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Order Soricomorpha Gregory, 1910

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Order Soricomorpha Gregory, 1910

By Neal Woodman and Jaime Péfaur

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Magnorder Epitheria

Order Soricomorpha Gregory, 1910

Neal Woodman and Jaime Péfaur

The Soricomorpha originally was proposed by Gregory (1910) as a “section” containing the shrews (Soricidae) and moles (Talpidae) within the suborder Lypotyphla, order Insectivora. More recent concepts of what constitutes the Soricomorpha vary. Typically, the order comprises shrews and solenodons (Solenodontidae), and possibly tenrecs (Tenrecidae; McKenna and Bell 1997) or moles (Arnason et al. 2002) or both (MacPhee and Novacek 1993). A possible relationship with gymnures and hedgehogs (Erinacidae) also has received support (Malia, Adkins, and Allard 2002). Previously, these five families had been included with golden moles (Chrysochloridae) in the order Lypotyphla, or along with elephant shrews (Macroscelididae) in the order Insectivora. However, recent analyses of phylogenetic relationships indicate that the seven families are not as closely related as previously believed (e.g., Stanhope et al. 1998; Mouchaty et al. 2000; Arnason et al. 2002; Malia, Adkins, and Allard 2002). Although consensus has yet to be reached on their relative phyletic positions, either to each other or to other mammalian groups, recent classifications (e.g., McKenna and Bell 1997) divide the Erinacidae, Soricidae, Solenodontidae, Talpidae, and Tenrecidae among many as four orders (Macroscelidea, Chrysochloridea, Erinaceomorpha, and Soricomorpha). Only one of these families, the Soricidae, is present in South America.

Family Soricidae G. Fischer, 1814

The Soricidae comprises 23 genera and more than 320 species distributed throughout Eurasia, Africa, North and Central America, and northwestern South America. Members of the family are sometimes considered primitive or generalized, but these labels ignore a well known suite of cranial and dental specializations unique to these animals.

Shrews are small mammals (head and body length, 35–150 mm; mass, 2–106 g), typically having small pinnae often concealed by fur, minute eyes, and an elongated, pointed snout. The long, flattened skull has incomplete zygomatic arches lacking jugals, free tympanic bones (auditory bullae are lacking), and a double articulation of the articular condyle of the dentary with the cranium. The clavicle is long and slender, and the pubic symphysis is open (innominate not in contact). The deciduous dentition is shed in utero. A pincer-like foraging apparatus is formed by the large, curved, first upper incisor and the long, procumbent, first lower incisor. Behind the first upper incisor, the anterior upper dentition (incisors, canine, and anterior premolars) is comparatively simple and undifferentiated, and these teeth are often referred to as “unicuspids.” Homologies of the unicuspid have been difficult to determine, and for this reason, dental formulae for individual species often disagree in the relative numbers of incisors, canines, and premolars. Only shrews of the subfamily Soricinae occur in the Americas. The red-pigmented dentition in most New World genera (except *Megasorex* and *Notiosorex*) provides an additional characteristic that aids in distinguishing these mammals as shrews.

Although most authors attribute the name Soricidae to Gray (1821:300), Palmer (1904) and McKenna and Bell (1997) dated the name from G. Fischer's ([= Fischer von Waldheim] 1817:414) “*Familia Soricinorum*.” However, G. Fischer first used “*Familia Soricinorum*” in 1814 (p. x).

Genus *Cryptotis* Pomel, 1848

The small-eared shrews of the genus *Cryptotis* include at least 28 species that are discontinuously distributed from the eastern United States and southernmost Canada to Venezuela and Peru north of the Huancabamba Depression. Individual species occupy a variety of habitats from sea-level grasslands and second-growth woodlands in northern North America to humid montane forests and paramos of northern South America. In South America, *Cryptotis* is known only above 1,200 m. Shrews have been found in the Lower Montane Moist Forest, Lower Montane Wet Forest, Montane Wet Forest, Montane Rain Forest, Subalpine Páramo, and Subalpine Rain Páramo life zones of Holdridge (1947), as well as in disturbed cloud forest, secondary forest, and pasture lands (Woodman 2002).

Cryptotis are small to medium-sized shrews (length of head and body, 50–102 mm; tail, 12–53 mm; mass, 3–19 g). In South America, head and body length ranges from 60 to 102 mm; tail length, from 20 to 46 mm; and mass, from ca. 5 to 18 g. These medium-gray to nearly black small mammals all have red-pigmented teeth, and most have four

upper unicuspid. Upper unicuspid decrease in size posteriorly; the fourth unicuspid is always smaller than the third, and is occasionally absent in two species. The typical dental formula for *Cryptotis* often is given as 3/1, 1/1, 2/1, 3/3 = 30 (Hall 1981; F. A. Reid 1997). Choate (1970:208) gave the dental formula for the upper tooththrow as 1 (falciform incisor), 4 (unicuspids), 1 (premolar [P4]), and 3 (molars); the lower tooththrow as 1 (procumbent incisor), 1 (unicuspid), 1 (premolar [p4]), and 3 (molars). The fossil record of *Cryptotis* extends from late Miocene to Recent in North America (McKenna and Bell 1998).

Local vernacular names for shrews in South America include musarañas, ratones hocicudos, and ratones topos.

SYNONYMS:

Sorex: Say in James, 1823:163; not *Sorex* Linnaeus, 1758.

Corsira Gray, 1838a:123; part.

Brachysorex Duvernoy, 1842:37; part.

Galemys Pomel, 1848:249; part; preoccupied by *Galemys* Kaup, 1829 (Talpidae).

Musaraneus Pomel, 1848:249; part; *Musaraneus* is unavailable from Brisson (1762; see ICZN 1998), but is an available name from Pomel, 1848.

Cryptotis Pomel, 1848:249; type species "*M. cinereus* (*sorex* [*sic*] *cinereus* Bachm.)"; (= *Sorex parvus* Say in James, 1823); proposed as a subgenus of *Musaraneus* Pomel.

Blarina: Baird, 1857:51, 53; part; not *Blarina* Gray, 1838a.

Cryptotus Milne-Edwards, 1872b:256; incorrect subsequent spelling of *Cryptotis* Pomel.

Blarina: Coues, 1877:647; part; not *Blarina* Gray.

Soriciscus Coues, 1877:649; type species "*Sorex parvus* Say or *S. cinereus* Bachm." (= *Sorex parvus* Say in James, 1823) by original designation; proposed as a subgenus of *Blarina* Gray, 1838a.

Blarina (*Soriciscus*): J. A. Allen, 1895b:339, 340; not *Blarina* Gray.

Blarina: Merriam, 1897b:227; not *Blarina* Gray.

Blarina: O. Thomas, 1898c:457; not *Blarina* Gray.

Sorieiscus Elliot, 1901:382; incorrect subsequent spelling of *Soriciscus* Coues.

Cryptotis: Miller, 1911:221; first use as a genus.

Blarina: J. A. Allen, 1912:93; not *Blarina* Gray.

Blarina: O. Thomas, 1912c:409; not *Blarina* Gray.

Blarina: Stone, 1914:16; not *Blarina* Gray.

