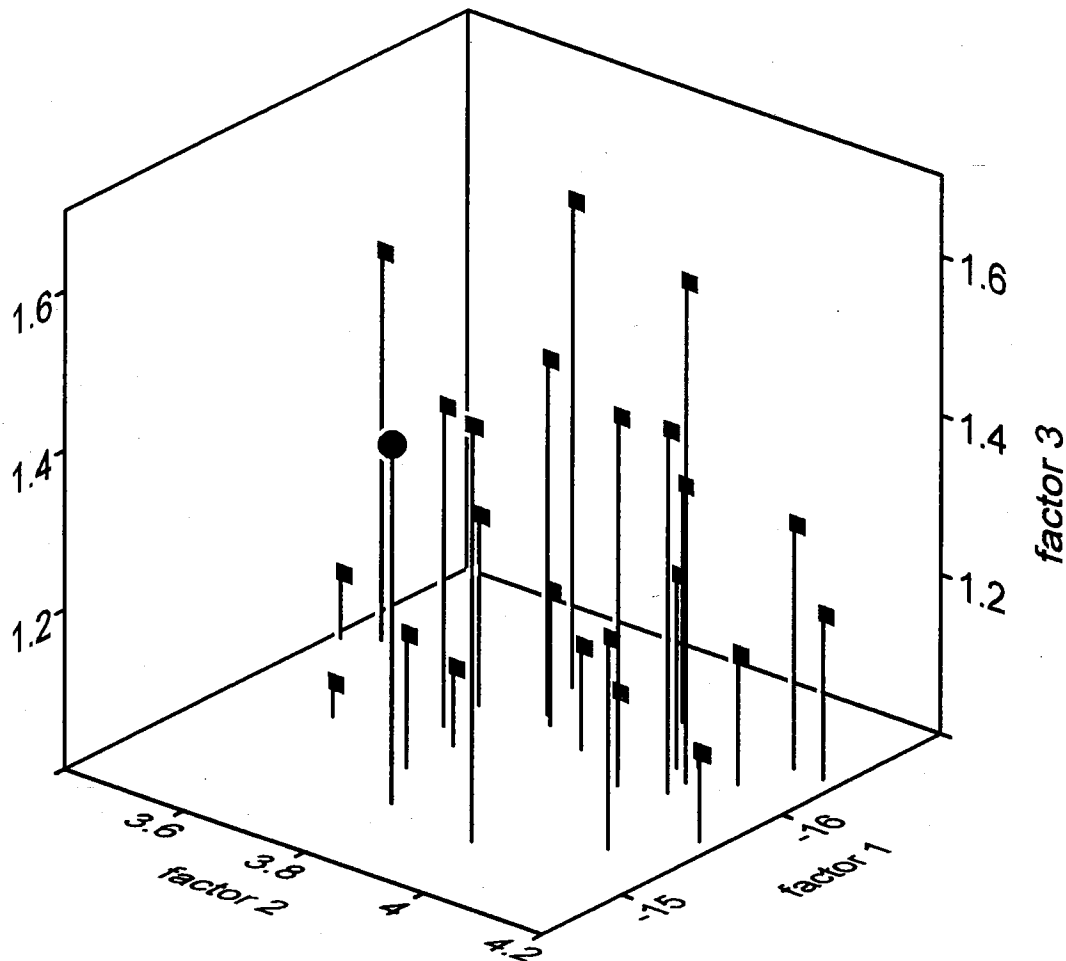


Fig. 2. Three-dimensional plot of the holotype of *Cryptotis avia* (solid circle) and 24 specimens of *Cryptotis thomasi* (solid squares) on factor axes 1, 2, and 3 from principle components analysis of nine cranial measurements. The first axis represents palatal length and maxillary tooththrow length (Table 2); the second axis is postorbital breadth and breadth across M2s; the third axis is postorbital breadth and zygomatic breadth contrasted with breadth across M2s.

