Taxonomic boundaries and geographic distributions revealed by an integrative systematic overview of the mountain coatis, *Nasuella* (Carnivora: Procyonidae)

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Abstract

The procyonid taxon *Nasuella* Hollister, 1915, is currently recognized as a monotypic genus comprising the single species *N. olivacea* (Gray, 1865), the Mountain Coati, found in montane habitats (*circa* 1300-4250 m) in the Andes of Venezuela, Colombia, and Ecuador. In this study we utilize museum specimens to examine the phylogenetic relationships, taxonomy and geographic distribution of *Nasuella* populations with an integrative systematic approach. Drawing on morphological comparisons of pelage, cranial, and dental characters, and molecular comparisons of the mitochondrial gene *cytochrome b* (from recent and historical samples), we confirm that *Nasuella* is closely related to other coatis (*Nasua*) and show that there are two deeply divergent lineages represented within the taxonomic bounds of *Nasuella*. We recognize and diagnose these taxa as two distinctive mountain coati species, corresponding to the Eastern Mountain Coati *Nasuella meridensis* (Thomas, 1901), endemic to the Venezuelan Andes, and the Western Mountain Coati *N. olivacea*, distributed in the Andes of Colombia and Ecuador. We use locality and habitat data associated with museum specimens to model the global geographic range of both species. From this we predict areas of undocumented (i.e., currently unvouchered) occurrence, areas of habitat loss associated with land use changes, and the geographic barrier separating the distributions of *N. meridensis* and *N. olivacea.* This newfound understanding of taxonomy and distribution should allow for a revised conservation assessment for mountain coatis.

Keywords: Andes, *cytochrome b*, ecomorphology, geographic range modeling, *Nasua*, *Nasuella*, phylogenetics, taxonomy

Barreras taxonómicas y distribución geográfica reveladas por una revisión integrativa y sistemática del Coatí de Montaña, *Nasuella* (Carnivora: Procyonidae)

Resumen

El grupo taxonómico prociónido actualmente reconocido como *Nasuella* Hollister, 1915, se encuentra considerado como un genero monotípico que abarca solamente a la especie *N. olivacea* (Gray, 1865), el Coatí de Montaña, y esta distribuido únicamente en hábitat montañoso (*circa* 1300-4250 m) de los andes de Venezuela, Colombia, y Ecuador. En este estudio utilizamos especímenes almacenados en museos internacionales para examinar las relaciones filogenéticas, la distribución geográfica y la taxonomía de poblaciones de *Nasuella* desde un punto de vista integratívo y sistemático. Nuestros resultados basados en comparaciones morfológicas de caracteres craneales y dentales, y de datos moleculares basados en secuencias del gen mitocondrial de *Citocromo b* (derivadas de ADN extraído de tejidos de especimenes congelados recientemente y de especimenes almacenados en etanol y también de hueso de ejemplares derivados de especímenes históricos utilizando protocolos de extracción de ADN antiguo) confirman que el género *Nasuella* se encuentra cercanamente relacionado a otros coatís del género *Nasua* y demuestran que hay dos linajes divergentes representados dentro de los márgenes taxonómicos de *Nasuella*. Reconocemos y diagnosticamos a estos dos grupos taxonómicos como especies distintas de Coatís de Montaña, correspondiente al Coatí de Montaña Oriental *Nasuella meridensis* (Thomas, 1901), endémico a los Andes de Venezuela; y al Coatí de Montaña Occidental *N. olivacea*, distribuido en los Andes de Colombia y Ecuador. Utilizamos datos de hábitat de cada localidad asociada con los ejemplares de museo para modelar el rango geográfico global de ambas especies; y para predecir las áreas en donde es posible que ocurran y que aun no han sido documentadas (*ej.* a base de ejemplares de museos), áreas de perdida de hábitat asociadas con cambios del uso de la tierra, y las barreras geográficas que separan la distribución de *N. meridensis* y *N. olivacea.* Este nuevo entendimiento de sus relaciones filogenéticas, distribución y taxonomía deben de permitir una revisión de la evaluación del estatus de conservación para los Coatís de Montaña.

Palabras clave: Andes, *Citocromo b*, ecomorfología, filogenia, modelamiento de rango geográfico, *Nasua, Nasuella*, taxonomía

Introduction

Of the six extant genera currently recognized in the carnivore family Procyonidae (*Bassaricyon* J. A. Allen, 1876; *Bassariscus* Coues, 1887; *Nasua* Storr, 1780; *Nasuella* Hollister, 1915; *Potos* E. Geoffroy Saint-Hilaire & F. G. Cuvier, 1795; and *Procyon* Storr, 1780), the geographically restricted *Nasuella* is by far the least studied. It is represented by a single recognized Andean endemic species - the Mountain Coati *N. olivacea* (Gray, 1865). Very little information about this intriguing procyonid has been published, such that it might be fairly argued that *Nasuella* is the least-studied carnivore genus globally.

Even the discovery and introduction of the scientific name of the species is shrouded in obscurity. The name first appeared, as *Nasua olivacea*, on the last page of an appendix to a listing of mammal specimens in the British Museum by John Edward Gray

(1843). Gray used the name without providing any description or clarification whatsoever (noting only the locality where the sole available specimen had been collected—"Santa Fé de Bogota", Colombia), so this initial presentation of the name is regarded as a *nomen nudum*, unavailable for use in nomenclature. A more official introduction of this name did not appear for another two decades, when, discussing the taxonomy of bears and raccoons, Gray (1865) introduced what is still essentially the current species-level taxonomy for coatis, and provided a very short accompanying description validating the use of *olivacea* for the Mountain Coati. Gray's description mentioned only the pelage coloration of the animal (rather than its small body size or highly distinctive skull and teeth—its principal distinguishing features): "olive-brown, grizzled; hairs black-brown, with a yellowish sub-terminal ring; under fur black; face pale; orbits, legs, and feet blackish brown; chest yellowish grey; tail short, with black rings and a black tip" (Gray 1865:703; reprinted a few years later in another museum catalogue: Gray 1869).

Probably because Gray's description offered no clear distinguishing features, and no other specimens became available, subsequent nineteenth century reviewers were forced to conclude that *N. olivacea* was a synonym of the more widespread South American coati *Nasua nasua* (referred to in literature at the time as "*Nasua rufa*") (e.g., Allen 1880, Sclater 1891). It was not until the beginning of the twentieth century, starting with a paper by Oldfield Thomas, that *olivacea* was recognized as a distinctive coati species (Thomas 1901) with several supposed subspecies (Thomas 1901, Allen 1913, Lönnberg 1913), and ultimately removed from other coatis to its own genus, *Nasuella* (Hollister 1915). Despite the improvement of this taxonomic understanding a century ago, the obscurity of *Nasuella* remains. The lack of any detailed information on *Nasuella* is striking, and pertains to all aspects of its biology. For example, as far as we are aware, the skull of *Nasuella* has only been figured once in the literature, and only in a single view, from a single specimen (the ventral view of the cranium, provided in the generic description of *Nasuella*) (Hollister 1915: plates 38-39). Even though reasonable samples of skins and skulls of *Nasuella* are available in world museum collections, no author has discussed patterns of geographic variation in the genus based on data from a variety of specimens encompassing its known geographic distribution, so it remains unclear if subspecies should be recognized within *N. olivacea* (Mondolfi 1987). *Nasuella* is the only procyonid genus (and one of very few carnivoran genera) that has not been featured in molecular genetic comparisons of any kind (Koepfli *et al*. 2007, Fulton & Strobeck 2007). Some fundamental references and field guides on Neotropical mammals do not illustrate or include accounts for *Nasuella* (Emmons & Feer 1990, 1997) or even mention it at all (Lord 2007); those that do discuss *Nasuella* offer very brief accounts (e.g., Eisenberg 1989, Eisenberg & Redford 1999). The most lengthy overview of coati taxonomy yet written, that of Decker (1991), does not mention *Nasuella* at all. (We note that Decker largely overlooked, or at least did not test, the taxonomic divisions among coatis briefly put forward earlier by Tate [1939:199–200], which we regard as the best appreciation of patterns of biological diversity in coatis published to date).

