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The shrews (*Cryptotis*) of Colombia: What do we know about them?

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In Colombia, shrews (*Cryptotis*) are represented by seven species associated with Andean, high Andean, and Paramo ecosystems of the three national Cordilleras. Of these species, five are endemic to the Andean region of the country. Despite representing the group of mammals with the highest rate of endemic species, the knowledge currently available on aspects such as natural history, distribution, and ecology is limited. This work assesses the current state of knowledge of the shrews of Colombia, discusses taxonomic issues, risks and threats related to conservation, and identifies research needs and priorities. We compile the information on shrews of Colombia available in the literature and databases. We include two of the known species of the country and one to be determined within a phylogenetic context. In general, the knowledge of the shrews of Colombia reveals the lack of ecological and genetic studies. There are unsolved taxonomic questions about the presence of certain species in the different mountain ranges of the country. There is an urgent need to generate molecular information to clarify the richness of the genus in Colombia which, according to our observations, has been underestimated. The knowledge about the shrews of Colombia is still scarce, even when some species were first described more than a hundred years ago. The need to conduct systematic studies and comprehensive morphological descriptions to clarify the richness of the shrews of Colombia is highlighted.

En Colombia, las musarañas (*Cryptotis*), están representadas por siete especies asociadas a ecosistemas andinos, altoandinos y paramunos de las tres cordilleras nacionales. De estas especies, cinco son endémicas de la región andina del país. A pesar de representar el grupo de mamíferos con mayor porcentaje de especies endémicas, el conocimiento que tenemos sobre aspectos como historia natural, distribución y ecología, es casi nulo. Este trabajo evalúa el estado actual de conocimiento de las musarañas de Colombia, discute problemas taxonómicos, riesgos y amenazas para su conservación e identifica necesidades y prioridades de investigación. Compilamos la información disponible en literatura y bases de datos sobre las musarañas de Colombia. Ubicamos a 2 de las especies conocidas en el país y una por determinar en un contexto filogenético. La tendencia general en el conocimiento de las musarañas de Colombia es hacia la ausencia de estudios ecológicos y genéticos. Además, aún persisten dudas taxonómicas con respecto a la presencia de ciertas especies en las diferentes cordilleras del país. Existe una necesidad urgente de generar información molecular para clarificar la riqueza real del género en Colombia que, de acuerdo con nuestras observaciones, ha sido subestimada. El conocimiento sobre las musarañas de Colombia es aún precario, a pesar de que algunas especies fueron descritas hace más de cien años. Se resalta la necesidad de generar estudios sistemáticos y de profundizar en descripciones morfológicas más completas que permitan clarificar la riqueza de musarañas presentes en Colombia.

Key words: Andes; distribution; endemism; Eulipotyphla; Soricidae; taxonomy.

Introduction

South American shrews (Eulipotyphla: Soricidae: *Cryptotis*) represent an adaptive radiation of small mammals that live in mountain ecosystems, displaying the highest richness in northern South America (Woodman and Péfaur 2008). In Colombia, a country located in the northwest of South America, seven species are currently recognized (*Cryptotis brachyonyx*, *C. colombianus*, *C. medellinius*, *C. perijensis*, *C. squamipes*, *C. tamensis*, and *C. thomasi*), five of which are endemic to different sectors of the Andean region of the country (Woodman and Péfaur 2008; Solari *et al.* 2013; Ramírez-Chaves *et al.* 2016). The number of species registered in Colombia has nearly doubled over the past 30 years (by 1986, three confirmed species had been recorded and another one was considered as likely present; Cuervo Diaz *et al.* 1986), and the number of endemic species has almost tripled (by the year 2000, only two species were considered endemic, *C. colombianus* and *C. squamipes* out of a total of four recorded and one likely present species; Alberico *et al.* 2000).

In addition to the seven species recorded in the country, the likely presence of *C. mera* in Colombia has been suggested (Cuervo Diaz *et al.* 1986: as *Cryptotis nigrescens*) given its proximity to the records from Darien in Panama (Alberico *et al.* 2000; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008). Another species whose

presence has been suggested in Colombia is *C. equatoris*, which may be found in the Andes in southwest Colombia, department of Nariño, near Ecuador (Ramírez-Chaves and Noguera-Urbano 2011). However, records confirming its presence with respect to the current taxonomic proposals have not been validated yet; therefore, this species has been excluded from the recent lists of mammals of Colombia. Separately, it has been mentioned that *C. squamipes* may be a complex of at least three species restricted to Colombia (Woodman and Péfaur 2008). These facts indicate that the richness of *Cryptotis* in Colombia may have been underestimated.

The conservation status of shrews in Colombia has been evaluated from a global perspective; no regional assessments are currently available, despite the fact that at least five species are endemic to the country. The potential threats that shrews currently face are diverse, especially considering that these mammals are associated with the Andean region — one of the areas with the highest alteration rates by deforestation (70 to 93 % of the original area), with high concentrations of human settlements (Cavelier and Etter 1995; Rangel 2000) and a high susceptibility to climate change. In addition, this area supports the highest concentrations of human settlements in Colombia (Armenteras *et al.* 2003).

At a country level, none of the shrews is listed as a threatened species (MADS 2014; 2017). However, *C. brachyonyx* (listed globally as Data Deficient DD; Woodman 2008a) is considered as probably extinct or restricted to microhabitats inadequately sampled (Woodman and Péfaur 2008) since it has only been recorded in two localities (Woodman, 2003; 2008a).

In Colombia, the genus *Cryptotis* represents an important target group for research at various scales, given its large number of endemism and current threats. For this reason, this work aims to set the grounds for further studies in Colombia. To this end, this paper reviews, for each species recorded in the country, the current state of knowledge, distribution, risks and threats related to conservation, and research needs and priorities.

Materials and Methods

State of knowledge. We gathered the published literature available (articles, chapters in books, proceedings, and thesis) including information on the shrews of Colombia since the description of the first species in 1897 to 2018. This information was organized according to the following categories: a) Type of publication (journal articles, conference proceedings, book chapter, book, thesis). b) Relevance for the study (general, specific). c) Overview (summary papers with no new information). d) Research topics: I) Anatomy and Morphology. II) Taxonomy and Systematics. III) Biogeography, Current Distribution, and Records (we only considered lists of species that included data not previously available in other publications). IV) Threats and Relationship with Humans / Conservation (threats, conservation, cultural aspects). V) Ecology and Natural History (abundance, behavior, predation, diet, reproduction, habitat use). VI) Genetics. The keywords used in searches under different combinations included: Colombia + *Blarina*, *Cryptotis*, *avia, avius, brachyonyx*, *colombiana*, *colombianus*, *medellinia*, *medellinius*, *perijensis*, *squamipes*, *tamensis*, *thomasi.* We report the available information for each species according to the topics searched.

Research Needs and Priorities. To define research priorities, we calculated the "research effort" (adapted from Andrade-Ponce *et al.* 2016) by assigning a score based on the number of topics investigated for each species (Categories I to VI based on the current state of knowledge). The maximum score in this category was 60, which is the sum of each topic in the literature that obtained a score of 10 if a species had at least 10 studies for that topic. If the species had less than 10 studies, the score of each topic was calculated as the sum of the number of studies for that species. Thus, species with no published information for a given topic were scored as zero for that topic, while species with information in at least one publication for the six topics obtained a score of 6. Low research effort scores (<30) or <5 for each individual topic point to high research needs.

Distribution. We searched different sources of information to derive an approximation of the areas of distribution of shrews in Colombia. These included the Information System on Colombian Biodiversity, an initiative that provides open access on the biodiversity of Colombia (SiB Colombia; https://sibcolombia.net/el-sib-colombia) and the Global Biodiversity Information Facility database (GBIF; http://www.gbif.org). The search considered the genus, specific name of the species, and Colombia (GBIF 2018; https://www.gbif.org/occurrence/search?q=Cryptotis&country=CO; doi 10.15468/dl.hjv2ad). We also reviewed the records available in Woodman and Péfaur (2008) and the distribution maps published in the Red List of the International Union for the Conservation of Nature (IUCN 2018; https://www.iucnredlist.org). These were used to construct a map of species richness by overlaying the distribution areas of each species. All the geographic analyzes were conducted using the "raster" and "sp" packages (Hijmans 2018) (Pebesma and Bivand 2005) in R (R Development Core Team 2018) and ArcMap (ESRI 2016).

