Pontifícia Universidade Católica do Rio Grande do Sul
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# História evolutiva de *Conepatus* (Carnivora: Mephitidae): padrões biogeográficos de diversificação, investigação filogenética e revisão taxonômica do gênero

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PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL
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# HISTÓRIA EVOLUTIVA DE *CONEPATUS* (CARNIVORA: MEPHITIDAE): PADRÕES BIOGEOGRÁFICOS DE DIVERSIFICAÇÃO, INVESTIGAÇÃO FILOGENÉTICA E REVISÃO TAXONÔMICA DO GÊNERO

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**TESE DE DOUTORADO**
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# RESUMO

*Conepatus* (Mammalia: Carnivora) compreende um dos grupos de mamíferos neotropicais menos conhecidos. Apesar de apresentar uma extensa área de distribuição, indo do sul da América do Norte ao extremo sul da América do Sul, poucos estudos foram conduzidos até o momento sobre o gênero. A falta de conhecimento envolvendo ecologia, morfologia e distribuição das diferentes populações dificulta estudos comparativos, fazendo com que grande parte da diversidade do grupo permaneça desconhecida. O problema mais básico, contudo, parece ser a falta de estudos envolvendo sua história evolutiva e relações filogenéticas, disciplinas balizadoras da taxonomia moderna. Uma classificação taxonômica sólida é primordial para o estudo de qualquer grupo, já que é o princípio que norteia a descrição dos demais aspectos de uma determinada população. Além das contribuições taxonômicas, conhecer a história evolutiva de um táxon é importante também por que é a partir do entendimento cumulativo da estrutura da diversidade de vários grupos que se pode entender grandes padrões históricos. Assim, para contribuir com o conhecimento relativo a essas questões fundamentais, este estudo procurou revisar vários aspectos deste gênero. Entre eles estão padrões filogenéticos, evolutivos, morfológicos, de distribuição e de estrutura populacional, culminando assim em uma revisão taxonômica. Para tanto, foram realizadas análises moleculares baseadas em 1.902 pares de base pertencentes a três fragmentos do DNA mitocondrial, além de oito locos de microssatélites nucleares. Também foram conduzidos dois tipos de análise morfológica. A primeira baseou-se em um painel de 29 medidas de crânio e dentes para identificar padrões de estrutura populacional, enquanto a segunda procurou por diferenças no padrão corporal geral entre algumas das populações identificadas. Finalmente, realizou-se uma extensa busca por registros de ocorrência geográfica do gênero em publicações originais e bases de dados de coleções científicas. Os resultados obtidos indicam que *Conepatus* é um gênero bastante estruturado geograficamente, apresentando, no mínimo, 10 grupos distintos. Também é possível afirmar que ao menos alguns dos grupos identificados apresentam um nível perceptível de diferenciação morfológica em termos de aspectos corporais gerais, o que reforça a idéia de estruturação neste grupo. A respeito dos padrões de distribuição, fica claro que o gênero habita quase que exclusivamente áreas de campo e florestas secas, sendo raramente encontrado em florestas densas. Algumas descontinuidades de distribuição podem ser percebidas, podendo estar diretamente ligadas ao isolamento total ou parcial dos grupos. A história evolutiva do gênero é complexa, e parece estar ligada a padrões biogeográficos amplos. A coalescência dos grupos da América do Sul e Central é de cerca de 3,2 milhões de anos atrás (MAA), apoiando a hipótese de que o gênero invadiu o continente sul-americano logo após o fechamento do Istmo do Panamá, há 2.8 MAA. A coalescência das amostras sul-americanas, contudo, é bem mais recente (cerca de 0.85 MAA), sugerindo uma evolução complexa, possivelmente ligada à dinâmica vegetacional intrincada da América do Sul ao longo das eras glaciais do Pleistoceno. Finalmente, a revisão taxonômica proposta sugere que os 10 grupos identificados sejam elevados à categoria de espécie, devido ao padrão observado de diferenciação entre estas linhagens.

# ABSTRACT

**Evolutionary history of *Conepatus* (Carnivora: Mephitidae): biogeographic patterns of diversification, phylogenetics investigation and taxonomic revision** – *Conepatus* (Mammalia: Carnivora) comprises one of the least known groups of Neotropical mammals. Despite its broad distribution, ranging from southern North America to southernmost South America, few studies have been conducted on this genus. The lack of knowledge regarding the ecology, morphology and distribution of different populations hampers comparative studies, resulting in much of the group's diversity remaining unknown. The most basic problem, however, seems to be the lack of studies regarding the evolutionary history and phylogenetic relationships among its populations, which are the main grounds for modern taxonomic classifications. A solid taxonomic arrangement is critical, since it is the principle that guides the description of all other aspects of a given population. Finally, understanding the evolutionary history of a taxon is important not only due to taxonomic concerns, but also because it is the cumulative knowledge on the diversification of different groups that allows the description of major biogeographic patterns. Attempting to shed light on several of these aspects, this study investigated phylogenetic patterns, evolutionary history, population structure, morphological variation and general distribution of *Conepatus*, which altogether led to a taxonomic revision. To accomplish this, molecular analyses were performed, based on 1,902 base pairs of the mitochondrial DNA and eight microsatellite loci. We also conducted two types of morphological surveys. The first one was based on a panel of 29 craniodental measurements, while the second one investigated the differentiation of external body features among previously identified populations. Finally, we performed an extensive search for geographic records in original publications and scientific collection databases. Overall, the results indicated that *Conepatus* is a highly structured genus, encompassing at least 10 distinct geographic groups. In addition, at least some of these groups presented a noticeable level of morphological differentiation in terms of general body aspects, which reinforces the identified population structure. With respect to distributional aspects, *Conepatus* seems to inhabit almost exclusively open habitats and dry forests, rarely being found in moist dense forests. Some distributional discontinuities could be identified, which may be directly linked to the complete or partial isolation between groups. The evolution of the genus is complex, and appears to be linked to broad biogeographic patterns. The coalescence of Central and South American groups was estimated in *ca.* 3.2 million years ago (MYA), supporting the hypothesis that this genus colonized South America right after the complete closure of the Panama Isthmus, *ca.* 2.8 MYA, during the Great American Biotic Interchange. The coalescence of the South American populations, however, is far more recent (*ca.* 0.85 MYA), suggesting a complex evolutionary history, possibly linked to the peculiar vegetation dynamics that took place in South America during the cycles of Pleistocene ice ages. Finally, a new taxonomic arrangement is proposed, suggesting that all 10 identified groups could be elevated to the rank of species, due to the observed pattern of differentiation among these lineages.

# APRESENTAÇÃO

A presente tese de doutoramento está estruturada na forma de artigos científicos (Capítulos II e III), acompanhados de introdução e conclusões gerais (Capítulos I e IV, respectivamente). Introdução e conclusões gerais estão redigidas em português, seguindo as normas da revista *Zoological Journal of the Linnean Society* para referências bibliográficas. Os artigos estão em fase de finalização e serão submetidos aos periódicos científicos *Journal of Heredity* (artigo que representa o Capítulo II) e *Zoological Journal of the Linnean Society* (Capítulo III), após a incorporação das recomendações recebidas da banca examinadora. As normas de submissão de cada uma das revistas estão anexadas no final do presente documento (Anexos I e II). Adicionalmente, está anexado um artigo em que o doutorando é o segundo autor (Anexo III), publicado no periódico *Small Carnivore Conservation*, durante o primeiro ano do período deste doutoramento (2009). Este artigo faz uma revisão geral do conhecimento à época sobre duas das espécies sul-americanas de *Conepatus*, *C. chinga* e C. semistriatus, e também apresenta alguns resultados iniciais dos estudos desenvolvidos por este doutorando e seus colaboradores.

# CAPÍTULO I – INTRODUÇÃO GERAL

Zorrilhos, jaratatacas, jitiras, jacarambevas ou cangambás. Estes são alguns dos nomes populares pelos quais são conhecidos os membros do gênero *Conepatus* no Brasil. Nos países de língua espanhola recebem outras diversas denominações: zorrinos, zorrillos, zorros hediondos, chingues ou mapurites. No inglês, hog-nosed skunks ou rooter skunks. Todas estas denominações se referem a um grupo de animais bastante conspícuos. São mamíferos de pequeno a médio porte, pesando de 0,5 a 4 quilos e medindo de 40 centímetros a quase 1 metro de comprimento, sendo aproximadamente um terço deste tamanho devido à cauda. O corpo é fusiforme, com focinho alongado e unhas grandes. A coloração dos pelos de fundo vai do negro ao marrom, com uma característica coloração branca no dorso (Dragoo, 2009).

O padrão da coloração dorsal varia enormemente, tanto entre populações quanto dentro das mesmas, sendo inclusive motivo de controvérsias taxonômicas ao longo da história. Há desde indivíduos com uma faixa contínua e larga, que se estende desde a cabeça até a cauda, até animais sem praticamente qualquer pelo branco. Indivíduos intermediários geralmente apresentam duas listras brancas, que podem variar tanto na largura quanto no comprimento, com diferentes padrões de manchas na cabeça e cauda (Figura 1). Recentemente, um indivíduo aparentemente albino foi também registrado na Argentina (Castillo, 2011). Muitos autores basearam-se nas diferenças de coloração para sugerir agrupamentos taxonômicos, mas estudos recentes mostram que a variação de pelagem dentro de uma mesma população é tão grande que a torna pouco aplicável para a delimitação de táxons (Van Gelder, 1968; Dragoo *et al.*, 2003; Schiaffini *et al.*, 2013).

Parece claro, contudo, que tal combinação de cores os torna inconfundíveis, o que talvez tenha relação direta com a sua característica mais conhecida. Característica esta que compartilham com os outros gêneros da família a que pertencem, Mephitidae (Wozencraft, 2005). Os mefitídeos possuem um par de glândulas perianais capazes de produzir e armazenar uma quantidade considerável de uma secreção líquida fétida, utilizada como defesa (Dragoo, 2009). Em situação de perigo, os indivíduos levantam a cauda e borrifam a substância a até um metro de distância na direção da ameaça, que é imediatamente afastada (Brazil, 1924). Alguns autores associam esta coloração conspícua com aposematismo, isto é, uma vez que o agressor a relacione com o forte odor, passa a evitá-la (Stankowich *et al*., 2011). A potência singular desta defesa química atraiu o interesse de vários pesquisadores, que tentam rastrear seus componentes moleculares desde 1862. Wood (1999) publicou uma revisão bastante informativa sobre o tema, incluindo o histórico da pesquisa e uma tabela comparativa com os principais componentes encontrados em espécies dos três gêneros americanos de Mephitidae. Segundo este autor, a composição da secreção de *C. leuconotus* contém 71% de (*E*)-2-buteno-1-tiol, um composto organossulfurado que parece assim ser o responsável pelo forte odor, altamente eficiente como arma de defesa. Coincidentemente ou não, a predação de zorrilhos por outros animais já foi eventualmente registrada (Yáñez *et al*., 1986; Foster *et al*., 2010), mas parece rara.

**Figura 1. Aparência geral e variação morfológica e de coloração de indivíduos do gênero *Conepatus* de diferentes regiões da sua distribuição. A – Patagônia, América do Sul (Crédito: Dênis Sana); B – Pampas, Brasil (Crédito: Manoel LF Rodrigues); C – Arizona, EUA (Crédito: Saguaro National Park, disponível em http://www.inaturalist.org); D – Cusco, Peru (Crédito: Edward Hurme, disponível em http://www.inaturalist.org).**

A eficiência na defesa contra predadores naturais talvez seja uma das explicações para o grande sucesso do gênero em termos de distribuição, já que

*Conepatus* é um dos gêneros de mamíferos neotropicais com maior área de ocorrência. Sua distribuição e hábitos parecem estar ligados a ambientes de campo (Nowak, 1999), mas alguns registros em áreas de floresta densa (*e.g.* Cáceres, 2004) e a falta de uma revisão detalhada acerca das áreas de ocorrência deixam alguns pontos dessa discussão em aberto. A distribuição conjunta das quatro espécies atualmente reconhecidas vai da Patagônia até o sul da América do Norte, sendo registrada em quase todos os países da América do Sul e Central, além de México e Estados Unidos (Figura 2).

**Figura 2. Distribuição das quatro espécies atualmente reconhecidas de *Conepatus*, baseada nos mapas da Lista Vermelha da IUCN (IUCN, 2012). Amarelo – *C. humboldtii;* Verde – *C. chinga*; Vermelho – *C. semistriatus*; Azul – *C. leuconotus.***

Ao mesmo tempo, algumas características da biologia destes animais também parecem estar relacionadas ao seu grande sucesso em vários e diferentes ambientes. Apesar de poucas populações já terem sido estudadas quanto a este quesito, os poucos trabalhos são congruentes, apontando um padrão geral que será apresentado a seguir. Zorrilhos são animais noturnos, solitários e com comportamento territorialista pouco desenvolvido (Fuller *et al*., 1987; Donadio *et al*., 2001; Castillo *et al*., 2011a Kasper *et al*., 2012a). O forrageamento é intenso e dura quase todo o período de atividade do indivíduo, quando ele revira o solo utilizando suas fortes garras e boa capacidade olfatória à procura de insetos e larvas (Kasper *et al*., 2009; Dragoo, 2009). Alternativamente, zorrilhos podem se alimentar de outros invertebrados, ovos, peixes, sapos e aves, além de carcaças de outros animais e até plantas e frutas (Travaini *et al*., 1998; Donadio *et al*., 2004; Medina *et al*., 2009; Peters *et al*., 2011), o que os torna bastante generalistas e, portanto, mais plásticos em termos de adaptação a diferentes condições ambientais. Também usam suas garras para cavar buracos, os quais usam como tocas, onde geralmente repousam durante o período diurno. Alternativamente, também se abrigam em cavidades deixadas por outros animais, ocos de árvores e mesmo elementos da vegetação, mudando com frequência o local de refúgio (Castillo *et al*., 2011b; Kasper *et al*., 2012a). Finalmente, pouco se sabe sobre sua reprodução. Parecem se reproduzir uma vez ao ano, tendo geralmente de dois a três filhotes. Há cuidado parental por parte das mães até que os filhotes dispersem, alguns meses após o nascimento (Kasper *et al*., 2009; Dragoo, 2009). A capacidade reprodutiva relativamente alta é outro fator que pode contribuir para o sucesso do gênero.

Contudo, apesar de estarem presentes em vários ambientes, sendo até mesmo abundantes em alguns deles (*e.g.* Kasper *et al*., 2012b), o gênero está entre os grupos de mamíferos neotropicais menos conhecidos (Oliveira, 2006). Poucas populações foram estudadas quanto à sua morfologia, ecologia e distribuição precisa, e quase toda a biologia descrita para o grupo está baseada em alguns poucos estudos conduzidos com populações do sul da América do Sul (Argentina, Chile, Uruguai e sul do Brasil). A distribuição geográfica disponibilizada pela Lista Vermelha da IUCN (IUCN, 2012) é claramente incorreta, deixando de incluir algumas regiões onde a presença de indivíduos do gênero é notória, como boa parte do Brasil e o centro da Argentina (como exemplo de registros geográficos para estas localidades ver Cavalcanti, 2010; Peters *et al*., 2011; Schiafiini *et al*. 2013). Dessa maneira, estudos comparativos e de revisão do gênero ficam bastante comprometidos, o que pode levar a uma subestimativa da diversidade real de formas e hábitos que compõem o gênero. Também importante, a falta de estudos comparativos impede que se gerem hipóteses de estruturação geográfica, uma vez que é a partir de diferenças aparentes entre as diversas populações que se pode suspeitar que duas ou mais delas estejam total ou parcialmente isoladas.

A taxonomia, de fato, é um dos problemas mais claros e urgentes no grupo, uma vez que uma sólida delimitação de unidades taxonômicas é a base para que futuros estudos descritivos caracterizem os diferentes grupos, identificando também possíveis ameaças regionais à sua conservação. Até o momento não existem revisões amplas e modernas do gênero, o que está diretamente relacionado ao escasso conhecimento sobre sua história evolutiva e relações filogenéticas internas. A seção seguinte visa a revisar os aspectos já estudados e as principais limitações no conhecimento referente à evolução e taxonomia de *Conepatus* dentro do contexto da sua família, Mephitidae.

### *Taxonomia e história evolutiva de Mephitidae*

Carnivora é uma das ordens mais populares entre os mamíferos, incluindo vários animais conhecidos pelo público em geral, como felinos, hienas, canídeos, ursos, lontras, focas, leões marinhos e os próprios zorrilhos. Classicamente, 11 famílias eram reconhecidas pela literatura (Nowak, 1999), mas recentes avanços moleculares na área elevaram este número para 16, resolvendo boa parte das incertezas taxonômicas do grupo (Eizirik *et al*., 2010). Entre as novas famílias está Mephitidae, anteriormente colocada dentro de Mustelidae como subfamília Mephitinae devido ao compartilhamento de alguns caracteres, agora sabidamente homoplásicos: glândulas perianais maiores que em outros carnívoros e perda de algumas estruturas dentárias. As glândulas dos mefitídeos, no entanto, são ainda mais desenvolvidas que nos mustelídeos, dando à família sua característica mais típica, que ao mesmo tempo é a sinapomorfia que sempre os uniu: a defesa química (Dragoo, 2009). A elevação do grupo para o nível de família foi primeiramente proposta por Dragoo & Honeycutt 1997, sendo definitivamente confirmada por estudos mais completos e robustos publicados posteriormente (Flynn *et al*., 2005; Eizirik *et al*., 2010).

Mephitidae é uma família essencialmente americana, composta por quatro gêneros e 12 espécies. Destas, apenas as duas espécies de *Mydaus* (*M. javanensis* e *M. marchei*) são exclusivamente asiáticas, ocorrendo nas Filipinas, Malásia, Ilha de Java e Indonésia. Os três outros gêneros (*Mephitis*, *Spilogale* e *Conepatus*) se distribuem exclusivamente pelas Américas. Enquanto *Mephitis* e *Spilogale* têm distribuição restrita às Américas do Norte e Central, *Conepatus* tem ocorrência mais ampla, ocorrendo também na América do Sul (Wozencraft, 2005). Apesar de apresentarem alguma variação no tamanho, os componentes deste grupo são todos mamíferos de pequeno a médio porte, apresentando uma coloração de fundo escuro com manchas claras bastante característica e possivelmente aposemática (Stankowich *et al*., 2011) (Figura 3). O hábito alimentar do grupo parece ser essencialmente onívoro, com ênfase em insetos. Todos possuem garras fortes e têm por hábito revirar o solo em busca de insetos e larvas, estando presentes nos mais diferentes ambientes das Américas (Dragoo, 2009).

A evidência fóssil indica que a origem da família é a Eurásia, onde apresentava ampla distribuição e diversidade considerável ao redor do Mioceno Médio. O fóssil mais antigo de um mefitídeo conhecido até hoje – um crânio do gênero *Palaeomephitis* – é datado em cerca de 11-12 milhões de anos atrás (MAA) (Wolsan, 1999). Pelo menos três gêneros – e possivelmente mais – presentes em diferentes regiões da Ásia e da Europa são atribuídos a esta família entre o Mioceno (23 – 5,3 MAA) e o Plioceno (5,3 – 3,6 MAA) (Wang *et al*., 2005). A relação filogenética dos gêneros atuais apoia essa hipótese, já que a posição de *Mydaus* como grupo mais basal é reconstruída por abordagens moleculares recentes com alto suporte (Eizirik *et al*., 2010). Acredita-se que em algum ponto do Mioceno uma única invasão do continente americano tenha ocorrido, provavelmente através do estreito de Bering, dando origem ao grupo dos mefitídeos do Novo Mundo. A datação molecular de Eizirik *et al*. (2010) estima a separação entre as linhagens da Eurásia e das Américas em cerca de 20 MAA (IC 95%: 14,6 – 28,2 MAA), sugerindo uma origem ainda mais antiga para a família inteira. No entanto, devido à falta de registros fósseis anteriores a 12 MAA e aos poucos pontos internos de calibração fóssil utilizados para a análise de datação, esta estimativa pode estar superestimada.

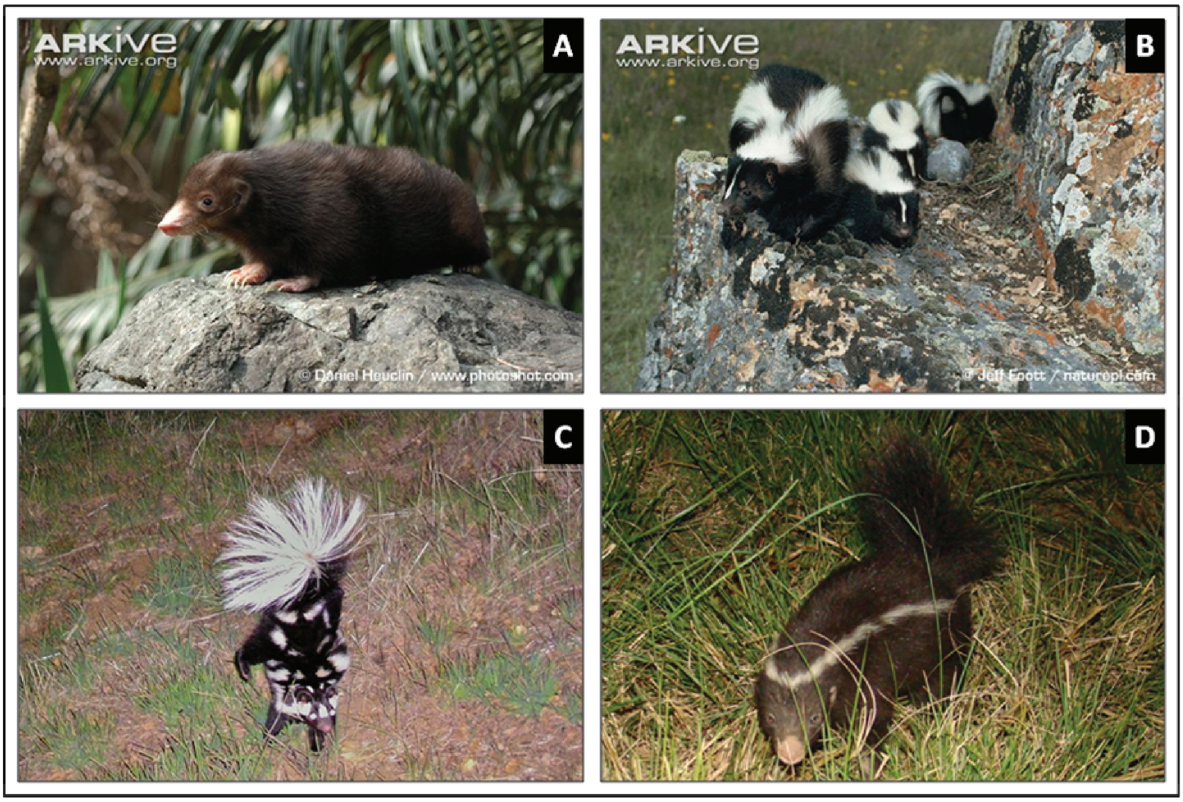

**Figura 3. Representantes dos quatro gêneros atuais de Mephitidae. A – *Mydaus marchei* (Crédito: Daniel Heuclin, disponível em Http://www.arkive.org); B – *Mephitis mephitis* (Crédito: Jeff Foott, disponível em http://www.arkive.org); C – *Spilogale gracilis* (Crédito: ramdomtruth (usuário), disponível em http://www.flickr.com); D – *Conepatus chinga* (Crédito: Carlos Benhur Kasper).**

Em relação à linhagem do Novo Mundo, o mais antigo fóssil conhecido pertence ao gênero *Martinogale*, com idade estimada de 9,3 milhões de anos (MA) (Wang *et al*., 2005). Este parece ser o mefitídeo americano mais basal, apresentando registros fósseis espalhados pelo Mioceno tardio, embora sua monofilia não seja clara (Wang *et al*., 2005; Wang & Castañeda, 2008). Uma forma mais recente e intermediária, *Buisnictis*, aparece no início do Plioceno, e logo a seguir uma explosão de diversidade parece ter tido início, com vários novos grupos sendo registrados em várias bacias sedimentares da América do Norte. Os primeiros membros dos gêneros atuais parecem ter origem neste episódio de diversificação, sugerindo que a coalescência do grupo-coroa dos mefitídeos americanos esteja entre o fim do Mioceno e o início do Plioceno (Kurtén & Anderson, 1980; Wang *et al*., 2005). Atualmente, o mais antigo registro de um gênero americano moderno se refere a um espécime de *Conepatus* do México, com 4,8 MA de idade (Wang & Catañeda, 2008). Já os fósseis mais antigos de *Mephitis* e *Spilogale* têm entre 1,8 e 3 MA de idade (Kurtén & Anderson, 1980) sugerindo que estes gêneros sejam mais recentes. Mais uma vez, os dados moleculares de Eizirik *et al*. (2010) corroboram este cenário, uma vez que *Conepatus* aparece como grupo basal, com alto suporte. A estimativa de ponto para a idade deste nó é muito próxima daquela do fóssil mais antigo de um mefitídeo americano (~9,2 MA), de forma que no momento não se pode inferir se o mesmo se trata de um táxon basal (*stem taxon*) ou de um representante do grupo-coroa desta linhagem.

### *Taxonomia e história evolutiva de* ***Conepatus***

Quatro espécies são atualmente aceitas para *Conepatus* (Wozencraft, 2005): *C. leuconotus* para a América do Norte e Central; *C. semistriatus* para América Central, norte da América do Sul e nordeste brasileiro; *C. chinga* para a porção central da América do Sul; e *C. humboldtii* para a Patagônia (Figura 2). O histórico da taxonomia do grupo, no entanto, é complexo. A problemática envolvendo *Conepatus* parece ser fruto da grande variação morfológica existente no grupo, referente tanto ao tamanho e formas corporais quanto aos padrões de pelagem. Muitos táxons foram descritos, entre o final do século XIX e início do século XX, por naturalistas europeus que coletavam ou recebiam carregamentos de coletas realizadas em diferentes pontos nas Américas. Baseando-se em um ou poucos espécimes, estes naturalistas atribuíam quase qualquer padrão variante a um novo táxon, como pode ser percebido nos textos de Oldfield Thomas, do Museu Britânico de História Natural. Sozinho, ele descreveu mais de dez táxons para o gênero. Uma passagem da descrição de *C. arequipae* (Thomas, 1900: 467), ilustra esta postura (trecho traduzido para o português por este autor):

> “**... Este zorrilho é um intermediário entre *C. quitensis* e *C. rex*. Ele se diferencia do primeiro pelo seu tamanho menor, pela natureza mais definitivamente reversa dos pelos da nuca, e pelas listras brancas terminando na região lombar e não passando para trás, para a raiz da cauda. De *C. rex*, por outro lado, ele se diferencia pelo tamanho consideravelmente maior e pelas listras brancas serem totalmente separadas uma da outra pela linha preta mediana.”**

A primeira espécie de *Conepatus*, *C. chinga*, foi descrita por Molina (1782), originalmente como *Viverra chinga*. Algumas outras espécies foram descritas nos anos seguintes, como *C. semistriatus* Boddaert, 1785 e *C. leuconotus* Lichtenstein 1832, originalmente *Viverra semistriatus* e *Mephitis leuconota*, respectivamente (Dragoo, 2009). Foi apenas em 1837 que Gray cunhou o nome *Conepatus,* ao descrever *C. humboldtii*, e sugeriu que algumas espécies já descritas fossem incorporadas ao novo gênero. Muitas espécies e subespécies foram então descritas para *Conepatus*, principalmente na virada do século XX, chegando a totalizar mais de 20 táxons.

As primeiras revisões do gênero surgiram em meados do século XX. Cabrera (1958) sinonimizou vários táxons e deu à taxonomia do grupo o padrão geral que é seguido por muitos autores até hoje. Ele incluiu vários táxons com ocorrência para Uruguai, sul do Brasil e Argentina em *C. chinga,* do Chile, dando à espécie um padrão de distribuição muito próximo ao aceito atualmente. Também foi este autor que incluiu as populações da América Central, centro do Brasil, Colômbia, Venezuela e Equador e norte do Peru em *C. semistriatus*, gerando o padrão disjunto que hoje se observa em todas as distribuições da espécie presentes na literatura. Alguns anos depois, em 1965, Kipp realizou um estudo comparativo, e, baseando-se principalmente em amostras de pele, fez algumas proposições taxonômicas (Van Gelder, 1968; Schiaffini *et al*., 2013). O arranjo geral proposto por esta autora não foi seguido, mas duas de suas proposições foram incorporadas ao esquema de Cabrera: a inclusão de *C. rex* (Peru, Bolívia, norte da Argentina e norte do Chile) em *C. chinga*, e a de *C. castaneus* (Argentina, entre o sul da província de Buenos Aires e norte de Rio Negro) em *C. humboldtii*. Assim, pode-se dizer que o arranjo taxonômico seguido hoje pelos principais autores (*e.g.* Wozencraft, 2005; Dragoo, 2009) é baseado em Cabrera, com pequenas modificações incorporadas a partir de Kipp.

Estes autores, contudo, não incluíram os táxons norte-americanos nas suas revisões. As duas espécies tradicionalmente aceitas para a América do Norte, *C. leuconotus* e *C. mesoleucus*, e suas respectivas subespécies, foram revisadas por Dragoo *et al*. (2003), que ao não encontrar padrões geográficos de diferenciação morfológica ou molecular propôs que ambas fossem sinonimizadas. Chega-se assim ao arranjo taxonômico atualmente aceito, com quatro espécies. Entretanto, a falta de uma revisão geral, comparativa e com ferramentas taxonômicas modernas, além do desencontro de informações entre alguns autores importantes, deixa várias questões em aberto. Alguns pesquisadores admitem inclusive que todas as espécies atualmente reconhecidas no gênero possam ser coespecíficas (Nowak, 1999). Em recente compilação sobre a família, Dragoo (2009) enfatiza a grande necessidade de um estudo de revisão sobre o gênero.

A falta de um arranjo taxonômico consistente para *Conepatus* é também um reflexo da escassez de estudos envolvendo a história evolutiva do gênero, principalmente no que se refere às populações sul-americanas. A filogenética é a disciplina-base da taxonomia moderna, o que faz com que cada vez mais as revisões taxonômicas sejam conduzidas em conjunto com o estudo da evolução do grupo. Poucos estudos até hoje abordaram este aspecto, e a história evolutiva de *Conepatus* permanece com muitos pontos desconhecidos.

Acredita-se que a origem do gênero deu-se na América do Norte, dentro de uma explosão de diversidade da família Mephitidae que ocorreu no início do Plioceno (ver acima). O registro fóssil indica que o gênero já estava presente na região da atual América Central antes do fechamento total do Istmo do Panamá (Wang & Castañeda, 2008). Este evento geológico, que começou há aproximadamente 12 MA e culminou na total conexão dos dois continentes há aproximadamente 2,8 MA (Woodburne, 2010), deu origem a um dos mais importantes eventos biogeográficos da história dos mamíferos, o Grande Intercâmbio Americano de Fauna. Muitos táxons da fauna endêmica sul-americana, como preguiças e gambás, invadiram o continente do norte. Mas a maior migração em termos de número de táxons foi no sentido norte-sul, podendo-se citar veados, porcos-do-mato, camelídeos e diversas famílias de carnívoros como principais representantes. Dentre os representantes da família Mephitidae, *Conepatus* é o único que parece ter invadido e prosperado na América do Sul (Marshall *et al*., 1982).

A invasão dos diferentes táxons, contudo, não foi simultânea. Existem ondas migratórias descritas mesmo antes do fechamento completo do Istmo, como no caso da invasão dos procionídeos (sentido norte-sul) e preguiças (sul-norte) (Marshall *et al*., 1982; Woodburne, 2010). Algumas das primeiras revisões sobre o tema indicavam que *Conepatus* teria participado da primeira onda migratória após o fechamento completo, aproximadamente 2,6 MAA, devido a um registro fóssil desta época encontrado na Argentina (*e.g.* Marshall *et al*., 1982). Posteriormente a idade precisa deste fóssil foi colocada em dúvida, sendo este um tema ainda em debate (para uma revisão ver

Wang & Castañeda, 2008). A provável presença do gênero na América Central no período do fechamento do istmo, bem como a cobertura vegetal aberta que se estendia tanto pela América Central como pela maior parte da América do Sul à época (Woodburne, 2010), fortalecem a hipótese de que *Conepatus* possa ter sido um dos primeiros gêneros a migrar do norte para o sul. Contudo, segundo Wang & Castañeda (2008), teria havido duas entradas distintas de *Conepatus* no continente sul-americano, uma delas dando origem às linhagens do sul (*C. chinga* e *C. humboldtii*) e outra dando origem à população do Brasil central, mais proximamente relacionada a linhagens centro-americanas atuais. Estudos evolutivos que possam investigar a estruturação populacional do grupo e datar a separação entre as linhagens norte e sul-americanas poderiam contribuir significativamente com este debate.

Outro aspecto diretamente ligado ao estudo evolutivo do gênero é a análise da estruturação geográfica de *Conepatus* na América do Sul através de ferramentas modernas, a qual ainda se encontra em um estágio inicial. Até 2012 nenhum trabalho havia sido publicado sobre o tema. Schiaffini *et al*. (2013), em um estudo simultâneo com a presente tese, foram os primeiros a publicar dados confrontando a estrutura taxonômica tradicional com uma investigação envolvendo dados moleculares e morfológicos. Os autores testaram a existência de *C. humboldtii* e *C. chinga* buscando por uma possível estruturação geográfica consistente da variação encontrada. Ao não serem capazes de encontrá-la, os autores sugerem a sinonimização das duas espécies, em caso semelhante ao de Dragoo *et al*. (2003), que propuseram a mesma medida para as espécies norte-americanas. Em conjunto, estes resultados revelam a urgência de uma revisão mais ampla da taxonomia de *Conepatus* através de um estudo que investigue seus padrões de estruturação geográfica ao longo de toda sua distribuição.

Ao mesmo tempo, a partir do ponto de vista evolutivo, a delimitação taxonômica e espacial das populações, em conjunto com a datação dos seus eventos de divergência, torna possível realizar inferências a respeito de quais e como foram os processos responsáveis pela diversidade observada atualmente (*e.g.* Johnson *et al*., 2006; Patou *et al*., 2008). Esse conhecimento também é de suma importância, uma vez que a caracterização dos processos que afetaram um determinado táxon pode ser analisada em conjunto com os processos que afetaram outros grupos, para que se entendam grandes padrões de diversificação. *Conepatus*, por exemplo, pode ser utilizado como referência para táxons que estejam intimamente relacionados com os ambientes de campo da América do Sul, os quais sabidamente apresentam uma história complexa.

Nos últimos 2 milhões de anos a Terra tem passado por períodos alternados de glaciação e interglaciação (Sigman & Boyle, 2000). Os períodos glaciais são mais frios, e assim uma maior parte da água do planeta fica retida nas calotas polares. O clima fica então mais seco, o que pode favorecer a expansão das savanas. O processo contrário acontece nos períodos interglaciais, quando o clima é mais quente, úmido e assim mais propício à expansão de florestas. A alternância entre estes dois tipos de período, associados a fatores edáficos e climáticos locais, fez com que a vegetação da América do Sul tenha tido uma evolução complexa, com períodos de expansão das florestas sobre os campos e vice-versa (para uma revisão ver Pinheiro & Monteiro, 2010). Como os zorrilhos parecem ter seus hábitos diretamente relacionados a ambientes abertos, eventuais retrações dos campos podem ter levado populações a ser reduzidas ou mesmo se extinguir localmente, com o contrário acontecendo com a expansão destes ambientes.

Diante de todo o exposto, uma investigação que aborde ao mesmo tempo os aspectos evolutivos e taxonômicos do grupo contribuirá significativamente não só para o conhecimento mais detalhado de *Conepatus*, mas também com futuros estudos que caracterizem a variação biológica das populações sul-americanas, bem como com um entendimento mais completo de questões ligadas ao Grande Intercâmbio Americano de Fauna e à evolução complexa dos ambientes campestres da América do Sul.

### *Ferramentas de estudo*

A utilização de ferramentas moleculares em investigações filogenéticas e evolutivas é cada vez mais frequente, devido à facilidade em gerar caracteres informativos independentes e a crescente gama de análises associadas que estão se tornando possíveis, como as de datação de coalescência. Estudos que investiguem a história evolutiva de apenas uma espécie, ou grupos de espécies próximas, tratam de uma escala de tempo que vai de alguns milhares até poucos milhões de anos, sendo assim realizadas com marcadores de evolução mais rápida, como DNA mitocondrial (DNAmt) e DNA microssatélite (*e.g.* Escorza-Treviño & Dizon, 2000). Apesar de possuir informação filogenética facilmente acessível, o DNAmt apresenta padrão de herança matrilinear, tornado sua história passível de vieses por eventuais diferenças comportamentais entre machos e fêmeas. As regiões de DNA microssatélite, por sua vez, se caracterizam por apresentarem altíssimos níveis de mutação e conseqüente variabilidade. Apresentam a vantagem de serem usualmente biparentais e potencialmente neutros, fora raras exceções (Ellegren, 2004). Raramente são utilizados como fonte de informação filogenética, mas sua alta variabilidade lhes confere grande poder na detecção de estruturação populacional, mesmo que recente. Assim, a utilização conjunta de DNAmt e microssatélites é muito difundida (*e.g.* Escorza-Treviño & Dizon, 2000; Tchaika *et al*. 2007).

Abordagens morfológicas detalhadas também têm sido empregadas em estudos de estruturação geográfica (*e.g.* Bornholdt, 2012; Schiaffini *et al*., 2013). Estas devem ser distinguidas do emprego tradicional da morfologia na descrição dos táxons (ver acima), uma vez que se baseiam em um número maior de caracteres independentes e empregam metodologias estatísticas mais rigorosas. Quase a totalidade destes estudos utiliza medidas de crânio, mandíbula e dentes, uma vez que este é o tipo de material mais comumente disponível nas coleções científicas. A análise morfométrica tem a vantagem de buscar por padrões de estruturação geográfica e ao mesmo tempo fornecer padrões morfológicos para determinadas populações. Assim, novos indivíduos podem ser adicionados à análise e alocados em algum dos grupos descritos.

Finalmente, uma caracterização detalhada da história evolutiva e taxonomia de um grupo passa também pelo conhecimento preciso de suas áreas de ocorrência. Mais de uma versão para a distribuição de *Conepatus* está presente hoje na literatura, e nenhuma parece ser suficientemente correta. A versão disponibilizada pela Lista Vermelha da IUCN (IUCN, 2012) baseia-se em dados do *Global Mammal Assessment* (Schipper *et al*., 2008), uma das revisões mais recentes e importantes sobre as espécies de mamíferos. No entanto, como discutido anteriormente, os mapas apresentados para as espécies do gênero necessitam ser revisados. Além de deixar de incluir regiões com notória presença de *Conepatus*, eles incorporam a região de costa do Equador e Colômbia, onde a cobertura vegetal é majoritariamente de floresta densa, uma questão que também precisa ser melhor investigada. Finalmente, uma revisão detalhada das áreas de ocorrência do gênero pode permitir que se verifiquem descontinuidades de distribuição, as quais podem auxiliar na identificação dos padrões de estruturação populacional de *Conepatus*.

### *Conceitos de espécie*

A definição de espécies é um dos tópicos mais debatidos e controversos da biologia. Apesar de a espécie ser a unidade fundamental para descrição e comparação da biodiversidade, até hoje não há consenso geral sobre o seu conceito ou critério de reconhecimento. Ao longo das últimas décadas, dezenas de conceitos foram sugeridos (para uma lista dos mais importantes, ver Mayden, 2002), quase sempre refletindo as diferentes características biológicas dos grupos ou áreas da biologia com as quais os autores trabalhavam. Todos receberam críticas ao longo do tempo, principalmente pela falta de aplicabilidade em todos os grupos que compõem a árvore da vida. Poucos conceitos conseguem lidar, por exemplo, com grupos formados por seres assexuados. Recentemente, alguns autores têm sugerido que o conceito de espécies e o critério para delimitá-las devem ser tópicos dissociados, propondo uma unificação dos conceitos existentes (*e.g.* Mayden, 2002; de Queiroz, 2007; Naomi, 2011). Esta unificação de conceitos parece ser a abordagem mais aplicável frente ao imenso debate sobre o tema, sendo assim discutida a seguir.

Mayden (1999, 2002) e de Queiroz (2005, 2007) vêm propondo, respectivamente, uma abordagem hierárquica e de unificação de conceitos. Ambas as propostas são bastante semelhantes em vários pontos, mas com pequenas diferenças, como discutido por Naomi (2011). A ideia central é a dissociação entre conceituação e delimitação de espécies, questões que os autores consideram terem sido misturadas durante muito tempo. Ambos propõem que o conceito norteador utilizado seja o de que uma espécie é uma linhagem independente, uma metapopulação com uma história evolutiva definida e única, semelhante ao conceito evolutivo de espécie (Wiley, 1978). Reconhecendo-se esse como o conceito filosófico, os autores propõem que outros conceitos de espécie (como o biológico, o ecológico e o filogenético) sejam utilizados como ferramentas de identificação do processo evolutivo de especiação. Desta maneira, os autores sugerem a unificação dos diversos conceitos, ideia que aparentemente foi bem aceita pela comunidade científica.

Em uma revisão das ideias destes autores, Naomi (2011) ressalta pequenos problemas com ambas as ideias, e sugere sua correção através da uma unificação que utiliza elementos das duas propostas. As divergências entre estas três visões são mínimas, e envolvem principalmente a filosofia por trás e o raciocínio desenvolvido para chegar ao resultado final. Em termos de aplicação prática, todas são bastante semelhantes. No contexto desta tese, uma vez que a mesma versa sobre uma espécie sexuada, a abordagem proposta por esses três autores é bastante compatível e aplicável, e assim será adotada. Assim, o conceito de espécie a ser adotado neste estudo é o evolutivo, sendo os outros conceitos modernos utilizados como critérios de delimitação. Tais critérios serão principalmente o filogenético e o biológico, ou seja, o isolamento reprodutivo aparente.