Lack of any detailed research to date on *Nasuella* also means that its conservation status is poorly understood. Indeed, a recent effort to rigorously document the current conservation status of all extant mammals (Schipper *et al*. 2008) classified it as "Data Deficient" (Reid & Helgen 2008), making it one of very few generic-level carnivoran lineages so categorized. In total, previously published accounts of *Nasuella* involve only very cursory discussions of geographic variation (Gray 1865, Thomas 1901, Allen 1913, Lönnberg 1913, Cabrera 1958, Mondolfi 1987); comments on geographic distribution (Thomas 1901, Allen 1912, 1913, 1916, Lönnberg 1913, Bisbal 1989, Linares 1998, Eisenberg & Redford 1999, Guzmán-Lenis 2004, Ramírez-Chaves *et al*. 2008, Balaguera-Reina *et al*. 2009); brief anatomical and ecomorphological comparisons (Hollister 1915, Tate 1939, Mondolfi 1987, Decker & Wonzencraft 1991, Friscia *et al*. 2007); and limited discussions of ecology and behavior (Rodríguez-Bolaños 2000, 2003, Jarrín-V. 2001).

Our approach in this study has been to use information associated with museum specimens to provide the first detailed review of *Nasuella* across the known geographic range of the genus. First, we draw on skins and skulls stored in selected museums to review patterns of morphological geographic variation (and the appropriateness of trinomial distinctions) in *Nasuella*. Second, we undertake molecular comparisons of the mitochondrial gene *cytochrome b* (abbreviated *cyt b*), extracted both from recently-collected frozen and ethanol-stored tissues, and from historical museum samples using ancient DNA protocols, to offer an independent perspective on geographic variation and intrageneric divergences. Third, we utilize locality and habitat data derived from museum specimen labels to predict the global geographic distribution of *Nasuella*. Crucially, all three approaches (morphological observations, mitochondrial DNA comparisons, and geographic range modeling) identify remarkable disjunction (morphological, genetic, and geographic) between *Nasuella* samples collected in the Andes of Venezuela and those collected in the Andes of Colombia and Ecuador. This marked divergence, unanticipated in previous discussions of *Nasuella*, necessitates changes to the species-level taxonomy of *Nasuella* and requires a re-evaluation of the conservation status of the implicated taxa.

Methods

Morphology

We have studied all *Nasuella* specimens in the collections of the American Museum of Natural History, New York (AMNH); the Natural History Museum, London (BMNH); the Museo de Zoologia, Universidad Politecnica, Quito, Ecuador (EPN); the Field Museum of Natural History, Chicago (FMNH); the Naturhistoriska Riksmuseet, Stockholm, Sweden (NMS); the Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador (QCAZ); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). This includes the type specimens of all named taxa within *Nasuella*, almost all specimens previously reported in the literature, and many never previously reported. As far as we are aware, these holdings represent the great majority (>90%) of Mountain Coati specimens in museums, but we also recognize that we have missed important holdings in Colombian and Venezuelan collections in preparing this study (cf. Linares 1998, Guzmán-Lenis 2004).

Standard external measurements for museum specimens—head-body length (HB) and tail length (TV)—were recorded by the original museum collectors in the field, as noted on museum specimen tags and labels. Craniodental variables were measured by the first author with digital calipers to the nearest 0.1 mm.

Table 1. Selected external, cranial, and dental measurements and ratios in adult specimens of the two species of Mountain Coatis, Nasuella olivacea *and* N. meridensis *(see Methods for abbreviations; based on specimens at AMNH, BMNH, FMNH, NMS, and USNM). The two species differ little in overall skull size, but* N. meridensis *has markedly smaller teeth than* N. olivacea, *both absolutely and proportionally.*

Variable	*N. olivacea* Colombia, Ecuador	*N. meridensis* Venezuela
HB	449 ± 19.4	479 ± 50.7
	409 – 487	430 – 540
	n = 15	*n* = 4
TV	247 ± 14.5	242 ± 53.9
	220 – 270	192 – 300
	n = 15	*n* = 4
TV/HB	55%	50%
	49 – 61%	43 – 60%
	n = 15	*n* = 4
GLS	106.2 ± 6.19	107.5 ± 5.27
	96.7 – 115.9	101.0 – 115.3
	n = 19	*n* = 7
ZYG	50.4 ± 5.42	47.1 ± 4.02
	40.5 – 57.5	43.4 – 53.8
	n = 22	*n* = 9
ZYG/GLS	47%	44%
	41 – 55%	41 – 48%
	n = 19	*n* = 7
M1 L	5.24 ± 0.27	4.38 ± 0.22
	4.6 – 5.7	4.1 – 4.6
	n = 31	n = 9
M1 W	4.54 ± 0.25	3.93 ± 0.15
	4.1 – 5.9	3.7 – 4.1
	n = 32	n = 9

Tabled values are mean ± SD, range and sample size (*n*).

Single-tooth measurements are measured across the crown. All measurements of length are in millimeters. Measurements reported here include greatest length of skull (GLS), zygomatic width (ZYG), length of the first upper molar (M1 L), and width of the first upper molar (M1 W). Limited sexual dimorphism is evident in sexed *Nasuella* samples from the same region (with only zygomatic width significantly larger in males in *t*-test comparisons), such that external and craniodental measurements are pooled in our summary statistics, which are intended to demonstrate a few key points of comparison between *N. olivacea* and *N. meridensis* (Table 1). In addition to measuring skulls and teeth, we examined variation in qualitative morphological attributes between *Nasuella* populations.

DNA Sequencing

Sequences for *Nasuella olivacea* and *N. meridensis* have not previously been reported in the literature and were newly generated from fresh and historical museum materials for this study. "Fresh" *Nasuella* tissues were sampled from recently collected voucher specimens from Ecuador at QCAZ and EPN (a skin clip from a whole specimen stored in ethanol and a sample of tongue from a frozen whole specimen, Table 2). Tiny fragments of turbinate bones were also sampled from the nasal cavities of *Nasuella* skulls from Colombia and Venezuela stored at the USNM (Table 2). In addition, we used sequences from representatives of *Nasua nasua* and *Nasua narica* (selecting sequences from widely separated geographic localities in order to capture as much intraspecific divergence as possible within our limited comparative sample). Newly reported *Nasua* sequences were generated in a previous study that examined the phylogeography of South American coatis (Tsuchiya-Jerep 2009) and for a pending study of variation in *N. narica* (Koepfli *in litt*.). We also obtained previously-published *cyt b* sequences for *Nasua* and other procyonid taxa from GenBank (Table 2).

Total genomic DNA from tissue samples was extracted using the QIAGEN DNeasy kit (QIAGEN, Valencia, CA, USA) and the respective protocol for animal tissues. Polymerase chain reaction (PCR) and sequencing reactions were carried out with primers LGL 765 and LGL 766 from Bickham *et al.* (2004) and using an MJ thermocycler (MJ Research, Waltham, MA, USA) under the following conditions, repeated for 35 cycles: denaturation at 94°C for 1 min, annealing at 50°C for 1 min, extension at 72°C for 1

Table 2. Taxa and samples used in molecular comparisons.