Molecular Characterization of Some Species and their Phylogenetic Relationships. No genetic information is currently available for the Colombian species of *Cryptotis.* Hence, the Cytochrome b (*Cytb*) mitochondrial marker was characterized for some species; it has been used repeatedly in studies addressing systematics, taxonomy, and phylogeography (Guevara and Cervantes 2014; Moreno-Cárdenas 2017; Zeballos *et al.* 2018). Tissues were obtained from three specimens from different localities throughout the country. The first corresponds to *C. thomasi*, collected in the department of Cundinamarca and deposited in the Collection of Mammals of Instituto de Ciencias Naturales (ICN) under collector

number YMS 31 (no catalogued). The second, identified as *C. squamipes,* was collected in the municipality of El Tambo, department of Cauca, and deposited in the Collection of Mammals of the Museum of Natural History at Universidad del Cauca (MHNUC 1572). The third was collected as part of the Santander BIO Project in the municipality of Santa Bárbara, department of Santander, and deposited in the Collection of Mammals of the Museum of Natural History at Universidad Industrial de Santander (UIS-MZ 1594). The taxonomic identity of the third specimen (UIS-MZ 1594) is uncertain, as it does not display all the morphological traits of the species recorded in the area (*C. tamensis, C. meridensis*), so that this work refers to it as *Cryptotis* sp.

Genomic DNA was extracted from approximately 25 mg of tissue (preserved in 96 % ethanol), using the "GeneJet Genomic DNA Purification Kit" (Thermo-Scientific), following the manufacturer's specifications. Cytochrome B (1,140 bp) was amplified with primers MVZ05 (5'-CGA AGC TTG ATA TGA AAA ACC ATC GTT G; Smith and Patton 1993) and H15915 (5'-AAC TGC AGT CAT CTC CGG TTT ACA AGA C; Irwin *et al.* 1991), as per the protocols described in the work of Guevara and Cervantes (2014). PCR reactions were carried out in a Multigene TC9600-G Thermal Cycler (Labnet International, Inc.). The success and quality of PCR reactions were confirmed by viewing the products in 0.8 % agarose gels using the EZ-VISION fluorescent agent (AMRESCO, Inc.). Those amplified fragments with the highest intensity and the expected band size were sent to the "Sequencing and Molecular Analysis Service" (SSiGMol) at Universidad Nacional de Colombia. These were purified and sequenced in a 3500 ABI sequencer (Applied Biosystems). The inspection of electropherograms, as well as the edition, and assemblage of consensus from the sequences received (forward and reverse) were carried out with Geneious R11 (Biomatters Limited). To confirm that the material generated represents endogenous DNA of shrews, all consensuses were subjected to comparisons with the BLAST algorithm (Altshul 1990). Consensus sequences were submitted to GenBank under accession numbers MK681774 (*Cryptotis* sp), MK681775 (*C. thomasi*), and MK681776 (*C. squamipes*).

The *Cytb* sequences for all *Cryptotis* species available in the GenBank public repository were downloaded, as well as those of external groups used by Guevara and Cervantes (2014) in their analysis (Appendix 1). These sequences were aligned, along with those produced in the present work, using the MUSCLE 3.8.425 (Edgar 2004) algorithm implemented in Geneious R11. The nucleotide evolution model was determined through the best fit to the final matrix using the Akaike Information Criterion (AIC) in the program jModelTest 2.1.10 (Darriba *et al.* 2012).

A Bayesian inference analysis was run in MrBayes 3.2.6 (Ronquist *et al.* 2012). To ensure the convergence of topologies, two runs were conducted in parallel, each with four Markov chains that started from trees generated at random and were maintained over 15,000,000 generations, with parameters sampled at 1000-generation intervals. The stationary phase and convergence were monitored in the Tracer program version 1.6 (Rambaut *et al.* 2014). Twenty-five percent of sampling points prior to the asymptote were discarded (burn-in), and the remaining trees (11,250) were pooled to calculate the *a posteriori* probability of clades in a consensus tree. A node was deemed as having significant support when its *a posteriori* probability was greater than 0.95 (Gutierrez *et al.* 2017).

Uncorrected average genetic distances (p) and the distances corrected according to the Kimura-2-parameter model (K2P; Kimura 1980) were estimated from the complete matrix of sequences in MEGA version 7.0 (Kumar *et al.* 2015). The values obtained were compared with those reported for the genus *Cryptotis* by Guevara and Cervantes (2014) and Zeballos *et al.* (2018).

Results

State of Knowledge, Research Needs, and Priorities. We found 50 studies on the seven *Cryptotis* species in Colombia. Of these, 72 % were scientific articles; 10 %, books and book chapters; 6 %, degree dissertations and thesis; and 12 %, electronic documents and conference abstracts. The species with the highest number of studies was *Cryptotis colombianus* (n = 16) and the least studied was *C. perijensis* (n = 3). The topics most frequently addressed refer to taxonomy and distribution records (Table 1).

The information reviewed indicates uncertainty regarding taxonomic and geographic information related to records of shrews of Colombia available in databases. The search in SiB Colombia showed 191 records in total (Table 2), with 122 corresponding to five species (*C. colombianus*, *C. medellinius*, *C. meridensis*, *C. squamipes*, and *C. thomasi*) distributed in Colombia. A total of 56 questionable records were found, representing specimens identified to genus. Seven support the presence of *C. meridensis* (species distributed in Venezuela) and six that have retained the name *C. avia,* currently considered as a synonym of *C. thomasi* (Woodman and Péfaur 2008).

GBIF produced 193 records concentrated in the north of the Central and Western Cordilleras (Antioquia and Cundinamarca; Figure 1). The best represented species was *C. thomasi* (n = 147), while two species have no available records in this

Table 1. Research effort on shrews (*Cryptotis*) of Colombia. The highest possible research effort score is 60. I) Anatomy and Morphology; II) Taxonomy and Systematics; III) Biogeography, Distribution, and Records; IV) Threats and Relationships with Humans / Conservation; V) Ecology and Natural History; VI) Genetics.

Species	Number of publications by topic						Effort
	I	II	III	IV	V	VI	
Cryptotis brachyonyx	2	2	2	3	1	0	10
Cryptotis colombianus	6	5	12	2	5	0	28
Cryptotis medellinius	5	4	7	4	7	0	27
Cryptotis perijensis	1	1	1	0	0	0	3
Cryptotis squamipes	3	3	7	3	2	0	18
Cryptotis tamensis	4	4	5	2	3	0	18
Cryptotis thomasi	8	6	10	1	3	0	25

Table 2. Geographic information available for shrews of the genus *Cryptotis* of Colombia from different sources.

Species	Woodman and Péfaur (2008)	SiB Colombia 2018	GBIF 2018	IUCN 2018
Cryptotis brachyonyx	2	0	0	1
Cryptotis colombianus	2	22	16	1
Cryptotis medellinius	4	7	6	1
Cryptotis perijensis	0	0	0	0
Cryptotis squamipes	4	14	12	1
Cryptotis tamensis	3	0	12	1
Cryptotis thomasi	2	79	147	1

database (*C. brachyonyx* and *C. perijensis*). The information proposed by Woodman and Péfaur (2008) indicated that the best represented species are *C. squamipes* and *C. medellinius,* with four records each. As regards the geographic information available on the IUCN website, six species of shrews are reported for Colombia, except for *C. perijensis*. There are only two localities reported for *C. perijensis*, from which a buffer was drawn around each locality using the disperal distance for a species in the same genus (*C. parvus*, radius 280 m; Choate and Fleharty 1973). The exploratory analysis of overlapping areas of distribution of shrews showed the probable existence of two areas with sympatric shrews. One is located between Medellín and Manizales, on the Western and Central Cordilleras (*C. colombianus* and *C. medellinius*); the second, in the north-eastern hills of Bogotá (*C. thomasi* and *C. brachyonyx*, Figure 2). Some species of shrews could

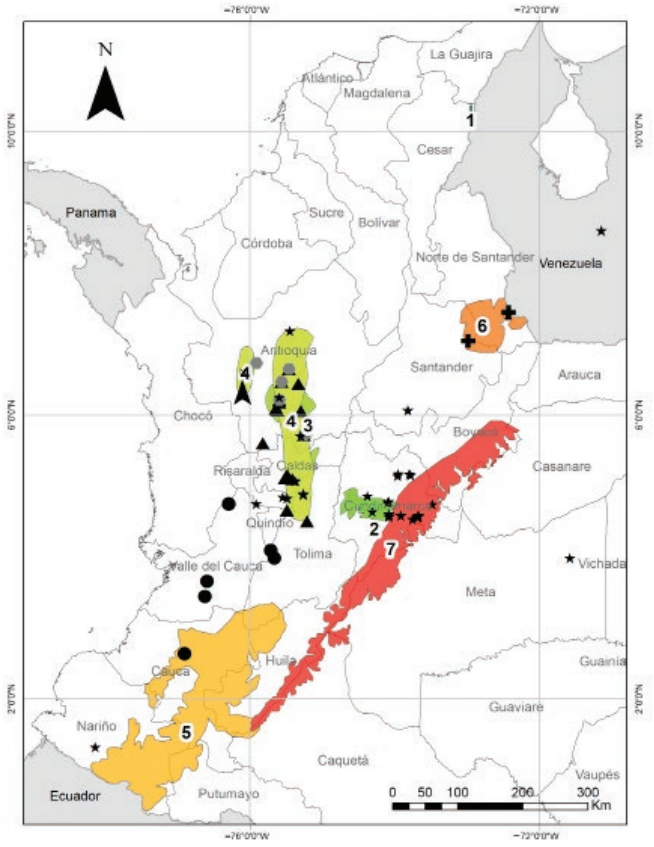

Figure 1. Geographic distribution of shrews in Colombia from IUCN maps (numbers) and GBIF available records (symbols). 1) *C. perijensis* (no GBIF records). 2) *C. brachyonyx* (no GBIF records). 3) *C. colombianus* (triangle). 4) *C. medellinius* (grey hexagon). 5) *C. squamipes* (circle). 6) *C. tamensis* (cross). 7) *C. thomasi* (star).