Blarina: H. E. Anthony, 1921a:5; not *Blarina* Gray.

Blarina: Hibbard, 1953:29; not *Blarina* Gray.

Cryptotys Saban, 1958:846; incorrect subsequent spelling of *Cryptotis* Pomel.

Xenosorex Schaldach, 1966:289; type species *Notiosorex phillipsii* Schaldach, 1966, by original designation; proposed as a subgenus of *Notiosorex*: Schaldach, 1966; not *Notiosorex* Coues, 1877.

Criptotis Durant and Péfaur, 1984:6; incorrect subsequent spelling of *Cryptotis* Pomel.

Cripotitis Aagaard, 1982:276; incorrect subsequent spelling of *Cryptotis* Pomel.

Criptotis Durant and Díaz, 1995:87; incorrect subsequent spelling of *Cryptotis* Pomel.

REMARKS: *Sorex surinamensis* Gmelin, 1788:114, and *Blarina pyrrhonota* Jentink, 1910b:167, are two taxa with complex taxonomic histories long associated with South American soricids. Each species was described on the basis of a single specimen believed at the time to have originated from Surinam. *Sorex surinamensis* supposedly was the first species of shrew to be described from South America or from anywhere else in the New World (Gmelin 1788:114). The type specimen has not been located, therefore, verification of its identity is not possible. O. Thomas (1888b:357), Trouessart (1898:1242), and Cabrera (1919:42; 1925:135) considered the original description of *S. surinamensis* to have been based on a marsupial, and they listed the name in their synonymies of the Guianan Short-tailed Opossum, *Monodelphis breviceaudata* (as either *Didelphys breviceaudata* or *Peramys breviceaudatus*). However, Trouessart (1897:188) also listed *S. surinamensis* as a possible synonym of *B. pyrrhonota*, another name believed to have been based on a shrew from Surinam. In contrast, Tate (1932:223) stated clearly that the descriptions of both *S. surinamensis* and *B. pyrrhonota* represented soricids and suggested that both names may have been based on the same individual. He also cast doubt on whether either species occurred in Surinam, suggesting that the specimen on which Jentink based *B. pyrrhonota* was mislabeled. Cabrera (1958:47) treated *S. surinamensis* as a species of *Cryptotis* and included *B. pyrrhonota* as a junior synonym.

Blarina pyrrhonota was first mentioned by Jentink (1888:16), but was not described until much later (Jentink 1910b:167). As noted previously, Trouessart (1897:188, 1904:138) treated *B. pyrrhonota* as a South American species and suggested that *S. surinamensis* might be a synonym. Cabrera (1925:135) listed *pyrrhonota* (*sic*) as a species of *Cryptotis*, but, apparently unaware of Jentink's (1910b) subsequent validation, he said the name was a *nomen nudum* because it lacked a formal description. In accord with Tate (1932), Cabrera (1958:47) subsequently treated *B. pyrrhonota* as a synonym of *Cryptotis surinamensis*. Husson (1963) provided the first detailed redescription of the holotype of *B. pyrrhonota* and concluded that it was a *Sorex*, probably the common European shrew, *Sorex araneus*. The original label had been lost, obscuring the history of the specimen, and he noted that there was no evidence that it was also the basis for Gmelin's (1788) description of *S. surinamensis*, as suggested by Tate

(1932). Modern taxonomic accounts tend to treat both *B. pyrrhonota* and *S. surinamensis* as synonyms of *S. araneus* (e.g., Hutterer 1993).

Recent taxonomic treatments of *Cryptotis* partition the species among four informal species groups based upon external, cranial, dental, and postcranial characteristics (Choate 1970; Woodman 1996, 2002; Woodman and Timm 1993, 1999, 2000; Woodman, Cuartas-Calle, and Delgado 2003): the *C. mexicana*-group in Mexico and northern Central America; the *C. nigrescens*-group distributed from Mexico to Colombia; the *C. parva*-group occurring from Canada to Costa Rica; and the *C. thomasi*-group in the Andes of northern South America. Most South American *Cryptotis* are members of the *C. thomasi*-group, which is distinguished by a number of derived characters, including modifications of the forelimbs (Woodman 1996, 2002; Woodman, Cuartas-Calle, and Delgado 2003; Woodman and Morgan, *in press*). In addition, two species (*C. colombiana*, *C. mera*) are allied with the more primitive and mostly Central American *Cryptotis nigrescens*-group (Woodman 1996; Woodman and Timm 1993; Woodman, Cuartas-Calle, and Delgado 2003).

For the most part, our current knowledge of South American shrews is limited to an incomplete understanding of their taxonomies, distributions, and associations with other small mammals, vegetation communities, and climatic zones. Few solid scientific studies of reproduction, feeding habits, and other aspects of their life histories have been undertaken. There are abundant opportunities for local researchers to undertake meaningful comparative studies of ecology, behavior, physiology, and additional aspects of the biology of these shrews.

The following key should be considered a rough guide to identifying species of shrews in South America. The genus is under active study at this time and although 11 species are included in the key, some named "species" are known to be complexes comprising two or more species. Several species are documented by only a handful of often-incomplete specimens, so the full range of morphological variation is incompletely documented. In the Cordillera Central and Cordillera Oriental of Colombia, a species from the *C. nigrescens*-group occurs sympatrically with a member of the *C. thomasi*-group, and a similar situation is expected in the poorly explored Cordillera Occidental (Woodman and Timm 1993; Woodman 1996). Through much of the highlands of northwestern South America, species of *Cryptotis* are parapatric, so location can be helpful in determining species identity. However, distributions remain poorly documented throughout the Andes, and potential contact zones between neighboring species are unsampled in nearly all cases. Specimens of shrews are relatively rare in collections, and vouchers always must be prepared and deposited

in a reputable institution where they will be available for study.

Editor's note: The gender of *Cryptotis* has been treated inconsistently (e.g., compare Miller and Kellogg 1955; Cabrera 1958). Based on his interpretation of classical usage, Woodman (1993) argued that the gender of a generic name ending in *-otis* is feminine; he has been consistent in following that interpretation (e.g., Woodman, 1996, 2002, 2003b; Woodman and Timm 1993, 1999; Woodman and Díaz de Pascual 2004). Gardner (2005a), based on his understanding of Article 30.1.4.2 (ICZN 1999) and arguments presented by Pritchard (1994) and David and Gosselin (2002), determined that the gender of *Cryptotis* is masculine. Nevertheless, pending action by the International Commission on Zoological Nomenclature, Woodman herein treats *Cryptotis* as feminine.