### *Objetivos*

Frente a todo o exposto acima, os objetivos desta tese são: (i) investigar o padrão geral de estruturação geográfica das populações de *Conepatus*; (ii) realizar uma revisão detalhada da distribuição do gênero; (iii) investigar a história evolutiva de *Conepatus*, relacionando padrões de diversificação com eventos biogeográficos e vegetacionais históricos importantes; e (iv) utilizar todos os dados gerados e compilados para realizar uma revisão taxonômica de *Conepatus*.

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# CAPÍTULO II

**Artigo Científico**

## Complex evolution and highly structured populations of South American hog-nosed skunks (*Conepatus*)

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# Complex evolution and highly structured populations of South American hog-nosed skunks (*Conepatus*)

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*Running Title*: Phylogeny and evolution of *Conepatus*

## Abstract

Six carnivoran families invaded South America during the Great American Biotic Interchange (GABI), originating a fascinating endemic fauna. *Conepatus*, the only representative of the Mephitidae that immigrated, comprises the group of invaders for which the diversification times and patterns are the least understood, which is reflected in poor taxonomic and biogeographic knowledge. Here we investigated the evolutionary history of *Conepatus* by analyzing 1,902 base pairs of mitochondrial DNA and eight autosomal microsatellite loci. Our results indicate that South American populations represent a distinct lineage relative to Central and North American species. The estimated time for this basal south-north split (*ca.* 3.2 million years ago) is consistent with an early invasion of South America during the GABI. The mitochondrial lineage from central Brazil is significantly divergent from that found in Mexico, indicating that they do not belong to the same species (*C. semistriatus*) as traditionally assumed. Also, the extant genetic diversity of *C. chinga* is highly structured geographically, suggesting the presence of at least three major phylogroups with additional internal subdivision. The evolution and demography of these groups seem to have been closely connected to the history of South American grasslands, with phylogeographic partitions associated with well-defined natural barriers. Altogether, these results shed light onto the evolutionary history of *Conepatus*, and indicate the need for a taxonomic revision of this group, which is critical to support the design of detailed research programs and adequate conservation strategies targeting these species.

*Keywords:* Mephitidae, phylogeny, molecular dating, taxonomy, demography, conservation

## Introduction

The Great American Biotic Interchange (GABI) is one of the main events driving mammal evolution in the American Continent. The complete closure of the Panama landbridge, *ca.* 2.8 million years ago (MYA) (Woodburne 2010), triggered waves of invasion by many mammalian taxa in both directions (Marshall et al. 1982; Webb 2006). In the case of the order Carnivora, at least six different families migrated from North to South America at different points during and after the isthmus formation, giving rise to a spectacular endemic carnivore radiation in the southern continent (Eizirik 2012). The evolutionary history of such colonizer taxa is, however, often difficult to trace. Taken together, the recent age of the invasions and the rapid lineage diversifications that ensued pose challenges to phylogenetic reconstruction due to the narrow time that each branch had to accumulate apomorphies. In addition to this particular evolutionary history, South America has experienced a complex vegetational dynamics that also affected the evolution of several mammalian taxa in that continent. During the last two million years, the Earth has undergone several alternating glacial and interglacial cycles (Sigman and Boyle 2010). Glacial periods are colder and therefore dryer, causing open environments (e.g. grasslands, savannas) to flourish. On the other hand, interglacial periods are warmer and moister, favoring the expansion of forests. This expansion-reduction dynamics has affected several South American biomes, such as the Cerrado, and therefore could have influenced the evolutionary history of taxa closely associated to them (for a review see Pinheiro and Monteiro 2010). Together, the GABI and the complex vegetational dynamics are two of the most important factors that have shaped the evolution of South American mammals, and therefore their understanding is essential in the process of describing the history and diversity of such taxa. On a broader context, the characterization of the evolutionary history of individual taxa can also help shed light on biogeographic events and processes that affected entire communities or biomes.

Most carnivoran families that colonized South America during the GABI have already been studied at some level, enabling at least a basic understanding of their diversification patterns (for a review see Eizirik 2012). However, this is not the case of *Conepatus*, the only genus of Mephitidae that invaded and flourished in the southern continent. The exact time of invasion is still uncertain, and the subsequent evolution of the genus is still poorly characterized. The exact species-level composition, population structure and phylogenetic relationship among different groups have all received very little attention so far, as has the role played by the complex vegetation dynamics of South America in shaping the genus’ diversity. Therefore, Mephitidae remains the group with the least understood diversification patterns among the Carnivora involved in the GABI.

Currently, there are four accepted species of *Conepatus*: *C. leuconotus* in southern North America and part of Central America; *C. semistriatus* in Central and northern South America, in addition to a disjunct population in northern/central Brazil (*C. s. amazonicus*); *C. chinga* in the central/southern portion of South America; and *C. humboldtii* in southernmost South America (Wozencraft 2005) (Figure 1). However, recent studies have challenged the traditional taxonomic arrangement of the genus, indicating the need for a modern revision based on a more detailed understanding of the phylogeny and evolutionary history of the group (Dragoo et al. 2003; Schiaffini et al. 2013). A few studies have already been conducted on this issue, but several points need further attention. Fossil evidence strongly indicates that *Conepatus* has originated in North America along with other New World skunk lineages, in the early Pliocene or earlier (Wolsan 1999; Wang et al. 2005). The oldest *Conepatus* fossil was found in Mexico and dated at 4.8 million years ago (MYA), long before the closure of the Panama Isthmus (Wang and Castañeda 2008). For South America, the oldest *Conepatus* record comes from the Chapadmalalan formation in Argentina, dated at 2.5 MYA (Hunt 1996). This date would make *Conepatus* one of the first genera to invade the continent after the complete formation of the landbridge (Marshall et al. 1982). However, the association of this fossil with that particular formation was contested later by some authors, originating a debate that persists until the present (for a review see Wang and Castañeda (2008). Therefore, this issue still needs to be better characterized given its importance to understand the evolutionary history of the genus.

Another important issue that needs further investigation is the phylogeographic structure of *Conepatus* and the main diversification events that shaped the evolution of the genus. In this context, Wang and Castañeda (2008) proposed a gradual divergence pattern, from north to south, based on a phylogenetic reconstruction that relied on fossil and present osteological material. They suggested that *C. leuconotus* is the most basal skunk, with the Central American group (*C. semistriatus*) being the sister clade of the South American one. The dates of both divergence events would be very old, occurring before the closure of the Panama Isthmus. Finally, they postulated two South American invasions: one lineage giving rise to an endemic South American group (*C. chinga* and *C. humboldtii*) and another occupying central and northeastern Brazil (*C. s. amazonicus*), but still closely related to Central American lineages. However, it is worth mentioning that their phylogeny was based on only 38 morphological characters, and did not include any individual from Central Brazil. It is therefore interesting to perform a broader phylogenetic assessment of the relationships among major *Conepatus* lineages, including estimates of their divergence times. It is also important to test the evolutionary scenario proposed in that previous study, along with its biogeographic ramifications.

In addition to the large-scale evolutionary history of the main *Conepatus* lineages, the internal structure within each species also requires more detailed characterization. It is very common for species with broad distributions to present subdivided populations (Avise 2008). Among the South American *Conepatus* species, *C. chinga* has the broadest predicted distribution, ranging from southern Peru, southern Bolivia and northern Chile through northern Argentina, Paraguay, Uruguay and southern Brazil (Figure 1) (IUCN 2012). A total of seven subspecies are currently accepted (Dragoo 2009), but so far no study has investigated the phylogeography of this species, so as to directly assess the historical discontinuities among these and other regional populations. From a biogeographic perspective, there are a few potential barriers when considering the geographic distribution of *C. chinga*: the Andes, major rivers, and forested areas such as the Amazon Forest. Addressing this issue is critical to allow the design of adequate conservation assessments of these animals, since their distribution could result in the differentiation of local populations in distinct MUs (Management Units), ESUs (Evolutionarily Significant Units) or even species (Moritz 1994). In the IUCN Red List (IUCN 2012) *C. chinga* is referred to as ‘Least Concern’ (Lc), and the species is not listed on any appendix of CITES. However, threats to local populations could be greatly underestimated due to lack of knowledge of the phylogeographic structure. Although apparently abundant in some of its occurrence areas, a high mortality rate is recorded in some regions due to road-killing and hunting pressure (Kasper et al. 2009; Peters et al. 2011). Furthermore, South American savannas are among the most endangered ecosystems in that continent (Jarvis et al. 2010), which could represent a major threat to the genus since it seems to be strongly associated to this type of environment (Dragoo 2009) The exact impact of such pressures has not been characterized so far, and that, along with the lack of knowledge on species-level partitions, can make conservation problems remain undetectable.

Another South American population that needs attention is the one from Central and Northeastern Brazil. It is traditionally considered to be a disjunct population of *C. semistriatus*, whose main distribution area, the one that includes the species type, ranges from Mexico to Northern South America (Dragoo 2009). Brazilian *C. semistriatus* is described as a distinct subspecies, *C. s. amazonicus*, but even its exact geographic range is presently not well established. However, a more critical concern is the taxonomic position of this population, which needs to be investigated with modern phylogenetic tools. Considering that *Conepatus* seems to be strongly related to field environments, it is easily noted that a significant barrier – the entire Amazon Forest – would separate *C. s. amazonicus* from the rest of the species' distribution. As all the conservation issues mentioned for *C. chinga* can also apply to this population (*e.g.* Alves et al*.* 2009), an investigation of its phylogenetic position among *Conepatus* could help further taxonomic and biological studies and enable proper conservation plans on its behalf.

As for the investigation of large-scale evolutionary patterns and species internal structure, several types of molecular characters have been used with increased frequency and robustness. Since intra-specific level studies usually deal with recent evolutionary processes, the most used markers in these cases are rapidly-evolving DNA regions, such as mitochondrial DNA (mtDNA) segments (Avise 2008). Together with mtDNA, microsatellite loci are useful tools, since they can also provide insights on recent evolutionary history, but with the addition of biparental information (*e.g.* Charruau et al*.* 2011; Barton and Wisely 2012). So far, no study has characterized in detail any mtDNA region for use in such surveys, nor any microsatellite locus has been characterized for use in the South American populations of the genus.

Thus, the goals of this study were to: (i) characterize mtDNA and autosomal microsatellite loci which can be utilized in the present and in future investigations of *Conepatus* phylogeny, intraspecific structure and evolutionary history; and to use such regions in (ii) an analysis of *C. chinga* intraspecific structure, aiming to better understand the phylogeography and population history of this species, and (iii) an evolutionary assessment of *C. semistriatus* populations from Central Brazil, aiming to test whether they form a monophyletic group with putative conspecifics from North/Central America. We also aimed to (iv) construct a comprehensive phylogeny of genus *Conepatus*, with more detailed emphasis on South American lineages; and (v) combine molecular dating estimates and demographic history reconstructions to draw inferences on the evolution of the genus in South America.

## Materials and Methods

### *Samples*

Our sampling scheme was aimed at covering as much as possible the presumed diversity of species belonging to *Conepatus*, encompassing much of the geographic distribution of the genus, with emphasis on South American populations (Table 1 and Figure 1). In particular, we included areas that had not been surveyed by previous evolutionary or taxonomic studies (e.g. the Cerrado biome in Central Brazil), aiming to investigate their phylogeographic affiliations. Samples were obtained through direct collection of tissue from road-killed or free-ranging animals captured for field ecology studies. Blood samples were stored in a salt saturated solution (100mM Tris, 100mM EDTA, 2% SDS), and muscle/skin samples were preserved in 70-96% ethanol; all samples were stored at room temperature.

Regarding *C. chinga*, 104 samples from its predicted distribution were obtained: five samples from central Chile (between Los Ríos y Coquimbo Regions), 20 from central and northern Argentina (from Cordoba, Buenos Aires, Mendoza, Corrientes and Entre Ríos provinces), seven from Uruguay (from Canelones, Maldonado and Rocha provinces), and 72 from southern Brazil (Rio Grande do Sul and Santa Catarina states). In the latter region, two different biomes can be recognized: a southern portion which belongs to the 'Uruguayan Savannas' (comprised by southern Brazil and Uruguay), component of the 'Pampas' biome (56 out of 72 samples), and a northern one, comprising altitude grasslands locally called 'Campos de Cima da Serra' (16 out of 72 samples), hereafter Southern Brazil Altitude Grasslands. Both biomes are open environments dominated by grasslands, which are geographically close to each other but historically separated by a stretch of Atlantic Forest (IBGE 2004).

As for *C. semistriatus,* samples of 34 individuals from central Brazil (encompassing both the Cerrado and Caatinga biomes) were analyzed, along with one additional sample collected in Yucatán province, Mexico. A single sample of *C. humboldtii* was obtained, from southern Chile (Aisén Region). Finally, we also included two *C. leuconotus* samples, one from the United States (Texas State) and another one from Mexico (Oaxaca province).

Therefore the major phylogenetic diversity of *Conepatus* that is currently accepted was included in this study. An initial division of the South American samples in distinct populations, defined by geographic origin, was established: southern Brazil Altitude Grasslands (SB-AG), southern Brazil Uruguayan Savannas (S BRA), Uruguay Uruguayan Savannas (URU), central/northern Argentina (ARG), central Chile (C CHI), southern Chile (S CHI) and central Brazil (C BRA) (see Figure 1). However, due to the consistent analyses outcomes, a rearrangement was necessary, in order to facilitate the visualization of the results. First, southern Brazil Uruguayan Savannas (S BRA) and Uruguay Uruguayan Savannas (URU) were unified in a single population, the Uruguayan Savannas (US). Additionally, Argentinean samples were subdivided in two distinct populations: eastern Argentina (E ARG – Corrientes and Entre Ríos provinces), and northern/central Argentina (N/C ARG – Cordoba, Buenos Aires and Mendoza provinces). Table 1 shows sample information organized by population, including putative species (according to the current literature), geographic and biome origin and collectors. Southern Brazil and Uruguay were kept separate in this table in order to provide more detailed information.

*DNA isolation and PCR amplification*

Genomic DNA was isolated from tissue samples through a standard Proteinase-K/phenol-chloroform protocol (Sambrook and Russel 2001). Three different regions of the mtDNA were chosen on the basis of their informativeness potential, and amplified through Polymerase Chain Reactions (PCRs): partial *ND5* gene, using primers ND5-DF1 and ND5-DR1 (Trigo et al*.* 2008); partial *Cytochrome-B* gene, using primers L15162 and L15915 (Irwin et al*.* 1991); and a segment that includes partial *ATP6* and *Cytochrome Oxidase-III* genes, hereafter referred to as segment 7a following a nomenclature based on Delisle and Strobeck (2002). The latter was amplified using the forward primer mtDNA7H (Delisle and Strobeck 2002) in combination with the reverse primer MCi7R1 (5' – CAAGTAATAGATACTCCGGAGGCTAG – 3') designed in this study using the software Primer3 (Rozen and Skaletsky 2000) and an alignment containing mtDNA sequences of *Spilogale putorius* (Genebank accession code NC_010497.1) and multiple canids. Two different sequencing approaches were followed, depending on the target analysis. A subset of the entire set of individuals (dataset A), representative of all geographic groups, was chosen to be sequenced for all three mtDNA regions, for use in phylogenetic analyses. The final number of individuals sequenced for all three segments was 36. A second dataset (dataset B), comprising all sampled individuals, was constructed to assess haplotype frequency information and thus be more appropriate for demographic and population structure analyses. Due to initial assessments of PCR efficiency, *ND5* was the chosen segment to be amplified for all available individuals, yielding a final alignment with 133 animals.

For the microsatellite analyses, we employed the 10 dinucleotide loci described by Dragoo et al. (2009). After efficiency tests, only eight out of the initial 10 loci were amplified for all the populations (loci Meph22-16 and Meph22-19 were excluded). A maximum number of 30 individuals per population was surveyed, yielding a final number of 88 individuals typed. Chilean populations could not be typed due to technical limitations of our Chile-based molecular laboratory. Microsatellite primers were ordered with a universal M13-tail added to the 5' end of the forward primer (Boutin-Ganache et al*.* 2001). Thus, a third M13 primer tagged with a fluorescent label (6-FAM, NED or HEX) was included in the reactions in order to label the PCR products with the desired fluorescent dye.

PCRs were conducted in a 20 µl volume, containing 1x PCR Buffer (Invitrogen), 200 µM dNTPs, 0.1 µM of each primer (which included a third M-13 fluorescently labeled primer, diluted 15 times in relation to the others, in the case of the microsatellite

PCRs), 1.5 to 2.5 mM of $MgCl_2$, 0.2 to 0.5 unit of *Platinum* Taq DNA Polymerase (Invitrogen) and 10-50 ng of template DNA. PCR conditions were kept constant for all three mtDNA segments and microsatellite loci, beginning with initial denaturation at 94°C for 3min; then 10 touchdown cycles of denaturation at 94°C for 45s, annealing at 60-51°C for 45s and extension at 72°C for 1min 30s; followed by 30 to 35 cycles of denaturation at 94°C for 45s, annealing at 50°C for 45s and extension at 72°C for 1min30s; and ending with a final extension at 72°C for 3min.

Mitochondrial PCR products were checked and quantified through visualization on a 1% agarose gel stained with GelRed 10x (Biotium), using DNA Ladder (Invitrogen) as a size and concentration marker. The products were then purified either by ammonium acetate precipitation or enzymatic purification (employing Exonuclease I and Shrimp Alkaline Phosphatase). Finally, purified products were sequenced using the *DYEnamic ET Dye Terminator Sequencing Kit* (GE Healthcare) and a MEGABACE 1000 (GE Healthcare) automated DNA sequencer. For nearly all sequences, both forward and reverse strands were sequenced. Microsatellite fluorescently-labeled PCR products were multiplexed and genotyped in a MEGABACE 1000 (GE Healthcare) sequencer, utilizing an ET-ROX 550 size standard (GE Healthcare).

### *Mitochondrial DNA sequence analysis*

Consensus sequences were generated using Phred/Phrap/Consed (Gordon et al*.* 1998), and then manually checked and edited using Chromas 2.0 (http://www.technelysium.com.au/chromas.html) and Bioedit 7.0.9.0 (Hall 1999). Sequences were aligned with the ClustalW algorithm implemented in Bioedit, and concatenated with Dambe 5.2.40 (Xia and Xie 2001). To characterize the selected mtDNA segments and to provide a baseline of their diversity to be used in this and other evolutionary studies, molecular diversity indices, such as nucleotide diversity (Pi) and haplotype diversity (*h*), were generated for each segment using MEGA 5.1 (Tamura et al*.* 2011) and Arlequin 3.5 (Excoffier and Lischer 2010). Separate estimates were made for each population.

Median-joining networks were drawn with Network 4.6.0.1 (Bandelt et al*.* 1999) using dataset B (*ND5*, 133 individuals), in order to assess information on haplotype ancestry, geographic structure and historical demography. The same dataset was used to analyze geographic structure through tests of population differentiation such as fixation indices ($F_{st}$), as implemented in Arlequin 3.5.

Phylogenetic analyses were carried out using two different search optimization criteria. First, Maximum Likelihood (ML) was employed, using the RaxML plataform, through the RaxML BlackBox web server (Stamatakis et al*.* 2008). Dataset A was used, adding one individual each of *Mephitis mephitis* and *Spilogale putorius* as outgroups, whose sequences were obtained directly from Genbank (accession numbers HM106332.1 and NC_010497, respectively). We implemented a gamma model of rate heterogeneity among sites, with an estimated proportion of invariable sites. The algorithm automatically conducts bootstrap searches to provide support values for the final trees. A second phylogenetic analysis was conducted using Bayesian inference, employing the package Beast 1.7.4 (Drummond et al. 2012). Before running this software, substitution models were estimated for each of the three different mtDNA segments via the Corrected Akaike Information Criterion (AICc) and Bayesian Information Criterion (BIC), both implemented in jModelTest 0.1.1 (Posada, 2008). In addition to the phylogenetic topology, node dates were also estimated with Beast. Dating estimates were calibrated with a set of fossil and molecular dating priors located within the Mephitidae tree. Analyses were run assuming substitution models HKY+G with four categories for both *Cytb* and *7a*, and HKY+I for *ND5* (as estimated through jModelTest). The uncorrelated lognormal relaxed molecular clock was used to estimate a molecular rate for each of the three segments at all nodes. A Yule process of speciation was defined as the tree prior, and the starting tree was generated randomly. Two points of calibration were defined, namely: (1) the split between *Spilogale*+*Mephitis* and *Conepatus* (Eizirik et al. 2010); and (2) the split between *Spilogale* and *Mephitis*. The prior for node 1 was defined as a Gamma distribution with the following parameters: Shape = 3, Scale = 1.6 and Offset = 4.8. The offset value was based on the age of the oldest fossil of the extant mephitid genera (Wang & Castañeda 2008). The shape and scale of the Gamma distribution were set so as to match the parameters (mean and 95% credibility interval) of the molecular dating reported by Eizirik et al. (2010) for this node. The prior for node 2 was also set as a gamma distribution (with Shape = 3, Scale = 1.3 and Offset = 1.8), also matching the parameters of the molecular dating performed by Eizirik et al. (2010). The offset value was defined by the oldest *Spilogale* and *Mephitis* fossil records (Kurtén and Anderson 1980). Finally, fifty million generations were run, with parameters sampled every 5,000 steps. Results were analyzed with Tracer v1.5 and the trees visualized with FigTree v1.3.1, both of them included in the Beast package.

To access past variation in the population size of the different populations, we conducted two different kinds of demographic analyses, both of them utilizing dataset B. We initially assessed each of the phylogeographic groups with statistical tests of neutrality, including Tajima's D and Fu's Fs, as implemented in Arlequin 3.5, and Fu and Li's D* and F*, as implemented in DnaSP 5.10 (Rozas et al. 2003). Additionally, we investigated the molecular signatures of past variations in effective population size with a Bayesian Skyline Reconstruction, as implemented in Beast 1.7.4. A separate run was performed for each phylogenetic group, with the tree prior set to Bayesian Skyline. We assumed a strict clock model, and the mean substitution rate estimated in the previous phylogenetic and dating analyses (2.779E-8/year). The substitution model was set to HKY+I, following the previous assessment with jModelTest.

### *Microsatellite data analysis*

General diversity indices for the microsatellite loci (number of alleles, expected and observed heterozygosity and allele size range) were calculated with Cervus 3.0.3 (Marshall et al*.* 1998). HW-equilibrium and linkage disequilibrium tests were performed in Arlequin 3.5, applying the Bonferroni correction to the statistical significance level given the use of multiple comparisons. We also utilized Arlequin to estimate $F_{st}$ and $R_{st}$ for all population pairs. $D_{est}$ fixation indices were calculated through the web-based platform SMOGD (Crawford 2010). It is important to mention that no statistical significance test is available for the $D_{est}$ analysis, for which only the classical $F_{st}$ levels of differentiation are adopted to interpret the results.

Finally, we also conducted a Bayesian analysis of population structure using the software Structure 2.3.2.1 (Pritchard et al*.* 2000), to investigate which number of distinct genetic groups would best fit our microsatellite data. The run parameters were: 100,000 steps of burn-in plus 1,000,000 MCMC iterations, under the admixture model; the number of clusters tested (parameter *K*) ranged from 1 to 10, and for each value of *K* we performed 15 different runs.

## Results

### *Mitochondrial DNA markers*

We generated sequences for the three assayed mtDNA segments: *ND5* – 642 base pairs (bp); *Cytochrome-b (cytb)* – 631 bp; and *7a* – 629 bp. Considering all segments jointly, a total of 1,902 bp was generated and kept in the final alignment for each of the completely sequenced individuals. Table 2 shows basic molecular diversity indices by segment for each population. The final number of sequences generated for *Cytb* and *7a* is larger than 36 (the final number of individuals of dataset A) because for some individuals we obtained good quality sequences for only one of these two segments. When considering individuals from all different populations, diversity indices found for the three different segments were relatively similar, ranging from 1.58 to 2.39% in nucleotide diversity and from 17 to 34 in total number of haplotypes. However, values varied hugely among different populations. Central/northern Argentina presented very high levels of diversity for all indices, in opposition to very low values found for central Brazil and southern Brazil (both populations) + Uruguay populations. Central Chile and eastern Argentina also presented low diversity, but these results can be biased by their small sample size. It is worth mentioning, however, that even with few individuals sampled, many diversity indices of these latter two populations were higher than those of central Brazil and southern Brazil (both populations) + Uruguay.

The network drawn from the *ND5* sequences is shown in Figure 2a. The general structure of the network shows four major phylogeographic groups: southern Brazil (both populations) + Uruguay (A); Argentina (both populations) + central Brazil (B), central Chile (C) and southern Chile (D). Clades A, B and C are major representatives of current *C. chinga* mtDNA diversity, while southern Chile is a putative representative of the Patagonian species *C. humboldtii*. The South American representative of *C. semistriatus*, i.e. the central Brazil population, is clearly nested inside the Argentinean *C. chinga* diversity (group B-II). Another population nested inside phylogroup B is Eastern Argentina (group B-I), comprised by samples from the Entre Ríos and Corrientes provinces (see Figure 2a). Regarding phylogroup A, we found a haplotype that was exclusive of individuals from the Southern Brazil Altitude Grasslands biome, and almost all individuals from this Biome bore this haplotype (CC-N05; group A-I). The only exception was one individual from the municipality of Campestre da Serra (contained in the SB-AG biome), which presented the haplotype CC-N06, shared with individuals from the Uruguayan Savannas biome. Phylogroup C was formed by the central Chile samples, a population that is clearly separated from phylogroup B by the major Cordillera of the Andes. Finally, group D was formed by a single sample from southern Chile, which was clearly separated from phylogroups B and C. It is important to note that almost all of the identified geographic groups and subgroups were separated from one another by several mutational steps, which is quite remarkable considering that the network was drawn based on a single 642-bp segment containing only 63 variable sites. The only group that did not follow this pattern was the central/north Argentina population, which presented the most structured diversity and may represent to some extent the basal diversity for the whole group. Still, it is possible to visualize the proximity among all the Argentinean haplotypes. Finally, the positions of *C. semistriatus* sample from Mexico and both samples of *C. leuconotus* from USA are not shown in Figure 2a due to the great divergence (*ca.* 100 mutational steps) from the core network.

Regarding the mtDNA $F_{st}$ analysis, a first round was conducted keeping the populations from the Uruguayan Savannas of southern Brazil and Uruguay separated. As the $F_{st}$ value for this population pair was very low and statistically not significant, a second round of analysis was conducted, this time joining these populations as a single

Uruguayan Savannas (US) unit. The results of the second round of mtDNA $F_{st}$ analysis is shown on Table 3, and corroborate most of the network conclusions. As would be expected from the lack of haplotype sharing among major phylogroups (A, B and C), pairwise values among them are very high, ranging from 0.25 to 0.98. The lowest values were found within major phylogroups, such as SB-AG versus Uruguayan Savannas and between Argentinean populations. On the other hand, values between major phylogroups were very high, most of them being higher than 0.9. Values of *p* for all pairwise comparisons were highly significant (see Table 3).

The tree generated with both phylogenetic approaches presented very similar topologies, so that only the one found with the Bayesian analysis is shown (Figure 2b; support values in Table 4). Despite slight differences in the hierarchical structure within the main clades, both trees agree almost completely in the composition and support of such groups. Disagreements refer only to the poorly supported clades (nodes 11 and 12), with the support values found with the Bayesian analysis being slightly higher. The phylogenetic relationships among mephitids show *Conepatus* clearly as a basal group relative to *Spilogale* and *Mephitis*. Regarding the internal arrangement of *Conepatus*, three major groups can be noted: *C. leuconotus* from the USA and Mexico; *C. semistriatus* from Mexico; and a third one that includes all South American samples. Regarding the hierarchical structure of these three groups, the strongest trend is to position South America as a basal clade relative to *C. leuconotus* and Mexican *C. semistriatus,* but support values for this relationship are moderate. It is worth mentioning that the monophyletic regional groups found with the phylogenetic analyses are perfectly congruent with those recovered in the network analysis and present high support values, corroborating the existence of such mitochondrial clades. The lowest support for a regional clade was that of phylogroup B (Argentina + Central Brazil), with a bootstrap value of 70% in the ML tree. However, the posterior probability of this clade in the Bayesian analysis was 1.0, strongly supporting its recognition. Finally, it is important to note that the exact hierarchical structure among the regional groups was not well resolved in any of the trees (nodes 11 and 12).

The dating estimates for each of the well-supported nodes, including the mean and 95% credibility interval, are shown in Table 4. The tree root age was estimated at around 7 MYA, with the coalescence of the extant diversity of *Conepatus* being slightly older than 3 MYA. Interestingly, the coalescence estimate of the South American *Conepatus* clade was considerably younger, *ca.* 0.85 MYA. Also, all South American populations (phylogroups) had relatively young coalescence times, with the central/northern Argentina population being the oldest, around 0.5 MYA. The Central Brazil and Southern Brazil (both populations)/Uruguay populations presented very similar coalescence times, *ca.* 0.1 MYA. The Central Chilean population, with only five samples and three haplotypes, presented an older coalescence estimate, indicating that the very recent coalescence times of the two well-sampled Brazilian populations are even more remarkable.

Only two populations presented signals of past demographic changes (Table 5, Figure 3). First, the Central Brazil population presented several signals of population growth. Its network structure (Figure 2a, group B-II) presented a star-shape, which indicates a recent expansion event. Of the neutrality tests, only Tajima's D showed statistically significant negative results, but Fu's Fs was also clearly negative, albeit marginally non-significant (p = 0.06). Finally, the Bayesian Skyline Reconstruction showed a considerable effective size growth event for this population, starting ca. 20,000 years ago (Figure 3a). Another population presenting growth signals was southern Brazil-Uruguay, although these results were not as straightforward as those from central Brazil. Fu's Fs was the only neutrality test yielding significantly negative results, and the Bayesian Skyline Reconstruction indicated a very recent change in effective population size, *ca.* 1,000 years ago (Figure 3b). All other populations showed no significant changes in population size, as inferred from the neutrality tests or the Bayesian Skyline Reconstruction (result not shown).

### *Microsatellite analyses*

Table 6 summarizes the basic information regarding the microsatellite loci surveyed, including locus name and fluorescent label, multiplex arrangement, number of individuals typed per population for each locus, basic diversity indices and results from the HW-equilibrium test per locus and population. No linkage disequilibrium was detected. Only one locus (Meph42-15) was monomorphic for all populations, and thus was not utilized in the subsequent analyses. All other loci were polymorphic and informative, and final missing data across all loci and individuals was around 25%. In general, diversity indices were moderate to low for all populations surveyed, except for central/northern Argentina. The mean expected heterozygosity across loci (excluding Meph42-15) for each population ranged from 0.45 (Eastern Argentina) to 0.71 (northern/central Argentina), with a mean of 0.55. The central Brazil and southern Brazil-Uruguay groups presented considerably lower diversity indices than would be expected given their predicted broad distributions and large populations. These results are congruent with the mtDNA diversity indices, for which central/northern Argentina also showed the highest levels.

The microsatellite-based fixation indices are shown on Table 3. Similarly to the analogous analysis performed with the mtDNA data, a first round of tests was conducted keeping the populations of the Uruguayan Savannas biome from southern Brazil and Uruguay separated. As the results for all three fixation indices were very low or statistically non-significant for this particular pair (results not shown), a second round was performed uniting these populations in a single Uruguayan Savannas group. The values found in this final round were similar across the three fixation indices ($F_{st}$, $R_{st}$ and $D_{est}$) for all population pairs. All values were statistically significant for both $F_{st}$ and $R_{st}$, and higher than 0.15 for $D_{est}$. In general, $R_{st}$ values were the highest, indicating that the allele sizes are an important parameter underlying population distinctiveness. Altogether, the microsatellite biparental information expressed in the fixation indices corroborated the existence of the phylogroups identified with the mtDNA, pointing to the existence of five isolated populations: Uruguayan Savannas (Uruguay + southern Brazil Uruguayan Savannas); southern Brazil Altitude Grasslands; eastern Argentina; central/northern Argentina; and central Brazil.

The results obtained with the Bayesian approach implemented in Structure were mostly concordant with those of the microsatellite fixation indices. Table 7 shows the mean likelihood and variance calculated across 15 iterations for each *K* (number of assumed clusters) tested. The best mean likelihood value was obtained for *K* = 4 populations, but *K* = 5 resulted in a very similar value. The best likelihood across all *K* values and all iterations was obtained for one of the iterations of *K* = 5 (result not shown). Figure 4 shows the bar plots generated for the iteration with the highest likelihood value of *K* = 4 and *K* = 5, and Table 8 shows the genetic distribution of each population in each of the identified clusters. It can be seen that results assuming both *K* = 4 and *K* = 5 agree in identifying the existence of clusters that roughly correspond to the populations of southern Brazil Altitude Grasslands, Uruguayan Savannas, central/northern Argentina and central Brazil. Eastern Argentina seems to be the least identifiable population, always clustering with Uruguayan Savannas individuals. However, it is interesting to note that eastern Argentina individuals always cluster together, which indicates the existence of some internal consistence. For *K* = 5, Table 8 shows that each population is mostly allocated in a unique cluster (bold values). These results show a strong signal of population structure among the surveyed South American populations, corroborating the results obtained wtih the other analyses.

## Discussion

This is the first comparative assessment of different mtDNA segments for use in phylogenetic approaches targeting *Conepatus* (but see the parallel study by Schiaffini et al. [2013], which also included different mtDNA segments). Results of the diversity tests and from the whole set of analyses show that the selected fragments are appropriate markers for evolutionary surveys with this genus. Future studies that target similar goals may also include this set of genes, which would also be useful in the context of allowing direct data comparison and combined analyses. Similarly, it was the first time that a set of microsatellite loci was characterized for utilization in South American skunks, and further studies may employ the same markers to generate comparable results. Together, the set of mtDNA and nuclear markers utilized in this study proved to be complementary and informative, being useful for evolutionary and demographic analyses.

Results from both mitochondrial and microsatellite surveys are highly concordant and encourage us to rethink several aspects of the evolutionary history of *Conepatus*, in some cases leading to challenges to the presently accepted taxonomic structure of the genus. Foremost, all South American populations sampled here comprise a monophyletic group. It was not completely defined whether *C. leuconotus* and Mexican *C. semistriatus* lineages are also monophyletic, since the support value for this clade was not substantial. Further segments should be added to this survey in order to clarify this issue. However, this phylogenetic configuration seems to be a tendency and, if confirmed, the genus would have a single basal divergence originating northern and southern clades. A first consequence of such conclusion would be the support for the inference of a single invasion of South America by the genus. The divergence date between the northern and the southern clade, around 3 MYA, is perfectly consistent with a split caused by an early South American colonization after the closure of the Panama landbridge, around 2.8 MYA (Woodburne 2010). The 2.5 MYA date of the first South American *Conepatus* fossil, from Argentina, remains to be confirmed, but the hypothesis of the genus being present in the first wave of colonization during the GABI could not be ruled out by our results. On the contrary, although our dating estimates are not sufficiently precise, they fit better with an early entry scenario than a later colonization episode. Another important consequence of this phylogenetic arrangement is that central Brazilian *Conepatus* is not closely related to *C. semistriatus* from Mexico, but instead it is part of an Argentinean radiation of *Conepatus*, as it is clearly nested within the diversity of those lineages (see Figures 2a – 2b). This finding has important taxonomic implications, and also changes the current evolutionary hypothesis of two South American invasions by this genus. Taxonomically, *C. semistriatus amazonicus* must be renamed, which should be performed on the basis of additional analyses of molecular and morphological characters.

Another interesting result is that the South American clade has a recent coalescence time relative to the divergence from the northern clade. As the invasion of South America seems to have occurred early during the GABI, i.e. close to 2.8 MYA, one could expect a rapid expansion, with multiple early lineages arising right after that date. This seems to be the case of some other carnivoran lineages invading from the north during the GABI, such as the felids of the genus *Leopardus* (for a detailed review, see Eizirik 2012). In contrast, the coalescence of the southern *Conepatus* clade seems to be a little younger than 1 MYA. Together with the phylogenetic tree topology and the lack of hierarchical resolution above the phylogroup level, this result indicates that extant mtDNA lineages occurring in this area descend from a very recent and rapid colonization of different grassland environments of southern South America (south of the Amazon Forest), stemming from one or few source regions.

A likely candidate for such geographic origin is central/northern Argentina. This area presents the highest and most structured internal mtDNA diversity, and appears at a central position in the *ND5* Network. Also, its microsatellite diversity is considerably higher than all other surveyed populations. These results are compatible with a scenario of extinction-recolonization of the South American grasslands, possibly related to the dynamics of field-like environments of South America during the world glacial-interglacial cycles that started around 2 million years ago (Sigman and Boyle 2000). It is well known that during this time great changes in the vegetation cover of South America occurred: forests advanced over grasslands in warmer/moister interglacial periods and the opposite scenario took place in colder/dryer glacial periods (Pinheiro and Monteiro 2010).

The beginning of the last Glacial Period, *ca.* 110 kiloyears ago (KYA), is one of such episodes that potentially allowed an expansion of grassland territories in South America (Werneck et al*.* 2012), and this event could have influenced the flourishing of some *Conepatus* populations. Interestingly, both central Brazil and southern Brazil-Uruguay populations present very similar coalescence times, around 100 KYA years ago, which may indicate that both biomes could have expanded, enabling its associated fauna to prosper. An alternative, non-exclusive hypothesis is that the retraction of forests increased the connectivity among grassland areas, facilitating the invasion of formerly isolated regions by *Conepatus*.

On the other hand, the joint coalescence time of the central Brazil population with Argentinean haplotypes is much older, around 400 KYA (result not shown). This result may indicate that the invasion of the central Brazil grasslands (currently Cerrado and Caatinga biomes) occurred long before the population expansion. Similarly, the divergence time of southern Brazil-Uruguay from the Argentinean population is also older, suggesting that the colonization and population expansion events may not be linked. Alternatively, such older coalescences may reflect the genealogical history of the ancestral population, prior to the invasion of the new areas, which poses an interesting avenue for future phylogeographic investigation.

Several glacial-interglacial cycles are described for the last 2 million years (Sigman and Boyle 2000). Therefore, climatic and vegetational changes in this continent could have been a major force driving *Conepatus* evolution, which may be true for many other grassland-dwelling taxa that also seem to have experienced a complex evolutionary history. Maned wolves (*Chrysocyon brachyurus*), for example, also present a signature for a recent population expansion in the Brazilian Cerrado (Bonatto *in prep.*), while the pampas cat (*Leopardus colocolo*) seem to have invaded this biome coming from Argentina at some time in the past (Santos 2012). Therefore, additional analyses of the evolutionary history of *Conepatus* could shed light on our understanding of the faunal dynamics that occurred in South American grasslands in the last 3 million years.

Regarding the internal diversity of the southern *Conepatus* clade, it is clearly a highly structured lineage. Although the hierarchical relationships among regional groups are still not well resolved, their existence is very strongly supported by both mitochondrial and microsatellite data. All analyses consistently show no differentiation between the Uruguayan Savannas in southern Brazil and in Uruguay, strongly indicating that this biome holds a single evolutionary population of *Conepatus*. All other populations tested were solidly confirmed as distinct units, with the suggestion of an additional, unexpected population in eastern Argentina. Altogether, these results indicate the existence of at least four major phylogroups, some of them presenting internal, nested clades: (A) Southern Brazil + Uruguay, (B) Central/Northern Argentina + Central Brazil, (C) Central Chile and (D) Southern Chile. Clades A and B are the ones that present nested populations (see Figures 2a – 2b).

Group A occupies two biomes of southern Brazil and Uruguay, delimited on the western edge by a major river, the Uruguay, and on the north by the Atlantic Forest (see Figure 2c). The largest portion of the group's occurrence area lies in the Brazilian and Uruguayan components of the Pampas biome, known as the Uruguayan Savannas. A nested group (A-I) occupies the isolated altitude grasslands known as the 'Campos de Cima da Serra', and seems to comprise a distinct demographic unit given the results obtained with both mtDNA and microsatellites. Field researchers already noticed a frequency difference in the coloration (presence of white areas) of the back and tail of individuals observed in this population, relative to those from the Uruguayan Savannas (C.B. Kasper *pers. comm.*). The former ones would have more white hairs in the back, and many of them also present a mostly white tail. On the other hand, the latter ones seem to have a darker fur, with very few of them presenting a significant amount of white tail hairs. This morphological distinction should be further investigated and characterized, in the light of our results indicating a genetic disjunction between these areas. Interestingly, this difference was apparently noticed also by early naturalists (Inhering 1911: 258). A likely scenario that explains this pattern is the colonization or recolonization of this area by individuals from the Uruguayan Savannas, since its mtDNA diversity is nested within Group A. Finally, regarding Group A as a whole, it presents a moderate signal of population expansion, detected by some of the demographic analyses and the skyline plot performed with BEAST. This expansion seems to have occurred *ca*. 1,000 years ago, with no obvious link with major climatic or vegetation shifts. The event could be related to some change in the ecological structure of the Uruguayan Savannas, but such shift would be very difficult to identify.

Group B is the most diverse and structured one, delimited on its eastern portion by the same Uruguay River and on its western portion by the Andes (see Figure 2c). The internal diversity of this group presents some deeply divergent haplotypes subgroups. However, when considering Western, Central and Northern Argentina, no geographic structure was detected, and the haplotypes seem to be randomly dispersed. However, when considering eastern Argentina, a very unexpected but consistent phylogroup was detected by the phylogenetic, network and microsatellite analyses. Geographically, it seems to be limited by the Uruguay and Parana Rivers, which is plausible considering that the distribution of group A is also delimited by a river. Further studies are needed in order to better characterize the genetic diversity, morphology and evolutionary history of this clade.