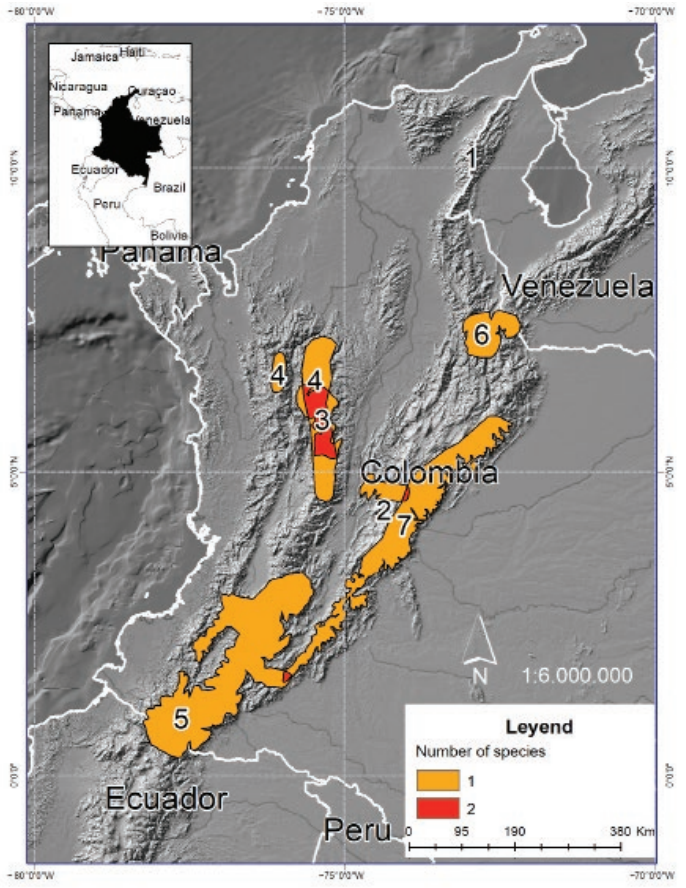

Figure 2. Overlapping areas of distribution of the shrews of Colombia based on the distributions proposed by IUCN (2018). The areas of sympatry of two species are marked in red. Numbers indicate the names of species: 1) *C. perijensis*. 2) *C. brachyonyx*. 3) *C. colombianus*. 4) *C. medellinius*. 5) *C. squamipes*. 6) *C. tamensis*. 7) *C. thomasi*.

be represented in at least ten conservation areas (Figure 3). The state of knowledge and distribution of the species studied are summarized below.

Cryptotis brachyonyx. It is known from four records obtained throughout more than a century. The latest was obtained in 1925. Although these specimens were initially assigned to *C. colombianus* (Woodman and Timm, 1993), distributed as two isolated populations in the Central and Eastern cordilleras of Colombia, the reassessment by Woodman (2003) assigned the population of the Eastern Cordillera to *C. brachyonyx,* and those living in the Central Cordillera to *C. colombianus.* The description was based on the combined analysis of cranial characters, axial skeleton, and external characters. The characters described assign this species within the *"nigrescens"* group, which also includes *C. colombianus*. The rest of the Colombian shrews belong to the "*thomasi*" group (Table 3). *C. brachyonyx* is known only from its original publication (Woodman, 2003) and two additional documents mentioning aspects on its conservation status (Woodman 2008a; Woodman and Péfaur 2008), anatomy, and ecology. *C. brachyonyx* has a very low research effort, thus having the highest need for research of all species of shrews that are endemic to Colombia (Table 1).

Distribution: Endemic to Colombia. It is known only from two localities in the department of Cundinamarca,

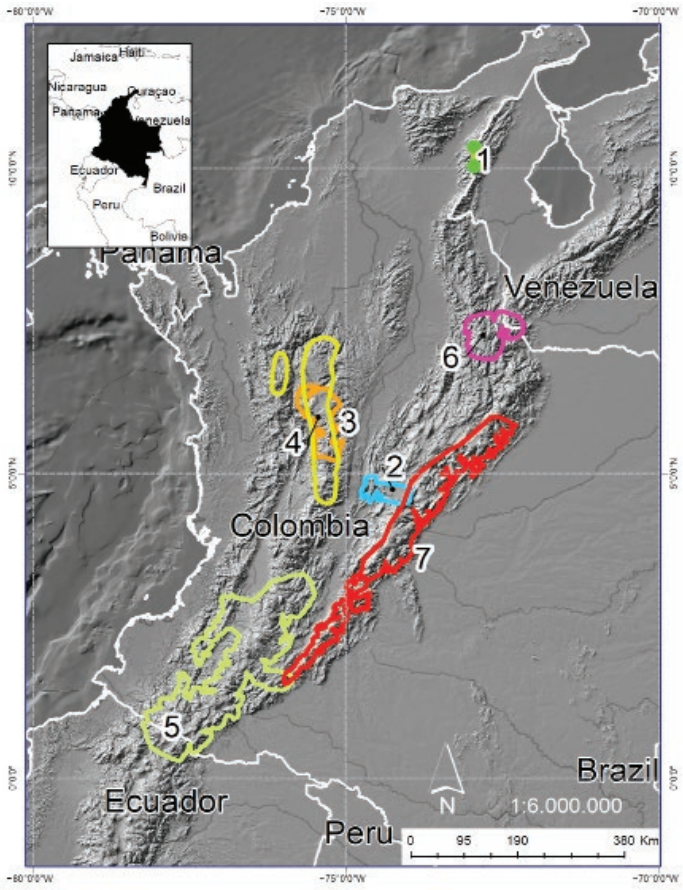

Figure 3. Overlay of the areas of distribution of shrews on conservation areas in Colombia. Numbers indicate the names of species: 1) *C. perijensis*. 2) *C. brachyonyx*. 3) *C. colombianus*. 4) *C. medellinius*. 5) *C. squamipes*. 6) *C. tamensis*. 7) *C. thomasi*.

Eastern Cordillera, within an elevational range of 1,300 to 2,715 masl. A specimen from San Juan de Rio Seco was previously reported as *Cryptotis colombianus* (Woodman 1996; Woodman, 2003).

Conservation status: It is listed as Data Deficient at global level (Woodman 2008a).

Cryptotis colombianus was described from a single specimen collected in the Negrito river, Sonsón, Antioquia; there are studies on its anatomy (6 studies; Woodman and Timm, 1993; Woodman 1996; Woodman, 2003; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008; Marín Cardona 2009), taxonomy and nomenclature (5; Woodman and Timm, 1993; Vivar *et al.* 1997; Woodman *et al.* 2003; Woodman and Péfaur 2008; Marín Cardona 2009), biogeography and current distribution (12; Woodman and Timm, 1993; Woodman 1996; Woodman *et al.* 2003; Cuartas-Calle and Muñoz Arango 2003; Castaño *et al.* 2003; Woodman and Péfaur 2008; Marín Cardona 2009; Castaño 2012; Escobar-Lasso *et al.* 2013; Solari *et al.* 2013; 2015; Noguera-Urbano and Escalante 2015; Castaño *et al.* 2017), threats and conservation (2; Díaz-Pulido *et al.* 2015; Woodman 2017), ecology and natural history (5; Woodman *et al.* 2003; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008; Marín Cardona 2009; Solari *et al.* 2015). It shows a moderate research effort (Table 1).

Distribution: Endemic to Colombia. It is known from the Central Cordillera in the departments of Antioquia, Caldas, and Risaralda, in an elevational range between 1,750 and 2,150 masl (Woodman and Timm, 1993; Woodman *et al.* 2003; Cuartas-Calle and Muñoz Arango 2003; Castaño 2012; Escobar-Lasso *et al.* 2013; Solari *et al.* 2015; Castaño *et al.* 2017). A specimen from San Juan de Rioseco (Cundinamarca), in the Eastern Cordillera previously reported as *Cryptotis colombianus* corresponds to *C. brachyonyx* (Woodman 1996; Woodman, 2003).

