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FERNANDO HEBERSON MENEZES LIMA

**SISTEMÁTICA DOS PORCOS-ESPINHOS DO GÊNERO *COENDOU* LACÉPÈDE,
1799 (RODENTIA: ERETHIZONTIDAE)**

FORTALEZA

2023

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(RODENTIA: ERETHIZONTIDAE)

Tese apresentada ao Programa de Pós-Graduação em Sistemática, Uso e Conservação da Biodiversidade, da Universidade Federal do Ceará como requisito parcial para a obtenção do título de doutor. Área de concentração: Taxonomia, Sistemática e Evolução Biológica.

Orientador: Dr. Itayguara Ribeiro da Costa
Coorientador: Dr. Pedro Cordeiro Estrela de Andrade Pinto

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BANCA EXAMINADORA

Prof. Dr. Itayguara Ribeiro da Costa (Orientador)
Universidade Federal do Ceará

Prof. Dr. Pedro Cordeiro Estrela de Andrade Pinto (Coorientador)
Universidade Federal da Paraíba

Prof. Dr. Vicente Vieira Faria (Interno)
Universidade Federal do Ceará

Prof. Dra. Thais Kubik Martins (Externo)
Universidade Federal do Ceará

Dr. Aldo Caccavo de Araujo (Externo)
Museu Nacional da Universidade Federal do Rio de Janeiro

Prof. Dr. José Anderson Feijó da Silva (Externo)
Institute of Zoology, Chinese Academy of Sciences

Prof. Dr. Hugo Fernandes-Ferreira (Suplente interno)
Universidade Estadual do Ceará

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RESUMO

Os porcos-espinhos do novo mundo são roedores de médio porte da família Erethizontidae, que é dividida em três gêneros, *Chaetomys*, *Erethizon* e *Coendou*, em 18 espécies, cuja maioria está em *Coendou*, sendo os gêneros *Chaetomys* e *Erethizon* monoespecíficos. Os porcos-espinhos do gênero *Coendou* possuem hábitos noturnos, arbóreos e folívoros que os tornam de difícil coleta, limitando a quantidade de informação disponível em coleções científicas e para análises genéticas. Assim, informações sobre variação morfológica, distribuição e biologia dos porcos-espinhos são confusas e incompletas, em especial de espécies amazônicas. Consequentemente, há uma carência de material de qualidade como referência para identificação das espécies do grupo, concomitando em um histórico taxonômico confuso. Tradicionalmente, o gênero *Coendou* é dividido em dois subgêneros, *Coendou* e *Sphiggurus*, contudo, até então, não havia concordância a respeito de quais seriam os caracteres diagnósticos. Análises filogenéticas e revisões taxonômicas pretéritas descreveram duas novas espécies de *Coendou* e apontaram que os caracteres diagnósticos descritos para esses subgêneros são homoplásicos, tornando *Coendou* e *Sphiggurus* polifilético e parafilético, respectivamente. Pela sistemática integrativa, aqui descrevemos um terceiro subgênero, nomeado de *Caaporamys*, e novos caracteres diagnósticos para os existentes, solucionando a classificação subgenérica do grupo. Adicionalmente, as espécies do complexo *Coendou prehensilis* foram delimitadas, sendo três espécies: *C. prehensilis*, *C. longicaudatus* e *C. baturitensis*, que são espécies de distribuição alopátrica e podem ser diagnosticadas pelos espinhos e caracteres cranianos. Por fim, *Coendou roosmalenorum* teve a sua posição filogenética e distribuição definidos, sendo uma espécie do subgênero *Caaporamys* com ocorrência restrita à província Madeira.

Palavras-chave: taxonomia; espinhos; distribuição; filogenia.

ABSTRACT

The new world porcupines are medium sized rodents of the Erethizontidae family, which is divided into three genera, *Chaetomys*, *Erethizon* and *Coendou*, with and 18 species. *Chaetomys* and *Erethizon* are monospecific and almost all species are in the genus *Coendou*. The porcupines are hard to record and capture due their arboreal, nocturnal, and florivorous habits, which restricts the amount of information available in scientific collections and genetic samples. In this way, information on morphological variation, distribution and biology of porcupines are messy and incomplete, mainly in Amazonian species. Consequently, it lacks quality samples as identification references of the porcupine species, resulting in a chaotic taxonomical history. Traditionally, the genus *Coendou* is divided in two subgenera, *Coendou* and *Sphiggurus*, although, there is no concordance about the diagnostic characters. Previous phylogenetic analyses and taxonomic assessments described new species and suggested the diagnostic characters of both subgenera are homoplasies. As a result, the interpretation that *Coendou* and *Sphiggurus* are, respectively, polyphyletic, and paraphyletic. Here, through an integrative systematic approach, we described a third subgenus, named *Caaporamys*, and new diagnostic characters for the subgeneric classification. Therefore, the subgeneric classification of the genus *Coendou* is solved. Additionally, the species of *Coendou prehensilis* complex were delimited: *Coendou prehensilis*, *Coendou longicaudatus* and *Coendou baturitensis*. The species are allopatric and can be identified through quills and cranial traits. Finally, *Coendou rosmalenorum* has its phylogenetics position and distribution investigated, confirming its position as a *Caaporamys* species distributed in Madeira Province.

Keywords: taxonomy; quills; distribution; phylogeny.

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1 INTRODUÇÃO GERAL

Os porcos-espinhos neotropicais, roedores caviomorfos da família Erethizontidae, são herbívoros noturnos de hábitos arborícolas de tamanho médio (de um a 10kg), caracterizados pela presença de pelos modificados em espinhos, cauda preênsil dorsalmente, pólex ausentes e hálux reduzidos (EISENBERG; REDFORD, 1999; ELLERMAN, 1940; EMMONS, 1997; VOSS, 2015). São comumente chamados de ouriço-caixeiro, luís-caixeiro, cuandu ou porco-espinho. A família Erethizontidae é composta por três gêneros e 17 espécies com ocorrência do Sul do Canadá ao Norte da Argentina (FEIJÓ; LANGGUTH, 2013; VOSS, 2015).

No Brasil, até então, são reconhecidas 10 espécies de eretizontídeos: *Coendou prehensilis* (LINNAEUS, 1758), *C. baturitensis* (FEIJÓ; LANGGUTH, 2013), *C. bicolor* (TSCHUDI, 1844), *C. nycthemera* (OLFERS, 1818), *C. speratus* (MENDES-PONTES *et al.*, 2013), *C. insidiosus* (OLFERS, 1818), *C. spinosus* (CUVIER, 1823), *C. melanurus* (WAGNER, 1842), *C. roosmalenorum* (VOSS; SILVA), 2001 e *Chaetomys subspinosus* (OLFERS, 1818) (FEIJÓ; LANGGUTH, 2013; FREITAS; FRANÇA; VERÍSSIMO, 2013; VOSS, 2015).

Quanto à sistemática, a biologia e os limites de distribuição das espécies de porcos-espinhos são pouco conhecidos, devido aos seus hábitos arborícolas, noturnos e por não caírem em armadilhas comumente utilizadas em inventários de mamíferos terrestres não-voadores (EMMONS, 1997). Dessa forma, algumas espécies carecem de estudos sobre distribuição e história natural, como o *C. roosmalenorum*, que foi descrito em 2001 e sem nenhum estudo subsequente. Por outro lado, espécies são descritas por um material obtido de forma oportunista, quando se encontra um espécime morto, como ocorreu com o *C. baturitensis* (FEIJÓ; LANGGUTH, 2013) ou quando um estudo foca especificamente nos porcos-espinhos, como no caso de *C. speratus* (MENDES PONTES *et al.*, 2013). Naturalmente, a dificuldade de coleta de espécimes de porco-espinho resulta em escassez de material de qualidade em coleções científicas, dessa forma, há pouco material de referência para estudos taxonômicos com o grupo.

A família Erethizontidae era dividida tradicionalmente em cinco gêneros: *Chaetomys* Gray, 1843, *Erethizon* F. Cuvier, 1823, *Echinoprocta* Gray, 1865, *Sphiggurus* F. Cuvier, 1825 e *Coendou* Lacépède, 1799 (WOODS; KILPATRICK, 2005). Os três últimos estavam envolvidos em divergências sobre as suas validades e as suas delimitações (BONVICINO; PENNA-FIRME; BRAGGIO, 2002; EMMONS, 1997; HANDLEY; PINE, 1992; VOSS; HUBBARD; JANSA, 2013; VOSS, 2011). Alguns autores consideram

Sphiggurus e *Echinoprocta* como sinônimos de *Coendou* (ELLERMAN, 1940; HANDLEY; PINE, 1992; MCKENNA; BELL, 1997; VOSS; SILVA, 2001; VOSS; HUBBARD; JANSÁ, 2013; VOSS, 2011). Handley e Pine (1992) argumentam que não existem caracteres morfológicos marcantes para distinguir *Sphiggurus* e *Coendou*. Posteriormente, Voss *et al.* (2013), pela análise de filogenia molecular baseada em sequências do gene mitocondrial do citocromo b da maioria das espécies do gênero, demonstraram que os caracteres anteriormente considerados como diagnósticos de *Coendou*, surgiram de forma independente sendo identificados como homoplasias. Portanto, *Sphiggurus* é um agrupamento parafilético, *Coendou* um grupo polifilético e *Echinoprocta* como apenas um morfótipo de *Coendou* de cauda curta, corroborando com Handley e Pine (1992). Devido à prioridade taxonômica do nome mais antigo, *Sphiggurus* e *Echinoprocta* passam a ser sinônimos de *Coendou*. Todavia, os autores não apresentaram caracteres morfológicos diagnósticos para os três grupos encontrados na análise de máxima parcimônia e verossimilhança.

Ficou claro nas análises de Voss *et al.* (2013) que a homoplasia em caracteres morfológicos foi uma das principais fontes de impasse taxonômico. A compreensão dos padrões de homoplasia em caracteres morfológicos é um tema teórico fundamental para a sistemática (GAUBERT *et al.*, 2005), mas também para a compreensão das modalidades de evolução de caracteres morfológicos. Ao contrário de caracteres moleculares que possuem modelos de evolução conhecidos que permitem estimar estatisticamente a homoplasia esperada, os modelos de evolução para caracteres morfológicos são muito simples, quando comparados com os padrões previstos de evolução morfológica (LEWIS, 2001) limitando a capacidade de estimar a homoplasia morfológica. A pelagem é um dos caracteres mais importantes para a taxonomia clássica de *Coendou* e deveria ser objeto de uma análise evolutiva para entender a sua plasticidade e como ser utilizada, de forma quantitativa, para estudos sistemáticos do gênero.

Dentro desse contexto, este trabalho tem como objetivos:

- a) Delimitar as espécies de porcos-espinhos do gênero *Coendou* por uma abordagem integrativa, testando-as com evidências morfológicas, morfométricas, moleculares e biogeográficas;
- b) Estimar as relações de parentescos entre as espécies do grupo, por dados moleculares e morfológicos;
- c) Identificar caracteres diagnósticos para a classificação quanto ao nível de espécie e de subgênero;
- d) Reavaliar a distribuição de espécies de *Coendou*.

2 Capítulo 1: Major range extensions for three species of porcupines (Rodentia: Erethizontidae: *Coendou*) from the Brazilian Amazon

Fernando Heberon Menezes, Guilherme Siniciato Terra Garbino, Thiago Borges Fernandes Semedo, Mendelson Lima, Anderson Feijó, Pedro Cordeiro-Estrela, Itayguara Ribeiro da Costa

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Abstract:

We report range extensions for three species of Amazonian erethizontids, *Coendou bicolor*, *C. ichillus*, and *C. nycthemera*. We record *C. ichillus* for the first time in Brazil, from Rio Japurá, state of Amazonas. We record *C. bicolor* for the first time in the state of Amazonas, which represents a range extension of approximately 905 km. We also extend the occurrence of *C. nycthemera* 620 km to the south into Mato Grosso state. All records are based on museum specimens, highlighting the importance of scientific collections as biodiversity databases, and emphasizing the lack of research on Amazonian porcupines.

Keywords:

Coendou bicolor; *Coendou ichillus*; *Coendou nycthemera*; museum specimens; new record

Resumo:

Aqui nós relatamos ampliação de distribuição de três espécies de eretizontídeos amazônicos: *Coendou bicolor*, *C. ichillus* e *C. nycthemera*. Nós registramos pela primeira vez *C. ichillus* no Brasil, no Rio Japurá, estado do Amazonas. Registramos *C. bicolor* pela primeira vez no estado Amazonas, o que representa uma ampliação de distribuição de aproximadamente 905 km. Também estendemos a ocorrência de *C. nycthemera* 620 km ao sul, no estado de Mato Grosso. Todos os registros são baseados em espécimes de museu, enfatizando a importância das coleções científicas como bancos de dados da biodiversidade e a destacando ausência de pesquisas para porcos-espinhos amazônicos.

Palavras-chave:

Coendou bicolor; *Coendou ichillus*; *Coendou nycthemera*; espécime de museu; novo registro

2.1 Introduction

New World porcupines from the family Erethizontidae, are nocturnal and arboreal rodents with hairs modified into sharpened quills and prehensile tails (Emmons 1997). Erethizontids are distributed from Canada to Uruguay and Argentina (Emmons 1997, Voss 2015). There are 17 species recognized in the family Erethizontidae of which 15 belong to genus *Coendou* Lacépède, 1799 (Voss 2015, Feijó & Langguth 2013, Mendes Pontes et al. 2013). Brazil is the country with the highest diversity of erethizontids, which includes the Atlantic forest endemic *Chaetomys subspinosus* and nine species of *Coendou*, of which five are endemic to the country, i.e., *C. nycthemera*, *C. insidiosus*, *C. roosmalenorum*, *C. baturitensis* and *C. speratus* (Feijó & Langguth 2013, Voss 2015, Mendes Pontes et al. 2013, de Freitas et al. 2013).

As cryptic animals, rarely observed in the wild and underrepresented in collections, there are several gaps in the knowledge about the distribution of most of the porcupine species (Leite et al. 2011, Voss et al. 2013, Feijó & Langguth 2013, Mendes Pontes et al. 2013). The records are limited to a small number of specimens (e.g. *Coendou melanurus* as pointed by Voss et al. 2001) or biased towards the surroundings of urban centres and river margins (see maps 405-417 in Voss 2015). Several new distributional records of porcupine species were made recently: *Coendou bicolor* (Wagner 1842) had new records from Brazil (de Freitas et al.

2013) and a possible record for Colombia (Ramírez-Chaves et al. 2016), *Coendou speratus* Mendes Pontes et al. 2013 had a distributional gap filled in northeastern Brazil (Nascimento & dos Santos 2014), *Coendou ichillus* Voss & da Silva 2001 had new records from Peru (Gregory et al. 2015) and Colombia (Ramírez-Chaves et al. 2016), and *Coendou rufescens* (Gray, 1865) had new records for Ecuador (Narváez-Romero et al. 2018).

In this report, we present new geographical records and updated distribution maps of three species of Amazonian *Coendou*, with the first records of *C. ichillus* for Brazil and major range extensions of *C. bicolor* and *C. nycthemera*.

2.2 Material and Methods

Specimens of erethizontids were examined in the scientific collections of Universidade do Estado de Mato Grosso, campus Alta Floresta (CZAF) in Alta Floresta, Mato Grosso state, Brazil; Museu de Zoologia da Universidade de São Paulo (MZUSP) in São Paulo, São Paulo state, Brazil and Museu Paraense Emílio Goeldi (MPEG) in Belém, Pará state, Brazil. Specimens are composed of stuffed and open skins.

The external measurements are the length of head-and-body (HBL) and length of tail (LT) following the protocol in Voss & Angermann (1997). External measurements were extracted from specimen labels. We estimated the area (in km²) of species distribution range based on the minimum convex polygon using ArcMap software version 10.2.

2.3 Results

Figure 1 shows the updated distribution map of *Coendou bicolor*, *C. ichillus*, and *C. nycthemera*, and Table 1 has the detailed localities. We did not map the record of “*Coendou* cf. *bicolor*” for Boyacá, Colombia (Ramírez-Chaves et al. 2016) because the it is based on a cranium without associated skin, and the authors did not consider *C. bicolor* distinguishable from *C. prehensilis* by cranial characters alone.

The new records of *C. nycthemera* are based on three specimens, an adult male and a female from the right bank of Rio Teles Pires, and a juvenile (sex undetermined) from the opposite bank of the same river (CZAF-MA 9, 10, 11, Figure 2b) (Table 1). All three records were made on the vicinities of a hydroelectric power plant, the Usina Hidrelétrica Teles Pires, Mato Grosso state, and were previously identified as “*Coendou melanurus*”. Brandão et al. (2019) cited “*Coendou* cf. *nycthemera*” based on one of the specimens from CZAF reported here, but the authors could not confirm the identity of the specimens at that time. The new records extend the known geographic range of *C. nycthemera* approximately 620 km from the closest locality to the northwest (Igarapé Auará, on the left bank of Rio Madeira) and of 950 km from the closest locality to the northeast (Capitariquará, on Rio Tocantins), representing a southward area extension of about 41% (Figure 1).

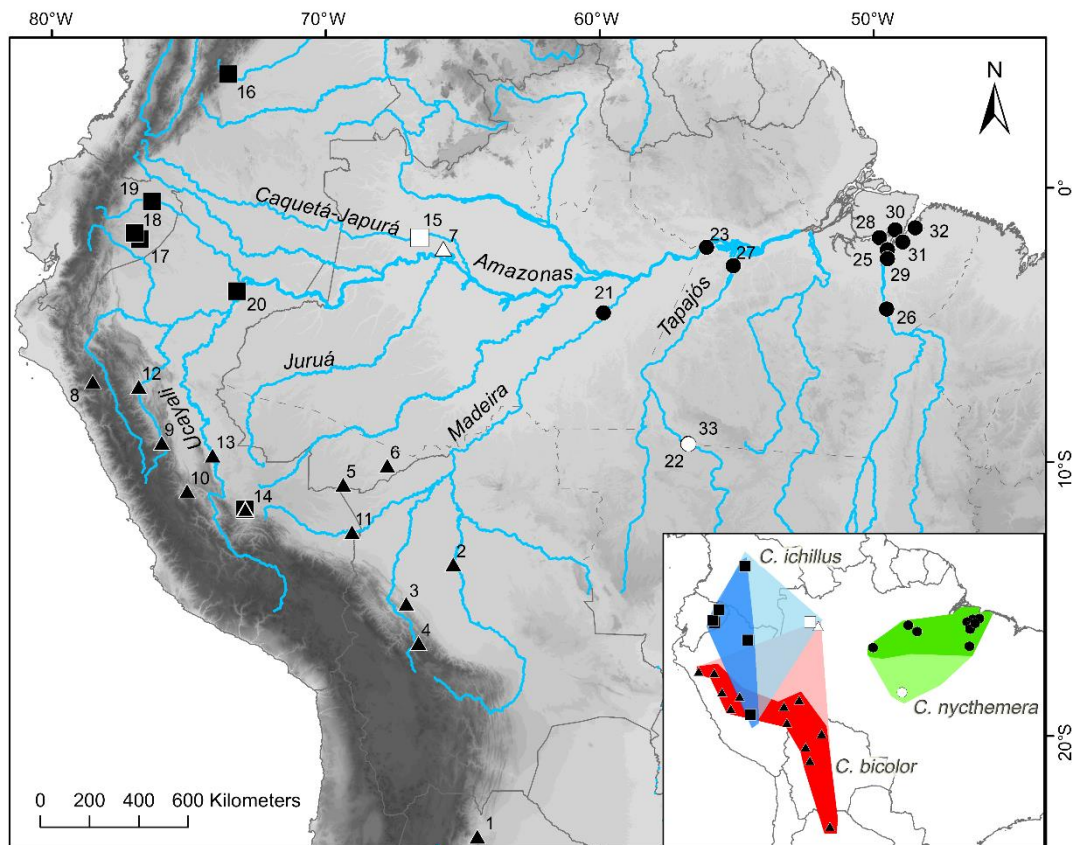


Figure 1. Updated distribution map of *Coendou bicolor* (triangles), *C. ichillus* (squares), and *C. nycthemera* (circles). New records are represented by white symbols. Detailed locality data is in Table 1. Inset map shows the previous distribution (darker shades) and the updated polygon (lighter shades) of *C. bicolor* (red), *C. ichillus* (blue), and *C. nycthemera* (green).

Coendou nycthemera can be externally diagnosed from its congeners by its size, length of villous hairs relative to quills, and color pattern of dorsal quills (Table 2). *Coendou nycthemera* is slightly smaller than *C. melanurus* and significantly smaller than *Coendou baturitensis* Feijó & Langguth 2013 and the Amazonian populations named as *Coendou prehensilis* (Linnaeus 1758) (Table 2). The distal band of the tricolored quills of *C. nycthemera* is very short, inconspicuous or absent, and its colour may be whitish, yellowish or orangish (Figure 3d). Furthermore, *Coendou nycthemera* differs from the similar-sized *C. melanurus* and *Coendou roosmalenorum* by lacking a long, villous fur covering its quills (Voss & Angermann 1997, Handley & Pine 1992). The distal band of the tricolored quills of *C. melanurus* are always light yellowish (Voss et al. 2001). *Coendou nycthemera* has only bicolored quills on its rump while *C. baturitensis* and Amazonian *C. prehensilis* have tricolored and bicolored quills on rump. It also differs from *C. baturitensis* by the dark brownish or black short medial band of the tricolored quills and distal band of bicolored quills (Figure 3). In *C. baturitensis* the medial band of the tricolored quills and the distal band of the bicolored quills are light brownish (Feijó & Langguth 2013).

Table 1. Locality records of *Coendou bicolor*, *C. ichillus*, and *C. nycthemera*. Localities are ordered by species, country, state/department, and locality, and the #ID refers to map in figure 1.

#ID	Species	Country	Department/ State/Province	Locality	Coordinates	Source
1	<i>C. bicolor</i>	Argentina	Jujuy	Yuto	23°39'S 64°28'W	Lucero (1987)
2	<i>C. bicolor</i>	Bolivia	Beni	Puerto Caballo	13°43'S 65°21'W	Voss (2015)
3	<i>C. bicolor</i>	Bolivia	Beni	Yucumo	15°10'S 67°04'W	Voss (2015)
4	<i>C. bicolor</i>	Bolivia	Cochabamba	Charuplaya	16°36'S 66°37'W	Voss (2015)
5	<i>C. bicolor</i>	Brazil	Acre	Brasiléia	10°48'38"S 69°22'05"W	Freitas et al. (2013)
6	<i>C. bicolor</i>	Brazil	Acre	Senador Guimard, on AC-040 road	10°07'12"S 67°45'15"W	Freitas et al. (2013)
7	<i>C. bicolor</i>	Brazil	Amazonas	Reserva de Desenvolvimento Sustentável Mamirauá	2°12'54.43"S 65°42'35.53"W	MPEG 24574, 37122
8	<i>C. bicolor</i>	Peru	Cajamarca	2.5 km N of Monte Seco	7°03'51.32"S 78°30'25.80"W	Voss (2015)
9	<i>C. bicolor</i>	Peru	Huánuco	Tingo María	9°17'38.07"S 75°59'39.02"W	Voss (2015)
10	<i>C. bicolor</i>	Peru	Junín	Chanchamayo	11°03'25.73"S 75°03'39.99"W	Voss (2015)
11	<i>C. bicolor</i>	Peru	Madre de Dios	Reserva Cuzco Amazónico	12°33'00"S 69°02'60"W	Voss (2015)
12	<i>C. bicolor</i>	Peru	San Martín	Área de Conservación Municipal Mishquiyacu- Rumiyacu y Almendra	7°14'40.16"S 76°49'33.47"W	Voss (2015)
13	<i>C. bicolor</i>	Peru	Ucayali	Río Alto Ucayali	9°45'00"S 74°07'59.99"W	Voss (2015)
14	<i>C. bicolor</i> and <i>C. ichillus</i>	Peru	Cusco	Confluence of Ríos Camisea and Urubamba	11°43'16.80"S 72°56'31.20"W	Gregory et al. (2015)
15	<i>C. ichillus</i>	Brazil	Amazonas	Limoeiro, Japurá, Rio Japurá	1°49'S 66°35'W	MZUSP 11465
16	<i>C. ichillus</i>	Colombia	Meta	Villavicencio, km 30 carretera a Caños Negros	4°09'25"N 73°33'21"W	Ramírez-Chaves et al. (2016)
17	<i>C. ichillus</i>	Ecuador	Pastaza	Río Conambo	1°52'S 76°46'60"W	Voss and da Silva (2001)
18	<i>C. ichillus</i>	Ecuador	Pastaza	Río Yana Rumi	1°38'S 76°59'W	Voss and da Silva (2001)
19	<i>C. ichillus</i>	Ecuador	Sucumbios	La Selva Jungle Lodge	0°30'S 76°21'60"W	Voss and da Silva (2001)
20	<i>C. ichillus</i>	Peru	Loreto	Iquitos	3°45'60"S 73°15'W	Voss and da Silva (2001)
21	<i>C. nycthemera</i>	Brazil	Amazonas	Igarapé Auará, Rio Madeira, left bank	4°33'S 59°52'W	Voss (2015)
22	<i>C. nycthemera</i>	Brazil	Mato Grosso	Teles Pires Hydroelectric Reservoir, left bank of Rio Teles Pires	9°19'S 56°47'W	CZAF-MA 10
23	<i>C. nycthemera</i>	Brazil	Pará	ALCOA harbor, Juruti	2°10'S 56°06'W	MPEG 38377
24	<i>C. nycthemera</i>	Brazil	Pará	Belém	1°27'S 48°29'W	Voss (2015)
25	<i>C. nycthemera</i>	Brazil	Pará	Cametá	2°15'S 49°30'W	Voss (2015)
26	<i>C. nycthemera</i>	Brazil	Pará	Capitariquará, extreme South of Ilha Tocantins, rio Tocantins, 78 km S and 16 km E, Tucuruí	4°25'S 49°32'W	MPEG 12496
27	<i>C. nycthemera</i>	Brazil	Pará	Caxiricatuba	2°50'S 55°08'W	MZUSP 5035
28	<i>C. nycthemera</i>	Brazil	Pará	Curralinho, Marajó island	1°48'S 49°47'W	Voss (2015)
29	<i>C. nycthemera</i>	Brazil	Pará	Mocajuba	2°34'S 49°30'W	Voss (2015)
30	<i>C. nycthemera</i>	Brazil	Pará	Muaná	1°31'S 49°13'W	Voss (2015)
31	<i>C. nycthemera</i>	Brazil	Pará	Rio Meruú, left margin, PA- 151, Km 18. Igarapé-Miri	1°58'S 48°57'W	MPEG 24191
32	<i>C. nycthemera</i>	Brazil	Pará	Santa Teresinha, Km 87-94 of the BR-010 road	1°16'S 48°05'W	MZUSP 25591
33	<i>C. nycthemera</i>	Brazil	Pará	Teles Pires Hydroelectric Reservoir, right bank of Rio Teles Pires	9°20'S 56°46'W	CZAF-MA 9, CZAF-MA 11.