Taxon	Locality	Source (catalog/reference)	Genbank number
Bassaricyon gabbii	Panama, Limbo plot	Koepfli *et al.* (2007)	DQ660300
Bassaricyon alleni	Peruvian Amazon, Rio Cenapa	Koepfli *et al.* (2007)	DQ660299
Nasua nasua	Bolivia, Santa Cruz	Koepfli *et al.* (2007)	DQ660303
Nasua nasua	Brazil, Ceará	Tsuchiya-Jerep (2009)	GQ214530
Nasua narica	Panama	Koepfli *et al.* (2007)	DQ660302
Nasua narica	USA, New Mexico	Koepfli *in litt*	unpublished
Nasuella olivacea	Ecuador, Papallacta	EPN 3414	GQ169038
Nasuella olivacea	Ecuador, Pichincha	QCAZ 8687	GQ169039
Nasuella olivacea	Colombia, Cauca, Malvasa, 3500 m	USNM 309043	GQ169040
Nasuella meridensis	Venezuela, Timotes, Merida, 3 km W near Paramiro, 3000 m	USNM 372854	GQ169041

min. The PCR reagents in a 25 µL reaction were 0.2 µL AmpliTaq (5 units μL^{-1}, Applied Biosystems, Foster City, CA, USA), 1µL per primer (10 µM), 2.5 µL dNTP (2 µM), 2 µL $MgCl_2$ (25 mM), 2.5 µL AmpliTaq Buffer (Applied Biosystems), 2µL BSA (0.01 mg/µL), 1 µL genomic DNA and 12.8 µL sterile water.

Total genomic DNA from turbinate bone samples was extracted following ancient DNA protocols established by Wisely *et al*. (2004). All pre-PCR protocols were conducted in an isolated ancient DNA laboratory located in a separate building from the one containing the primary DNA laboratory. Polymerase chain reaction and sequencing of ancient DNA samples were carried out using an additional pair of internal primers designed from procyonid sequences generated in this study. A 427 bp fragment of the 5' end of *cyt b* was amplified using primer LGL 765 from Bickham *et al.* (2004) as the forward primer and H15149Pro as an internal reverse primer (5'-CTCCTCAAAAGGATATTTGYCCTCA -3': the 3' end corresponds to base 14,576 of the *Canis lupus* [Wolf] mtDNA sequence). The PCR profile was modified to include 50 cycles, with reagents as described above.

Polymerase chain reaction products were amplified for sequencing using a 10 µL reaction mixture of 2 µL of PCR product, 0.8 µL of primer (10 µM), 1.5 µL Big Dye 5 x Buffer (Applied Biosystems), 1 µL Big Dye version 3 (Applied Biosystems) and 4.7 µL sterile water. The reaction was run using an MJ thermocycler (MJ Research) with denaturation at 96°C for 10 s, annealing at 50°C for 10 s and extension at 60°C for 4 min: this was repeated for 25 cycles. The product was cleaned using a sephadex-based filtration method, and sequences of both strands were resolved in a 50 cm array using the ABI PRISM 3130 Genetic Analyzer (Applied Biosystems). Sequences were aligned and edited in Sequencher version 4.7 (Gene Codes Corporation).

Phylogenetic analyses

Phylogenetic analyses were conducted using two approaches. First, we used sequences from a 366-bp fragment from the 5' end of *cyt b*, enabling the inclusion of the two *Nasuella* sequences obtained from the turbinate samples while reducing the effect of missing information due to the short length of the sequences. Second, short sequences were excluded from the analyses, and only samples for which the entire *cyt b* gene had been sequenced were used to assess the strength of the generic relationships and to provide further evidence for branch support and divergence estimates. The sequence data were analyzed using maximum parsimony, maximum-likelihood, Bayesian, and distance methods. PAUP* 4.0b10 (Swofford 2003) was used for neighbor-joining and maximum parsimony analyses; maximum likelihood analyses were conducted using GARLI 0.96b (Zwickl 2006). We used the olingo species *Bassaricyon gabbii* and *B. alleni* as outgroup taxa because *Bassaricyon* has been previously shown to be the sister group to the coatis in recent, more detailed phylogenetic studies (Koepfli *et al.* 2007, Fulton & Strobeck 2007).

A neighbor-joining tree was created using the HKY85 method with pair-wise distances calculated using the Kimura 2-parameter (K2P) model. The branch and bound search method was used for the maximum parsimony analyses. Parsimony bootstrap support was estimated using the heuristic search method with 100 random stepwise taxon additions for 1000 replicates. The maximum likelihood analysis was conducted using the following parameters; rate matrix = (14.127, 187.864, 16.570, 0.728, 335.001, 1.000); base frequencies (A = 0.2714, C = 0.2834, G = 0.1806, T = 0.2646); proportion of invariable sites = 0.0099; gamma distribution shape parameter = 0.2377 for the short *cyt b* sequences. For the entire *cyt b* sequences, the parameters were: rate matrix = (2.688, 104.784, 3.938, 0.182, 80.935, 1.000); base frequencies (A = 0.3200, C = 0.3109, G = 0.1299, T = 0.2391); proportion of invariable sites = 0.0196; gamma distribution shape parameter = 0.2408. These parameters, and the best model of evolution (GTR+G+I), were estimated using GARLI. Maximum likelihood bootstrap support was estimated with 500 replicates.

MrModeltest version 2.2 (Nylander 2004) was used to find the best model for the Bayesian analyses under the Akaike information criterion. The parameters were then applied in MrBayes version 3.1 (Huelsenbeck & Ronquist 2001). The model parameters were set to nst = 6 with a proportion of invariable sites (GTR + I). Two replicates of the Bayesian analysis were run, each using 1,000,000 generations in four chains, with a heating parameter of 0.05, and sampling frequency of 100 steps.

Molecular divergence estimates were generated in MEGA4 (Tamura *et al.* 2007). A distance tree was generated using the HKY85 model with a constant rate applied across the tree. Divergences were calibrated using the 12 mya estimate of divergence between *Bassaricyon* and *Nasua* calculated by Koepfli *et al.* (2007).

Geographic Range Modeling

We used Maximum Entropy Modeling (Maxent) (Phillips *et al*. 2005) to predict the geographic range of *Nasuella* species based on 33 vouchered localities derived from our specimen examinations (list of localities available on request) and 20 environmental variables representing potential vegetation and climate. Localities were georeferenced with data derived from museum specimen tags, often with clarifying reference to the ornithological gazetteers prepared by Paynter (1982, 1993, 1997). For potential vegetation we used the 15 major habitat types classified as ecological biomes (Olson *et al*. 2001). For climate we used 19 BIOCLIM variables representing annual trends, seasonality, and extremes in temperature and precipitation across portions of Central and South America (derived from Hijmans *et al*. [2005] as described at http://www.worldclim.org/bioclim.htm). Because there were so few records for *N. meridensis*, we constructed the model for the genus and later distinguished the two species based on the location of voucher specimens. We used all vouchered specimen localities in our dataset to train the final model. We also tested model performance by running 10 iterations while randomly withholding 20% of the points as test locations. To produce geographic ranges showing presence/absence of a species we used the average equal training sensitivity and specificity for the 10 test models as our probability cutoff value (Phillips *et al*. 2005). To evaluate the present conservation status in these areas we overlapped predicted ranges with estimates of modern land use (Eva *et al*. 2004).

Results

Morphological comparisons

Morphological comparisons of *Nasuella* specimens deposited in world museums revealed: 1) outstanding morphological distinctions between *Nasuella* collected in the Venezuelan Andes *versus* *Nasuella* from Colombia and Ecuador; and 2) more subtle, but consistent, distinctions between *Nasuella* from Ecuador and Colombia.

Distinctions between Venezuelan and other *Nasuella* samples include differences in pelage coloration, differences in qualitative craniodental characteristics, and differences in the size and proportion of the teeth, especially the premolars and molars. Compared to *Nasuella* from Colombia and Ecuador, Venezuelan animals generally have paler, more olive-brown fur (more reddish or blackish in skins from Colombia and Ecuador), a blackish mid-dorsal stripe on the back (not as apparent in skins from Colombia and Ecuador), and a slightly shorter tail on average (Table 1). Qualitative craniodental distinctions between Venezuelan and other *Nasuella* involve the configuration of the bony palate (extending farther behind the molar row) and palatal shelf (less markedly depressed posteriorly), the anterior alveolar foramen (usually extending farther anterior of the infraorbital foramen), and the configuration of the dentary, in which the posterior processes tend to be more broadly dissociated posteriorly (Fig. 1). The most striking distinction between Venezuelan and other *Nasuella* is the grossly reduced dentition of Venezuelan animals, such that each premolar and molar is absolutely smaller in dimensions of length and width compared to Colombian and Ecuadoran *Nasuella* samples (e.g. Figs 1 and 2; Table 1). Because the skull is the same size in Venezuelan animals as in other populations, this distinction in the size of the teeth constitutes a rather extraordinary distinction in proportional terms (Fig. 1, Table 1).