Conservation status: It is listed as Least Concern (Woodman 2008b; 2017). It has been listed as threatened in the country (Díaz-Pulido *et al.* 2015); however, it requires new assessments.

Cryptotis medellinius. It was described based on specimens collected in the northern part of the municipality of Medellín (San Pedro), Colombia (Thomas, 1921). Its description was based on specimens acquired by the British Museum from an exchange with Brother Nicéforo María. According to the original description, the type locality of *C. medellinius* is the municipality of San Pedro, 30 km north of Medellín (Thomas, 1921). Similar to all shrews of Colom-

Table 3. General morphological characters by group of *Cryptotis* species of Colombia.

Species	Group	Endemism	Date	
			Collection	Description
Cryptotis brachyonyx	*C. nigrescens*	Yes	1895	2003
Cryptotis colombianus	The species in this group are considered as having higher mobility capabilities based on the structure of the humerus, which is less complex and robust, relative to other more fossorial species. (Woodman and Timm 1993; Woodman et al., 2003). In general, these shrews have small body and forefoot, although with a proportionally longer tail. These prefer low to medium altitudinal ranges, although it has not been confirmed for the Colombian species of this group.	Yes	1950	1993
Cryptotis medellinius	*C. thomasi*	Yes	1920	1921
Cryptotis perijensis	These are the largest South American shrews, although with proportionately shorter tail. The forelimbs have a more robust general pattern including a more complex humerus and forefoot with wider claws, interpreted as an adaptation to a more fossorial habit (Woodman and Gaffney 2014). These are considered as shrews inhabiting higher elevations.	No	1989	2015
Cryptotis squamipes		Yes	1911	1912
Cryptotis tamensis		No	1968	2002
Cryptotis thomasi		Yes	1895	1897

bia, the description of *C. medellinius* was based on the morphological analysis of cranial, dental, and external characters (Thomas, 1921). These allocate it within the "*thomasi*" group; it is larger compared to *C. brachyonyx* and *C. colombianus*.

There are studies on its anatomy and morphology (5 studies; Thomas, 1921; Woodman 2002; Cuartas-Calle and Muñoz Arango 2003; Woodman *et al.* 2003; Woodman and Péfaur 2008), taxonomy and systematics (4; Thomas, 1921; Vivar *et al.* 1997; Woodman *et al.* 2003; Woodman and Péfaur 2008), biogeography and current distribution (7; Tate 1932; Sanchez 2000, as *C. colombiana*; Sánchez and Alvear 2003; Woodman 2002; Woodman *et al.* 2003; Woodman and Péfaur 2008; Delgado-V 2009; Noguera-Urbano and Escalante 2015), and statements on its ecology and natural history (7; Sanchez 2000, as *C. colombiana*; Woodman 2002; Sánchez and Alvear 2003; Delgado-V 2002; Cuartas-Calle and Muñoz Arango 2003; Woodman *et al.* 2003; Woodman and Péfaur 2008). It shows a moderate research effort (Table 1).

Distribution: Endemic to Colombia. It is known from the northern part of the Central and Western Cordilleras of Colombia within an elevational range between 1,800 and 3,800 m, in the departments of Antioquia, Caldas, and Risaralda. The southern limit of distribution in each mountain range is uncertain, no specimen has been reported in the southern part of Paso de Quindío in the Central Cordillera nor in the southern part of Páramo de Frontino in the Western Cordillera (Vivar *et al.* 1997; Woodman 2002; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008; Delgado-V 2009). This species inhabits Premontane Moist Forest, Low Montane Forest, Montane Forest; and Low Montane and Montane Rainforest (Cuartas-Calle and Muñoz Arango 2003).

Conservation status: It is currently listed as Least Concern (Naylor and Roach 2016a). Its vulnerability risk is similar to that of *C. colombianus* and *C. squamipes* (Díaz-Pulido *et al.* 2015). It was previously listed as Data Deficient (Cuartas-Calle and Muñoz Arango 2003).

Cryptotis perijensis. It was described based on a specimen collected in 1989 in the department of Cesar, near Finca El Suspiro, at 2,100 m a.s.l. in northern Colombia (Duarte and Viloria 1992). Since it was described less than four years ago, the knowledge about this species is virtually nil (Table 1). The morphological information and distribution available come from the first record (Quiroga Carmona and Woodman, 2015), according to which it was assigned to *C. thomasi* (Duarte and Viloria 1992). There is a second record, also identified as *C. thomasi* (Corredor-Carrillo and Muñoz-Saba 2007) from Serranía del Perijá, between 2,850 and 3,100 masl, near the municipality of San José de Oriente in the department of Cesar, Colombia. The set of morphological traits related to dental and cranial anatomy allowed to assign *C. perijensis* to the "*thomasi*" group. It shows a very low research effort (Table 1).

Distribution: known in Colombia from two localities in Serranía del Perijá, department of Cesar, in an elevational range between 2,000 and 3,100 masl (Duarte and Viloria 1992; Corredor-Carrillo and Muñoz-Saba 2007; Quiroga Carmona and Woodman, 2015).

Conservation status: it has not been assessed to date.

Cryptotis squamipes. It was originally described as *Blarina* (*Cryptotis*) *squamipes* based on a single specimen collected at 3,151 masl in the Western Cordillera, 64 km west of Popayán (currently in the municipality of El Tambo, Cauca) in June 1911. There are studies on its anatomy and morphology (3 studies; Allen 1912; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008); taxonomy and systematics (3; Allen 1912; Woodman and Péfaur 2008; Guevara López 2010); biogeography and current distribution (7; Allen 1912; Tate 1932; Cuervo Diaz *et al.* 1986; Cuartas-Calle and Muñoz Arango 2003; Rivas-Pava *et al.* 2007; Woodman and Péfaur 2008; Rojas-Díaz *et al.* 2012), and ecology and natural history (2; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008). The research effort for this species is low (Table 1).

Distribution: Endemic to Colombia. It is known from the following localities: Farallones, Tenerife and Finca Zingara, department of Valle del Cauca, and in Cerro Munchique, department of Cauca, of the Western Cordillera and southern part of the Central Cordillera. It inhabits an elevational range from 1,500 to 3,375 m (Allen 1912; Cuervo Diaz *et al.* 1986; Woodman and Péfaur 2008).

Conservation status: It is listed as Least Concern (Naylor and Roach 2016b), showing a vulnerability risk similar to that of *C. colombianus* and *C. medellinius* (Díaz-Pulido *et al.* 2015). It was previously listed as Data Deficient (Cuartas-Calle and Muñoz Arango 2003).

Cryptotis tamensis. It was described based on one specimen collected in 1968 from the locality of Buena Vista, Tachira state, Venezuela, near Serranía de Perijá and Páramo of Tama, municipality of San Cristóbal, department of Norte de Santander, Colombia (Woodman, 2002). *C. tamensis* has been assigned to the "*thomasi*" group. In addition, a series of morphological and morphometric traits have been proposed for its taxonomic validation (Woodman, 2002). Studies on this species address its anatomy, morphology, taxonomy, and systematics (4 studies; Woodman, 2002; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008; Estupiñán-Saavedra 2009); biogeography and current distribution (5; Woodman 2002; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008; Estupiñán-Saavedra 2009; Cáceres Martinez *et al.* 2017), conservation (2; Cáceres Martinez *et al.* 2017; Woodman and Quiroga-Carmona 2018), and ecology and natural history (3; Woodman 2002; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008). Similar to *C. squamipes*, the research effort for this species is low (Table 1).

Distribution: In Colombia, the species is known from the upper part of the Táchira river, Páramo de Tamá, municipality of Surata, department of Norte de Santander, and Finca

El Rasgón, Vereda La Cristalina, municipality of Piedecuesta, department of Santander, in the Western Cordillera. The elevational range is between 2,385 and 3,000 masl (Woodman 2002; Woodman and Péfaur 2008; Estupiñán-Saavedra 2009).

Conservation status: It is listed as Least Concern (Woodman and Quiroga-Carmona 2018). It was previously listed as Data Deficient (Cuartas-Calle and Muñoz Arango 2003).