Figure 2. Skins in dorsal view of **a)** *Coendou bicolor* (MPEG 37122), **b)** *C. nycthemera* (CZAF-MA 10), and **c)** *C. ichillus* (MZUSP 11465).

The range extension of *Coendou bicolor* is based on two specimens previously identified as *Coendou prehensilis*, a juvenile of unknown sex (MPEG 24574) and an adult female (MPEG 37122, Figure 2a), both from Estação Ecológica Mamirauá, Uarini, in Amazonas State (Table 1). These records expand the known distribution of *C. bicolor* in approximately 905 km northeast from Senador Guimard, Acre, Brazil, the closest record in Brazil (de Freitas et al. 2013) and approximately 1,250 km northeast from Río Alto Ucayali, Ucayali, Peru, the closest record outside Brazil (Voss 2015). The new record comprises an eastward area extension of 53% (Figure 1). *Coendou bicolor* is a large porcupine (Table 2) and has no distal bands on its quills (Figure 3c) and no tricolored quill on the rump, differing from the Amazonian *C. prehensilis* and the northeastern Brazil *C. baturitensis*, both of which have tricolored quills (Figure 3a-b). *Coendou bicolor* has no villous fur covering its quills (Voss 2011) differing from *C. melanurus* (Voss et al. 2001) and *C. roosmalenorum* (Voss & da Silva 2001).

Table 2. External diagnostic characters of the Brazilian Amazonian porcupines.

	Size	Villous hair	Long dorsal quills	Short dorsal quills
<i>C. nycthemera</i>	Small (HBL: 344±22mm; LT: 313±25mm) (Voss & Angermann 1997)	Do not cover the quills	Tricolored or bicolored. Basal band short and yellowish, medial band blackish and long. Distal band, when present, very short. May be whitish, yellowish or orangish	Bicolored. Short basal band yellowish and long distal band blackish
<i>C. bicolor</i>	Large (Mean HBL: 457mm; Mean LT: 422 mm) (Voss 2011)	Do not cover the quills	Bicolored. Short basal band slightly yellowish; long distal band blackish	Bicolored. Short basal band yellowish; long distal band blackish
<i>C. ichillus</i>	Small (HBL: 275mm; LT: 245mm)*	Do not cover the quills	Substituted by Tricolored bristle-quills. Basal band is yellowish, medial band is blackish and distal band is whitish. All bands above the same length	Bicolored. Yellowish basal band and blackish distal band, above the same length
Amazonian <i>C. prehensilis</i>	Large (HBL: 451±25mm; LT: 453±31mm)(Voss 2011)	Do not cover the quills	Bicolored and tricolored. Tricolored quills have basal band slightly yellowish, long blackish medial band and short whitish distal band. Bicolored quills have slightly yellowish basal band and the blackish distal band	Bicolored and tricolored. Tricolored quills have basal band yellowish, long blackish medial band and short whitish distal band. Bicolored quills have yellowish basal band and the blackish distal band
<i>C. melanurus</i>	Small (Mean HBL: 385mm; Mean LT: 373mm) (Voss et al. 2001, p.136)	Cover the quills	Substituted by very slim bristle-quills. Long yellowish basal band, blackish medial band and slightly yellowish distal band	Bicolored. Long strongly yellowish basal band with an inconspicuous blackish distal band
<i>C. rosmalenorum</i>	Small (HBL ~290mm; LT ~250mm) (Voss & da Silva 2001)	Cover the quills	Substituted by bristle- quills. Long yellowish basal band, blackish medial band and slightly yellowish distal band	Bicolored. Long strongly yellowish basal band with a short blackish distal band
<i>C. baturitensis</i>	Large (HBL: 500mm; LT: 460mm) (Feijó & Langguth 2013)	Do not cover the quills	Bicolored and tricolored. Tricolored quills have whitish basal band, long brownish medial band and short whitish distal band. Bicolored quills have short whitish basal band and long brownish distal band	Bicolored and tricolored. Tricolored quills have whitish basal band, long brownish medial band and short whitish distal band. Bicolored quills have short whitish basal band and long brownish distal band

* based on measurements of the examined specimens

The record of *Coendou ichillus* is based on an adult male (MZUSP 11465, Figure 2c), collected on November 21, 1977, on the margins of Rio Japurá, Limoeiro in Amazonas State (Table 1). The specimen is preserved as an open skin with the cranium removed and was previously identified as “*Coendou prehensilis*” by P.E. Vanzolini. This is the first record of *C. ichillus* in Brazil and extends its distribution eastwards in approximately 790 km from Iquitos, Peru, the closest known record (Voss & da Silva 2001), representing an increase of 55% on its estimated distribution area (Figure 1). *Coendou ichillus* is a medium-sized porcupine (Table 2) that differs from the similar *C. melanurus* and *C. rosmalenorum* by the absence of long hairs covering its quills (Voss & da Silva 2001). It is also distinct from the larger *C. prehensilis* and *C. baturitensis* by the lack of tricolored quills on the rump and the presence of bristle-like quills on the dorsum (Figure 3g).

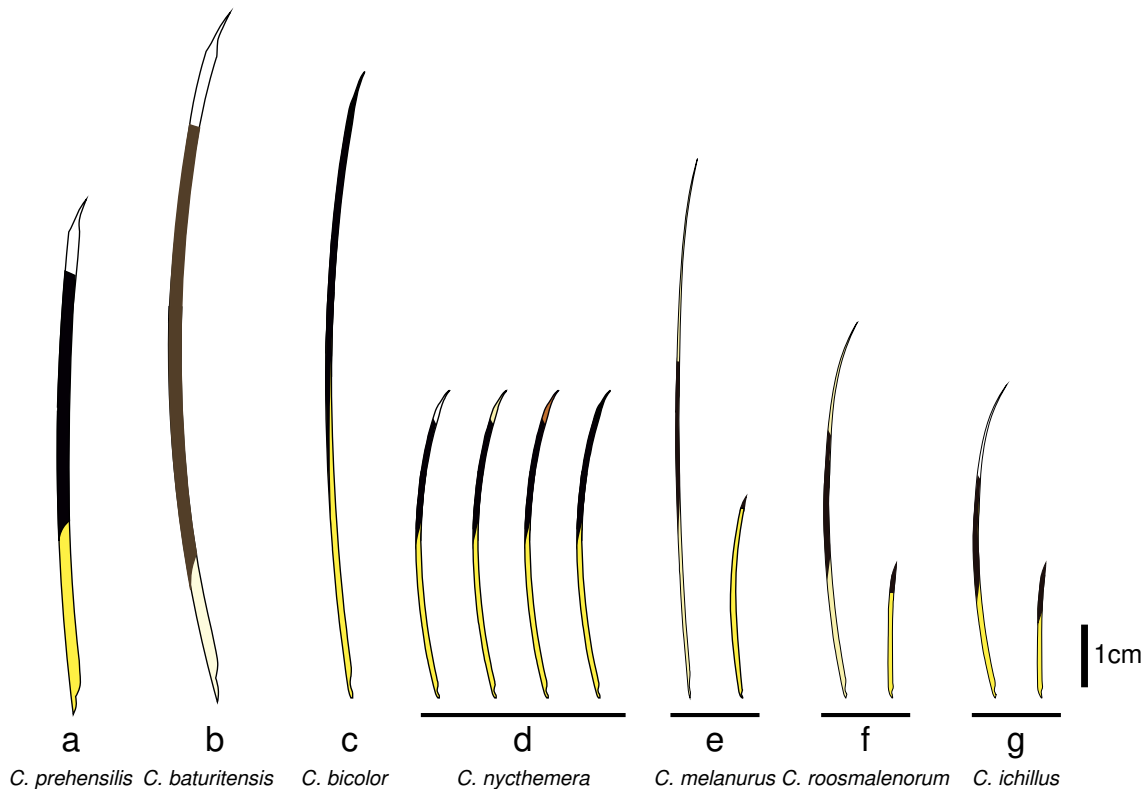


Figure 3. Quills and bristle-quills of selected species of Brazilian porcupines. **a)** Amazonian *C. prehensilis* long tricolored quill, **b)** *C. baturitensis* long tricolored quill, **c)** *C. bicolor* long bicolored quill, **d)** *C. nycthemera* long quills with different distal band colors, **e)** *C. melanurus* tricolored bristle-quill and bicolored quill, **f)** *C. roosmalenorum* tricolored bristle-quill and bicolored quill, and **g)** *C. ichillus* tricolored bristle-quill and bicolored quill.

2.4 Discussion

Natural history information on *Coendou* species is scant in the literature, especially for the Amazonian taxa (Voss, 2015). Even their distribution ranges are poorly defined. For example, Voss (2015) considered *C. nycthemera* associated with the lower Amazonas, Madeira, and Tocantins rivers. With the new record presented here, we demonstrate that *C. nycthemera* occurs further south, at the margins of Rio Teles Pires in Mato Grosso (Figure 1). Considering the new potential distribution of *C. nycthemera*, it is plausible that it also occurs in the Amazon of the state of Maranhão, as suggested by de Oliveira et al. (2007), and in the northern tip of the state of Tocantins.

Coendou bicolor was previously thought to occur exclusively along the Andean foothills and in adjacent lowland forest (Voss, 2015), our record from the Brazilian state of Amazonas expands its potential distribution area in about 53% towards central Amazon. Similarly, *C. ichillus* had a restricted distribution limited to east Ecuador, north Peru, and Colombia, and the record from Rio Japurá increases by 55% its potential range (Figure 1). Altogether, our findings contribute significantly to a better delimitation of the range of these three Amazonian porcupines.

Our study also sheds light on sympatric patterns across *Coendou* species. Approximately 100 km south to the new localities of *C. nycthemera* reported here, we (GSTG

and TBFS) observed a larger *Coendou*, here identified as *C. prehensilis* (ca. 10°20'S 56°58'W – Figure 4), suggesting that the two taxa are sympatric in the region, as recorded elsewhere (Handley & Pine 1992). The new localities for *C. bicolor* (locality 7 in Figure 1) and *C. ichillus* (locality 15 in Figure 1) are just 100 km apart in the north-western region of Amazonas state and support the hypothesis that the two taxa occur in sympatry throughout much of their range, as observed by Gregory et al. (2015), who photographed both species using the same branches of a tree in southwestern Peru.



Figure 4. *Coendou prehensilis* observed close to Nova Monte Verde, Mato Grosso, Brazil.

The three species reported here can be easily differentiated from their congeners based on external traits that can be assessed in the field or in museums. Particularly, the quill morphology is a key character to *Coendou* taxonomy (see Table 2, Figure 3). It is noteworthy that all the new records presented here are based on misidentified museum specimens. Some individuals, as the *C. ichillus* from MZUSP, were collected about 40 years ago. These results highlight both the importance of scientific collections in preserving a still unknown biodiversity and how poorly known is our knowledge about the taxonomy and distribution of Neotropical porcupines. The knowledge about porcupines is limited even if some porcupine species appear to be relatively abundant. For example, 59 individuals of *C. melanurus* were captured over 18 months in an area of 105 km² in the wildlife rescue of Petit Saut hydroelectric dam in French Guiana (Vié 1999).

From a conservation viewpoint, the areas where *C. nycthemera* was recorded, in southern (localities 22, 33 in Figure 1) and eastern Amazonia (localities 25, 26, and 28–32, in Figure 1) are under intense pressure from cattle ranching, agriculture developments, and selective logging (Gascon et al. 2001, Yoshikawa & Sanga-Ngoie 2011, Silva & Lima 2018). Therefore, our new record documents an arboreal mammal that is likely being affected by intense deforestation in the southern Amazon of Mato Grosso, in the same manner as monkeys such as *Mico emiliae*, *Saguinus niger*, and the recently described *Callicebus grovesi*, all of which occur in the region (Garbino et al. 2015, Boubli et al. 2019).

Our paper brings new data on the geographical distribution of *Coendou* species, recording for the first time *C. ichillus* for Brazil and reporting major range extensions for *C. bicolor* and *C. nycthemera*. With the new record of *C. ichillus* for Brazil, there are now 10 species of *Coendou* confirmed in the country (de Freitas et al. 2013, Voss 2015). Considering the most up-to-date catalogue of the Brazilian mammals (Quintela et al. in press), there are now 744 species of mammals in the country.

All records presented herein are based on scientific collections, reinforcing their importance as repositories of an unknown mammalian diversity, even for large species such as erethizontids. We would like to point out that due to the Brazilian cuts imposed by the current federal government to science (de Oliveira Andrade 2019), it is likely that studies of biodiversity and museum's collections will have irreversible impacts to the mammalogy academia and during this new anti-science government.

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References

- BOUBLI, J.P. et al. 2019. On a new species of titi monkey (Primates: *Plecturocebus* Byrne et al., 2016), from Alta Floresta, southern Amazon, Brazil. *Mol. Phylogenet. Evol.* 132(July 2018):117–137.
- BRANDÃO, M.V., GARBINO, G.S.T., SEMEDO, T.B.F., FEIJÓ, A., DO NASCIMENTO, F.O., FERNANDES-FERREIRA, H., ROSSI, R.V., DALPONTE, J. & CARMIGNOTTO, A.P. 2019. Mammals of Mato Grosso, Brazil: Annotated species list and historical review. *Mastozoología Neotrop.* 26(2):1–44.
- EMMONS, L.H. 1997. *Neotropical Rainforest Mammals: A field guide*. The University of Chicago Press, Chicago.
- FEIJÓ, A. & LANGGUTH, A. 2013. Mamíferos de médio e grande porte do Nordeste do Brasil: Distribuição e taxonomia, com descrição de novas espécies. *Rev. Nord. Biol.* 22(1):3–225.
- DE FREITAS, M.A., DE FRANÇA, D.P.F. & VERÍSSIMO, D. 2013. First record of the Bicoloured-spined Porcupine *Coendou bicolor* (Tschudi, 1844) for Brazil. *Check List* 9(1):94.
- GARBINO, G.S.T., SEMEDO, T.B.F. & PANSONATO, A. 2015. Notes on the western black-handed tamarin, *Saguinus niger* (É. Geoffroy, 1803) (Primates) from an Amazonia-Cerrado ecotone in central-western Brazil: new data on its southern limits. *Mastozoología Neotrop.* 22(2):311–318.

- GASCON, C., BIERREGAARD JR, R.O., LAURANCE, W.F. & RANKIN-DE-MERONA, J. 2001. Deforestation and forest fragmentation in the Amazon. In Lessons from Amazonia: The ecology and conservation of a fragmented forest (R. O. Bierregaard Jr, C. Gascon, T. E. Lovejoy, & R. Mesquita, eds) Yale University Press, New Haven, p.22–30.
- GREGORY, T., LUNDE, D.P., ZAMORA-MEZA, H.T., CARRASCO-RUEDA, F., ZAMORA MEZA, H.T. & CARRASCO-RUEDA, F. 2015. Records of *Coendou ichillus* (Rodentia, Erethizontidae) from the Lower Urubamba Region of Peru. *Zookeys* 509(June):109–121.
- HANDLEY, C.O. & PINE, R.H. 1992. A new species of prehensile-tailed porcupine, genus *Coendou* Lacépède, from Brazil. *Mammalia* 56(2):237–244.
- LEITE, Y.L.R., CALDARA JR, V., LOSS, A.C., COSTA, L.P., MELO, É.R.A., GADELHA, J.R. & MENDES PONTES, A.R. 2011. Designation of a neotype for the Brazilian porcupine, *Coendou prehensilis* (Linnaeus, 1758). *Zootaxa* 279130–40.
- LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 10th, vol ed. Laurentii Salvii, Stockholm.
- LUCERO, M.M. 1987. Sobre la presencia de dos taxa de *Coendou* en el Norte Argentino (Mammalia, Erethizontidae). *Acta Zool. Lilloana* 3937–41.
- MENDES PONTES, A.R., GADELHA, J.R., MELO, É.R.A., DE SÁ, F.B., LOSS, A.C., CALDARA JR, V., COSTA, L.P. & LEITE, Y.L.R. 2013. A new species of porcupine, genus *Coendou* (Rodentia: Erethizontidae) from the Atlantic forest of northeastern Brazil. *Zootaxa* 3636(3):421.
- NARVÁEZ-ROMERO, C., REYES-PUIG, C., VALLE, D. & BRITO, J. 2018. New records and estimation of the potential distribution of the stump-tailed porcupine *Coendou rufescens*. *Therya* 9(2):137–146.
- NASCIMENTO, A.L. da C.P. & DOS SANTOS, J.W. 2014. *Coendou speratus* Mendes Pontes, Gadelha, Melo, Sá, Loss, Caldara Jr., Costa & Leite, 2013 (Mammalia, Rodentia, Erethizontidae) in northeastern Brazil: Filling gaps in its geographical distribution. *Check List* 10(5):1223–1225.
- DE OLIVEIRA ANDRADE, R. 2019. Brazil's budget cuts threaten more than 80,000 science scholarships. *Nature* 572(7771):575–576.
- DE OLIVEIRA, T.G., GERUDE, R.G. & E SILVA-JÚNIOR, J. de S. 2007. Unexpected mammalian records in the state of Maranhão. *Bol. do Mus. Parana. Emílio Goeld* 2(2):23–32.
- QUINTELA, F.M., ROCA, C.A. & FEIJÓ, A. Updated and annotated checklist of recent mammals from Brazil. *Anais da Academia Brasileira de Ciências. An. da Acad. Bras. Ciência*.
- RAMÍREZ-CHAVES, H.E., SUÁREZ-CASTRO, A.F., MORALES-MARTÍNEZ, D.M. & VALLEJO-PAREJA, M.C. 2016. Richness and distribution of porcupines (Erethizontidae: *Coendou*) from Colombia. *Mammalia* 80(2):181–191.
- SILVA, C.A. & LIMA, M. 2018. Soy Moratorium in Mato Grosso: Deforestation undermines the agreement. *Land use policy* 71(November):540–542.

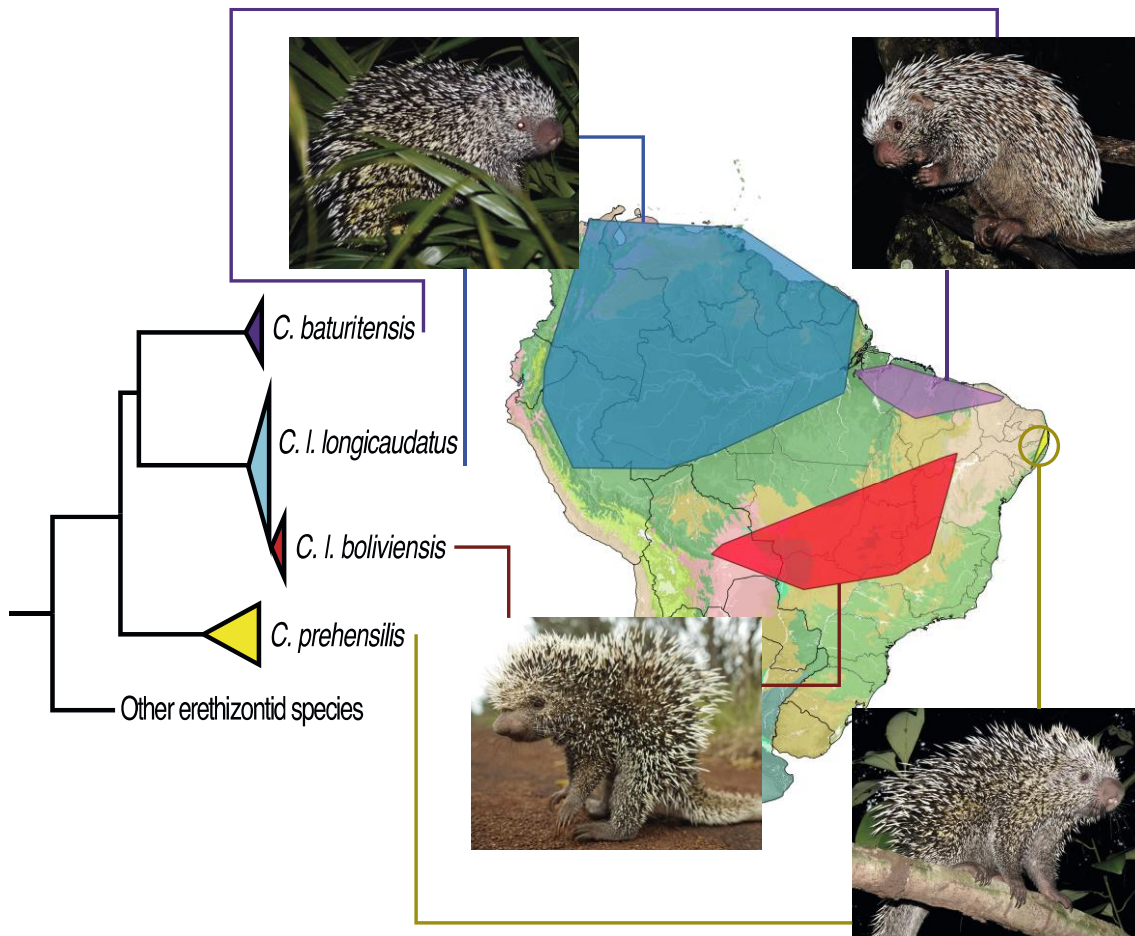
- VIÉ, J.-C. 1999. Wildlife rescues - The case of the Petit Saut hydroelectric dam in French Guiana. *Oryx* 33(2):115–126.
- VOSS, R.S. 2011. Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae) 3. An annotated Checklist on the species of *Coendou* Lacépède, 1799. *Am. Museum Novit.* (3720):1–36.
- VOSS, R.S. 2015. Superfamily Erethizontoidea Bonaparte, 1845. In *Mammals of South America, Volume 2: Rodents* (J. L. Patton, U. F. J. Pardiñas, & G. D'Elía, eds) The University of Chicago Press, Chicago, p.786–805.
- VOSS, R.S. & ANGERMANN, R. 1997. Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae). 1. Type material described by Olfers (1818) and Kuhl (1820) in the Berlin Zoological Museum. *Am. Museum Novit.* (3214):1–44.
- VOSS, R.S., HUBBARD, C. & JANSA, S.A. 2013. Phylogenetic relationships of New World porcupines (Rodentia, Erethizontidae): implications for taxonomy, morphological evolution, and biogeography. *Am. Museum Novit.* (3769):1–36.
- VOSS, R.S., LUNDE, D.P. & SIMMONS, N.B. 2001. The Mammals of Paracou, French Guiana: a neotropical lowland rainforest fauna Part 2. Nonvolant species. *Bull. Am. Museum Nat. Hist.* 2631–236.
- VOSS, R.S. & DA SILVA, M.N.F. 2001. Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae). 2 . A review of the *Coendou vestitus* group with descriptions of two new species from Amazonia. *Am. Museum Novit.* (3351):1–36.
- YOSHIKAWA, S. & SANGA-NGOIE, K. 2011. Deforestation dynamics in Mato Grosso in the southern Brazilian Amazon using GIS and NOAA/AVHRR data. *Int. J. Remote Sens.* 32(2):523–544.