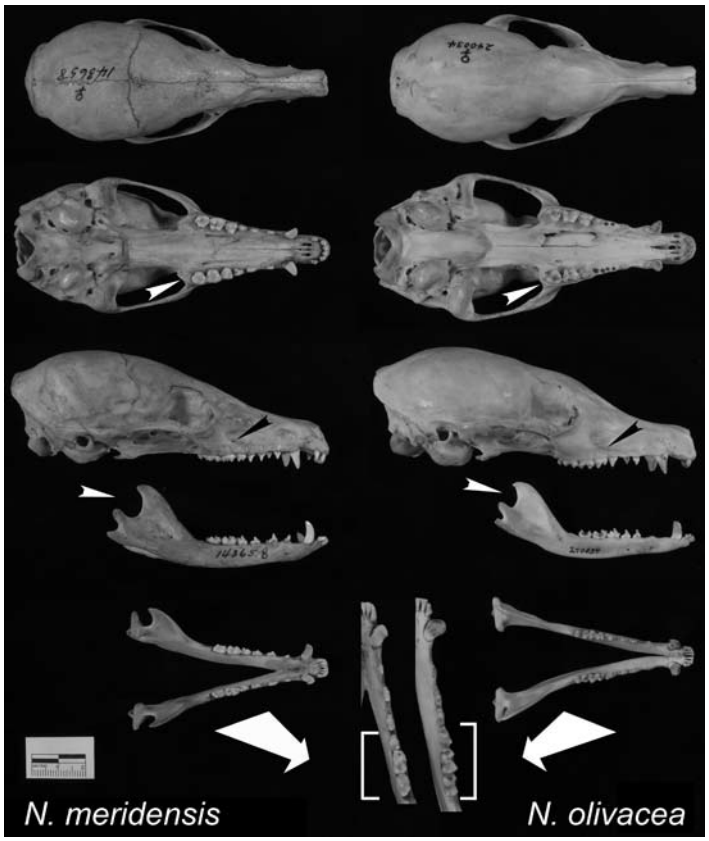

Fig. 1. Skulls and teeth in the two species of Nasuella*. Left,* N. meridensis*, USNM 143658 (older subadult or young adult female, from Guache, Montes De La Culata, 3000 m, Merida, Venezuela). Right,* N. olivacea olivacea*, USNM 240034 (adult female, from Choachi, Colombia). Scale bar = 20 mm. From top to bottom, shown are dorsal, ventral, and lateral views of crania, lateral view of the mandibles, and dorsal view of the mandibles with enlarged (circa x 2) view of the mandibular toothrow. White arrows in the ventral view of the crania highlight the palate behind the last molar, which is extended in* N. meridensis *relative to* N. olivacea*, and the smaller teeth of* N. meridensis*. Black arrows in the lateral view of the crania highlight the position of the anterior alveolar foramen (cf. Decker 1991), which is usually situated farther anterior of the infraorbital foramen in* N. meridensis*. White arrows in the lateral view of the mandible illustrate the configuration of the posterior processes of the dentary, in which the juxtaposition of the coronoid and condyloid processes is generally more expansively "excavated" in* N. meridensis*. The ventral view of the mandible and the close-up view of the mandibular toothrow illustrate the much smaller teeth of* N. meridensis *relative to* N. olivacea*.*

Specimens from Colombia and Ecuador are similar in most aspects, and have teeth that are equivalent in size (e.g., Fig. 2). Relative to Colombian samples, animals from Ecuador have consistently smaller skulls on average (maximum observed skull length is 105 in our Ecuadoran samples, versus 116 in Colombian skulls) and have darker, more blackish fur, and tail rings that are less clearly defined.

Molecular phylogenetics

We obtained the same topology and high support values for all analyses (Figs 3 and 4), providing strong support for the monophyly of each species, but paraphyly for the genus *Nasua* with respect to *Nasuella* (*Nasuella* is recovered as the sister lineage to *Nasua narica*; support for this finding is particularly strong for the analyses of the complete *cyt b* sequences—Fig. 4).

All analyses of short sequences produce a single moderate to strongly supported topology for the monophyly of *Nasuella* (Fig. 3). The sequence from the *Nasuella* sample from Venezuela represents a lineage basal to those from Ecuador and Colombia. Within this Ecuador – Colombia clade there is only a 1.9-2.9% sequence divergence under the K2P model, but the divergence between this clade and the Venezuela sequence based on the K2P distance is three times greater ranging from 8.0 to 9.1%. The longer sequences show a 2.1% K2P distance between the two *Nasuella* from Ecuador. The pairwise divergence estimates for the short *cyt b* sequences proved to be similar to divergence estimates from the entire *cyt b* data set. For the other samples, based on analyses

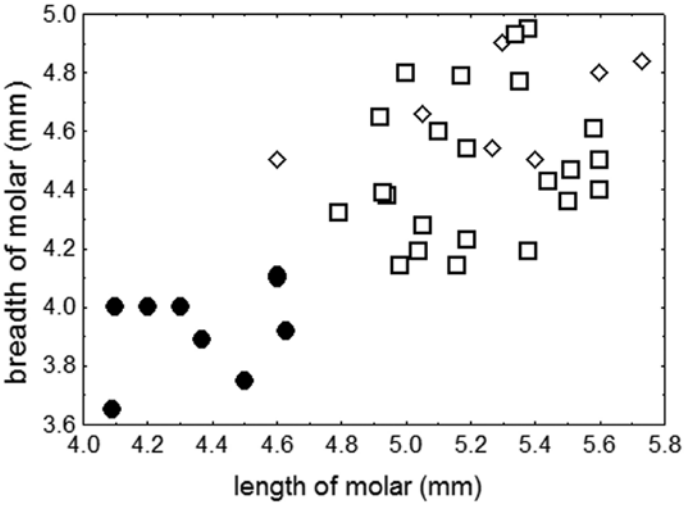

Fig. 2. Size distinction in the upper first molar (M1) in N. meridensis *(closed symbols) and* N. olivacea *(open symbols). Symbols: Closed dots* = N. meridensis *(Venezuela); open squares* = N. o. olivacea *(Colombia); open diamonds*= N. o. quitensis *(Ecuador).*

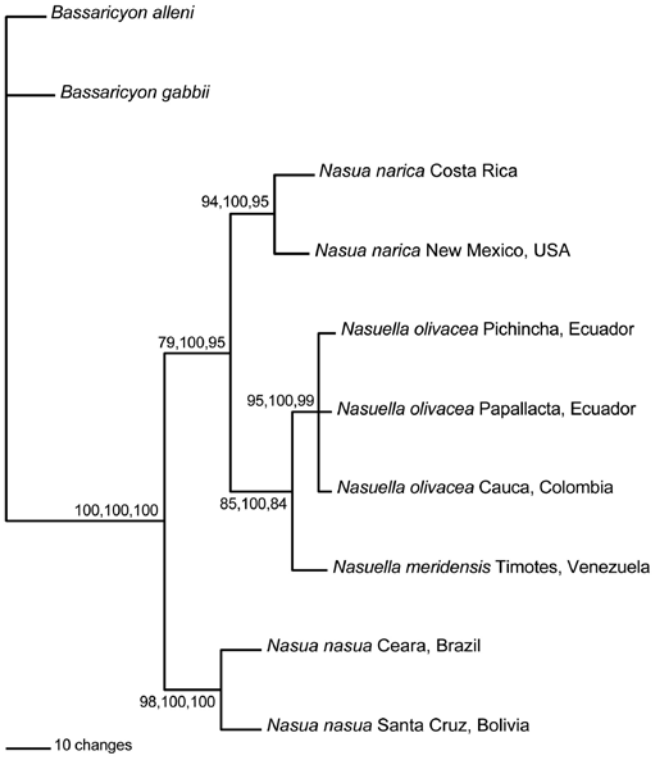

Fig. 3. Molecular relationships of coatis based on partial cytochrome b *sequences. One of three most parsimonious trees (length = 167, retention index = 0.763, consistency index = 0.760) from the partial sequence of the* cyt b *gene (366 bp). This comparison allows for the inclusion of the short sequence generated from DNA extracted from the turbinate bones of a specimen of* N. meridensis*. Branch support values represent maximum parsimony and maximum likelihood bootstrap support, followed by Bayesian posterior probabilities values, respectively.*