Cryptotis thomasi (Merriam) 1897

Blarina thomasi Merriam, 1897:227.

B.[larina] thomasi Thomas, 1898:457.

[Blarina] thomasi Trouessart, 1905:138; Anthony, 1921:5.

B.[larina] thomasi Thomas, 1912:409; Stone, 1914:16.

C.[ryptotis] thomasi Thomas, 1921:354; Choate & Fleharty, 1974:1 (in part); Corbet & Hill, 1980:28 (in part); Corbet & Hill, 1991:32 (in part).

Cryptotis thomasi G. M. Allen, 1923:37 (in

part); Tate, 1932:226; Cabrera & Yepes, 1960:54; Hershkovitz, 1969:18 (in part); Honacki et al., 1982:86 (in part); Eisenberg, 1989:71 (in part); Hutterer, 1993 (in part).

Cryptotis avia G. M. Allen, 1923:37; Tate, 1932:226; Honacki et al., 1982:85; Eisenberg, 1989:70; Hutterer, 1993.

[Cryptotis] avia Cabrera, 1925:133.

[Cryptotis] thomasi Cabrera, 1925:135.

Cryptotis avius Cabrera, 1958:46.

Cryptotis thomasi thomasi Cabrera, 1958:46.

Table 2.—Factor loadings from principal components analysis of cranial variables of the holotype of *Cryptotis avia* and 24 *Cryptotis thomasi*. Abbreviations are explained in Table 1.

Variable	Factor 1	Factor 2	Factor 3
PL	-0.643	-0.318	-0.074
TR	-0.553	-0.220	0.134
MTR	-0.296	0.205	0.171
M2B	-0.276	0.641	-0.502
UTR	-0.231	-0.030	-0.219
ZP	-0.161	-0.064	0.434
WM1	-0.126	0.245	-0.155
PO	-0.107	0.556	0.654
U1B	-0.103	0.152	-0.081

C.[ryptotis] avia Cabrera & Yepes, 1960: 55; Choate & Fleharty, 1974:1; Corbet & Hill, 1980:27; Corbet & Hill, 1991:31.

Specimens examined (42).—Colombia: no locality (MCZ 27596). Cundinamarca: Bogotá (AMNH 34605); Bogotá, San Cristóbal, 2800–2900 m (FMNH 71030–71034, 71036, 71037); Bogotá, San Francisco, 3000–3500 m (FMNH 71023–71029, 71035); Chipaque [Chipaque] (USNM 251960); El Verjón [Páramo el Verjón] (AMNH 62789, 62790, MCZ 20091—holotype of *C. avia*); Laguna del Verjón, (MCZ 19995); Fusayasugá (MCZ 27599); Hacienda Santa Barbara, Monserrate, Bogotá, D. E., 3300 m (ICN 9649, 9650, 9652, 9658); Páramo de Bogotá, 2900 m (AMNH 37381); Páramo de Chisacá, km 30, 3100 m (ICN 5223); Páramo de Choachí, 3000 m (AMNH 38405, MCZ 19885, 20090, 20092, 27597, 27598); Páramo de Monserrate, near Cerro del Rompedro, 3200 m (ROM 51870); Plains of Bogotá (USNM 80903–80906); Reserva Biológica Carpana, Municipio Junin, 3000 m (ICN 10995, 10996); Represa del Neusa, Tausa (ICN 9659).

Distribution of *Cryptotis colombiana* Woodman & Timm (1993)

The only other specimen currently identified in a major systematic collection as *C. avia* is AMNH 70597. This consists of a

skin and skull of a young adult (toothwear class 1 of Rudd 1955) of unknown sex collected in November 1925 by Nicéforo Maria (original number 111) at San Juan de Ríoseco, Cundinamarca Dept., Colombia (Fig. 1). San Juan de Ríoseco (4°51'N, 74°38'W) is at ca. 1300 m in the western foothills of the Eastern Cordillera of Colombia, about 18 km NE of Ambalema (Paynter & Traylor 1981) and ca. 70 km west of the type locality of *C. avia*. The specimen is a small- to medium-sized *Cryptotis* (Table 1), and given its similar preparation and close geographical association with the holotype of *C. avia*, it is easy to see why it was referred to that species.