3 Capítulo 2: Integrative systematics of Neotropical porcupines of *Coendou prehensilis* complex (Rodentia: Erethizontidae)

Fernando Heberon Menezes, Anderson Feijó, Hugo Fernandes-Ferreira, Itayguara Ribeiro da Costa & Pedro Cordeiro-Estrela

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Graphical Abstract



Abstract:

Coendou comprises the most speciose genus in Erethizontidae, with 15 currently recognized species. Although several taxonomic studies in the last two decades have unveiled part of its diversity, the most widespread Neotropical taxon *Coendou prehensilis* has received limited attention. Here, we combined morphological and molecular datasets to infer the phylogenetic relationships of the species in the genus and revise the taxonomy of the *C. prehensilis* complex. We found four morphotypes and three well-supported monophyletic clades within *C. prehensilis*. These three clades represent valid species: *C. prehensilis* (restricted to the north of the Atlantic Forest), *C. baturitensis* (occurring in the eastern Amazonian and montane forests enclaves in the Caatinga), and *C. longicaudatus* (two subspecies, *C. l. longicaudatus* from the Amazon and *C. l. boliviensis* from Cerrado and Chaco). Furthermore, we recovered three morphologically diagnosable clades within *Coendou*, for which we assigned subgeneric names. *Coendou* (*Coendou*) comprises six species (*C. baturitensis*, *C. longicaudatus*, *C. mexicanus*, *C. prehensilis*, *C. quichua*, and *C. rufescens*), *Coendou* (*Sphiggurus*) includes five taxa (*C. bicolor*, *C. insidiosus*, *C. nycthemera*, *C. speratus*, and *C. spinosus*), and the third subgenus we named

Coendou (*Caaporamys*) subgen. nov, comprising *C. melanurus* (type species), *C. vestitus*, *C. pruinus*, *C. ichillus*, and *C. roosmalenorum*.

Keywords: *baturitensis*, *boliviensis*, *longicaudatus*, Pernambuco Endemism Centre, quill

Resumo:

Coendou é o gênero de Erethizontidae mais especioso, com 15 espécies reconhecidas. Nas últimas duas décadas, diversos estudos taxonômicos revelaram parte da sua diversidade. Todavia, a espécie neotropical com maior distribuição, *Coendou prehensilis*, recebeu pouca atenção. Aqui, nós combinamos bancos de dados morfológicos e moleculares para inferir relações filogenéticas das espécies dentro do gênero para avaliar o estado taxonômico do complexo *C. prehensilis*. Nós encontramos quatro morfótipos e três clados monofiléticos bem-suportados dentro de *C. prehensilis*. Estes três clados representam espécies válidas: *C. prehensilis* (restrito ao norte da Mata Atlântica), *C. baturitensis* (ocorrendo no leste Amazônico até áreas florestadas de altitude da Caatinga) e *C. longicaudatus* (com duas subespécies, *C. l. longicaudatus* da Amazônia e *C. l. boliviensis* do Cerrado e Chaco). Além disso, nós reconhecemos três clados morfológicamente diagnosticáveis dentro de *Coendou*, os quais nós atribuímos nomes subgenéricos. *Coendou* (*Coendou*) com seis espécies (*C. baturitensis*, *C. longicaudatus*, *C. mexicanus*, *C. prehensilis*, *C. quichua* e *C. rufescens*), *Coendou* (*Sphiggurus*) com cinco táxons (*C. bicolor*, *C. insidiosus*, *C. nycthemera*, *C. speratus* e *C. spinosus*) e o terceiro subgênero nós nomeamos *Coendou* (*Caaporamys*) subgen. nov, composto por *C. melanurus* (espécie-tipo), *C. vestitus*, *C. pruinus*, *C. ichillus* e *C. roosmalenorum*.

Palavras-chave: *baturitensis*, *boliviensis*, *longicaudatus*, Centro de Endemismo de Pernambuco, espinho

3.1 Introduction

The New World porcupines, family Erethizontidae, are a group of at least 17 species of large herbivorous arboreal rodents, ranging from 1 to 10 kg, with their fur modified into quills, lacking thumbs, presenting a bulbous snout and a dorsally coiling prehensile tail (Eisenberg & Redford, 1999; Ellerman, 1940; Emmons, 1997; Feijó & Langguth, 2013; Voss, 2015). Erethizontids are distributed from northern Argentina to northern Canada (Emmons, 1997; Voss, 2015) and are classified into three genera: *Chaetomys* Gray, 1850, *Erethizon* F. Cuvier, 1823, and *Coendou* Lacépède, 1799.

Studies on *Coendou* in the last decades resulted in many taxonomic changes and new species descriptions. Leite *et al.* (2011) designated the neotype of *Coendou prehensilis* (Linnaeus, 1758). Three monographs were published about the family's taxonomy (Voss, 2011, 2015; Voss & Angermann, 1997; Voss & da Silva, 2001). Geographic variation was examined and detailed for hairy dwarf porcupines of eastern Brazil, *Coendou spinosus* (F. Cuvier, 1823) and *Coendou insidiosus* (Olfers, 1818) (Caldara Júnior & Leite, 2012). Four species were described: *Coendou ichillus* Voss & da Silva, 2001, *Coendou roosmalenorum* Voss & da Silva, 2001, *Coendou speratus* Mendes Pontes *et al.*, 2013, and *Coendou baturitensis* Feijó & Langguth, 2013. Additionally, phylogenetic relationships among some erethizontid species

have been inferred by molecular data (Bonvicino et al., 2002; Leite et al., 2011; Mendes Pontes et al., 2013). However, limited taxonomic and geographical sampling hampered a comprehensive phylogenetic hypothesis for the family. Only one work included 13 of the 17 known erethizontid species (Voss et al., 2013), but it lacked sequences of *C. baturitensis*, *C. speratus*, *C. insidiosus* and *C. roosmalenorum*.

Coendou prehensilis is the recognized species with the broadest distribution, ranging from Northern Argentina to the Guianas and reported in all tropical south American biomes (Ramírez-Chaves et al., 2020; Torres-Martínez et al., 2019; Voss, 2015). It exhibits remarkable morphological variation (Leite et al., 2011; Voss, 2011) especially in the colour pattern of the quills (Feijó & Langguth, 2013). Individuals from the Atlantic Forest biome are medium to small size, while animals from other regions are medium to large size (Feijó & Langguth, 2013). Such variation raised a suspicion that the name *Coendou prehensilis* might have been applied to a complex of closely related species (Cabrera, 1961; Husson, 1978; Leite et al., 2011; Voss, 2011). For example, Cabrera (1961) recognized morphological variation within *C. prehensilis*, which led him to recognize three subspecies, followed by Husson (1978). Feijó & Langguth (2013), based on external and cranial traits, described *Coendou baturitensis*, as part of the *C. prehensilis* complex. Later, Voss (2015) treated it as a junior synonym of *C. prehensilis*.

Previous phylogenetic studies on the *Coendou prehensilis* complex have consistently recovered two monophyletic lineages: one with central and north-western South American specimens and another with a single sequence of the neotype of the *Coendou prehensilis* from north-eastern Brazil (Leite et al., 2011; Voss et al., 2013). Accordingly, unique morphological traits were reported for each lineage (Feijó & Langguth, 2013; Leite et al., 2011). Nevertheless, comprehensive analyses of the geographic variation of the whole *C. prehensilis* complex are lacking. Here, we combined morphological and molecular datasets to infer the phylogenetic relationships of the genus *Coendou* and revise the taxonomy of the *C. prehensilis* complex through an integrative approach.

3.2 Material and Methods

3.2.1 Examined specimens

We examined morphologically 280 specimens of erethizontids, of which 140 are diagnosable specimens with complete skins and/or skulls of the *C. prehensilis* complex (See appendix 1 for a list of all examined specimens). The specimens are housed in the collection of Mammals of the Universidade Federal da Paraíba, João Pessoa, Brazil (UFPB), collection of

Mammals of the Universidade Federal de Pernambuco, Recife, Brazil (UFPE), collection of Mammals of the Universidade de Brasília, Brasília, Brazil (UnB), Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP), Museu Nacional do Rio de Janeiro, UFRJ, Rio de Janeiro, Brazil (MNRJ), Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG), American Museum of Natural History, New York, USA (AMNH) and Field Museum of Natural History, Chicago, USA (FMNH).

Furthermore, living specimens from the Baturité's Range (the type locality of *C. baturitensis*), Mulungu, Ceará, Brazil, were examined and had blood and quills samples collected under Brazilian license SISBIO n° 44678-3.

3.2.2 Morphological description

We scored morphological character states of the skin and the skull. A new nomenclature for the porcupine body regions, band colours and mechanical regions of the quills is proposed to score the external morphological character states. Specimens of the *Coendou prehensilis* complex that share most of the character states were grouped in morphotypes and their localities plotted on a map to assess their distribution. The morphotypes are interpreted as species, subspecies or intraspecific variation. Heuristic age determination follows Voss & da Silva (2001).

We also assessed the external and cranial morphometric variation of the morphotypes. External measurements were obtained from the specimens' labels: weight (W), head and body length (HBL), length of tail (LT), and length of hindfoot with claws (HF). Cranial measurements were taken with digital calipers to the nearest 0.01 mm following the criteria described by Voss & da Silva (2001) and we added two new measurements: the anterior height of rostrum (AHR, anterior extreme of upper incisive foramen to nasal tip), and the posterior height of rostrum (PHR, anterior base of the zygomatic process of the jugal to the nasal above the lacrimal location; see Figure S1 for details). We assumed there is no sexual dimorphism in porcupine species following the findings of Caldara Júnior & Leite (2012) for the *Coendou insidiosus* complex. We considered only adult specimens for the description of morphotypes.

3.2.3 Living specimens and sampling collection

Quills, blood samples, measurements and external morphology datasets were collected from two living individuals from Mulungu municipality in Baturité's Range, Ceará State, Brazil, the type locality of *Coendou baturitensis*. The individuals were lifted by the tail,

contained in a box and sedated via intramuscular injection in the tail with ketamine 20mg/kg and midazolam 2 mg/kg by the responsible veterinarian. The quills are housed in the Collection of Mammals of the Universidade Federal da Paraíba under numbers UFPB 9390 (juvenile female) and UFPB 9391 (adult male).

3.2.4 DNA purification, amplification and sequencing

The DNA from blood samples of UFPB 9391 was obtained through the Wizard® Genomic DNA Purification Kit. The DNA of UFPB 9412 (an adult female), UFPB 9780 (a sex-undetermined adult) and UFPB 9781 (an adult female) were extracted from fresh muscle samples preserved in PA ethanol at 4°C through a standard CTAB extraction protocol (Doyle & Doyle, 1987). The Polymerase Chain Reaction (PCR) was performed with the GoTaq® Green Master Mix 2X kit with primers MVZ 05 (sense) 5' CGAAGCTTGATATGAAAACCATCGTTG (Smith & Patton, 1993) and UMMZ 04 5' TCTTCATTTYWGGTTTACAAGAC (antisense) (Jansa et al., 1999) to amplify the complete cytochrome *b* (*cyt b*) sequence. PCR conditions were Initial Denaturation at 95°C for 2 minutes, 39 cycles at 95°C/30s, 44°C/45s and 73°C/90s with final extension of 73°C/ 8min. The expected amplicon length is about 1200 bp. The PCR product with the primers used for the amplification were sent for sequencing in the Laboratory of Histopathology at Instituto de Ciências do Mar (Labomar) of the Universidade Federal do Ceará, Ceará, Brazil. For sequencing, we used an additional primer, MZV16 (antisense) 5' AAATAGGAARTATCAYTCTGGTTTRAT (Smith & Patton, 1993). The new sequences are deposited in GenBank with accession numbers KY784123-KY784126.

3.2.5 Morphometric analyses

We explored the cranial morphometric variation in *Coendou prehensilis* complex through univariate and multivariate analyses. Only adult individuals were included in the statistical analyses. In order to increase the sample size in multivariate analyses, we imputed missing data using the Amelia R package (Honaker et al., 2011) with species as a crossfactor. To increase the predictive power of imputations, we excluded specimens with numerous missing values, the final dataset included 72 specimens with only 3.8% of missing data. We evaluated the reliability of the estimation using the overimpute function which treats observed values as missing and estimates the observed values and their confidence intervals with the model used to estimate missing values. The breadth of morphospace variation within *C.*

prehensilis was assessed via principal component analysis (PCA) using the log-transformed cranial measurements. The separation among morphotypes was quantified via discriminant function analysis (DFA) with leave-one-out cross-validation. We obtained similar results in the multivariate analyses when removing all individuals with missing data.

3.2.6 Phylogenetic analyses

Phylogenetic relationships were inferred based on morphological and molecular data, as separate and combined partitions.

3.2.6.1 Morphological Data

The coding of morphological characters was made in a nexus file following Maddison *et al.* (1997). We performed Maximum Parsimony analysis (MP1) in PAUP4.0a150 (Swofford, 2002; Wilgenbusch & Swofford, 2003) with jack-knife resampling method (1000 replicates) with a heuristic search using the tree-bisection-reconnection (TBR) as the branch-swapping algorithm. Gaps were treated as “additional state”. *Chaetomys subspinosus* (Olfers, 1818) and *Erethizon dorsatum* (Linnaeus, 1758) were used as outgroups. Most parsimonious trees were summarized as a 50% majority-rule consensus tree. We listed apomorphies and calculated the consistency indexes (CI) for each character to identify homoplasy patterns.

3.2.6.2 Molecular Data

We used a total of 59 sequences for phylogenetic analyses: our new 4 sequences and 56 available erethizontid’s cytochrome *b* sequences previously deposited in GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>) (Appendix 2). It was almost all erethizontid’s sequences except the unique available sequence of *Coendou pruinus* Thomas, 1905 because it is very short with only 248 nucleotides (KC463880). The alignment was performed by the Muscle algorithm in MEGA 7 Software (Kumar *et al.*, 2016). We did not trim the final alignment and treated the gaps as missing data, resulting in an alignment size of 1140 nucleotides (Alignment S1). Model selection for probabilistic analyses was carried out with JModelTest 2 (Darriba *et al.*, 2012). The model TN93 (Tamura & Nei, 1993) with gamma distribution (+G) was selected because it had the lowest BIC (Bayesian Information Criterion) and AIC (Akaike Information Criterion) scores (see Sullivan & Joyce, 2005). Two phylogenetic analyses were performed: Maximum Likelihood (ML) and Bayesian Inference (BI). *Chaetomys subspinosus* and *E. dorsatum* were used as outgroups for the analyses.

The Maximum Likelihood (ML) consensus tree was inferred from 1000 pseudo replicates (Felsenstein, 1985) using PhyML 3.1 (Guindon *et al.*, 2010) with an initial BioNJ

tree method (Guindon & Gascuel, 2003) and NNI search algorithm with TN93 nucleotide substitution model and a discrete gamma distribution model with 4 categories (+G=0.222). Estimated nucleotide frequencies are $f(A)=0.32516$, $f(C)=0.28747$, $f(G)=0.09416$ and $f(T)=0.29320$. Bayesian Inference (BI1) was inferred with a GTR+G model in MrBayes 3.2 (Huelsenbeck & Ronquist, 2001; Ronquist et al., 2012; Ronquist & Huelsenbeck, 2003) with 4 chains over 10 million generations sampled every 100. The first 25% of samples were discarded as burn-in to estimate consensus trees and evolutionary parameters.

3.2.6.3 Combined data

We performed two analyses with combined molecular and morphological datasets (Alignment S2). First, we performed a Maximum Parsimony (MP2) analysis with 1000 bootstrap replicates in PAUP4. Gaps were treated as "additional state". Starting tree(s) obtained via stepwise addition and the tree-bisection-reconnection (TBR) algorithm with reconnection limit of 8. Branches collapse (creating polytomies) if maximum branch length is zero.

Second, we inferred a Bayesian Inference (BI2) tree based employing a partitioned model. The morphological dataset considered only variable characters and employed the parsimonious model of Lewis (2001). For the molecular data we employed the GTR+G model with the same search parameters as described above for BI1. The analysis was performed in MrBayes v. 3.1.2 (Ronquist et al., 2012). To quantify the contribution of the morphological and molecular datasets to node support, we used the Partitioned Bremer Index (Bremer, 1994; Lambkin et al., 2002).

3.3 Results

3.3.1 Pelage

Here, we describe a new way of interpreting the porcupine external morphology in order to distinguish the quills of the dorsal crest from those of the rump (Figure 1a). The external morphology was described using the different quill types and their position on the body. Furthermore, we also propose a new nomenclature for porcupine quills based on the pigmentation banding pattern and functional mechanical regions (Figure 1b). The pigmented bands are enumerated from 1 to n , from proximal to distal. The band 1 (B1) is the nearest to the tegument insertion of the quill, bristle or any modified hair of the porcupine. The upcoming bands receive the following ordinal number. The apical band is the n^{th} band (B_n) which n is also the total number of bands. Therefore, in a three-banded quill, the basal band is the B1, the medial band B2 and the distal band B3. Mechanical regions of the quill are tripartite: 1) The

bulb is the region that anchors the quill to the tegument, 2) the *mucronis* (Latin: a point that pricks, masculine) is the mechanical region of thinner diameter than the rest of the quill at its apex after the quill body constriction, 3) the quill body consists of almost all its length and has a broader diameter than the bulb and the *mucronis*.

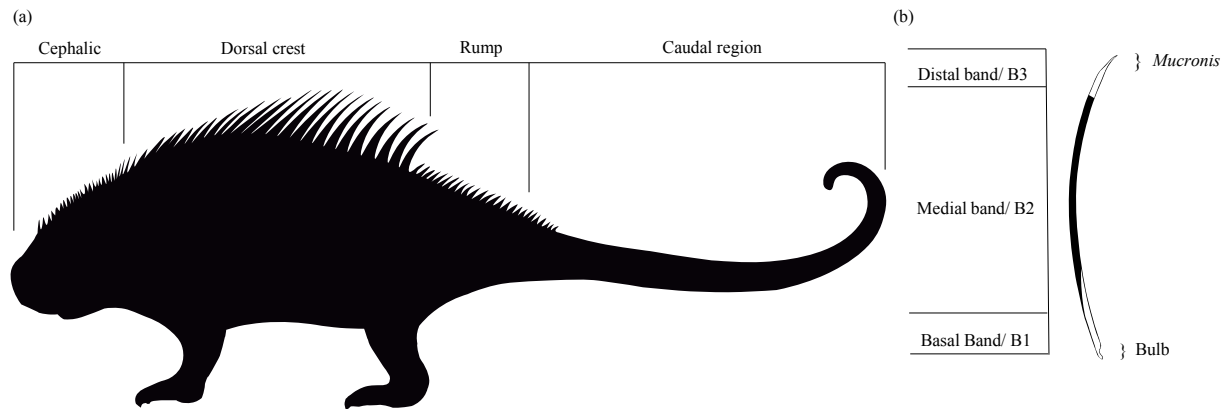


Figure 1. (a) Nomenclature of the body regions of *Coendou* used in this study. The dorsal crest exhibits long and flexible quills and the rump shows short and inflexible quills. (b) Nomenclature of the different regions of an *Erethizontid* quill. The pigmented or nonpigmented bands are numbered based on their position relative to the tegument. The mechanical parts are the bulb, the quill body and the *mucronis*. Artwork by F.H. Menezes.

There are two types of banding pattern in erethizontid quills: the first has a darker medial band (B2) between the lighter basal (B1) and the distal (B3) bands, this is the tricoloured quill banding pattern; the second type lacks a lighter distal band (B3), named the bicoloured quill banding pattern, given it presents only a lighter basal band (B1) and a darker distal band (B2). The distal band (B2) of bicoloured quills is considered homologous to the medial band (B2) of tricoloured quills, therefore we recommend the use of numbered band nomenclature.

3.3.2 Character states

We scored 38 external and cranial characters of 12 species of erethizontids, plus the four morphotypes of the *Coendou prehensilis* complex (Table 1). The external morphological characters are based on the scheme of body regions here proposed (Figure 1). We used only species for which we have examined at least one specimen. The species with only one or/and incomplete specimens had their character states complemented with previous literature descriptions. List of characters and their states and coding follows (Figures 2-4): **Char. 1** – Fur covering quills on the dorsal crest: absent (0), present (1). **Char. 2** – Dorsal fur distribution: absent (0), present on rump (1), absent on rump (2). When present, the villous fur covers all the dorsum or is absent only on the rump. The characters 1 and 2 were considered as separated to

obtain independent values of consistency and retention indices since the villous fur covering the dorsal quills was used as a diagnostic character to *Sphiggurus* (e.g., Woods & Kilpatrick, 2005). **Char. 3** – Ventral pelage: soft (0), rough (1). The ventral pelage of porcupines can be composed of villous and soft fur or spiny hairs. The spiny pelage is made of hard and inflexible aristiform hairs with barbless *mucronis* which is absent in the soft pelage. **Char. 4** – Quill shape: non-wavy (0), wavy (1). Some species present quills with a wavy body, as the broomstraw-spines of *Chaetomys subspinosus* (see Voss & Angermann, 1997 for details), while other species have curved quill bodies (Figure 1b). **Char. 5** – Dorsal crest composition: inflexible straight quills (0), flexible curved quills (1), bristle quills (2). Some quills are hard and inflexible with a long barbed *mucronis*, other ones are flexible and long with a barbless *mucronis*, the bristle-quills present a barbless terminal filament rather than a *mucronis* (see Voss & da Silva, 2001 for details on bristle-quills). The bands of bristle-quills are treated as homologous to the bands of long quills of the dorsal crest. **Char. 6** – Diameter of quills or bristle-quills of the dorsal crest: thin (0), thick (1). Thin < 1.4 mm < thick in adult specimens. **Char. 7** – Tetracoloured quills: absent (0), present (1). **Char. 8** – Tricoloured quill location: posterior half of dorsum (0), head and flanks (1), all dorsum (2), almost all dorsum except rump (3). **Char. 9** – Bicoloured quills location: head and thoracic dorsum (0), uniformly along dorsum (1), mainly on rump (2), only on rump (3). The distribution of bicoloured quills could be restricted to specific body areas, densely in some areas or uniformly found in all dorsum. **Char. 10** – Coloration of B1 and B2 of dorsal crest quills and bristle-quills: B1 whitish, B2 brownish (0), B1 slightly yellowish, B2 brownish (1), B1 strongly yellowish, B2 dark brownish (2), B1 strongly yellowish, B2 blackish (3). **Char. 11** – Coloration of B3 of dorsal crest: whitish (0), slightly yellowish (1), yellowish (2), orangish (3). **Char. 12** – B2 relative length to B1: shorter (0), about the same length (1), longer (2). **Char. 13** – B3 relative length to B2: shorter (0), about the same length (1), longer (2), inconspicuous (3). **Char. 14** – Quills on limbs: absent (0), present (1). **Char. 15** – Tail colour type: coloured (0), blackish (1). The quills of the tail can be tricoloured or bicoloured with a very long blackish B2. **Char. 16** – Tail relative length to the body: long (0), short (1). The tail is considered long if it has at least 65% of the body length. **Char. 17** – Incisive enamel colour: orange (0), yellowish (1). **Char. 18** – Molar occlusion pattern viewed frontally: vertical (0), diagonal (1). **Char. 19** – Rostrum width: narrow (0), wide (1). **Char. 20** – Nasals length: short (0), long (1). The naso-frontal sutures of short nasals do not surpass the pre-orbital processes of frontals in dorsal view, while the naso-frontal sutures of long nasals surpass the pre-orbital processes in dorsal view. **Char. 21** – Medial masseter scar

shape: elliptical and narrow (0), oval and wide (1), triangular (2). **Char. 22** – Lacrimal sutures: absent (0), present (1). **Char. 23** – Relative parietal length: shorter than interparietal (0), longer than interparietal (1), about interparietal length (2). **Char. 24** – Temporal scars drawing in dorsal view: calix shape (0), V-shaped (1), Y-shaped (2). **Char. 25** – Lambdoidal ridge: inconspicuous (0), present but weakly developed (1), strongly laterally developed (2). **Char. 26** – Palatal keel: absent (0), present (1). **Char. 27** – Pterygoid contact with auditory bullae: absent (0), present (1). **Char. 28** – Alisphenoid contact with auditory bullae constituting a fenestra: absent (0), present (1). **Char. 29** – Alisphenoid ossification: incomplete and open sphenopterygoid canal (0), complete with an alisphenoid bridge over the sphenopterygoid canal (1). Based on Voss & da Silva (2001). **Char. 30** – Dorsal contact between auditory bullae and alisphenoid: absent (0), present (1). **Char. 31** – The dorsal roof of the external auditory meatus: smooth (0), keeled (1). Based on Voss (2011). **Char. 32** – Nasals profile and nasofrontal inflation: flattened (0), posterior half-inflated (1), totally inflated (2). The skull dorsal region in porcupines varies greatly among the species. Some species have a flattened dorsal region without curvatures in the first two-thirds, except by a slight curvature immediately above the orbital region or with a slight inflation pronounced in the nasofrontal region. Furthermore, in some species, the posterior half of the nasal is inflated, with the anterior half-flatted. In *C. baturitensis*, the nasal is totally inflated. **Char. 33** – Orbito-temporal fossa depth: shallow (0), keeled and shallow (1), deep (2), hypertrophied keel (3). **Char. 34** – Postorbital edge linked to orbito-temporal keel: without link (0), linked (1). **Char. 35** – Shape of superior edge of orbito-temporal fossa: semi-circular (0), triangular (1). **Char. 36** – Angular process: narrow without alar projections (0), wide with dorsoventrally alar projections (1), Z-shaped (2). **Char. 37** – Coronoid process: absent (0), reduced (1), developed (2). The coronoid process is inconspicuous in some species, with only a small tip without any curvature. While a well-developed coronoid process presents a slightly curvature. The cranial and mandibular characters (Char. 19-37) are illustrated in figures 2-4. **Char. 38** – Neonate pelage colouration: whitish (0), cream-coloured (1), golden (2), orangish (3), brownish (4) and blackish (5). The colour of the neonate's pelage is different from the adult villous pelage colours. The vivid colours observed in living neonates tend to fade after the preservation process. Therefore, the living individuals have brighter colours than the museum specimens. The codification of neonates of *C. prehensilis* complex, *C. spinosus* and *C. insidiosus* was based on living or recently dead and preserved specimens while the codification of *C. nycthemera* was based only on preserved specimens. The states of character 38 were considered constant for each species

and were assessed based on 13 specimens (MNRJ 1361, MNRJ 42814, MNRJ 46935, MPEG 418, MPEG 421, MPEG 12598, MZUSP 20931, UFPB 1237, UFPB (FHM 23), UFPB (FHM 24), MNRJ 75670, MNRJ 79052 and MZUSP 25591). The states of characters 1 to 37 are exclusive of adult specimens. All characters are assumed to have unordered rather than ordered states.