KEY TO SOUTH AMERICAN SPECIES OF *CRYPTOTIS*:

1. Body size small, length of head and body (HB) 60–76 mm; pelage more-or-less uniformly dark with little contrast between dorsum and ventrum; manus not enlarged; foreclaws not elongate; length of tail (LT) long relative to length of head and body (LT/HB 34–57%); typically only three unicuspid visible in lateral view of upper toothrow; unicuspid typically large in lateral view, with straight or convex postero-ventral margins; anterior element of ectoloph of M1 approximately equal in size to posterior element; anterior border of coronoid process joins horizontal ramus of mandible at a high angle (*C. nigrescens*-group, Colombia) 2
- 1'. Body size small to large (HB 58–102 mm); pelage variable; manus broad and foreclaws usually long; tail may be short to long (LT/HB 28–60%); three or four unicuspid visible in lateral view of upper toothrow; unicuspid slender in lateral view, with concave to deeply concave postero-ventral margins; anterior element of ectoloph of M1 smaller than posterior element; anterior border of coronoid process joins horizontal ramus of mandible at a low angle. *C. thomasi*-group) 4
2. Foramen of tympanic process of petromastoid usually absent, or if present, minute; fourth unicuspid large, averaging 50% (36–64%) of surface area of third unicuspid; tail shorter, less than 1/2 the length of HB, and LT/HB averaging 39% (34–46%); HB averaging 69 mm (67–79 mm); occurs along or near Colombia's border with Panama *Cryptotis mera*
- 2'. Foramen on posterior or posteromedial edge of tympanic process of petromastoid conspicuously large; fourth unicuspid smaller, averaging 42.5% (32–61%) of surface area of third unicuspid; tail longer, LT/HB averaging 47% (36–57%) 3

3. Palate broad, breadth across molars (M2-M2) 6.0-6.4 mm; posterolingual cuspules on cingulae of anterior three unicuspid obvious; lower sigmoid notch of mandible typically shallow; entoconid of m3 absent; HB averaging 65 mm (60-76 mm); occurs in Colombia *Cryptotis colombiana*
- 3'. Palate narrower, breadth across molars (M2-M2) 5.7-5.9 mm; posterolingual cuspules of anterior three unicuspid minute; lower sigmoid notch of mandible variable, shallow to moderately deep; entoconid of m3 present but minute; occurs in Colombia *Cryptotis brachyonyx*
4. Length of tail less than 29 mm 5
- 4'. Length of tail more than 29 mm 7
5. Size large, HB averages 87 mm (74-96 mm); tail short, averaging 24 mm (20-27 mm); LT/HB averaging 29% (21-36%); dorsal pelage medium to dark brown; red pigment typically extends into hypoconal basin of M1 and M2; lower sigmoid notch shallow to very shallow; large, obvious foramen on posterior edge of tympanic process of petromastoid; fourth unicuspid large, averaging 50% of surface area of third unicuspid; known from Colombia *Cryptotis thomasi*
- 5'. Medium-size to large, HB averaging 75-80 mm (range 58-89 mm); tail moderately long, both absolutely (LT averaging 21-31 mm, range 21-38 mm) and relatively (LT/HB averaging 38-39%, range 26-54%); pelage color variable; red pigment typically absent from hypoconal basin of upper molars; lower sigmoid notch shallow to deep; typically a minute foramen on posterior edge of tympanic process of petromastoid; known from Ecuador 6
6. Head and body length averaging 80 mm (65-86 mm); dorsal pelage medium gray, appearing speckled; palate narrow relative to length-of-palate (M2-M2/PL averaging 63%, range 58-66%); fourth unicuspid large, averaging 51% of surface area of third unicuspid; coronoid process moderately high, averaging 66% (62-70%) of length of mandible; length of mandible behind m3 long, averaging 82% (77-87%) of length of mandible; lower sigmoid notch moderately deep to deep; minute entoconid occasionally present on m3; tail moderately long, both absolutely (LT averaging 31 mm, range 22-38 mm) and relatively (LT/HB averaging 38%, range 30-54%); known from southern Ecuador . . . *Cryptotis montivaga*
- 6'. Head and body length averaging 75 mm (58-89 mm); dorsal pelage dark chocolate brown; palate moderately broad (M2-M2/PL averaging 65%, range 58-69%); fourth unicuspid large, averaging 58% of surface area of third unicuspid; coronoid process low, averaging 63%, (range 58-69%) of length of mandible; length of mandible behind m3 moderately long, averaging 76% (range 71-82%) of total length of mandible; lower sigmoid notch shallow to moderately deep; entoconid absent from m3; tail moderately long, both absolutely (LT averages 29 mm, range 21-34 mm) and relatively (LT/HB averages 39%, range 26-50%); known from northern and central Ecuador *Cryptotis equatoris*
7. Fourth unicuspid typically reduced, averaging 19-29% (range 2-49%) of surface area of third unicuspid; body size large (HB averaging 84-88 mm, range 74-102 mm); medium-sized foramen normally visible on posterior edge of tympanic process of petromastoid; known from Colombia and Venezuela 8
- 7'. Fourth unicuspid typically large, averaging 40-58% (25-81%) of surface area of third unicuspid; body size small to large (HB averaging 68-85 mm, range 58-98 mm); foramen on posterior edge of tympanic process of petromastoid absent, minute, or huge, but not medium-sized; known from Colombia, Ecuador, and Peru 10
8. Fourth unicuspid extremely reduced, averaging 19% (2-37%) of surface area of third unicuspid, absent on one or both sides of cranium in approximately 25% of specimens; M3 simple; length of mandible behind m3 long, averaging 81% (74-87%); HB averaging 88 mm (76-102 mm); fourth unicuspid not visible in lateral view of skull; posterolingual cuspules typically absent in anterior three unicuspid; coronoid process high, averaging 70% (63-76%) of length of mandible; known from Venezuela *C. meridensis*
- 8'. Fourth unicuspid reduced, averaging 29% (12-49%) of surface area of third unicuspid; M3 complex or simple; length of mandible behind m3 moderate, averaging 77-78% (72-81%) of total length of mandible 9
9. Fourth unicuspid usually visible in lateral view of skull; posterolingual cuspules usually present on anterior three unicuspid; M3 simple or complex; coronoid process moderately high, averaging 65% (62-68%) relative to length of mandible; HB averaging 86 mm (80-91 mm); known from Colombia and Venezuela *Cryptotis tamensis*
- 9'. Fourth unicuspid usually not visible in lateral view of skull; posterolingual cuspules usually absent from anterior three unicuspid; M3 complex; coronoid process high, averaging 71% (65-77%) of length of mandible; HB averaging 84 mm (74-92 mm); known from Colombia *Cryptotis squamipes*
10. Size large (HB averaging 85 mm, range 77-98 mm); huge, obvious foramen on posterior edge of tympanic process of petromastoid; known from Colombia *Cryptotis medellinia*
- 10'. Size small to large (HB 58-89 mm); foramen on posterior edge of tympanic process small to absent 11

11. Medium-sized to large (HB averaging 75–80 mm, range 58–89 mm); M3 typically simple; entoconid usually absent on m3 6
- 11'. Size small (HB averaging 68 mm, range 63–73 mm); M3 complex; entoconid present on m3; known from Peru *Cryptotis peruiensis*

Cryptotis brachyonyx Woodman, 2003*Short-clawed Colombian Shrew*

SYNONYMS:

Blarina thomasi: Merriam, 1897b: 227; part.

[*Blarina (Cryptotis)*] *thomasi*: Trouessart, 1904:138; part; not *Blarina thomasi* Merriam.