Cryptotis thomasi was the first valid shrew species for South America (Merriam 1897), initially described as *Blarina thomasi*. It was described from five of the 10 specimens collected in Hacienda "La Selva" in Sabana de Bogotá in 1895. Studies on this species address its anatomy and morphology (8 studies; Merriam 1897; Allen 1923; Vivar *et al.* 1997; Woodman 2002; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008; Estupiñán-Saavedra 2009; Vianchá Sánchez *et al.* 2012), taxonomy and systematics (6; Allen 1923; Woodman 1996; Vivar *et al.* 1997; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008; Estupiñán-Saavedra 2009), biogeography and current distribution (10; Merriam 1897; Cuervo Diaz *et al.* 1986; López-Arévalo *et al.* 1993; Woodman 2002; Cuartas-Calle and Muñoz Arango 2003; Otálora Ardila 2003; Estupiñán-Saavedra 2009; Vianchá Sánchez *et al.* 2012; Liévano Latorre and López Arévalo 2015; Medina *et al.* 2015), and ecology and natural history (3; López-Arévalo *et al.* 1993; Cuartas-Calle and Muñoz Arango 2003; Woodman and Péfaur 2008; Liévano Latorre and López Arévalo 2015). It is one of the species most recorded in the literature, along with *C. colombianus* and *C. medellinius* (Table 1).

Distribution: Endemic to Colombia. It is known from the following localities: Parque Natural Municipal Rancheria, municipality of Paipa; Neusa dam and Páramo of Chisacá, in the department of Cundinamarca, central and north-eastern part of the Eastern Cordillera, among other localities in the departments of Boyacá, Cundinamarca, and Santander. It lives in an altitudinal range of 2,800 to 3,500 m. The southern limit of its distribution is located in the northern part of Paso de Las Cruces, department of Huila, and the northern limits are associated to the headwaters of the valleys and tributaries of the Chicamocha and Upía rivers (Woodman 2002; Estupiñán-Saavedra 2009).

Conservation status: It is currently listed as Least Concern (Naylor *et al.* 2018).

Molecular Characterization of Some Species and their Phylogenetic Relationships. This work characterizes for the first-time species of the genus *Cryptotis* from Colombia at the molecular level, at least for one mitochondrial marker (*Cytb*). Sequences comprising almost the entire coding region of the gene were successfully obtained for *C. thomasi*, *C. squamipes* and a third species whose taxonomic determination has not been solved yet (*Cryptotis* sp.). The matrix included in the phylogenetic analyses consisted of a total of 114 sequences, with 25 corresponding to the external groups used by Guevara and Cervantes (2014) and 89 to 26 species of the genus *Cryptotis* (Appendix 1).

In the Bayesian topology retrieved, *Cryptotis* appears as a monophyletic group with high support (pp = 1), whose sister genus is *Blarina* (Figure 4). However, some nodes that reflect the deepest phylogenetic relationships, *i. e.*, those between groups of species, tend to show a low level of support. This is in line with previous work using the same marker or a combination of mitochondrial and nuclear markers, which nonetheless failed to achieve a final resolution of the phylogenetic scenario of *Cryptotis* (Guevara and Cervantes 2014; He *et al.* 2015; Moreno-Cárdenas 2017).

According to the analysis performed, the species in the "*parvus*" group form a monophyletic group with high support (pp = 1). The monophyly and relationships within the other species remain unclear. This is particularly evident in the "*mexicanus*" and "*goldmani*" groups because, although some species form monophyletic subgroups, these appear phylogenetically scattered without a clear association matching the morphological definitions (Figure 4).

Similar to the work of Moreno-Cárdenas (2017), the Bayesian topology obtained here points to a close relationship between the "*thomasi*" and "*nigrescens*" groups (pp = 0.99), while revealing an unexpected association between these and some members of the "*mexicanus*" group (*C.*

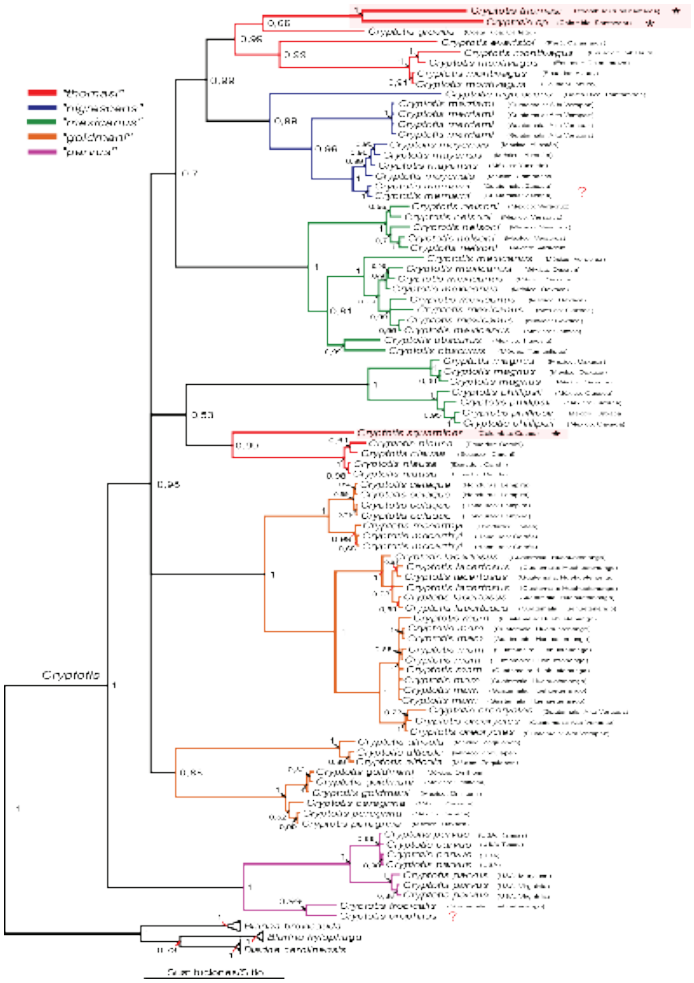

Figure 4. Bayesian Phylogeny of Cytochrome B (*Cytb*). The new information corresponding to species of *Cryptotis* of Colombia is marked with asterisks (*). The groups of species were defined based on the work of He *et al.* (2015). Access numbers of each sequence are listed in Appendix 1.

Table 4. Percentage of genetic divergence (genetic distances of *Cytb* corrected according to the Kimura-2-parameter model x 100) between the species of the "*thomasi*" group (according to the morphological definition), including those of Colombian origin characterized in this work. The divergence values between sibling and geographically close species are highlighted in bold.

	Group/Specie	1	2	3	4	5
1	*Cryptotis thomasi*	-	-	-	-	-
2	*Cryptotis* sp.	**8.7 %**	-	-	-	-
3	*Cryptotis squamipes*	14.6 %	15.0 %	-	-	-
4	*Cryptotis niausa*	14.2 %	14.4 %	**9.8%**	-	-
5	*Cryptotis montivagus*	13.5 %	14.6 %	14.0 %	12.4 %	-
6	*Cryptotis evaristoi*	13.5 %	12.9 %	14.7 %	13.9 %	10.6 %

nelsoni, C. mexicanus and *C. obscurus*), although with little statistical support (pp = 0.70). However, the molecular evidence seemingly contrasts the traditional morphological definition of these two groups. On the one hand, all species recovered within the "*nigrescens*" group were consistent with the morphology (*C. nigrescens, C. merriami*, and *C. mayensis*; pp = 0.99), while the "*thomasi*" group shows an unexpected pattern of relationships. With a high statistical support (pp = 0.99), this group was recovered as monophyletic and is made up mainly of Andean species: *C. montivagus* and *C. evaristoi*, from Ecuador, and *C. thomasi* and *Cryptotis* sp., from Colombia (Figure 4). An aspect worth mentioning is that a species from Central America (*Cryptotis gracilis*), supposedly with a morphology akin to the "*goldmani*" group, is closely related to the two Colombian species. Likewise, contrary to the morphological definition of this group, another Colombian species (*C. squamipes*) and an Ecuadorian species (*C. niausa*) were recovered as sister lineages (pp = 0.99) and were unexpectedly associated with some members of the "*mexicanus*" group. Considering these findings and the fact that the mitochondrial topology of the work of Moreno-Cárdenas (2017) reports a relationship with low support (pp = 0.60) between *C. niausa* and other members of the "*nigrescens*" group, it is reasonable to hypothesize that *C. niausa*, as well as *C. squamipes* and possibly also *C. gracilis*, are "relict species". However, this assumption requires further data to establish whether or not these are associated with the *Cryptotis* morphological groups currently defined.

The phylogenetic analyses and genetic distances of *Cytb* support the taxonomic identity of the three Colombian species, while reflecting a pattern of affinity based on geographic proximity. *Cryptotis* sp. and *C. thomasi*, both sister species within the "*thomasi*" group and distributed in the Eastern Cordillera of Colombia, exhibit a distance of 8.7 % between them (Table 4). Similarly, *C. squamipes* differed from its Ecuadorian sister species (*C. niausa*) by an average distance of 9.8 % and both are distributed in the orographic region shared between the southwest of Colombia and northern Ecuador. The differences between these three Colombian species and the other species of *Cryptotis* involve a distance that exceeds 12 %.