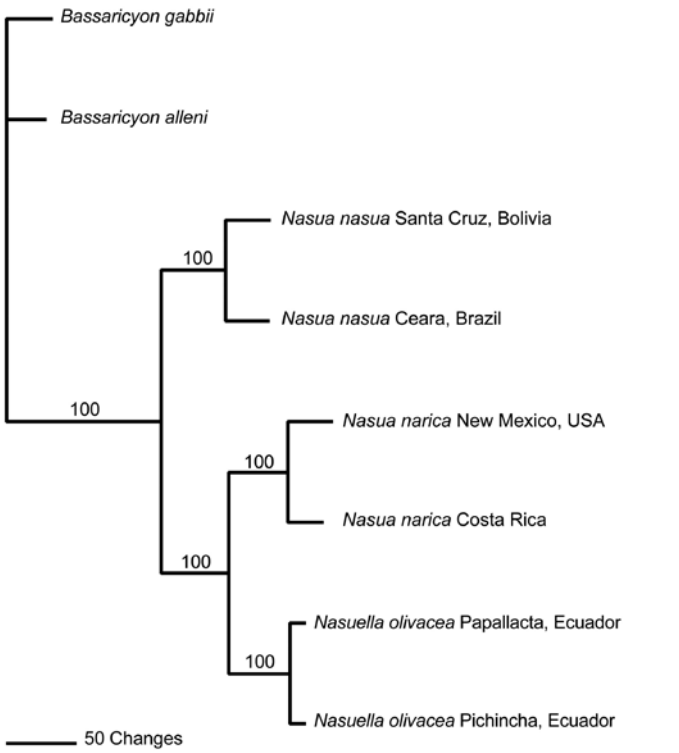

Fig. 4. Molecular relationships of coatis based on complete cytochrome b sequences. The single most parsimonious tree (length = 495, retention index = 0.764, consistency index = 0.792) from the complete cyt b *gene (1140 bp). This comparison excludes the short sequence generated from DNA extracted from the turbinate of a specimen of* N. meridensis*. Branch support values shown for all branches were the same in all analyses (maximum parsimony and maximum likelihood bootstrap values and Bayesian posterior probabilities).*

of the short and long sequences, the distance between the two *N. narica* sequences was 4.4% and 4.9% and between the *N. nasua* was 7.4 and 6.0% respectively. The divergence values within *Nasua* were 18.5-19.3%, and the divergence values between *N. narica* and *Nasuella* (Ecuador) was 9.7-12.6%.

Geographic range modeling

The distribution model was judged to have performed well based on high values for area under the curve of the final model (AUC = 0.995) and unregularized training gain (3.986). Models also performed well when we withheld 20% of the locations to test a model built on the remaining 80% of the locations (test AUC = 0.974, unregularized training gain = 3.38). The full Maxent distribution model shows most lowland areas as unsuitable, with some moderately appropriate conditions in the highlands of Central America and the Guianan shield, but the highest quality areas in the Andes (Fig. 5). The relative contributions of the environmental variables were highest for three associated with temperature. Temperature seasonality (estimated as standard deviation) had the highest contribution (40.1%) followed by the maximum temperature of the warmest month (24.0%) and mean temperature of the warmest quarter (22.9%).

To create a presence/absence range map we calculated the average probability value giving equal training sensitivity and specificity averaged across our 10 test models (p = 0.151, Fig. 6).

There was a clean break in the predicted range between Venezuela and the rest of the Andes, suggesting that geographic isolation may have contributed to the evolution of two deeply divergent allopatric species, *N. olivacea* and *N. meridensis*, as indicated by our mo-

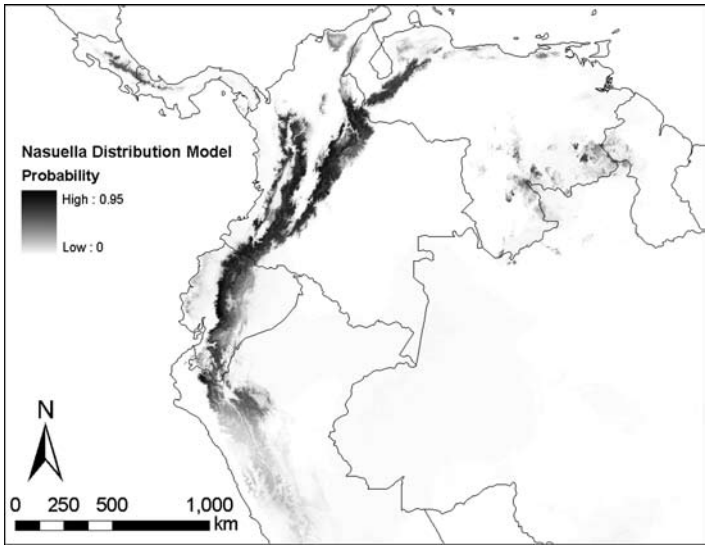

Fig. 5. Bioclimatic distribution models and localities for Nasuella*. Generated from Maxent using 33 vouchered occurrence records, 19 bioclimatic variables, and one potential habitat variable.*

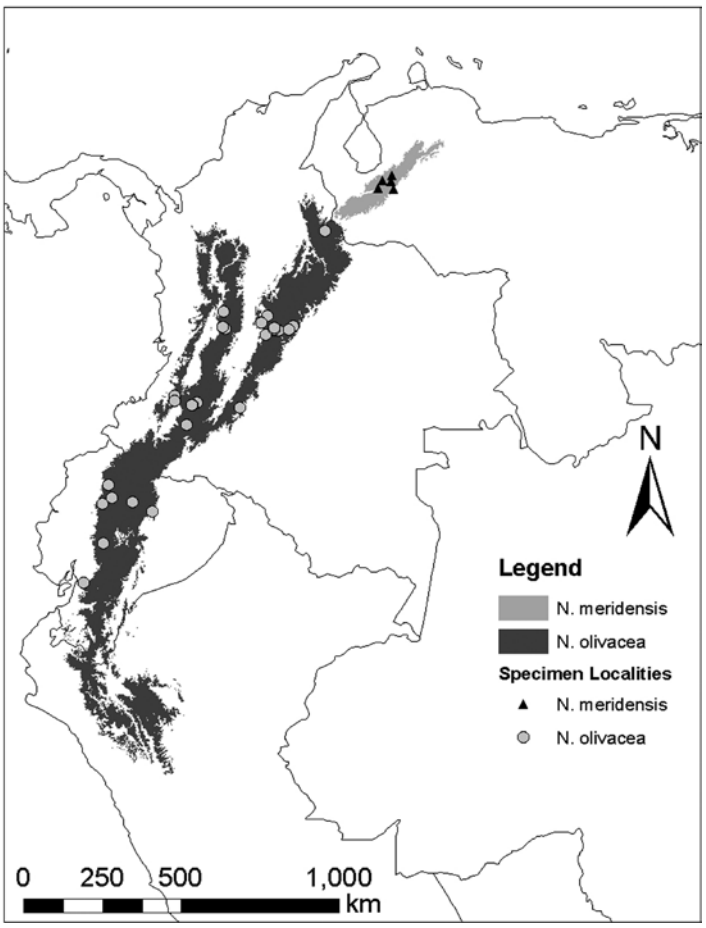

Fig. 6. Predicted distribution for Nasuella *based on bioclimatic models. To create these binary maps we used the average minimum training presence for 10 test models as our cutoff. In addition, we excluded areas of high probability that were outside of the known range of the species if they were separated by unsuitable habitat. The distribution model was made using all records for the genus and later divided between the two species based on specimen records.*