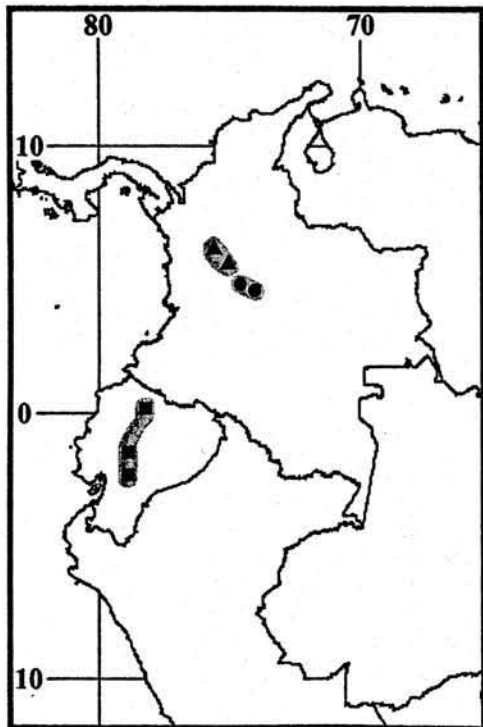
Cryptotis thomasi: O. Thomas, 1921f:354; part; not *Blarina thomasi* Merriam.

Cryptotis thomasi thomasi: Cabrera, 1958:48; part; not *Blarina thomasi* Merriam.

Cryptotis colombiana: Woodman, 1996:417; part; not *Cryptotis colombiana* Woodman and Timm, 1993.

Cryptotis brachyonyx Woodman, 2003b:855; type locality "Colombia: Department of Cundinamarca: 'La Selva, near Bogotá.'"

DISTRIBUTION: *Cryptotis brachyonyx* is known from the Cordillera Oriental in central and eastern departamento de Cundinamarca, Colombia, between 1,300 and 2,715 m elevation.



Map 82 Marginal localities for *Cryptotis brachyonyx* ●, *Cryptotis colombiana* ▲, and *Cryptotis equatoris* ■

MARGINAL LOCALITIES (Map 82; from Woodman 2003b): COLOMBIA: Cundinamarca: Plains of Bogotá; Cundinamarca, San Juan de Río seco.

SUBSPECIES: *Cryptotis brachyonyx* is monotypic.

NATURAL HISTORY: The habitat probably includes the Premontane Moist Forest, Premontane Wet Forest, Lower Montane Moist Forest, Montane Moist Forest, and/or Montane Wet Forest life zones on the Cordillera Oriental in central and eastern departamento de Cundinamarca, Colombia. Its life history is unknown.

Remarks: La Selva was the name of George O. Child's estate on the Plains of Bogotá, the elevation of which he estimated as approximately 8,900 ft. Woodman (2003b) allied *Cryptotis brachyonyx* with the *Cryptotis nigrescens*-group of Central American.

Cryptotis brachyonyx is sympatric with *Cryptotis thomasi*, and they share the same general type locality. However, all four known specimens of *C. brachyonyx* were collected prior to 1925. The overall scarcity of *C. brachyonyx* and its absence in later collections led Woodman (2003b) to suggest that the species is either extinct, or restricted to specific microhabitats that have not been adequately sampled.

Cryptotis colombiana Woodman and Timm, 1993
Colombian Shrew

SYNONYMS:

Cryptotis thomasi: Hershkovitz, 1969:18; part; not *Blarina thomasi* Merriam.

Cryptotis colombiana Woodman and Timm, 1993:24; type locality "Colombia; Central Cordillera; Antioquia Dept., Sonsón; 15 km E of Río Negrito; 1750 m"; here corrected to Río Negrito, 15 km E of Sonsón, Antioquia, Colombia.

DISTRIBUTION: *Cryptotis colombiana* is known from the central portions of the Cordillera Central and the Cordillera Oriental of Colombia between 1,750 and 2,150 m elevation.

MARGINAL LOCALITIES (Map 82): COLOMBIA: Antioquia, Vereda San Antonio de Prado (MUA 060); Antioquia, Finca Los Sauces (MUA 12001).

SUBSPECIES: *Cryptotis colombiana* is monotypic.

NATURAL HISTORY: The region of the Cordillera Central where *C. colombiana* has been found corresponds to the Lower Montane Wet Forest life zone. The original vegetation is cloud forest characterized by constant fog, high humidity, and a diverse assemblage of trees covered with epiphytes. Much of the area today includes agricultural fields, pastures, secondary successional brush and woodlands, and disturbed primary forest having a thick understory. Individuals have been captured in an overgrown cattle pasture surrounded by moss-covered rock outcroppings,

along the rocky bank of a small stream running through a grove of secondary-growth trees, and in minimally disturbed primary forest (C. A. Cuartas-Calle, *in litt.*). Remains of *C. colombiana* have been recovered from pellets of the Barn Owl (*Tyto alba*) and Tropical Screech-owl (*Otus choliba*) (C. A. Cuartas-Calle, *in litt.*).

REMARKS: Woodman and Timm (1993), Woodman (1996), and Woodman, Cuartas-Calle, and Delgado (2003) allied *Cryptotis colombiana* with the *Cryptotis nigrescens*-group of Central America.

Cryptotis equatoris (O. Thomas, 1912)

Ecuadorian Shrew

SYNONYMS:

Blarina equatoris O. Thomas, 1912c:409; type locality "Sinche, Guabanda [=Guaranda], 4000 m." Bolívar, Ecuador.

Blarina aequatoris: Lönnberg, 1921:4; incorrect subsequent spelling of *Blarina equatoris* O. Thomas.

Blarina osgoodi Stone, 1914:16, type locality "Hacienda Garzón, Mt. Pichincha, 10,500 ft. altitude," Pichincha, Ecuador.

[*Cryptotis*] *equatoris*: O. Thomas, 1921f:354; first use of current name combination.

C[*ryptotis*]. *osgoodi*: Tate, 1932:225; name combination.

Cryptotis thomasi equatoris: Cabrera, 1958:47; name combination.

Cryptotis e[*quatoris*]. *equatoris*: Vivar, Pacheco, and Valqui, 1997:6; name combination.

Cryptotis equatoris osgoodi: Vivar, Pacheco, and Valqui, 1997:7; name combination.

DISTRIBUTION: *Cryptotis equatoris* occurs in the Andes of central and northern Ecuador between 1,675 and 4,055 m elevation.

MARGINAL LOCALITIES (Map 82): ECUADOR: Pichincha (Pichincha-Imbabura border), Mojanda, western side (NHR A586313); Bolívar, Sinche (type locality of *Blarina equatoris* O. Thomas); Cañar, Chical (AMNH 62923).

SUBSPECIES: *C. equatoris* is monotypic.

NATURAL HISTORY: Very little is known about the natural history of *C. equatoris*. Chapman (1926) described the vegetation of the type locality as open, with a predominance of grasses, but with several forest patches. Given the broad elevational distribution of the species, it should occur in a variety of wet montane forest and páramo habitats.