Table 1. Data matrix of character states of examined species of erethizontids and the morphotypes of *Coendou prehensilis* complex.

Groups	1	2	3	
	1234567890	1234567890	1234567890	12345678
<i>Chaetomys subspinosus</i>	0001001000	0B01000000	2021111111	0021021?
<i>Erethizon dorsatum</i>	1200100212	-1-0010100	A01220001A	0031A115
<i>Coendou roosmalenorum</i>	1200200-12	2021100100	00?010001A	1010012?
<i>Co. ichillus</i>	0000200-12	0021100100	10?1010010	0000012?
<i>Co. melanurus</i>	1100200-12	211110?110	00?00?0010	10100?2?
<i>Co. bicolor</i>	0000100-12	-23100?110	10?0?00000	1100102?
<i>Co. nycthemera</i>	0000100313	C331000100	A020011111	00100024
<i>Co. speratus</i>	0000100332	3000000100	1020100111	0010002?
<i>Co. insidiosus N</i>	1100100112	3000000100	102A000111	00000023
<i>Co. spinosus C</i>	1100100312	3000000100	0020000111	00100023
<i>Co. spinosus S</i>	1100100312	2000000100	0020000111	00100023
<i>Co. quichua</i>	0010110322	010100111?	???????????	10???????
<i>Co. prehensilis</i>	0010110232	1021000110	AA1B1000A0	01210AB2
<i>Co. l. longicaudatus</i>	0010110222	0101000110	101BBAAA0	11B0AA24
<i>Co. l. boliviensis</i>	00101102CB	0011000110	101BBA00AA	11A0A023
<i>Co. baturitensis</i>	0010110221	0201001111	100B2A0010	12D01A20

The characters were listed by 10 states per species. Polymorphic entries: A= (01), B= (12), C= (23) and D= (012). Missing data are coded by question marks.

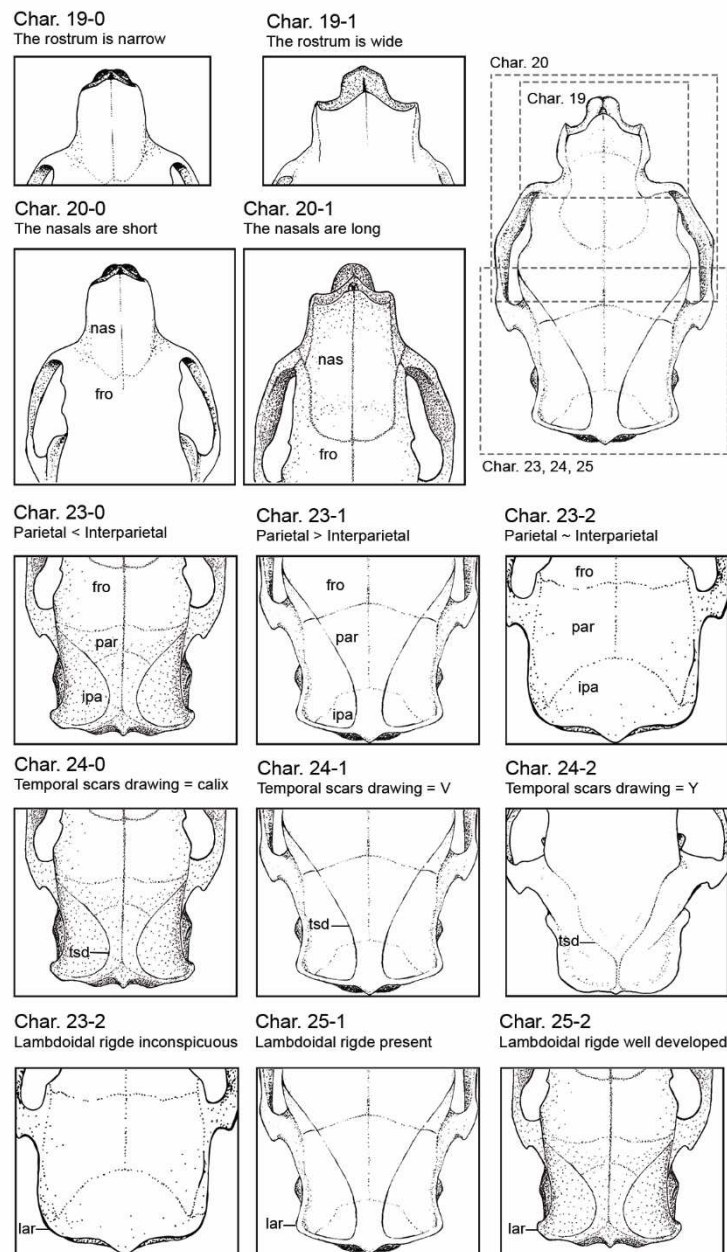


Figure 2. Selected cranial characters states of the Erethizontidae in dorsal view. nas – nasal, fro – frontal, par – parietal, ipa – interparietal, tsd - temporal scars drawing, lar – lambdoidal ridge. Artwork by F.H. Menezes.

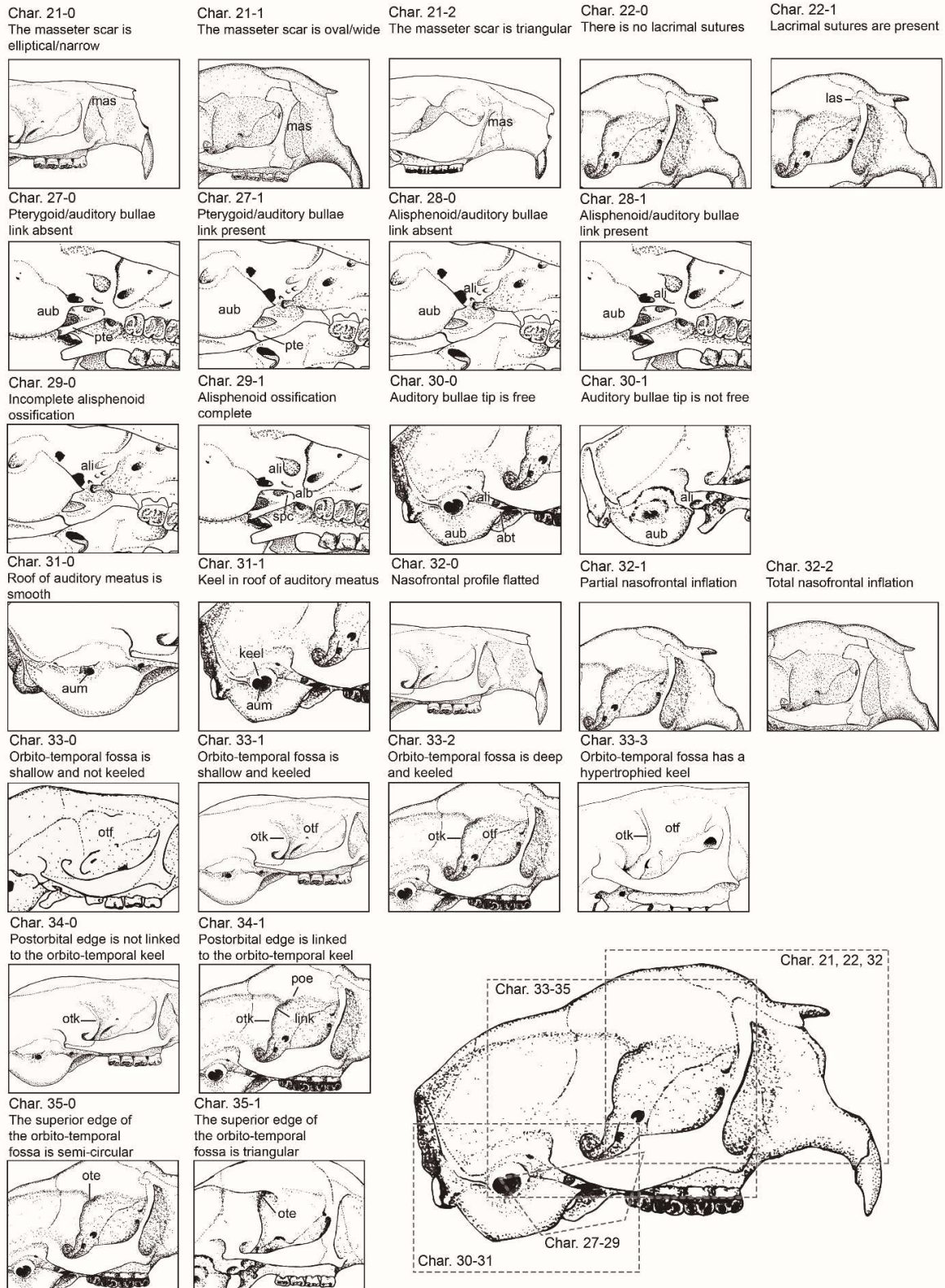


Figure 3. Selected cranial character states of the Erethizontidae in lateral view. mas – masseter scar, las – lacrimal scar, aub – auditory bullae, pte – pterygoid, ali – alisphenoid, alb – alisphenoidal bridge, spc – sphenopterygoid canal, abt – auditory bullae tip, aum – auditory meatus, otf – orbito-temporal fossa, otk – orbito-temporal keel, poe – post-orbital edge, ote – orbito-temporal superior edge. Artwork by F.H. Menezes.

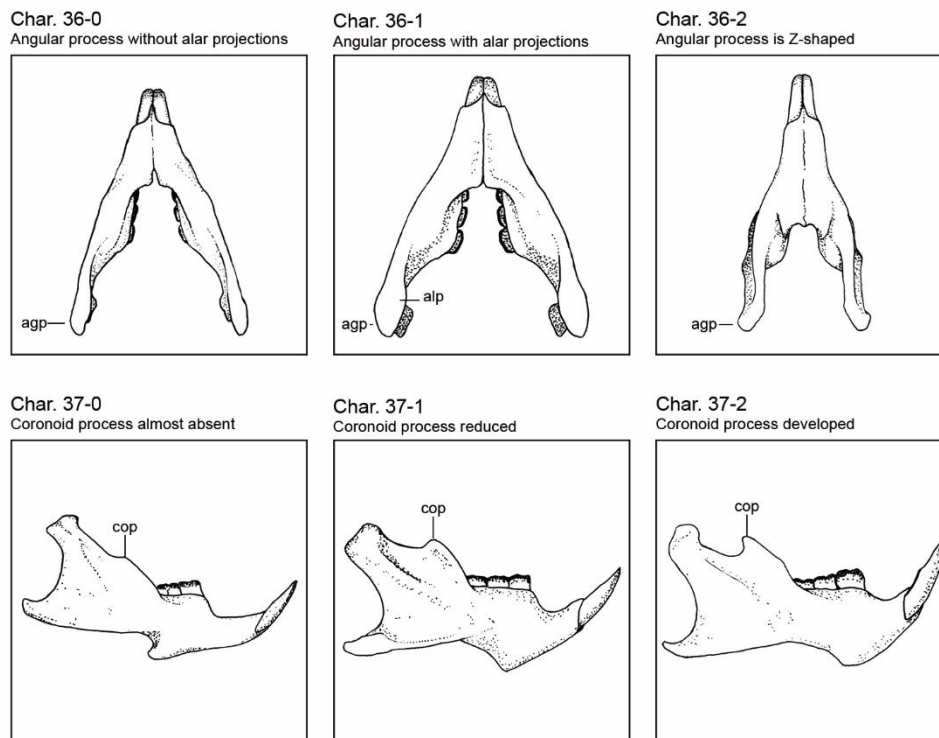


Figure 4. Selected mandibular character states of the Erethizontidae in ventral (top) and lateral (bottom) views. agp – angular process, alp – alar process, cop – coronoid process. Artwork by F.H. Menezes.

3.3.3 Morphotypes

We found 16 morphotypes of erethizontids (Table 1). Two of them correspond to the outgroups (*Chaetomys subspinosus* and *Erethizon dorsatum*) used in the phylogenetic analysis of the combined morphological and molecular data. The fourteen remaining morphotypes belong to the genus *Coendou*. Three represent the hairy dwarf porcupines of eastern Brazil: two of them consist of *Coendou spinosus*, as previously reported by Caldara Júnior & Leite (2012), and one refers to *Coendou insidiosus*. Seven morphotypes represent fully recognized species of *Coendou*: *C. melanurus* (Wagner, 1842), *C. roosmalenorum*, *C. ichillus*, *C. bicolor* (Tschudi, 1844), *C. nycthemera* (Olfers, 1818), *C. speratus*, and *C. quichua* Thomas, 1899. The following species were not included because no specimens were examined: *Coendou rufescens* (Gray, 1865), *Coendou mexicanus* (Kerr, 1792), *Coendou vestitus* Thomas, 1899 and *Coendou pruinosus*. We recognized the remaining four morphotypes as part of the *C. prehensilis* complex. We assigned each morphotype to a Latin name based on the oldest valid name and the congruent description. The four morphotypes represent three species: *Coendou prehensilis* (Linnaeus, 1758), *Coendou baturitensis* Feijó & Langguth, 2013, and *Coendou longicaudatus*

Daudin, 1802 with two subspecies: *Coendou longicaudatus longicaudatus* Daudin, 1802 and *Coendou longicaudatus boliviensis* (Brandt, 1835). See the taxonomy account below for a full description of each taxon.

The four morphotypes of the *C. prehensilis* complex share some common features (Tables S1-S2). The dorsal villous pelage of adults is composed of scarce shaggy monocoloured or tricoloured fur, which never covers the quills (Char. 1:0 CI 0.33). The dorsal crest exhibits thick (Char. 6:1 CI 1.00), long and flexible tricoloured quills with a short barbless *mucronis* (Char. 5:1 CI 1.00). The tricoloured quills are present on almost all the dorsum except the rump (Char. 8:3 CI 0.75). The rump is composed of short bicoloured quills with barbed and relatively long *mucronis*. The B1 of the rump quills is usually more yellowish than quills of the other regions. The ventral pelage of adults is composed of tricoloured and sometimes bicoloured aristiform fur (Char. 3:1 CI 1.00). The B1 of the ventral pelage is whitish or light yellow, B2 is brownish or blackish and B3 is usually whitish. There are quills on the limbs (Char. 14:1 CI 0.33). The tail is long and has bicoloured and tricoloured quills dorsally in its basal third portion (Char. 15:0 CI 1.00). They have post cranial vibrissae emerging laterally on their anterior and posterior limbs, probably with a mechanoreceptor function. These vibrissae are long, thick and flexible with some colour variation. Post cranial vibrissae are bicoloured with dark B1 and yellowish B2, or tricoloured with a darker pattern than tricoloured quills, or monocoloured black or darkish brown. The skull of adults exhibits a wide and high rostrum with total (Char. 32:2 CI 0.67) or partial nasofrontal inflation (Char. 32:1). The lambdoidal ridge is laterally evident in dorsal view (Char. 25:1-2 CI 0.88). The temporal scars are Y (Char. 24:1) or V-shaped (Char. 24:2 CI 0.97) and converge posteriorly. The maxillary teeth are pentalophodont.

The neonates of the four *C. prehensilis* complex morphotypes exhibit a smooth villous pelage covering all body surfaces. This pelage is monocoloured and we found whitish, cream-coloured, orange and rust-brownish specimens (Char. 38 CI 0.80). The quills are thin and almost whitish with some tricoloured and bicoloured with inconspicuous B2. The skull of neonates has a large uninflated rostrum. Some degree of nasofrontal inflation is noticeable during the ontogeny, mainly in subadult specimens.

Cranially, the morphotypes of the *C. prehensilis* complex present similar features with exclusive character states limited to *C. prehensilis* and *C. baturitensis* (Table 2, Figure 5). The skull of *C. prehensilis* is smaller, while the skull of the other morphotypes exhibits a similar size (Table 3, Figure 6). *Coendou baturitensis* exhibits the longest nasal and the shortest parietal (Table 3). Externally, they are easily diagnosable by their quill band colours (Char. 10-13)

(Figure 7) and by the distribution of each type of quill on the body and its curvature (Char. 5-9) (Table 2). The morphotypes present different colour patterns based on the distribution of quill types (Figure 8).

Table 2. Diagnostic traits of the four morphotypes of the *C. prehensilis* complex. Body measurements given as mean (min.–max.) N.

Character condition	<i>C. prehensilis</i>	<i>C. l. longicaudatus</i>	<i>C. l. boliviensis</i>	<i>C. baturitensis</i>
Size	Medium-small	Medium	Large	Medium
Weight (g)	2656(2350–2900) 3	3750(3100-4200) 6	4056(2330-5570) 10	3457(3415-3500) 2
Head and body length (mm)	402.5(290–480) 4	502.1(450-530) 7	512.1(470-570) 11	498.6(460-549) 5
Tail length (mm)	386.5(310–430) 4	521.5(460-600) 10	522.1(470-578) 11	426.6(325-470) 5
Hindfoot with claws length (mm)	83.33(80–85) 3	100.3(87-110) 10	97.1(87-105) 8	87.6(80-105) 5
Ear length (mm)	10 (-) 1	14(10-17) 3	11.5(8-15) 9	27.6(20-33) 3
TL in relative HBL (%)	97.5 (86.9-106.9) 4	106.9 (88.4-126.6) 7	102.3 (82.4-121.9) 11	86.5 (59.1-102.1) 5
Distribution of bicoloured quills (CI 0.875)	Rump agglomerated (Char. 9:3)	Uniformly distributed (Char. 9:1)	Rump agglomerated (Char. 9:3)	Uniformly distributed (Char. 9:1)
length of anterior quills and Band colours	B1 <u>Long and light yellowish</u> B2† <u>Short and dark brownish</u> B3 <u>Long and light yellowish</u>	<u>Medium</u> and whitish <u>Medium</u> and dark brownish <u>Short</u> and whitish	Long and whitish Short and brownish Medium and whitish	<u>Short</u> and whitish <u>Long</u> and brownish Medium and whitish
Posterior quills colours	B1 <u>Strongly yellowish</u> B3 <u>Light yellowish</u>	Yellowish Whitish	Yellowish Whitish	<u>Light yellowish</u> Whitish
Curvature of dorsal crest quills	Slightly curved	Slightly curved	Curved	Curved
Nasal length (CI 1.00)	Short (Char. 20:0)	Short (Char. 20:0)	Short (Char. 20:0)	<u>Long</u> (Char. 20:1)
Parietal length (CI 0.667)	Longer than interparietal (Char. 23:1)	Longer than interparietal (Char. 23:1)	Longer than interparietal (Char. 23:1)	<u>Shorter than interparietal</u> (Char. 23:0)
Lacrimal sutures (CI 1.00)	<u>Present</u> (Char. 22:1) or absent (Char. 22:0)	Absent (Char. 22:0)	Absent (Char. 22:0)	Absent (Char. 22:0)
Lambdoidal ridges (CI 0.88)	Present but weakly developed (Char. 25:1)	Present but weakly developed (Char. 25:1) or strongly laterally developed (Char. 25:2)	Present but weakly developed (Char. 25:1) or strongly laterally developed (Char. 25:2)	Strongly laterally developed (Char. 25:2)
Nasofrontal inflation (CI 0.667)	Partial (Char. 32:1)	Partial (Char. 32:1)	Partial (Char. 32:1)	<u>Complete</u> (Char. 32:2)
Medial masseter scar shape (CI 0.818)	<u>Elliptical and narrow</u> (Char. 21:0) or oval and wide (Char. 21:1)	Oval and wide (Char. 21:1)	Oval and wide (Char. 21:1)	Oval and wide (Char. 21:1)

Orbito-temporal fossa depth (CI 0.906) and its superior margin shape (Char. 35 CI 0.958)	Deep (Char. 33:2) and curved (Char. 35:0)	Deep or keeled shallow (Char. 33:1 or 2) and curved or triangular (Char. 35:0 or 1)	Shallow, keeled or not (Char. 33:0 or 1) and curved or triangular (Char. 35:0 or 1)	Shallow or deep, keeled or not (Char. 33:0, 1 or 2) and triangular (Char. 35:1)
Post-orbital edge (CI 0.50)	<u>Linked to orbito-temporal fossa keel</u> (Char. 34:1)	Not linked to orbito-temporal fossa keel (Char. 34:0)	Not linked to orbito-temporal fossa keel (Char. 34:0)	Not linked to orbito-temporal fossa keel (Char. 34:0)
Enamel colour (CI 0.50)	Orangish (Char. 17:0)	Orangish (Char. 17:0)	Orangish (Char. 17:0)	<u>Yellowish</u> (Char. 17:1)
Palatal keel (CI 0.923)	Absent (Char. 26:0)	Absent or present (Char. 26:0-1)	Absent or present (Char. 26:0-1)	Absent or present (Char. 26:0-1)
Alisphenoid ossification (CI 1.00)	Partial or complete (Char. 29:0-1)	Partial or complete (Char. 29:0-1)	Partial or complete (Char. 29:0-1)	Complete (Char. 29:1)
Auditory bullae with link (CI 0.895) or dorsal contact with alisphenoid (CI 0.8)	With no link or contact (Char. 28:0; Char. 30:0)	<u>Link present</u> or absent (Char. 28:0-1) and no dorsal contact (Char. 30:0)	With no link (Char. 28:0) and dorsal <u>contact can be present</u> or not (Char. 30:1)	With no link or contact (Char. 28:0; Char. 30:0)
Pterygoid linked to auditory bullae (CI 0.944)	Absent (Char. 27:0)	Absent or present (Char. 27:0-1)	Absent (Char. 27:0)	Absent (Char. 27:0)
Dorsal roof of the external auditory meatus (CI 0.250)	<u>Not keeled</u> (Char. 31-0)	Keeled (Char. 31-1)	Keeled (Char. 31-1)	Keeled (Char. 31-1)
Coronoid process (CI 1.00)	<u>Reduced</u> or developed (Char. 37:1-2)	Developed (Char. 37:2)	Developed (Char. 37:2)	Developed (Char. 37:2)
Angular process (CI 0.958)	Narrow or wide with dorsoventrally alar projections (Char. 36:1)	Narrow or wide with dorsoventrally alar projections (Char. 36:1)	Narrow without alar projections (Char. 36:0)	Narrow or wide with dorsoventrally alar projections (Char. 36:1)

†B2 of posterior quills has the same colour tones of anterior quills.
Only adult and non-pregnant specimens were considered to obtain the body measurements.
Exclusive character conditions for each morphotype are underlined.

By comparing cranial measurements across the morphotypes, the first two principal components (together explained 52.4% of the variation) show that the three species of *C. prehensilis* complex occupy different morphospaces (Figure 6). The two subspecies of *C. longicaudatus* show a marked overlap. The four taxa, however, can be clearly separated in the discriminant analysis (Figure 6). The correct classification percentage among the three species after leave-one-out cross-validation is 93% (*C. prehensilis*: 81.2%, *C. longicaudatus*: 97.7%, *C. baturitensis*: 92.3%).