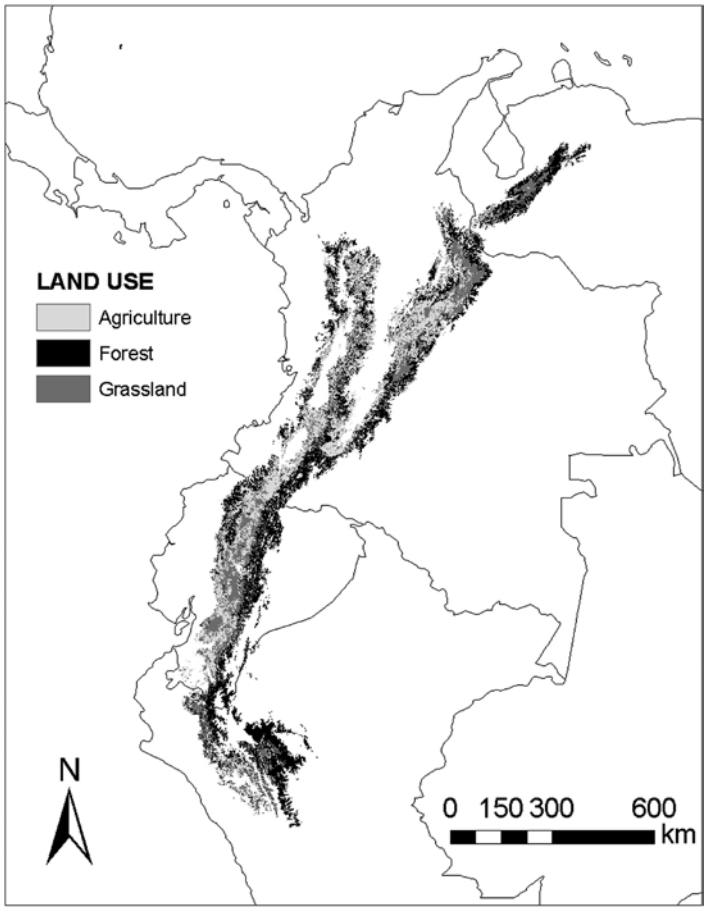

Fig. 7. Present land use across the predicted geographic distribution of Nasuella *(*N. olivacea *and* N. meridensis*). Land use data from Eva et al. (2004).*

lecular and morphological comparisons. Although *N. olivacea* has a relatively large range, only 36% of this area is presently forested (Table 3). Furthermore, these forests are highly fragmented, especially by agriculture along the central axis of its range. *Nasuella meridensis* has a smaller range, but apparently less disturbed by agriculture than *N. olivacea* (Fig. 7).

Discussion

Our examinations of museum skulls and skins reveal striking qualitative and morphometric distinctions between Mountain Coati populations from the Venezuelan Andes compared to populations from Colombia and Ecuador, which suggest considerable ecomorphological distinction between these forms. Presumably some of these differences, especially the excessively reduced teeth of Venezuelan animals, reflect functionally important distinctions such as differences in feeding mode and ecology, but this awaits further clarifying study.

These morphological distinctions are complemented by remarkably high sequence divergence in the *cytochrome b* gene (8-9%) between Venezuelan and other populations of *Nasuella*. This level of morphological and molecular divergence clearly indicates that these are deeply divergent lineages, and we recommend that they be recognized as two distinct, and clearly diagnosable, allopatric species. Though these taxa have been regarded as conspecific in the past, the name *meridensis*, applied by Thomas (1901) to Mountain Coati populations from the Merida Andes, is an available name for the Venezuelan taxon. The type locality of *N. olivacea* (Gray 1865) is the vicinity of Bogota in Colombia (Cabrera 1958); remaining species-level synonyms of *N. olivacea* include *lagunetae* (J. A. Allen 1913), with type locality "La Guneta (alt. 10,300 ft.), West Quindio Andes, Cauca, Colombia", and *quitensis* (Lönnberg 1913), with syntypes originating from Lloa and Gualea in Ecuador. To us, distinctions between Colombian and Ecuadoran samples of *N. olivacea* in both skull size and pelage (with Ecuadoran animals having significantly smaller skulls and darker fur) and mtDNA (2-3% divergence in *cyt b*) support the traditional recognition (e.g., Lönnberg 1913, Wozencraft 2005) of separate subspecies in Colombia (*N. o. olivacea*) and Ecuador (*N. o. quitensis*); the precise geographic boundaries of these subspecies remain to be determined.

Nasuella was originally diagnosed as a genus distinct from *Nasua* especially on the basis of its smaller body size, shorter tail, and more gracile skull and teeth (Hollister 1915), and has been recognized as a separate genus since its description. An intriguing result from analysis of coati *cyt b* sequences is the lack of support for monophyly of the two species classified in the genus *Nasua* (*N. nasua* and *N. narica*) relative to *Nasuella*. Instead, *Nasuella* (i.e., *N. olivacea* + *N. meridensis*) is recovered as the sister line-

Table 3. Present land use in the predicted range of N. olivacea *and* N. meridensis. *"Other" includes various inappropriate habitats (urban areas, ice, and lakes). Areas are in square kilometers.*

	N. olivacea		***N. meridensis***	
	Area	**%**	**Area**	**%**
Forest	101,784	36.2	10,413	53.8
Grassland	75,712	26.9	5,953	30.8
Agriculture	101,042	35.9	2,728	14.1
Other	2,445	0.9	249	1.3
Total	280,983		19,342	

age to *N. narica*, with high support. Thus it seems likely that the genus *Nasua* as currently recognized is not monophyletic, and that all coatis may instead be better classified as a single genus, *Nasua* (i.e., with *Nasuella* as a synonym), representing three deeply divergent evolutionary lineages—South American *N. nasua*; North American *N. narica* (with *N. nelsoni* of Cozumel); and Andean *N. olivacea* and *N. meridensis*. We continue to use *Nasuella* as a genus name in this paper pending additional clarifying morphological and genetic comparisons, particularly involving biparental (nuclear DNA) markers, which, in tandem with our mtDNA data, should allow for a more definitive resolution of coati evolutionary history.

Our review of the known and predicted geographic distribution of *Nasuella* identifies a narrow but very clear geographic gap in predicted occurrence between *N. meridensis* and *N. olivacea* in the vicinity of the Colombian-Venezuelan border (Figs 5 and 6). We speculate that this current distributional discrepancy also reflects the ancient biogeographic origin of these two allopatric taxa, for example by a climate-associated vicariant event that isolated these two populations in high montane habitats across this divide. Whatever the origin of the two species' current distributions, their distinctness has clearly been maintained in the face of fluctuating Pleistocene climate episodes during which montane forests may have periodically extended to considerably lower elevations than they do today (e.g., Schubert 1974), perhaps marginalizing the current biogeographic gap between these Andean regions.

One potentially substantive result of the geographic modeling analyses presented here is the identification of areas where, even though geographic records are currently lacking, Mountain Coatis may occur. Priorities for renewed survey efforts aimed at documenting the full geographic distribution of *Nasuella* include the southern portion of the predicted range, which extends into northern Peru. Some authors have previously suggested the possibility that the distribution of *Nasuella* may extend into Peru (e.g., Eisenberg 1989, Eisenberg & Redford 1999), but we know of no vouchered records to date. If present there, Peru might provide some of the largest remaining forested habitat in the range of *N. olivacea*, so this is important to establish. Another priority area for field surveys is the northern extension of the western cordillera of Colombia; candidate habitat is present in this region, but we are not aware of any records from this area to date. Other islands of potential habitat, isolated from the known range of *Nasuella*, are to be found in areas of northern Colombia as well as the Darien Mountains of Panama, and these offer further survey priorities.