Finally, still regarding Group B, one of the most interesting findings of this study was that the mtDNA diversity present in Central Brazil is clearly nested within the Argentinean clade. This result raises the strong hypothesis of a colonization of the Brazilian Cerrado and Caatinga biomes through the dispersal of Argentinean individuals across the Paraguayan Chaco and Brazilian Pantanal regions. At the same time, the high levels of microsatellite divergence and the clear mtDNA differentiation points to a lack of current gene flow, indicating that this is an isolated population with an already very distinct evolutionary history. Regarding demographic tests, this group presented the most significant signals of population expansion. The Bayesian skyline reconstruction showed a strong effective size growth around 20 KYA, the approximate time of the last glacial maximum (LGM), between 26 and 19 KYA (Clark et al*.* 2009). The LGM was traditionally associated with Cerrado expansion and its advance over forested environments by several authors (*e.g.* Behling 1998), and therefore could be the driving force behind this recent population expansion (but see Werneck et al*.* 2012).

Group C is comprised by the central Chilean samples, occurring west of the Andes (Figure 2c). As might be expected, this great cordillera prevents the gene flow among these organisms, leading to separate evolutionary histories of groups B and C. The small number of available samples from Central Chile hampers more detailed analyses of their diversity, internal structure and demographic history. However, it is important to mention that even with only five individuals sampled, diversity levels were higher and coalescence time were deeper for this group than for other areas with better coverage, possibly indicating an older and more diversified population. Further studies are needed in order to better characterize its evolutionary history and internal structure, being the addition of microsatellite data perhaps the most immediate issue.

Finally, Group D was represented by a single sample from Southern Chile, and the disjunction of Groups C and D remains to be further investigated. Going from north to south in Chile, a geographic section that contains several large lakes is known as the 'Los Lagos Region'. Some of these lakes prevent most of the passage over land, since they spread from the Pacific Ocean to the Andes foothills. These geographic elements can represent the physical barriers that separate groups C and D, but a more detailed sampling around this region is necessary in order to better understand this disjunction. At the same time, this 'group D' sample is a putative *C. humboldtii* individual, and its position in the South American *Conepatus* clade is worth mentioning. Despite the low support of the group that presents this sample as an internal lineage in relation to *C. chinga* populations, if this hierarchical structure is maintained in further investigations, the whole taxonomic structure of South America *Conepatus* should be reevaluated, as this would no longer be recognized as more deeply divergent group than the other units identified here. As for Group C, microsatellite data should be also generated for Group D, ir order to confirm the genetic structure pattern found.

## Conclusion

The broad picture of *Conepatus* evolutionary history is just beginning to be understood. Very few studies have so far focused on this genus, hampering the understanding of a taxon that is closely linked to the GABI and to the evolution of South American savannas. Our results are consistent with the hypothesis that *Conepatus* could have been one of the first northern genera to invade and occupy South American grassland right after the closure of the Panama Isthmus. This invasion seems to be the cause of a North-South split in this genus, although more data is necessary to better assess this hypothesis. Our data support a single invasion of southern and central South America (south of the Amazonian Forest), but the young coalesce time of extant lineages within his group suggests a dynamics of extinction-recolonization of grassland biomes. This complex history seems to be linked to the climatic and vegetational cyclic changes of the last Ice Age, which also seem to be the most likely driving force of the complex demographic history of some populations. Altogether, these results show that a finer understanding of the evolutionary history of a taxon such as *Conepatus* could shed light on the history of vegetation and faunal dynamics of South America.

Regarding the structure of the South American *Conepatus* clade, our data provide important and solid insights, which challenge the current taxonomic paradigm pertaining to this genus. We can recognize five distinct Evolutionarily Significant Units (ESUs): (i) Central Chile; (ii) Northern/Central Argentina; (iii) Northeastern Argentina; (iv) Central Brazil [Cerrado and Caatinga biomes]; and (v) Southern Brazil/Uruguay. All of them have been detected by the mtDNA survey, confirmed by microsatellite analyses (except for the Chilean populations) and present an evident geographic delimitation, thus comprising distinct evolutionary entities. Furthermore, we recognize the southern Brazil Altitude Grasslands (*Campos de Cima da Serra*) population as an MU, nested within the Southern Brazil/Uruguay clade. All of these units need focused research attention, in order to better characterize their internal genetic diversity, evolutionary history, demographic dynamics, morphological and ecological features, as well as exact geographic ranges. From a conservation perspective, all of the mentioned units must be managed and protected independently, which implies a dramatic change relative to presently employed strategies.

This study includes one sample of a putative *C. humboldtii* individual, and if that identification is correct our results indicate that this species is part of the radiation stemming from northern Argentina. Its exact phylogenetic relationship with the other South American *Conepatus* populations must be investigated in more detail, and a broad study including samples from both Chilean and Argentinean Patagonia is necessary in order to characterize the evolutionary history of this taxon. Interestignly, a recently published, parallel study employing mtDNA data and morphological analyses (Schiaffini et al. 2013) failed to identify a clear distinction between *C. humboldtii* and *C. chinga*, illustrating the need for further taxonomic analyses targeting this group.

Although this study could not address all outstanding taxonomic and evolutionary issues pertaining to *Conepatus*, it helped shed light on several issues, and indicated important avenues for further research. Follow-up studies should involve more molecular markers, a broader geographic sampling and more representatives of putative taxa. Important occurrence areas of *Conepatus* could not be sampled in this study, such as the Argentinean Patagonia, Paraguay, Bolivia, Peru, Ecuador, Venezuela, the United States and several Central American countries. Considering the apparent propensity of *Conepatus* populations to become isolated by several geographic elements, it is quite likely that still many other ESUs can exist throughout the genus' distribution. Therefore, further comparative studies should be developed in order to better understand the evolutionary history of *Conepatus*, the GABI and the open habitats which harbor these widespread carnivores.

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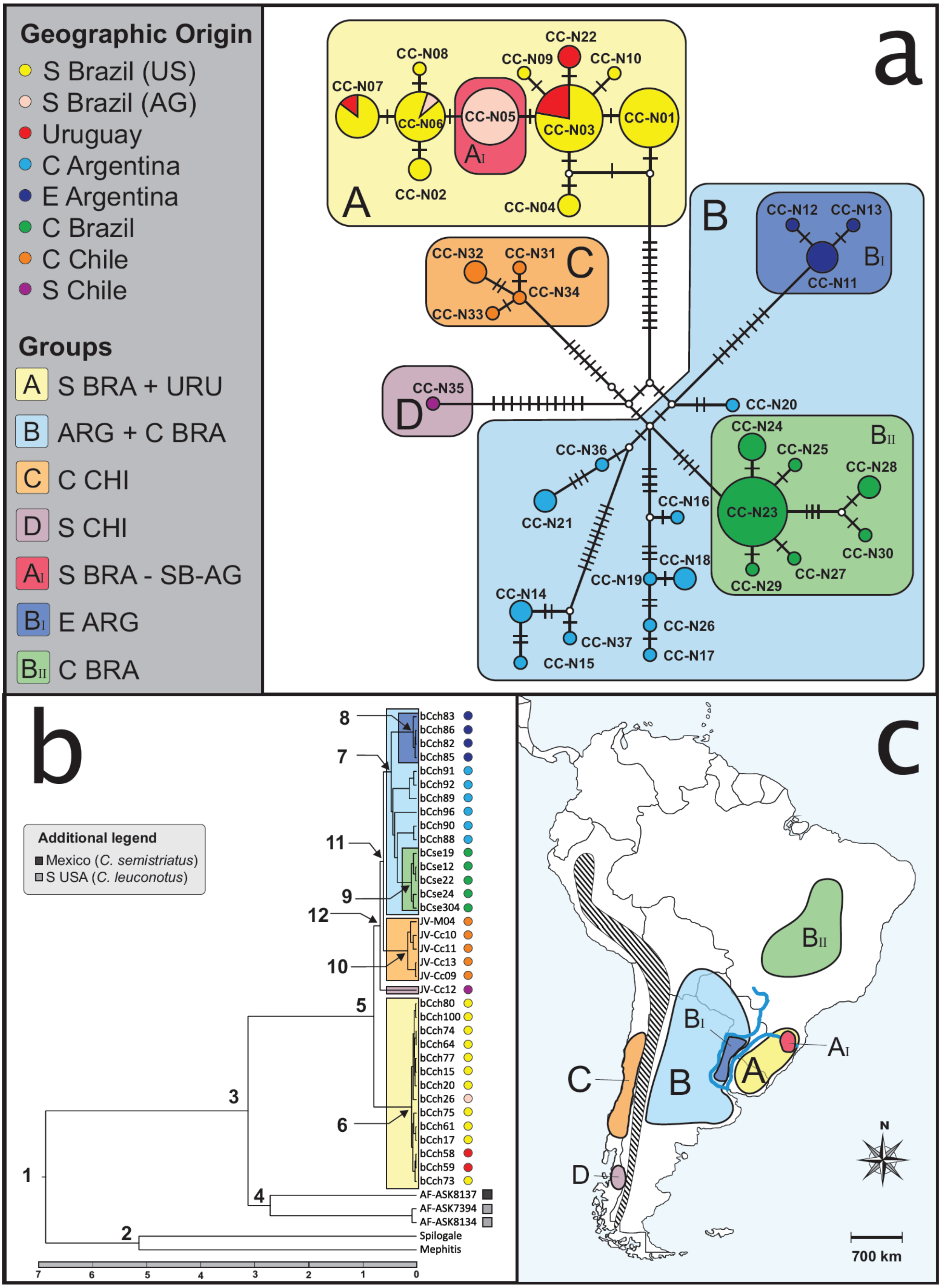
## Figures and Tables

**Figure 1.** Sample collection points (circles) plotted against the geographic distribution of the currently accepted *Conepatus* species (colored areas), following the IUCN Red List (IUCN 2012). Gray filled circles represent points from which only one sample was obtained. White filled circles indicate that two or more (up to seven) samples were collected at the same or adjacent localities. Dashed lines delimit populations to which the samples were initially assigned (see text and Table 1 for details and population codes). The total number of individuals sampled for each initial population is given in parenthesis. Color codes of the distribution for each *Conepatus* species are as follows: *C. humboldtii* – yellow; *C. chinga* – green; *C. semistriatus* – red; and *C. leuconotus* – blue.



a
Geographic Origin
S Brazil (US)
S Brazil (AG)
Uruguay
C Argentina
E Argentina
C Brazil
C Chile
S Chile
Groups
A S BRA + URU
B ARG + C BRA
C C CHI
D S CHI
AI S BRA - SB-AG
BI E ARG
BII C BRA
CC-N01
CC-N02
CC-N03
CC-N04
CC-N05
CC-N06
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CC-N32
CC-N33
CC-N34
CC-N35
CC-N36
CC-N37
A
AI
B
BI
BII
C
D
b
Additional legend
Mexico (C. semistriatus)
S USA (C. leuconotus)
1
2
3
4
5
6
7
8
9
10
11
12
bCch83
bCch86
bCch82
bCch85
bCch91
bCch92
bCch89
bCch96
bCch90
bCch88
bCse19
bCse12
bCse22
bCse24
bCse304
JV-M04
JV-Cc10
JV-Cc11
JV-Cc13
JV-Cc09
JV-Cc12
bCch80
bCch100
bCch74
bCch64
bCch77
bCch15
bCch20
bCch26
bCch75
bCch61
bCch17
bCch58
bCch59
bCch73
AF-ASK8137
AF-ASK7394
AF-ASK8134
Spilogale
Mephitis
7
6
5
4
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c
BII
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700 km

**Figure 2.** Phylogroups recovered by mtDNA analyses and their distribution plotted on a map of South America. Color legend applies to all panels. (a) Haplotype network drawn from 642 bp of *ND5* gene sequences of 132 *Conepatus* individuals, representing eight different geographic origins in South America. Each cross bar along network connectors represents one mutational step, and small white circles represent extinct/unsampled haplotypes; (b) Phylogenetic tree generated with the Bayesian analysis performed using Beast, showing the relationship among 38 ingroup and two outgroup individuals inferred from 1,902 bp of mtDNA. Ingroup individuals represent eight distinct South American geographic origins with additional *C. leuconotus* and *C. semistriatus* samples from Central/North America. Numbers next to nodes or pointing arrows indicate the node number (see Table 4 for support values and node dating estimates). The bar below the tree indicates time in million years before the present; (c) Geographic distribution of network phylogroups and tree-based clades visualized on a map of South America. Blue lines represent the Uruguay and Paraná Rivers and the hatched shape along the Pacific coast represents the southern portion of the Andes Cordillera (see text for more details).

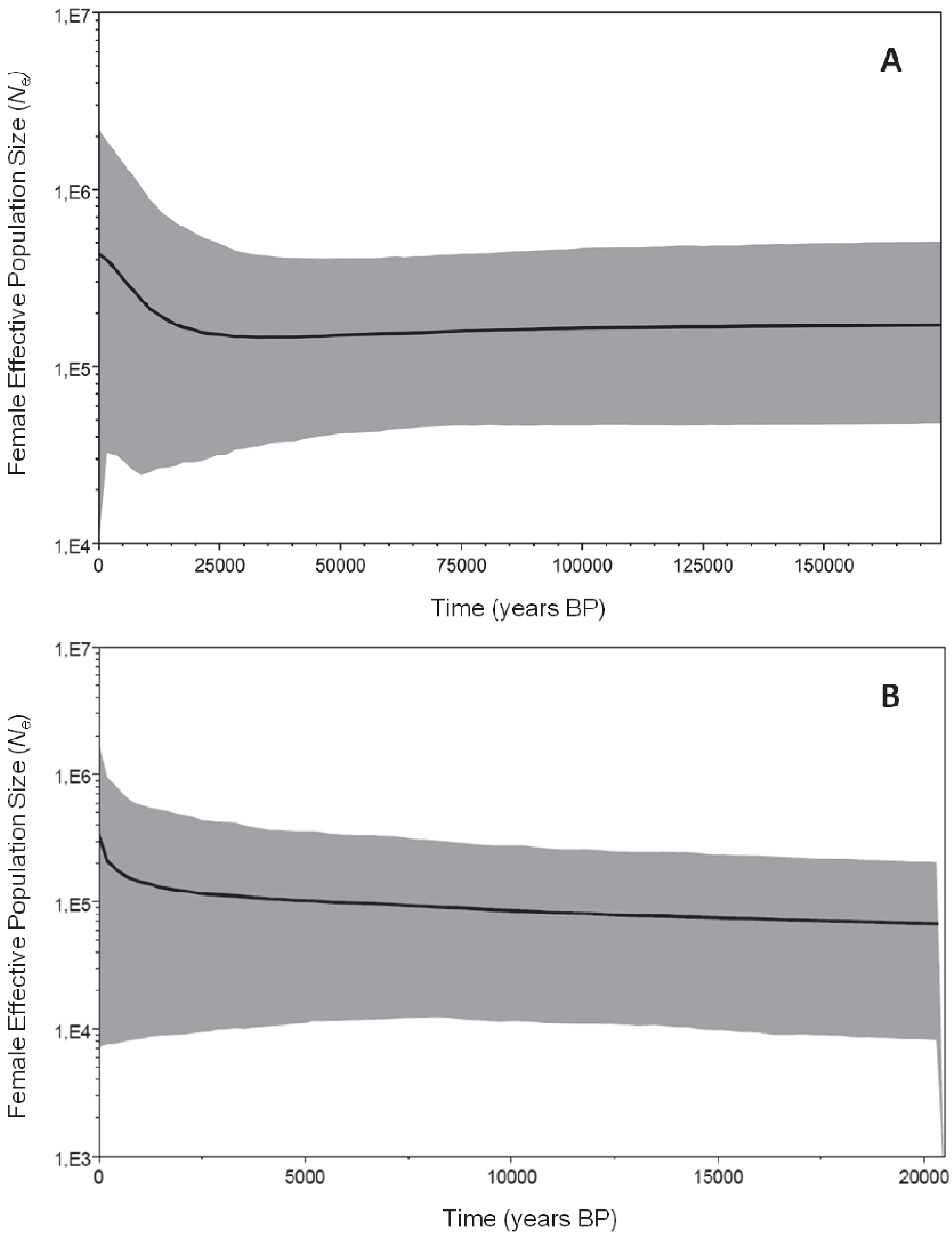

**Figure 3.** Bayesian Skyline Reconstruction plots representing the past effective population size of two different populations: (A) Central Brazil (31 individuals) and (B) Southern Brazil-Uruguay (76 individuals). The *X* axis represents the time in years before present (BP), while the *Y* axis represents the female effective population size ($N_e$). The reconstruction was conducted with 642 bp of the *ND5* mitochondrial gene, assuming a strict molecular clock and utilizing a $2.779^{-8}$ substitutions/site per year rate, as calculated from the phylogenetic analysis performed with Beast. The solid black line represents the mean population size, while the grey shade represents the 95% credibility interval.

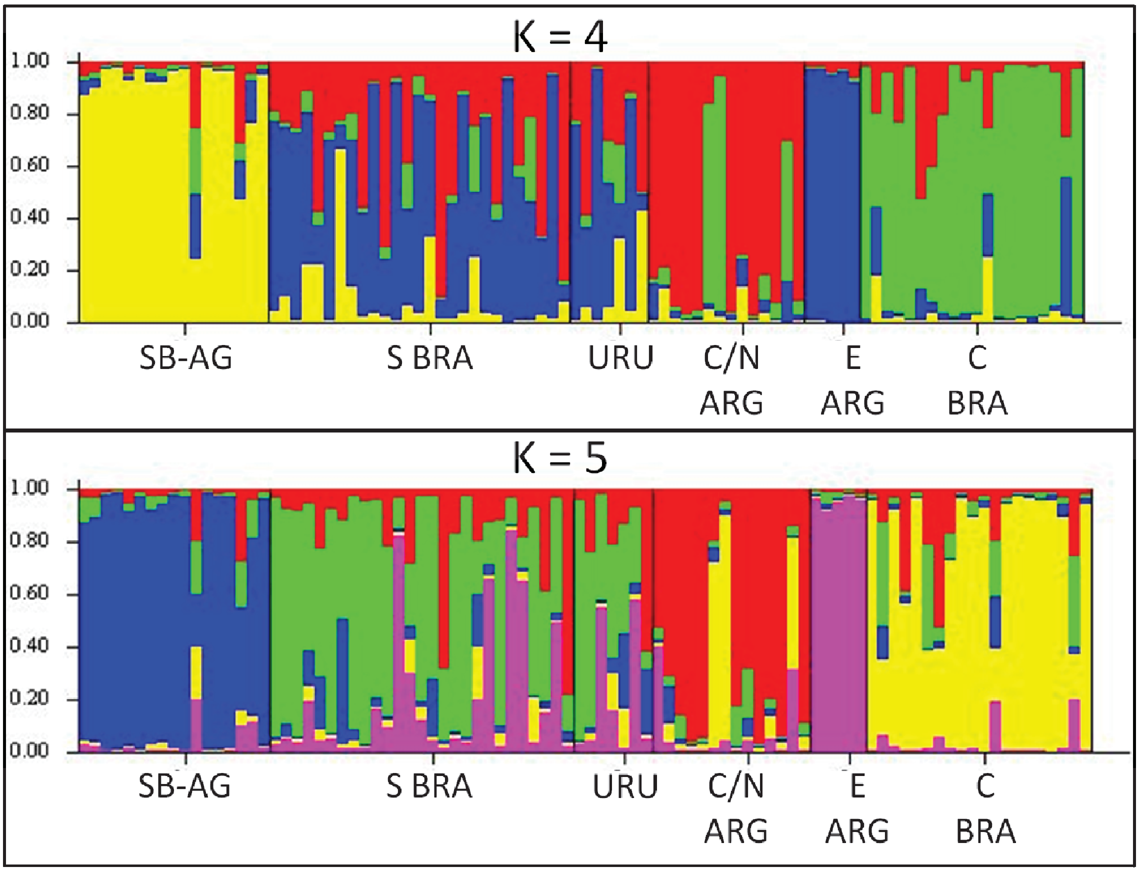

**Figure 4.** Bar plots drawn on the basis of the results of the Bayesian analysis performed with the software Structure, considering the runs with best values of likelihood among *K* = 4 (above) and *K* = 5 (below). 'K' represents the number of genetically-defined population units, with each assumed unit/cluster shown as a distinct color. Runs were performed with a dataset containing 88 individuals and seven microsatellite loci. Each bar represents one individual, and black lines between some of them represent divisions between different geographic population. The *Y* axis represents the percentage of genetic composition of each individual with respect to the inferred clusters (colors). Populations: Southern Brazil Altitude Grasslands (SB-AG), Southern Brazil Uruguayan Savannas (S BRA), Uruguay Uruguayan Savannas (URU) Central/Northern Argentina (C/N ARG), Eastern Argentina (E ARG) and Central Brazil (C BRA).

**Table 1.** Information regarding each sample utilized in this study, including putative species (following the current literature), geographic origin, initial population assignment (see text for details) and collectors.

| ID | Putative Species | City | State/Department/Region | Country | Population (this study) | Collector |
|---|---|---|---|---|---|---|
| bCch-002 | *C. chinga* | Viamão | Rio Grande do Sul | Brazil | S BRA | E. Eizirik |
| bCch-003 | *C. chinga* | Cristal | Rio Grande do Sul | Brazil | S BRA | Pró-Carnívoros Association |
| bCch-004 | *C. chinga* | Pelotas | Rio Grande do Sul | Brazil | S BRA | Pró-Carnívoros Association |
| bCch-005 | *C. chinga* | Pedro Osório | Rio Grande do Sul | Brazil | S BRA | Pró-Carnívoros Association |
| bCch-006 | *C. chinga* | Arroio Grande | Rio Grande do Sul | Brazil | S BRA | Pró-Carnívoros Association |
| bCch-007 | *C. chinga* | Arroio Grande | Rio Grande do Sul | Brazil | S BRA | Pró-Carnívoros Association |
| bCch-008 | *C. chinga* | São Francisco de Paula | Rio Grande do Sul | Brazil | SB-AG | Pró-Carnívoros Association |
| bCch-009 | *C. chinga* | Tainhas | Rio Grande do Sul | Brazil | S BRA | Pró-Carnívoros Association |
| bCch-010 | *C. chinga* | Lagoa Vermelha | Rio Grande do Sul | Brazil | SB-AG | Pró-Carnívoros Association |
| bCch-011 | *C. chinga* | Vacaria | Rio Grande do Sul | Brazil | SB-AG | Pró-Carnívoros Association |
| bCch-013 | *C. chinga* | Arambaré | Rio Grande do Sul | Brazil | S BRA | Pró-Carnívoros Association |
| bCch-014 | *C. chinga* | Camaquã | Rio Grande do Sul | Brazil | S BRA | Pró-Carnívoros Association |
| bCch-015 | *C. chinga* | Capão do Leão | Rio Grande do Sul | Brazil | S BRA | Pró-Carnívoros Association |
| bCch-016 | *C. chinga* | Cachoeira do Sul | Rio Grande do Sul | Brazil | S BRA | E. Eizirik, M. Fontoura-Rodrigues, R. Morato |
| bCch-017 | *C. chinga* | Rio Grande | Rio Grande do Sul | Brazil | S BRA | P. B. Chaves |
| bCch-018 | *C. chinga* | Rio Grande | Rio Grande do Sul | Brazil | S BRA | P. B. Chaves |
| bCch-019 | *C. chinga* | Santa Vitória do Palmar | Rio Grande do Sul | Brazil | S BRA | P. B. Chaves |
| bCch-020 | *C. chinga* | Uruguaiana | Rio Grande do Sul | Brazil | S BRA | J. Koenemann |
| bCch-022 | *C. chinga* | Osório | Rio Grande do Sul | Brazil | S BRA | M. Tavares |
| bCch-023 | *C. chinga* | Anita Garibaldi | Santa Catarina | Brazil | SB-AG | C. B. Kasper |
| bCch-024 | *C. chinga* | Campo Belo do Sul | Santa Catarina | Brazil | SB-AG | C. B. Kasper |
| bCch-025 | *C. chinga* | Campestre da Serra | Rio Grande do Sul | Brazil | SB-AG | C. B. Kasper |
| bCch-026 | *C. chinga* | Alfredo Wagner | Santa Catarina | Brazil | SB-AG | J. Cheren |
| bCch-027 | *C. chinga* | São Cristóvão do Sul | Santa Catarina | Brazil | SB-AG | J. Cheren |
| bCch-029 | *C. chinga* | Triunfo | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-030 | *C. chinga* | Soledade | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-031 | *C. chinga* | Campestre da Serra | Rio Grande do Sul | Brazil | SB-AG | C. B. Kasper |
| bCch-034 | *C. chinga* | Campo Belo do Sul | Santa Catarina | Brazil | SB-AG | C. B. Kasper, M. Piccoli (BAESA) |

**Table 1.** (continued)

| ID | Putative Species | City | State/Department/Region | Country | Population (this study) | Collector |
|---|---|---|---|---|---|---|
| bCch-035 | *C. chinga* | Capão Alto | Santa Catarina | Brazil | SB-AG | C. B. Kasper, M. Piccoli (BAESA) |
| bCch-036 | *C. chinga* | Campo Belo do Sul | Santa Catarina | Brazil | SB-AG | C. B. Kasper, M. Piccoli (BAESA) |
| bCch-037 | *C. chinga* | Bom Jesus | Rio Grande do Sul | Brazil | SB-AG | C. B. Kasper, M. Piccoli (BAESA) |
| bCch-038 | *C. chinga* | Anita Garibaldi | Santa Catarina | Brazil | SB-AG | C. B. Kasper, M. Piccoli (BAESA) |
| bCch-039 | *C. chinga* | Capão Alto | Santa Catarina | Brazil | SB-AG | C. B. Kasper, M. Piccoli (BAESA) |
| bCch-040 | *C. chinga* | Campo Belo do Sul | Santa Catarina | Brazil | SB-AG | C. B. Kasper, M. Piccoli (BAESA) |
| bCch-041 | *C. chinga* | Piratini | Rio Grande do Sul | Brazil | S BRA | F. Mazim |
| bCch-042 | *C. chinga* | Piratini | Rio Grande do Sul | Brazil | S BRA | F. Mazim |
| bCch-043 | *C. chinga* | Cachoeira do Sul | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-044 | *C. chinga* | Rosário do Sul | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-048 | *C. chinga* | Rio Grande | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-049 | *C. chinga* | Rio Grande | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-050 | *C. chinga* | Cerrito | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-051 | *C. chinga* | Pedro Osório | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-052 | *C. chinga* | Pedro Osório | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-053 | *C. chinga* | Tapes | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-054 | *C. chinga* | Pedro Osório | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-055 | *C. chinga* | Arroio Grande | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-056 | *C. chinga* | Arroio Grande | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper, G. N. Cavalcanti, M. Fontoura-Rodrigues |
| bCch-057 | *C. chinga* | Osório | Rio Grande do Sul | Brazil | S BRA | H. Figueiró (Fundação Zoobotânica RS) |
| bCch-058 | *C. chinga* | Barra de Valizas | Rocha | Uruguay | URU | M. Fontoura-Rodrigues, M. Reck, D. Dal'Bosco |
| bCch-059 | *C. chinga* | Barra de Valizas | Rocha | Uruguay | URU | M. Fontoura-Rodrigues, M. Reck, D. Dal'Bosco |
| bCch-060 | *C. chinga* | Santa Vitória do Palmar | Rio Grande do Sul | Brazil | S BRA | M. Fontoura-Rodrigues, M. Reck, D. Dal'Bosco |
| bCch-061 | *C. chinga* | Arroio Grande | Rio Grande do Sul | Brazil | S BRA | F. Mazim |
| bCch-062 | *C. chinga* | Cristal | Rio Grande do Sul | Brazil | S BRA | F. Mazim |
| bCch-063 | *C. chinga* | Canguçu | Rio Grande do Sul | Brazil | S BRA | F. Mazim |
| bCch-064 | *C. chinga* | Arroio Grande | Rio Grande do Sul | Brazil | S BRA | F. Mazim |
| bCch-065 | *C. chinga* | Barra do Ribeiro | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |

**Table 1.** (continued)

| ID | Putative Species | City | State/Department/Region | Country | Population (this study) | Collector |
|---|---|---|---|---|---|---|
| bCch-066 | *C. chinga* | Tapes | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-067 | *C. chinga* | Osório | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-068 | *C. chinga* | Cristal | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-069 | *C. chinga* | Tapes | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-070 | *C. chinga* | Osório | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-071 | *C. chinga* | Encruzilhada do Sul | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-072 | *C. chinga* | Cristal | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-073 | *C. chinga* | Santo Antônio da Patrulha | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-074 | *C. chinga* | Pantano Grande | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-075 | *C. chinga* | Encruzilhada do Sul | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-076 | *C. chinga* | Canguçú | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-077 | *C. chinga* | Ibirubá | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper |
| bCch-078 | *C. chinga* | Cachoeira do Sul | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-079 | *C. chinga* | Cachoeira do Sul | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-080 | *C. chinga* | Alegrete | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-081 | *C. chinga* | Alegrete | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-082 | *C. chinga* | Cuatro Bocas | Corrientes | Argentina | E ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-083 | *C. chinga* | Los Conquistadores | Entre Rios | Argentina | E ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-084 | *C. chinga* | Federal | Entre Rios | Argentina | E ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-085 | *C. chinga* | Federal | Entre Rios | Argentina | E ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-086 | *C. chinga* | Bovril | Entre Rios | Argentina | E ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-087 | *C. chinga* | Pareditas | Mendoza | Argentina | C/N ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-088 | *C. chinga* | Pareditas | Mendoza | Argentina | C/N ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-089 | *C. chinga* | El Nehuil | Mendoza | Argentina | C/N ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-090 | *C. chinga* | Coronel Dorrego | Buenos Aires | Argentina | C/N ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-091 | *C. chinga* | Coronel Dorrego | Buenos Aires | Argentina | C/N ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-092 | *C. chinga* | Coronel Dorrego | Buenos Aires | Argentina | C/N ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-093 | *C. chinga* | Coronel Dorrego | Buenos Aires | Argentina | C/N ARG | C. B. Kasper, M. Fontoura-Rodrigues |

**Table 1. (continued)**

| ID | Putative Species | City | State/Department/Region | Country | Population (this study) | Collector |
|---|---|---|---|---|---|---|
| bCch-094 | *C. chinga* | Benito juarez | Buenos Aires | Argentina | C/N ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-095 | *C. chinga* | Alzaga | Buenos Aires | Argentina | C/N ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-096 | *C. chinga* | Cachari | Buenos Aires | Argentina | C/N ARG | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-097 | *C. chinga* | Ciudad de la Costa | Canelones | Uruguay | URU | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-098 | *C. chinga* | José Ignácio | Maldonado | Uruguay | URU | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-099 | *C. chinga* | José Ignácio | Maldonado | Uruguay | URU | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-100 | *C. chinga* | Santa Vitória do Palmar | Rio Grande do Sul | Brazil | S BRA | C. B. Kasper, M. Fontoura-Rodrigues |
| bCch-101 | *C. chinga* | Gualegay | Entre Rios | Argentina | E ARG | J. Pereira |
| bCch-102 | *C. chinga* | ? | Cordoba/Buenos Aires | Argentina | C/N ARG | R. Palacios |
| bCch-103 | *C. chinga* | ? | Cordoba/Buenos Aires | Argentina | C/N ARG | R. Palacios |
| bCch-104 | *C. chinga* | ? | Cordoba/Buenos Aires | Argentina | C/N ARG | R. Palacios |
| bCch-105 | *C. chinga* | ? | Cordoba/Buenos Aires | Argentina | C/N ARG | R. Palacios |
| bCch-106 | *C. chinga* | Tapes | Rio Grande do Sul | Brazil | S BRA | P. B. Chaves |
| bCch-107 | *C. chinga* | Castillos | Rocha | Uruguay | URU | P. B. Chaves |
| bCch-108 | *C. chinga* | La Barra | Maldonado | Uruguay | URU | M. Favarini |
| bCse-001 | *C. semistriatus* | São Roque | Minas Gerais | Brazil | C BRA | CENAP |
| bCse-002 | *C. semistriatus* | Formiga | Minas Gerais | Brazil | C BRA | J. May |
| bCse-003 | *C. semistriatus* | Formiga | Minas Gerais | Brazil | C BRA | F. Rodrigues |
| bCse-004 | *C. semistriatus* | Piumhí | Minas Gerais | Brazil | C BRA | J. May Jr. |
| bCse-005 | *C. semistriatus* | Três Marias | Minas Gerais | Brazil | C BRA | F. Rodrigues |
| bCse-006 | *C. semistriatus* | Piumhí | Minas Gerais | Brazil | C BRA | J. May Jr. |
| bCse-007 | *C. semistriatus* | São Roque de Minas | Minas Gerais | Brazil | C BRA | J. May Jr. |
| bCse-008 | *C. semistriatus* | Batalha | Piauí | Brazil | C BRA | G. N. Cavalcanti |
| bCse-009 | *C. semistriatus* | José de Freitas | Piauí | Brazil | C BRA | G. N. Cavalcanti |
| bCse-010 | *C. semistriatus* | Cabeceiras | Piauí | Brazil | C BRA | G. N. Cavalcanti |
| bCse-011 | *C. semistriatus* | Cabeceiras | Piauí | Brazil | C BRA | G. N. Cavalcanti |
| bCse-012 | *C. semistriatus* | Pirapora | Goiás | Brazil | C BRA | F. Grazziotin, A. Garda |
| bCse-014 | *C. semistriatus* | Soledade de Minas | Minas Gerais | Brazil | C BRA | C. B. Kasper, T. G. Oliveira, M. Tsuchiya, M. Fontoura-Rodrigues |
| bCse-015 | *C. semistriatus* | Cristalina | Goiás | Brazil | C BRA | F. Jerep, T. Carvalho |

**Table 1.** (continued)

| ID | Putative Species | City | State/Department/Region | Country | Population (this study) | Collector |
|---|---|---|---|---|---|---|
| bCse-016 | *C. semistriatus* | Três Marias | Minas Gerais | Brazil | C BRA | G. N. Cavalcanti |
| bCse-017 | *C. semistriatus* | Cristino Castro | Piauí | Brazil | C BRA | G. N. Cavalcanti |
| bCse-019 | *C. semistriatus* | Ribeiro Gonçalves | Piauí | Brazil | C BRA | C. B. Kasper |
| bCse-020 | *C. semistriatus* | Barão de Cocais | Minas Gerais | Brazil | C BRA | D. Saraiva |
| bCse-021 | *C. semistriatus* | Curvelo | Minas Gerais | Brazil | C BRA | D. Saraiva |
| bCse-022 | *C. semistriatus* | Três Marias | Minas Gerais | Brazil | C BRA | D. Saraiva |
| bCse-023 | *C. semistriatus* | Três Marias | Minas Gerais | Brazil | C BRA | D. Saraiva |
| bCse-024 | *C. semistriatus* | Curvelo | Minas Gerais | Brazil | C BRA | D. Saraiva |
| bCse-026 | *C. semistriatus* | Iguatú | Ceará | Brazil | C BRA | G. N. Cavalcanti |
| bCse-027 | *C. semistriatus* | Valença | Piauí | Brazil | C BRA | G. N. Cavalcanti |
| bCse-301 | *C. semistriatus* | Mineiros | Goiás | Brazil | C BRA | L. Silveira |
| bCse-302 | *C. semistriatus* | Valença | Piauí | Brazil | C BRA | G. N. Cavalcanti |
| bCse-303 | *C. semistriatus* | Mineiros | Goiás | Brazil | C BRA | L. Silveira, A. Jacomo, M. Furtado, C. Kashivakura |
| bCse-304 | *C. semistriatus* | Mineiros | Goiás | Brazil | C BRA | L. Silveira, A. Jacomo, M. Furtado, C. Kashivakura |
| bCse-306 | *C. semistriatus* | Mineiros | Goiás | Brazil | C BRA | L. Silveira, A. Jacomo, M. Furtado, C. Kashivakura |
| bCse-307 | *C. semistriatus* | Mineiros | Goiás | Brazil | C BRA | L. Silveira, A. Jacomo, M. Furtado, C. Kashivakura |
| bCse-308 | *C. semistriatus* | Mineiros | Goiás | Brazil | C BRA | L. Silveira, A. Jacomo, M. Furtado, C. Kashivakura |
| bCse-309 | *C. semistriatus* | Mineiros | Goiás | Brazil | C BRA | L. Silveira, A. Jacomo, M. Furtado, C. Kashivakura |
| bCse-310 | *C. semistriatus* | Mineiros | Goiás | Brazil | C BRA | L. Silveira, A. Jacomo, M. Furtado, C. Kashivakura |
| bCse-311 | *C. semistriatus* | Mineiros | Goiás | Brazil | C BRA | L. Silveira, A. Jacomo, M. Furtado, C. Kashivakura |
| JV-M04 | *C. chinga* | Curicó | Maule | Chile | C CHI | J. Vianna |
| JV-Cc09 | *C. chinga* | Santo Domingo | Valparaíso | Chile | C CHI | J. Vianna |
| JV-Cc10 | *C. chinga* | Puente Iñaque | Los Ríos | Chile | C CHI | J. Vianna |
| JV-Cc13 | *C. chinga* | Los Vilos | Coquimbo | Chile | C CHI | J. Vianna |
| JV-Cc11 | *C. chinga* | Paso Puyehua | Los Lagos | Chile | C CHI | J. Vianna |
| JV-Cc12 | *C. humboldtii* | Puerto Aisén | Aisén | Chile | S CHI | J. Vianna |
| AF-ASK8137 | *C. semistriatus* | Merida | Yucatán | Mexico | CSE | A. Ferguson |
| AF-ASK7394 | *C. leuconotus* | McCulloch | Texas | USA | CLE | A. Ferguson |
| AF-ASK8134 | *C. leuconotus* | San Francisco del Mar | Oaxaca | Mexico | CLE | A. Ferguson |

**Table 2.** Genetic diversity observed in mitochondrial DNA fragments sampled in multiple *Conepatus* sp. populations. The total fragment length analyzed, in base pairs, is given beside each fragment name.

| | ND5 (642 bp) | | | | | cytb (631 bp) | | | | | 7a (629 bp) | | | | | Overall (1,902 bp) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Population | N | S | h | Hd | Pi (%) | N | S | h | Hd | Pi (%) | N | S | h | Hd | Pi (%) | N | S | h | Hd | Pi (%) |
| [US]+[SB-AG] | 76 | 7 | 7 | 0.69 | 0.21 | 36 | 10 | 8 | 0.64 | 0.16 | 17 | 3 | 4 | 0.49 | 0.09 | 16 | 15 | 11 | 0.93 | 0.18 |
| C/N ARG | 14 | 34 | 11 | 0.97 | 1.86 | 9 | 24 | 8 | 0.97 | 1.49 | 7 | 20 | 4 | 0.81 | 1.45 | 7 | 72 | 6 | 0.95 | 1.65 |
| E ARG | 6 | 2 | 3 | 0.60 | 0.11 | 5 | 2 | 3 | 0.70 | 0.16 | 4 | 2 | 3 | 0.83 | 0.16 | 4 | 5 | 4 | 1.00 | 0.13 |
| C BRA | 31 | 9 | 7 | 0.50 | 0.18 | 6 | 1 | 2 | 0.33 | 0.05 | 6 | 4 | 4 | 0.80 | 0.25 | 5 | 9 | 4 | 0.90 | 0.21 |
| C CHI | 5 | 6 | 4 | 0.90 | 0.47 | 0 | - | - | - | - | 0 | - | - | - | - | 0 | - | - | - | - |
| Overall | 133* | 63 | 32 | 0.87 | 2.39 | 56 | 52 | 21 | 0.84 | 1.93 | 41 | 36 | 17 | 0.87 | 1.58 | 32 | 216 | 29 | 0.98 | 5.37 |

Number of individuals sampled (N), number of segregating sites (S), observed number of haplotypes (h), haplotype diversity (Hd) and nucleotide diversity (Pi).

Populations: Uruguayan Savannas + Southern Brazil Altitude Grasslands ([US]+[SB-AG]), Central/Northern Argentina (C/N ARG), Eastern Argentina (E ARG), Central Brazil (C BRA) and Central Chile (C CHI).

*The single sample from Southern Chile was included only in the overall statistics.

**Table 3.** Pairwise fixation indices estimated among *Conepatus* sp. populations.

| | SB-AG | US | C/N ARG | E ARG | C BRA |
|---|---|---|---|---|---|
| **mtDNA** | | | | | |
| $F_{st}$ | | | | | |
| US | 0.251*** | - | - | - | - |
| C/N ARG | 0.768*** | 0.833*** | - | - | - |
| E ARG | 0.988*** | 0.921*** | 0.536*** | - | - |
| C BRA | 0.965*** | 0.926*** | 0.564*** | 0.924*** | - |
| C CHI | 0.968*** | 0.919*** | 0.539*** | 0.909*** | 0.916*** |
| **Microsatellites** | | | | | |
| $F_{st}$ | | | | | |
| US | 0.228*** | - | - | - | - |
| C/N ARG | 0.143*** | 0.148*** | - | - | - |
| E ARG | 0.355*** | 0.35*** | 0.24*** | - | - |
| C BRA | 0.207*** | 0.129*** | 0.113*** | 0.31*** | - |
| $R_{st}$ | | | | | |
| US | 0.196* | - | - | - | - |
| C/N ARG | 0.227*** | 0.279*** | - | - | - |
| E ARG | 0.721*** | 0.320* | 0.586*** | - | - |
| C BRA | 0.463*** | 0.539*** | 0.466*** | 0.78*** | - |
| $D_{est}$ | | | | | |
| US | 0.368 | - | - | - | - |
| C/N ARG | 0.378 | 0.246 | - | - | - |
| E ARG | 0.463 | 0.195 | 0.416 | - | - |
| C BRA | 0.378 | 0.183 | 0.23 | 0.383 | - |

$D_{est}$ analysis does not output statistical significance tests.

Statistical significance for $F_{st}$ and $R_{st}$ tests: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Populations: Southern Brazil Altitude Grasslands (SB-AG), Uruguayan Savannas (US), Central/Northern Argentina (C/N ARG), Eastern Argentina (E ARG), Central Brazil (C BRA) and Central Chile (C CHI).

Comparisons with the Central Chile populations were carried out only with mtDNA (*ND5*) because microsatellite data were not generated for that population.