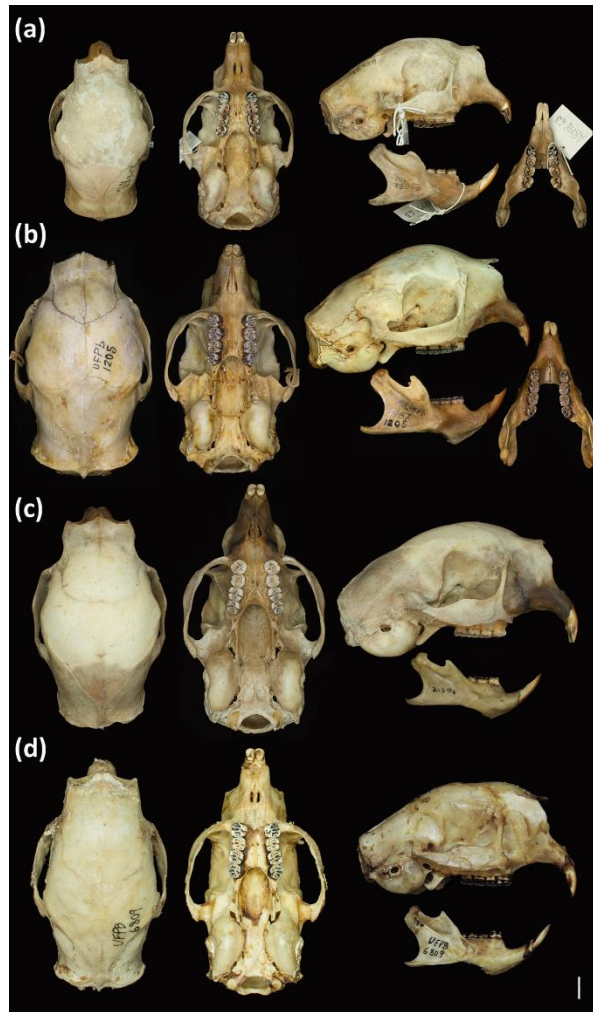


Figure 5. Skulls and mandibles of *Coendou prehensilis* complex morphotypes. (a) Skull and mandible of the neotype of *Coendou prehensilis* (MNRJ 73383). (b) skull and mandible of *C. longicaudatus longicaudatus* (UFPB 1205 from Samuel Hydroelectric Dam, Candeias do Jamari, Rondônia, Brazil). (c) Skull (MZUSP 32335, from Manso Hydroelectric power dam, Chapada dos Guimarães, Mato Grosso, Brazil) and mandible (FMNH 21396, from Buena Vista, Santa Cruz, Bolivia) of *C. longicaudatus boliviensis*. (d) Skull and mandible of the holotype of *Coendou baturitensis* (UFPB 6809, from Baturité range, Ceará, Brazil). Scale bar 10mm.

The separation of *C. prehensilis* from the other two species along the DFA2 axis is mainly related to its smaller size, longer maxillary toothrow, narrower P4 and narrower braincase (Figure 6, Table S3). *Coendou baturitensis* is clearly differentiated from *C. longicaudatus* along the DFA1 axis. The former has longer nasals, larger M1, higher rostrum, and narrower zygomatic breadth in relation to *C. longicaudatus* (Table 3, Figure 6). In addition, the two subspecies of *C. longicaudatus* cluster apart along the DFA3, where *C. l. longicaudatus* show longer zygomatic length, deeper upper incisors, shorter upper molars row, a narrower nasal aperture and a shorter diastema when compared to *C. l. boliviensis* (Tables 3, Figure S1). Interestingly, we found the two subspecies of *C. longicaudatus* tend to have longer tails

(averaging about 102.3% of HBL for *C. l. boliviensis*, and 106.3% for *C. l. longicaudatus*) than *C. baturitensis* (average 86.5% of HBL) and *C. prehensilis* (average 97%) (Table 2).

Table 3: Cranial measurements by morphotype of *C. prehensilis* complex. Mean \pm Standard deviation (Min–Max) N.

Measurements	<i>C. prehensilis</i>	<i>C. l. longicaudatus</i>	<i>C. l. boliviensis</i>	<i>C. baturitensis</i>
CIL	86.2 \pm 5.5 (75.7–94.4) 14	92.9 \pm 4.9 (81.6–101.6) 18	94.1 \pm 3 (89.1–99.4) 19	94.3 \pm 4.3 (89.9–103.3) 12
LD	23.5 \pm 2.7 (18.3–27.7) 15	24.7 \pm 2.4 (20–28.1) 18	25.7 \pm 1.4 (23.8–28.9) 19	25.7 \pm 1.9 (22.2–29.9) 13
LIF	7.5 \pm 1.61 (5.1–9.8) 15	8.4 \pm 1.7 (5.8–11.7) 18	8.3 \pm 1.1 (7.0–10.7) 18	7.4 \pm 1.7 (4.2–9.6) 13
BIF	4.2 \pm 0.5 (3.4–5) 15	4.8 \pm 0.7 (3.9–6.1) 18	4.9 \pm 0.6 (3.6–6) 18	3.6 \pm 0.5 (2.7–4.4) 13
MTR	19.4 \pm 0.8 (18.2–20.6) 14	20.4 \pm 1 (18.8–22.1) 17	20.7 \pm 1.1 (18.8–22) 18	21.3 \pm 0.9 (19.2–22.7) 11
LM	14.5 \pm 0.5 (13.7–15.3) 14	15.3 \pm 0.6 (14.5–16.6) 17	15.4 \pm 0.9 (13.1–16.4) 18	15.7 \pm 0.7 (13.9–16.5) 11
BP4	5.3 \pm 0.4 (4.7–5.9) 15	5.9 \pm 0.4 (5.2–7) 17	5.8 \pm 0.3 (5.2–6.2) 18	5.9 \pm 0.4 (5.2–6.5) 13
BM1	5.4 \pm 0.31 (4.9–5.7) 15	5.6 \pm 0.3 (5–6.3) 17	5.5 \pm .03 (5–5.9) 18	5.5 \pm 0.3 (5.1–6.1) 12
APB	5.2 \pm 0.61 (4.1–6.1) 15	6.7 \pm 1 (3.5–8) 18	6.1 \pm 0.7 (4.7–7.2) 19	5.3 \pm 0.8 (3.7–6.6) 13
PPB	8.3 \pm 0.6 (6.9–8.9) 14	9.8 \pm 0.9 (7.7–11.6) 18	9.3 \pm 1 (6.8–10.8) 19	9.2 \pm 0.8 (8.1–10.5) 11
PZB	51.3 \pm 1.9 (48.1–54.8) 14	55.5 \pm 2.8 (51.1–61.2) 18	55.4 \pm 2 (51.1–58.8) 18	53.6 \pm 1.6 (51.0–55.9) 13
HIF	13.1 \pm 1.5 (10.5–14.9) 15	14.7 \pm 2.2 (9.8–17.4) 18	14.5 \pm 1.1 (12.1–16.4) 19	14.8 \pm 1.4 (12.9–16.5) 13
ZL	36.6 \pm 3.73 (31.1–41.6) 15	40.4 \pm 3.5 (36.2–49.8) 18	37.3 \pm 2.4 (32.5–43.1) 19	36.0 \pm 2.4 (33.0–41.3) 13
LN	32.93 \pm 4.4 (26.24–40.59) 12	31.6 \pm 5.3 (20.6–38.9) 10	33.9 \pm 3 (28.8–38.5) 16	41.3 \pm 3.8 (36.3–48.7) 11
BNA	22.54 \pm 1.48 (20.13–25.54) 15	22.9 \pm 1.2 (20.9–24.9) 17	24.0 \pm 1.2 (22.4–26.5) 18	23.8 \pm 1.2 (21.5–25.6) 13
BB	36.52 \pm 1.47 (32.55–38.52) 15	39.3 \pm 1.8 (35.8–42.4) 18	39.7 \pm 1.8 (37.2–44.4) 19	39.0 \pm 0.9 (37.6–40.7) 13
DI	4.39 \pm 0.2 (4.06–4.68) 15	4.6 \pm 0.5 (4–6) 18	4.4 \pm 0.3 (4.1–5) 17	4.5 \pm 0.3 (4.0–5.2) 12
BIT	6.95 \pm 0.84 (5.82–8.43) 15	7.1 \pm 0.5 (6.3–7.8) 17	6.9 \pm 0.5 (6.1–7.7) 16	7.5 \pm 0.3 (7.1–8.0) 11
AHR	27.12 \pm 1.92 (22.66–30.05) 15	27.8 \pm 1.8 (25.3–30.7) 16	28.4 \pm 1.6 (25.6–32.4) 19	30.7 \pm 2.1 (27.7–33.5) 13
PHR	34.11 \pm 3.46 (27.4–42.25) 15	37.7 \pm 6.7 (22.4–46.9) 18	40.4 \pm 2.9 (35.9–45.9) 19	43.0 \pm 3.9 (37.9–50.0) 13

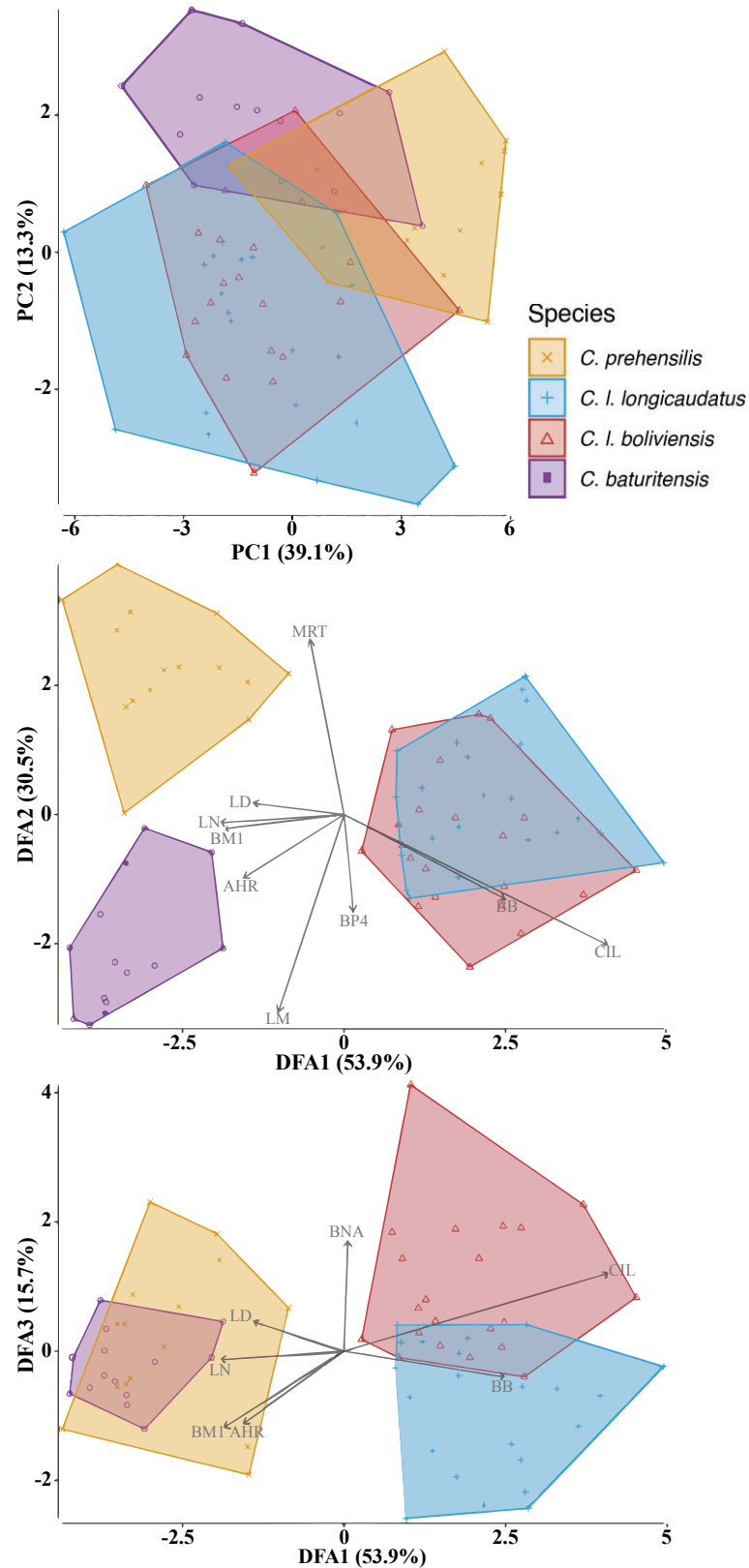


Figure 6. Scatterplot of the first and second principal components (top panel), the first and second discriminant axes (centre), and the first and third discriminant axes (bottom panel) of the log-transformed cranial measurements of the *Coendou prehensilis* complex clustered by morphotypes corresponding to species/subspecies.

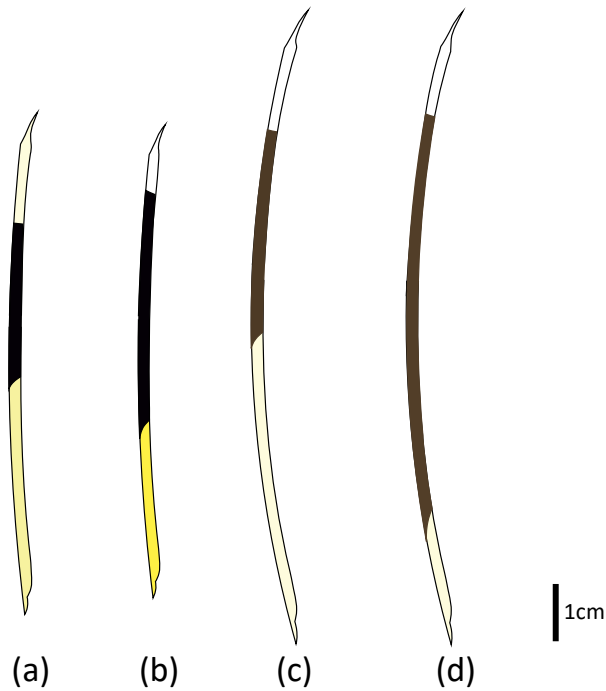


Figure 7. Scheme of band colour and length of tricoloured quills of the four morphotypes of the *Coendou prehensilis* complex corresponding to characters 10 to 13. (a) Tricoloured quill of *C. prehensilis* (Char. 10:2 CI 1.00, 11:1 CI 0.75, 12:0 CI 0.50, 13:2 CI 0.50.), (b) tricoloured quill of *C. longicaudatus longicaudatus* (Char. 10:2, 11:0, 12:1, 13:0). (c) tricoloured quill of *C. longicaudatus boliviensis* (Char. 10:1, 11:0, 12:0, 13:1). (d) tricoloured quill of morphotype *C. baturitensis* (Char. 10:1, 11:0, 12:2, 13:0).

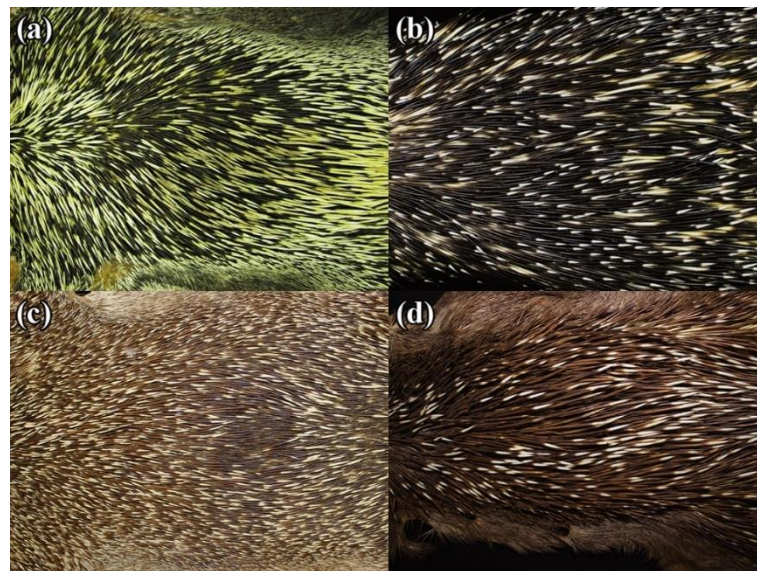


Figure 8. Colour pattern of *Coendou prehensilis* complex morphotypes. The anterior part of dorsum is on the left and posterior part on the right. (a) *C. prehensilis* (MNRJ 73383), note the quills with strong yellowish colour of B1/B3 and the short blackish B2; (b) *C. longicaudatus longicaudatus* (UFPB 1205), note the quills with very short whitish B3; (c) *C. longicaudatus boliviensis* (FMNH 21709), note the long whitish B3 and short brownish B2; and (d) *C. baturitensis* (MZUSP 13486), note the very long brownish B2 and short whitish B3. The

state of character 9 is: 2 in *Coendou longicaudatus longicaudatus* and *C. baturitensis*, 3 in *C. prehensilis* and *C. longicaudatus boliviensis*.

The localities of the specimens for each morphotype of the *C. prehensilis* complex delimit allopatric distributions for the four morphotypes (Figure 9). The figure 9 considers geographical information of specimens examined morphologically and also the sequenced specimens with congruent morphotypes.

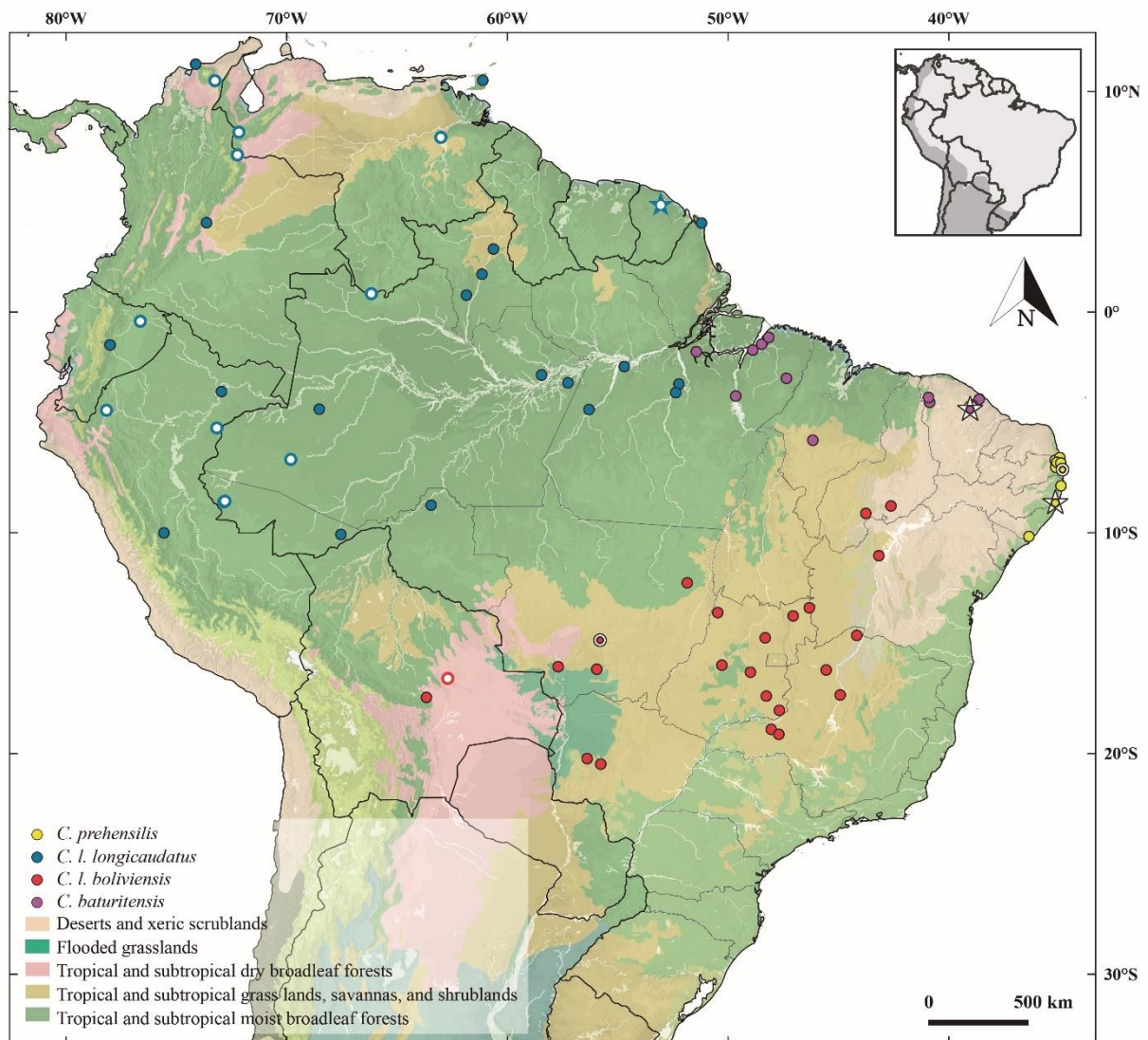


Figure 9. Localities of specimens of the *Coendou prehensilis* complex mapped onto South American biomes. The species and subspecies are represented by different colours. The simple coloured points represent localities of specimens examined only morphologically, the white points with inner coloured points are localities with specimens sequenced for *cyt b* and analysed morphologically. The white spotted points are localities exclusively with specimens exclusively sequenced for *cyt b*. The stars represent type localities. The upper-right insert shows the distribution of *Coendou prehensilis* in light grey according to IUCN.

3.3.4 Phylogenetic Relationships

The Maximum Parsimony tree obtained from morphological data (MP1) analysis has 30 parsimony informative characters. The consensus tree has length 124 (min 62, max 161), Consistency Index (CI) 0.50 and a Retention Index (RI) of 0.37. Eight morphological characters are uninformative (autapomorphies) and 29 are informative. The MP1 consensus tree shows the four morphotypes of *C. prehensilis* with *Coendou quichua* in a polytomy, *C. roosmalenorum* and *C. melanurus* are grouped together, and another polytomy comprised of the morphotypes of the hairy dwarf porcupines of eastern Brazil, *C. insidiosus* and *C. spinosus* (Figure S2). See supporting information (Table S1) for the transformation list.

The Maximum Likelihood (ML) and Bayesian Inference (BI1) analyses of the cytochrome *b* generated consensus trees with the same topology (Figure S3). The genus *Coendou* has three well-supported clades of species with a topology similar to the trees obtained by Voss *et al.* (2013). Most *Coendou* species show well-supported monophyletic groups except *C. spinosus* which is paraphyletic (Figure S3). The *Coendou prehensilis* complex is recovered as a monophyletic clade with high support (BS 96, PP 100) composed of three main lineages. The first divergence separates the neotype of *Coendou prehensilis* and one individual from João Pessoa, Paraíba (Northeastern Brazil), from all other species of the complex. The second divergence separates three individuals from the Baturité range, the type locality of *Coendou baturitensis*, from a clade encompassing all other *C. prehensilis* complex individuals from central and western Amazon and Cerrado biomes. This latter clade includes individuals of *C. longicaudatus longicaudatus* and *C. longicaudatus boliviensis*. These three main clades are well supported in both ML and BI. Specimens of *C. l. boliviensis* are monophyletic (BS 97, PP 100) within a polytomy of *C. longicaudatus* lineage. Therefore, *C. l. longicaudatus* is a paraphyletic clade.

The trees obtained by Maximum Parsimony (MP2) and Bayesian Inference (BI2) with combined morphological and molecular datasets show fully congruent topologies with those inferred from the molecular dataset, ML and BI1 trees (Figure 10), however, they showed a stronger resolution than the molecular dataset alone. Almost all species presented posterior probability values (PP) of 100 and bootstrap support (BS) values above 90%. The MP2 tree has a length of 1364 (min. 795, max. 4186), a CI of 0.583 and a RI of 0.832. A total of 694 characters are constant, 123 characters are uninformative (autapomorphies) and 360 are informative. Partitioned Bremer indices show that almost all clades have congruent

morphological and molecular signals under parsimony except for the genus *Coendou* and the *Coendou prehensilis* complex, in which signal conflict is detected (Figure 10).

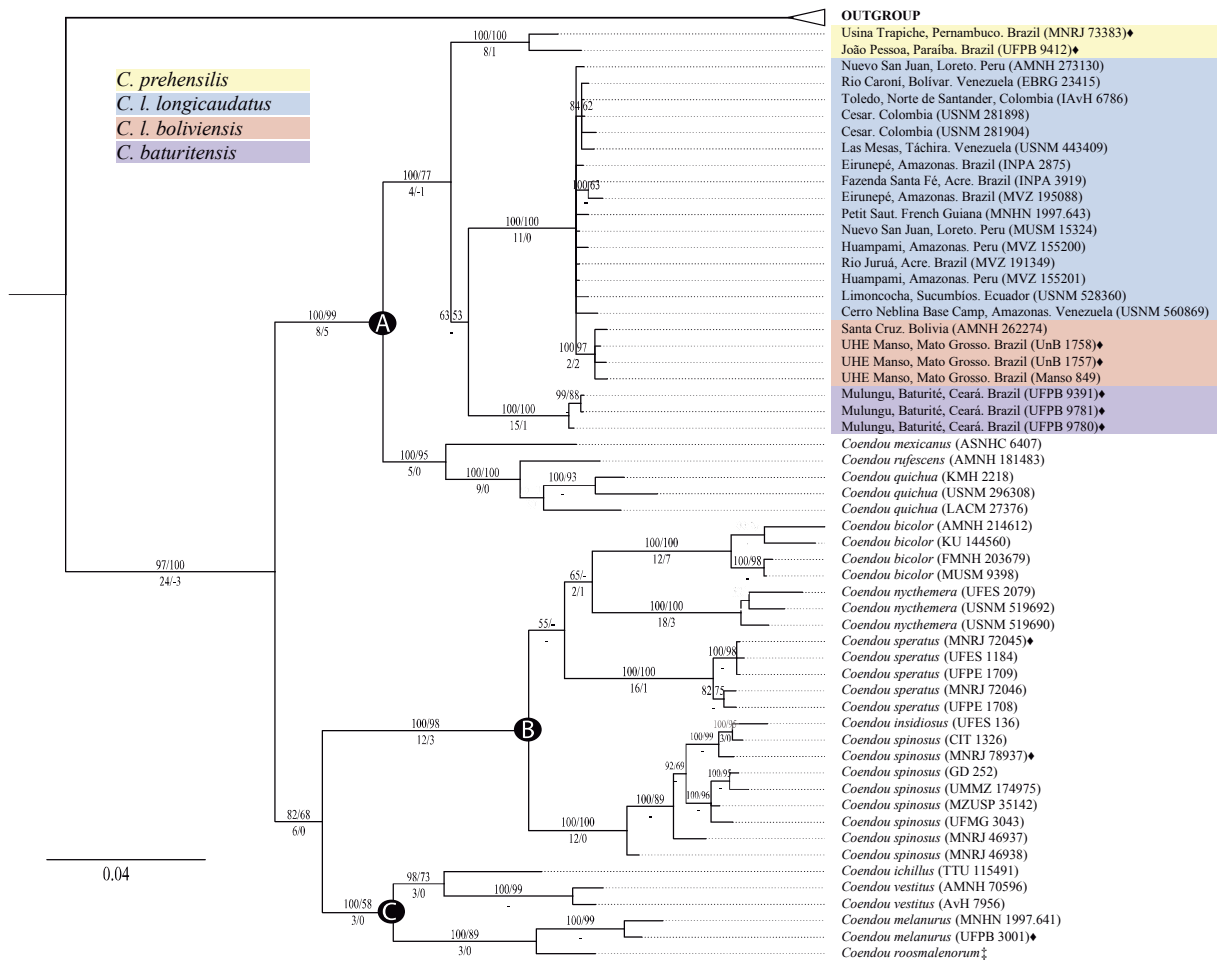


Figure 10. Phylogenetic tree of the Erethizontidae obtained by Bayesian Inference (BI2) with morphological and *cyt b* sequences combined. The sequences of each morphotype of *Coendou prehensilis* complex are grouped by colours with the localities replacing the species name. The values above the branches represent the posterior probability values of BI2 branches (left) the bootstrap proportion of MP2 branches (right). The values below the branches are the partitioned Bremer decay index for the molecular and morphological datasets respectively. Capital letters at nodes correspond to the main clades with subgeneric names A: *Coendou*, B: *Sphiggurus*, C: *Caaporamys* subgen. nov.