We offer this revision of taxonomic boundaries, along with an overview of the geographic distribution of *Nasuella*, as necessary steps along a path toward generating a better understanding of the conservation status of Mountain Coatis, and identifying priorities that may assist in conservation planning and management initiatives for Mountain Coatis. Importantly, recognition of two species of *Nasuella* requires that conservation considerations be made separately for both, and demonstrates that these taxa each have smaller geographic ranges than the combined range of "*N. olivacea*" as previously recognized (e.g., *N. meridensis* has a relatively limited distribution, restricted to high montane habitats in the Venezuelan Andes). The conservation status of "*N. olivacea*" (i.e., embracing both Mountain Coati species) is currently regarded as "Data Deficient", especially because of "ongoing uncertainty surrounding the potential impacts of habitat loss and habitat conversion to agriculture" on Mountain Coati populations (Reid & Helgen 2008, Schipper *et al*. 2008). Our analyses suggest that a large proportion of the potential geographic range of *Nasuella*, especially of the Western Mountain Coati, is dominated by agricultural landscapes, which now fragment cloud forest habitats throughout the Andes—habitats on which *Nasuella* presumably depends (see also Balaguera-Reina *et al.* 2009). We hope that the new information brought to light here can be combined with better "on the ground" knowledge of Mountain Coatis—information such as the presence and security of *Nasuella* populations in protected areas, the extent to which *Nasuella* occurs in agricultural habitats, and the severity of threats such as deforestation and hunting—to provide a more insightful prognosis for the conservation of these remarkable Andean carnivores.

Taxonomy

***Nasuella olivacea* (Gray 1865)**

Suggested English common name: Western Mountain Coati.
Diagnosis: Body size smaller, tail shorter, and teeth markedly smaller than in the species of *Nasua*; distinguished from *N. meridensis* in having more saturate pelage (more rufous or blackish), usually without a blackish mid-dorsal stripe; much larger teeth, especially premolars and molars (e.g. Figs 1 and 2); a shorter lateral extension of the palate behind the upper molars (Fig. 1); the (postdental) "palatal shelf" posteriorly depressed; and the anterior alveolar foramen situated within or just anterior to the infraorbital foramen.
Distribution: *Nasuella olivacea* is endemic to the Andes of Colombia and Ecuador (Fig. 6), where it is known from cloud forest and paramo habitats, at elevations between 1300 and 4250 meters (specimens at AMNH, BMNH, EPN, FMNH, NMS, QCAZ, USNM, Balaguera-Reina *et al*. 2009). Some information on the ecology and behavior of this species in Colombia has been published in the past decade (Rodríguez-Bolaños 2000, 2003).
Subspecies: We recommend that two subspecies can be admitted on current evidence, with the precise geographic boundary between the two currently undefined.
N. o. olivacea (Gray 1865). Skull growing larger (greatest length 97-116 mm in adults), pelage paler (more brown), with dark tail rings usually evident on the tail. Distributed throughout the Andes of Colombia (*lagunetae* J.A. Allen 1913, is a synonym; see above).
N. o. quitensis (Lönnberg 1913). Skull smaller (greatest length 97-105 mm in adults), pelage darker (more blackish), with dark tail rings less clearly visible on the tail. Distributed throughout the Andes of Ecuador.

***Nasuella meridensis* (Thomas 1901)**

Suggested English common name: Eastern Mountain Coati.
Diagnosis: Body size smaller, tail shorter, and teeth markedly smaller than in the species of *Nasua*; distinguished from *N. olivacea* in having more olivaceous pelage, usually with a blackish dorsal stripe; much smaller teeth, especially premolars and molars (e.g. Figs 1 and 2); a longer lateral extension of the palate behind the upper molars (Fig. 1); the (postdental) "palatal shelf" less posteriorly depressed; and the anterior alveolar foramen situated farther anterior relative to the infraorbital foramen.
Distribution: *Nasuella meridensis* is endemic to the Venezuelan Andes (Fig. 6), where it is known from cloud forest and paramo habitats, at elevations between 2000 and 4000 meters (Thomas 1901, Handley 1976, Bisbal 1989, Linares 1998). We know of no ecological or behavioral studies of *N. meridensis* to date, but selected ecological attributes of their montane habitats have been subject to informative overview studies (e.g., Ataroff & Rada 2000, Barthlott *et al*. 2001, Janzen *et al*. 1976, Kelly *et al*. 1994, Marquez *et al*. 2004, Paoletti *et al*. 1991, Pérez 1992). The species is monotypic (i.e., no subspecies can be recognized).

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References

Allen, J. A. 1880. On the coatis (genus *Nasua*, Storr). *Bulletin of the United States Geological and Geographical Survey* 5:153–174.

Allen, J. A. 1912. Mammals from western Colombia. *Bulletin of the American Museum of Natural History* 31: 71–95.

Allen, J. A. 1913. New mammals from Colombia and Ecuador. *Bulletin of the American Museum of Natural History* 32: 469–484.

Allen, J. A. 1916. List of mammals collected in Colombia by the American Museum of Natural History expeditions, 1910–1915. *Bulletin of the American Museum of Natural History* 35: 191–238.

Ataroff, M. & Rada, F. 2000. Deforestation impact on water dynamics in a Venezuelan Andean cloud forest. *Ambio* 29: 440–444.

Balaguera-Reina, S. A., Cepeda, A., Zárrate-Charry, D., & González-Maya, J.F. 2009. The state of knowledge of Western Mountain Coati *Nasuella olivacea* in Colombia, and extent of occurrence in the Northern Andes. *Small Carnivore Conservation* 41: 35–40.

Barthlott, W., Schmit-Neuerberg, V., Nieder, J. & Engwald, S. 2001. Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. *Plant Ecology* 152: 145–156.

Bickham, J. W., Patton, J. C., Schlitter, D. A., Rautenbach, I. L. & Honeycutt, R. L. 2004. Molecular phylogenetics, karyotypic diversity, and partition of the genus *Myotis* (Chiroptera: Vespertilionidae) *Molecular Phylogenetics and Evolution* 33: 333–338.

Bisbal, F. J. 1989. Distribution and habitat association of the carnivores in Venezuela. Pp. 339–362 in Redford, K. & Eisenberg, J. (Eds) *Advances in Neotropical Mammalogy*. Sandhill Crane Press. Gainesville, Florida, USA.

Cabrera, A. 1957 (1958). Catálogo de los mamíferos de América del Sur. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciencias Zoológicas*, 4(1):iv + 308 pp.

Decker, D. M. 1991. Systematics of the coatis, genus *Nasua* (Mammalia: Procyonidae). *Proceedings of the Biological Society of Washington* 104: 370–386.

Decker, D. M. & Wozencraft, W. C. 1991. Phylogenetic analysis of Recent procyonid genera. *Journal of Mammalogy* 72: 42–55.

Eisenberg, J. F. 1989. *Mammals of the Neotropics, volume 1. The northern Neotropics—Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana*. University of Chicago Press, Chicago, USA.

Eisenberg, J. F. & Redford, K. H. 1999. *Mammals of the Neotropics, volume 3. The central Neotropics*. University of Chicago Press, Chicago, USA.

Emmons, L. H. & Feer, F. 1990. *Neotropical rainforest mammals: a field guide*. University of Chicago Press, Chicago, USA.

Emmons, L. H., & Feer, F. 1997. *Neotropical rainforest mammals: a field guide*. Second edition. University of Chicago Press, Chicago, USA.

Eva, H. D., Belward, A. S., De Miranda, E. E., Di Bella, C. M., Gond, V., Huber, O., Jones, S., Sgrenzaroli, M. & Fritz, S. 2004. A land cover map of South America. *Global Change Biology* 10: 731–744.

Friscia, A. R., Van Valkenburgh, B. & Biknevicius, A. R. 2007. An ecomorphological analysis of extant small carnivorans. *Journal of Zoology (London)* 282: 82–100.

Fulton, T. L. & Strobeck, C. 2007. Novel phylogeny of the raccoon family (Procyonidae: Carnivora) based on nuclear and mitochondrial DNA evidence. *Molecular Phylogenetics and Evolution* 43: 1171–1177.