**Table 4.** Support values and age estimates for each node displayed on Figure 2b. The support values provided are Posterior Probabilities (PP), calculated with Beast, and Bootstrap support (BS) calculated with RaxML. Node ages were estimated with Beast, in million years ago, and are shown as the mean followed by the 95% credibility interval boundaries.

| Node | Node Name | Support | | Node Age (MYA) | | |
|---|---|---|---|---|---|---|
| | | PP | BS | Mean | Lower 95% | Upper 95% |
| 1 | Mephitidae | NP | NP | 6.86 | 5.07 | 9.25 |
| 2 | *Spilogale* + *Mephitis* | 1.0 | 100 | 5.09 | 3.42 | 7.09 |
| 3 | *Conepatus* | 1.0 | 100 | 3.18 | 2.04 | 4.51 |
| 4 | *C. leuconotus* + *C. semistriatus* | 0.76 | - | 2.87 | 1.75 | 4.18 |
| 5 | South American Clade | 1.0 | 100 | 0.84 | 0.5 | 1.22 |
| 6 | S Brazil* + Uruguay | 1.0 | 100 | 0.1 | 0.05 | 0.16 |
| 7 | Argentina** + C Brazil | 0.99 | 70 | 0.5 | 0.3 | 0.73 |
| 8 | E Argentina | 1.0 | 100 | 0.06 | 0.02 | 0.12 |
| 9 | C Brazil | 1.0 | 99 | 0.1 | 0.04 | 0.17 |
| 10 | C Chile | 1.0 | 100 | 0.18 | 0.06 | 0.32 |
| 11 | (Argentina + C Brazil) + C Chile) | 0.61 | - | NP | NP | NP |
| 12 | (Argentina + C Brazil) + C Chile) + S Chile | 0.53 | - | NP | NP | NP |

Not Significant: - ; Not Performed: NP.

Abbreviations: S, Southern; C, Central; E, Eastern.

* Including Southern Brazil Altitude Grasslands

** Including Eastern Argentina

**Table 5.** Statistical neutrality tests performed with distinct *Conepatus* sp. populations. P values for each test are provided next to each result.

| | | Tajima's D | | Fu and Li's D* | | Fu and Li's F* | | Fu's Fs | |
|---|---|---|---|---|---|---|---|---|---|
| Population | N | Value | p | Value | p | Value | p | Value | p |
| [US]+[SB-AG] | 76 | -0.622 | 0.308 | -0.463 | > 0.10 | -0.696 | > 0.10 | -6.039 | 0.01* |
| C/N ARG | 14 | 0.501 | 0.744 | 0.635 | > 0.10 | 0.687 | > 0.10 | -0.919 | 0.307 |
| E ARG | 6 | -1.131 | 0.155 | -1.155 | > 0.10 | -1.195 | > 0.10 | -0.858 | 0.081 |
| C BRA | 31 | -1.571 | 0.041* | -0.981 | > 0.10 | -1.359 | > 0.10 | -2.329 | 0.065 |
| C CHI | 5 | 0.286 | 0.667 | 0.286 | > 0.10 | 0.296 | > 0.10 | -0.331 | 0.301 |

*Statistically significant value ($p < 0.05$).

Populations: Uruguayan Savannas + Southern Brazil Altitude Grasslands ([US]+[SB-AG]), Central/Northern Argentina (N/C ARG), Eastern Argentina (E ARG), Central Brazil (C BRA) and Central Chile (C CHI).

**Table 6.** Diversity indices of eight microsatellite loci assessed across five populations surveyed in this study.

| | *Multiplex 1* | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Meph42-73 (F) | | | | | Meph22-14 (F) | | | | | Meph42-15 (H) | | | | | Meph42-25 (N) | | | | |
| Population | N | A | S | $H_o$ | $H_e$ | N | A | S | $H_o$ | $H_e$ | N | A | S | $H_o$ | $H_e$ | N | A | S | $H_o$ | $H_e$ |
| SB-AG | 15 | 2 | 158-164 | 0.467 | 0.480 | 9 | 4 | 270-280 | 1.000 | 0.732 | 14 | 1 | 193 | 0.0 | 0.0 | 15 | 6 | 221-253 | 0.733 | 0.703 |
| US | 30 | 2 | 158-164 | 0.167 | 0.305 | 19 | 11 | 256-280 | 0.842 | 0.910 | 33 | 1 | 193 | 0.0 | 0.0 | 30 | 17 | 221-259 | 0.900 | 0.946 |
| C/N ARG | 13 | 5 | 158-172 | 0.769 | 0.720 | 10 | 7 | 254-276 | 0.700 | 0.779 | 13 | 1 | 193 | 0.0 | 0.0 | 12 | 13 | 211-259 | 0.833 | 0.946 |
| E ARG | 5 | 2 | 170-172 | 0.200 | 0.200 | 4 | 4 | 268-276 | 0.750 | 0.821 | 5 | 1 | 193 | 0.0 | 0.0 | 5 | 6 | 233-247 | 0.600 | 0.778 |
| C BRA | 16 | 5 | 156-164 | 0.625 | 0.780 | 14 | 9 | 264-282 | 1.000 | 0.884 | 17 | 1 | 193 | 0.0 | 0.0 | 18 | 9 | 211-249 | 0.444* | 0.843 |
| Overall | 79 | 8 | 156-172 | 0.418 | 0.673 | 56 | 15 | 254-282 | 0.875 | 0.900 | 82 | 1 | 193 | 0.0 | 0.0 | 80 | 24 | 211-259 | 0.738 | 0.944 |

**Table 6.** (continued)

| | *Multiplex 2* | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Meph22-26 (F) | | | | | Meph22-70 (N) | | | | | Meph22-89 (F) | | | | | Meph42-67 (H) | | | | |
| Population | N | A | S | $H_o$ | $H_e$ | N | A | S | $H_o$ | $H_e$ | N | A | S | $H_o$ | $H_e$ | N | A | S | $H_o$ | $H_e$ |
| SB-AG | 9 | 3 | 253-259 | 0.667 | 0.503 | 9 | 3 | 198-206 | 0.444 | 0.569 | 9 | 1 | 168 | 0.000 | 0.000 | 15 | 2 | 235-237 | 0.667 | 0.497 |
| US | 26 | 8 | 251-267 | 0.885 | 0.779 | 22 | 2 | 196-198 | 0.000 | 0.089 | 11 | 4 | 154-184 | 0.091 | 0.403* | 32 | 2 | 235-237 | 0.063 | 0.062 |
| C/N ARG | 11 | 9 | 245-267 | 0.727 | 0.887 | 7 | 9 | 198-232 | 0.857 | 0.934 | 2 | 2 | 156-162 | 0.500 | 0.500 | 12 | 2 | 235-237 | 0.250 | 0.228 |
| E ARG | 5 | 3 | 251-257 | 0.600 | 0.711 | 5 | 3 | 184-196 | 0.000 | 0.622 | 0 | 0 | - | 0.000 | 0.000 | 5 | 1 | 235 | 0.000 | 0.000 |
| C BRA | 12 | 8 | 245-261 | 0.667 | 0.844 | 17 | 3 | 198-202 | 0.353 | 0.314 | 0 | 0 | - | 0.000 | 0.000 | 17 | 3 | 233-237 | 0.353 | 0.392 |
| Overall | 63 | 12 | 245-267 | 0.762 | 0.851 | 60 | 14 | 184-232 | 0.267 | 0.554 | 22 | 6 | 154-184 | 0.091 | 0.366 | 81 | 3 | 233-237 | 0.259 | 0.266 |

Sample size (N), observed number of alleles (A), size range of the PCR fragment (S), observed heterozygosity (Ho) and expected heterozygosity (He)
Populations: Southern Brazil Altitude Grasslands (SB-AG), Uruguayan Savannas (US), Central/Northern Argentina (C/N ARG), Eastern Argentina (E ARG), and Central Brazil (C BRA).
The letter in parentheses next to each microsatellite locus represents the fluorophore employed for the multiplex approach: F - 6-FAM, N - NED, H - HEX.
*Departure from HW-Equilibrium detected and statistically significant after Bonferroni Correction.

**Table 7.** Mean likelihood (Ln P(D)) and likelihood variance (Var[LnP(D)]) values across 15 iterations for each *K*, as assessed with the software Structure (see text for details).

| K | Ln P(D) | Var[LnP(D)] |
|---|---|---|
| 1 | -1561.05 | 33.94 |
| 2 | -1472.80 | 103.23 |
| 3 | -1425.49 | 226.07 |
| 4* | -1374.43 | 249.97 |
| 5 | -1379.21 | 379.84 |
| 6 | -1492.71 | 646.39 |
| 7 | -1503.57 | 717.15 |
| 8 | -1474.85 | 702.66 |
| 9 | -1509.25 | 788.84 |
| 10 | -1566.61 | 898.10 |

*Best K likelihood value.

**Table 8.** Distribution of genetic assignment of each *Conepatus* population to the genetic clusters (C1 - C5) inferred with the software Structure.

| | K = 4 | | | | K = 5 | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Population | C1 | C2 | C3 | C4 | C1 | C2 | C3 | C4 | C5 |
| SB-AG | **0.891** | 0.038 | 0.043 | 0.029 | **0.843** | 0.043 | 0.045 | 0.045 | 0.023 |
| S BRA | *0.115* | **0.503** | *0.317* | 0.064 | 0.067 | **0.476** | *0.160* | *0.262* | 0.036 |
| URU | *0.165* | **0.469** | *0.286* | 0.080 | 0.099 | **0.386** | *0.191* | *0.272* | 0.053 |
| C/N ARG | 0.042 | 0.041 | **0.706** | *0.211* | 0.029 | 0.043 | **0.675** | 0.093 | *0.160* |
| E ARG | 0.009 | **0.948** | 0.033 | 0.010 | 0.007 | 0.012 | 0.008 | **0.968** | 0.005 |
| C BRA | 0.041 | 0.060 | *0.104* | **0.795** | 0.034 | 0.075 | *0.112* | 0.049 | **0.731** |

**Bold:** the highest values of genetic content of each Conepatus population.
*Italic:* values of genetic content higher than 10%.
Populations: Southern Brazil Altitude Grasslands (SB-AG), Southern Brazil, excluding SB-AG (S BRA), Uruguay (URU), Central/Northern Argentina (C/N ARG), Eastern Argentina (E ARG), and Central Brazil (C BRA).

# CAPÍTULO III

**Artigo Científico**

# Taxonomic revision of *Conepatus* (Carnivora: Mephitidae) based on molecular phylogenetics, morphological comparisons and distributional patterns

**Manoel Ludwig da Fontoura-Rodrigues,** Carlos Benhur Kasper, Gitana Nunes Cavalcanti, Diego Castillo, Kristofer Michael Helgen, **Eduardo Eizirik**

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# Taxonomic revision of *Conepatus* (Carnivora: Mephitidae) based on molecular phylogenetics, morphological comparisons and distributional patterns

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*Running Title*: Taxonomic revision of *Conepatus*

## Abstract

*Conepatus* is one of the least studied Neotropical mammalian genera, whose current taxonomic and geographic structure is poorly defined. It therefore requires prompt taxonomic revision in order to provide the basis for detailed descriptive and comparative studies on the biology, ecology and evolution of the species contained in this group. Since modern taxonomic concepts involve an understanding of the evolutionary divergence among populations, morphological diagnosis and distributional delimitation, we focused on these three aspects to assess and revise the genus' taxonomy. In order to do so, we initially performed a detailed distributional assessment of the genus as a whole, to serve as basic layer. We then conducted an analysis of population differentiation based on 29 craniodental variables and previously collected molecular data. Finally, we compared some of the identified populations in terms of differences in general body measurements, to test if the population structure found with more detailed approaches can also be detected by inspecting the general appearance of the individuals. We found at least 10 distinct evolutionary units in *Conepatus*, in contrast to the four species that are currently accepted. Most of them are highly associated to a particular geographic region, so that their specific range can be clearly delimited. General body measurements are clearly associated with population disjunctions, making them suitable for the initial characterization of additional populations. We suggest that all 10 evolutionary units identified here should be recognized taxonomically, and discuss conceptual and nomenclatural aspects that can guide such proposition.

*Keywords*: conservation – craniodental measurements – evolution – ESUs – hog-nosed skunks

## Introduction

Although mammals are often considered to be a well-known group within the Tree of Life, many taxa contained in this class remain poorly understood. Even among orders such as the Carnivora, which have been the target of numerous phylogenetic investigations, there are several taxa for which even basic taxonomic questions are not adequately solved (Patterson, 2001). Such uncertainties include aspects such as species delimitation, geographic distribution and diagnostic morphological traits. This lack of knowledge can seriously harm the efficacy of conservation efforts, since it hampers a proper evaluation of conservation status and the design of adequate action plans. Since mammals are often among the most affected vertebrates in impacted environments (Schipper *et al*., 2008), resolving such basic issues are a priority in the context of performing adequate assessments of threat and making conservation-related decisions.

Several cases of such paucity of basic knowledge affect Neotropical taxa, including carnivoran genera such as *Conepatus* Gray, 1837 (Carnivora: Mephitidae), which comprises the hog-nosed skunks (Wozencraft, 2005). This genus presents one of the largest distributions among the Carnivora, inhabiting several biomes in South America, Central America and southern North America (Figure 1). Despite being common in many of these areas, very little is known about the basic biology of these animals, including their behavior, ecology and geographic distribution (Oliveira, 2006). Moreover, the lack of evolutionary studies targeting these animals has traditionally hampered a proper systematic assessment of the group, leading to important taxonomic uncertainties. Until recently, the taxonomic arrangement of *Conepatus* consisted in a five-species division: *C. mesoleucus* and *C. leuconotus* in North America; *C. semistriatus* in Central and northern South America, as well as in a disjunct area located in Central Brazil; and *C. chinga* and *C. humboldtii* in South America (Wozencraft, 1993). The two North American species, formerly separated mainly by size and color patterns, were recently synonymized under *C. leuconotus* (Dragoo *et al*., 2003). Regarding the South American species, it was only recently that their evolutionary history began to be investigated using modern phylogenetic approaches, performed on the basis of molecular and morphological characters (Schiaffini *et al.* 2013; Fontoura-Rodrigues *et al.* [in prep.] ***[ver capítulo II desta tese]***). The study by Schiaffini *et al.* (2013) focused on populations from southern South America, using mtDNA sequences and morphological data (skull, mandible and pelage features), and failed to identify clear-cut differences between *C. chinga* and *C. humboldtii*, leading those authors to question the validity of their specie-level status. In contrast, the study by Fontoura-Rodrigues *et al.* (in prep.), based on mtDNA and nuclear microsatellite data, identified several distinct evolutionary units in *Conepatus*, which occur in different regions of South America and whose phylogeographic pattern challenges the currently accepted taxonomic structure of the genus. Since these authors did not present a formal taxonomic reevaluation, there is a need for further assessment of the identified phylogroups, so as to define at what level they should be recognized, and how to treat them from a nomenclatural perspective. Such reassessment must be in accordance with the taxonomic history of the genus, following the form and priority order of the names previously proposed by original authors.

Similarly to what happened to several other Neotropical taxa, most *Conepatus* species were described by European naturalists from the XVIII to the XX centuries, most of them based on a few or even a single specimen. The British naturalist Oldfield Thomas alone described more than ten different species from several South American countries (*e.g.* Thomas, 1898, 1900, 1902, 1905). The first major taxonomic revisions were conducted by Cabrera (1958) and Kipp (1965), who proposed the synonymization of several previously described species and established the basis for the modern taxonomic disposition mentioned above. However, the arrangement employed by most authors today is a mosaic of these early reviews, and does not stem from a direct evaluation based on a broad comparison of primary data. Most importantly, it is now well established that modern phylogenetic approaches, based on morphological and/or molecular data, are important to accomplish a more accurate taxonomic assessment. The study by Dragoo *et al*. (2003) showed that the traditional surveys that identified most taxonomic units in *Conepatus* – based mainly on color patterns and body size of a few individuals – are not appropriate or sufficient. Therefore, a modern taxonomic proposition must be designed based on modern tools and concepts, such as the Evolutionarily Significant Units (ESUs) (Moritz, 1994; for a review see Fraser & Bernatchez, 2001), which are usually based on genetic analyses. At the same time, modern morphological comparisons, often based on several different craniometrical measurements and several individuals, can also reveal population differentiation by taking into account a wider range of intraspecific variation and discern a more robust signal coming from a large number of variables (*e.g.* Huggenberger *et al*., 2002; Bornholdt *et al*., in press). This approach has already been utilized in the genus to show the lack of internal structure in the Uruguayan population (Van Gelder, 1968), and also in the recent study by Schiaffini *et al.* (2013). In addition to population structure, the modern application of the ESU concept usually incorporates two other components: local adaptation (inferred from morphological diagnostic characters and/or ecological features) and allopatry (Eizirik *et al*., 2006). Moreover, in some cases geographic units initially identified as distinct ESUs may in fact warrant species-level recognition upon further scrutiny, and may or may not bear the same properties. Since cryptic species and sympatric speciation are found in nature, such features cannot be interpreted as clearly determinant, but their presence is often important to substantiate a solid taxon description. Therefore, whenever possible, morphological traits and distributional patterns should be investigated alongside the characterization of population distinctiveness based on molecular tools.

Regarding the geographic range of the genus, several uncertainties still persist. Although a major consensus exists pointing to savannas and other open environments as the main habitat type for the genus, several records from forested environments challenge this view (*e.g.* Cáceres, 2004; Oliveira *et al*., 2007). So far, no comprehensive review has been conducted on this topic, which includes museum data and original publication records; moreover the reports on the geographic range of some particular populations are clearly outdated. For example, the *Conepatus* population occurring in central/northern Brazil has long been considered to be restricted to the northeastern region (the Caatinga biome) by many authors. Only recently did Dragoo (2009) include central Brazil (the Cerrado biome) as an area of occurrence of that group, although he did not provide a precise characterization of its distribution in this region. Many records for central and northeastern Brazil are available, and therefore a precise distribution delimitation is necessary in order to better characterize that population. A similar situation is the uncertain occurrence area of *Conepatus* in southern Brazil. This population is known to occur in the Pampas region (*e.g.* Cabrera, 1958) as well as in an isolated altitude grasslands biome, locally called 'Campos de Cima da Serra'. However, no described distribution delimits these particular occurrence areas, which is required in order to better characterize this population. Finally, the occurrence area of the genus in other South American countries, such as Chile, Colombia and Venezuela, must also be delimited more precisely, which would support a more complete taxonomic assessment.

As discussed above, a proper taxonomic review must rely on population structure, detailed geographic distribution and morphological diagnosis. Therefore, the objectives of this study were to (i) draw a detailed characterization of the genus' geographic occurrence, with precise distributional limits; (ii) integrate the inferences on genetic structure reported by Fontoura-Rodrigues *et al.* (in prep.) with a novel assessment of craniodental measurements to assess the evolutionary distinctiveness of geographic units identified in *Conepatus*; (iii) use general body measurements of four specific populations to test whether the large-scale population structure can be detected by external morphological traits; and (iv) combine the inferences derived from all data types to suggest a taxonomic revision for *Conepatus*. *C. leuconotus* was not included in the structure analyses, as this taxonomic unit has already been revised by Dragoo *et al*. (2003). We follow his taxonomic considerations regarding that species in the final section.

## Material and Methods

### *Assessment of Geographic Distribution*

In order to characterize the occurrence areas of *Conepatus* at a detailed level, we gathered two types of records bearing the geographic origin of individuals: (i) museum collection databases; and (ii) original data published in scientific journals. In the case of publications, we incorporated only direct visualization, photograph or track records, without considering indirect records (such as interviews) or citations to other papers. As for museum records, we accessed the online database of 37 North American mammal collections through the MaNIS portal (http://manisnet.org – Stein & Wieczorek, 2004). We also consulted the mammal collections of the following institutions, through their online databases or direct contact with the in-charge curators: Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; the London's Natural History Museum, UK; Berlin's Museum für Naturkunde, Germany; and Paris' Muséum National d'Histoire Naturelle, France. The minimum precision cutoff for each record was defined as city/municipality for South American countries, Mexico and United States; and state-level origin for Central American countries. Records were located with the help of the Google Maps tool (http://maps.google.com/maps) and then plotted onto a map of the Americas presenting a simplified scheme of major vegetation types, based on Dinerstein *et al.* (1995): moist forests; dry forests, xerofitics and desert environments; savannas; and flooded grasslands. A precise distributional map was then drawn on the basis of exact record points, also employing the range of biomes in which the genus occurs to predict its likely overall distribution. Therefore, if a particular biome presented records that covered most of its area, the predicted distribution was drawn to include its totality.

### *Molecular data*

One of the main bases for our taxonomic revision was the genetic structure and phylogeny described by Fontoura-Rodrigues *et al.* (in prep). That study suggested the existence of six distinct ESUs, distributed as follows: (i) Central Chile; (ii) Southern Chile (iii) Northern/Central Argentina; (iv) Northeastern Argentina; (v) Central Brazil; and (vi) Southern Brazil/Uruguay. By performing additional analyses on the same data set, as well as comparing the results among data sets, we sought to assess whether these ESUs might warrant formal taxonomic recognition.

Using the mitochondrial DNA data generated by Fontoura-Rodrigues *et al.* (in prep.), we investigated specific phylogenetic configurations that allowed an assessment of different taxonomic arrangements. In order to do that, we employed a hypothesis-testing approach utilizing Bayes factors, as described and implemented in Mr.Bayes (Ronquist & Huelsenbeck, 2003) to compare the suitability of three distinct scenarios of evolutionary relationships. Two such scenarios corresponded to currently accepted taxonomic arrangements (Wozencraft, 2005), and a third referred to the phylogenetic disposition of a particular branch in the phylogenetic tree reported by Fontoura-Rodrigues *et al*. The first scenario tested the current taxonomic postulation that central Brazilian *Conepatus* populations are part of the Central American *C. semistriatus* clade. For such, we designed a constrained group of central Brazil population and the Mexico *C. semistriatus* sample. In the second scenario, we tested the postulation that *C. humboldtii* and *C. chinga* are two reciprocally monophyletic clades. In order to do so, we enforced a phylogenetic constraint putting the Chilean *C. humboldtii* sample as a basal lineage in relation to all other sampled populations. Finally, the third scenario involved a constraint to test the position of the southern Brazilian/Uruguayan population as the most basal lineage relative to all other South American clades, an arrangement recovered by Fontoura-Rodrigues *et al*. (*in prep.*) but which received low support in their tree. For each of the three tests, we conducted two phylogenetic searches, one employing a constraint enforcing the specific scenario of interest and another one employing a similar but negative constrain (*i.e.* excluding the arrangement proposed by the positive constraint). The suitability of each alternative hypothesis was verified in terms of the harmonic mean of the marginal likelihood of the phylogenetic search enforcing it. This value is expressed in log units, and a difference of 3-5 units is considered to be strong evidence in favor of a given hypothesis, while >5 units is considered to be very strong evidence (Kass and Raftery, 1995). Run parameters included 100,000 MCMC steps and assumption of the HKY + G (4 groups) substitution model (based on the results reported by Fontoura-Rodrigues et al. [in prep.]).

*Morphological data*

Two separate morphological surveys were conducted. First, the population structure of *Conepatus* was assessed through a detailed craniodental panel of measurements taken from several individuals representing distinct geographic regions. A second survey was conducted based on general body measurements, a kind of information traditionally described by field researchers, to test if the population structure found with molecular markers and craniodental characters is reflected on external morphological differentiation in *Conepatus*. All statistical analyses were performed with IBM SPSS Statistics v. 21.0 (IBM, 2012).

*Morphological data – Population structure*

For the first survey, 29 independent craniodental measurements were taken from *Conepatus* individuals deposited in the mammalian collections of two institutions: Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; and the National Museum of Natural History, Smithsonian Institution, Washington D. C., USA. A list with all measurements names, codes and descriptions is provided in Table 1. Skulls were evaluated regarding developmental stage and integrity, and only intact adult specimens (*i.e.* with complete permanent dentition and fusion of the skull bone sutures) with known geographic origin were included in the following analyses. All measurements were taken by the first author. Table 2 provides museum codes, geographic origin and general information regarding the 48 specimens utilized for this survey. Since a large number of specimens bore no associated sex information, individuals were assembled in a single analysis group so as to maximize the power of the geographic assessment power, even though sexual dimorphism has already been described for some *Conepatus* populations (Dragoo, 2009).

Normality of all 29 measurements was tested to verify the need for any transformation. As all variables presented no significant departure from a normal distribution, no transformation was performed (Field, 2005). Multivariate statistical tests were then conducted in order to assess the occurrence of any geographic clustering. An exploratory survey was conducted with a Principal Component Analysis (PCA) of the covariance matrix, plotting the first two components (PC1 and PC2) in a dispersion graph to visually identify the presence of clusters. Based on this assessment a Discriminant Function Analysis (DFA) was performed, in order to statistically test the validity of the putative groups. Due to a cluster overlap possibly caused by spurious similarity (see Results section for details) we conducted two additional DFAs, in order to address two specific questions: (i) is there a population disjunction between Central America and central/northern South American populations?; and (ii) are there discontinuities among South America populations?

### *Morphological data – External Differentiation among populations*

For the second survey, general body measurements were obtained from individuals of four distinct geographic regions. Measurements taken were: total body length (TLgth), tail length (Tail), hind foot length (HFoot), ear length (Ear) and total weight (Wght). Two proportions were also included: tail length/total length (T/TL) and total weight/head and body length (W/HB). Population 1, from Southern Brazil, was sampled in the municipality of Arroio Grande, Rio Grande do Sul state (32°13.8’ S, 53°4.8’ W). A total of 18 individuals (seven males and 11 females) was included. Population 2, from central Brazil, was sampled in the Emas National Park, Goiás state (17°10.2’ S, 52°31.8’), comprising 10 individuals (eight males and two females). Population 3, from central Argentina, comprised 25 individuals (11 males and 14 females) sampled in two nearby localities in the Buenos Aires province. Finally, Population 4 comprised 13 individuals (five males and eight females) sampled in Northern Venezuela, including the Falcon, Monagas and Zulia States. Measurement data were provided upon request by the authors of the following original publications: population 1 – Kasper *et al*. (2012); population 2 – Cavalcanti (2010); population 3 – Castillo *et al*. (2011). Population 4 was sampled by the Smithsonian Venezuelan Project, and the measurement data were obtained directly from the National Museum of Natural History online database; measurements of one extra individual available in Allen &

Carriker (1911) were included. All individuals included sex information, so analyses were conducted separately for males and females due to the previous report of cases of sexual dimorphism in *Conepatus* (Dragoo, 2009).

Statistical treatment was similar to that of the first morphological survey. Variables were initially tested for normality. As some of them presented departure from a normal distribution, variables were log-transformed, thus reaching normality. An exploratory analysis was performed with a PCA to test the presence of clusters, and to assess whether they matched the four sampled populations. Subsequently, a DFA was performed to statistically test the clusters identified in the PCA.

## Results

### *Distribution areas*

All the compiled records are shown on Table 3, which includes information regarding source institutions/publications, collector/author, geographic origin, and year of collection. A total of 364 records from 19 institutions and 272 records from 54 publications were compiled, resulting in a final number of 636 distinct geographic records. Several additional records were discarded from both museum and publication sources due to redundancy in geographic location. To characterize the genus' distribution more accurately, we employed buffer circles with a diameter of ~50 kilometers to represent each record. When two or more records overlapped due to adjacent origins, we only plotted one of them. Also, when the reported location could not be reliably ascertained, the record was discarded. As a consequence, the final number of distinct geographic records plotted on the map was 295 (Figure 2). A map with the resulting distribution of *Conepatus* is shown on Figure 3.

The general distribution pattern indicates that Co*nepatus* is present in almost all grassland, savanna, desert, xeric and dry forested environments of South and Central America, as well as southern North America. The only type of vegetation from which the genus seems to be absent is dense moist forests, despite a few records in such environments. This occupation pattern results in a distribution that includes a large portion of Central and South America, encompassing many different biomes. *Conepatus* seems to be absent only from a few major biomes in these continents, namely the Atlantic Forest, Amazon Forest, 'North Colombia – Panama' moist forests and the Atacama Desert. At the same time, some potential discontinuities could be noted, as between Central/Northern Chile and Argentina, Central and South America and also Northern and Southern Colombia. These absence areas could be related to a lack of sampling effort, or represent real population disjunctions. In this context, results from the population structure analyses can help with the interpretation of these distribution patterns.

Finally, five records were considered doubtful, but were still plotted on the map (red circles – Figure 2) due to the relevance of their geographic origins in terms of potential impacts on the general distributional pattern: (i) Tierra del Fuego, in southernmost Patagonia; (ii) the Brazilian Pantanal flood plain; (iii) Joinville, in Santa Catarina State, southern Brazil; (iv) Serra do Mar, Paraná State, southern Brazil; and (v) Ilha de Maracá, Roraima, northern Brazil.

*Molecular data*

Bayes Factor results consistently refuted two taxonomic arrangements that are currently accepted in *Conepatus*, but did not clearly resolve the phylogenetic uncertainty tested in the third scenario (Table 4). First, the difference between the harmonic means of the marginal likelihood of the run with the *C. semistriatus* constraint (where the monophyly of the samples from Mexico and Central Brazil is enforced) was 38.07 units lower than the scenario with the opposite constraint. Since a difference larger than 5 units is considered to be a strong signal in favor of a given hypothesis, it is clear that the constrained scenario is significantly worse. Second, the scenario where *C. chinga* is constrained to present reciprocal monophyly with *C. humboldtii* was 5.69 units lower than the scenario with the negative constraint. Again, this result indicates strong evidence against this separation in two lineages, as currently accepted. Finally, the scenario in which the southern Brazil population was tested as the most basal South American lineage had weak support (1.75 units higher than the alternative constraint), so that this assessment was not conclusive.

*Morphological data – Population structure*

Data regarding the population structure assessed with the first morphological survey showed some robust tendencies regarding population differentiation. The PCA plot of the first two principal components (Figure 4A) showed that individuals from nearby geographic origins tended to form clusters, indicating the existence of morphological consistency uniting some geographic populations. Clusters that could be visually identified were: (1) Central America, (2) Venezuela/Northern Colombia, (3) Ecuador/Peru and (4) Uruguay + Southern Brazil + Southern/Central Argentina. Furthermore, we noted that some of these geographic clusters showed a clear divergence, while others showed some degree of overlap. In order to facilitate the visualization of the clustering patterns, we attempted to minimize the potential noise caused by any spurious (e.g. plesiomorphic) character sharing. To do so, we divided the results of the PCA analysis into different plots. Each plot shows a specific scenario of hypothesis testing: Figure 4B shows only the clusters identified in South America (*i.e.* clusters 2, 3 and 4), and Figure 4C shows only the clusters of Northern South America and Central America (*i.e.* clusters 1, 2 and 3). Clusters 1 and 4 were never included in the same plot due to the deep genetic separation found by Fontoura-Rodrigues *et al.* (in prep.) between the lineages occurring in these two regions. When these sets of populations are thus assessed separately, it became easier to visually conclude that there is very little overlap between distinct geographical clusters in the PCA plot. Regarding the PCA parameters, the first principal component (PC1) explained 72.1% of the total variation, while the second (PC2) explained 7.23%, totalizing 79.33% (Table 5). The main contributors to PC1 were the variables Bas, Zyg, WaCan, Mast and IOrb, while LMoL, LMoW, UPML, JaH and UMoL were the main contributors to PC2. These results indicate that skull size is the main driver of PC1, while PC2 mostly reflects variance in dental characters.

Results from the DFA were mostly consistent with those from PCA. The plot of CV1 against CV2 showed a trend for cluster separation, although it was not as straightforward as the PCA plot (Figure 4D). Canonical variates (CV) 1 (86.55%) and 2 (10.2%) together accounted for 96.75% of the discriminating power (Table 5). CV1 was mostly influenced by the variables Zyg and CrH, while CV2 was more correlated with the variables CrH, WaInc, WaCan, and CaW. Several of the 29 craniodental variables showed significant differentiation among groups (Table 6), indicating a consistent trend of morphological distinction among putative geographic clusters. The analysis of predicted group membership showed a considerable level of correspondence between the original and final cluster assignment (79.2% - Table 7A). However, the assignment of group 1 (Southern Brazil – Argentina – Uruguay) presented very poor levels of concordance (14.3%), with many individuals clustering together with group 2 (Ecuador-Peru). On the other hand, when populations 1 and 4 (Central America) were not analyzed together, correspondence levels of both DFA assignments increased substantially (92.7% when groups 1, 2 and 3 are included, and 85.3% when groups 2, 3 and 4 are included – Table 7B and 7C). This pattern indicates that some character sharing between groups 1 and 4 (possibly caused by symplesiomorphy or convergence, given the large geographic separation of these groups) might be biasing the original analysis at some level. Still, most of the population structure pattern was also clearly discerned in the original analysis, with the distinction between populations 1 and 2 being the only result that was not straightforward. Altogether, these results support the inference that there is consistent and significant differentiation in craniodental morphology among Central and South American populations of *Conepatus*.

*Morphological data – External differentiation among populations*

Results from the PCA and DFA indicate that the general external morphology is affected by population discontinuities. Plots of the PC1 against PC2 for both males and females (Figures 5A and 5B) showed that predicted populations tend to form clusters, with little or no overlap between them. The main case of overlap involved the southern *vs.* central Brazilian populations, which do not seem to be closely related, based on the mtDNA analysis reported by Fontoura-Rodrigues *et al*. (*in prep.*). Therefore, this overlap may be caused by spurious (e.g. plesiomorphic or convergent) character sharing. On the other hand, the PCA results can be used to shed light three distinct evolutionary hypotheses. First, current taxonomic understanding assumes that Venezuelan and Central Brazilian populations belong to the same species (*C. semistriatus*), as should also be the case for southern Brazil and Central Argentina (*C. chinga*). In contrast, the phylogenetic results reported by Fontoura-Rodrigues *et al*. (in prep.) indicate that the central Brazilian population is closely related to the Argentinean one. Assessing these three scenarios in the light of the PCA results, it is possible to note that general body morphology supports the distinction between Venezuela and Central Brazil, and also between southern Brazil and central Argentina. Finally, the PCA results indicated that, in spite of being closely related as inferred by the mtDNA results, central Brazilian and central Argentinean populations can be distinguished by general body measurements. With respect to the PCA parameters, PC1 explained 48.65% and 56.25% of the variance in males in females, respectively. PC2 explained 34.14% and 23.49%, totalizing 82.79 and 79.74% of the total variance in males in females, respectively (Table 8). In the case of males, Tlgth and Tail were the main contributors to PC1, while Tail and T/TL were the main drivers of PC2. As for females, Tail and HFoot were the two most important variables for PC1 and PC2 was explained mainly by Tlgth and Tail. Wgth was also an important parameter for the PC1 of both males and females. Although the identification of any clear pattern is difficult here, probably due to the small number of variables, it is possible to note that tail length is the most important variable explaining the variance in both males and females. The male PC1 is driven mostly by size, while the PC2 is more related to form. PC1 and PC2 in females are both related to size, with the hind foot length being particularly important to PC1 and the total length to PC2.

The DFA results also corroborate the existence of the predicted geographic units (Figures 5C and 5D). All variable means were significantly distinct between populations (Table 9), indicating that traditional body measurements can distinguish the predicted populations. Canonical variates (CV) 1 and 2 together corresponded to 97% and 97.8% of the total variance for males and females, respectively (Table 8).In the case of males, CV1 was driven mainly by Tlgth and Tail, corresponding to 63.9% of the variance. The main contributors to CV2 were Wgth and T/TL, with 33.1% of the variance. As for females, CV1 was mainly explained by Tlgth and HFoot (56.5%) while Tail and HFoot were the main contributors to CV2 (41.3%). Altogether, these PCA and DFA results indicate that geographic population structure, as identified by molecular data and craniodental characters, also induces perceptible differentiation in traditional body measurements usually taken in field surveys.

## Discussion

### *Geographic Distribution*

The general pattern of *Conepatus* distribution is mostly congruent with what could be predicted from the literature, including known aspects of the genus' biology, which postulates that hog-nosed skunks are highly associated with open environments (*e.g.* Dragoo, 2009). Some important additions and reconsiderations, however, can be gleaned from our analysis. Foremost, it is the first time that a precise distributional map is drawn for Brazil, a country that contains a portion of the genus' range, spanning at least three distinct major biomes. Many authors have considered only the Caatinga biome, in northeastern Brazil, as an occurrence area for *Conepatus* (*e.g.* Eisenberg & Redford, 1999; IUCN, 2012). It is clear, however, that this population also occupies the Cerrado, a biome that encompasses a large area of Central Brazil. Also, the range of the southern Brazilian population was drawn more precisely, and includes two distinct biomes: the Uruguayan Savannas (part of the Pampas biome) and an altitude grassland biome locally called "Campos de Cima da Serra". A finer distribution was also drawn for the northern portion of South America, including Ecuador, Colombia and Venezuela. Some authors have included the coast of Ecuador and Colombia in the genus' distribution (Figure 1), a region that is mostly covered by dense forest. However, we could find no confirmed record of *Conepatus* for those areas, which is concordant with the observed pattern of these organisms being absent from that kind of environment.

On a broader context, the overall presence of *Conepatus* in dense forests could be assessed in several areas. Based on sporadic records of hog-nosed skunks in such areas, some researchers have proposed that it is possible that *Conepatus* may also inhabit biomes such as the Atlantic and Amazon Forests, in addition to savannas and dry forests (*e.g.* Oliveira *et al.*, 2007). However, our database shows that very few records are located in moist forests, and even those data points come from sites that are very close to open environments. A potential argument to dispute our conclusion is a possible lack of studies in such dense vegetation environments, such as the Amazon Forest. However, other well-known environments, such as the Atlantic Forest, present very few records. Furthermore, the few records located inside moist forests can have direct relation with two factors. First, large areas originally covered with dense vegetation are currently being severely modified by human activities, which turn forests into plantation areas or other open environments. The Brazilian Atlantic Forest is restricted to only 11-16% of its original cover (Ribeiro *et al*., 2009), and many of the records located in this biome could represent recently cleared areas. This phenomenon has already been recorded for another typical savanna-dwelling species, the maned wolf (*Chrysocyon brachyurus*), which seems to have recently expanded its range from the Cerrado into the Atlantic Forest borders (Queirolo *et al*., 2011). Second, *Conepatus* is described to be very tolerant to human disturbance. Many authors recorded hog-nosed skunks in farms or near urban centers, being even common in such areas (Bateman & Fleming, 2012; Kasper *et al*., 2012). Combined, the deforestation and the tolerance of these animals to human-impacted areas can lead to the presence of *Conepatus* in regions of the South America that were originally densely forested. Nevertheless, it is important to note that Central America’s individuals seem to be indeed present in moist as well as in dry forests. This pattern may indicate distinct habits of this population, which needs to be further investigated.

Some doubtful records were identified and plotted due to the potential relevance of the implicated information. Each of these regions/biomes should be further investigated in order to better assess the presence or absence of the genus. In the map provided on Figure 3, the potential occurrence areas derived from the presence of *Conepatus* in such geographic points are presented. Hereafter all five records are discussed in detail.

Tierra del Fuego, in southernmost Patagonia, has already been mentioned as a region where skunks are absent (Osgood, 1943), and we only found a single record, considering both museums and literature sources. This specimen is deposited in the USNM of Washington DC, with catalog number M-36928, but no precise collection location is provided except for “Tierra del Fuego”, Argentina. Therefore, the presence of the genus in this island is still uncertain.

The Brazilian Pantanal is a flood plain located among savannas and dry forests. Although some authors cite the presence of the genus in this biome (Cáceres *et al*., 2008), no direct record or precise location could be retrieved. Therefore, it is not possible at present to conclude if the genus occurs throughout this area (perhaps at very low densities), or only on the edges of this biome, or even if it is present in the Pantanal at all.

Very few of the compiled records are located in the Brazilian Atlantic Forest, and due to the deforestation process it is possible that all of them represent cases induced by the tolerance level of these animals to human-impacted areas. However, two of these records are located in a densely forested area. The first one is a museum record from Berlin’s Museum für Naturkunde, with catalog number 61677. The only geographic information of the specimen collection is “Joinville”, which is the name of a well-known Brazilian city. However, due to the lack of any other information, it is not appropriate to consider this record as a precise occurrence point. The second record consists of the sighting of an individual in the Serra do Mar Mountains, Paraná State (Cáceres, 2004), which is in fact close to the city of Joinville and could indicate a distribution patch. However, this is the only record of a *Conepatus* individual in such a dense forested area, and no photographic evidence or methodological detail was provided. This does not in itself imply that the record is not correct, but such outlier observation should be confirmed by additional studies before it could be conclusively accepted. Therefore, the presence of *Conepatus* in densely forested areas of the Atlantic Forest remains undocumented.

Finally, the most interesting record is located in the Maracá Fluvial Island, in Roraima State, Brazil. This island is covered with dense Amazon Forest and savanna patches, near a large patch of the Amazonian Savannas (see map in Figure 2). This is one of the most enigmatic biomes of South America, since very few descriptive studies have been conducted so far in such areas. From a vegetational perspective, the Amazonian Savannas seem to be linked to the Cerrado Biome (Ratter *et al*., 1997), which could also lead to faunal similarities. However, the exact mammal composition of these patches is still poorly known, and the presence of *Conepatus* has never been confirmed. Barnett & da Cunha (1994) reported the only *Conepatus* record for this biome, which could indicate the existence of the most isolated and perhaps relict population of *Conepatus*, implying the need for immediate research attention. However, the authors did not provide any methodological details for this record, preventing any precise conclusion at this time.

Finally, regarding the biomes from which *Conepatus* is absent, it is clear that the genus has a restricted occurrence in the densely forested areas of Central and South America. However, in addition to the Atlantic, Amazon, North Colombia and Central America moist forests, *Conepatus* is apparently absent from the Atacama desert. It is possible that the extreme conditions of such an environment limit its occupation by this adaptable genus. A final note regarding the general pattern of *Conepatus* distribution is the presence of individuals on a very broad range of altitude, from zero to above 4,000 meters above sea level. Together with the wide variety of vegetation occupied by *Conepatus*, this data reinforces the remarkable ecological plasticity of the hog-nosed skunks.