REMARKS: The holotype and one other specimen of *C. equatoris* were collected by Perry O. Simons during his stay from 12 to 25 December 1898 at a locality given simply as "Sinche, Guaranda, 4000 m" (Chubb 1919). O. Thomas (1912c) mistakenly spelled Guaranda as "Guabanda." Sinche is not listed by USBGN (1987), and the name has been interpreted as referring to Sinchig (01°32'S, 78°59'W),

a village 10 km north of the town of Guaranda (Paynter, 1993). In November 1923, G. H. H. Tate spent time collecting at a "Hacienda Sinche" (ca. 01°32'55"S, 78°56'45"W; Instituto Geográfico Militar de Ecuador, Guaranda quadrangle, NIV-C3; 1:50,000), at 10,400 ft (= 3,170 m) elevation. Based on hand-drawn maps in Tate's original field notes deposited in the AMNH, Hacienda Sinche is north-east of Guaranda. On specimen labels, this locality is written simply as "Sinche," and it probably is the same locality where Simons collected.

Vivar, Pacheco, and Valqui (1997) described differences in size between samples of *C. equatoris* from near the type locality and from Cerro Pichincha near the type locality of *Blarina osgoodi*, and they recognized these populations as distinct subspecies. However, they failed to investigate intervening populations, and they relied upon unnecessarily small samples to justify their separation of these taxa. *Cryptotis equatoris* may eventually prove to be a complex comprising two or more species, but understanding the interrelationships of these populations will require a comprehensive review of the taxon throughout its geographic distribution.

Cryptotis medellinia O. Thomas, 1921

Medellín Shrew

SYNONYMS:

Cryptotis medellinius O. Thomas, 1921f:354; type locality "San Pedro, 30 km. north of Medellín," Antioquia, Colombia.

Cryptotis medellinus: Tate, 1932:224; incorrect subsequent spelling of *Cryptotis medellinius* O. Thomas.

Cryptotis thomasi medellinius: Cabrera, 1958:48; name combination.

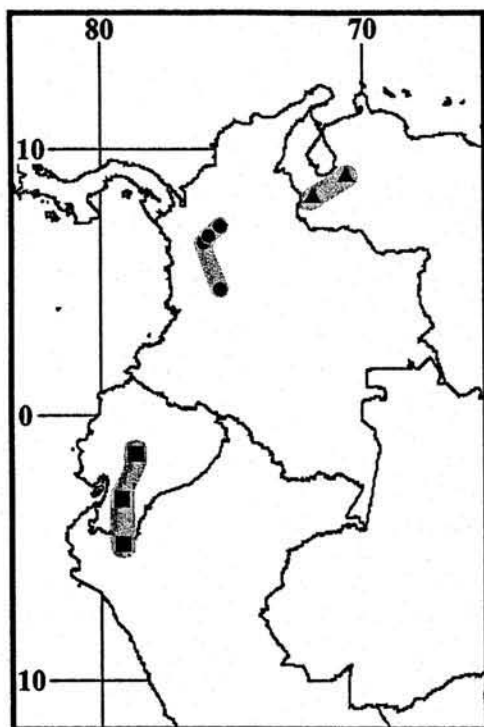
[*Cryptotis*] *medellinia*: Woodman, 1993:545; spelling changed to feminine gender.

DISTRIBUTION: *Cryptotis medellinia* is known from northern half of the Cordillera Central and the northern tip of the Cordillera Occidental of Colombia between 2,000 and 3,800 m elevation (Woodman 2002).

MARGINAL LOCALITIES (Map 83): COLOMBIA: Antioquia, Ventanas (FMNH 69812); Antioquia, Vereda Pajarito (MUA [field number CC 70]); Antioquia, Páramo Frontino (FMNH 71021). Risaralda, La Pastora (ICN, unnumbered).

SUBSPECIES: *Cryptotis medellinia* is monotypic.

NATURAL HISTORY: The distribution of *C. medellinia* may include Premontane Wet Forest, Lower Montane Wet Forest, Lower Montane Rain Forest, Montane Wet Forest (Cuartas and Muñoz 2000a, 2003b), and Montane Rain Forest life zones. Little is known of the natural history of *C. medellinia*. Specimens have been taken in a moss-lined runway in cut-over scrub vegetation, along a forest trail



Map 83 Marginal localities for *Cryptotis medellinia* ●, *Cryptotis meridensis* ▲, and *Cryptotis montivaga* ■

(J. L. Patton field notes, MVZ), in Andean forest at 2600 m, and an area reforested with *Alnus acuminata* at 3200 m (Sánchez and Alvear 2003). In addition, an individual was found dead in an area reforested with *Pinus* (Sánchez, Sánchez-Palomino, and Cadena 2004). Data on reproduction are scarce. A lactating female was taken in February, and one pregnant with 2 fetuses was captured in October (Sánchez and Alvear 2003). Remains of *C. medellinia* have been recovered from Barn Owl (*Tyto alba*) pellets (C. A. Cuartas-Calle, *in litt.*) and from scats of the crab-eating fox (*Cerdocyon thous*; Delgado 2002).

Cryptotis mera Goldman, 1912

Goldman's Shrew

SYNONYMS:

Cryptotis merus Goldman, 1912b:17; type locality "from head of Rio Limon (altitude 4,500 feet), Mount Pirri, eastern Panama."

Cryptotis mera: Hall and Kelson, 1959:61; gender agreement.

Cryptotis nigrescens mera: Handley, 1966: 756; name combination.

Cryptotis nigrescens nigrescens: Choate, 1970:279; part; not *Blarina nigrescens* J. A. Allen, 1895b.

DISTRIBUTION: *Cryptotis mera* is known only from Cerro Pirre (Serranía Pirre), and from Cerro Tacarcuna and

Cerro Malí (Serranía de Darién), between 1,370 and 1,525 m elevation (Woodman and Timm 1993). The border between Panama and Colombia passes through the Pirre and Darién highlands where this species has been taken; *C. mera* undoubtedly occurs in Colombia as well.

MARGINAL LOCALITIES: Currently known only from Panama near the border with Colombia; not mapped.

SUBSPECIES: *Cryptotis mera* is monotypic.

NATURAL HISTORY: Little is known of the natural history of *C. mera*. The two highland regions where this shrew has been found correspond to the Premontane Rain Forest and Lower Montane Rain Forest life zones (Tosi 1971). Goldman (1912b) described the Serranía de Pirre as a region of unbroken, dense cloud forest with abundant epiphytes and high annual rainfall.

REMARKS: Woodman and Timm (1993) recognized *C. mera* as a species distinct from *C. nigrescens*, but continued to ally it with the mostly Central American *Cryptotis nigrescens*-group.

Cryptotis meridensis (O. Thomas, 1898)

Mérida Shrew

SYNONYMS:

Blarina meridensis O. Thomas, 1898c:457; type locality "Merida, alt. 2165 m., Mérida, Venezuela; corrected to "Montes del Valle Merida 2165 m" by Woodman (2002) based on label information.

C[ryptotis]. meridensis: O. Thomas, 1921f:354; first use of current name combination.

Cryptotis thomasi meridensis: Cabrera, 1958:48; part; name combination.

Cryptotis thomasi thomasi: A. Díaz, Péfaur, and Durant 1997:293; part; not *Blarina thomasi* Merriam.

Cryptotis meridensis meridensis: Linares, 1998:106; part.