The skin of the AMNH specimen is in fair condition, but the left hind leg is detached. The braincase is broken, although most pieces appear to be present. The upper dentition lacks LU1 and LU2. The right mandible is missing, and the left mandible lacks I1. This individual possesses a number of characters that distinguish it from *Cryptotis thomasi* (and other members of the *C. thomasi* group) and that place it within the *Cryptotis nigrescens* group. It has small forefeet and small foreclaws; broad upper unicuspid with straight posteroventral occlusal surfaces; a relatively shorter, broader mandible; a relatively tall coronoid process of the mandible, with steep, concave anterior border; the articular condyle is shorter and broader; p4 is shorter and higher crowned.

AMNH 70597 shares a number of cranial characteristics with the holotype of *Cryptotis colombiana*. These include: two large dorsal foramina close to the sagittal suture; no ventral extension of the sinus canal nor an associated foramen posterior to the dorsal articular facets; a moderately well-developed foramen dorsal to each dorsal articular facet; the high, wide anterior process of petromastoid (Fig. 3); a large foramen on the posteromedial edge of the tympanic process of the petromastoid. The latter two characters appear to be derived within the *Cryptotis nigrescens* group. An enlarged

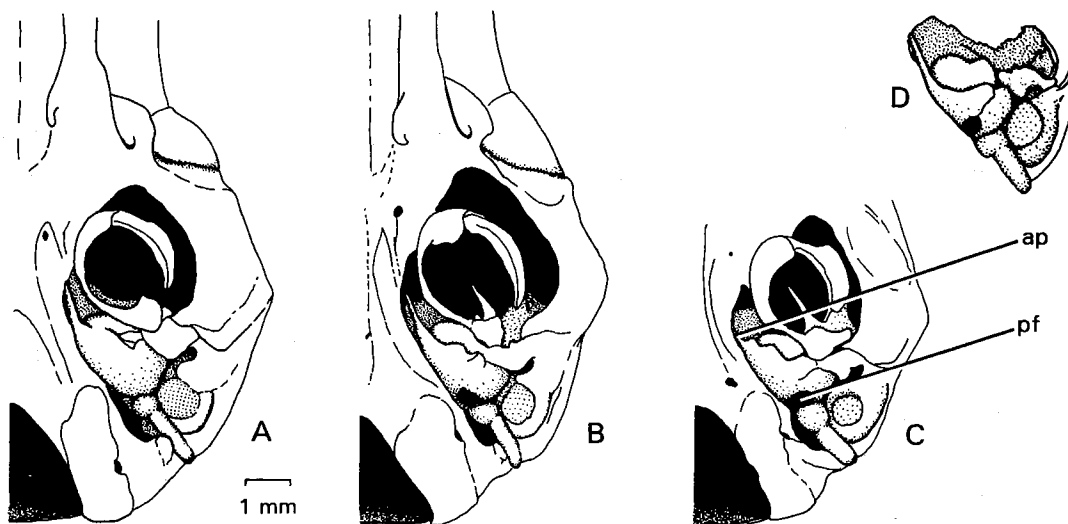


Fig. 3. Ventral view of the left tympanic region of skulls of *Cryptotis*, illustrating the location of the anterior process of the petromastoid (ap) and the foramen on the posterior edge of the tympanic process of the petromastoid (pf): A) *C. meridensis* (FMNH 12981), B) *C. thomasi* (ICN 9650), C) the holotype of *C. colombiana* (FMNH 69816), and D) the disarticulated right otic capsule of *C. colombiana* (AMNH 70597). The left anterior process of the petromastoid of FMNH 69816 is incomplete (but see Woodman & Timm 1993: Fig. 18).