Table 5. Species richness of shrews (*Cryptotis*) in South American countries. *Likely presence in Colombia.

Country	Number of species	Endemic	Non-endemic
Colombia	7	**5:** *brachyonyx, colombianus, medellinius, squamipes, thomasi*	*perijensis, tamensis*
Venezuela	6	**4:** *aroensis, dinirensis, meridensis, venezuelensis*	*perijensis, tamensis*
Ecuador	4	**3:** *equatoris*, niausa*, osgoodi*	*noctivagus*
Peru	3	**2:** *evaristoi,* peruviensis	noctivagus

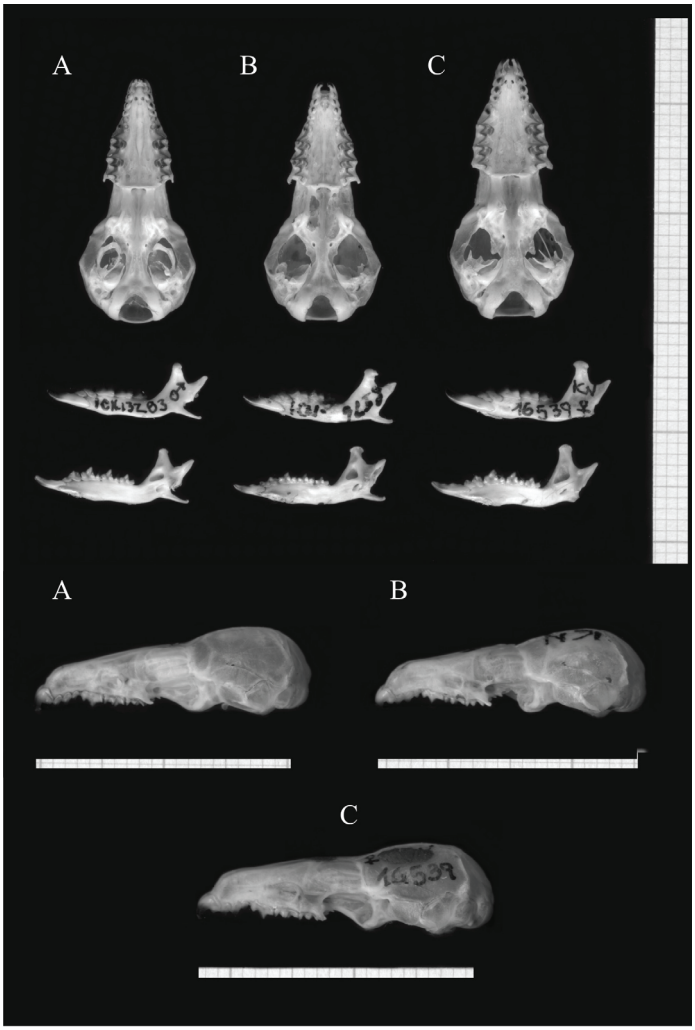

Figure 5. Details of the skull: A. *Cryptotis* from the department of Nariño. B. *Cryptotis thomasi*, C. *Cryptotis* cf. *colombianus*.

Discussion

In general, the topics least addressed for Colombian shrews include ecology, natural history, systematics, biogeography, and genetics. We have identified research needs in nearly all topics evaluated, mainly in ecology, genetics, and molecular techniques (Table 1). The lack of molecular studies is partly due to the lack of joint efforts to conduct the molecular characterization of the species distributed in Colombia, as well as regarding policies dealing with access to these resources from the national government. This has led to a lag relative to other South American countries that are home to a lower diversity of shrews (Moreno-Cárdenas 2017; Zeballos *et al.* 2018). The lack of information

about natural history and ecology partly results from the lack of implementation of appropriate methods to study shrews in the field coupled with the absence of research lines designed to that end. There are four priority areas of research for the species of shrews in Colombia.

Species Richness and Systematics. The lack of phylogenies involving all species living in Colombia and the missing morphological information associated with molecular analyses to support proper identification of voucher specimens in national collections have limited the understanding of species richness and distribution. Although Colombia is a country rich in shrew species relative to other South American countries (Table 5; Solari *et al*. 2013; Quiroga-Cardona and DoNascimiento 2016; Moreno Cárdenas and Román-Carrión 2017; Zeballos *et al*. 2018), this number appears to be underestimated, given the complexity of the Andean ecosystems. For example, there are reports on the presence of *Cryptotis* specimens lacking the morphological traits of the species known for the Central Cordillera (Sánchez and Alvear 2003; Rojas-Díaz *et al*. 2012; Figure 5). At least two of the known species in the country (*e. g., C. squamipes* and *C. medellinius*) may actually be species complexes (Woodman and Péfaur 2008). Furthermore, the presence of *C. equatoris* in Colombia is a subject that warrants further analysis.

Specimens tentatively identified as *C. equatoris* from the southwest of Colombia and deposited in Universidad de Nariño (PSO-CZ 483, 516) were collected at localities adjacent to those where this species was recorded in Ecuador (Moreno Cárdenas and Albuja V. 2014). The specimens are dark colored, similar to literature reports for *C. equatoris* and *C. osgoodi* (Moreno Cárdenas and Albuja V. 2014). Likewise, there are specimens from the department of Nariño deposited at the Institute of Natural Sciences, Universidad Nacional de Colombia (Figure 5a) and the PSO-CZ collection, which are grayish-brown, a color also observed in Ecuadorian species such as *C. niausa* (Moreno Cárdenas and Albuja V. 2014). However, a reevaluation of these specimens is required in accordance with the characteristics proposed in recent reviews (Moreno Cárdenas and Albuja V. 2014; Moreno Cárdenas and Román-Carrión 2017; Zeballos *et al*. 2018). If these records were confirmed with molecular information, the richness of shrews in Colombia would increase to nine species, with the possibility of an additional one, seemingly not described yet and discussed below.

Considering the availability of molecular information on shrews from North and Central America, as well as those inhabiting Ecuador and Peru, the inclusion of the Colombian species is necessary to understand aspects of the evolution and diversification of *Cryptotis*, especially in the ecosystems of the northern Andes of South America. The present work accomplishes the characterization of only two species out of seven knowns to inhabit in Colombia, in addition to a third with a questionable taxonomic determination. The latter, collected in ecosystems in the municipality of Santa Bárbara, department of Santander, shows a distribution adjacent to that of *C. tamensis* and close to that of *C. meridensis*, but exhibits a distinctive morphology. Molecular analyses of the three species will likely reveal the influence of either ecological mechanisms — as *C. tamensis* inhabits mainly forests while *Cryptotis* sp. has been collected in moorlands — or vicariant processes, as the ranges of *C. meridensis* and *Cryptotis* sp. are apparently separated by the Táchira depression, which would have led to the genetic differentiation between them.

The inclusion of *C. thomasi, Cryptotis* sp., and *C. squamipes* within a phylogenetic context of the genus sets the basis for further studies to elucidate aspects currently unknown. Particularly, *C. squamipes*, traditionally considered as a member of the "*thomasi*" group, seems to be a "relict species" along with *C. niausa*, without a clear association to any of the species groups defined based on morphological traits. This, coupled with the fact that the "*mexicanus*" and "*goldmani*" groups were not recovered as monophyletic, supports the contradiction observed between morphology and molecular characteristics. In this sense, the groups of species within *Cryptotis* should be reevaluated in light of new evidence, which will be partly achieved through the characterization of various molecular markers in a larger number of species.

Biogeography. Another area that deserves research on the shrews of Colombia is biogeography. The geographic information about the shrews in Colombia is heterogeneous and biased for most species (*e. g.,* some records reported for *C. thomasi* are located outside of the Andean ecosystems; Figure 1). In general, the online databases have biases, errors, and lack of information associated with some specimens (Noguera-Urbano and Escalante 2014). In the case of the shrews of Colombia, the analysis of the geographic evidence (distribution maps and localities from databases) reveals little consistency between data sources. For this reason, the estimated distribution may be questionable for some of these species. This finding evidences the need to conduct reviews of the genus including all the specimens deposited in the various collections, both in the country and abroad. Some progress has been made on this topic (Estupiñán-Saavedra 2009; Marín Cardona 2009). The research priorities in this area include explorations in mountainous places where no shrews have been recorded, together with filtering and release of field information, and the evaluation of morphological and molecular traits to allow the identification both in the field and in the laboratory. This information will yield a better picture on the distribution of the species of shrews of Colombia.