DISTRIBUTION: *Cryptotis meridensis* is found in the Cordillera de los Andes of Trujillo, Mérida, and eastern Táchira, Venezuela, between 1,640 and 3,950 m elevation (Woodman and Díaz de Pascual 2004).

MARGINAL LOCALITIES (Map 83): VENEZUELA: Trujillo, Río Motatán site E-II (Durant and Díaz 1995); Mérida: Páramo de Mariño (Durant, Díaz, and Díaz de Pascual 1994).

SUBSPECIES: *Cryptotis meridensis* is monotypic.

NATURAL HISTORY: *Cryptotis meridensis* has been studied more comprehensively than any other South American soricid, yet our knowledge of the ecology and habits of this species remains rudimentary. Woodman and Díaz de Pascual (2004) summarized the natural history of this species in their *Mammalian Species* account. The Mérida Shrew inhabits cloud forest and paramo environments and has been documented in Lower Montane Moist Forest, Lower Montane Rain Forest, Montane Wet Forest,

Montane Rain Forest, Subalpine Paramo, Subalpine Rain Páramo, and Lower Montane Wet Forest life zones (Handley 1976; Aagaard 1982; Durant, Díaz, and Díaz de Pascual 1994; Durant and Díaz 1995). At higher elevations at which it occurs, mean annual temperatures can be as low as 2°C, with extreme daily temperature fluctuations and daily frosts in the colder seasons. In other regions that it inhabits, mean annual temperatures can reach 17°C. The species is found primarily in relatively wet environments, with mean annual precipitation from 1,023 to greater than 2,000 mm (Azócar and Monasterio 1980; Durant and Péfaur 1984; Durant and Díaz 1995; A. Díaz, Péfaur, and Durant 1997). The Mérida Shrew may require a thick and extensive moss layer in páramo in which to construct runways, tunnels, and nests. In forested habitats, it uses runways in soil under litter, fallen logs, and rocks (Durant and Péfaur 1984; Durant, Díaz, and Díaz de Pascual 1994; Durant and Díaz 1995; A. Díaz, Péfaur, and Durant 1997). The nest of *C. meridensis* comprises an inner layer of grasses and sedges and an outer layer constructed from parts of frailejón (*Espeletia schultzii*) and romerillo (*Hypericum laricifolium*) (A. Díaz, Péfaur, and Durant 1997). The Mérida Shrews consumes a diversity of invertebrates that includes centipedes, earthworms, pill bugs, snails, spiders, and the larvae, pupae, and adults of a variety of insects. Soil-dwelling invertebrates dominate the diet, and earthworms were the most frequently encountered prey, suggesting that it forages more in the subsurface than on the soil surface (Díaz de Pascual and de Ascensão 2000). Other prey may include lizards, nestlings of rodents, and eggs and chicks of ground-nesting birds (A. Díaz et al. 1995), and individuals were observed opportunistically feeding on a rice rat (*Oryzomys meridensis*) and a trap-killed conspecific (Aagaard 1982; Woodman and Díaz de Pascual 2004). *Cryptotis meridensis* is preyed upon in turn by the opossums (*Didelphis pernigra*), weasels (*Mustela frenata*), and birds of prey, such as the Barn Owl (*Tyto alba*) (A. Díaz, Péfaur, and Durant 1997; Araujo and Molinari 2000). The Mérida Shrew can be relatively abundant in mammal communities in which it occurs. It is commonly one of the three most abundant small mammals in páramo and cloud forest environments in long-term studies using snap-traps, live-traps, or pitfall-traps (Aagaard 1982; A. Díaz et al. 1995; Durant and Díaz 1995; Díaz de Pascual 1993, 1994; Woodman and Díaz de Pascual 2004). As with other small mammals, population levels fluctuate seasonally and annually. Peaks in abundance may be timed in relation to local peaks in rainfall (Aagaard 1982; Durant and Díaz 1995; Woodman 2002; Woodman and Díaz de Pascual 2004). Reproduction occurs throughout the year. Pregnant or lactating females were captured at Monte Zerpa Cloud Forest in every month of the year, with the greatest proportion of pregnant females in April and the fewest in July

and December. The typical litter consists of 3 pups, with a known range of 2–4 pups (Woodman and Díaz de Pascual 2004).

REMARKS: Woodman (2002) noted that the skin label attached to the holotype of *Cryptotis meridensis* has “Montes del Valle Merida 2165 m” as the complete locality, rather than the abbreviated type locality reported by O. Thomas (1898c). Woodman (2002) recently recognized the population of *Cryptotis* from the Tamá highlands along the Venezuela-Colombia border as *C. tamensis*; thereby, restricting the name *C. meridensis* to the population inhabiting the Cordillera de Los Andes near Mérida. These actions leave in doubt the identities of populations of *Cryptotis* from El Junquito in the Coastal Highlands west of Caracas (Ojasti and Mondolfi 1968) and from the Sierra de Perijá (Guajira), Cordillera Oriental of Colombia (Duarte and Vilorio 1992), each of which is documented by a single skull (Woodman 2002). Collection and study of statistically significant samples of complete specimens of shrews from each locality (indicated by question marks in Map 83) will be required to determine the relationships of shrews comprising those two populations.

Durant and Péfaur (1984) commented on differences in pelage color and texture between *C. meridensis* from open paramo and closed cloud forest environments. Although Soriano, Utrera, and Sosa (1990) were unable to corroborate this variation, Woodman (2002) noted some differences in pelage among individuals representing different habitats, but stated that these differences were not diagnostic.

Cryptotis montivaga (H. E. Anthony, 1921)

Grizzled Ecuadorian Shrew

SYNONYMS:

Blarina montivaga H. E. Anthony, 1921a:5; type locality “Bestion, Prov. del Azuay,” Ecuador.

[*Cryptotis*] *montivaga*: Cabrera, 1925:134; first use of current name combination.

Cryptotis montivagus: Cabrera, 1958:47; name combination and incorrect gender concordance.

DISTRIBUTION: *Cryptotis montivaga* occurs in the provinces of Chimborazo, Azuay, and Loja, Ecuador, at elevations between 2,500 and 3,800 m.

MARGINAL LOCALITIES (Map 83): ECUADOR: Chimborazo, Urbina (AMNH 64623); Azuay, Bestion (type locality of *Blarina montivaga* H. E. Anthony); Loja, Podocarpus National Park (Barnett 1999).

SUBSPECIES: *Cryptotis montivaga* is monotypic.

NATURAL HISTORY: Barnett (1993, 1999) reported capturing 12 *C. montivaga*: 1 at 2,700 m in montane forest dominated by *Podocarpus* and *Ocotea*, 5 in quenoa (*Polylepis*) forest at 3,700–4,000 m, and 6 in streamside scrub at 3,450–4,000 m; none were taken in grassland

(paramo) habitats. Elevations recorded on skin labels of these specimens in the BMNH range from 3,300 to 3,800 m.

Reproductive data for *C. montivaga* are mostly lacking. Barnett (1999) reported a female pregnant with two embryos when captured in August. Two females, one captured in July and the other in August, were lactating. Analysis of stomach contents of five individuals revealed remains of beetles, spiders, caterpillars, and possibly arthropod larvae (Barnett 1993). Remains of *C. montivaga* have been recovered from owl pellets found in Podocarpus National Park (Barnett 1999).