anterior process of the petromastoid is not found in any other member of the genus *Cryptotis*, nor in any species of *Blarina* or *Sorex* (the sister taxa of *Cryptotis*—George 1986) that I have inspected. A large foramen in the tympanic process is found among some South American members of the *Cryptotis thomasi* group, including *C. thomasi* (Fig. 3). However, it is not found in any other member of the *C. nigrescens* group, nor is it present in any species of any other genus of soricine that I have inspected. There is a temptation to suggest that this character might be environmentally-induced, given the Andean distribution of *C. colombiana* and species in the *C. thomasi* group. However, not all Andean members of the *C. thomasi* group possess this foramen (e.g., *Cryptotis meridensis*). Moreover, *C. colombiana* and *C. thomasi* do not inhabit similar habitats within the Andes. *Cryptotis thomasi* is restricted to high elevation (>2700 m), moist paramo, whereas *C. colombiana* occurs at much lower elevations (<2000 m) and may occur in a wider variety of habitats, including the rela-

tively dry, western side of the Eastern Cordillera.

If an enlarged anterior process of the petromastoid and a large foramen in the tympanic process are derived within the *Cryptotis nigrescens* group, the two characters link the holotype of *Cryptotis colombiana* and AMNH 70597 phylogenetically and distinguish them from all other members of the *C. nigrescens* group.

Several characters distinguish the two specimens of *Cryptotis colombiana*. The AMNH specimen is smaller overall and not as robust as the holotype; the rostrum, post-orbital area, and palate are narrower; the zygomatic plate is relatively narrower; the upper molars are much smaller, resulting in a shorter molariform toothrow (Table 1); the foramen on the posterior edge of the tympanic process of the petromastoid is more medially located (Fig. 3); the articular process of the mandible is much narrower and there is a distinct notch between the upper and lower articular surfaces; there is a vestigial entoconid in the talonid of m3; the

teeth are more heavily pigmented and not nearly as bulbous.

The AMNH specimen is from the Eastern Cordillera of the Colombian Andes, whereas the holotype of *Cryptotis colombiana* is from the Central Cordillera (Fig. 1). With the exception of the specialized *Cryptotis mayensis* from the Yucatan Peninsula, Mexico, the *Cryptotis nigrescens* group consists of middle- to high-elevation species that do not occur below 800 m (Woodman & Timm 1993). The Central and Eastern Cordilleras are separated by the deep valley of the Río Magdalena that flows at elevations below 500 m north of Neiva. The vegetation of the valley is quite distinct from the upper slopes of either cordillera (R. Anderson, in. lit.), and the valley probably acts as an effective barrier to gene flow. Additional collections of these shrews will help us to better understand their distribution in Colombia and to understand the range of morphological variation in the characters listed above. However, the current scarcity of specimens of *C. colombiana* prevents adequate appraisal of variation within this species, and it is most helpful at this time to refer AMNH 70597 to *C. colombiana*. The two specimens appear to be more closely related phylogenetically to each other than to any other known taxon, and whether they represent distinct species or are members of a single, morphologically diverse species, they have the same biogeographic significance relative to the distribution and history of the *C. nigrescens* group. Woodman & Timm (1993) hypothesized that *C. colombiana*, or a close relative, should occur at high elevation in the Western Cordillera of Colombia, which is located between the known geographic ranges of *C. colombiana* and its geographically closest relative in the *C. nigrescens* group, *C. mera*. The discovery of *C. colombiana* in the Eastern Cordillera reinforces that idea.

The account for *Cryptotis colombiana* is amended to include the new material:

Cryptotis colombiana
Woodman & Timm 1993

Cryptotis thomasi Hershkovitz, 1969:18 (in part).

Cryptotis colombiana Woodman & Timm, 1993.

Specimens examined (2).—Colombia: Antioquia: Sonsón, 15 km E of Río Negro, 1750 m (FMNH 69816—holotype). Cundinamarca: San Juan de Río seco (AMNH 70597).

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