Distribution maps are currently available for six of the seven species reported in Colombia. We believe that this may be due to the speed of information updating on the distribution of mammals. *C. perijensis* is a species described just recently (Quiroga Carmona and Woodman, 2015); this information is expected to be available soon in databases, and the recorded localities will likely increase. The growing knowledge about the distribution of species will improve management and decision-making in the conservation

of shrew species (Guevara *et al.* 2015). In addition, there are spatial inconsistencies between records and distribution maps available in databases. For example, the distribution proposed for *C. squamipes* by IUCN and Woodman and Péfaur (2008) indicates that this species is distributed from Nariño to southern Tolima or the center of the Valle del Cauca, respectively. On the other hand, GBIF records indicate that this species is distributed from Cauca to the north of Valle del Cauca, and only one record overlaps the distribution map.

The number of records available for the different species has increased since the proposals of Woodman and Péfaur (2008). However, this increase in the number of records does not involve data quality. This is evident in the outdated scientific names associated with the records or the absence of the specific name for some of those records. Therefore, the information on the distribution and sites of sympatry of shrew species should be updated and verified, since estimates derived from uncertain distributions cast doubts as to their interpretation.

The adaptation of shrews to Andean ecosystems point to the need to improve the conservation strategies in these areas, considering that this region is subject of the highest transformation rates in forest environments (Cavelier and Etter 1995; Rangel 2000; Armenteras *et al.* 2003) and the highest vulnerability to the impacts derived from the rising temperature. However, the overlap of distribution ranges with at least ten conservation areas of Colombia is highly likely, as these species inhabit mostly high-mountain areas in the country (Woodman and Péfaur 2008). Their presence in these areas involve new management challenges, given the little natural connectivity between high-mountain areas as a consequence of human activities.

Ecology and Natural History. It has been shown that shrews comprise an important component in the diet of carnivores and birds of prey. In particular, they are among the most common preys in the diet of owls (*Tyto*; Delgado-V. and Ramírez 2009). Despite the importance of the records of shrews obtained from food pellets, mainly of nocturnal birds of prey in Colombia, the absence of well-defined cranio-dental and postcranial traits restrain our ability to identify bone fragments to species. In addition, this limitation affects our understanding of the interactions between shrews and their predators.

The lack of knowledge on the natural history and ecology of shrews is a concern. Filling these information gaps requires the conduction of field monitoring and compilation of data associated with voucher specimens deposited in biological collections, especially as regards reproductive seasons, local abundances, and ecological interactions (*i. e.,* parasites).

Conservation Status. Although no focal studies are currently available on the conservation status of the shrews of Colombia, several general threats have been identified that may affect the populations inhabiting the country. As regards the threats that shrews currently face, these species are highly sensitive to any alterations to high-mountain ecosystems, including both the transformation of ecosystems and deforestation, and the impacts of climate change. For example, the Andean forest and páramos show a tendency to shrink as a result of climatic variations; thus, páramos in Colombia currently represent 5 % of the original area (Flantua *et al.* 2014; Hazzi *et al.* 2018). This reduction related to climatic variations poses risks to shrews because the reduction of ecosystems translates into smaller distribution areas of the associated flora and fauna. If it is considered that high-mountain ecosystems reached up to 1,900 or 2,200 m a.s.l. during glacial periods of the Quaternary (Hooghiemstra 2006; van der Hammen *et al.* 1974; Jimenez-Rivillas *et al.* 2018), an overall reduction in the sizes of populations of all species of *Cryptotis* can be inferred. However, further studies including the review of localities, research on fossils, phylogeographic analysis, and modeling of distribution ranges may support this hypothesis.

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Appendix 1.

List of sequences included in the phylogenetic and distance analyzes. Abbreviations: ASNHC (Angelo State Natural History collections, Angelo State University, San Angelo, Texas, USA), CNMA (National Collection of Mammals, Instituto de Biología, UNAM, México), CMNH (Carnegie Museum of Natural, History, Pittsburgh, Pennsylvania, USA), HA (Abe H private collection), ICN (Collection of Mammals, Instituto de Ciencias Naturales, Bogotá, Colombia), KIZ (Kunming Institute of Zoology, Kunming, China), KU (Kansas University Museum, USA), MVZ (The Museum of Vertebrate Zoology, Berkeley, USA), LACM (Natural History Museum of Los Angeles County, USA), MHNUC (Collection of Mammals, Museum of Natural History, Universidad del Cauca, Popayán, Colombia), MHP (Sternberg Museum of Natural History, Fort Hays State University, USA), MUSA (Museum of Natural History, Universidad Nacional de San Agustín, Perú), MVZ (Museum of Vertebrate Zoology at Berkeley, USA), QCAZ (Museum of Zoology, Pontificia Universidad Católica del Ecuador), ROM (Royal Ontario Museum, Canadá), TK (Natural Science Research Laboratory, Texas Tech University, USA), UIS-MZ (Collection of Mammals, Museum of Natural History, Universidad Industrial de Santander), USNM (National Museum of Natural History; Smithsonian Institution; Washington, DC, USA), ZIN (Zoological Institute of the Russian Academy of Sciences, Rusia).

Taxón	Voucher	Código de acceso	Localidad	Cytb (pb)	Fuente
Blarina brevicauda	USNM 569100	KT876835	USA: Pennsylvania	1107	He *et al*. (2015)
Blarina brevicauda	USNM 569118	KT876836	USA: Virginia	1107	He *et al*. (2015)
Blarina brevicauda	USNM 570202	KT876837	USA: Maine	1107	He *et al*. (2015)
Blarina carolinensis		JF912171		452	Pfau *et al*. (2011)
Blarina carolinensis	TK164126	JF912173	USA: Arkansas	452	Pfau *et al*. (2011)
Blarina hylophaga	MHP KK766	JF912177		452	Pfau *et al*. (2011)
Blarina hylophaga	MHP KK767	JF912178		452	Pfau *et al*. (2011)
Blarinella griselda	ZIN:97788	KY249527	Vietnam: Sa Pa	1076	Bannikova *et al*. (2017)
Blarinella quadraticauda		JF719721		1140	No published
Chimarrogale himalayica		AB107875	Taiwán: Nantou	1140	Ohdachi *et al*. (2006)
Chimarrogale platycephalus	HA7789*	AB108769	Japón: Shiga	1140	Ohdachi *et al*. (2006)
Chodsigoa parca	KIZ 201212894 028696	KX765508	China: Yunnan	1140	Chen *et al*. (2017)
Crocidura fuliginosa	MVZ186404	EU122212	Vietnam	1140	Meegaskumbura *et al*. (2007)
Episoriculus leucops	HA7127	AB175111	Nepal: Syng Gomba	1140	Ohdachi *et al*. (2006)
Episoriculus umbrinus	ZIN 96263	MF577030	Vietnam: Lao Cai	1123	Abramov *et al*. (2017)
Megasorex gigas	LACM 055131	AB175150	México: Colima	1140	Ohdachi *et al*. (2006)
Nectogale elegans	19715	GU981294	China: Yunnan	1140	He *et al*. (2010)
Neomys anomalus		DQ991055	España	1140	Castiglia *et al*. (2007)
Notiosorex crawfordi	LACM LAF1313	AB175148	México: Baja California	1140	Ohdachi *et al*. (2006)
Notiosorex crawfordi	LACM LAF1295	AB175149	México: Baja California	1140	Ohdachi *et al*. (2006)
Sorex raddei		GU827404	Rusia: Vyselki	1046	Orlov *et al*. (2011)
Sorex satunini		GU827402	Rusia: Vyselki	1038	Orlov *et al*. (2011)
Sorex volnuchini		GU827400	Rusia: Vyselki	1045	No published
Soriculus nigrescens	19710	GU981300	China: Yunnan	1140	He *et al*. (2010)
Soriculus nigrescens	19711	GU981301	China: Yunnan	1140	He *et al*. (2010)
Cryptotis alticola	CNMA 44765	KF551854	México: Zoquiapan	1140	Guevara and Cervantes (2014)
Cryptotis alticola	CNMA 44766	KF551855	México: Zoquiapan	1140	Guevara and Cervantes (2014)
Cryptotis alticola	CNMA 44768	KF551856	México: Zoquiapan	1140	Guevara and Cervantes (2014)
Cryptotis celaque	CMNH SP13226	MF158092		1119	Baird *et al*. (2018)
Cryptotis celaque	CMNH SP13228	MF158093		1120	Baird *et al*. (2018)
Cryptotis celaque	CMNH SP13229	MF158094		1119	Baird *et al*. (2018)
Cryptotis celaque	CMNH SP13234	MF158095		1117	Baird *et al*. (2018)
Cryptotis evaristoi	MUSA 7428	MH352617	Perú: Cajamarca	1116	Zeballos *et al* (2018)
Cryptotis goldmani	LACM LAF1596	AB175136	México: Guerrero	1140	Ohdachi *et al*. (2006)
Cryptotis goldmani	LACM LAF1599	AB175137	México: Guerrero	1140	Ohdachi *et al*. (2006)
Cryptotis goldmani	LACM LAF1595	AB175138	México: Guerrero	1140	Ohdachi *et al*. (2006)
Cryptotis gracilis	USNM 568678	KT876838	Costa Rica: Cartago	412	He *et al*. (2015)
Cryptotis lacertosus	USNM 569368	KT876839	Guatemala: Huehuetenango	1107	He *et al*. (2015)