*Population structure*

On a broad perspective, our results corroborate and extend the conclusions of Fontoura-Rodrigues *et al*. (in prep.). In that study, the authors investigated the genetic structure of *Conepatus* in the central/southern portion of South America (south of the Amazon Forest), and showed that this genus is highly prone to evolve population discontinuities. The detailed craniodental survey conducted in the present study is in accordance with this pattern, and shows that northern populations of *Conepatus* (Peru, Ecuador, Colombia, Venezuela and Central America) also present a disjunct structure. It is important to mention that our sampling panel was limited in terms of geographic distribution and number of individuals, enabling only large-scale structural patterns to be identified. Nevertheless, the strong morphological clusters identified with clear geographical correlation, even when investigated with a limited sampling, indicate that the pattern is not spurious, but rather consistent. Only one population disjunction (Ecuador-Peru *versus* Uruguay-Southern Brazil-Argentina) could not be confirmed with the DFA, but the overall PCA and the complementary partitioned DFA indicate that these populations are distinct. In fact, a possible reason for the lack of resolution regarding the southern cluster is that its seven individuals are likely representatives of three different populations, as described by the previous genetic assessment. Another obstacle to a clearer resolution regarding that cluster is its apparent morphological similarity, in terms of craniodental measurements, to the Central American cluster. This overlap is most likely spurious, since molecular data indicate that these populations have been separated for around 3.2 million years. Therefore, analyzing all results of the craniodental survey, it is possible to identify three additional *Conepatus* populations in relation to the six described by Fontoura-Rodrigues *et al*.: (vii) Ecuador-Peru; (viii) Venezuela-Northern Colombia; and (ix) Central America. The fourth cluster identified (Uruguay-Argentina-Southern Brazil) seems to represent distinct local populations, and based on the present results it is possible to infer only that they are distinct from Ecuador-Peru cluster. A final population of *Conepatus* that will be considered here is the one revised by Dragoo *et al*. (2003): (x) *C. leuconotus*.

Plotting this general pattern of population structure against the occurrence map of the genus, it is possible to associate some of the population disjunctions with distribution discontinuities, enabling the proposition of an approximate geographic delimitation for each unit. First, the Central American cluster is probably separated from the South American populations by dense forests that cover most of Panama, as well as the northern region of Colombia. Along Central America, the limits of this population seem to be the distribution of *C. leuconotus* and also some densely forested areas in Nicaragua and Honduras. The existence of two different taxonomic units in Central America seems clear, also being detected by Fontoura-Rodrigues *et al*. (in prep.). The occurrence area of *C. leuconotus* also seems to be well established (Dragoo *et al*., 2003). However, a specific study aiming to understand the exact barriers that separate these units, including an investigation regarding possible sympatric areas and an in-depth morphological comparison, should be conducted in order to better characterize these populations. Regarding northern South America, the Venezuela-North Colombia population seems to be separated from the Ecuador-Peru cluster by a distributional discontinuity. This gap, however, could be caused by lack of sampling effort, since the specific biome from where *Conepatus* seems to be absent (Magdalena Dry Forests, Colombia) presents three records in its northern portion (Figure 2). A detailed survey should be conducted in that region in order to assess the exact occurrence areas, possible barriers and detailed population structure of those populations. It is worth mentioning, though, that other authors have already noticed some level of differentiation between southern and northern Colombia hog-nosed skunks, indicating that the candidate barrier that separates these two clusters is probably located between these two Colombian regions (Ramírez-Chaves & Noguera-Urbano, 2010). Finally, the Ecuador-Peru cluster is clearly limited by the Amazon Forest on its western portion, but the barriers that separate it from the southern South American populations (*i.e.* Argentina, Uruguay, and Brazil), are not clear. No individuals from Bolivia, Paraguay and North Argentina could be included in this survey, and as this region is located exactly between those clusters, it is probably critical to understand this separation. A specific survey should be conducted in that region, not only to understand the separation of those clusters, but also to characterize the populations that inhabit that particular area, since Bolivia and Paraguay are amongst the least studied areas with respect to hog-nosed skunks.

Extending the combined analysis of detailed distribution against population structure to the ESUs identified in the genetic assessment by Fontoura-Rodrigues *et al*. (in prep.), it is possible to notice some interesting patterns. Regarding the central Chile population, it seems clear that *Conepatus* is not present in the highest portions of the Andes Cordillera, which likely explains its separation from the Argentinean individuals. However, the southern portion of the Andes is not so high, and due to the distribution of *Conepatus* in region, it seems plausible that southern Chilean animals might be able to cross the mountains and maintain gene flow with Argentinean individuals. This would be in accordance to current taxonomic understanding, which predicts that *C. humboldtii* occupies both the Chilean and Argentinean Patagonia (Wozencraft, 2005; Dragoo, 2009), but this assumption should be taken with caution. Again, a specific survey should be conducted to better understand the disjunction between central and southern Chilean populations, as well as to characterize the population structure of the Chilean and Argentinean Patagonia hog-nosed skunks.

A final point that is worth mentioning is that the central Brazilian and central Argentinean populations, although clearly differentiated, seem to be in contact in terms of their distribution, which raises the question of what could be the main barrier that separates them. Once again, Paraguay and northern Argentina seem to be key regions to be investigated in order to better understand this issue.

### *Major morphological differentiation among populations*

Regarding the morphological assessment based on general body measurements, the results are highly concordant with the structure pattern found with molecular markers and detailed craniodental approaches. Even employing a few variables, multivariate analyses were able to detect significant differences among all populations, which indicates that population disjunctions are driving external morphological differentiation. It is important to mention that our study did not include individuals of all populations detected in the structure surveys, preventing the conclusion that all of them can be distinguished by such measurements. However, the observed concordance increases the support for the detected pattern. At the same time, it also shows that this traditional panel of variables, which are usually described by field researchers and easily comparable, can be a useful tool for the investigation of population discontinuities. We recommend that, when possible, field assessments should include and report this type of data.

### *Molecular data*

The hypotheses tested with the use of Bayes factors are conclusive in discarding two of the most important current taxonomic arrangements of *Conepatus*. First, the understanding that central Brazilian hog-nosed skunks are part of the *C. semistriatus* diversity was strongly refuted. The good support for the alternative scenario, in which that population was found to be closely related to Argentinean *C. chinga* (Fontoura-Rodrigues *et al.*, *in prep.*), already constituted strong evidence that the traditional taxonomic disposition was wrong, which is now further corroborated by our results. The second test showed strong evidence that *C. chinga* and *C. humboldtii* are not reciprocally monophyletic. The most likely scenario is that *C. humboldtii* is part of the '*C. chinga*' diversity, which also has important taxonomic consequences. The third test (the 'Southern Brazil-Uruguay' group as a basal lineage relative to all South American populations) did not show significant results in favor of any specific hypothesis, leaving this issue still unresolved. This indicates that our dataset has no power to determine this phylogenetic arrangement with precision, probably due to the recent and rapid radiation of the genus in South America. A deeper survey, utilizing a larger number and diversity of molecular markers, should therefore be conducted in order to better characterize the internal hierarchical arrangement of South American groups. With respect to taxonomic consequences, central Brazilian *Conepatus* must be removed from *C. semistriatus*, and a new name should be allocated to this population unit. Also, either *C. humboldtii* must be included in *C. chinga* or, alternatively, all the evolutionary clades of *C. chinga* presenting similar levels of divergence must be elevated to the species level.

### *Taxonomic revision*

Based on the results of the detailed distribution, population structure and morphological differentiation, several evolutionary units could be identified. Most of them have clear geographic delimitations and were detected by more than one independent approach (*i.e.* mitochondrial DNA, microsatellites, craniodental morphological survey and/or general body measurements). Also, our specific Bayes factor tests assessing the current taxonomic organization indicate that a major rearrangement should be conducted. Based in these results, we suggest a new taxonomic arrangement for *Conepatus* (Table 10, Figure 6). Scientific name proposals follow the major review of Cabrera (1958) in relation to synonymizations and geographic origin of taxon types. Basically, whenever a taxonomic unit was identified and geographically delimited, the oldest taxon reported by Cabrera for any locality within that area was employed to name the specific epithet. A ‘splitter’ approach was adopted, and each evolutionary unit was considered to constitute a different species. The reasons for this approach were twofold. First, the age of the basal diversification of the South American group is *ca.* 0.85 million year ago (MYR), a split time commonly associated with the separation of taxonomic units in species or even groups of species. This is the case of the South American foxes (six species in the genus *Lycalopex*, with a coalescence time of *ca.* 1 MYR – Perini *et al*., 2010) and some Neotropical cats (coalescence time of *Leopardus geoffroyi* and *L. guigna* is *ca.* 0.74 MYR – Johnson *et al*., 2006). The second reason is mostly practical. *Conepatus* has recently invaded South America and radiated, occupying several biomes in that continent. Combined, the large occurrence area and the recent and complex evolutionary history of the genus make a detailed and conclusive phylogenetic approach very difficult to achieve in the near future, which could cause several taxonomic units to remain poorly named. In addition, the apparent tendency of these animals to evolve geographically differentiated populations raises the possibility of additional subdivisions being found as more detailed surveys are conducted. Naming every robust evolutionary unit as a species makes them stable to whichever phylogenetic configuration becomes consolidated at higher hierarchical levels, and at the same time prevents possible taxonomic subdivisions nested within them to be named as ‘sub-subspecies’. Still, as several geographic locations were not sampled in detail for this study, and distribution patterns still need further information, the taxonomic arrangement proposed is open to reconfigurations and reviews. Nevertheless, it could be taken as a working basis for future taxonomic studies focusing on *Conepatus*.

## Concluding remarks

The genus *Conepatus* is only beginning to be better understood. The lack of studies regarding its evolution, ecology, taxonomy and biogeography has been an impediment for broad comparative studies, and much of the genus’ diversity seems to be still unknown. Only recently a few studies started to describe the detailed ecology and morphology of these animals at specific locations (Cavalcanti, 2010; Castillo *et al*., 2011; Kasper *et al*., 2012), but given the broad occurrence area of the genus, it is still only the beginning. Combined with the genetic assessment of Fontoura-Rodrigues *et al*. (in prep.), this study starts to shed some light on the general population structure and natural history of *Conepatus* as a whole, and it is clear that our results raise more questions than complete answers. They can be used, however, as a guide for future surveys, since they establish some large-scale and clear patterns.

*Conepatus* is a highly structured genus, presenting several and even unexpected population discontinuities. The flow of individuals seems to be limited by mountains, rivers and dense vegetation cover, and therefore further population structure surveys should be as detailed as possible, as almost all regions of South America present such elements in abundance. Traditional body measurements are likely to reflect these population disjunctions, being potentially good markers to identify them in initial, exploratory investigations. On the other hand, detailed craniodental surveys seem to be highly effective in the identification of population structure, and as skull material of *Conepatus* is relatively abundant in several mammalian collections around the world, this approach can be further utilized to improve the knowledge regarding the population structure of the genus.

The taxonomic proposal we put forth is based on solid results that strongly indicate population isolation and differentiation, most of them confirmed by more than one approach, including molecular (mtDNA and/or microsatellites) and/or morphological (craniodental panel and/or general body measurements) data. Also, the geographic patterns seem robust as well, since most distributional limits are readily identifiable. However, it is important to note that not all approaches were conducted with all populations, which should be performed as soon as possible to confirm or revise the arrangement proposed here. Much still needs to be done, and this taxonomic organization will certainly need adjustments, improvements and also criticism, in order to become more accurate and informative over time.

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**Table 1.** Skull, jaw and teeth measurement names, codes and descriptions, utilized in the population differentiation survey. When applicable, measurements were taken on the left side of the skull and jaw.

| Measurement Name | Code | Description |
|---|---|---|
| Basilar | **Bas** | From the anteriormost border of the foramen magnum to the internal plane of the first upper incisors |
| Condylobasal | **CoBa** | From the posteriormost parts of the occipital condyles to the anteriormost portions of te premaxillae |
| Zygomatic | **Zyg** | Greatest width across zygmoatic arches |
| Mastoid | **Mast** | Width across tips of the mastoid processes |
| Interorbital | **IOrb** | Least distance across frontal bones at the level of the frontomaxillary sutures |
| Postorbital | **POrb** | Least distance across frontal bones posterior to the postorbital projections |
| Palatilar | **Palat** | From one of the indentations at the posterior of the palatine bones to the internal plane of the first upper incisors |
| Facial Length | **FaL** | Least length from inside of orbit to the premaxillae between incisors |
| Nasal Retraction | **Nas** | From mid-point of frontal inflation to the front of nasals |
| Cranium Height | **CrH** | From between basi-sphenoid and basioccipital to the dorsal surface of the parietal bones |
| Cranium Width | **CrW** | Cranium maximum width measured above the mastoid processes |
| Bulla Lenght | **BuL** | From the anterior thin process to the end of the bulla convexity |
| Bulla Width | **BuW** | From the intern line of the bulla convexity to |
| Maxillary Tooth Row | **MaTR** | Lenght of the upper tooth row, from the last molar to the canine, measured in the aveoli |
| Width ac. Incisors | **WaInc** | Width across upper incisors |
| Width ac. Canines | **WaCan** | Width across upper canines |
| Width ac. Molars | **WaMol** | Width across upper molars |
| N Canine Length | **CanL** | Upper canine diameter |
| Canine Width | **CanW** | Upper canine width |
| Large Upper Premolar Lenght | **UPML** | Large upper premolar length |
| Large Upper Premolar Width | **UPMW** | Large upper premolar width |
| Upper Molar Length | **UMoL** | Upper molar length |
| Upper Molar Width | **UMoW** | Upper molar width |
| Jaw Height | **JaH** | From the dorsalmost point of the coronoid process of the mandible perpendicular to the line formed between the ventral portion of the ramus and the ventral portion of the angular process, in the plane of te ramus |
| Jaw Lenght | **JaW** | From the mandibular symphysis at the alveoli of the first incisors to the posteriormost portion of the angular process, in the plane of the ramus |
| Jaw Tooth Row | **JaTR** | Lenght of the upper tooth row, from the first molar to the canine, measured in the aveoli |
| Width ac. Lower Premolar | **WaLPM** | Width across lower premolars |
| Lower Molar Length | **LMoL** | Lower molar length |
| Lower Molar Width | **LMoW** | Lower molar width |

**Table 2.** Collection information for all individuals utilized in the craniodental survey.

| Code | Institution | Acronym | Scientific Name | Sex | Stage | Country | State | Locality | Collector | Year |
|---|---|---|---|---|---|---|---|---|---|---|
| MC-001 | FZBRS | MCN 1767 | C. chinga | F | 4 | Brazil | Rio Grande do Sul | Rio Grande | Eduardo Borsatto | 1986 |
| MC-004 | FZBRS | MCN 2588 | C. chinga | U | 4 | Argentina | Cordoba | Cerro Los Gigantes | Demetrio Luiz Guadagnim | 1993 |
| MC-009 | FZBRS | MCN 3068 | C. chinga | U | 4 | Brazil | Rio Grande do Sul | Dom Feliciano | Kita (PUCRS) | 2002 |
| MC-012 | USNM | 172857 | C. c. rex | U | 5 | Peru |  | Chicama Valley | AF Hrdlicka | 1910 |
| MC-013 | USNM | 176320 | C. c. rex | U | 4 | Peru |  | Huarochiri | AF Hrdlicka | 1913 |
| MC-014 | USNM | 194319 | C. c. rex | M | 4 | Peru | Cuzco | Tocopoquee | E Heller | 1915 |
| MC-015 | USNM | 194320 | C. c. rex | F | 4 | Peru | Cuzco | Occobamba Valley | E Heller | 1915 |
| MC-017 | USNM | 194323 | C. c. rex | M | 3 | Peru | Cuzco | Matchu Picchu | E Heller | 1915 |
| MC-018 | USNM | 194324 | C. c. rex | U | 5 | Peru | Cuzco | Orca | E Heller | 1915 |
| MC-019 | USNM | 259436 | C. c. suffocans | M | 4 | Uruguay | Rocha | San Vicente de Castillos | CC Samborn | 1926 |
| MC-025 | USNM | 568103 | C. chinga | U | 4 | Ecuador | Pichincha | San Domingo de los Colorados |  | 1979 |
| MH-001 | USNM | 172791 | C. humboldtii | U | 4 | Argentina |  | San Jose | AF Hrdlicka | 1910 |
| MH-003 | USNM | 172793 | C. humboldtii | U | 4 | Argentina |  | Tello | AF Hrdlicka | 1910 |
| MH-004 | USNM | 172794 | C. humboldtii | U | 3 | Argentina |  | Tello | AF Hrdlicka | 1910 |
| MS-001 | USNM | 132512 | C. s. conepatl | U | 3 | Mexico | Veracruz | Perez | J Friesser | 1903 |
| MS-002 | USNM | 65762 | C. s. conepatl | F | 4 | Mexico | Veracruz | Catemaco | Nelson & Goldman | 1894 |
| MS-003 | USNM | 65763 | C. s. conepatl | M | 4 | Mexico | Veracruz | Catemaco | Nelson & Goldman | 1894 |
| MS-004 | USNM | 281452 | C. s. semistriatus | M | 4 | Colombia | Magadalena | Colon. Agric. de Caracolicito | Hershkovitz | 1942 |
| MS-009 | USNM | 281457 | C. s. semistriatus | M | 3 | Colombia | Cesar | Valledupar | Hershkovitz | 1942 |
| MS-010 | USNM | 281458 | C. s. semistriatus | F | 3 | Colombia | Cesar | Valledupar | Hershkovitz | 1942 |
| MS-011 | USNM | 281459 | C. s. semistriatus | F | 3 | Colombia | Cesar | Valledupar | Hershkovitz | 1942 |
| MS-012 | USNM | 281460 | C. s. semistriatus | M | 4 | Colombia | Cesar | Valledupar | Hershkovitz | 1942 |
| MS-016 | USNM | 281464 | C. s. semistriatus | M | 4 | Colombia | La Guajira | Fonseca | Hershkovitz | 1943 |
| MS-017 | USNM | 281465 | C. s. semistriatus | F | 4 | Colombia | La Guajira | Fonseca | Hershkovitz | 1943 |
| MS-020 | USNM | 61205 | C. s. trichurus | U | 4 | Costa Rica |  |  |  |  |
| MS-021 | USNM | 61275 | C. semistriatus | U | 4 | Guatemala |  |  |  |  |
| MS-022 | USNM | 296626 | C. s. semistriatus | F | 4 | Venezuela | Monagas | Caicara | FD Smith Jr. | 1952 |
| MS-025 | USNM | 388244 | C. s. semistriatus | M | 4 | Venezuela | Monagas | Maturin | Smithsonian Venezuelan Project | 1966 |

**Table 2.** (continued)

| Code | Institution | Acronym | Scientific Name | Sex | Stage | Country | State | Locality | Collector | Year |
|---|---|---|---|---|---|---|---|---|---|---|
| MS-026 | USNM | 443285 | C. s. semistriatus | F | 4 | Venezuela | Falcon | Cataparida | Smithsonian Venezuelan Project | 1968 |
| MS-027 | USNM | 443286 | C. s. semistriatus | F | 5 | Venezuela | Falcon | Cataparida | Smithsonian Venezuelan Project | 1968 |
| MS-028 | USNM | 443289 | C. s. semistriatus | F | 4 | Venezuela | Falcon | Cataparida | Smithsonian Venezuelan Project | 1968 |
| MS-029 | USNM | 443290 | C. s. semistriatus | M | 4 | Venezuela | Falcon | Cataparida | Smithsonian Venezuelan Project | 1968 |
| MS-030 | USNM | 443291 | C. s. semistriatus | M | 4 | Venezuela | Falcon | Cataparida | Smithsonian Venezuelan Project | 1968 |
| MS-031 | USNM | 443293 | C. s. semistriatus | F | 4 | Venezuela | Falcon | Cataparida | Smithsonian Venezuelan Project | 1968 |
| MS-032 | USNM | 443294 | C. s. semistriatus | F | 5 | Venezuela | Falcon | Cataparida | Smithsonian Venezuelan Project | 1968 |
| MS-033 | USNM | 443295 | C. s. semistriatus | F | 4 | Venezuela | Falcon | Cataparida | Smithsonian Venezuelan Project | 1968 |
| MS-034 | USNM | 443296 | C. s. semistriatus | F | 4 | Venezuela | Falcon | Cataparida | Smithsonian Venezuelan Project | 1968 |
| MS-035 | USNM | 443414 | C. s. semistriatus | F | 3 | Venezuela | Falcon | Coro | Smithsonian Venezuelan Project | 1968 |
| MS-036 | USNM | 443576 | C. s. semistriatus | M | 5 | Venezuela | Zulia | Encontrados | Smithsonian Venezuelan Project | 1968 |
| MS-037 | USNM | 324236 | C. s. trichurus | M | 3 | Panama | Chiriqui | Bamdito | CO Handley Jr. | 1962 |
| MS-038 | USNM | 332037 | C. s. trichurus | U | 5 | Panama | Chiriqui | El Volcan | E Tyson | 1962 |
| MS-039 | USNM | 335773 | C. s. trichurus | M | 3 | Panama | Bocas del Toro | Sibube | CO Handley Jr. | 1963 |
| MS-040 | USNM | 363346 | C. s. trichurus | M | 5 | Panama | Chiriqui | Progreso | Greenwell & Fleming | 1966 |
| MS-041 | USNM | 8610/A6948 | C. s. yucatanicus | U | 4 | Mexico |  | Merida | A Schott | 1866 |
| MS-042 | USNM | 108503 | C. s. yucatanicus | M | 3 | Mexico | Yucatan | La Vega | Nelson & Goldman | 1901 |
| MS-043 | USNM | 337832 | C. s. yucatanicus | M | 5 | Nicaragua | Chontales | Villa Somoza | JN Clanton | 1963 |
| MS-044 | USNM | 338870 | C. s. yucatanicus | F | 4 | Nicaragua | Jinotega | HCA La Trampa | MK Clark | 1964 |
| MS-045 | USNM | 361359 | C. s. yucatanicus | F | 4 | Nicaragua | Rio San Juan | La Esperanza | MK Clark | 1965 |

Code: assigned code (this study)
Institutions: Mammal collection where individuals are deposited.
Sex: Female, F; Male, M; Unknown, U.
Stage: young adult, 3; adult, 4; old adult, 5.
Country, State and Locality: information regarding collection point of each specimen.
Collector: specimen colector.
Year: year of collection.

**Table 3A.** General information regarding the geographic records collected from museum specimens to develop a detailed distributional map of *Conepatus*.