◆ Specimens examined in this study, ‡ Only morphological characters available.

All individuals attributed to *C. prehensilis* and *C. baturitensis* were consistently recovered as monophyletic allopatric lineages and therefore considered as valid species. The individuals of the *C. prehensilis* complex from central-western Amazon and Cerrado biomes are respectively referred to *Coendou longicaudatus longicaudatus* and *C. longicaudatus boliviensis*. The subspecies classification is based on the fact they are easily diagnosable externally, show cranial morphometric differences, occur in different biomes, but are not

reciprocally monophyletic. Therefore, we recognize three species as part of the *C. prehensilis* complex: *Coendou prehensilis* (Linnaeus, 1758), *Coendou baturitensis* Feijó & Langguth, 2013, and *Coendou longicaudatus* Daudin, 1802 with two subspecies.

3.4 Discussion

3.4.1 Taxonomic assessment

Our comprehensive study of the *Coendou prehensilis* complex, combining morphological, morphometric and molecular datasets from a large part of its distribution, allowed us to clarify the taxonomy of this widespread Neotropical group. Our main findings include the recognition of three species previously held within *Coendou prehensilis*, confirming the specific status of *Coendou baturitensis* and revalidating *Coendou longicaudatus*. The inclusion of *C. baturitensis* individuals in the phylogenetic analyses and an additional sequence of *C. prehensilis* from Northeastern Brazil were decisive for our new classification. It is noteworthy that no previous systematic revision of the *C. prehensilis* complex examined animals from the Atlantic Forest, Cerrado, Chaco, Caatinga and Amazonian biomes altogether, allowing the identification of the autapomorphies, synapomorphies and combination of diagnostic characters here presented. Indeed, prior to the designation of the neotype of *Coendou prehensilis* (Leite et al., 2011), no taxonomic study had examined porcupines from the Brazilian Northeastern region. Most of the studies limited their analyses to specimens from Amazonia Forest, Bolivian Chaco or Central Brazils. Therefore, the authors had used either *longicaudatus* or *boliviensis* specimens as representative of the morphological characteristics of *C. prehensilis* to compare with other *Coendou* morphotypes, in order to describe new species or to synonymize taxa. Leite *et al.* (2011) and Feijó & Langguth (2013) were the first to compare and describe specimens of *Coendou prehensilis* complex from Northeastern Brazil. It is also noteworthy that at least three aspects of the systematics of the *Coendou* are still unclear: 1) the precise phylogenetic position of *C. rosmalenorum*, for which no DNA sequence data are available; 2) The relationship between *C. insidiosus* and *C. spinosus*, which seem to be not reciprocally monophyletic (as also noted in Mendes Pontes et al., 2013); and 3) the relationships within the *C. longicaudatus* subspecies, which requires the analysis of additional molecular markers for an improved resolution

3.4.2 Subgeneric classification of *Coendou*

Traditionally, the species of *Coendou* were divided into two genera (or subgenera): *Sphiggurus* F. Cuvier, 1823 and *Coendou* Lacépède, 1799 (Allen, 1904; Cabrera, 1961; Ellerman, 1940; Feijó & Langguth, 2013; Husson, 1978; Tate, 1935). This classification was based on the nasofrontal sinus inflation and/or on the length of the dorsal fur (Bonvicino et al., 2002, 2008; Feijó & Langguth, 2013; Voss, 2011, 2015; Woods & Kilpatrick, 2005). Nevertheless, these characters were considered insufficient to distinguish the two (sub)genera (Emmons, 1997; Handley & Pine, 1992; Voss, 2011) and the dorsal fur was recovered as a homoplastic trait (Voss et al., 2013), leading recent authors to abandon the subgeneric classification in *Coendou* (Voss, 2015; but see Feijó & Langguth, 2013). In this study, we recovered three well-supported lineages within *Coendou* that show distinct morphological traits (Figure 7). A similar topology was found by Voss *et al.* (2013), but their third lineage (our clade C in Figure 10) had weak support. Additionally, for Voss *et al.* (2013), the three lineages were not morphologically diagnosable. Here, we advocate for the subgeneric classification in *Coendou* given that each of the three main clades have unique morphological synapomorphies and were consistently recovered as monophyletic in our analyses.

The subgeneric groups are designated by their oldest available names for the genus nominal taxa. Group A represents the subgenus *Coendou*, based on *Coendou prehensilis*, the nominotypical taxon, and is composed of the Andean and Trans-Andean porcupines: *Coendou (Coendou) prehensilis*, *C. (Co.) longicaudatus*, *C. (Co.) baturitensis*, *C. (Co.) quichua*, *C. (Co.) mexicanus* and *C. (Co.) rufescens*. This group has the following putative synapomorphies: the quills are thick, the dorsal crest is composed of flexible quills, the ventral pelage is rough and the tail exhibits tricoloured and bicoloured quills. No specimens of *C. (Co.) mexicanus* and *Coendou (Co.) rufescens* were examined. Group B represents the subgenus *Sphiggurus*, based on *Sphiggure spinosa* F. Cuvier, 1823 (its original spelling, but maintained as *Sphiggurus* due to its prevailing subsequent usage as in Voss, 2011:6) and it is composed of five species: *Coendou (Sphiggurus) insidiosus*, *C. (S.) spinosus*, *C. (S.) nycthemera*, *C. (S.) bicolor* and *C. (S.) speratus*. These species possess thin quills, the dorsal crest is composed of flexible tricoloured or bicoloured quills, soft ventral pelage and the tail exhibits tricoloured and bicoloured quills. There are four additional valid generic names for porcupine species: *Sinetheres* F. Cuvier, 1823, *Cercolabes* Brandt, 1835, *Echinoprocta*, Gray, 1865 and *Cryptosphingurus* Miranda Ribeiro, 1936. However, their type species are grouped in the two former subgenera. Therefore, the group C has no subgeneric name available as determined by

the articles 42-44 of the International Code of Zoological Nomenclature, so we propose the name *Caaporamys* **subgen. nov.** (Caaporã's Rat, masculine. Zoobank's act [DC888480-8EAF-4C0A-9AC1-2BF4B3ED8590](https://zoobank.org/DC888480-8EAF-4C0A-9AC1-2BF4B3ED8590)). Caaporã (or Caipora) is an Amazonian indigenous deity, guardian of the animals; the name means “who lives in the forest” in Tupi-Guarani languages, the most widespread indigenous linguistic family of Brazil. *Caaporamys* comprises the smallest species of *Coendou* and is equivalent to the *vestitus* group of Voss and Silva (2001). It is composed of five species: *Coendou (Caaporamys) melanurus* designated as type species, *C. (Ca.) vestitus*, *C. (Ca.) pruinusosus*, *C. (Ca.) ichillus* and *C. (Ca.) roosmalenorum*. These species have thin quills, the dorsal crest is composed of tricoloured bristle-quills, soft ventral pelage and the tail has an overall blackish colour because of its bicoloured quills with a long and blackish B2.

3.4.3 Quill banding colour pattern as an important taxonomic tool for porcupines

The quills are an important taxonomic character in the family Erethizontidae (Handley & Pine, 1992; Leite et al., 2011; Mendes Pontes et al., 2013; Voss & Angermann, 1997; Voss & da Silva, 2001). Although there are numerous studies describing the functional morphology of the erethizontid quills (e.g., Cho et al., 2012; Vincent & Owers, 1986; Yang et al., 2013), the distinction of functional quill types are not widely used as taxonomic characters. The quills of erethizontids have a cortex compounded of juxtaposed scales, which are the barbs in the *mucronis* region (Chernova, 2002; Cho et al., 2012; Vincent & Owers, 1986). The diversity of function of quill types in *Coendou* species likely relates to distinct defensive strategies. For example, the long tricoloured quills have barbless *mucronis* while short bicoloured quills have barbed *mucronis*. The barbed *mucronis* represents an anchoring system in the tegument of a potential aggressor (Chernova, 2002; Cho et al., 2012; Vincent & Owers, 1986), what makes the quills commonly found in agonistic encounters with domestic dogs (e.g., Johnson et al., 2006; Rangel & Neiva, 2013) and sometimes lethal to large predators as cougars, *Puma concolor* (as reported by Elbroch et al., 2016). The fact that the long tri-banded quills are barbless suggests the importance of the preservation of these quills when a porcupine is attacked, with potential trade-offs between the cost of loss and protection types. In our study, we show that the distribution of long tricoloured and short bicoloured quills along the body is useful to differentiate species and subspecies in *Coendou* and might also reflect distinct evolutionary strategies of porcupines' lineages.

Previous taxonomic studies on quill morphology of porcupines applied a divergent nomenclature from the functional trichology studies. The term ‘tip’ refers to the n^{th} band in taxonomic works, referring to the region homogeneously coloured at the distal part of the hair (e.g., Leite et al., 2011; Mendes Pontes et al., 2013), while the same term refers to *mucronis* in functional trichology descriptions (Chernova, 2002; Cho et al., 2012; e.g., Vincent & Owers, 1986). The term ‘tip’ has also been used to refer to the n^{th} band and the *mucronis* in the same work (e.g., Voss & da Silva, 2001). The confusion of the term “tip”, in this case, does not make clear whether the *mucronis* region is equivalent to band n . Moreover, the name “tip” does not represent the mechanical function performed by *mucronis*. Therefore, our nomenclature aims to highlight the mechanical and functional differences among the regions of quills.

The colour tones and length of each band and its position in the bicoloured and tricoloured quills define the colour pattern of the porcupine. The colour patterns appear to be conservative in the species of the *Coendou prehensilis* complex as well as almost all of the examined species of erethizontid, except for the *C. insidiosus/C. spinosus* complex (Caldara Júnior & Leite, 2012). Therefore, our study shows that the location and banding pattern of each type of quill on the porcupine dorsum has proven to be of high value as diagnostic characters. Furthermore, the coloration of the porcupine quills is aposematic, an ecological trait (Inbar & Lev-Yadun, 2005; Stankowich & Campbell, 2016), which reinforces its importance in porcupine biology. We thus encourage future taxonomic studies on porcupines to explore the colour tones and distribution of the quill types. Additionally, this trait can be easily assessed in live animals or on sylvatic and domesticated predators, which can be a useful tool for species identification in the field or occurrence confirmation.

3.4.4 Biogeography of Neotropical forested biomes

Because of their herbivorous diet, arboreal habits, and medium size, porcupines are strongly associated with forested ecosystems. The distribution of the four taxa of the *C. prehensilis* complex suggests that the species occur in both dry and moist forests, as well as in forests ecosystems within savannahs, e.g., in the Cerrado biome. Occupation of these ecosystems is emblematic in *C. baturitensis* that occurs both in the eastern Amazon forests and in mid altitude moist forest enclaves remnants within the Caatingabiome, generally grouped under the term *brejos de altitudes* or moist altitude forests (Moro et al., 2015), what reinforces previously known past connections between the Amazon and the Atlantic forests (Costa, 2003; Vanzolini & Williams, 1981), the two major tropical moist forest biomes of the Americas.

Moreover, the *brejos de altitude* fauna is usually composed of endemic species of forest dwellers. Some species found in *brejos de altitude* have a disjunct distribution with their populations or sister species in the eastern portion of the Amazon, including reptiles (e.g., genera *Atractus*, *Enyalius*, *Pseustes*), anurans (e.g., genus *Adelophryne*), birds (e.g., *Pipra fasciicauda* and *Selenidera gouldii*), and mammals (e.g., *Makalata*, *Proechimys roberti*) (Borges-Nojosa, 2007; Girão et al., 2007; Leite & Loss, 2015; Loebmann & Haddad, 2010). This pattern is also found in other species from the northern Atlantic forest Lowlands as in the howler monkey *Alouatta belzebul* and the kinkajou *Potos flavus*, or at the generic and specific level in other small mammals (Costa et al., 2000).

The available information about the species limits in the *C. prehensilis* complex suggests they are allopatric and loosely associated with particular biomes and ecoregions. However, sympatry among species from distinct subgenera seems to be common in Neotropical porcupines (as reported by Gregory et al., 2015; Menezes et al., 2020; Ramírez-Chaves et al., 2016, 2019). For example, *C. (Co.) baturitensis* is sympatric with *Coendou (Sphiggurus) nycthemera* in the eastern amazon forest, and *C. (Co.) l. boliviensis* exists in sympatry with *Coendou (Sphiggurus) spinosus* in the transition zone between Atlantic Forest and Cerrado in southeastern Brazil (see the examined specimens in supporting information). The distribution of *C. (Co.) l. longicaudatus* overlaps with almost all Amazonian porcupine species, with documented sympatry with *Coendou (Sphiggurus) bicolor* and *Coendou (Caaporamys) ichillus* (Menezes et al., 2020). *C. (Co.) prehensilis* occurs in sympatry with *Coendou (Sphiggurus) speratus* in the Pernambuco Endemism Centre (PEC) (Feijó & Langguth, 2013; Mendes Pontes et al., 2013). This ecoregion is one of the most important Brazilian biodiversity hotspots and encompasses a coastal block of Atlantic Forest between the states of Alagoas and Rio Grande do Norte. The area represents less than 5% of the original Brazilian Atlantic Rainforest, but it is home to more than 60% of all the bird species and 8% of the vascular plants related in this biome (Tabarelli & Roda, 2005). In addition to *C. prehensilis* and *C. speratus*, there are other mammal species endemic to PEC such as *Sapajus flavius*, *Hylaeamys oniscus* and *Sylvilagus brasiliensis* (Garbino et al., 2018; Mendes Pontes et al., 2016).

3.4.5 Conservation

Our new taxonomic arrangement will likely cause profound changes in the evaluation of the conservation status of the whole group. *Coendou prehensilis* is considered as Least Concern by international (Marinho-Filho & Emmons, 2016) and Brazilian (ICMBio, 2018) red

lists due to its previous wide distribution and presumed large population. Our study, however, shows that this species is restricted to the Pernambuco Endemism Centre (Figure 9), which despite its impressive ecological importance, has lost 94.6% of its original forest cover mainly due to sugarcane plantation over the last 500 years (Mendes Pontes et al., 2016; Ribeiro et al., 2009). This habitat loss is reflected by a severe defaunation, resulting in the local extinction of seven species of medium and large-sized mammals, which represents 20.6% of the original richness of this group (Garbino et al., 2018). It is relevant to point out that the other endemic mammal species from PEC are threatened: the blonde capuchin *Sapajus flavius*, the tapeti *Sylvilagus brasiliensis*, and the congeneric species *Coendou (S.) speratus* are considered as endangered by the IUCN (Roach & Mendes Pontes, 2020; Ruedas & Smith, 2019; Valença Montenegro et al., 2020) and the Brazilian Red List (ICMBio, 2018). In addition to endemism, *S. flavius* and *C. speratus* share similar habits, habitats and threats with *C. prehensilis*. Therefore, it is likely to expect an increase in conservation concerns for the Brazilian Porcupine. Among the 11 localities here recorded for *C. prehensilis*, nine are from the Atlantic Forest of Paraíba state, where most of the specimens were collected in the protected area Guaribas Biological Reserve (Feijó et al., 2016). This area could be prioritized to develop biological and ecological research regarding this species and to promote conservation actions.

The conservation status of *Coendou baturitensis*, currently classified as Data Deficient (ICMBio, 2018; Roach, 2016), also requires a re-evaluation. In the northeastern portion of Brazil, this species is distributed in or close to forested remnants (*brejos de altitude*) inserted in the Caatinga biome and that have faced accentuated deforestation, overexploitation of natural resources, introduction of invasive species, pollution of water resources, and real estate speculation (de Oliveira et al., 2007; Fernandes-Ferreira et al., 2015; Tabarelli et al., 2010). The Amazonian populations are in one of the most threatened regions of this biome, the Eastern Amazon. This region faces high rates of deforestation caused by agriculture, livestock, logging and hydroelectric plants (Lees et al., 2016; Silva Junior et al., 2020; Vieira et al., 2008) including the Belo Monte Dam located in the Xingu River, the west limit of *C. baturitensis* distribution. In addition, the species is hunted mainly for food purposes throughout its range. In the Baturité range, for example, the hunting of this porcupine increases during the mango harvest, one of its favourite diet items according to local interviewees. Luckily, in some localities, there is a consumption taboo associated with *C. baturitensis*. The folk knowledge claims that the consumption of its meat can lead to bad luck (Alves et al., 2016).

The ample distribution of *Coendou longicaudatus* and its presence in several protected areas are certainly positive factors for its conservation status. Nevertheless, there are several threats associated with this species that are gradually and worryingly increasing. Deforestation in the Brazilian Amazon, Cerrado and Pantanal has sharply risen in the last years. Since 2013, official deforestation rates have been on an upward trend, worsening in the last two years. In 2019, the vegetational loss increased 34% when compared to 2018. The Brazilian Amazon, for example, lost 11,088 km² of forested area, the highest rate in the decade (Escobar, 2020; Silva Junior et al., 2021). Cerrado is one of the most impacted biomes in the world, with over 20,400 km² of native vegetation suppressed between 2017 and 2019 (Assis et al., 2019). Over 22,000 fires were recorded in Pantanal in 2020, the highest rate in its entire history and which surpasses the records of 2019, 2018 and 2017 together (INPE, 2021). The increased investment in livestock and soy production as well as the loosening of environmental laws are the main reasons for the documented loss in these biomes. Other causes include logging, mining, construction of dams, global climate changes, and the continuous use of fires for traditional and non-traditional communities for agricultural purposes (Fearnside et al., 2013; Pivello, 2011; Silva Junior et al., 2021; Sontner et al., 2017; Trigueiro et al., 2020). In addition, hunting of *Coendou* spp. for food use is also documented in these areas (Baía Júnior et al., 2010).

It is important to note that it is a major challenge to adequately estimate the impact of the threats discussed above on the populations of the *Coendou prehensilis* complex and therefore of all species and subspecies recognized in this study. Except for some restricted ecological records (e.g., Griffiths et al., 2020; Ramírez-Chaves et al., 2020), there is practically no research focused on their natural history such as reproduction, diet, population density and home range of this group. Thus, it is urgent to conduct studies to fill these gaps in order to establish accurate assessments and effective conservation strategies.

3.5 Taxonomic accounts

FAMILY ERETHIZONTIDAE Bonaparte, 1845

GENUS *COENDOU* Lacépède, 1799

3.5.1 *Coendou* (*Coendou*) *prehensilis* (*Linnaeus*, 1758)

Yellow Quill-Tipped Porcupine

Figures 5a, 7a, 8a, 11a, 12a

Type material: MNRJ 73383, neotype designated by Leite *et al.* (2011). Adult male collected by Antônio Rossano Mendes Pontes (field number ARMP 63) on May 12, 2009. The specimen consists of a well-preserved skin, skull and mandible (Figure 2a). The *cyt b* sequence of the neotype is archived in GenBank with accession number HM462243.

Type locality: “Asia, America meridionalis” (Linnaeus, 1758), posteriorly fixed to “Pernambuco” by Thomas (1911). The neotype was collected in Mata Xanguá, Usina Trapiche, municipality of Sirinhaém, state of Pernambuco, Brazil, coordinates 8°38'50"S 35°10'15"W, elevation 100 m (Leite *et al.*, 2011).

Etymology: *prehensilis* refers to the characteristic prehensile tail of the erethizontid porcupines.

Diagnosis: Small-medium sized porcupine (Table 2). *Coendou prehensilis* presents the dorsal crest composed mainly of tricoloured quills and the rump of bicoloured quills (Figure 11a). The brown villous pelage, sometimes tricoloured, never covers the quills in adults. The B1 of tricoloured and bicoloured quills is light yellowish on the cephalic portion and strongly yellowish on the rump, while intermediary yellow tones in the dorsal crest. The B2 is blackish and short compared to B1 and B3 in tricoloured quills. The B3 of tricoloured quills is white yellowish and sometimes half of B2 length (Figure 7a). The general body colour pattern is light yellowish with dark brownish dashes, due to the predominance of tricoloured quills with long B3 (Figure 8a). The tricoloured quills of the dorsal crest are shorter than 10 cm and are slightly curved. Among the four taxa of *C. prehensilis* complex, the skull of *C. prehensilis* (Figure 5a) is the smallest and shows the lowest rostrum (Table 3). The nasals have only the posterior half inflated and the naso-frontal suture is not close to the postorbital processes in dorsal view. The interparietal is short and triangular shaped and the fronto-parietal and parietal-interparietal sutures are distant in dorsal view. Some specimens of *C. prehensilis* (e.g., MZUSP 8456, UFPB 6762, UFPB 9516, UFPB 9790) exhibit the lacrimal sutures not completely obliterated in adults, a unique character among *Coendou*. The lacrimal sutures are not visible even in neonates of other species. The neonates of *C. prehensilis* have cream-coloured pelage (Figure 12a). The neonates are born with thin white quills on their dorsum covered by villous furs. The body sides and paws have a lighter cream-coloured fur pattern than the dorsum. The skin of the tail and paws are dark greyish.

Distribution: *Coendou prehensilis* is restricted to the north portion of the Atlantic Forest, where its south limit is the right margin of the São Francisco River, region known as the Pernambuco Endemism Centre (Figure 9). Examined specimens were collected in three

Brazilian States: Paraíba (cities of Cabedelo, João Pessoa, Mamanguape, Sapé, Rio Tinto and Mataraca), Pernambuco (Igarassu and Sinharém), and Alagoas (Penedo, Murici).

Remarks: *Coendou prehensilis* is the type species of the genus *Coendou* Lacépède, 1799. Except for two studies (Feijó & Langguth, 2013; Leite et al., 2011), all previous papers referring to “*Coendou prehensilis*” actually describe and present data from *Coendou longicaudatus* (Menezes et al., 2020; Moraes-Santos, 1997; Ramírez-Chaves et al., 2020; e.g., Roberts et al., 1985) and even *Coendou baturitensis* (as in Moraes-Santos, 1997). Therefore, natural history information about this species is virtually unknown.

Eight of the 18 examined specimens of this species were collected between 2015 and 2017, all from Paraíba State. It reflects the scarcity of past research efforts directed to porcupines in Northeastern Brazil.