Gray, J. E. 1843. *List of the specimens of Mammalia in the collection of the British Museum*. George Woodfall and Son, London, UK.

Gray, J. E. 1865. A revision of the genera and species of ursine animals (Ursidae) founded on the collection in the British Museum. *Proceedings of the Zoological Society of London* 1864: 677–709.

Gray, J. E. 1869. *Catalogue of carnivorous, pachydermatous, and edentate mammals in the British Museum*. Taylor and Francis, London, UK.

Guzmán-Lenis, A. R. 2004. Revisión preliminary de la familia Procyonidae en Colombia. *Acta Biológica Colombiana* 9: 69–76.

Handley, C. O., Jr. 1976. Mammals of the Smithsonian Venezuelan Project. *Brigham Young University Science Bulletin, Biological Series* 20(5): 1–91.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

Hollister, N. 1915. The genera and subgenera of raccoons and their allies. *Proceedings of the United States National Museum* 49: 143–150.

Huelsenbeck, J. P. & Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.

Janzen, D. H., Ataroff, M., Farinas, M., Reyes, S., Rincon, N., Soler, A., Soriano, P. & Vera, M. 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica* 8: 193–203.

Jarrín-V., P. 2001. *Mamíferos en la niebla: Otonga, un bosque nublado del Ecuador*. Museo de Zoología, Centro e Biodiversidad y Ambiente, Pontificia Universidad Católica del Ecuador.

Kelly, D. L., Tanner, E. V. J., Nic Lughadha, E. M. & Kapos, V. 1994. Floristics and biogeography of a rain forest in the Venezuelan Andes. *Journal of Biogeography* 21: 421–440.

Koepfli, K. P., Gompper, M. E., Eizirik, E., Ho, C.-C., Linden, L., Maldonado, J. E. & Wayne, R. K. 2007. Phylogeny of the Procyonidae (Mammalia: Carnivora): molecules, morphology, and the Great

American Interchange. *Molecular Phylogenetics and Evolution* 43: 1076–1095.

Linares, O. J. 1998. *Mamíferos de Venezuela*. Sociedad Conservacionista Audubon de Venezuela, Caracas, Venezuela.

Lönnberg, E. 1913. Mammals from Ecuador and related forms. *Arkiv för Zoologi* 8(16): 1–36.

Lord, R. 2007. *Mammals of South America*. Johns Hopkins University Press, Baltimore, Maryland, USA.

Marquez, E. J., Farinas, N. R., Briceno, B. & Rada, F. J. 2004. Distribution of grasses along an altitudinal gradient in a Venezuelan paramo. *Revista Chilena de Historia Natural* 77: 649–660.

Mondolfi, E. 1987. Baculum of the lesser Andean coati, *Nasuella olivacea* (Gray), and of the larger grison, *Galictis vittata* (Schreber). *Fieldiana Zoology* 39: 447–454.

Nylander, J. A. A. 2004. *MrModeltest v2*. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Lamoreux, J. F., Ricketts, T. H., Itoua, I., Wettengel, W. W., Kura, Y., Hedao, P. & Kassem, K. 2001. Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience* 51: 933–938.

Paoletti, M. G., Taylor, R. A. J., Stinner, B. R., Stinner, D. H. & Benzing, D. H. 1991. Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. *Journal of Tropical Ecology* 7: 373–383.

Paynter, R. A., Jr. 1982. *Ornithological Gazetteer of Venezuela*. Museum of Comparative Zoology, Cambridge, Massachusetts, USA.

Paynter, R. A., Jr. 1993. *Ornithological Gazetteer of Ecuador, second edition*. Museum of Comparative Zoology, Cambridge, Massachusetts, USA.

Paynter, R. A., Jr. 1997. *Ornithological Gazetteer of Colombia, second edition*. Museum of Comparative Zoology, Cambridge, Massachusetts, USA.

Pérez, F. L. 1992. The ecological impact of cattle on caulescent Andean rosettes in a high Venezuelan paramo. *Mountain Research and Development* 12: 29–46.

Phillips, S. J., Anderson, R. P. & Schapire, R. E. 2005. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259.

Ramírez-Chaves, H., Pérez, W. & Ramírez-Mosquera, J. 2008. Mamíferos presentes en el municipio de Popayán, Cauca, Colombia. *Boletín Cientifico Museo Historia Natural* 12: 65–89.

Reid, F. & Helgen, K. 2008. *Nasuella olivacea*. In: IUCN 2009. *IUCN Red List of Threatened Species*. Version 2009.1. <www.iucnredlist.org>. Downloaded on 25 May 2009.

Rodríguez-Bolaños, A, Cadena, A. & Sánchez, P. 2000. Trophic characteristics in social groups of the Mountain coati, *Nasuella olivacea* (Carnivora: Procyonidae). *Small Carnivore Conservation* 23: 1–25.

Rodríguez-Bolaños, A., Sánchez, P. & Cadena, A. 2003. Patterns of activity and home range of Mountain Coati *Nasuella olivacea*. *Small Carnivore Conservation* 23: 1–5.

Schipper, J. *et al*. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322: 225–230.

Schubert, C. 1974. Late Pleistocene Mérida glaciation, Venezuelan Andes. *Boreas* 3: 147–151.

Sclater, W. L. 1891. *Catalogue of Mammalia in the Indian Museum, Calcutta. Part II. Rodentia, Ungulata, Proboscidea, Hyracoidea, Carnivora, Cetacea, Sirenia, Marsupialia, Monotremata.* Trustees of the Indian Museum, Calcutta, India.

Swofford, D. L. 2003. *PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods), Version 4.0b10*. Sinauer Associates, Sunderland, Massachusetts, USA.

Tamura, K., Dudley, J., Nei, M. & Kumar, S. 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution* 24: 1596–1599.

Tate, G. H. H. 1939. The mammals of the Guiana region. *Bulletin of the American Museum of Natural History* 76: 151–229.

Thomas, O. 1901. New Neotropical mammals, with a note on the species of *Reithrodon*. Annals and Magazine of Natural History (series 7) 8: 246–255.

Tsuchiya-Jerep M. T. N. 2009. *Filogeografia, história demográfica e diversidade molecular de duas espécies neotropicais da família Procyonidae (Mammalia, Carnivora):* Nasua nasua *e* Procyon cancrivorus. Pontificia Universidade Catolica do Rio Grande do Sul (M.Sc. thesis), Porto Alegre, Brazil.

Wisely, S. M., Maldonado, J. E. & Fleischer, R.C. 2004. A technique for sampling ancient DNA that minimizes damage to museum specimens. *Conservation Genetics* 5: 105–107.

Wozencraft, W.C. 2005. Order Carnivora. Pp. 532–628. In Wilson, D.E. & Reeder, D.M. (eds.) *Mammal Species of the World*, Third Edition. The Johns Hopkins University Press, Baltimore.

Zwickl, D. J. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation, The University of Texas at Austin. (downloaded from www.bio.utexas.edu/faculty/antisense/garli/Garli.html)

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CORRIGENDUM

Helgen, K. M., Kays, R., Helgen, L. E., Tsuchiya-Jerep, M. T. N., Pinto, C. M., Koepfli, K. P., Eizirik, E. & Maldonado, J. E. 2009. Taxonomic boundaries and geographic distributions revealed by an integrative systematic overview of the mountain coatis, *Nasuella* (Carnivora: Procyonidae). *Small Carnivore Conservation* 41: 65–74.

Fig. 3 (page 70) revised. Molecular relationships of coatis based on partial cytochrome b sequences. One of three most parsimonious trees (length = 167, retention index = 0.763, consistency index =0.760) from the partial sequence of the cyt b gene (366 bp). This comparison allows for the inclusion of the short sequence generated from DNA extracted from the turbinate bones of a specimen of N. meridensis. Branch support values represent maximum parsimony and maximum likelihood bootstrap support, followed by Bayesian posterior probabilities values, respectively.

The bootstrap support values for the maximum likelihood estimate were incorrect in the original article. Our overall taxonomic conclusions remain unchanged.