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | AMNH | M-41530 | Argentina | Santiago del Estero | | | Santiago del Estero | Lavalle | Miller; Boyle | | |
| **2** | **AMNH** | **M-36928** | **Argentina** | **Tierra del Fuego** | | | | | **L. E. Miller** | | |
| 3 | AMNH | M-36932 | Argentina | Entre Rios | | | Parana | | L. E. Miller | | |
| 4 | AMNH | M-94317 | Argentina | Chubut | | | Escalante | 100 kilometers northwest of Comodoro Rivadavia | | | |
| 5 | AMNH | M-94328 | Argentina | Chubut | | | Sarmiento | Colhue Huapi Lake | | | |
| 6 | AMNH | M-94330 | Argentina | Chubut | | | Sarmiento | Colhue Huapi Lake | | | |
| 7 | AMNH | M-41529 | Argentina | Tucuman | | | Tafi Viejo | Tafi | Miller; Boyle | | |
| 8 | AMNH | M-25669 | Argentina | Santa Cruz | | | Corpen Aike | Chico River | A. E. Colburn | | |
| 9 | AMNH | M-260327 | Bolivia | Santa Cruz | -18,27 | -62,08 | Cordillera | 5 kilometers southeast of Tita | S. Anderson | | 295 m |
| 10 | AMNH | M-264464 | Bolivia | Tarija | -21,26 | -63,55 | Gran Chaco | Tapuco | S. Anderson | | 1500 m |
| 11 | AMNH | M-247712 | Bolivia | La Paz | | | Tamayo | 5 kilometers east of Ulla Ulla | S. Anderson | | 4460 m |
| 12 | AMNH | M-39011 | Bolivia | Cochabamba | | | Carrasco | Tujma River | W. D. Miller | | 8200 ft |
| 13 | AMNH | M-133945 | Brazil | Goias | | | Anapolis | | R. M. Gilmore | | 1000 m |
| 14 | AMNH | M-133946 | Brazil | Mato Grosso do Sul | | | Maracaju | | R. M. Gilmore | | |
| 15 | AMNH | M-235994 | Brazil | Rio Grande do Sul | | | Uruguaiana | | A. Ximenez | | |
| 16 | AMNH | M-235512 | Brazil | Rio Grande do Sul | | | Rio Grande | Quinta | A. Ximenez | | |
| 17 | AMNH | M-33290 | Chile | Araucania | | | Cautin | Temuco, Maquegua | J. A. Wolffsohn | | |
| 18 | AMNH | M-33291 | Chile | Araucania | | | Cautin | Temuco, Maquegua | J. A. Wolffsohn | | |
| 19 | AMNH | M-93324 | Chile | Araucania | | | Malleco | Angol | D. S. Bullock | | 70 m |
| 20 | AMNH | M-130049 | Chile | Magallanes | | | Punta Arenas | | F. M. Chapman | | |
| 21 | AMNH | M-38423 | Colombia | Cundinamarca | | | Bogota | Las Balcillas | M. Gonzalez | | |
| 22 | AMNH | M-38424 | Colombia | Cundinamarca | | | Bogota | Las Balcillas | M. Gonzalez | | |
| 23 | AMNH | M-15480 | Colombia | Magdalena | | | Santa Marta | Playa Brava | A.E.E. | | |
| 24 | AMNH | M-14632 | Colombia | Magdalena | | | Santa Marta | Bonda | H. H. Smith | | 150 ft |
| 25 | AMNH | MS-3634 | Costa Rica | Limon | | | Guacimo | Jimenez | G. K. Cherrie | | |
| 26 | AMNH | M-135269 | Costa Rica | San Jose | | | Escazu | Escazu | C. F. Underwood | | 3200 ft |
| 27 | AMNH | M-19205 | Costa Rica | San Jose | | | Parrita | Pozo Azul | M. A. Carriker, Jr. | | |
| 28 | AMNH | M-135270 | Costa Rica | San Jose | | | Santa Ana | La Hondura | C. F. Underwood | | 2500 ft |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 29 | AMNH | M-19206 | Costa Rica | Cartago | | | Cartago | Irazu Volcano, R. Jimenez Ranch | M. A. Carriker, Jr. | | |
| 30 | AMNH | M-141858 | Costa Rica | San Jose | | | Alajuelita | Santa Teresa, Peralta | P. E. Crowe | | |
| 31 | AMNH | MO-2794 | Costa Rica | Limon | | | Guacimo | Jimenez | | | |
| 32 | AMNH | M-66719 | Ecuador | Pichincha | | | Quito | Mount Antisana | H. E. Anthony | | |
| 33 | AMNH | M-187838 | Ecuador | Pichincha | | | Quito | 25 miles south of Quito | R. G. Van Gelder | | 12000 ft |
| 34 | AMNH | M-67085 | Ecuador | Bolivar | | | Guaranda | Sinchig | G. H. H. Tate | | |
| 35 | AMNH | M-36466 | Ecuador | Pichincha | | | Quito | | W. B. Richardson | | |
| 36 | AMNH | M-17201 | Mexico | Veracruz-Llave | | | Paso Nuevo | | A. E. Colburn | | |
| 37 | AMNH | M-17202 | Mexico | Veracruz-Llave | | | Paso Nuevo | | A. E. Colburn | | |
| 38 | AMNH | M-172190 | Mexico | Veracruz-Llave | | | Catemaco | Lake Catemaco | D. Jennings | | |
| 39 | AMNH | M-212835 | Mexico | Yucatan | | | Opichen | Actun Spukil | R. T. Hatt | | |
| 40 | AMNH | M-18900 | Panama | Chiriqui | | | Boqueron | | J. H. Batty | | |
| 41 | AMNH | M-248468 | Paraguay | Boqueron | | | | 50 kilometers west southwest of Fortin Madrejon | P. Myers | | |
| 42 | AMNH | M-238425 | Peru | Ancash | | | Recuay | Carpa, Cordillera Blanca | F. Vuilleumier | | 4050 m |
| 43 | AMNH | M-205889 | Uruguay | Soriano | | | Cardona | 3 kilometers east of Cardona | M. D. Tuttle | | |
| 44 | AMNH | M-205837 | Uruguay | Cerro Largo | | | Melo | 6 kilometers southeast of Melo | J. C. Barlow | | |
| 45 | AMNH | M-205838 | Uruguay | Cerro Largo | | | Melo | 6 kilometers southeast of Melo | J. C. Barlow | | |
| 46 | AMNH | M-205839 | Uruguay | Cerro Largo | | | | 20 kilometers northwest of Paso del Dragon | A. Langguth | | |
| 47 | AMNH | M-205836 | Uruguay | Artigas | | | | 6 kilometers north northwest of Belen | R. G. Van Gelder | | |
| 48 | AMNH | M-205869 | Uruguay | Lavalleja | | | Zapican | 12 kilometers west southwest of Zapican | M. D. Tuttle | | |
| 49 | AMNH | M-205873 | Uruguay | Rocha | | | Lascano | 22 kilometers southeast of Lascano | J. C. Barlow | | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 50 | AMNH | M-205879 | Uruguay | Tacuarembo | | | Tacuarembo | 10 kilometers north of Tacuarembo | M. D. Tuttle | | |
| 51 | AMNH | M-205885 | Uruguay | Tacuarembo | | | Tacuarembo | 40 kilometers northwest of Tacuarembo | A. Ximenez | | |
| 52 | AMNH | M-205886 | Uruguay | Tacuarembo | | | Tacuarembo | 15 kilometers northwest of Tacuarembo | K. F. Koopman | | |
| 53 | AMNH | M-205888 | Uruguay | Tacuarembo | | | Tacuarembo | 10 kilometers north of Tacuarembo | M. D. Tuttle | | |
| 54 | AMNH | M-205887 | Uruguay | Tacuarembo | | | Tacuarembo | 10 kilometers north of Tacuarembo | K. F. Koopman | | |
| 55 | AMNH | M-205901 | Uruguay | Treinta y Tres | | | Vergara | 13 kilometers west southwest of Vergara | A. Langguth | | |
| 56 | AMNH | M-205899 | Uruguay | Treinta y Tres | | | | 15 kilometers northwest of Tacuari River mouth | T. J. McIntyre | | |
| 57 | AMNH | M-205895 | Uruguay | Treinta y Tres | | | | 16 kilometers south southwest of Tacuari River mouth | A. Ximenez | | |
| 58 | AMNH | M-205859 | Uruguay | Rio Negro | | | | 15 kilometers south of of Paysandu, Negro stream | R. G. Van Gelder | | |
| 59 | AMNH | M-205900 | Uruguay | Treinta y Tres | | | | 80 kilometers northeast of Treinta y Tres, Tacuari River | A. Langguth | | |
| 60 | AMNH | M-205840 | Uruguay | Cerro Largo | | | Melo | 20 kilometers southeast of Melo, Tacuari River, Sierra de Vaz | S. Anderson | | |
| 61 | AMNH | M-205898 | Uruguay | Treinta y Tres | | | | 10 kilometers west of Tacuari River mouth | J. C. Barlow | | |
| 62 | AMNH | M-205897 | Uruguay | Treinta y Tres | | | | 10 kilometers west of Tacuari River mouth | S. Anderson | | |
| 63 | AMNH | MO-605 | United StatesA | Arizona | | | Pinal Co. | | | | |
| 64 | AMNH | M-144821 | Venezuela | Aragua | | | Girardot | Rancho Grande | C. W. Beebe | | |
| 65 | AMNH | M-69609 | Venezuela | Sucre | | | Sucre | Neveri | G. H. H. Tate | | |
| 66 | AMNH | M-32073 | Venezuela | Yaracuy | | | Bolivar | El Hacha, Bolivar R.R. | M. A. Carriker, Jr. | | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 67 | AMNH | M-21634 | Venezuela | Merida | | | Libertador | Merida | S. B. Gabaldon | | |
| 68 | AMNH | M-21635 | Venezuela | Merida | | | Libertador | Merida | S. B. Gabaldon | | |
| 69 | AMNH | M-135481 | Venezuela | Guarico | | | Zaraza | | A. Roe | | 60 m |
| 70 | AMNH | MO-605 | United StatesA | Arizona | | | Pinal Co. | | | | |
| 71 | AMNH | 4605 | United StatesA | Texas | 29,69 | -98,57 | Bexar | San Antonio, 18 mi. NW, Camp Bullis | WJ Hamilton, Jr. | | |
| 72 | AMNH | 58867 | Mexico | Sonora | | | | Santa Cruz | Mearns & F. Holzner | | |
| 73 | AMNH | 91357 | Mexico | Sinaloa | | | | Santa Cruz De Alaya | J. Taylor | | |
| 74 | CU | 4605 | United States | Texas | 29,69 | -98,57 | Bexar | San Antonio, 18 mi. NW, Camp Bullis | WJ Hamilton, Jr. | 1943 | |
| 75 | FZBRS | 2588 | Argentina | Cordoba | | | | Cerro los Gigantes | D. L. Guadagnin | 1993 | |
| 76 | FZBRS | 1056 | Brazil | Rio Grande do Sul | | | | Quaraí | J.W.Thomé | 1983 | |
| 77 | FZBRS | 1767 | Brazil | Rio Grande do Sul | | | | Rio Grande | Eduardo Borsatto | 1986 | |
| 78 | FZBRS | 2513 | Brazil | Rio Grande do Sul | | | | Guaiba | Ana Maria Ribeiro & Jorge Ferigolo | 1992 | |
| 79 | FZBRS | 2517 | Brazil | Rio Grande do Sul | | | | Barra do Quaraí | Edison V. Oliveira | 1991 | |
| 80 | FZBRS | 2713 | Brazil | Rio Grande do Sul | | | | Santa Maria | Saul Milder | | |
| 81 | FZBRS | 3067 | Brazil | Rio Grande do Sul | | | | Aceguá | João Carlos Dotto | 1999 | |
| 82 | FZBRS | 3068 | Brazil | Rio Grande do Sul | | | | Dom Feliciano | Kita (PUCRS) | 2002 | |
| 83 | FZBRS | 3069 | Brazil | Rio Grande do Sul | | | | Rio Grande | Cibele Indrusiak | 2001 | |
| 84 | KU | 2042 | Argentina | Santa Cruz | -50,11 | -69,50 | | NO LOCALITY | MARTIN H T | | |
| 85 | KU | 2684 | Argentina | Santa Cruz | -51,56 | -68,96 | | CAPE FAIRWEATHER | MARTIN H T | 1905 | |
| 86 | KU | 32245 | Costa Rica | Cartago | 9,95 | -83,58 | | TURRIALBA, 12 KM SE OF; PILON DE AZUCAR PERALTA | WILLE A | 1949 | |
| 87 | KU | 19274 | Mexico | Veracruz | 18,04 | -94,53 | | COATZACOALCOS, 14 KM SW OF | DALQUEST W W | 1947 | |
| 88 | KU | 24546 | Mexico | Veracruz | 17,20 | -94,77 | | JESUS CARRANZA, 35 KM SE OF | DALQUEST W W | 1948 | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 89 | KU | 32224 | Mexico | Veracruz | 17,50 | -94,83 |  | JESUS CARRANZA, 20 KM ENE OF | DALQUEST W W | 1949 |  |
| 90 | KU | 93830 | Mexico | Yucatan | 21,19 | -88,15 |  | TIZIMIN, 6 KM N OF | CLIFTON P L | 1963 |  |
| 91 | KU | 95112 | Mexico | Yucatan | 21,19 | -88,15 |  | TIZIMIN, 6 KM N OF | CLIFTON P L | 1963 |  |
| 92 | KU | 71936 | Nicaragua | Managua | 0,00 | 0,00 |  | MANAGUA, 6 MI WSW OF | ALCORN J R | 1956 |  |
| 93 | KU | 104500 | Nicaragua | Chontales | 0,00 | 0,00 |  | VILLA SOMOZA | CLANTON J N | 1963 |  |
| 94 | KU | 110600 | Nicaragua | Chontales | 0,00 | 0,00 |  | VILLA SOMOZA, 1 KM N, 2.5 KM W OF | SMITH J D | 1967 |  |
| 95 | KU | 337831 | Nicaragua | Leon |  |  |  | Puerto Momotombo, 4 Km WNW, Hacienda Las Colinas | J. Clanton | 1962 |  |
| 96 | KU | 35518 | Mexico | Michoacan |  |  |  | Patzcuaro | E. Nelson |  |  |
| 97 | KU | 81721 | Mexico | Guanajuato |  |  |  | Santa Rosa | Nelson & E. Goldman |  |  |
| 98 | KU | 116953 | Mexico | Coahuila |  |  |  | Sierra Guadalupe | E. Nelson & E. Goldman |  |  |
| 99 | LACM | 59627 | Argentina | Chubut Prov | -42,41 | -71,09 |  | Lelegue | Kovacs, A | 1963 |  |
| 100 | LACM | 59628 | Argentina | Rio Negro Prov | -41,85 | -70,90 |  | Norquinco | Kovacs, A | 1968 |  |
| 101 | LACM | 26686 | Costa Rica | Puntarenas Prov | 9,52 | -84,32 |  | Parrita; Finca Ligia | USACR | 1964 |  |
| 102 | LSUMZ | 15923 | Argentina | Chubut Province | -42,20 | -70,83 |  | Cushamen | Kovacs (#911) | 1969 |  |
| 103 | LSUMZ | 16943 | Argentina | Chubut Province | -42,40 | -70,70 |  | Fofo-Cahuel | Kovacs (#904) | 1969 |  |
| 104 | LSUMZ | 16944 | Argentina | Chubut Province | -43,27 | -69,85 |  | Colanco-nuhe | Kovacs (#913) | 1969 |  |
| 105 | LSUMZ | 16945 | Argentina | Chubut Province | -42,40 | -70,70 |  | Fofo-Cahuel | Kovacs (#916) | 1969 |  |
| 106 | LSUMZ | 16946 | Argentina | Chubut Province | -42,20 | -70,83 |  | Cushamen | Kovacs (#1034) | 1970 |  |
| 107 | LSUMZ | 13375 | Costa Rica | Limón Province | 10,38 | -83,73 |  | Cariari | Gardner, Alfred L. (#10083) | 1967 |  |
| 108 | LSUMZ | 19353 | Peru | Piura Department | -4,56 | -81,27 |  | Ca. 2 km "down the road" from Talara to Lobitos | Thomas, Kim R. (#1122) | 1974 |  |
| 109 | MCZ | 19110 | Argentina |  |  |  |  | Huanuluan | J. L. Peters |  |  |
| 110 | MCZ | 24828 | Brazil |  |  |  |  | C. Piatry, N E Brazil | Glover Merrill Allen |  |  |
| 111 | MCZ | 27219 | Colombia |  |  |  |  | Choachi | Maria, Niceforo |  |  |
| 112 | MCZ | 27218 | Colombia |  |  |  |  | Choachi | Maria, Niceforo |  |  |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 113 | MCZ | 27341 | Ecuador | | | | | east Ecuador, northwest side of Mindo (?), altitude 11500 feet | Ludovic Soederstrom | | |
| 114 | MCZ | 10115 | Panama | | | | | Boquete [VERBATIM ELEVATION:4000] | Wilmot W. Brown Jr. | | |
| 115 | MCZ | 10116 | Panama | | | | | Boquete [VERBATIM ELEVATION:4500] | Wilmot W. Brown Jr. | | |
| 116 | MCZ | 5257 | Peru | | | | | Lake Titicaca | Samuel Walton Garman | | |
| 117 | MCZ | 5258 | Peru | | | | | Lake Titicaca | Samuel Walton Garman | | |
| 118 | MCZ | 5259 | Peru | | | | | Lake Titicaca, West shore | Samuel Walton Garman | | |
| 119 | MNHN | ZM-AC-A3150 | Argentina | | | | | Buenos Aires | Orbigny (d') | | |
| 120 | MNHN | ZM-AC-1995-188 | Chile | | | | Pce Magallanes | Cabeza del Mar | Pellé Eric | 1994 | |
| 121 | MNHN | ZM-MO-1932-2884 | Ecuador | | | | | Mera, Rio Pastara | Dorst | | |
| 122 | MNHN | ZM-MO-1872-57 | Guatemala | Santa Cruz | | | | | | | |
| 123 | MNHN | ZM-MO-1957-1294 | Peru | Pasco | | | | Huaron | | | |
| 124 | MNHN | ZM-MO-1957-1296 | Peru | Pasco | | | | Huaron | | | |
| 125 | MNHN | ZM-MO-1957-1297 | Peru | Puno | | | Checayani -Azaugaro | | Dorst Jean | | |
| 126 | MNHN | ZM-MO-1957-1298 | Peru | Puno | | | Checayani -Azaugaro | | | | |
| 127 | MNHN | ZM-MO-1970-301 | Peru | Puno | | | Checayani -Azaugaro | | Dorst Jean | | |
| 128 | MNHN | ZM-MO-1970-302 | Peru | | | | Checayani | | | | |
| 129 | MNHN | ZM-AC-A1988 | Uruguay | | | | | Montevideo | Eydoux Fortuné | | |
| 130 | MNHN | ZM-MO-1962-1643 | | | | | | Montevideo | Lasser F. | | |
| 131 | MSB | 56102 | Bolivia | Chuquisaca | -20,75 | -63,18 | | 6 KM W (BY ROAD) CARANDAYTI, 500 M; 20D45'S, 63D07'W | Bolivian Expedition 1985 | 1985 | |
| 132 | MSB | 57373 | Bolivia | Oruro | -19,13 | -66,12 | | 7 KM. S., 4 KM. E. CRUCE VENTILLA 3950M; 19.08S 66.07W | Bolivian Expedition 1986 | 1986 | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 133 | MSB | 67084 | Bolivia | Tarija | -21,43 | -63,92 |  | TAPECUA, 1500 m; 21D26'S,63D55'W. | Bolivian Expedition 1991 | 1991 |  |
| 134 | MSB | 210999 | Bolivia | Santa Cruz |  |  |  | 5 KM SE OF TITA, 0295 m. | Bolivian Expedition 1984, Sydney A. Anderson | 1984 |  |
| 135 | MSB | 50008 | Peru | Huanuco | -9,73 | -76,07 |  | 5 KM NE ACOMAYO, TINYAHUAYIN, 8400 FT | G. L. Graham | 1982 |  |
| 136 | MSU | MR.20038 | Argentina | Buenos Aires Province | -37,73 | -58,20 |  | Partido Balcarce | Peter L. Dalby | 1970 |  |
| 137 | MSU | MR.18700 | Argentina | Buenos Aires Province | -37,73 | -58,20 |  | dead on road, Ruta 226, approx. Km 90, Partido Balcarce | Peter L. Dalby | 1970 |  |
| 138 | MSU | MR.17865 | Argentina | Buenos Aires Province | -37,78 | -58,24 |  | Crovetto Field, Km 67, Ruta 226, Partido Balcarce | Peter L. Dalby | 1968 |  |
| 139 | MSU | MR.6306 | Chile | Malleco Province | -37,80 | -72,72 |  | Angol | Dillman S. Bullock |  |  |
| 140 | MSU | MR.6307 | Chile | Malleco Province | -38,43 | -72,23 |  | 30 km W Curacautin | John Keever Greer | 1962 |  |
| 141 | MSU | MR.9649 | Chile | Cautin Province | -38,73 | -72,60 |  | Temuco | Dillman S. Bullock | 1907 |  |
| 142 | MSU | MR.6308 | Chile | Malleco Province | -38,52 | -71,37 |  | Valley of Rio Lonquimay | John Keever Greer | 1961 |  |
| 143 | MSU | MR.6305 | Chile | Malleco Province | -37,80 | -72,72 |  | Angol | Dillman S. Bullock |  |  |
| 144 | MSU | MR.6304 | Chile | Malleco Province | -37,82 | -72,98 |  | Parque Nacional, 27 km WNW Angol | John Keever Greer | 1961 |  |
| 145 | MSU | MR.6303 | Chile | Malleco Province | -37,82 | -72,98 |  | Parque Nacional, 27 km WNW Angol | John Keever Greer | 1961 |  |
| 146 | MVZ | 21934 | Argentina | Provincia Santa Cruz | -50,01 | -68,51 |  | Santa Cruz | John R. Pemberton | 1915 |  |
| 147 | MVZ | 159443 | Argentina | Provincia Neuquen | -40,04 | -70,85 |  | Depto. Los Lagos, 3 km NW Confluencia | Oliver P. Pearson | 1980 |  |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 148 | MVZ | 159444 | Argentina | Provincia Neuquen | -39,09 | -70,32 | | Depto. Zapala, Parque Nacional Laguna Blanca | Oliver P. Pearson | 1980 | |
| 149 | MVZ | 162288 | Argentina | Provincia Rio Negro | -41,24 | -71,15 | | Depto. Pilcaniyeu, Estancia El Condor, 18 km SE Bariloche | Oliver P. Pearson | 1981 | |
| 150 | MVZ | 172241 | Argentina | Provincia Rio Negro | -41,20 | -71,06 | | Depto. Pilcaniyeu, 22 km ESE Bariloche, Estancia El Condor | Oliver P. Pearson | 1985 | 790-790 m |
| 151 | MVZ | 84332 | Ecuador | Provincia Tungurahua | -1,40 | -78,42 | | Runtun Hills, Banos | W. Clarke-MacIntyre | 1938 | 2000-2000 m |
| 152 | MVZ | 114775 | Peru | Departamento Puno | -15,03 | -69,93 | | Hacienda Calacala, 7 mi SW Putina | Carl B. Koford | 1951 | 13000-13000 ft |
| 153 | MVZ | 114776 | Peru | Departamento Puno | -16,43 | -69,67 | | Hacienda Pairumani, 24 mi S Ilave | Carl B. Koford | 1951 | 13000-13000 ft |
| 154 | MVZ | 114940 | Peru | Departamento Puno | -16,88 | -69,71 | | 10 mi S Mazo Cruz | Carl B. Koford | 1951 | |
| 155 | MVZ | 114941 | Peru | Departamento Puno | -16,43 | -69,67 | | Hacienda Pairumani, 24 mi S Ilave | Carl B. Koford | 1951 | 13000-13000 ft |
| 156 | MVZ | 121177 | Peru | Departamento Cajamarca | -6,90 | -79,05 | | Hacienda Taulis | Wilhelm Koepcke | 1952 | 2600-2600 m |
| 157 | MVZ | 121178 | Peru | Departamento Piura | -4,10 | -81,02 | | near Mancora | Wilhelm Koepcke | 1950 | 0-0 ft |
| 158 | MVZ | 135823 | Peru | Departamento Lima | | | | Lomas de Lachay, 22 km N and 11 km W Chancay | Carl B. Koford | 1967 | 1000-1000 ft |
| 159 | MVZ | 135824 | Peru | Departamento Piura | -4,51 | -81,13 | | Parinas, 7 km N and 15 km E Talara | Carl B. Koford | 1967 | |
| 160 | MVZ | 141630 | Peru | Departamento Lima | -13,08 | -76,37 | | 2 mi E Yauyos, Canete Valley | Oliver P. Pearson | 1971 | 8340-8340 ft |
| 161 | NHM | 1902.2.5.3 | Argentina | Mendoza | -31.00 | -69,00 | | San Juan | Thomas | 1902 | |
| 162 | NHM | 1902.1.1.11 | Bolivia | Beni | -16,00 | -66,00 | | Near Trinidad | Thomas | 1902 | |
| 163 | OMNH | 15157 | Argentina | Mendoza | -34,05 | -67,97 | Santa Rosa | Ñacuñán | | 1983 | |
| 164 | OMNH | 34537 | Argentina | Catamarca | -27,70 | -67,88 | Tinogasta | 34.6 km W Fiambalá (by road) | | 2006 | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 165 | OMNH | 35918 | Argentina | Catamarca | -28,27 | -65,87 | Ambato | 6 km S El Rodeo on Hwy 4 |  | 1990 |  |
| 166 | OMNH | 35919 | Argentina | Catamarca |  |  | Capayán | 5.2 km NW Chumbicha |  | 2003 |  |
| 167 | OMNH | 35920 | Argentina | Catamarca |  |  |  | Hwy 38, 17 km S La Merced S of km 613 |  | 1993 |  |
| 168 | OMNH | 35921 | Argentina | Chaco |  |  | Almirante Brown | 35 km NNW and 11 km NE El Mangrullo by road |  | 1990 |  |
| 169 | OMNH | 35923 | Argentina | Neuquen |  |  |  | 43 km NE Confluencia, DOR on Hwy 237 |  | 1991 |  |
| 170 | OMNH | 35924 | Argentina | San Juan |  |  | Sarmiento | Pedernal |  | 1990 |  |
| 171 | OMNH | 1460 | Argentina | Catamarca |  |  | Ambato | 6 km S of El Rodeo on Hwy 4 |  | 1990 |  |
| 172 | OMNH | 1592 | Argentina | Chaco |  |  | Almirante Brown | 35 km NNW and11 km NE El Mangrullo by road |  | 1990 |  |
| 173 | OMNH | 2328 | Argentina | Neuquen |  |  |  | 43 km NE Confluencia, DOR on Hwy 237 |  | 1991 |  |
| 174 | OMNH | 2328 | Argentina | Neuquen |  |  |  | 43 km NE Confluencia, DOR on Hwy 237 |  | 1991 |  |
| 175 | OMNH | 3839 | Argentina | Catamarca | 2848,70 | 6615,00 | Capayán | 5.2 km NW Chumbicha | Braun, J K | 2003 |  |
| 176 | OMNH | 4025 | Argentina | Tucumán |  |  | Tafí del Valle | Santa Cruz, 10 km al S de Tafí del Valle | Jayat, J P | 1998 |  |
| 177 | OMNH | 4025 | Argentina | Tucumán |  |  | Tafí del Valle | Santa Cruz, 10 km al S de Tafí del Valle | Jayat, J P | 1998 |  |
| 178 | ROM | 33524 | Belize |  | 17,77 | -88,37 |  | ROCKSTONE POND | PETERSON, RL; HEPPES, JB | 1964 |  |
| 179 | ROM | 95255 | Mexico | Campeche | 18,62 | -90,75 |  | 3.5 KM N OF ESCARCEGA, BY ROAD | ENGSTROM, MD; ET AL | 1989 |  |
| 180 | ROM | 80191 | Mexico | Coahuila |  |  |  | Carneros | Nelson & E. Goldman |  |  |
| 181 | TTU | 66634 | Argentina | La Pampa | -36,94 | -64,23 |  | PARQUE LURO | WREDE, M A |  |  |
| 182 | TTU | 11764 | United States | Texas | 30,70 | -104,92 |  | 15 MI SW LOBO, WHITE TANK EVANS RANCH | PACKARD, R L | 1965 |  |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 183 | UMMZ | 157158 | Argentina | Santa Cruz | -50,42 | -71,90 |  | ESTANCIA LA JOSEFINA, APPROX 50DEG 25'S, 71DEG 54'W | R.W. STORER | 1981 |  |
| 184 | UMMZ | 77293 | Ecuador | Imbabura | 0,78 | -78,30 |  | IBARRA,CAROLINA | P. HERSHKOVITZ | 1934 |  |
| 185 | UMMZ | 80292 | Mexico | Yucatán | 20,68 | -88,58 |  | CHICHEN ITZA | ANGEL CHANG | 1938 |  |
| 186 | UMMZ | 124451 | Paraguay | Chaco | -20,45 | -60,10 |  | 28.8KM BY RD W FORTIN MADREJON | P. MYERS | 1976 |  |
| 187 | UMMZ | 124452 | Paraguay | Chaco | -20,45 | -60,10 |  | 28.8KM BY RD W FORTIN MADREJON | P. MYERS | 1976 |  |
| 188 | USNM | 172794 | Argentina |  |  |  |  | Tello | A. Hrdlicka | 1910 |  |
| 189 | USNM | 331066 | Argentina |  |  |  |  | Azul, 40 Mi SE, Los Angeles Estancia | Lord & Jellison | 1962 |  |
| 190 | USNM | 264479 | Argentina |  |  |  | Patagonia | Gallegos | A. Colburn | 1898 |  |
| 191 | USNM | 172792 | Argentina | Buenos Aires |  |  |  | Necochea, N Of | A. Hrdlicka | 1910 |  |
| 192 | USNM | 172791 | Argentina |  |  |  |  | San Jose | A. Hrdlicka | 1910 |  |
| 193 | USNM | 171958 | Argentina |  |  |  | Patagonia | San Blas, 20 Mi S | A. Hrdlicka | 1910 |  |
| 194 | USNM | 172793 | Argentina |  |  |  |  | Tello | A. Hrdlicka | 1910 |  |
| 195 | USNM | 171957 | Argentina |  |  |  | Patagonia | San Blas, 20 Mi S | A. Hrdlicka | 1910 |  |
| 196 | USNM | 271410 | Bolivia | Cochabamba |  |  |  | Tiraque, 20 Mi S | R. Gilmore | 1937 |  |
| 197 | USNM | 391848 | Chile | Santiago |  |  |  | Santiago | Collector Unknown | 1946 |  |
| 198 | USNM | 391849 | Chile | Tarapaca |  |  |  | Parinacota | Collector Unknown |  |  |
| 199 | USNM | 391850 | Chile | Tarapaca |  |  |  | Parinacota | Collector Unknown |  |  |
| 200 | USNM | 281453 | Colombia | Magdalena |  |  |  | Colonia Agricola De Caracolicito | P. Hershkovitz | 1942 |  |
| 201 | USNM | 281457 | Colombia | Cesar |  |  | Valledupar District | Sierra Negra, Villanueva | P. Hershkovitz | 1942 |  |
| 202 | USNM | 281465 | Colombia | La Guajira |  |  | Fonseca District | Las Marimondas, East Andes | P. Hershkovitz | 1943 |  |
| 203 | USNM | 281462 | Colombia | Cesar |  |  | Valledupar District | Villanueva | P. Hershkovitz | 1943 |  |
| 204 | USNM | 281455 | Colombia | Cesar |  |  | Valledupar District | El Orinoco, Rio Cesar | P. Hershkovitz | 1942 |  |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 205 | USNM | 281454 | Colombia | Magdalena | | | | Colonia Agricola De Caracolicito | P. Hershkovitz | 1942 | |
| 206 | USNM | 281452 | Colombia | Magdalena | | | | Colonia Agricola De Caracolicito | P. Hershkovitz | 1942 | |
| 207 | USNM | 281458 | Colombia | Cesar | | | Valledupar District | Sierra Negra, Villanueva | P. Hershkovitz | 1942 | |
| 208 | USNM | 281456 | Colombia | Cesar | | | Valledupar District | El Orinoco, Rio Cesar | P. Hershkovitz | 1942 | |
| 209 | USNM | 281464 | Colombia | La Guajira | | | Fonseca District | Las Marimondas, East Andes | P. Hershkovitz | 1943 | |
| 210 | USNM | 281460 | Colombia | Cesar | | | Valledupar District | Sierra Negra, Villanueva | P. Hershkovitz | 1942 | |
| 211 | USNM | 281461 | Colombia | Cesar | | | Valledupar District | Villanueva | P. Hershkovitz | 1943 | |
| 212 | USNM | 281459 | Colombia | Cesar | | | Valledupar District | Sierra Negra, Villanueva | P. Hershkovitz | 1942 | |
| 213 | USNM | 281463 | Colombia | Cesar | | | Valledupar District | Villanueva | P. Hershkovitz | 1943 | |
| 214 | USNM | 568103 | Ecuador | Pichincha | | | | Rio Palenque Science Center, 47 Km South Santo Domingo De Los Colorados | Collector Unknown | 1979 | |
| 215 | USNM | 65762 | Mexico | Veracruz | | | | Catemaco | Nelson & E. Goldman | 1894 | |
| 216 | USNM | 63650 | Mexico | Veracruz | | | | Motzorongo | E. Nelson & E. Goldman | 1894 | |
| 217 | USNM | 65763 | Mexico | Veracruz | | | | Catemaco | Nelson & E. Goldman | 1894 | |
| 218 | USNM | 8610 | Mexico | | | | | Merida | A. Schott | 1866 | |
| 219 | USNM | 108503 | Mexico | Yucatan | | | | La Vega | Nelson & E. Goldman | 1901 | |
| 220 | USNM | 108502 | Mexico | Quintana Roo | | | | La Vega, Opposite Isla Cancun | E. Nelson & E. Goldman | 1901 | |
| 221 | USNM | 132512 | Mexico | Veracruz | | | | Perez | J. Friesser | 1903 | |
| 222 | USNM | 337832 | Nicaragua | Chontales | | | | Villa Somoza | J. Clanton | 1963 | |
| 223 | USNM | 361359 | Nicaragua | Rio San Juan | | | | La Esperanza | M. Clark | 1965 | |
| 224 | USNM | 338870 | Nicaragua | Jinotega | | | | Hca La Trampa | M. Clark | 1964 | |
| 225 | USNM | 332037 | Panama | Chiriqui | | | | El Volcan, 2 Mi NE | E. Tyson | 1962 | |
| 226 | USNM | 335773 | Panama | Bocas Del Toro | | | | Sibube | C. Handley & F. Greenwell | 1963 | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 227 | USNM | 363346 | Panama | Chiriqui | | | | Progreso | F. Greenwell & T. Fleming | 1966 | |
| 228 | USNM | 324236 | Panama | Chiriqui | | | | Cerro Punta, Bamdito | C. Handley & F. Greenwell | 1962 | |
| 229 | USNM | 176320 | Peru | | | | | Huarochiri, Near | A. Hrdlicka | | |
| 230 | USNM | 172857 | Peru | | | | | Chicama Valley | A. Hrdlicka | 1910 | |
| 231 | USNM | 194322 | Peru | Cusco | | | | Chospyoc, Huarocondo River | E. Heller | 1915 | |
| 232 | USNM | 194324 | Peru | Cusco | | | | Orca, Near Calca | E. Heller | 1915 | |
| 233 | USNM | 194319 | Peru | Cusco | | | | Occobamba Valley, Tocopoqueu | E. Heller | 1915 | |
| 234 | USNM | 194323 | Peru | Cusco | | | | Matchu Picchu, San Miguel Bridge | E. Heller | 1915 | |
| 235 | USNM | 194320 | Peru | Cusco | | | | Occobamba Valley | E. Heller | 1915 | |
| 236 | USNM | 259436 | Uruguay | | | | | Rocha, 15 Mi N Of San Vicente De Castillos | C. Sanborn | 1926 | |
| 237 | USNM | 296626 | Venezuela | Monagas | | | | Caicara | F. Smith | 1952 | |
| 238 | USNM | 372745 | Venezuela | Yaracuy | 10,62 | -68,40 | | Yaracuy, 19 Km NW Urama | Smithsonian Venezuelan Project | 1965 | |
| 239 | USNM | 443295 | Venezuela | Falcon | 11,17 | -70,62 | | Capatarida, 6 Km SSW Capatarida | Smithsonian Venezuelan Project | 1968 | |
| 240 | USNM | 443576 | Venezuela | Zulia | 9,18 | -72,70 | | Encontrados, 39 Km WNW, El Rosario | Smithsonian Venezuelan Project | 1968 | |
| 241 | USNM | 443289 | Venezuela | Falcon | 11,17 | -70,62 | | Capatarida | Smithsonian Venezuelan Project | 1968 | |
| 242 | USNM | 443414 | Venezuela | Falcon | 11,83 | -69,98 | | Coro, 49 Km N And 34 Km W | Smithsonian Venezuelan Project | 1968 | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 243 | USNM | 443290 | Venezuela | Falcon | 11,17 | -70,62 | | Capatarida, 5.5 Km NE, Orocodones | Smithsonian Venezuelan Project | 1968 | |
| 244 | USNM | 388244 | Venezuela | Monagas | 9,32 | -62,93 | | Maturin, 47 Km SE, Hato Mata De Bejuco | Smithsonian Venezuelan Project | 1966 | |
| 245 | USNM | 388241 | Venezuela | Monagas | 9,32 | -62,93 | | Maturin, 47 Km SE, Hato Mata De Bejuco | Smithsonian Venezuelan Project | 1966 | |
| 246 | USNM | 209149 | United States | Arizona | | | | Black River, 5 Mi Above Mouth Of White Creek | H. Jackson | | |
| 247 | USNM | 205376 | United States | Arizona | | | | Blue River, 12 M S, Cosper Ranch | E. Goldman | | |
| 248 | USNM | 205828 | United States | Arizona | | | | Blue River, Cosper Ranch | E. Holt | | |
| 249 | USNM | 61878 | United States | Arizona | | | | Fort Huachuca | E. Weibel | | |
| 250 | USNM | 214352 | United States | Arizona | | | | Fort Whipple, 3 Mi N | H. Jackson | | |
| 251 | USNM | 203906 | United States | Arizona | | | | Graham Mountains, Ash Creek | E. Holt | | |
| 252 | USNM | 21839 | United States | Arizona | | | | Huachuca Mountains | R. Lusk | | |
| 253 | USNM | A37285 | United States | Arizona | | | | La Osa, SW Of Laosa | E. Mearns | | |
| 254 | USNM | 214351 | United States | Arizona | | | | Mcmillenville, 8 Mi N | W. Taylor | | |
| 255 | USNM | 222830 | United States | Arizona | | | | Nantan Plateau, Near Sawmill, 25 Mi NE Rice, San Carlos Indian Reservation | W. Taylor | | |
| 256 | USNM | 205829 | United States | Arizona | | | | Prieto Plateau, Raspberry Creek, 3 Mi W, Cosper Ranch | E. Holt | | |
| 257 | USNM | 167890 | United States | Arizona | | | | Tucson, 15 mi S | H. Brown | | |
| 258 | USNM | 272467 | United States | Arizona | | | | Tucson, 36 Mi SE | A. Trowbridge | | |
| 259 | USNM | 167999 | United States | New Mexico | | | | Animas Valley, Cloverdale Ranch | H. Hotchkiss | | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 260 | USNM | 130092 | United States | New Mexico | | | | Capitan Mountains, SW Slope | J. Gaut | | |
| 261 | USNM | 530904 | United States | New Mexico | | | | Carlsbad Cave | V. Bailey | | |
| 262 | USNM | 244450 | United States | New Mexico | | | | Carlsbad Cave, In Walnut Canyon | V. Bailey | | |
| 263 | USNM | 158890 | United States | New Mexico | | | | Dry Creek | E. Goldman | | |
| 264 | USNM | 151219 | United States | New Mexico | | | | Gila National Forest, Diamond Creek | H. Hotchkiss | | |
| 265 | USNM | 159331 | United States | New Mexico | | | | Gila National Forest, E Diamond Creek | H. Hotchkiss | | |
| 266 | USNM | 167688 | United States | New Mexico | | | | Hillsboro | E. Goldman | | |
| 267 | USNM | 130670 | United States | New Mexico | | | | Jicarillo Mountains, NW Foothills | J. Gaut | | |
| 268 | USNM | 167689 | United States | New Mexico | | | | Lake Valley | E. Goldman | | |
| 269 | USNM | 147417 | United States | New Mexico | | | | Mimbres River, Head | V. Bailey | | |
| 270 | USNM | 147418 | United States | New Mexico | | | | Mimbres River, Head | V. Bailey | | |
| 271 | USNM | 248368 | United States | New Mexico | | | | Pinon, Near Sacramento River | E. Wright | | |
| 272 | USNM | 120050 | United States | New Mexico | | | | San Andreas Mountains, N Slope Salinas Peak | J. Gaut | | |
| 273 | USNM | 119857 | United States | New Mexico | | | | San Andreas Mountains, Sheep Mountain Summit | J. Gaut | | |
| 274 | USNM | 248214 | United States | Oklahoma | | | | Kenton | Collector Unknown | | |
| 275 | USNM | 11764 | United States | TEXAS | 30,70 | -104,92 | | 15 MI SW LOBO, WHITE TANK EVANS RANCH | PACKARD, R L | | |
| 276 | USNM | 274475 | United States | Texas | | | | Big Bend National Park, Day Canyon | J. Bankston | | |
| 277 | USNM | 274476 | United States | Texas | | | | Big Bend National Park, Emery Peak | J. Bankston | | |
| 278 | USNM | 136551 | United States | Texas | | | | Big Thicket, Sour Lake, 7 Mi NE | J. Gaut | | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 279 | USNM | 108764 | United States | Texas | | | | Boquillas | V. Bailey | | |
| 280 | USNM | A45131 | United States | Texas | | | | Brownsville | F. Armstrong | | |
| 281 | USNM | 116178 | United States | Texas | | | | Chesos Mountains | V. Bailey | | |
| 282 | USNM | 140360 | United States | Texas | | | | Cleveland, 12 Mi W | J. Gaut | | |
| 283 | USNM | 117648 | United States | Texas | | | | Davis Mountains, 15 Mi E Of Valentine | V. Bailey | | |
| 284 | USNM | 119013 | United States | Texas | | | | Devil'S River, 13 Mi Below Juno | V. Bailey | | |
| 285 | USNM | 24575 | United States | Texas | | | | Eagle Pass, 50 Mi SE, Blocker Rancho | C. Streator | | |
| 286 | USNM | 349999 | United States | Texas | | | | Fort Davis | V. Bailey | | |
| 287 | USNM | 119014 | United States | Texas | | | | Juno, 13 Mi S, Devils River | M. Cary | | |
| 288 | USNM | 126241 | United States | Texas | | | | Langtry, 8 Mi S | J. Gaut | | |
| 289 | USNM | 24840 | United States | Texas | | | | Laredo | W. Lloyd | | |
| 290 | USNM | 24842 | United States | Texas | | | | Laredo, 6 Mi S | W. Lloyd | | |
| 291 | USNM | 186455 | United States | Texas | | | | Mason | I. Henry | | |
| 292 | USNM | A31165 | United States | Texas | | | | Osman Canyon, Near Langtry | W. Lloyd | | |
| 293 | USNM | 244474 | United States | Texas | | | | San Angelo | S. Hill | | |
| 294 | USNM | 21659 | United States | Texas | | | | San Diego | T. Taylor | | |
| 295 | USNM | 274477 | United States | Texas | | | | Santa Elena Canyon | J. Bankston | | |
| 296 | USNM | 136533 | United States | Texas | | | | Sour Lake, 9 Mi NE | J. Gaut | | |
| 297 | USNM | 135098 | United States | Texas | | | | Tarkington | V. Bailey | | |
| 298 | USNM | 790 | United States | Texas | | | | West Texas | Pope | | |
| 299 | USNM | 9424 | Mexico | | | | | Santa Efegenia | F. Sumichrast | | |
| 300 | USNM | 20898 | Mexico | | | | | Hacienda Augostina | P. Jouy | | |
| 301 | USNM | 25555 | Mexico | Nuevo Leon | | | | Monterey | C. Streator | | |
| 302 | USNM | 25691 | Mexico | | | | | Lampazos, 18 Mi W | W. Lloyd | | |
| 303 | USNM | 27556 | Mexico | Tamaulipas | | | | Mier | W. Lloyd | | |
| 304 | USNM | 33252 | Mexico | Colima | | | | Manzanillo, Near Armeria | E. Nelson | | |
| 305 | USNM | 33253 | Mexico | Colima | | | | Colima | E. Nelson | | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 306 | USNM | 33254 | Mexico | Colima | | | | Hca Magdalena | E. Nelson | | |
| 307 | USNM | 34336 | Mexico | Jalisco | | | | Zapotlan | E. Nelson | | |
| 308 | USNM | 34407 | Mexico | Jalisco | | | | Etzatlan | E. Nelson | | |
| 309 | USNM | 35519 | Mexico | San Luis Potosi | | | | Hca La Parada | E. Nelson | | |
| 310 | USNM | 36172 | Mexico | Mexico | | | | Salazar | E. Nelson | | |
| 311 | USNM | 50833 | Mexico | San Luis Potosi | | | | Jeseu Maria, Mountains Near | Collector Unknown | | |
| 312 | USNM | 52697 | Mexico | Hidalgo | | | | El Chico | E. Nelson | | |
| 313 | USNM | 58926 | Mexico | Sonora | | | | San Jose Mountain | Collector Unknown | | |
| 314 | USNM | 68172 | Mexico | Oaxaca | | | | Cerro San Felipe | E. Nelson & E. Goldman | | |
| 315 | USNM | 70621 | Mexico | Guerrero | | | | Acapulco, sea level | Nelson & E. Goldman | | |
| 316 | USNM | 73480 | Mexico | Oaxaca | | | | Huilotepec | Nelson & E. Goldman | | |
| 317 | USNM | 74678 | Mexico | Guerrero | | | | Ometepec, Near | Nelson & E. Goldman | | |
| 318 | USNM | 74685 | Mexico | Oaxaca | | | | llano Grande | Nelson & E. Goldman | | |
| 319 | USNM | 82262 | Mexico | Jalisco | | | | Ameca | Nelson & E. Goldman | | |
| 320 | USNM | 90983 | Mexico | Zacatecas | | | | Plateado | Nelson & E. Goldman | | |
| 321 | USNM | 90985 | Mexico | Sinaloa | | | | Rosario | Nelson & E. Goldman | | |
| 322 | USNM | 92117 | Mexico | Zacatecas | | | | Valparaiso Mountains | Nelson & E. Goldman | | |
| 323 | USNM | 92980 | Mexico | Puebla | | | | Metlaltoyuca | E. Goldman | | |
| 324 | USNM | 95914 | Mexico | Sonora | | | | Camoa, Rio Mayo | E. Goldman | | |
| 325 | USNM | 98334 | Mexico | Chihuahua | | | | Near | Nelson & E. Goldman | | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 326 | USNM | 126145 | Mexico | Michoacan | | | | Mount Tancitaro | Nelson & E. Goldman | | |
| 327 | USNM | 132196 | Mexico | Chihuahua | | | | Colonia Garcia, 15 Mi W | J. Gaut | | |
| 328 | USNM | 510078 | Mexico | Nayarit | | | | Chacala | A. Gardner | | |
| 329 | USNM | 510079 | Mexico | Nayarit | | | | Estanzuela | A. Gardner | | |
| 330 | USNM | A3377 | Mexico | | | | | Durango, Rio Nasae | D. Couch | | |
| 331 | USNM | A46058 | Mexico | Sonora | | | | Nogales, 10 Mi S | J. Loring | | |
| 332 | USNM | 73481 | Mexico | Oaxaca | | | | Santa Domingo | Nelson & E. Goldman | | |
| 333 | UWBM | 41382 | Mexico | Veracruz | 18,45 | -95,21 | | Veracruz; San Andres | D. G. Kissenger | 1953 | |
| 334 | MFN | 26788 | Argentina | | | | | Rio St. Cruz | Konietzko | | |
| 335 | MFN | 48304 | Argentina | | | | | Ossa Marino | Dade | 1934 | |
| 336 | MFN | 45282 | Argentina | | | | | Osso Marino | Flemming | | |
| 337 | MFN | 48304 | Argentina | | | | | Osso Marino | Flemming | 1933 | |
| 338 | MFN | 48305 | Argentina | | | | | Osso Marino | Flemming | | |
| 339 | MFN | 64734 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 340 | MFN | 64735 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 341 | MFN | 64736 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 342 | MFN | 64737 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 343 | MFN | 64738 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 344 | MFN | 64739 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 345 | MFN | 64740 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 346 | MFN | 64741 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 347 | MFN | 64742 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 348 | MFN | 64743 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 349 | MFN | 64747 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 350 | MFN | 64748 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 351 | MFN | 64754 | Brazil | | | | | Rio Grande do Sul | Hensel | | |
| 352 | MFN | 61668 | Chile | | | | | Valdivia | Ohde | 1899 | |
| 353 | MFN | 61676 | Chile | | | | | Punta Arena | | | |
| 354 | MFN | 64744 | Guatemala | | | | | Finca la Providentia | H. Rolle | | |

**Table 3A.** (continued)

| Rec# | Institution | Acronym | Country | State/Province | Dec Lat | Dec Long | Locality 1 | Locality 2 | Collector | Year | Elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 355 | MFN | 64745 | Guatemala | | | | | Finca la Providentia | H. Rolle | | |
| 356 | MFN | 64749 | Guatemala | | | | | Finca la Providentia | H. Rolle | | |
| 357 | MFN | 64750 | Guatemala | | | | | Finca la Providentia | H. Rolle | | |
| 358 | MFN | 64751 | Guatemala | | | | | Finca la Providentia | H. Rolle | | |
| 359 | MFN | 64752 | Guatemala | | | | | Finca la Providentia | H. Rolle | | |
| 360 | MFN | 64753 | Guatemala | | | | | Finca la Providentia | H. Rolle | | |
| 361 | MFN | 64746 | Honduras | | | | | La Cumbre | Linnaea | | |
| 362 | MFN | 64755 | Mexico | | | | | Campostela | Schlüter | | |
| 363 | MFN | 61559 | Peru | | | | | Lauramarca | Garlepp | | |
| **364** | **MFN** | **61677** | | | | | | **Joinville** | **Rolle** | | |

Highlighted lines represent doubtful records.
Rec#: Record number (this study).
Institution: Mammalian Collection consulted. Detailed information provided below.
Acronym: Code in collection.
Dec Lat: Decimal Latitude.
Dec Long: Decimal Longitude.
Country: Country where specimen was collected.
State/Province: State/Province where specimen was collected.
Locality 1 and 2: city, district, county, farm, park and any additional specific information of collection point.
Year: year of specimen collection.
Elevation: above sea level of the collection point, given in meters (m) or feet (ft).
Institution codes: AMNH – American Museum of Naural History, New York, US; CU – Cornell University Museum of Vertebrates , Ithaca, US; FZBRS – Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; KU – University of Kansas Biodiversity Institute, Lawrence, US; LACM – Los Angeles County Museum of Natural History, Los Angeles, US; LSUMZ – Louisiana State University Museum of Natural Science, Baton Rouge, US; MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, US; MNHN – Muséum National d'Histoire Naturelle, Paris, France; MSB – Museum of Southwestern Biology, University of New Mexico, Albuquerque, US; MSU – Michigan State University Museum, East Lansing, US; MVZ – Museum of Vertebrate Zoology, University of California, Berkeley, US; NHM – British Natural History Museum, London, UK; OMNH – Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman, US; ROM – Royal Ontario Museum, Toronto, Canada; TTU – Museum of Texas Tech University, Lubbock, US; UMMZ – University of Michigan Museum of Zoology, Ann Arbor, US; USNM – National Museum of Natural History, Stithsonian Institute, Washington DC, US; UWBM – University of Washington Burke Museum, Seatle, US; MFN – Museum für Naturkunde, Berlin, Germany.

**Table 3B.** General information regarding the geographic records compiled from publications to develop a detailed distributional map of *Conepatus*.

| Rec# | Authors | Year | Country | State/Province | Coordinates | Locality/City/Park |
|---|---|---|---|---|---|---|
| 365 | Alberico et al | 2000 | Colombia | Cundinamarca | | |
| 366 | Alberico et al | 2000 | Colombia | Magdalena | | |
| 367 | Alberico et al | 2000 | Colombia | Nariño | | |
| 368 | Alberico et al | 2000 | Colombia | Norte de Santander | | |
| 369 | Allen et al | 1916 | Colombia | | | Balcillas, near Bogotá |
| 370 | Allen & Smith | 1904 | Colombia | Santa Marta | | Bonda |
| 371 | Allen & Smith | 1904 | Colombia | Santa Marta | | Playa Brava |
| 372 | Allen & Carriker | 1911 | Venezuela | Yaracuy | | El Hacha |
| 373 | Alves et al | 2009 | Brazil | Paraiba | -7.068185 -36.091752 | Pocinhos |
| 374 | Alves et al | 2012 | Brazil | São Paulo | -22.832833 -48.436369 | |
| 375 | Aris et al | 2008 | Peru | Ayacucho | | Anco |
| 376 | Barbarán | 2004 | Argentina | Jujuy | | |
| 377 | Barbarán | 2004 | Argentina | W Salta | | |
| **378** | **Barnett & Da Cunha** | **1994** | **Brazil** | **Roraima** | **3.409241 -61.592518** | |
| 379 | Bisbal | 1998 | Venezuela | Sucre | 10°41’-62°37’ | |
| 380 | Bitetti | 2009 | Argentina | Corrientes | -28.6 -57.817 | |
| 381 | Bocchiglieri et al | 2010 | Brazil | Bahia | -13°40’ -45°35’ | Jaborandi |
| 382 | Bruna et al | 2010 | Brazil | Minas Gerais | -19°10’ -48°23 | Panga Ecologic Station |
| **383** | **Cáceres** | **2004** | **Brazil** | **Paraná** | **-25°28’ -48°50’** | |
| **384** | **Cáceres et al** | **2008** | **Brazil** | **Mato Grosso do Sul** | | **Pantanal** |
| 385 | Câmara& Oliveira | 2012 | Brazil | Minas Gerais | -19.344837 -43.62417 | Serra do Cipó National Park |
| 386 | Cherem et al | 2004 | Brazil | Rio Grande do Sul | | Bom Jardim da Serra |
| 387 | Cherem et al | 2004 | Brazil | Rio Grande do Sul | | Bom Retiro |
| 388 | Cherem et al | 2004 | Brazil | Rio Grande do Sul | | São Joaquim |
| 389 | Cruz et al | 2005 | Brazil | Pernambuco | -8.428904 -38.543368 | RPPN Cantidiano Valgueiro |
| 390 | Cueva et al | 2010 | Ecuador | Pichincha | 0.118 -78.61 | |
| 391 | Falcão et al | 2012 | Brazil | Bahia | -16°18’00” -39°06’00” | RPPN Estação Veracel |
| 392 | Fáundez | 2012 | Chile | | -28.166667 -71 | |
| 393 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Viamão |
| 394 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Cristal |
| 395 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Pelotas |
| 396 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Pedro Osório |
| 397 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Arroio Grande |
| 398 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Arroio Grande |
| 399 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | São Francisco de Paula |
| 400 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Tainhas |
| 401 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Lagoa Vermelha |
| 402 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Vacaria |
| 403 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Arambaré |
| 404 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Camaquã |
| 405 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Capão do Leão |
| 406 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Cachoeira do Sul |
| 407 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Rio Grande |
| 408 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Rio Grande |
| 409 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Santa Vitória do Palmar |
| 410 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Uruguaiana |
| 411 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Osório |
| 412 | Fontoura-Rodrigues et al | in prep | Brazil | Santa Catarina | | Anita Garibaldi |
| 413 | Fontoura-Rodrigues et al | in prep | Brazil | Santa Catarina | | Campo Belo do Sul |
| 414 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Campestre da Serra |
| 415 | Fontoura-Rodrigues et al | in prep | Brazil | Santa Catarina | | Alfredo Wagner |
| 416 | Fontoura-Rodrigues et al | in prep | Brazil | Santa Catarina | | São Cristóvão do Sul |
| 417 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Triunfo |

**Table 3B**. (continued)

| Rec# | Authors | Year | Country | State/Province | Coordinates | Locality/City/Park |
|---|---|---|---|---|---|---|
| 418 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Soledade |
| 419 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Campestre da Serra |
| 420 | Fontoura-Rodrigues et al | in prep | Brazil | Santa Catarina | | Campo Belo do Sul |
| 421 | Fontoura-Rodrigues et al | in prep | Brazil | Santa Catarina | | Capão Alto |
| 422 | Fontoura-Rodrigues et al | in prep | Brazil | Santa Catarina | | Campo Belo do Sul |
| 423 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Bom Jesus |
| 424 | Fontoura-Rodrigues et al | in prep | Brazil | Santa Catarina | | Anita Garibaldi |
| 425 | Fontoura-Rodrigues et al | in prep | Brazil | Santa Catarina | | Capão Alto |
| 426 | Fontoura-Rodrigues et al | in prep | Brazil | Santa Catarina | | Campo Belo do Sul |
| 427 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Piratini |
| 428 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Piratini |
| 429 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Cachoeira do Sul |
| 430 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Rosário do Sul |
| 431 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Rio Grande |
| 432 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Rio Grande |
| 433 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Cerrito |
| 434 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Pedro Osório |
| 435 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Pedro Osório |
| 436 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Tapes |
| 437 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Pedro Osório |
| 438 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Arroio Grande |
| 439 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Arroio Grande |
| 440 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Osório |
| 441 | Fontoura-Rodrigues et al | in prep | Uruguay | Rocha | | Barra de Valizas |
| 442 | Fontoura-Rodrigues et al | in prep | Uruguay | Rocha | | Barra de Valizas |
| 443 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Santa Vitória do Palmar |
| 444 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Arroio Grande |
| 445 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Cristal |
| 446 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Canguçu |
| 447 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Arroio Grande |
| 448 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Barra do Ribeiro |
| 449 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Tapes |
| 450 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Osório |
| 451 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Cristal |
| 452 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Tapes |
| 453 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Osório |
| 454 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Encruzilhada do Sul |
| 455 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Cristal |
| 456 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Santo Antônio da Patrulha |
| 457 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Pantano Grande |
| 458 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Encruzilhada do Sul |
| 459 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Canguçú |
| 460 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Ibirubá |
| 461 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Cachoeira do Sul |
| 462 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Cachoeira do Sul |
| 463 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Alegrete |
| 464 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Alegrete |
| 465 | Fontoura-Rodrigues et al | in prep | Argentina | Corrientes | | Cuatro Bocas |
| 466 | Fontoura-Rodrigues et al | in prep | Argentina | Entre Rios | | Los Conquistadores |
| 467 | Fontoura-Rodrigues et al | in prep | Argentina | Entre Rios | | Federal |
| 468 | Fontoura-Rodrigues et al | in prep | Argentina | Entre Rios | | Federal |
| 469 | Fontoura-Rodrigues et al | in prep | Argentina | Entre Rios | | Bovril |
| 470 | Fontoura-Rodrigues et al | in prep | Argentina | Mendoza | | Pareditas |
| 471 | Fontoura-Rodrigues et al | in prep | Argentina | Mendoza | | Pareditas |
| 472 | Fontoura-Rodrigues et al | in prep | Argentina | Mendoza | | El Nahuil |
| 473 | Fontoura-Rodrigues et al | in prep | Argentina | Buenos Aires | | Coronel Dorrego |
| 474 | Fontoura-Rodrigues et al | in prep | Argentina | Buenos Aires | | Coronel Dorrego |
| 475 | Fontoura-Rodrigues et al | in prep | Argentina | Buenos Aires | | Coronel Dorrego |
| 476 | Fontoura-Rodrigues et al | in prep | Argentina | Buenos Aires | | Coronel Dorrego |