Cryptotis peruviansis Vivar, Pacheco, and Valqui, 1997
Peruvian Shrew

SYNONYMS:

Cryptotis thomasi: Hutterer, 1993:109; part; not *Blarina thomasi* Merriam.

Cryptotis peruviansis Vivar, Pacheco, and Valqui, 1997:7; type locality "Peru, Department Cajamarca, Las Ashitas, 3150 m, about 42 km W of Jaén (05°42'S, 79°08'W)."

DISTRIBUTION: *Cryptotis peruviansis* is known from the departments of Cajamarca and Piura, Peru, between 2,050 and 3,150 m elevation (Vivar, Pacheco, and Valqui 1997).

MARGINAL LOCALITIES (Map 84; from Vivar,

Pacheco, and Valqui 1997): PERU: Piura, Machete, on Zapalache-Carmen trail; Cajamarca, Las Ashitas (type locality of *Cryptotis peruviansis* Vivar, Pacheco, and Valqui).

SUBSPECIES: *Cryptotis peruviansis* is monotypic.

NATURAL HISTORY: The habitat at the type locality, on the eastern slope of Cerro Chinguela in the Río Samaniego Valley, was described as cloud forest dominated by *Podocarpus*. The holotype was collected in elfin forest consisting of shrubby trees with abundant epiphytes and mosses, classified as representing the Tropical Montane Rain Forest life zone (Vivar, Pacheco, and Valqui 1997).

Cryptotis squamipes (J. A. Allen, 1912)
Cali Shrew

SYNONYMS:

Blarina (Cryptotis) squamipes J. A. Allen, 1912:93; type locality "crest of Western Andes (alt. 10,340 ft.), 40 miles west of Popayan, Cauca, Colombia."

[*Cryptotis*]. *squamipes*: Tate, 1932:225; first use of current name combination.

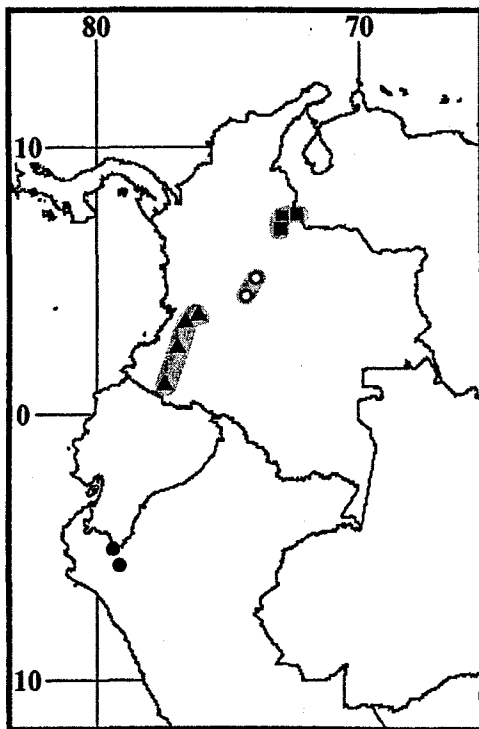
DISTRIBUTION: *Cryptotis squamipes* is known from the Cordillera del Sur of Colombia and the southern portions of the cordilleras Occidental and Central, at elevations from 1,500 to 3,375 m.

MARGINAL LOCALITIES (Map 84): COLOMBIA: Valle del Cauca, Tenerife (UV 7552); Valle del Cauca, Finca "Zingara" (UV 10143); Cauca, Cerro Munchique (FMNH 86716); Nariño, San Felipe (UV 11043)

SUBSPECIES: *Cryptotis squamipes*, as used herein, refers to a complex of at least three species that currently are under study.

NATURAL HISTORY: The holotype was collected in an area where "vegetation is scarce, scrubby and stunted" (Chapman 1917:32). The type locality is in Lower Montane Wet Forest (IGAC 1988), and the distribution of *C. squamipes* in the Cordillera Occidental probably corresponds closely to the distribution of this life zone.

REMARKS: A primary character that J. A. Allen (1912) used to distinguish *C. squamipes* was the scaliness of the feet, a feature also used by other authors to characterize this poorly known species. The feet of the holotype of *C. squamipes* have visible scales; however, the presence of obvious scales is not a diagnostic character. The upper surfaces of the feet of all species of *Cryptotis* are scaly, and the visibility of the scales depends to a large extent on the length and density of the over-laying hairs, characters that vary geographically in some species. The apparent scaliness of the feet also depends on the density and distribution of skin pigmentation, which vary among individual specimens and appear to be affected by type of preservation and subsequent exposure to light. In general, the feet of *C. thomasi* and *C. meridensis* tend to have more fur and less visible scales than



Map 84 Marginal localities for *Cryptotis peruviansis* ●, *Cryptotis squamipes* ▲, *Cryptotis tamensis* ■, and *Cryptotis thomasi* ○

do other species of Andean shrews. Among these and other Andean species, intraspecific variation in this character can equal, or exceed, interspecific variation. Moreover, the hind feet of the holotype of *C. squamipes* are aberrant and have abnormally developed claws. Malformation of the hind feet may have affected other morphological features of the feet as well, such as their hairiness, pigmentation, and apparent scaliness.

Cryptotis tamensis Woodman, 2002

Tamá Shrew

SYNONYMS:

Blarina meridensis: Osgood, 1912:62; not *Blarina meridensis* O. Thomas.

C[ryptotis]. meridensis: O. Thomas, 1921f:354; part; not *Blarina meridensis* O. Thomas.

Cryptotis thomasi meridensis: Cabrera, 1958:48; part; not *Blarina meridensis* O. Thomas.

Cryptotis meridensis meridensis: Linares, 1998:106; part; not *Blarina meridensis* O. Thomas.

Cryptotis tamensis Woodman, 2002:254; 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."

DISTRIBUTION: *Cryptotis tamensis* occurs in the Tamá highlands in western Táchira, Venezuela, and from southeastern Norte de Santander to northeastern Santander, Colombia, at elevations from 2,385 to 3,330 m.

MARGINAL LOCALITIES (Map 84; from Woodman 2002): VENEZUELA: Táchira, Buena Vista (type locality of *Cryptotis tamensis* Woodman). COLOMBIA: Santander, above Suratá; Santander, Finca El Rasgón.

SUBSPECIES: We treat *C. tamensis* as monotypic.

NATURAL HISTORY: The distribution of *C. tamensis* includes Lower Montane Wet Forest, Montane Wet Forest, and Montane Rain Forest life zones (Woodman 2002). In describing Páramo de Tamá, where he captured most of the known specimens of this species, Osgood (1912) noted that the term "páramo" regionally denoted the entire highlands, rather than being applied more specifically to the open, high-elevation vegetational formation. Grassland paramo is limited in this region, and most specimens of *C. tamensis* were taken in dense, epiphyte-rich cloud forest, although some were captured in agricultural pasture and disturbed cloud forest (Osgood 1912; Handley 1976). A lactating female and two gravid females, one with a single fetus, the second with two fetuses, were captured in March (Woodman 2002).