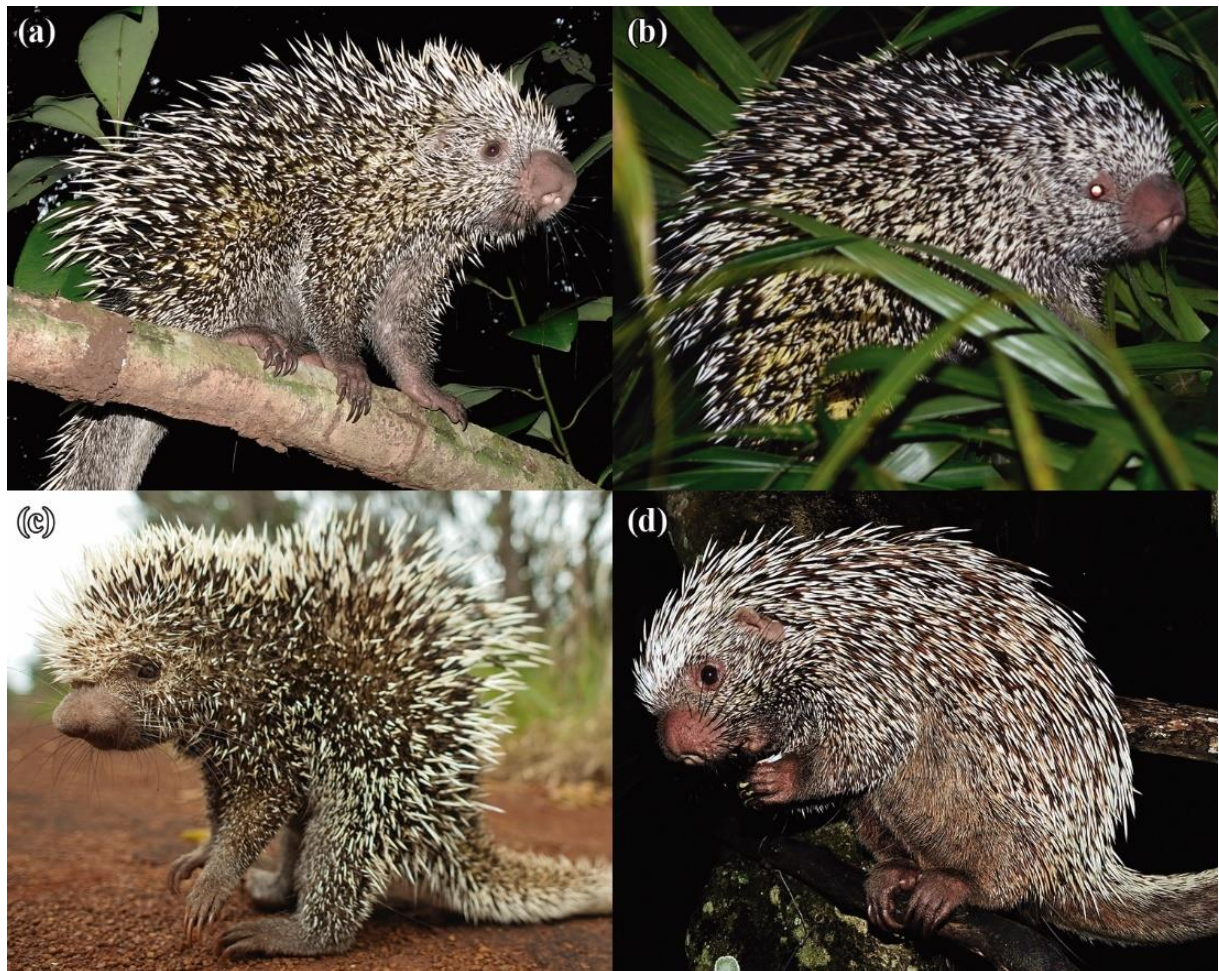


Figure 11. Living adults of *C. prehensilis* complex: (a) *Coendou prehensilis* from the Estação Ecológica de Murici, Alagoas state, Brazil. Note the bright yellowish colour of B1 of the quills in the rump and the long white B3. (b) *Coendou longicaudatus longicaudatus* from San Vicente del Caguán, Caquetá, Colombia. Note the short white B3. (c) Adult *Coendou longicaudatus boliviensis* from Volta Grande Environmental Station, Minas Gerais, Brazil. Note the long white B3 and short brownish B2 of the quills in the dorsum. (d) *Coendou baturitensis* from Mulungu,

Ceará, Brazil. Note the long brownish B2 and short whitish B1 and B3. Photographers (a-d): Marco Antonio de Freitas, Carlos A. Aya, João Marcos Rosa and Sanjay Veiga.



Figure 12. Dorsal view of neonates of (a) *C. prehensilis* (UFPB 10896) from SEMA 1, REBIO Guaribas, Mamanguape, Paraíba, Brazil; (b) *C. longicaudatus longicaudatus* (UFPB 1237) from Candeias do Jamari, Rondônia, Brazil; (c) *Coendou longicaudatus boliviensis* (UFPB 1616) from Nova Ponte Hydroelectric Dam, Nova Ponte, Minas Gerais, Brazil; (d) *Coendou baturitensis* (MNRJ 75670) from São Benedito, Ceará, Brazil. Scale bars 50mm.

3.5.2 *Coendou (Coendou) longicaudatus* Daudin, 1802

Long-Tailed Porcupine

Type: no type specimen available.

Type locality: Cayenne, French Guiana.

Etymology: reference to the long tail of ‘*Le Coendou*’ of Buffon (1789, p. 305): ‘*Le Coendou à longue queue*’ (the long-tailed *coendou*).

Diagnosis: Largest species of genus *Coendou* with a long tail (Table 2). The nasals have only the posterior half inflated. The lacrimal sutures are ever obliterated, even in neonate specimens. See under subspecies for detailed diagnosis.

Distribution: This species is widely distributed in the Amazonia and Cerrado biomes, with two confirmed records for the Bolivian Chaco. See more under subspecies.

Subspecies: Here, we recognize two subspecies of *C. longicaudatus*.

COENDOU (COENDOU) LONGICAUDATUS LONGICAUDATUS Daudin, 1802

Amazonian Long-Tailed Porcupine

Figures 5b, 7b, 8b, 11b, 12b

Type: no type specimen available.

Type locality: Cayenne, French Guiana.

Etymology: reference to the long tail of ‘*Le Coendou*’ of Buffon (1789, p. 305): ‘*Le Coendou à longue queue*’ (the long-tailed *coendou*).

Diagnosis: The Amazonian long-tailed porcupine shows a dark brown with short white dashes general colour pattern in dorsal view (Figure 11b). This general colour pattern is due to the presence of some bicoloured quills among the tricoloured quills of the dorsal crest and short whitish B3 of the tricoloured quills. The B2 of tricoloured quills is dark brown and comprises about half of the total quill length (Figure 7b). The B3 is most whitish and sometimes light yellowish around the rump. The B1 of anterior quills is light yellowish and the posterior quills exhibit a B1 very yellowish, mainly on the rump (Figure 8b). The dorsal crest tricoloured quills are shorter than 10 cm and slightly curved. Cranially, the nasofrontal suture is not close to the postorbital processes in dorsal view (Figure 5b). The interparietal is short and triangular shaped in dorsal view. The auditory bullae can be linked to the alisphenoid. The neonate of this subspecies exhibits rust-brown long soft fur (Figure 12b), delicate bicoloured quills with a gradient in which its basal third is whitish and the two distal thirds are rust-brown. Most of the

quills are dirty white coloured distributed on the entire dorsal surface, without any differentiation in colour bands. In addition, rare tricoloured quills can be found on the basal portion of the tail. These tricoloured quills have dirty whitish B1 and B3 with a very short blackish B2.

Distribution: This taxon is widely distributed in the Amazon Forest, east of the Andes (Figure 9). The examined specimens are limited to the west bank of the Xingu River.

Remarks: *longicaudatus* is the second oldest available name of *C. prehensilis* complex (Cabrera, 1961; Husson, 1978) and its description is congruent with the Amazonian morphotype. Unfortunately, we did not have access to the sequenced specimens of *C. l. longicaudatus*. Nevertheless, we examined a specimen (MZUSP 25230) from the border between Brazil and French Guiana (210 km apart from the type locality) and the photo of the sequenced specimen INPA 2875 (Voss et al., 2013, fig. 5) is completely congruent with our Amazonian morphotype.

COENDOU (COENDOU) LONGICAUDATUS BOLIVIENSIS (Gray, 1850)

Cerrado's Long-Tailed Porcupine

Figures 5c, 7c, 8c, 11c, 12c

Type: BMNH 47.11.22.6. It consists of a skin and skull collected by Mr. Bridges.

Type locality: "Bolivia", probably near Santa Cruz de la Sierra, Bolivia (suggested by Voss, 2011).

Etymology: The specific epithet refers to the country of origin of the type specimen.

Diagnosis: This subspecies is the largest and heaviest South American porcupine (Figure 11c). It shows a brown and white mixed general colour pattern (Figure 8c). The dorsal crest is composed mostly of tricoloured quills with rare or no bicoloured quills. The B3 of tricoloured quills is whitish and relatively long (when compared with the B3 of *C. l. longicaudatus*) (Figure 7c). The B2 is shorter than B1 and has a lighter brown colour than the B2 of *C. prehensilis* and *C. l. longicaudatus*. The B1 is generally whitish but yellowish in the rump. The tricoloured quills in the dorsal crest are longer than 10 cm and very curved. The nasal is short and the parietal is long. Some individuals exhibit the auditory bullae dorsally in contact with the alisphenoid forming a foramen. Cranially, *C. l. boliviensis* has a shorter zygomatic length, larger upper molars row, and wider nasal aperture in comparison with *C. l. longicaudatus*. The villous pelage of neonate of *C. l. boliviensis* completely covers the quills. The neonate pelage is orange and the quills are thin and mostly white (Figure 12c). The

subadults show a light brownish villous pelage mixed with the dorsal quills, this pelage is conspicuous on the rump region. The lacrimal sutures are not visible in any development stage. The skull of the neonate has a large uninflated rostrum. No diagnostic feature is present on neonate skulls.

Distribution: This subspecies seems to be strictly associated with forested vegetation in the diagonal open/dry formations of South America. Our records include individuals from both Bolivian Chaco and Brazilian Cerrado (Figure 9). We did not find any evidence of this taxon in the Caatinga biome and the Atlantic Forest at the right bank of the São Francisco River.

Remarks: *Cercolabes (Synetheres) platycentrotus* Brandt, 1835 was also applied to individuals from central Brazil (Miranda Ribeiro, 1936; Tate, 1935; Waterhouse, 1848) and it is an older name than *C. boliviensis* (Gray, 1850) and would have priority. However, Brandt (1835) considers *Cercolabes platycentrotus* very similar to *Cercolabes prehensilis*, the only difference is the longitudinal grooves in the quills of *C. platycentrotus*, which Voss (2011) considered an artifact of preservation or a developmental pathology of the holotype. Because of that uninformative description, the fading colour of the quills of the holotype, and the lack of a place of origin of *C. platycentrotus*, the name was treated as *nomen dubium* by Voss (2011), with which we agree.

The karyotype (2n 74, FN 82) reported by Lima (1994) refers to a subadult male of *C. l. boliviensis* collected in UHE Nova Ponte, Minas Gerais State, Brazil and deposited in Mammal Collection of Universidade Federal da Paraíba (UFPB 1617). No karyological information is available to *C. prehensilis*, *C. l. longicaudatus* and *C. baturitensis*.

3.5.3 Coendou (*Coendou*) *baturitensis* Feijó & Langguth, 2013

Baturite Porcupine

Figures 5d, 7d, 8d, 11d, 12d

Type material: The holotype (UFPB 6809) is an adult specimen collected by H. Fernandes-Ferreira on August 21, 2012 (Figure S4). It consists of a skull and mandible with all teeth (Figure 5D). The paratype (MNRJ 34504) consists of a skull with all teeth and a flat skin of an adult female collected by Alfonso Mota on January 19, 1954.

Type locality: The holotype was collected in the Community Sítio Barreiros, municipality of Aratuba, Ceará state, Brazil. This site is part of the Baturité range.

Etymology: The specific epithet refers to the locality of origin of the type specimens, Baturité range.

Diagnosis: The Baturité's Porcupine is a medium to large-sized species (Table 2, Figure 11d). The dorsal crest is composed of a homogeneous mixture of long tricoloured and bicoloured quills. The B2 is light brown, the same brown tone presented in the B2 of most specimens of *C. l. boliviensis*. The B2 is longer than B1 in tricoloured and bicoloured quills. The B3 is the same length or slightly longer than B1 in the long tricoloured quills (Figure 7d). In short tricoloured quills, the B3 is sometimes shorter than B1 or about the same length. The long B2 of tricoloured quills and the abundant short bicoloured quills present in the dorsal crest give this species an overall brown background colour pattern with some whitish dashes (Figure 8d). Adults of *Coendou baturitensis* present tricoloured quills longer than 10 cm and very curved. The ventral surface has a general colour pattern mixed between brownish and greyish tones, with some individuals with strong rust brownish tones. The nasofrontal inflation is complete and the rostrum is the highest among the other species of the complex (Figure 5d). The naso–frontal suture is located near to the postorbital process in dorsal view. The interparietal is wide and the fronto–parietal and parietal–interparietal sutures are close in dorsal view. The lacrimal sutures are never evident in any ontogenetic stage. The neonate of *C. baturitensis* has a white woolly pelage that covers the dorsum, with no visible quills (Fig 12d). Its belly has a whitish or light brownish pelage. The juveniles of this species have white villous pelage with furs uniformly spread over the dorsum among the quills. This white pelage disappears with maturation and is completely absent in adults. During the development, the density of villous fur of the ventral surface reduces and is replaced by the hard-spiny pelage of adults. The dark grey tail has few ontogenetic variations. The most remarkable variation is the increase of quill density during maturation. The tegument of snout, limb and tail present the same general coloration in neonates, juveniles, subadults and adults. The lacrimal sutures are not visible in neonate skulls.

Distribution: The species occurs in eastern Amazon (Pará and Maranhão states) and montane forested enclaves (*Brejos de altitude*) in Ceará state in Northeastern Brazil. This species appears restricted to forested areas. It was previously known only for the Baturité Range (its type locality). Here, we register the presence of *C. baturitensis* in new localities of Ceará, Maranhão and Pará states (Figure 9). These new localities increase in about 1460 km westward from the previously known distribution of the species. We confirmed the presence of *C. baturitensis* through collected quills in Pacatuba, Ceará. The presence of *C. baturitensis* for the Ibiapaba region, Ceará, was confirmed by the capture of one living specimen from Ubajara which was released with some quills collected (UFPB 9392), and by a neonate from São

Benedito (MNRJ 75670) (Figure 12d). This neonate was anteriorly used only to document the presence of the genus in the Ibiapaba Range (Feijó & Langguth 2013).

Remarks: Voss (2015) considered *C. baturitensis* synonymy of *C. prehensilis*, arguing it falls within the variation of the widespread *C. prehensilis*, opinion followed by Gutiérrez & Marinho-Filho (2017). However, none of these authors have examined individuals of *C. baturitensis*. Here, we presented additional morphological diagnostic traits and confirmed the monophyly of the species.

Moojen (1952, p. 104) placed the type locality of *Cercolabes tricolor* Gray (1850) to Igarapé-Açu, a municipality in the east portion of the Pará State, within the distribution of *C. baturitensis* here documented. However, the actual collection locality of *C. tricolor* is unknown (Voss, 2011) and Moojen (1952) when describing “*C. tricolor*” provides characters of *C. (S.) nycthemera*, a sympatric species with *C. baturitensis* in Pará.

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References

- Allen, J. A. (1904). Report on mammals from the district of Santa Marta, Colombia, collected by Mr. Herbert H. Smith, with field notes by Mr. Smith. *Bulletin of the American Museum of Natural History*, 20(35), 407–468. <http://digitallibrary.amnh.org/handle/2246/667>
- Alves, R., Feijó, A., Barboza, R., Souto, W., Fernandes-Ferreira, H., Cordeiro-Estrela, P., & Langguth, A. (2016). Game mammals of the Caatinga biome. *Ethnobiology and Conservation*, 5(5), 1–51. <https://doi.org/10.15451/ec2016-7-5.5-1-51>
- Assis, L. F. F. G., Ferreira, K. R., Vinhas, L., Maurano, L., Almeida, C., Carvalho, A., Rodrigues, J., Maciel, A., & Camargo, C. (2019). TerraBrasilis: A Spatial Data Analytics Infrastructure for Large-Scale Thematic Mapping. *ISPRS International Journal of Geo-Information*, 8(11), 513. <https://doi.org/10.3390/ijgi8110513>
- Baía Júnior, P. C., Guimarães, D. A., & Le Pendu, Y. (2010). Non-legalized commerce in game meat in the Brazilian Amazon: A case study. *Revista de Biologia Tropical*, 58(3), 1079–1088. <https://doi.org/10.15517/rbt.v58i2.5264>
- Bonvicino, C. R., de Oliveira, J. A., & D’Andrea, P. S. (2008). *Guia dos roedores do Brasil: Com chaves para gêneros baseadas em caracteres externos*. Centro Pan-Americano de Febre Aftosa.
- Bonvicino, C. R., Penna-Firme, V., & Braggio, E. (2002). Molecular and Karyologic Evidence of the Taxonomic Status of *Coendou* and *Sphiggurus* (Rodentia: Hystricognathi). *Journal of Mammalogy*, 83(4), 1071–1076.
- Borges-Nojosa, D. M. (2007). Diversidade de anfíbios e répteis da serra de Baturité, Ceará. In T. S. de Oliveira & F. S. de Araújo (Eds.), *Diversidade e Conservação da Biota na Serra de Baturité, Ceará* (pp. 225–247). Universidade Federal do Ceará.
- Brandt, J. F. (1835). Mammalium rodentium exoticorum novorum vel minus rite cognitorum musei academici zoologici descriptiones et icones. *Mémoires de l’Académie Impériale Des Sciences de St. Pétersbourg, Ser. 6.*, 3, 357–442.
- Bremer, K. (1994). Branch support and tree stability. In *Cladistics* (Vol. 10, pp. 295–304).
- Buffon, G.-L. L. (1789). *Histoire naturelle générale et particulière: Supplément. Tome XII*. Thierry Hoquet (Université de Nanterre - Paris X). <http://www.buffon.cnrs.fr/>
- Cabrera, A. (1961). Catálogo de los mamíferos de América del Sur. *Revista Del Museo Argentino de Ciencias Naturales*, 4(2), 599–600.
- Caldara Júnior, V., & Leite, Y. L. R. (2012). Geographic variation in hairy dwarf porcupines of Coendou from eastern Brazil (Mammalia: Erethizontidae). *Zoologia*, 29(4), 318–336. <https://doi.org/10.1590/S1984-46702012000400005>
- Chernova, O. F. (2002). New Findings of a Specialized Spine Cuticle in Porcupines (Rodentia: Hystricomorpha) and Tenrecs (Insectivora: Tenrecidae). *Doklady Biological Sciences*, 384(4), 267–270. <https://doi.org/10.1023/A:1016094230305>
- Cho, W. K., Ankrum, J. A., Guo, D., Chester, S. A., Yang, S. Y., Kashyap, A., Campbell, G. A., Wood, R. J., Rijal, R. K., Karnik, R., Langer, R., & Karp, J. M. (2012). Microstructured barbs on the North American porcupine quill enable easy tissue penetration and difficult removal. *PNAS*, 109(52), 21289–21294. <https://doi.org/10.1073/pnas.1216441109>

- Costa, L. P. (2003). The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. *Journal of Biogeography*, *30*, 71–86.
- Costa, L. P., Leite, Y. L. R., Fonseca, G. A. B., & Fonseca, M. T. (2000). Biogeography of South American forest mammals: Endemism and diversity in the Atlantic Forest. *Biotropica*, *32*(4 B), 872–881. <https://doi.org/10.1111/j.1744-7429.2000.tb00625.x>
- Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, *9*(8), 772–772. <https://doi.org/10.1038/nmeth.2109>
- Daudin, F. M. (1802). Tableau des divisions, sous-divisions, ordres et genres de mammifères, par le Citoyen Lacepède; avec l'indication de toutes les espèces décrites par Buffon, et leur distribution dans chacun des genres. In B. G. Lacépède (Ed.), *Histoire naturelle par Buffon 14* (pp. 143–195). P. Didot et Firmin Didot.
- de Oliveira, T. S., Figueiredo, M. A., Nogueira, R. S., Sousa, S. C., Souza, S. S. G., Romero, R. E., & Tavares, R. C. (2007). Histórico dos impactos antrópicos e aspectos geoambientais da Serra de Baturité, Ceará. In T. S. de Oliveira & F. S. de Araújo (Eds.), *Diversidade e Conservação da Biota na Serra de Baturité, Ceará* (pp. 17–72). Universidade Federal do Ceará.
- Doyle, J. J., & Doyle, J. L. A. (1987). A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemistry Bulletin*, *19*, 11–15.
- Eisenberg, J. F., & Redford, K. H. (1999). *Mammals of the Neotropics: The Central Neotropics. Vol. 3*. The University of Chicago Press.
- Elbroch, L. M., Hoogesteijn, R., & Quigley, H. (2016). Cougars (*Puma concolor*) Killed by North American Porcupines (*Erethizon dorsatum*). *The Canadian Field-Naturalist*, *130*(1), 53. <https://doi.org/10.22621/cfn.v130i1.1793>
- Ellerman, J. R. (1940). *The families and genera of living Rodents. Volume I. Rodents other than Muridae* (2nd ed.). The British Museum (Natural History).
- Emmons, L. H. (1997). *Neotropical Rainforest Mammals: A field guide*. The University of Chicago Press.
- Escobar, H. (2020). Deforestation in the Brazilian Amazon is still rising sharply. *Science*, *369*(6504), 613. <https://doi.org/10.1126/science.369.6504.613>
- Fearnside, P. M., Figueiredo, A. M. R., & Bonjour, S. C. M. (2013). Amazonian forest loss and the long reach of China's influence. *Environment, Development and Sustainability*, *15*(2), 325–338. <https://doi.org/10.1007/s10668-012-9412-2>
- Feijó, A., & Langguth, A. (2013). Mamíferos de médio e grande porte do Nordeste do Brasil: Distribuição e taxonomia, com descrição de novas espécies. *Revista Nordestina de Biologia*, *22*(1), 3–225.
- Feijó, A., Nunes, H., & Langguth, A. (2016). Mamíferos da Reserva Biológica Guaribas, Paraíba, Brasil. *Revista Nordestina de Biologia*, *24*(1), 57–74.
- Felsenstein, J. (1985). Confidence Limits on Phylogenies: An Approach using the Bootstrap. *Evolution*, *39*(04), 783–791.
- Fernandes-Ferreira, H., Gurgel-Filho, N. M., Feijó, A., Mendonça, S. V., Alves, R. R. N., & Langguth, A. (2015). Non-volant mammals from Baturité Ridge, Ceará state, Northeast Brazil. *Check List*, *11*(3), 1630. <https://doi.org/10.15560/11.3.1630>
- Garbino, G. S. T., Rezende, G. C., Fernandes-Ferreira, H., & Feijó, A. (2018). Reconsidering mammal extinctions in the Pernambuco Endemism Center of the Brazilian Atlantic Forest. *Animal Biodiversity and Conservation*, *41*(1), 175–184.