**Table 3B**. (continued)

| Rec# | Authors | Year | Country | State/Province | Coordinates | Locality/City/Park |
|---|---|---|---|---|---|---|
| 477 | Fontoura-Rodrigues et al | in prep | Argentina | Buenos Aires | | Benito juarez |
| 478 | Fontoura-Rodrigues et al | in prep | Argentina | Buenos Aires | | Alzaga |
| 479 | Fontoura-Rodrigues et al | in prep | Argentina | Buenos Aires | | Cachari |
| 480 | Fontoura-Rodrigues et al | in prep | Uruguay | Canelones | | Ciudad de la Costa |
| 481 | Fontoura-Rodrigues et al | in prep | Uruguay | Maldonado | | José Ignácio |
| 482 | Fontoura-Rodrigues et al | in prep | Uruguay | Maldonado | | José Ignácio |
| 483 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Santa Vitória do Palmar |
| 484 | Fontoura-Rodrigues et al | in prep | Argentina | Entre Rios | | Gualegay |
| 485 | Fontoura-Rodrigues et al | in prep | Argentina | Cordoba/Buenos Aires | | ? |
| 486 | Fontoura-Rodrigues et al | in prep | Argentina | Cordoba/Buenos Aires | | ? |
| 487 | Fontoura-Rodrigues et al | in prep | Argentina | Cordoba/Buenos Aires | | ? |
| 488 | Fontoura-Rodrigues et al | in prep | Argentina | Cordoba/Buenos Aires | | ? |
| 489 | Fontoura-Rodrigues et al | in prep | Brazil | Rio Grande do Sul | | Tapes |
| 490 | Fontoura-Rodrigues et al | in prep | Uruguay | Rocha | | Castillos |
| 491 | Fontoura-Rodrigues et al | in prep | Uruguay | Maldonado | | La Barra |
| 492 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | São Roque |
| 493 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Formiga |
| 494 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Formiga |
| 495 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Piumhí |
| 496 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Três Marias |
| 497 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Piumhí |
| 498 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | São Roque de Minas |
| 499 | Fontoura-Rodrigues et al | in prep | Brazil | Piauí | | Batalha |
| 500 | Fontoura-Rodrigues et al | in prep | Brazil | Piauí | | José de Freitas |
| 501 | Fontoura-Rodrigues et al | in prep | Brazil | Piauí | | Cabeceiras |
| 502 | Fontoura-Rodrigues et al | in prep | Brazil | Piauí | | Cabeceiras |
| 503 | Fontoura-Rodrigues et al | in prep | Brazil | Piauí | | Pirapora |
| 504 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Soledade de Minas |
| 505 | Fontoura-Rodrigues et al | in prep | Brazil | Goiás | | Cristalina |
| 506 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Três Marias |
| 507 | Fontoura-Rodrigues et al | in prep | Brazil | Piauí | | Cristino Castro |
| 508 | Fontoura-Rodrigues et al | in prep | Brazil | Piauí | | Ribeiro Gonçalves |
| 509 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Barão de Cocais |
| 510 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Curvelo |
| 511 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Três Marias |
| 512 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Três Marias |
| 513 | Fontoura-Rodrigues et al | in prep | Brazil | Minas Gerais | | Curvelo |
| 514 | Fontoura-Rodrigues et al | in prep | Brazil | Ceará | | Iguatú |
| 515 | Fontoura-Rodrigues et al | in prep | Brazil | Piauí | | Valença |
| 516 | Fontoura-Rodrigues et al | in prep | Brazil | Goiás | | Mineiros |
| 517 | Fontoura-Rodrigues et al | in prep | Brazil | Piauí | | Valença |
| 518 | Fontoura-Rodrigues et al | in prep | Brazil | Goiás | | Mineiros |
| 519 | Fontoura-Rodrigues et al | in prep | Brazil | Goiás | | Mineiros |
| 520 | Fontoura-Rodrigues et al | in prep | Brazil | Goiás | | Mineiros |
| 521 | Fontoura-Rodrigues et al | in prep | Brazil | Goiás | | Mineiros |
| 522 | Fontoura-Rodrigues et al | in prep | Brazil | Goiás | | Mineiros |
| 523 | Fontoura-Rodrigues et al | in prep | Brazil | Goiás | | Mineiros |
| 524 | Fontoura-Rodrigues et al | in prep | Brazil | Goiás | | Mineiros |
| 525 | Fontoura-Rodrigues et al | in prep | Brazil | Goiás | | Mineiros |
| 526 | Fontoura-Rodrigues et al | in prep | Brazil | Maule | | Curicó |
| 527 | Fontoura-Rodrigues et al | in prep | Chile | Valparaíso | | Santo Domingo |
| 528 | Fontoura-Rodrigues et al | in prep | Chile | Los Ríos | | Puente Iñaque |
| 529 | Fontoura-Rodrigues et al | in prep | Chile | Coquimbo | | Los Vilos |
| 530 | Fontoura-Rodrigues et al | in prep | Chile | Los Lagos | | Paso Puyehua |
| 531 | Fontoura-Rodrigues et al | in prep | Chile | Aisén | | Puerto Aisén |
| 532 | Fontoura-Rodrigues et al | in prep | Mexico | Yucatán | | Merida |
| 533 | Fontoura-Rodrigues et al | in prep | United States | Texas | | McCulloch |

**Table 3B**. (continued)

| Rec# | Authors | Year | Country | State/Province | Coordinates | Locality/City/Park |
|---|---|---|---|---|---|---|
| 534 | Fontoura-Rodrigues et al | in prep | Mexico | Oaxaca | | San Francisco del Mar |
| 535 | Freitas | 2010 | Brazil | Sergipe | -10.035795 -37.408551 | Porto da Folha |
| 536 | Geise et al | 2004 | Brazil | Rio de Janeiro | -22.331499 -44.583477 | Itatiaia National Park |
| 537 | GómezPuerta et al | 2009 | Peru | | -14.445319 -71.048584 | |
| 538 | Herrera et al | 2005 | Brazil | Piauí | -8.439772 -42.333485 | PARNA Serra da Capivara |
| 539 | Huertas & Donegan | 2006 | Colombia | Santander | 06°37’16” -73°30’01” | Honduras Alto |
| 540 | IUCN | 1982 | Argentina | Neuquen | -39.047986 -70.41275 | Laguna Blanca National Park |
| 541 | IUCN | 1982 | Argentina | Chaco | -26.83333 -59.66667 | Gran Chaco National Park |
| 542 | IUCN | 1982 | Argentina | Formosa | -24.283333° -61.8° | Formosa National Park |
| 543 | IUCN | 1982 | Argentina | La Pampa | -37.986557 -65.595417 | Lihuel-Calel National Park |
| 544 | IUCN | 1982 | Argentina | Santa Cruz | -50 -73.249444 | Los Glaciares National Park |
| 545 | IUCN | 1982 | Bolivia | La Paz | -14.75 -69 | Ulla Ulla National Park |
| 546 | IUCN | 1982 | Chile | Malleco | -37.055177 -73.212891 | Nahuelbuta National Park |
| 547 | IUCN | 1982 | Chile | | -30.689297 -71.680298 | Fray Jorge National Park |
| 548 | IUCN | 1982 | Peru | Lima | -11.403976 -77.360916 | Lachay National Park |
| 549 | Jayat et al | 1999 | Argentina | Jujuy | | Yuto |
| 550 | Jayat et al | 1999 | Argentina | Jujuy | | San Antonio |
| 551 | Jayat et al | 1999 | Argentina | Jujuy | | Cochinoca |
| 552 | Jayat et al | 1999 | Argentina | Jujuy | | Criadero de Abrapampa |
| 553 | Jayat et al | 1999 | Argentina | Jujuy | | Purmamarca |
| 554 | Jayat et al | 1999 | Argentina | Jujuy | | El Perchel |
| 555 | Jayat et al | 1999 | Argentina | Jujuy | | Humahuaca |
| 556 | Jayat et al | 1999 | Argentina | Jujuy | | Pozuelos |
| 557 | Jayat et al | 1999 | Argentina | Jujuy | | Tres Cruces |
| 558 | Jayat et al | 1999 | Argentina | Salta | | Incahuasi |
| 559 | Jayat et al | 1999 | Argentina | Salta | | Lizoite |
| 560 | Jayat et al | 1999 | Argentina | Salta | | Santa Victoria |
| 561 | Jayat et al | 1999 | Argentina | Salta | | Valle Lizoite |
| 562 | Jayat et al | 1999 | Argentina | Santiago del Estero | | Añatuya |
| 563 | Jayat et al | 1999 | Argentina | Santiago del Estero | | Quimilí |
| 564 | Jayat et al | 1999 | Argentina | Santiago del Estero | | Huyamampa |
| 565 | Jimenez et al | 2010 | Peru | | -6.41 -79.06 | Pagaibamba Park |
| 566 | Johnson et al | 1988 | Chile | | | Torres del Paine National Park |
| 567 | Lessa et al | 2012 | Brazil | Minas Gerais | -16°56’08” -46°16’05” | |
| 568 | Linares | 1998 | Venezuela | | | Llanos biome (visually plotted in map) |
| 569 | Linares | 1999 | Venezuela | | | Llanos biome (visually plotted in map) |
| 570 | Linares | 2000 | Venezuela | | | Llanos biome (visually plotted in map) |
| 571 | Linares | 2001 | Venezuela | | | Llanos biome (visually plotted in map) |
| 572 | Linares | 2002 | Venezuela | | | Llanos biome (visually plotted in map) |
| 573 | Linares | 2003 | Venezuela | | | Llanos biome (visually plotted in map) |
| 574 | Llanos-Cuentas et al | 1999 | Peru | Bolognesi | | Ancash |
| 575 | Lyra-Jorge et al | 2008 | Brazil | São Paulo | -21°31'15" -47°34'42" | |

**Table 3B**. (continued)

| Rec# | Authors | Year | Country | State/Province | Coordinates | Locality/City/Park |
|---|---|---|---|---|---|---|
| 576 | Nunes et al | 2012 | Brazil | Minas Gerais | -20.715278 -42.4475 | Serra do Brigadeiro Park |
| 577 | Oliveira et al | 2007 | Brazil | | -04°17’ -46°23’ | |
| 578 | Oliveira et al | 2007 | Brazil | | -04°23’ -44°39’ | |
| 579 | Oliveira et al | 2007 | Brazil | | -04°33’ -44°55’ | |
| 580 | Oliveira et al | 2007 | Brazil | | -04°23’ -44°20’ | |
| 581 | Oliveira et al | 2007 | Brazil | | -04°27’ -43°53’ | |
| 582 | Oliveira et al | 2007 | Brazil | | -04°58’ -43°10’ | |
| 583 | Oliveira et al | 2007 | Brazil | | -05°-05’ -42°50’ | |
| 584 | Oliveira et al | 2007 | Brazil | | -03°52’ -45°17’ | |
| 585 | Oliveira et al | 2007 | Brazil | | -04°33’ -45°07’ | |
| 586 | Oliveira et al | 2007 | Brazil | | -04°12’ -44°50’ | |
| 587 | Oliveira et al | 2007 | Brazil | | -04°-06’ -44°57’ | |
| 588 | Oliveira et al | 2007 | Brazil | | -04°12’ -44°35’ | |
| 589 | Oliveira et al | 2007 | Brazil | | -04°-04’ -44°58’ | |
| 590 | Oliveira et al | 2007 | Brazil | | -04°57’ -44°28’ | |
| 591 | Oliveira et al | 2007 | Brazil | | -04°23’ -44°20’ | |
| 592 | Oliveira et al | 2007 | Brazil | | -04°39’ -43°36’ | |
| 593 | Oliveira et al | 2007 | Brazil | | -04°47’ -42°50’ | |
| 594 | Oliveira et al | 2007 | Brazil | | -04°51’ -43°21’ | |
| | | | | | | |
| 595 | Osgood | 1943 | Chile | | 41° 17' 0.88" S 72° 15' 36.30" W | Puerto Varas |
| 596 | Osgood | 1943 | Chile | | | valdivia |
| 597 | Osgood | 1943 | Chile | | | Rinihue |
| 598 | Osgood | 1943 | Chile | | | Rio Nirehuao |
| 599 | Osgood | 1943 | Chile | | | Huanuluan |
| 600 | Osgood | 1943 | Chile | | | Tacna |
| 601 | Osgood | 1943 | Peru | | | Cailloma |
| 602 | Osgood | 1943 | Peru | | | Arequipa |
| 603 | Osgood | 1943 | Peru | | -15.95 -69.98 | Puno |
| 604 | Osgood | 1943 | Peru | | -14.0875 -75.763333 | Huacallani |
| 605 | Osgood | 1943 | Peru | | | Salinas |
| 606 | Osgood | 1943 | Peru | | | Sumbay |
| | | | | | | |
| 607 | Pacheco et al | 2004 | Bolivia | | | Sajama National Park |
| 608 | Penido & da Silva | 2012 | Brazil | Minas Gerais | -20°26’47” -44°36’38” | Mata do Cedro Ecologic Station |
| 609 | Peters et al | 2011 | Brazil | Rio Grande do Sul | | Southern Half of RS State |
| 610 | Pozo & Trujilo | 2005 | Ecuador | | -0.078278 -77.838135 | Cayambe Coca Ecological Reserve |
| 611 | Ramirez-Chavez & Noguera-Urbano | 2010 | Colombia | Nariño | | La Florida |
| 612 | Ramirez-Chavez & Noguera-Urbano | 2010 | Colombia | Nariño | | Pasto |
| 613 | Ramirez-Chavez & Noguera-Urbano | 2010 | Colombia | Nariño | | Sandoná |
| 614 | Ramirez-Chavez & Noguera-Urbano | 2010 | Colombia | Nariño | | Sapuyes |
| 615 | Ramirez-Chavez & Noguera-Urbano | 2010 | Colombia | Nariño | | Tuquerres |
| 616 | Ramirez-Chavez & Noguera-Urbano | 2010 | Colombia | Nariño | | Ospina |
| 617 | Ramirez-Chavez & Noguera-Urbano | 2010 | Colombia | Nariño | | Potosí |
| 618 | Ramirez-Chavez & Noguera-Urbano | 2010 | Colombia | Nariño | | Puerres |
| 619 | Ramirez-Chavez & Noguera-Urbano | 2010 | Colombia | Nariño | | Nariño |
| 620 | Rumiz et al | 1998 | Bolivia | Cochabamba | | Carrasco National Park |
| 621 | Santos et al | 2004 | Brazil | Rio Grande do Sul | | Aparados da Serra National Park |

**Table 3B**. (continued)

| Rec# | Authors | Year | Country | State/Province | Coordinates | Locality/City/Park |
|---|---|---|---|---|---|---|
| 622 | Telleria et al | 1999 | Bolivia | La Paz | | Inquisivi province |
| 623 | Thomas | 1902 | Bolivia | | | Choro |
| 624 | Thomas | 1902 | Bolivia | | | Cochabamba |
| 625 | Thomas | 1898 | Bolivia | | | Esperanza, Mount Sahama |
| 626 | Thomas | 1905 | Costa Rica | | | Boquete |
| 627 | Thomas | 1900 | Peru | Arequipo | | Sumbay |
| 628 | Thomas | 1900 | Peru | | | Callao |
| 629 | Tirira & Boada | 2009 | Ecuador | Carchi | 00°36’N 77°40’W | |
| 630 | Tirira & Boada | 2009 | Ecuador | Carcho | 00°34’N 77°42 | |
| 631 | Travaini et al | 1998 | Argentina | | 70°30’—71°30’W; 39°30’—40°20’S | |
| 632 | Yahnke et al | 1998 | Paraguay | Amambay | | Cerro Cora Park |
| 633 | Yahnke et al | 1998 | Paraguay | Boquerón | | Teniente Enciso Park |
| 634 | Yahnke et al | 1998 | Paraguay | Chaco | | Defensores del Chaco Park |
| 635 | Zapata et al | 2001 | Argentina | Santa Cruz | 47°47’S 65°49’W | |
| 636 | Zapata-Ríos et al | 2006 | Ecuador | | 02°35' -77°46' | |

Highlighted lines represent doubtful records.
Rec#: Record number (this study), in continuity to Table 3A.
Authors: publication authors.
Year: year of publication.
Country: Country where specimen was collected.
State/Province: State/Province where specimen was collected.
Coordinates: geographical coordinates given in either latitude/longitude or decimal latitude/longitude system.
Locality/City/Park: district, county, farm, park and any additional specific information of collection point.

**Table 4.** Bayes factor results, expressed as the harmonic means of the marginal likelihood for each phylogenetic search, in log units. A difference of 3-5 units is considered to be strong evidence in favor of a given hypothesis, while a difference of >5 units is considered to be very strong evidence (Kass and Raftery, 1995).

| | *C. semistriatus* | | *C. humboldtii - C. chinga* | | *Southern Brazil / Uruguay basal* | |
|---|---|---|---|---|---|---|
| Run | Constrained | Not constrained | Constrained | Not constrained | Constrained | Not constrained |
| 1 | -6488.83 | -6451.85 | -6455.66 | -6449.07 | -6434.27 | -6436.39 |
| 2 | -6495.56 | -6457.49 | -6450.57 | -6449.45 | -6440.26 | -6442.01 |
| Total | -6494.87 | -6456.8 | -6454.97 | -6449.28 | -6439.57 | -6441.32 |

*C. semistriatus* constraint: Central America and Central Brazil populations being monophyletic in relation to all other South America populations.

*C. humboldtii* - *C. chinga* constrain: Southern Chile sample being basal in relation to all other *C. chinga* populations.

Southern Brazil basal constrain: Southern Brazil/Uruguay population being basal in relation to all other South American populations.

**Table 5.** Structure matrix of the first and second functions of the PCA and DFA, conducted for the population differentiation assessment based on 29 craniodental variables. The eigenvalue and cumulative variance are presented for both analyses. Wilk's Lambda, Chi-square statistic, degrees of freedom, significance values and canonical correlation values are provided for DFA.

| | PCA | | DFA | |
|---|---|---|---|---|
| Variables | PC1 | PC2 | CV1 | CV2 |
| Bas | **0.961** | -0.141 | -0.016 | 0.049 |
| CoBa | 0.764 | -0.489 | -0.018 | 0.041 |
| Zyg | **0.944** | 0.006 | -0.004 | 0.062 |
| Mast | **0.915** | -0.173 | -0.010 | 0.021 |
| IOrb | **0.915** | 0.123 | -0.016 | **0.123** |
| POrb | 0.664 | 0.254 | 0.007 | 0.065 |
| Palat | 0.827 | 0.142 | -0.009 | 0.081 |
| FaL | 0.871 | -0.192 | -0.024 | 0.038 |
| Nas | 0.074 | -0.494 | -0.038 | -0.095 |
| CrH | 0.472 | -0.302 | -0.013 | -0.038 |
| CrW | 0.811 | -0.160 | -0.025 | 0.027 |
| BuL | 0.603 | -0.226 | -0.007 | 0.021 |
| BuW | 0.443 | 0.107 | 0.004 | 0.024 |
| MaTR | 0.861 | 0.182 | -0.001 | 0.062 |
| WaInc | 0.797 | 0.064 | -0.034 | 0.094 |
| WaCan | **0.919** | 0.098 | -0.003 | 0.063 |
| WaMol | 0.890 | 0.203 | 0.008 | **0.117** |
| CaL | 0.665 | -0.264 | -0.009 | 0.000 |
| CaW | 0.677 | -0.213 | -0.007 | 0.024 |
| UPML | 0.525 | **0.386** | **0.041** | 0.087 |
| UPMW | 0.632 | -0.090 | -0.042 | 0.018 |
| UMoL | 0.431 | **0.376** | -0.247 | 0.031 |
| UMoW | 0.656 | 0.352 | -0.205 | -0.090 |
| JaH | 0.819 | 0.277 | **0.049** | -0.033 |
| JaW | 0.853 | **0.382** | -0.055 | 0.022 |
| JaTR | 0.843 | 0.360 | -0.002 | -0.028 |
| WaLPM | 0.706 | 0.155 | **0.073** | **0.206** |
| LMoL | 0.655 | **0.484** | -0.152 | -0.144 |
| LMoW | 0.60 | **0.39** | -0.067 | -0.126 |
| Wilk's Lambda | - | - | 0.000 | 0.005 |
| Chi-square statistic | - | - | 128.78 | 62.11 |
| d.f. | - | - | 63 | 40 |
| *P*-value | - | - | 0.000* | 0.014* |
| Canonical correlation | - | - | 0.998 | 0.986 |
| Eigenvalue | 124.36 | 12.48 | 328.49 | 61.26 |
| Cumulative variance (%) | 72.10 | 79.33 | 83.70 | 99.30 |

Highest contribution values for principal component and discriminant functions are presented in bold. Asterisks represent statistically significant values.

**Table 6.** Difference significance values of the variable means between groups in the DFA, conducted for the population structure investigation based on 29 craniodental variables.

| Variable | Wilks' Lambda | *F*-value | *P*-value |
|---|---|---|---|
| Bas | 0.718 | 2.746 | 0.068 |
| CoBa | 0.743 | 2.423 | 0.094 |
| Zyg | 0.786 | 1.901 | 0.160 |
| Mast | 0.829 | 1.440 | 0.259 |
| IOrb | 0.448 | 8.610 | 0.000* |
| POrb | 0.615 | 4.379 | 0.015* |
| Palat | 0.685 | 3.212 | 0.043* |
| FaL | 0.719 | 2.741 | 0.069 |
| Nas | 0.454 | 8.435 | 0.000* |
| CrH | 0.861 | 1.130 | 0.360 |
| CrW | 0.721 | 2.713 | 0.071 |
| BuL | 0.886 | 0.898 | 0.459 |
| BuW | 0.954 | 0.335 | 0.800 |
| MaTR | 0.779 | 1.987 | 0.147 |
| WaInc | 0.485 | 7.422 | 0.001* |
| WaCan | 0.784 | 1.931 | 0.155 |
| WaMol | 0.503 | 6.906 | 0.002* |
| CaL | 0.973 | 0.198 | 0.897 |
| CaW | 0.940 | 0.443 | 0.725 |
| UPML | 0.425 | 9.460 | 0.000* |
| UPMW | 0.538 | 5.999 | 0.004* |
| UMoL | 0.498 | 7.063 | 0.002* |
| UMoW | 0.358 | 12.573 | 0.000* |
| JaH | 0.671 | 3.437 | 0.035* |
| JaW | 0.646 | 3.837 | 0.024* |
| JaTR | 0.806 | 1.685 | 0.201 |
| WaLPM | 0.718 | 2.750 | 0.068 |
| LMoL | 0.538 | 6.007 | 0.004* |
| LMoW | 0.748 | 2.361 | 0.100 |

Asterisks represent statistically significant values.

**Table 7.** Results of the assignment tests performed by the DFA conducted for the population structure investigation based on 29 craniodental variables. Correspondence between original and predicted group membership is provided in form of number of individuals (count) and percentage. Table A refers to the survey conducted with all individuals and populations. Tables B and C refer to surveys in which a particular populations was not included (see text for details). Clusters: Southern Brazil, Argentina and Uruguay (S Bra-Arg-Uru); Peru and Ecuador (Peru-Ecuador); Venezuela and Northern Colombia (Ven-Col); Central America (C America).

| Table A | | Predicted Group Membership | | | | |
|---|---|---|---|---|---|---|
| | Original Groups | S Bra-Arg-Uru | Peru-Ecuador | Ven-Col | C America | Total |
| **Count** | S Bra-Arg-Uru | 1 | 4 | 0 | 2 | 7 |
| | Peru-Ecuador | 0 | 6 | 0 | 1 | 7 |
| | Ven-Col | 1 | 0 | 19 | 0 | 20 |
| | C America | 0 | 1 | 1 | 12 | 14 |
| **Percentage** | S Bra-Arg-Uru | 14.3 | 57.1 | 0.0 | 28.6 | 100.0 |
| | Peru-Ecuador | 0.0 | 85.7 | 0.0 | 14.3 | 100.0 |
| | Ven-Col | 5.0 | 0.0 | 95.0 | 0.0 | 100.0 |
| | C America | 0.0 | 7.1 | 7.1 | 85.7 | 100.0 |

79.2% of original grouped cases correctly classified.

| Table B | | Predicted Group Membership | | | |
|---|---|---|---|---|---|
| | Original Groups | Peru-Ecuador | Ven-Col | C America | Total |
| **Count** | Peru-Ecuador | 6 | 0 | 1 | 7 |
| | Ven-Col | 0 | 20 | 0 | 20 |
| | C America | 1 | 1 | 12 | 14 |
| **Percentage** | Peru-Ecuador | 85.7 | 0.0 | 14.3 | 100.0 |
| | Ven-Col | 0.0 | 100.0 | 0.0 | 100.0 |
| | C America | 7.1 | 7.1 | 85.7 | 100.0 |

92.7% of original grouped cases correctly classified.

| Table C | | Predicted Group Membership | | | |
|---|---|---|---|---|---|
| | Original Groups | S Bra-Arg-Uru | Peru-Ecuador | Ven-Col | Total |
| **Count** | S Bra-Arg-Uru | 5 | 1 | 1 | 7 |
| | Peru-Ecuador | 1 | 6 | 0 | 7 |
| | Ven-Col | 0 | 2 | 18 | 20 |
| **Percentage** | S Bra-Arg-Uru | 71.4 | 14.3 | 14.3 | 100.0 |
| | Peru-Ecuador | 14.3 | 85.7 | 0.0 | 100.0 |
| | Ven-Col | 0.0 | 10.0 | 90.0 | 100.0 |

85.3% of original grouped cases correctly classified.

**Table 8.** Structure matrix of first and second functions of PCA and DFA, conducted for the morphological comparison survey based on general body measurements. The eigenvalue and cumulative variance are presented for both analyses. Wilk's Lambda, Chi-square statistic, degrees of freedom, significance values and canonical correlation values are provided for DFA. Results are given separately for males and females.

| | PCA | | | | DFA | | | |
|---|---|---|---|---|---|---|---|---|
| | Males | | Females | | Males | | Females | |
| Variable | PC1 | PC2 | PC1 | PC2 | CV1 | CV2 | CV1 | CV2 |
| Tlgth | **0.886** | 0.039 | 0.322 | **0.903** | **0.837** | -0.133 | **0.534** | -0.17 |
| Tail | **0.787** | **0.578** | **0.83** | **0.418** | **0.66** | 0.161 | 0.016 | **0.746** |
| Hfoot | 0.684 | 0.212 | **0.876** | 0.073 | 0.383 | 0.045 | **0.535** | **0.641** |
| Wgth | 0.743 | -0.66 | 0.799 | -0.147 | 0.176 | **0.974** | 0.392 | 0.117 |
| T/TL | 0.337 | **0.856** | 0.767 | -0.162 | 0.296 | **0.819** | 0.498 | 0.124 |
| W/HB | 0.615 | -0.705 | 0.764 | -0.603 | 0.347 | -0.263 | 0.471 | -0.07 |
| Wilsk's Lambda | - | - | - | - | 0.047 | 0.253 | 0.046 | 0.224 |
| Chi-square statistic | - | - | - | - | 52 | 23.35 | 63.3 | 30.63 |
| d.f. | - | - | - | - | 12 | 6 | 15 | 8 |
| *P*-value | - | - | - | - | 0.000* | 0.001* | 0.000 | 0.000 |
| Canonical Correlation | - | - | - | - | 0.903 | 0.833 | 0.893 | 0.861 |
| Eigen value | 2.91 | 2.04 | 3.37 | 1.41 | 4.39 | 2.27 | 3.92 | 2.85 |
| Cumulative variance | 48.65 | 82.79 | 56.25 | 79.74 | 63.9 | 97.00 | 56.5 | 97.8 |

Highest contribution values for principal component and discriminant functions are presented in bold.
Asterisks represent statistically significant values.

**Table 9.** Difference significance values of the variable means between groups in the DFA, conducted for the morphological comparison survey based on general body measurements.

| | Males | | | Females | | |
|---|---|---|---|---|---|---|
| Variable | Wilks' Lambda | F | *P*-value | Wilks' Lambda | F | *P*-value |
| TLgth | 0.33 | 12.10 | 0.000* | 0.38 | 11.95 | 0.000* |
| Tail | 0.24 | 19.02 | 0.000* | 0.30 | 16.93 | 0.000* |
| HFoot | 0.60 | 4.03 | 0.02* | 0.52 | 6.81 | 0.000* |
| Wght | 0.34 | 11.69 | 0.000* | 0.58 | 5.23 | 0.01* |
| T/TL | 0.54 | 5.05 | 0.01* | 0.49 | 7.79 | 0.000* |
| W/HB | 0.30 | 14.12 | 0.000* | 0.45 | 8.90 | 0.000* |

Asterisks represent statistically significant values.

**Table 10.** Integrated taxonomic proposition based on molecular, morphological and distribution data. Scientific names follow Cabrera (1958). Dragoo (2009) was consulted for *C. conepatl*.

| Population | Geographic range | Occurrence Biomes | Reference | Method supporting population distinctiveness | Scientific name | Author |
|---|---|---|---|---|---|---|
| i | Central Chile | Chilean Matorral | Fontoura-Rodrigues *et al*. (in prep.) | 1 | *C. chinga* | Molina, 1782 |
| ii | Southern Chile (+ Southern Argentina?) | Patagonia | Fontoura-Rodrigues *et al*. (in prep.) | 1 | *C. humboldtii* | Gray, 1837 |
| iii | Central/Northern Argentina | Chacos and Argentinean Pampas | Fontoura-Rodrigues *et al*. (in prep.) | 1, 2, 4 | *C. suffocans* | Illiger, 1815 |
| iv | Entre Ríos + Corrientes Departments (Argentina) | Argentinean Pampas | Fontoura-Rodrigues *et al*. (in prep.) | 1, 2 | *C.* sp. nov. | - |
| v | Central Brazil | Cerrado and Caatinga | Fontoura-Rodrigues *et al*. (in prep.) | 1, 2, 4 | *C. amazonicus* | Lichtenstein, 1838 |
| vi | Southern Brazil + Uruguay | Uruguayan Savannas (Pampas) and Campos de Cima da Serra | Fontoura-Rodrigues *et al*. (in prep.) | 1, 2, 4 | *C.* sp. nov. | - |
| vii | Southern Colombia + Equador + Peru | Andes Montane Vegetation and Peru's shore Deserts | This study | 3 | *C. quitensis* | Humboldt, 1812 |
| viii | Northern Colombia + Venezuela | Llanos and Venezuelan/Colombian dry forests | This study | 3, 4 | *C. semistriatus* | Boddaert, 1785 |
| ix | Eastern/Southern Central America | Savannas and dry forests of Central America | This study | 3 | *C. conepatl* | Gmelin, 1788 |
| x | Southern North America + Western/Northern Central America | Deserts and dry forests of Southern USA, Mexico and Central America | Dragoo *et al*. 2003 | 1, 3 | *C. leuconotus* | Lichtenstein, 1832 |

Structure detection methods: 1 – mitochondrial DNA; 2 – microsatellites; 3 – craniodental measurements; and 4 – general body measurements.

**Figure 1.** Geographic distributions of the four currently recognized *Conepatus* species, based on the map currently available in the IUCN Redlist (IUCN, 2012). Circles represent the approximate locality of the type for each species, following Cabrera (1958). Species code: *C. humboldtii*, horizontal stripes; *C. chinga*, dark gray; *C. semistriatus*, diagonal stripes; and *C. leuconotus*, light gray.

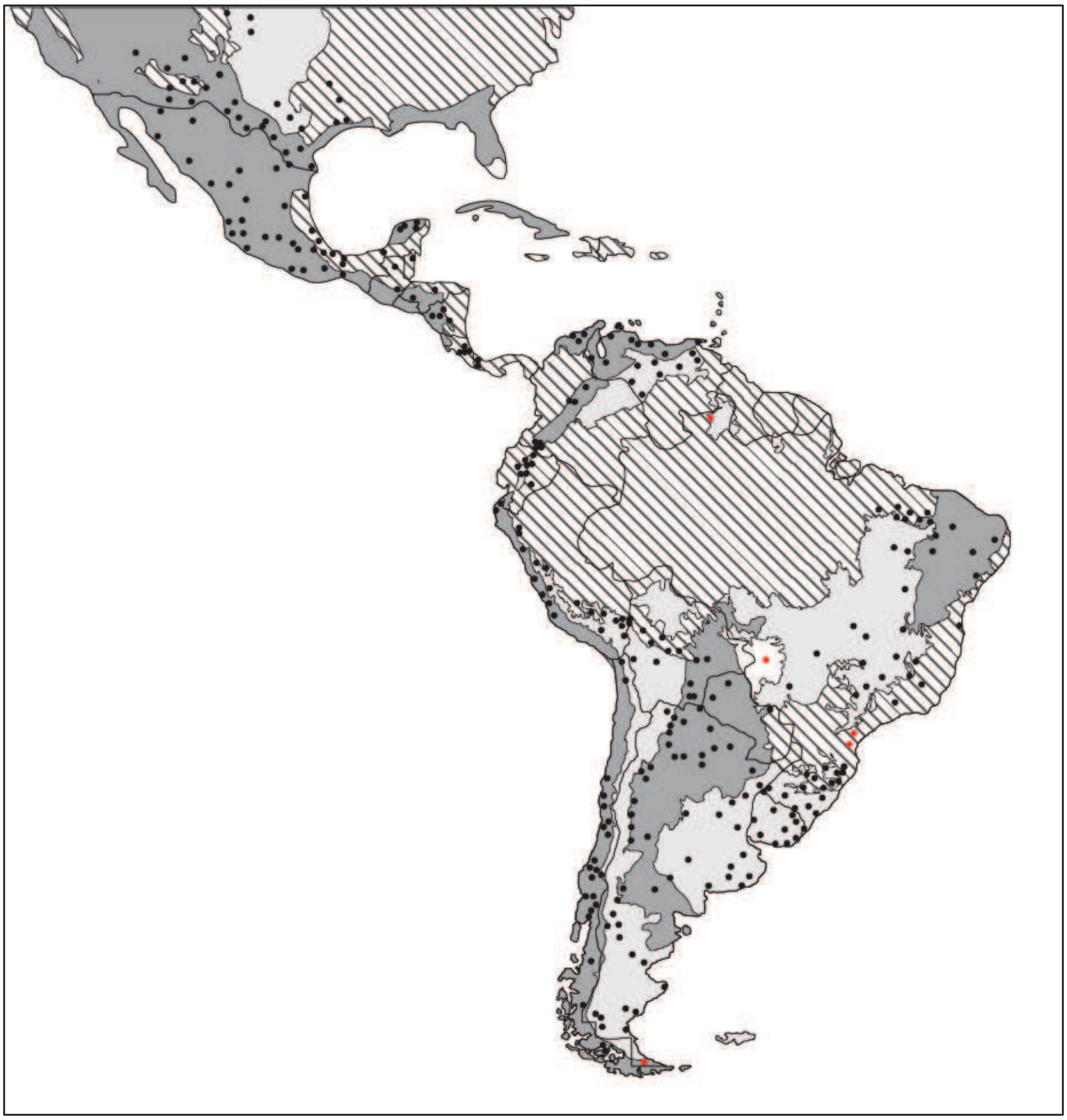

**Figure 2.** The 295 geographical records collected from museum specimen and publication records of *Conepatus* plotted on a vegetational map of the Americas. Each record is represented by a black circle of roughly 50 km in diameter. The five red circles represent doubtful records, plotted on the map due to the relevance of their geographical location. Vegetation types were divided as follows: dense forests, diagonal stripes; savannas and grasslands, light gray; dry forests, xerofitics and desert environments, dark gray; flood plains, white.

**Figure 3.** Predicted geographic distribution of *Conepatus* (in light gray) based on the 295 geographical records collected and plotted in figure 2. Dark gray areas represent biomes or regions from which doubtful records were collected, and therefore should not be included in the final distribution map until confirmed by further studies.

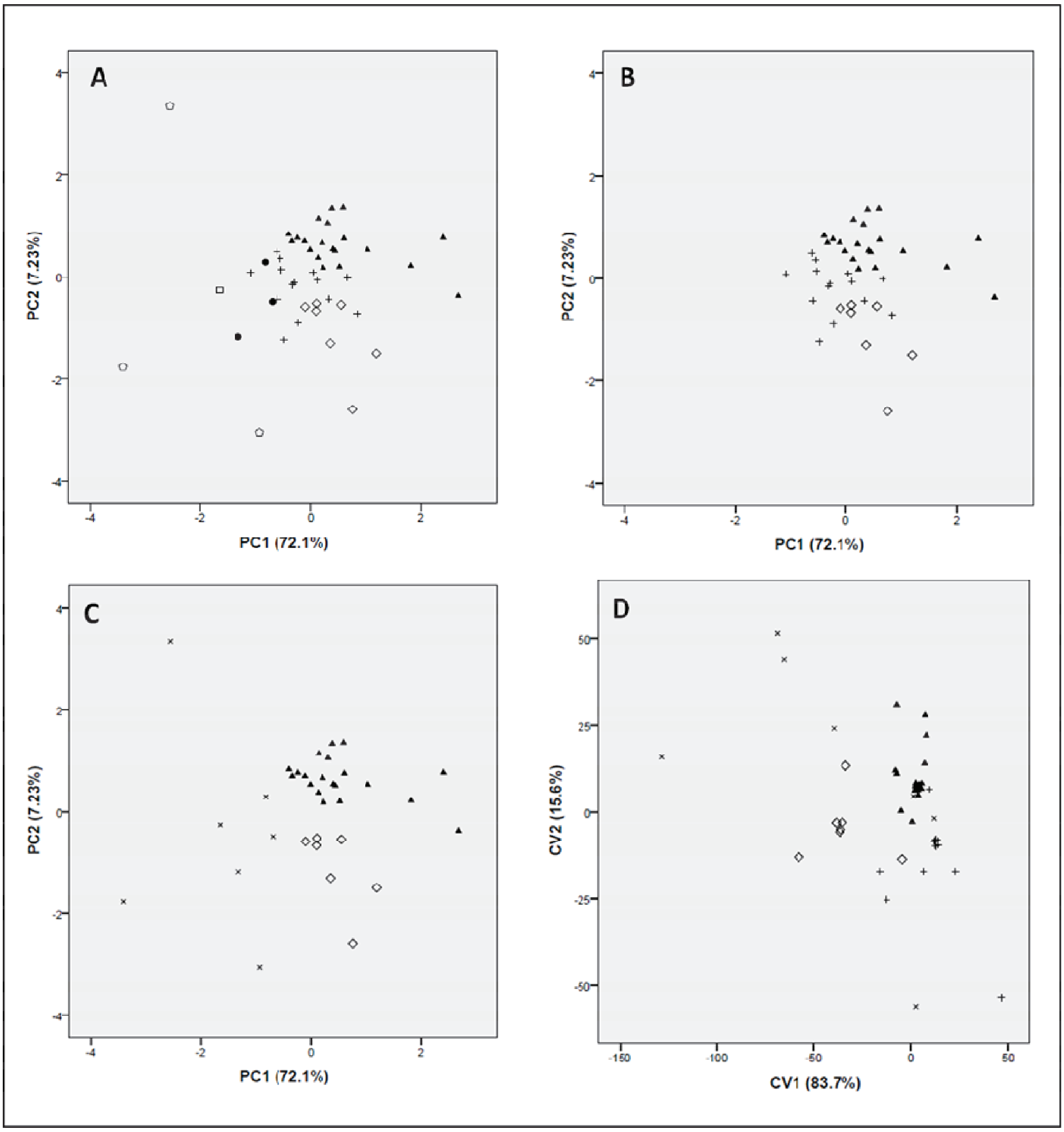
A
B
C
D
PC1 (72.1%)
PC2 (7.23%)
CV1 (83.7%)
CV2 (15.6%)
-4
-2
0
2
4
-150
-100
-50
0
50
-50
-25
25
50

**Figure 4.** PCA (A, B and C) and DFA (D) plots derived from a database of 29 craniodental measurements. The PCA is presented in three different configurations: A – all individuals; B – only northern South American and Central American individuals; C – only South American individuals. PCA results are represented by the first principal component (PC1) plotted against the second one (PC2), with the respective percentages of variance explanation shown in parentheses. The DFA plot (D) is represented by the first canonical variate (CV1) plotted against the second one (CV2), with the respective percentage of discriminatory power shown in parentheses. Geographic origin codes are as follows: Southern Argentina, white pentagons; Central Argentina, white squares; Southern Brazil and Uruguay, black circles; Peru and Ecuador, white diamonds; Venezuela and Northern Colombia, black triangles; Central America, vertical crosses. When Southern Brazil, Uruguay and Argentina are unified in a single population, individuals are represented by diagonal crosses (Xs). No sex division was performed to conduct these analyses.

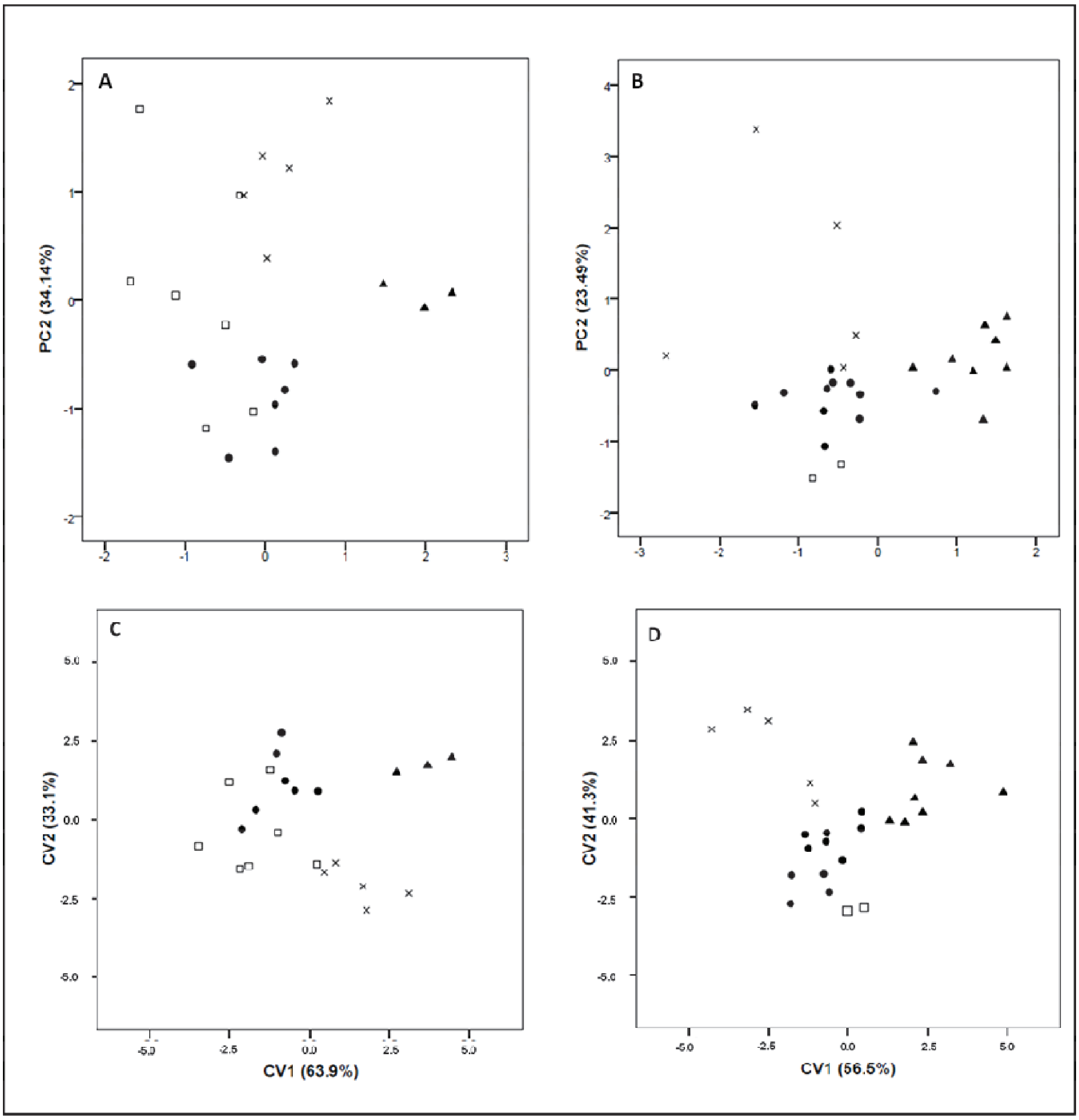

**Figure 5.** PCA (A and B) and DFA (C and D) plots regarding the survey with general body measurements. PCA plots are represented by the first principal component (PC1) against the second (PC2), with respective percentages of variance explanation between parentheses. The DFA plot is represented by the first canonical variate (CV1) plotted against the second (CV2), with respective percentage of the discriminatory power between parentheses. Geographic origin codes are as follows: Central Argentina, diagonal crosses (Xs); Southern Brazil, black circles; Venezuela, black triangles; Central Brazil, white squares. Figures A and C represent the male dataset, while figures B and D represent the female dataset.