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Cryptotis lacertosus	USNM 569420	KT876840	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis lacertosus	USNM 569431	KT876841	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis lacertosus	USNM 569442	KT876842	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis lacertosus	USNM 569443	KT876843	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis lacertosus	USNM 569503	KT876844	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis magna	LACM LAF1514	AB175139	México: Oaxaca	1140	Ohdachi *et al*. (2006)
Cryptotis magna	LACM LAF1550	AB175140	México: Oaxaca	1140	Ohdachi *et al*. (2006)
Cryptotis magna	LACM LAF1515	AB175141	México: Oaxaca	1140	Ohdachi *et al*. (2006)
Cryptotis mam	USNM 569554	KT876845	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis mam	USNM 569555	KT876846	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis mam	USNM 570248	KT876847	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis mam	USNM 570256	KT876848	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis mam	USNM 570257	KT876849	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis mam	USNM 570313	KT876850	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis mam	USNM 570314	KT876851	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis mam	USNM 570337	KT876852	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis mam	USNM 570340	KT876853	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis mayensis	ROM 96535-FN30563	KT876854	México: Campeche	1107	He *et al*. (2015)
Cryptotis mayensis	CNMA:46150	KF551857	México: Yucatán	1140	Guevara and Cervantes (2014)
Cryptotis mayensis	CNMA:46151	KF551858	México: Yucatán	1140	Guevara and Cervantes (2014)
Cryptotis mayensis	CNMA:46152	KF551859	México: Yucatán	1140	Guevara and Cervantes (2014)
Cryptotis mccarthyi	CMNH SP12828	MF158096		1120	Baird *et al*. (2018)
Cryptotis mccarthyi	CMNH SP12836	MF158097		1121	Baird *et al*. (2018)
Cryptotis mccarthyi	CMNH SP12934	MF158098		1120	Baird *et al*. (2018)
Cryptotis merriami	USNM 570108	KT876855	Guatemala: Alta Verapaz	1107	He *et al*. (2015)
Cryptotis merriami	USNM 570112	KT876856	Guatemala: Alta Verapaz	1107	He *et al*. (2015)
Cryptotis merriami	USNM 570122	KT876857	Guatemala: Alta Verapaz	1107	He *et al*. (2015)
Cryptotis merriami	USNM 570132	KT876858	Guatemala: Alta Verapaz	1107	He *et al*. (2015)
Cryptotis merriami	USNM 57049	KT876859	Guatemala: Zacapa	1107	He *et al*. (2015)
Cryptotis merriami	USNM 570125	KT876860	Guatemala: Zacapa	1107	He *et al*. (2015)
Cryptotis mexicanus	LACM LAF1506	KT876861	México: Oaxaca	1107	He *et al*. (2015)
Cryptotis mexicanus	LACM LAF1510	AB127979	México: Oaxaca	630	No published
Cryptotis mexicanus	LACM LAF1509	AB175142	México: Oaxaca	1140	Ohdachi *et al*. (2006)
Cryptotis mexicanus	LACM LAF1511	AB175143	México: Oaxaca	1140	Ohdachi *et al*. (2006)
Cryptotis mexicanus	CNMA 41951	KF551836	México: Veracruz	1140	Guevara and Cervantes (2014)
Cryptotis mexicanus	CNMA 43051	KF551837	México: Oaxaca	1140	Guevara and Cervantes (2014)
Cryptotis mexicanus	CNMA:43059	KF551838	México: Oaxaca	1140	Guevara and Cervantes (2014)
Cryptotis mexicanus	CNMA 43061	KF551839	México: Oaxaca	1140	Guevara and Cervantes (2014)
Cryptotis montivagus	QCAZ 4996	MH352622	Ecuador: Azuay	1098	Zeballos *et al* (2018)
Cryptotis montivagus	QCAZ 4997	MH352623	Ecuador: Azuay	1080	Zeballos *et al* (2018)
Cryptotis montivagus	QCAZ 8409	MH352620	Ecuador: Chimborazo	1086	Zeballos *et al* (2018)
Cryptotis montivagus	QCAZ 12037	MH352621	Ecuador: Chimborazo	1119	Zeballos *et al* (2018)
Cryptotis nelsoni	CNMA 41961	KF551840	México: Veracruz	1140	Guevara and Cervantes (2014)
Cryptotis nelsoni	CNMA 41964	KF551841	México: Veracruz	1140	Guevara and Cervantes (2014)
Cryptotis nelsoni	CNMA 41965	KF551842	México: Veracruz	1140	Guevara and Cervantes (2014)
Cryptotis nelsoni	CNMA 41969	KF551843	México: Veracruz	1140	Guevara and Cervantes (2014)
Cryptotis nelsoni	CNMA 41970	KF551844	México: Veracruz	1140	Guevara and Cervantes (2014)
Cryptotis niausa	QCAZ 11246	MH352619	Ecuador: Carchi	1119	Zeballos *et al* (2018)
Cryptotis niausa	QCAZ 12642	MH352624	Ecuador: Carchi	1123	Zeballos *et al* (2018)
Cryptotis niausa	QCAZ 12650	MH352625	Ecuador: Carchi	1123	Zeballos *et al* (2018)
Cryptotis niausa	QCAZ 12661	MH352626	Ecuador: Carchi	714	Zeballos *et al* (2018)
Cryptotis nigrescens	KU 143389	KT876862	Costa Rica: Punta Arenas	815	He *et al*. (2015)
Cryptotis obscurus	CNMA 42285	KF551846	México: Tlaxcala	1140	Guevara and Cervantes (2014)

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Cryptotis obscurus	CNMA 44637	KF551845	México: Tamaulipas	1140	Guevara and Cervantes (2014)
Cryptotis oreoryctes	USNM 569854	KT876863	Guatemala: Alta Verapaz	1107	He *et al*. (2015)
Cryptotis oreoryctes	USNM 569877	KT876864	Guatemala: Alta Verapaz	1107	He *et al*. (2015)
Cryptotis oreoryctes	USNM 569878	KT876865	Guatemala: Alta Verapaz	1107	He *et al*. (2015)
Cryptotis orophilus	CMNH SP11644	MF158113		1080	Baird *et al*. (2018)
Cryptotis parvus		AF395483		1138	Brant and Ortí (2002)
Cryptotis parvus		AF395484		1138	Brant and Ortí (2002)
Cryptotis parvus	USNM 568660	KT876866	USA: Virginia	1104	He *et al*. (2015)
Cryptotis parvus	USNM 569083	KT876867	USA: Virginia	1103	He *et al*. (2015)
Cryptotis parvus	USNM 570487	KT876868	USA: Maryland	774	He *et al*. (2015)
Cryptotis parvus	USNM 570510	KT876869	USA: Kansas	1107	He *et al*. (2015)
Cryptotis parvus	ANSHC 8192	AB175135	USA: Texas	1140	Ohdachi *et al*. (2006)
Cryptotis peregrinus	CNMA:45582	KF551848	México: Oaxaca	1140	Guevara and Cervantes (2014)
Cryptotis peregrinus	CNMA:45583	KF551849	México: Oaxaca	1140	Guevara and Cervantes (2014)
Cryptotis peregrinus	CNMA:45584	KF551847	México: Oaxaca	1140	Guevara and Cervantes (2014)
Cryptotis phillipsii	CNMA:4469	KF551850	México: Oaxaca	1140	Guevara and Cervantes (2014)
Cryptotis phillipsii	CNMA:44723	KF551853	México: Oaxaca	1140	Guevara and Cervantes (2014)
Cryptotis phillipsii	CNMA:44724	KF551852	México: Oaxaca	1140	Guevara and Cervantes (2014)
Cryptotis phillipsii	CNMA:44728	KF551851	México: Oaxaca	1140	Guevara and Cervantes (2014)
Cryptotis tropicalis	USNM 570435	KT876870	Guatemala: Huehuetenango	1107	He *et al*. (2015)
Cryptotis thomasi	ICN	MK681775	Colombia: Cundinamarca	1140	This work
Cryptotis squamipes	MHNUC 1572	MK681776	Colombia: Cauca	1140	This work
Cryptotis sp.	UIS-MZ-1594	MK681774	Colombia: Santander	1093	This work