REMARKS: By recognizing the population of *Cryptotis* from the Tamá highlands as a distinct species and restricting the name *C. meridensis* to the population inhabiting the

Cordillera de Los Andes near Mérida, Woodman (2002) placed in doubt the identities of populations of *Cryptotis* in the coastal highlands west of Caracas (Ojasti and Mondolfi 1968) and from the Sierra de Perijá (Duarte and Vilorio 1992; also see Map 83). These populations will require additional study to determine their relationships.

Cryptotis thomasi (Merriam, 1897)

Thomas's Shrew

SYNONYMS:

Blarina thomasi Merriam, 1897b:227; type locality "Plains of Bogota, [Cundinamarca,] Colombia (on G. O. Childs estate near city of Bogota, alt. about 9000 ft.)."

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

Cryptotis thomasi: O. Thomas, 1921f:354; first use of current name combination.

Cryptotis avia G. M. Allen, 1923a:37; type locality "El Verjón, in the Andes east of Bogotá," Cundinamarca, Colombia.

Cryptotis avius Cabrera, 1958:46; incorrect gender concordance.

Cryptotis thomasi thomasi: Cabrera, 1958:48; name combination.

DISTRIBUTION: *Cryptotis thomasi* is known from the central portion of the Cordillera Oriental in Cundinamarca, Colombia, at elevations between 2,800 and 3,500 m (Woodman 2002).

MARGINAL LOCALITIES (Map 84): COLOMBIA: Cundinamarca, Represa de Neusa (ICN 9659); Cundinamarca, Páramo de Chisacá (ICN 5223).

SUBSPECIES: *Cryptotis thomasi* is monotypic.

NATURAL HISTORY: The distribution of *C. thomasi* may include Lower Montane Moist Forest, Lower Montane Wet Forest, Montane Wet Forest, Montane Rain Forest, and Lower Andean Páramo life zones. Much of the information on the natural history of *C. thomasi* comes from a short capture-recapture study of the small mammal community in Andean cloud forest and páramo at Carpanta Biological Reserve (López-Arevalo, Montenegro-Díaz, and Cadena 1993). The study site, between 3000 and 3100 m, had a unimodal rainy season with mean annual precipitation of more than 3000 mm. Mean annual temperature was 8.8°C, with daily temperatures that could fluctuate between 0° and 29°C. *Cryptotis thomasi* was the most abundant (greatest number of individuals captured) of the 11 species of small mammals taken at the site. Most captures of this species were in páramo. The largest numbers of *C. thomasi* were captured in June, suggesting an increase in abundance or activity during the period preceding the peak of the rainy season in June and July. Reproductively active

females were found in April, June, and August, and two pregnant females were documented in each of the months of July and August. Pregnant females typically carried two fetuses. Examination of stomach contents revealed primarily remains of adult insects (López-Arevalo, Montenegro-Díaz, and Cadena 1993).

REMARKS: Woodman (1996) demonstrated that *Cryptotis avia* G. M. Allen, 1923a, is a synonym of *Blarina thomasi* Merriam.

Order Chiroptera Blumenbach, 1779

Alfred L. Gardner

Chiroptera, the only true flying mammals, are distinguished by wings supported primarily by the elongated radius, and elongated metacarpals and phalanges of digits II through V. The digits are connected by the wing membrane, which consists of a double layer of skin. Flight membranes include the propatagium (antebrachium) between shoulder and digit I; the dactylopatagium connecting the metacarpals and phalanges; the plagiopatagium connecting the wing to the side of the body, or in a few species, to the dorsum; and the uropatagium (interfemoral membrane), which varies between taxa from absent to extensive and extending well beyond the feet. Other adaptations for flight include lightening of the skull and post-cranial skeleton; reduction of the ulna; modifications of the shoulder girdle; thickening or fusion of thoracic vertebrae, ribs, and sternal elements; development of a keel on the sternum; and, in some taxa, fusion of anterior lumbar vertebrae and fusion of seventh cervical vertebra with the first thoracic. Modifications of the pelvic girdle appear to be related to pendant roosting posture and for maneuverability both in flight and when active on a substrate or at the roosting site. Development and specializations of the hind limbs, feet, and tail appear to be adaptations facilitating specific flight characteristics, the gathering of food, and the use of specific roosting sites (e.g., species of two families have suction disks on their thumbs and feet, permitting them to adhere to smooth surfaces). Living bats are represented by two suborders, the Megachiroptera and the Microchiroptera. Only microchiropterans occur in South American.

KEY TO THE FAMILIES OF SOUTH AMERICAN CHIROP- TERA:

1. Facial appendages (noseleaf, dermal outgrowths, flaps of skin on face or lips) 2
- 1'. No facial appendages. 3
2. Noseleaf present (main "spear" of noseleaf missing in the Desmodontinae), may be reduced to a hood-like dermal

outgrowth above the eyes in *Sphaeronycteris*, or a series of skin flaps on face in *Centurio* (these taxa lack a tail and have only a rudimentary uropatagium)

- Phyllostomidae
- 2'. No noseleaf or dermal outgrowths on face; lower lip with accessory skin folds and flaps; well-developed uropatagium and tail always present
- Mormoopidae
3. Either a series of tufts of pale fur on forearms, or pocket-like glands on propatagia or center of uropatagium; postorbital processes present (fused with margins of rostral shield in *Diclidurus*); palatal branch of premaxilla reduced (incomplete anterior palate); premaxillae movable, not fused to maxillae. Emballonuridae
- 3'. No tufts on forearms; no pocket-like glands on propatagia or on uropatagium; no postorbital processes; palatal branch of premaxilla may or may not be reduced; premaxillae fused to maxillae. 4
4. Upper lip full, smooth, and split by a cleft or deep fold in the midline below rhinarium; pinnae long, narrow, and pointed; wing membrane attaches to leg above ankle; feet and claws may be greatly elongated; tail half or less the length of uropatagium; anterior palate complete Noctilionidae
- 4'. No medial cleft dividing upper lip; pinnae not notably narrow and pointed; wing membrane attaches at ankle or along foot; feet not elongated; tail usually as long as or much longer than uropatagium 5
5. Each thumb and foot bears a round or oval-shaped disc (suction cup); tragus triangular; anterior palate complete (palatal branches of maxillae fused) . . . Thyropteridae
- 5'. No discs on thumb or foot; tragus of various form, but not triangular; anterior palate may be complete or incomplete 6
6. Thumb short, rudimentary, and, except for claw, entirely enclosed in propatagium. Furipteridae
- 6'. Thumb normal, not enclosed in propatagium. 7
7. Second digit consists only of metacarpal (phalanx lacking); tail as long as or longer than head and body, and except for tip, enclosed entirely in uropatagium
- Natalidae
- 7'. Second digit has rudimentary phalanx; tail as long as or considerably longer than uropatagium, but not longer than head and body. 8
8. Pinna of various shapes and sizes, may be very large, basal lobe present; tragus conspicuous, comparatively long, well developed, and its tip rounded or pointed
- Vespertilionidae
- 8'. Pinna wide, usually extending forward over eyes, lacking basal lobe; tragus small, truncated, and inconspicuous Molossidae