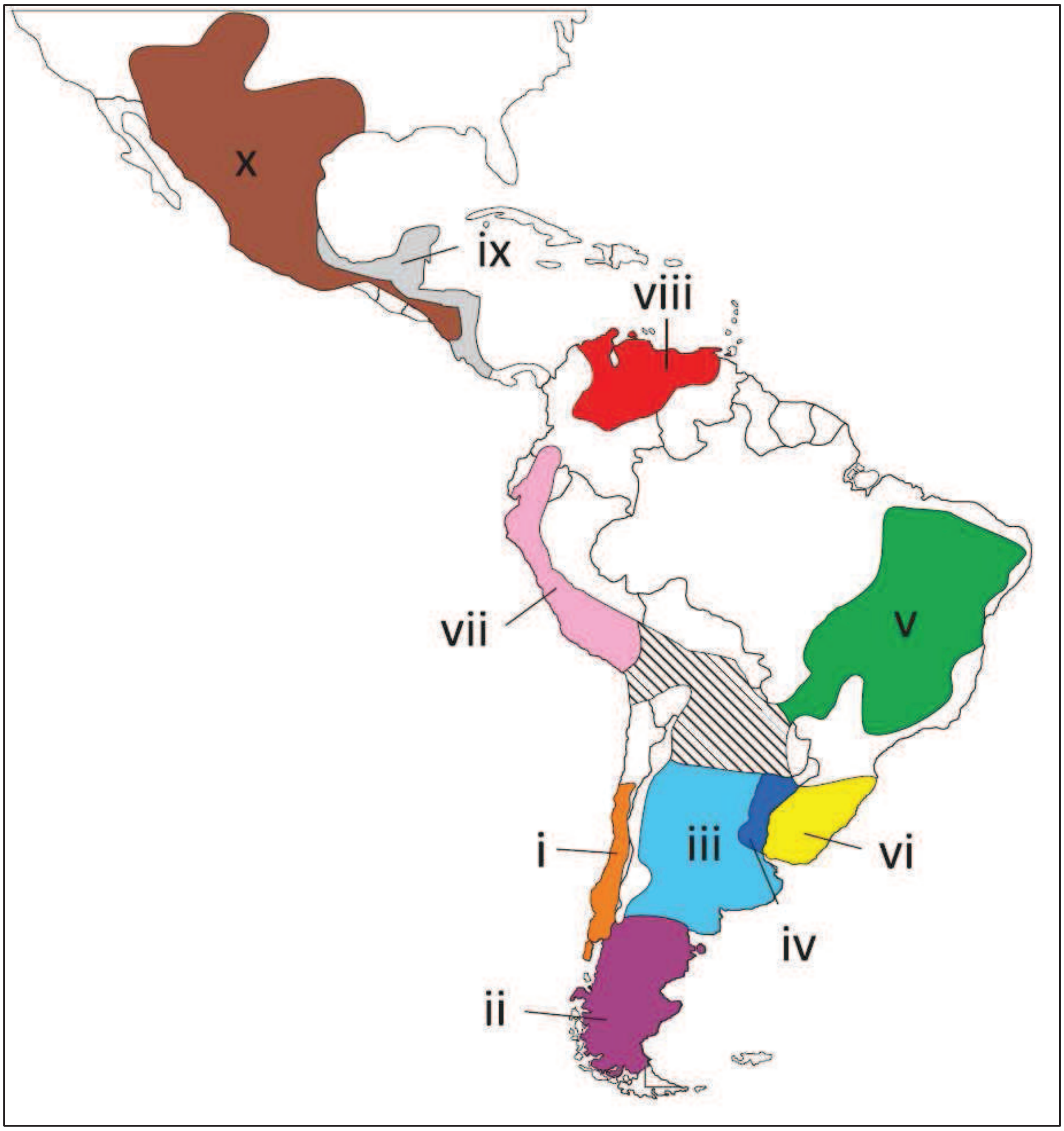

**Figure 6.** Final taxonomic proposal plotted over the genus' distributional map. Different colors indicate distinct populations that may warrant species-level recognition. Numbers refers to population identification codes listed in Table 10. The area with diagonal stripes refers to a region from which population structure information could not be generated, precluding its taxonomic assessment.

# CAPÍTULO IV – CONCLUSÕES GERAIS

O entendimento da história evolutiva e da estruturação populacional de *Conepatus* está apenas em seu início. O problema abordado por esta tese é complexo e extenso, com o agravante de ter sido pouquíssimo estudado até hoje. Como esperado, os resultados apresentados geram muitas questões adicionais, ao invés de preencher todas as lacunas existentes. Contudo, os dados gerados são bastante relevantes para o estudo de *Conepatus*, e poderão servir de base para futuras investigações complementares e revisões mais detalhadas.

Grande parte da história evolutiva do grupo permanece em aberto, mas alguns pontos começam a atingir um entendimento mais detalhado e robusto. Os resultados das análises filogenéticas e de datação realizadas neste estudo estão em concordância geral com o cenário evolutivo baseado nos registros fósseis e análises de datação publicadas anteriormente, como descrito no Capítulo 1. A estimativa de ponto para o nó *Spilogale* + *Mephitis* (5,09 MAA) é muito semelhante à da datação molecular de Eizirik *et al*. (2010), sugerindo que a coalescência destes gêneros no início do Plioceno (aproximadamente 5,2 MAA) é uma suposição robusta. Já para o nó (*Spilogale* + *Mephitis*) + *Conepatu*s a estimativa do presente estudo é um pouco mais recente (6,86 MAA) do que a de Eizirik *et al*. (2010) (9,2 MAA). Embora o intervalo de confiança de ambas as estimativas se sobreponham, a data mais recente parece estar mais de acordo com o registro fóssil conhecido até hoje. Mesmo considerando que a estimativa de Eizirik *et al*. (2010) não é mais antiga que o primeiro fóssil de Mephitidae conhecido para as Américas (*Martinogale*, 9,3 MAA), a posição filogenética de *Martinogale* parece basal e talvez até mesmo ancestral em relação aos gêneros que aparecem mais tardiamente no registro fóssil (Wang *et al*., 2005; Wang & Castañeda, 2008). Este fato sugere uma coalescência posterior a 9,3 MAA para o grupo coroa dos mefitídeos do Novo Mundo, e nesse contexto a data de aproximadamente 7 MAA encontrada pelo presente estudo parece se encaixar melhor. Outra razão para acreditar que esta estimativa pode ser mais precisa do que a de Eizirik *et al*. (2010) é a de que o presente estudo baseia-se em mais pontos internos de calibração fóssil, além de contar com uma amostragem mais completa dos grupos americanos de Mephitidae.

Já a data de invasão da América do Sul por *Conepatus* permanece em debate. A estimativa de ponto para a coalescência do gênero, considerando as amostras da América do Sul e do Norte, é de 3,18 MAA. Esta data é perfeitamente compatível com a entrada de *Conepatus* logo após o fechamento da ponte de terra, há 2,8 MA. A teoria da entrada precoce foi levantada pela descrição de um fóssil de 2,5 MA para a Argentina (*e.g.* Hunt, 1996). A idade precisa deste registro, contudo, é matéria de profundo debate entre paleontólogos, o que deixa a questão em aberto. Como discutido anteriormente, a presença do gênero na América Central desde 4,8 MAA (Wang & Castañeda, 2008) e a cobertura vegetal campestre que se estendia desde a América Central até boa parte da América do Sul no período do fechamento do istmo (Woodburne, 2010) são evidências que apoiam a hipótese de que *Conepatus* tenha estado presente na primeira onda migratória totalmente terrestre, como sugerido por Marshall *et al*. já em 1982. A datação do presente estudo se soma a estas evidências indiretas, e apesar de não ter poder para dar uma resposta definitiva sobre o tema, faz com que a teoria da colonização precoce de *Conepatus* seja corroborada.

Por outro lado, a coalescência das linhagens sul-americanas, com estimativa de ponto para 0,84 MAA, não corrobora esta teoria, apesar de também não refutá-la. É possível que, ao adicionar-se amostras de pontos mais setentrionais da distribuição do gênero, como Colômbia e Venezuela, a data desta coalescência se aproxime do ponto de fechamento do istmo e assim seja mais um elemento apontando na direção da colonização precoce. Esta é uma questão em aberto e deverá ser abordada por futuros estudos. Alternativamente, como foi debatido no Capítulo II, a data relativamente recente de coalescência dos grupos sul-americanos pode estar ligada à dinâmica complexa de avanço e recuo dos ambientes campestres na América do sul nos últimos 3 MA, afetados diretamente pelos ciclos glaciais dos últimos 2 milhões de anos (Sigman & Boyle, 2000; Pinheiro & Monteiro, 2010). Mesmo tendo colonizado a América do Sul logo após o fechamento do istmo, *Conepatus* pode ter passado por dinâmicas de extinção e recolonização dos ambientes campestres devido ao eventual encolhimento das savanas sul-americanas.

Analisando a estrutura populacional e níveis de variabilidade genética dos grupos daquele continente, o clado geográfico candidato a ter sido o centro de dispersão da atual diversidade é o da Argentina Central. Os resultados deste estudo indicam que uma das regiões colonizadas por indivíduos dessa população é a do atual Cerrado/Caatinga brasileiros. O grupo monofilético formado por todas as amostras do Brasil central está claramente colocado dentro da variabilidade do grupo argentino. Este, de fato, é um dos resultados mais importantes deste estudo, com consequências evolutivas e taxonômicas relevantes. Evolutivamente, a hipótese elegantemente levantada por Wang & Castañeda (2008) em que a América do Sul teria recebido duas ondas migratórias de *Conepatus*, uma colonizando o sul do continente e outra o centro do Brasil, é refutada pelos presentes dados. É possível que o continente sul-americano tenha recebido mais de uma onda de migrantes do gênero, mas para isso ter acontecido ela deve estar presente em alguma das populações mais setentrionais não amostradas, ou ter sido extinta. Taxonomicamente, a população que habita o Cerrado/Caatinga deve ser retirada de *C. semistriatus* e colocada em *C. chinga* ou constituir uma terceira espécie.

De maneira geral, *Conepatus* é um grupo com alto grau de estruturação geográfica, o que é um dos resultados mais interessantes e diretos deste estudo. Dada a vasta distribuição deste grupo ao longo das Américas, era esperado que descontinuidades populacionais fossem detectadas. O cenário encontrado, contudo, não deixa de ser impressionante, principalmente por se tratar de uma investigação ainda inicial, pouco refinada. No mínimo 10 unidades, com aparente significativo grau de separação, compõem este gênero, sendo nove identificadas por este estudo e uma adicional já revisada na literatura (*C. leuconotus* – Dragoo *et al*., 2003). Muitas delas foram detectadas através de mais de uma abordagem independente, seja ela morfológica ou molecular. A congruência entre as diferentes abordagens na detecção da separação de algumas das populações, associada a um padrão generalizado de estruturação encontrado pelas diferentes ferramentas, indica que o gênero apresenta um grande potencial de isolamento populacional. Foram detectados isolamentos causados pela presença de rios, montanhas e mesmo faixas de mata densa com relativamente baixa extensão. Estes resultados sugerem que estudos locais mais refinados possam encontrar ainda mais descontinuidades, o que significaria ainda outras unidades por ser descritas. Dentre os grupos de carnívoros que colonizaram a América do Sul a partir do fechamento do Istmo do Panamá, *Conepatus* parece representar a linhagem que mais se estruturou, com maior número de unidades identificadas do que os gêneros *Leopardus* (linhagem da jaguaritica – Johson *et al*., 2006) e *Lycalopex* (raposas sul-americanas – Lindblad-Toh *et al*., 2005).

Outro ponto interessante que deve ser mencionado é o de que parece haver pouca sobreposição entre os grupos identificados, isto é, na maioria dos casos é possível identificar as barreiras geográficas/vegetacionais que delimitam as populações. Ao mesmo tempo, muito ainda necessita ser investigado sobre este aspecto, já que os limites de várias populações ainda precisam ser melhor entendidos, como aqueles do grupo que ocupa o centro da Argentina. De qualquer maneira, parece claro que a descontinuidade de hábitat e a presença de rios podem ser importantes barreiras, e estudos subsequentes devem atentar para tais elementos.

Conjuntamente com a estruturação populacional e a delimitação geográfica de boa parte das unidades encontradas, foi possível verificar que diferenças morfológicas em termos de medidas gerais do corpo (*i.e.* comprimento total, comprimento da cauda, peso, etc.) são detectáveis entre algumas populações. Este resultado inicialmente serve como respaldo às infrências obtidas com as análises de estruturação mais refinadas (*i.e.* utilizando ferramentas moleculares ou o painel de 29 medidas craniométricas). Mas ao mesmo tempo, a possibilidade de detecção de diferenças populacionais através deste tipo de caracteres ganha uma nova importância, por se tratarem de medidas usualmente realizadas por pesquisadores de campo. Desta maneira, são ótimos candidatos para estudos comparativos exploratórios, o que justifica a sugestão de que, sempre que possível, pesquisadores de campo realizem e publiquem este tipo de dado.

Analisadas em conjunto, estruturação populacional, delimitação geográfica e diferenciação morfológica detectável sugerem a existência de um padrão coerente para os grupos encontrados. Apesar de estes três elementos não terem sido verificados para todas as 10 unidades, o que ressalta a necessidade de futuros estudos, pode ser notado um padrão geral que é consistente entre as diferentes populações. Todos os grupos identificados por análises detalhadas de estruturação populacional que foram posteriormente testados para existência de diferenças morfológicas gerais (*i.e.* medidas de corpo) apresentaram resultados que corroboraram a ideia de separação entre as populações. Não é possível afirmar que todas as nove unidades detectadas neste estudo apresentem padrões morfológicos gerais claramente diferenciáveis, uma vez que nem todas foram testadas para tal. Contudo, o padrão encontrado sugere que isto seja uma tendência, e assim este aspecto deve ser investigado em todas as populações para que comecem a ser melhor caracterizadas. Além disso, a união entre estes três elementos (estruturação populacional, delimitação espacial e diferenciação morfológica) indica que estes grupos apresentam plena justificativa para serem considerados ao menos Unidades Evolutivamente Significativas (UES) distintas (Eizirik, 1996; Eizirik *et al*., 2006), mas provavelmente se adequando a uma designação em nível de espécie. Neste sentido, e levando em consideração o conceito evolutivo de espécie e seus critérios associados (ver Capítulo I), na presente tese realizamos uma proposta taxonômica para o grupo, reconhecendo como espécies estas unidades evolutivas. Assim, em conjunto com a revisão já realizada por Dragoo *et al*. (2003), este estudo propõe a existência de 10 unidades taxonômicas distintas para *Conepatus*, sumarizadas na Tabela 10 e Figura 6 do Capítulo III.

A escolha por considerar cada população identificada como um táxon diferente, associada com a decisão de sugerir que todos os táxons sejam elevados ao nível de espécie, deve ser explicada, por se tratar de um potencial ponto de divergência entre os pesquisadores da área. Em primeiro lugar, cinco das nove populações foram detectadas através de mais de um método independente de investigação da estruturação geográfica (DNA mitocondrial, DNA microssatélite, morfometria do crânio ou morfologia geral): iii, iv, v, vi, e viii (ver Tabela 10, Capítulo III). Entre as quatro restantes, duas foram detectadas somente por DNA mitocondrial e duas somente pela análise craniométrica. Uma vez que os dados de microssatélites corroboraram todas as repartições encontradas através do DNA mitocondrial, pode-se prever que as populações do Chile (i e ii) estejam diferenciadas das populações Argentinas também com a análise deste tipo de marcador.

A respeito das populações detectadas apenas através das análises craniais (vii e ix), é possível verificar que os dados de distribuição geográfica corroboram a hipótese de que estejam mesmo isoladas. A população da América Central (ix) parece estar separada daquelas da América do Sul por uma vasta área de floresta densa que cobre boa parte do Panamá e o norte da Colômbia, funcionando como uma barreira. Caso esta barreira de alguma maneira não fosse efetiva, seria esperado que a população do norte da Colômbia e Venezuela (viii) fosse aquela com maior chance de fluxo e, portanto, mais crítica para se testar este isolamento. É possível perceber que as populações viii e ix não apresentam praticamente qualquer sobreposição nas análises multivariadas (por exemplo, PCA), o que indica falta de conectividade entre as duas (ou seleção diferencial afetando os caracteres analisados).

Já a população do sul da Bolívia, Equador e Peru (vii) parece estar separada das populações do sul do continente com base nos resultados das análises morfométricas. Contudo, é difícil precisar os limites desta população e uma possível barreira que a separa do centro da Argentina, uma vez que a distribuição entre estas duas áreas parece ser contínua. Este ponto merece especial atenção de futuras pesquisas. Em relação ao seu limite norte, a população vii encontra-se possivelmente disjunta da população da Venezuela e norte da Colômbia (população viii), apesar de esta descontinuidade ainda carecer de uma melhor caracterização. Ainda assim, as análises multivariadas mais uma vez demonstram a total falta de sobreposição entre as duas, sugerindo a ausência de conectividade entre as populações também nesse caso.

É importante mencionar uma sobreposição significativa nas análises multivariadas entre as populações vii e ix. Contudo, este aparente compartilhamento de caracteres morfológicos dificilmente deve ser ocasionado por fluxo gênico, devido à disposição geográfica dos dois grupos. Uma explicação plausível para este fato é uma possível retenção de diversidade ancestral nas duas populações alopátricas, com deslocamento de caracteres em uma terceira população, potencialmente simpátrica em relação às duas em algum momento da sua evolução (população viii). Assim, é possível que a população do norte da Colômbia e Venezuela tenha sofrido pressão seletiva (possivelmente aumentaram de tamanho, ver análise de PCA no Capítulo III) ao se adaptar para a exploração de um nicho distinto.

Finalmente, é preciso discutir os motivos que levaram à decisão de sugerir que todos os táxons identificados sejam elevados à categoria de espécie. A primeira razão diz respeito ao tempo de separação entre as linhagens. Através de uma análise das estimativas de datação para os diferentes grupos, presente no Capítulo II, é possível perceber que a divergência mais recente, que diz respeito à separação das populações do centro do Brasil e do centro da Argentina, ocorreu há aproximadamente 500 mil anos, enquanto a coalescência de todos os grupos é de aproximadamente 0,85 MA. Não há datas para a separação dos grupos setentrionais, uma vez que nenhuma amostra desta região foi obtida e incluída nas análises moleculares. Contudo, a forte diferenciação morfológica indica que os eventos de isolamento referentes à formação destas populações não deve ser consideravelmente mais recente. A fauna de mamíferos sul-americanos que migraram da América do Norte apresenta vários casos de separação igualmente recente entre espécies, como é o caso das raposas neotropicais (gênero *Lycalopex*). O tempo de coalescência de todas as seis espécies deste grupo (aproximadamente 1 MAA – Perini *et al*., 2010) se aproxima do tempo encontrado para as linhagens de *Conepatus* apenas da região sul do continente (0,84 milhão de anos). Outro caso próximo é a divergência entre o gato-do-mato-grande (*Leopardus geoffroyi*) e o gato-andino (*L. guigna*), de 0,74 MAA, ou mesmo da coalescência entre estas duas espécies e o gato-do-mato-pequeno (*L. tigrinus*), de 0,93 MAA (Johnson *et al*., 2006). Como esperado, o tempo de separação de várias espécies originadas pela radiação pós-invasão da América do Sul é recente, e não deve ser um impeditivo para que sejam tratadas como tal. Assim, o tempo de divergência parece não ser um impeditivo para que os táxons de *Conepatus* identificados sejam elevados à categoria de espécie.

Um segundo e importante motivo para esta sugestão diz respeito à necessidade urgente de uma organização taxonômica moderna para *Conepatus*. Como ficou evidente a partir das análises filogenéticas, o grupo apresenta uma história recente e complexa. Os grupos geográficos identificados apresentam alto valor de apoio estatístico, mas sua organização hierárquica ainda tem baixa resolução. A resolução deste aspecto possivelmente irá requerer uma abordagem multi-loco, talvez com o emprego de sequenciamento de DNA de nova geração (Shendure & Ji, 2008), envolvendo vários indivíduos de cada população. Além disso, irá requerer uma amostragem ampla, envolvendo regiões onde o estudo dos mamíferos em campo ainda é precário. A organização e execução de tal desenho amostral demandará um esforço enorme, e possivelmente não poderá ser completamente realizada dentro de poucos anos. Enquanto isso, novos pesquisadores que desejem descrever populações locais precisarão de nomes adequados e de um entendimento da estruturação geográfica mais preciso do que o que está dsiponível atualmente. Adicionalmente, a aparente propensão do gênero ao isolamento reprodutivo (inferido a partir dos dados genéticos) e diferenciação geográfica provavelmente fará com que unidades adicionais sejam encontradas assim que cada uma das grandes populações regionais comece a ser analisada em maior detalhe. Diante do arranjo proposto por este estudo, tais subgrupos poderiam ser descritos como subespécies.

Caso a estratégia oposta fosse adotada, optando-se por um arranjo em que os táxons aqui descritos fossem considerados subespécies dentro de uma espécie mais ampla (*e.g.* manter os grupos do Chile, Argentina, Uruguai e Rio Grande do Sul sob *C. chinga*), eventuais subdivisões a serem identificadas não poderiam ser nomeadas taxonomicamente com base nos procedimentos usuais, pois seriam sub-subespécies. Tal arranjo reduziria muito o poder organizacional da taxonomia do grupo, que afinal é a finalidade primordial da taxonomia como disciplina. Problemas adicionais, apesar de menos importantes, seriam a possível confusão gerada em coleções e estudos já publicados a respeito. Este seria o caso, por exemplo, de se considerar a população do Brasil central como parte de *C. chinga*, uma vez que já existe uma população classicamente chamada por este nome no sul do país. Chamar *C. humboldtii* de *C. chinga humboldtii* provavelmente também geraria muita confusão na literatura e em coleções científicas.

Dessa maneira, o arranjo taxonômico baseado em espécies distintas é mais simples, prontamente aplicável, menos sujeito a alterações por rearranjos filogenéticos de estudos futuros, e apresenta menor potencial de ocasionar confusões com os nomes classicamente atribuídos a várias populações. Adicionalmente, a elevação de populações locais ao nível de espécie, como a do próprio Rio Grande do Sul-Uruguai, possivelmente daria aos pesquisadores locais um maior incentivo para que tenham mais interesse em melhor caracterizá-las. Dessa maneira, o próprio estudo da evolução de *Conepatus* seria estimulado, permitindo que entendamos melhor a história não só do gênero como do Intercâmbio Americano de Fauna e dos campos sul-americanos. Obviamente, o arranjo aqui proposto deve ser encarado como um ponto de partida para novos e inúmeros estudos que critiquem, corroborem ou refutem as hipóteses taxonômicas e evolutivas aqui sugeridas, visto que vários aspectos foram apenas inicialmente caracterizados. Um dos pontos de maior urgência é o estudo das populações de Bolívia, Paraguai e norte da Argentina, caracterizando seus indivíduos e possíveis continuidades com outras populações. Além disso, esta é uma população central, sendo adjacente aos grupos do Chile, Peru, Argentina e Cerrado brasileiro, o que torna seu entendimento e delimitação importantes para a melhor caracterização de todas as populações mencionadas.

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# ANEXO I: NORMAS PARA SUBMISSÃO DE ARTIGOS CIENTÍFICOS AO PERIÓDICO *JOURNAL OF HEREDITY*

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Gould SJ. 1989. *Wonderful life: the Burgess Shale and the nature of history*. New York: W.W. Norton.

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# ANEXO III

**Artigo Científico**

## Recent advances in the knowledge of Molina's Hog-nosed Skunk Conepatus chinga and Striped Hog-nosed Skunk C. semistriatus in South America

Carlos Benhur Kasper, **Manoel L. da Fontoura-Rodrigues**, Gitana Nunes Cavalcanti, Thales Renato O. de Freitas, Flávio H. G. Rodrigues, Tadeu Gomes de Oliveira, **Eduardo Eizirik**

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# Recent advances in the knowledge of Molina's Hog-nosed Skunk *Conepatus chinga* and Striped Hog-nosed Skunk *C. semistriatus* in South America

Carlos Benhur KASPER[1], Manoel L. da FONTOURA-RODRIGUES[2], Gitana Nunes CAVALCANTI[3], Thales Renato O. de FREITAS[1], Flávio H. G. RODGRIGUES[3,5] Tadeu Gomes de OLIVEIRA[4,5] and Eduardo EIZIRIK[2,5]

## Abstract

Biological knowledge of South American hog-nosed skunks *Conepatus* remains scarce. Although common in several regions, even basic life-history aspects are poorly known, and important issues of taxonomy and biogeography are yet to be resolved. A better understanding of these species' evolutionary history, biology and ecology would provide a solid basis for conservation planning. Here we provide an overview of current research efforts targeting these issues in Molina's Hog-nosed Skunk *Conepatus chinga* and Striped Hog-nosed Skunk *C. semistriatus*. Preliminary data corroborating these species' evolutionary distinctiveness, and concerning distribution, habitat use, food habits, spatial ecology, life history, and reproductive biology are provided. We hope that these will serve as a basis for in-depth studies targeting these species and the role they play in Neotropical carnivore communities.

*Keywords:* conservation planning, distribution, ecology, life history, morphology, reproductive biology, taxonomy

## Avances recientes en el conocimiento sobre *Conepatus chinga* y *C. semistriatus* en Suramérica

## Resumen

El conocimiento biológico sobre las mofetas de Suramérica aún permanece escaso. A pesar de ser comunes en muchas regiones, aún se conoce muy poco, incluso de aspectos básicos de su historia natural, y asuntos importantes todavía necesitan ser resueltos con respecto a su taxonomía y biogeografía. Por esta razón existe una necesidad urgente de llenar estos vacios y de tener un mejor entendimiento de la historia evolutiva, biología y ecología de estas especies, con el fin de proveer una base sólida para la planificación de su conservación. Aquí proveemos un vistazo a los esfuerzos de investigación actuales enfocados a estos aspectos relacionados con *Conepatus chinga* y *C. semistriatus*. Reportamos datos preliminares corroborando la distinción evolutiva entre estas dos especies y proveemos algunos datos sobre su distribución, uso de hábitat, hábitos alimenticios, ecología espacial y biología reproductiva. Esperamos que estos esfuerzos puedan servir como base para estudios más profundos enfocados en estas especies y en el rol que juegan en las comunidades de carnívoros neotropicales.

*Palabras clave*: biología reproductiva, distribución, ecología, historia de vida, morfología, planificación para conservación, taxonomía

## Introduction

The family Mephitidae (skunks) comprises four genera, of which three occur exclusively in America: *Mephitis*, *Spilogale* and *Conepatus*. *Conepatus* (the hog-nosed skunks) is the only genus with species in both North (American Hog-nosed Skunk *C. leuconotus* and Striped Hog-nosed Skunk *C. semistriatus*) and South America (Molina's Hog-nosed Skunk *C. chinga*, *C. semistriatus* and Humboldt's Hog-nosed Skunk C. *humboldtii*); *Mephitis* and *Spilogale* occur exclusively in North America (Nowak 1999, Wozencraft 2005). In contrast to these two latter genera, *Conepatus* has received little attention from researchers, especially for the three South American species. In the last few years, our research group initiated studies concerning basic behaviour, distribution and ecology of *C. chinga* (Fig. 1) and *C. semistriatus* in Brazil. Molecular approaches are being employed to clarify taxonomy, biogeography and evolutionary history of the genus. Here we report first results of these ongoing efforts and project the future steps.

## Distribution, habitat use and taxonomy

One basic aspect is the geographic range of the two species. According to Redford & Eisenberg (1992) and Eisenberg & Redford (1999), *C. chinga* occurs from the northern region of Argentina to Uruguay, southern Bolivia, western Paraguay and central Chile. Recently, Cheida *et al.* (2006) and Cáceres (2004) reported it from the southern limits of Brazil to the Paraná (PR) and São Paulo (SP) states. However, records in the latter two states are rare, despite the fact that this region is one of the most studied in Brazil. Conspicuous, confirmed occurrence of *C. chinga* in Brazil is restricted to its southernmost states, Rio Grande do Sul (RS) and Santa Catarina (SC). The species's distribution in this region seems discontinuous, associated with two grassland regions historically separated by a broad patch of Atlantic Forest: the Brazilian Pampa in the southern part of RS and the Campos de Altitude region in Southern SC and northern RS. In sum, the species's occurrence seems strongly associated with Pampa and Chaco biomes, both characterised by open vegetation, cold temperatures and well-defined climatic seasons.

Use of forest areas by *C. chinga* is reported by Cáceres (2004) and Cheida *et al.* (2006) but is controversial. Cáceres (2004) suggested that its range is continuous along the mountains of the Serra do Mar, covered by dense Atlantic Forest. However, the record reported by Cáceres (2004), and many of our own records, suggest restriction to forest borders and to the *Araucaria* Forest, habitats

*Fig. 1. Hog-nosed Skunks; on the left:* Conepatus chinga *(Photo: Benhur Kasper), on the right:* C. semistriatus *(Photo: Jan Schipper).*

associated with grassland environments. In addition, it is possible that current fragmentation within forested regions is allowing the species's range to expand, a process also observed in species such as the Maned Wolf *Chrysocyon brachyurus* (R. de Paula verbally 2009). Thus, our view is that *C. chinga* is a grassland-dweller, not adapted to forested areas that may even bar its dispersal.

Regarding *C. semistriatus*, Eisenberg (1989) and Eisenberg & Redford (1999) suggested a geographic range from Mexico to northern Colombia, northern Venezuela, Peru and northeastern Brazil. Regarding this latter country, Cheida *et al.* (2006) extended the species's distribution to SP and also reported occurrence in the Cerrado (central Brazil) and Caatinga (northeastern Brazil) biomes. In agreement, our own records include the states of Maranhão, Goiás, Minas Gerais, São Paulo, Piauí, Bahia and Distrito Federal, all of which encompass a large portion of the Cerrado and/or Caatinga biomes, where the species seems relatively abundant. As reported by Cheida *et al.* (2006), the species does not seem to use forested areas, although some individuals could use densely covered sites as refuges, mainly in the dry season (Ferreira 2008). Some records point to use of Cerrado patches inside the Amazonian Forest and to transitional regions between the Cerrado and the Atlantic Forest, where open vegetation areas can be found.

Therefore, extensive forests probably constitute a barrier for *C. semistriatus* as well, raising the hypothesis that *C. semistriatus* and *C. chinga* populations could have been historically isolated by the broad extension of Atlantic Forest that covers most of the land between the Cerrado and the grassland environments of RS and SC states. This may also be so for other open-environment carnivores, such as Pampas Fox *Lycalopex gymnocercus* (RS and SC grasslands) and Hoary Fox *L. vetulus* (Cerrado).

However, uncertainties concerning the total geographic and reproductive isolation between *C. chinga* and *C. semistriatus* still persist. It is still uncertain which species has been recorded in SP state. Furthermore, the distribution limits of *C. semistriatus* in Brazil are also unclear. As *C. chinga* is thought to occur in the southern region of Bolivia and Paraguay, the possibility of additional contact zones cannot be discarded. Consequently, there may be some sympatry and gene flow between these two recognised species. Indeed, taxonomic delimitation within this genus has few systematic studies to confirm the traditionally described species (Cabrera 1958, Kipp 1965, Wozencraft 2005). A recent phylogenetic overview showed that two North American *Conepatus* species previously recognised through morphology (*C. leuconotus* and *C. mesoleucus*) actually comprise a single species (Dragoo *et al.* 2003). Similar taxonomic confusion could be involved with other species in the genus and should be investigated.

To elucidate these issues, we are initiating phylogenetic and phylogeographic studies based on molecular data. Our preliminary results, employing nucleotide sequences spanning about 550 base pairs (bp) of the mitochondrial DNA *NADH dehydrogenase 5* (*ND5*) gene from *Conepatus* individuals sampled in the grassland environments of RS and SC states, and also from three different points in the Cerrado, corroborate the recognition of two taxonomic entities. One clade, corresponding to *C. chinga*, seems to be restricted to the RS and SC grassland domains, while another, corresponding to *C. semistriatus*, was sampled only in the Cerrado field sites. The genetic distance between these two groups indicates that they diverged at least one million years ago. Additional genetic markers and more individuals have to be added to this survey to confirm the two clades and date their evolutionary divergence more precisely. Also, we aim to identify the limits of occurrence of both species and to investigate the possibility of any degree of gene flow, which is most likely in potential zones of sympatry. Furthermore, a broader taxonomic investigation of all *Conepatus* species, aiming to identify the number of valid taxa and to shed light on their evolution and phylogenetic relationships, is also of great interest for the design of adequate conservation strategies for this group, and may soon be feasible. For example, the validity of *C. humboldtii* demands investigation: there are no apparent ecological barriers between its range (Patagonian grasslands) and that of *C. chinga*.

## Ecology

There is currently very little information on the ecology of South American skunks. *Conepatus* is a specialised feeder of arthropods, mainly insects on the vegetation and within the soil (Redford & Eisenberg 1992). It is also an opportunistic predator, of small vertebrates and at carcasses of larger animals (Travaini *et al.* 1998, Donadio *et al.* 2004). Our field observations show that the foraging strategies of *C. chinga* and *C. semistriatus* mainly involve an active search for large insects such as beetles and larvae that live underground, digging the soil throughout almost their entire activity period. In some areas the consumption of vertebrates can be very important, as we observed for *C. chinga* in southeastern Brazil, where we have records of individuals feeding on fish (these being the first records of this item in their diets), amphibians, and eggs of both freshwater turtles and ground birds. Ingestion of eggs seems very frequent, with many turtle nests presenting characteristic signs of Molina's Hog-Nosed Skunk predation. In agreement, Gonçalves *et al.* (2007) noted that *C. chinga* is an important predator of nests of the turtle *Trachemys dorbigni* in southern Brazil. Regarding *C. semistriatus*, in addition to the high consumption of invertebrates (mainly beetles), some vertebrates have been recorded as being part of its diet as well. One individual was reported to feed on a dead bird, after attacking an owl nest. Silveira (1999) also reported the consumption of rodents and toads *Bufo* in the same region of the Cerrado.

Behavioural studies of both species are scarce. Rodrigues & Auricchio (1994) described *C. semistriatus* as solitary and non-territorial, with many individuals living in the same area, and males and females appearing together only in the breeding season. Data from a capture effort in Bahia state (Brazil) support these observations, with many individuals caught in a small area, where they seemed to have resting dens. Also, two individuals were caught at one time, in one trap. Behavioural observations of *C. chinga* are also very few, but nest sharing seems to be rare.

Concerning abundance estimates of *C. chinga*, there are two distinct patterns in the two different environments occupied in Brazil. In the Pampas it is among the most common carnivores, preliminary data showing 1.5 individuals/km². Conversely, *C. chinga* in the Campos de Altitude region seems to be very sparse: 280 km of line transects yielded only one sighting, and a 450 trap-night effort only one capture. It is not clear which factors cause this extreme variation in abundance, but they may relate to food availability and/or climate. Although *C. semistriatus* seems relatively abundant in Cerrado and Caatinga, there are no precise abundance estimates.

Other issues being studied are the spatial structure of home ranges and the activity patterns of *C. chinga*. The first survey found a home range of 1.9 km², shared by a male and a female, in Argentina (Donadio *et al.* 2001). Similarly, our preliminary observations indicate a mean home range of 1.9 km² (0.8 to 2.45 km²) for four males, with females showing much smaller home ranges (mean 0.8 km², range 0.3 to 1.2 km²), as measured for three individuals. The home ranges observed for *C. chinga* are much larger than those estimated for *C. humboldtii* (0.074–0.16 km²; Fuller *et al.* 1987) and *C. semistriatus* (0.18–0.53 km²; Sunquist *et al.* 1989), although caution should be taken in comparisons due to the limited number of sample individuals so far. More detailed survey might drastically change these preliminary results, especially for *C. semistriatus*, because it is larger than *C. chinga* and could plausibly use a larger home range.

Concerning activity patterns, as reported by Donadio *et al.* (2001), *C. chinga* in southern Brazil is almost exclusively nocturnal. Our first data indicate that it leaves its resting site about 30 minutes before sunset, remaining active until approximately 30 minutes before sunrise. At night, the activity is almost continuous, with few resting moments. Daytime activity is negligible, generally involving sleeping all day in resting or den sites. In the same study, Donadio *et al*. (2001) cited use of burrows as cover, each generally reused a few times. Our observations identified 14 types of resting sites, divided into four larger groups: burrows in the soil; under trunks and branches; within vegetation; and inside human-made structures. It seems to use several types of cover present in its home range, with different degrees of reuse. Further, each individual seems to use a central area, with several resting sites around it. The reuse of some resting sites may be intense, especially in the breeding season, when we recorded use of the same den for more than a month. Observations on the activity patterns on *C. semistriatus* in Mesoamerica are reported by González-Maya *et al.* (2009).

The proximity of hog-nosed skunks to houses or other human-made structures, along with high tolerance of people and domestic animals, seems strongly to affect their mortality rate. In our telemetry study focusing on *C. chinga*, of seven monitored individuals with home ranges near human dwellings, six died through human activity within six months of capture. Although usually not directly hunted or persecuted by farmers or other local people, the species is often killed by vehicles on roads and also by hunting dogs. In some roads of southernmost RS, *C. chinga* is one of the most frequent road-killed carnivores (F. Mazim verbally 2009). A similar situation may occur with *C. semistriatus*, which also seems to occupy human-modified landscapes and tolerates areas near town centres. The major observed threat is the high number of individuals killed on roads throughout the species's distribution. These data suggest that the species are very abundant in these areas; the impact of such mortality on populations is unknown.

Our observations indicate that *C. chinga* does not avoid the proximity of domestic dogs, nor of native wild canids such as Crab-eating Fox *Cerdocyon thous* and Pampas Fox. There is mortality from domestic dog attacks, but this overall proximity suggests no history of strong intraguild predation between these skunks and canids. This observation seems also to fit *C. semistriatus*, which may live near Crab-eating Fox and Maned Wolf, occasionally even chasing them off.

## Biology

Our *C. chinga* studies are also shedding some light on aspects of its biology and natural history. During capture for placement of radio-collars, we recorded morphometric data including body mass. In one studied population in southern Brazil there were significant differences between males and females in mean total length (58.8 cm for males and 55.3 cm for females) and mean body mass (2.26 kg and 1.58 kg), giving a remarkable sexual difference of 43%. Van Gerdal's (1968, *apud* Redford & Eisenberg 1992) assertion of sexual size dimorphism in Molina's Hog-nosed Skunk in Uruguay is therefore corroborated by our data.

Regarding reproduction of *C. chinga*, we recorded six litters, ranging from two to three pups (mean, 2.5). The reproductive period of *C. chinga* seems related to climatic seasons. Several matings were recorded in late winter and early spring (July–October), when we also found road-killed individuals carrying foetuses. In our telemetry survey, two females were observed with pups in the spring and early summer (October–January); one seemed to have given birth in September, being always seen with its pups until February, when the pups were no longer observed. In the summer (January and February), there were many observations of young individuals, apparently dispersing or searching for territories. Thus, we believe that birthing coincides with the beginning of the spring, and that the juveniles disperse in summer, after living 4–5 months with their mothers. There are still no such data for *C. semi-*

*striatus*, but our ongoing field efforts are also designed to address issues of this species's biology.

## Conclusions

Considering information from literature and our first surveys, we can recognise that *C. chinga* and *C. semistriatus* are: (i) two separate species—genetically and morphologically distinct and apparently occurring in two different (and perhaps isolated) habitats: Cerrado (*C. semistriatus*) and Pampa/Chaco (*C. chinga*); (ii) closely associated with grassland habitats; (iii) feeders mainly on insects, but also opportunistically on small vertebrates, larger carcasses and vertebrate eggs; (iv) nocturnal, solitary, with an apparently defined breeding season associated with warmer weather (early spring), and showing some degree of parental care (pups spend 4–5 months with their mothers) prior to juvenile dispersal; and (v) tolerant of human disturbance, although this is a major cause of mortality.

All these studies and field observations are in a very initial phase, and some current impressions may need to be re-evaluated as we gather more data. Moreover, it is also clear that these are very poorly known species, still requiring many studies to refine current understanding of ecology, behaviour, evolution and taxonomy. We hope that our ongoing efforts will enhance understanding of the biology of *Conepatus*, allowing design and implementation of effective conservation strategies.

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