- Girão, W., Albano, C., Pinto, P. T., & Silveira, L. F. (2007). Avifauna da serra de Baturité, Ceará: dos naturalistas à atualidade. In T. S. de Oliveira & F. S. de Araújo (Eds.), *Diversidade e Conservação da Biota na Serra de Baturité, Ceará* (pp. 187–224). Universidade Federal do Ceará.
- Gray, J. E. (1850). On the species of *Cercolabes* confounded under the name of *C. prehensilis*. *Annals and Magazine of Natural History*, 5(29), 380–381. <https://doi.org/10.1080/03745486009494929>
- Gregory, T., Lunde, D. P., Zamora-Meza, H. T., Carrasco-Rueda, F., Zamora Meza, H. T., & Carrasco-Rueda, F. (2015). Records of *Coendou ichillus* (Rodentia, Erethizontidae) from the Lower Urubamba Region of Peru. *ZooKeys*, 509(June), 109–121. <https://doi.org/10.3897/zookeys.509.9821>
- Griffiths, B. M., Gilmore, M. P., & Bowler, M. (2020). Predation of a Brazilian porcupine (*Coendou prehensilis*) by an ocelot (*Leopardus pardalis*) at a mineral lick in the Peruvian Amazon. *Food Webs*, 24, 2018–2020. <https://doi.org/10.1016/j.fooweb.2020.e00148>
- Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W., & Gascuel, O. (2010). New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology*, 59(3), 307–321. <https://doi.org/10.1093/sysbio/syq010>
- Guindon, S., & Gascuel, O. (2003). A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology*, 52(5), 696–704. <https://doi.org/10.1080/10635150390235520>
- Gutiérrez, E. E., & Marinho-Filho, J. (2017). The mammalian faunas endemic to the Cerrado and the Caatinga. *ZooKeys*, 644(January), 105–157. <https://doi.org/10.3897/zookeys.644.10827>
- Handley, C. O., & Pine, R. H. (1992). A new species of prehensile-tailed porcupine, genus *Coendou* Lacépède, from Brazil. *Mammalia*, 56(2), 237–244. <https://doi.org/10.1515/mamm-1992-0207>
- Honaker, J., King, G., & Blackwell, M. (2011). Amelia II: A Program for Missing Data. *Journal of Statistical Software*, 45(7). <https://doi.org/10.18637/jss.v045.i07>
- Huelsenbeck, J. P., & Ronquist, F. (2001). MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17(8), 754–755. <https://doi.org/10.1093/bioinformatics/17.8.754>
- Husson, A. M. (1978). *The Mammals of Suriname*. E. J. Brill.
- ICMBio. (2018). Livro vermelho da fauna brasileira ameaçada de extinção. Volume II - Mamíferos. In *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Vol. II*. ICMBio/MMA.
- Inbar, M., & Lev-Yadun, S. (2005). Conspicuous and aposematic spines in the animal kingdom. *Naturwissenschaften*, 92(4), 170–172. <https://doi.org/10.1007/s00114-005-0608-2>
- INPE. (2021). *Área Queimada*. Instituto Nacional de Pesquisas Espaciais. <http://queimadas.dgi.inpe.br/queimadas/aq1km/>
- Jansa, S. A., Goodman, S. M., & Tucker, P. K. (1999). Molecular phylogeny and biogeography of the native rodents of Madagascar (Muridae: Nesomyinae): a test of the single-origin hypothesis. *Cladistics*, 15(3), 253–270. <https://doi.org/10.1111/j.1096-0031.1999.tb00267.x>
- Johnson, M. D., Magnusson, K. D., Shmon, C. L., & Waldner, C. (2006). Porcupine quill injuries in dogs: A retrospective of 296 cases (1998-2002). *Canadian Veterinary Journal*, 47(7), 677–682.
- Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular Evolutionary Genetics

- Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution*, 33(7), 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Lambkin, C. L., Lee, M. S. Y., Winterton, S. L., & Yeates, D. K. (2002). Partitioned Bremer support and multiple trees. *Cladistics*, 18(4), 436–444. <https://doi.org/10.1111/j.1096-0031.2002.tb00159.x>
- Lees, A. C., Peres, C. A., Fearnside, P. M., Schneider, M., & Zuanon, J. A. S. (2016). Hydropower and the future of Amazonian biodiversity. *Biodiversity and Conservation*, 25(3), 451–466. <https://doi.org/10.1007/s10531-016-1072-3>
- Leite, Y. L. R., Caldara Júnior, V., Loss, A. C., Costa, L. P., Melo, É. R. A., Gadelha, J. R., & Mendes Pontes, A. R. (2011). Designation of a neotype for the Brazilian porcupine, *Coendou prehensilis* (Linnaeus, 1758). *Zootaxa*, 2791, 30–40.
- Leite, Y. L. R., & Loss, A. C. (2015). Genus *Phyllomys* Lund 1839. In J. L. Patton, U. F. J. Pardiñas, & G. D'Elia (Eds.), *Mammals of South America, Volume 2: Rodents* (pp. 915–928). University of Chicago Press.
- Lewis, P. O. (2001). A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, 50(6), 913–925. <https://doi.org/10.1080/106351501753462876>
- Lima, J. F. de S. (1994). Cariótipos em espécies de Dasyproctidae e Erethizontidae, com discussão da evolução cromossômica (Rodentia, Caviomorpha). *Brazilian Journal of Genetics Supplement*, 17, 135.
- Linnaeus, C. (1758). *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (10th, vol ed.). Laurentii Salvii.
- Loebmann, D., & Haddad, C. F. B. (2010). Amphibians and reptiles from a highly diverse area of the Caatinga domain: composition and conservation implications. *Biota Neotropica*, 10(3), 227–256. <https://doi.org/10.1590/S1676-06032010000300026>
- Marinho-Filho, J., & Emmons, L. H. (2016). *Coendou prehensilis*. *The IUCN Red List of Threatened Species*, T101228458A22214580. <https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T101228458A22214580.en>
- Mendes Pontes, A. R., Beltrão, A. C. M., Normande, I. C., Malta, A. de J. R., Silva Jr, A. P., & Santos, A. M. M. (2016). Mass Extinction and the Disappearance of Unknown Mammal Species: Scenario and Perspectives of a Biodiversity Hotspot's Hotspot. *PLOS ONE*, 11(5), e0150887. <https://doi.org/10.1371/journal.pone.0150887>
- Mendes Pontes, A. R., Gadelha, J. R., Melo, É. R. A., de Sá, F. B., Loss, A. C., Caldara Jr, V., Costa, L. P., & Leite, Y. L. R. (2013). A new species of porcupine, genus *Coendou* (Rodentia: Erethizontidae) from the Atlantic forest of northeastern Brazil. *Zootaxa*, 3636(3), 421. <https://doi.org/10.11646/zootaxa.3636.3.2>
- Menezes, F. H., Garbino, G. S. T., Semedo, T. B. F., Lima, M., Feijó, A., Cordeiro-Estrela, P., & da Costa, I. R. (2020). Major range extensions for three species of porcupines (Rodentia: Erethizontidae: *Coendou*) from the Brazilian Amazon. *Biota Neotropica*, 20(2), e20201030. <https://doi.org/10.1590/1676-0611-bn-2020-1030>
- Miranda Ribeiro, A. (1936). The new-born of the Brazilian tree-porcupine (*Coendou prehensilis* Linn.) and of the hairy tree-porcupine (*Sphingurus villosus* F. Cuv.). *Proceedings of the Zoological Society of London*, 106, 971–974.
- Moojen, J. (1952). *Os Roedores do Brasil*. Instituto Nacional do Livro.
- Moraes-Santos, H. M. (1997). Descrição do sínclânio de *Coendou prehensilis* (Erethizontidae) e a comparação com *Proechimys guyannensis guyannensis* (Echimyidae) (Rodentia, Caviomorpha). *Boletim Do Museu Paraense Emilio Goeldi*, 13(2), 95–189.

- Moro, M. F., Macedo, M. B., de Moura-Fé, M. M., Farias Castro, A. S., & da Costa, R. C. (2015). Vegetação, unidades fitoecológicas e diversidade paisagística do estado do Ceará. *Rodriguésia*, 66(3), 717–743. <https://doi.org/10.1590/2175-7860201566305>
- Pivello, V. R. (2011). The use of fire in the cerrado and Amazonian rainforests of Brazil: Past and present. *Fire Ecology*, 7(1), 24–39. <https://doi.org/10.4996/fireecology.0701024>
- Ramírez-Chaves, H. E., López-Ordóñez, J. P., Aya-Cuero, C. A., Velásquez-Guarín, D., Cardona-Giraldo, A., Atuesta-Dimian, N., Morales-Martínez, D. M., & Rodríguez-Posada, M. E. (2020). Filling distribution gaps: new records of the Brazilian Porcupine, *Coendou prehensilis* (Linnaeus, 1758) (Mammalia, Rodentia), in 10 departments of Colombia. *Check List*, 16(4), 927–932. <https://doi.org/10.15560/16.4.927>
- Ramírez-Chaves, H. E., Suárez-Castro, A. F., Morales-Martínez, D. M., & Vallejo-Pareja, M. C. (2016). Richness and distribution of porcupines (Erethizontidae: *Coendou*) from Colombia. *Mammalia*, 80(2), 181–191. <https://doi.org/10.1515/mammalia-2014-0158>
- Ramírez-Chaves, H. E., Torres-Martínez, M. M., Noguera-Urbano, E. A., Passos, F. C., & Colmenares-Pinzón, J. E. (2019). State of knowledge and potential distribution of the Colombian endemic brown hairy dwarf porcupine *Coendou vestitus* (Rodentia). *Mammalian Biology*, 99, 1–11. <https://doi.org/10.1016/j.mambio.2019.09.012>
- Rangel, C. H., & Neiva, C. H. M. B. (2013). Predação de vertebrados por cães *Canis lupus familiaris* (Mammalia: Carnivora) no Jardim Botânico do Rio de Janeiro. *Biodiversidade Brasileira*, 3(2), 261–269. <https://doi.org/10.37002/biobrasil.v%25vi%25i.345>
- Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., & Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, 142(6), 1141–1153. <https://doi.org/10.1016/j.biocon.2009.02.021>
- Roach, N. (2016). *Coendou baturitensis* (Baturite Porcupine). The IUCN Red List of Threatened Species 2016. <https://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T87411473A87411477.en>
- Roach, N., & Mendes Pontes, A. R. (2020). *Coendou speratus* (Dwarf Porcupine). *The IUCN Red List of Threatened Species 2020*, e.T46205559A166610234.
- Roberts, M., Brand, S., & Maliniak, E. (1985). The Biology of Captive Prehensile-Tailed Porcupines, *Coendou prehensilis*. *Journal of Mammalogy*, 66(3), 476–482. <https://doi.org/10.2307/1380922>
- Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19(12), 1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012). Mrbayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61(3), 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Ruedas, L., & Smith, A. T. (2019). *Sylvilagus brasiliensis* (Tapeti). The IUCN Red List of Threatened Species 2019. <https://dx.doi.org/10.2305/IUCN.UK.2019-2.RLTS.T87491102A45191186.en>
- Silva Junior, C. H. L., Celentano, D., Rousseau, G. X., de Moura, E. G., Varga, I. van D., Martinez, C., & Martins, M. B. (2020). Amazon forest on the edge of collapse in the Maranhão State, Brazil. *Land Use Policy*, 97(May), 104806. <https://doi.org/10.1016/j.landusepol.2020.104806>
- Silva Junior, C. H. L., Pessôa, A. C. M., Carvalho, N. S., Reis, J. B. C., Anderson, L. O., &

- Aragão, L. E. O. C. (2021). The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. *Nature Ecology and Evolution*, 5(2), 144–145. <https://doi.org/10.1038/s41559-020-01368-x>
- Smith, M. F., & Patton, J. L. (1993). The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. *Biological Journal of the Linnean Society*, 50(3), 149–177. <https://doi.org/10.1111/j.1095-8312.1993.tb00924.x>
- Sonter, L. J., Herrera, D., Barrett, D. J., Galford, G. L., Moran, C. J., & Soares-Filho, B. S. (2017). Mining drives extensive deforestation in the Brazilian Amazon. *Nature Communications*, 8(1), 1–7. <https://doi.org/10.1038/s41467-017-00557-w>
- Stankowich, T., & Campbell, L. A. (2016). Living in the danger zone: Exposure to predators and the evolution of spines and body armor in mammals. *Evolution*, 70(7), 1501–1511. <https://doi.org/10.1111/evo.12961>
- Sullivan, J., & Joyce, P. (2005). Model Selection in Phylogenetics. *Annual Review of Ecology, Evolution, and Systematics*, 36(1), 445–466. <https://doi.org/10.1146/annurev.ecolsys.36.102003.152633>
- Swofford, D. L. (2002). *PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates.
- Tabarelli, M., Aguiar, A. V., Ribeiro, M. C., Metzger, J. P., & Peres, C. A. (2010). Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. *Biological Conservation*, 143(10), 2328–2340. <https://doi.org/10.1016/j.biocon.2010.02.005>
- Tabarelli, M., & Roda, S. A. (2005). An opportunity for the Pernambuco Endemism Center. *Natureza & Conservação*, 3(2), 128–134.
- Tamura, K., & Nei, M. (1993). Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, 10(3), 512–526. <https://doi.org/10.1093/molbev/msl149>
- Tate, G. H. H. (1935). The Taxonomy of the Genera of Neotropical Hystricoid Rodents. *Bulletin of The American Museum of Natural History*, LXVIII(V), 295–447.
- Thomas, O. (1911). The Mammals of the Tenth Edition of Linnaeus; an attempt to fix the types of the genera and the exact bases and localities of the species. *Proceedings of the Zoological Society of London*, 81(1), 120–158. <https://doi.org/10.1111/j.1469-7998.1911.tb06995.x>
- Torres-Martínez, M. M., Ramírez-Chaves, H. E., Noguera-Urbano, E. A., Colmenares-Pinzón, J. E., Passos, F. C., & García, J. (2019). On the distribution of the Brazilian porcupine *Coendou prehensilis* (Erethizontidae) in Colombia. *Mammalia*, 83(3), 290–297. <https://doi.org/10.1515/mammalia-2018-0043>
- Trigueiro, W. R., Nabout, J. C., & Tessarolo, G. (2020). Uncovering the spatial variability of recent deforestation drivers in the Brazilian Cerrado. *Journal of Environmental Management*, 275(December 2019). <https://doi.org/10.1016/j.jenvman.2020.111243>
- Valença Montenegro, M., Bezerra, B., Fialho, M., Jerusalinsky, L., Lynch Alfaro, J., & Martins, A. B. (2020). *Sapajus flavius* (Blonde Capuchin). The IUCN Red List of Threatened Species 2020. <https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T136253A179782919.en>
- Vanzolini, P. E., & Williams, E. E. (1981). The vanishing refuge: A mechanism for ecogeographic speciation. *Papéis Avulsos de Zoologia*, 34(23), 251–255.
- Vieira, I. C. G., Toledo, P. M., Silva, J. M. C., & Higuchi, H. (2008). Deforestation and threats to the biodiversity of Amazonia. *Brazilian Journal of Biology*, 68(4 suppl), 949–956.

- <https://doi.org/10.1590/S1519-69842008000500004>
- Vincent, J. F. V., & Owers, P. (1986). Mechanical design of hedgehog spines and porcupine quills. *Journal of Zoology*, 210(1), 55–75. <https://doi.org/10.1111/j.1469-7998.1986.tb03620.x>
- Voss, R. S. (2011). Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae) 3. An annotated Checklist on the species of *Coendou* Lacépède, 1799. *American Museum Novitates*, 3720, 1–36.
- Voss, R. S. (2015). Superfamily Erethizontoidea Bonaparte, 1845. In J. L. Patton, U. F. J. Pardiñas, & G. D'Elía (Eds.), *Mammals of South America, Volume 2: Rodents* (pp. 786–805). The University of Chicago Press.
- Voss, R. S., & Angermann, R. (1997). Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae). 1. Type material described by Olfers (1818) and Kuhl (1820) in the Berlin Zoological Museum. *American Museum Novitates*, 3214, 1–44.
- Voss, R. S., & da Silva, M. N. F. (2001). Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae). 2. A review of the *Coendou vestitus* group with descriptions of two new species from Amazonia. *American Museum Novitates*, 3351, 1–36. [https://doi.org/10.1206/0003-0082\(2001\)351<0001:RNONPR>2.0.CO;2](https://doi.org/10.1206/0003-0082(2001)351<0001:RNONPR>2.0.CO;2)
- Voss, R. S., Hubbard, C., & Jansa, S. A. (2013). Phylogenetic relationships of New World porcupines (Rodentia, Erethizontidae): implications for taxonomy, morphological evolution, and biogeography. *American Museum Novitates*, 3769, 1–36. <https://doi.org/10.1206/3769.2>
- Waterhouse, G. R. (1848). *A natural history of the Mammalia, vol. II. Containing the order Rodentia, or gnawing Mammalia*. Hippolyte Ballière.
- Wilgenbusch, J. C., & Swofford, D. (2003). Inferring Evolutionary Trees with PAUP*. *Current Protocols in Bioinformatics*, Chapter 6, Unit 6.4. <https://doi.org/10.1002/0471250953.bi0604s00>
- Woods, C. A., & Kilpatrick, C. W. (2005). Infraorder Hystricognathi. In D. E. Wilson & D. M. Reeder (Eds.), *Mammal Species of the World: A Taxonomic and Geographic Reference* (2nd ed., pp. 1538–1600). Johns Hopkins University Press.
- Yang, W., Chao, C., & McKittrick, J. (2013). Axial compression of a hollow cylinder filled with foam: A study of porcupine quills. *Acta Biomaterialia*, 9(2), 5297–5304. <https://doi.org/10.1016/j.actbio.2012.09.004>

3.6 Appendix 1 - Examined specimens of Erethizontidae

†Sequenced specimens

Chaetomys subspinosus

BRAZIL Bahia: MNRJ 11202, MNRJ 11459, MNRJ 11460, MNRJ 11461, MNRJ 11462, MNRJ 11463, MNRJ 11464, MNRJ 11465, MNRJ 50682, MNRJ 81959, MNRJ 81960, MNRJ 81961, MNRJ 9680 – Ilhéus (14°48'S, 39°02'W). MNRJ 46250 – Nova Viçosa, Helvecia 1 (17°53'S, 39°23'W). **Espírito Santo:** MNRJ 81127 – Aracruz, Rodovia Aracruz–Comboios, Km 6 (19°49'S, 40°15'W). MNRJ 8278 – São José River (no GPS information). **Minas Gerais:** MNRJ 50683 – Serra do Caparaó (20°27'S, 41°50'W). **Unknown localities:** MNRJ 34503, MNRJ 81958, MNRJ 81962.

Erethizon dorsatum

UNITED STATES OF AMERICA **New Hampshire:** MNRJ 81956 – Carroll Municipality (43°52'N, 71°12'W). **Unknown localities:** MNRJ 898.

Coendou baturitensis

BRAZIL **Ceará:** UFPB 6809 – Aratuba, Comunidade Barreiros (4°25'S, 39° 1'W). UFPE 2387 – Baturité. UFPB 9390, UFPB 9391†, UFPB 9780†, UFPB 9781† – Mulungu, Maciço de Baturité (4°18'S, 39°0'W). UFPB 9518 – Pacatuba, Trilha do Letreiro, RPPN Sítio Monte Alegre (3°57'14.35"S, 38°37'23.29"W). MNRJ 34504 – Pacoti (4°13'S, 38°55'W). MNRJ 75670 – São Benedito, Cinta da Solidade (4°02'S, 40°50'W). UFPB 9392 – Ubajara, Igreja de Ubajara (3°52'16"S, 40°54'58"W). **Maranhão:** MPEG 20214 – Grajaú, Rod. Transmaranhão, Km 36, Faz. Sr. Adoam. (5°48'27.24", 46° 9'27.23"W). **Pará:** MPEG 38334 – Abaetetuba (1°43'S, 48°52'W). MPEG 418, MPEG 421, MPEG 6623, MPEG 8853, MPEG 9137, MPEG 11837 – Belém, Jardim Zoobotânico do Museu Paraense Emílio Goeldi (1°27'S, 48°28'W). MPEG 38854 – Melgaço, FLONA Caxiuanã (1°47'S, 51°26'W). MPEG 30679 – Paragominas (3°0'S, 47°21'W). MZUSP 13486 – Santo Antônio do Tauá (01°8'S, 48°09'W). MPEG 8872, MPEG 11876, MPEG 11899, MPEG 12316, MPEG 12598 – Tucuruí (3°48'S, 49°39'W).

Coendou bicolor

BRAZIL **Amazonas:** MPEG 24574, MPEG 37122 – Uarini, Reserva de Desenvolvimento Sustentável Mamirauá (2°12'S, 65°42'W).

Coendou ichillus

BRAZIL **Amazonas:** MZUSP 11465 – Japurá (1°49' S, 66°35' W). ECUADOR **Pastaza:** AMNH 126171, Pastaza River (No other information available).

Coendou insidiosus

BRAZIL **Bahia:** MNRJ 1361 – Feira de Santana (13°14'S, 39°00'W). MNRJ 11210, MNRJ 11211, MNRJ 11466, MNRJ 11467, MNRJ 68199 – Ilhéus (14°48'S, 39°02'W). MNRJ 55527 – Porto Seguro (16°26'S, 39°04'W). **Espírito Santo:** MNRJ 8277 – São José, Rio São José (19°17'S, 40°08'W). MNRJ 68200 (the exact locality is unknown).

Coendou longicaudatus longicaudatus

BRAZIL Acre: MZUSP 7345 – Iquíri River (the exact location is unknown). **Amazonas:** MNRJ 30481, MNRJ 30490 – Barreirinha, Ariaú River, right bank of Negro River (3°12'S, 57°15'W). MPEG 41760 – Jutaí, Roscujubim (4°24'S, 68°31'W). MZUSP 5040 – Silves (2°51'S, 58°27'W). **Pará:** MZUSP 20931 – Altamira, Cachoeira do Espelho, Xingu River (3°39'S, 52°22'W). MZUSP 25232 – Barreira, Tapajós River (no information about this locality could be recovered). MNRJ 7657 – Belterra, Santarém (2°28'S, 54°42'W). MZUSP 5042 – Bravo (no information about this locality could be recovered). MZUSP 25230 – Uruá, Parque Nacional da Amazônia (4°22'S, 56°46'W). MNRJ 2671 – Villa Braga, Rio Tapajós (4°25'S, 56°18'W). **Rondônia:** UFPB 1205, UFPB 1206, UFPB 1207, UFPB 1208, UFPB 1129, UFPB 1230, UFPB 1231, UFPB 1232, UFPB 1233, UFPB 1237, UFPB 1279, UFPB 1280, UFPB 1282, UFPB 1374 – Candeias do Jamari, UHE Samuel, Jamari River (8°45'1"S, 63°27'20"W). **Roraima:** FMNH 20031 – Boa Vista, Rio Branco (2°51'N, 60°37'4W). MNRJ 70735 – Caracarái, PARNA Viruá (1°43'N, 61°09'W). MZUSP 13683 – Catrimani River (the exact location is unknown). **Unknown localities:** MPEG 22481, MPEG 22482. **COLOMBIA Magdalena:** AMNH 15460 – Santa Marta, Bonda (11°14'N, 74°7'W). **Meta:** FMNH 87897, AMNH 136311 – Villavicencio (4°3'N, 73°37'W). **ECUADOR Pastaza:** Puyo, FMNH 43290 – Rio Capihuara (1°29'S, 78° 0'W). **PERU Maynas:** FMNH 86915, FMNH 86916, FMNH 86917 – Santa Cecilia (3°36'S, 72°57'W). **Pasco:** FMNH 41205 – Pozuzo (10° 0'S, 75°33'W). **TRINIDAD AND TOBAGO Trinidad:** FMNH 61862, FMNH 61863 – Mount Harris (10°29'N, 61° 6'W).

Coendou longicaudatus boliviensis

BOLIVIA Santa Cruz: FMNH 21396 – Buena vista (17°27'S, 63°40'W). **BRAZIL Bahia:** FMNH 21709 – Barra (11° 2'S, 43° 9'W). **Goiás:** MNRJ 4923, MNRJ 4924, MNRJ 4925, MNRJ 4936, MNRJ 4937, MNRJ 4938, MNRJ 34186 – Anápolis (16°19'S, 48°59'W). MZUSP 4271, MZUSP 4272, MZUSP 4273 – Cana Brava (13°37'S, 50°28'W). UnB 2802, UnB 2803 – Catalão, SETAS UHE Serra do Facão (18°02'46"S, 47°40'30"W). MZUSP 6984 – GO-70 (the exact locality is unknown). MNRJ 50162 – Minaçu, UHE Serra da Mesa (13°53'52,2"S, 48°19'02"W). MNRJ 2679 – Nova Roma, Rio Paraná (13°46'S, 47°03'W). MNRJ 2672 – São Domingos (13°24'S, 46°19'W). MNRJ 2670 – São Miguel River (unknown). MNRJ 2665 (The exact locality is unknown). **Minas Gerais:** UFPB 9410, UFPB 9411 – Indianópolis, UHE Miranda (18°54'33"S, 48°02'31"W). MNRJ 29080 – Matias Cardoso, Santa Idália Farm

(14°39'S, 44°10'W). UFPB 1616, UFPB 1617 – Nova Ponte, UHE Nova Ponte, Araguari River (19°07'S, 47°41'W). MZUSP 3115 – Pirapora (17°21'S, 44°55'W). MNRJ 2681 – Urucuaia, Urucuaia River (16°13'S, 45°33'W). **Mato Grosso:** MNRJ 64213, MNRJ 64569 – Barão de Melgaço, RPPN SESC Pantanal (16°11'S, 55°57'W). MNRJ 930 – Cárceres, Jauru River (16°04'S, 57°42'W). MZUSP 32335, UnB 1756, UnB 1757†, UnB 1758†, UnB 1759 – Chapada dos Guimarães, UHE Manso (14°52'S, 55°48'W). MZUSP 6983 – Cocalinho, Lago Dumbá Grande (14°29'26.89"S, 50°59'8.16"W). MZUSP 6357 – Palmeiras (12°16'S, 51°51'W). MNRJ 252 (the exact locality is unknown). **Mato Grosso do Sul:** MNRJ 65561 – Aquidauana, Foz do Rio Negro (20°29'S, 55°46'W). MNRJ 81806 – Miranda (20°14'S, 56°23'W). MZUSP 1859 – Porto Faia (no information about this locality could be recovered). **Piauí:** MZUSP (ARP 132) – Guaribas, PARNA Serra das Confusões (9°07'S, 43°45'W). UFPB 9589 – São Raimundo Nonato, PARNA Serra da Capivara, Caldeirão do Gato (8°47'S, 42°37'W).

Coendou melanurus

BRAZIL Roraima: UFPB 3001† – São José da Baliza, UHE Jatapu, Left Bank of Jatapu River (0°48'06"S, 59°16'59"W).

Coendou nycthemera

BRAZIL Pará: MPEG 6622, MPEG 6625, MPEG 6627, MPEG 6628, MPEG 8784, PEG 22451, MPEG 22478, MPEG 22479 – Belém, Jardim Zoobotânico do Museu Paraense Emílio Goeldi (1°27'S, 48°28'W). MNRJ 7652, MNRJ 7653, MNRJ 7654, MNRJ 81956 – Belterra, Santarém (2°28'S, 54°42'W). MZUSP 5031, MZUSP 5034, MZUSP 5036, MZUSP 5039 – Cometá (2°14'S, 49°30'W). MNRJ 4913, MNRJ 4914, MNRJ 4915, MNRJ 4916, MNRJ 4917, MNRJ 4918, MNRJ 4919, MNRJ 4920, MNRJ 4921, MNRJ 72043 – Currálinho (1°48'S, 49°48'W). MPEG 24191, MPEG 24192 – Igarapé-Miri (1°58'S, 48°57'W). MPEG 38377 – Juruti, Porto da ALCOA (2°9'S, 56° 5'W). MZUSP 25591 – Santa Teresinha, BR-010 Km 87-94 (1°18'S, 47°43'W). MPEG 12496 – Tucuruí (3°48'S, 49°39'W).

Coendou prehensilis

BRAZIL Alagoas: MZUSP 7531 – Penedo, Manimbu (10°10'S, 38°22'W). **Paraíba:** UFPB 931, UFPB 932, UFPB 9412†, UFPB 9789 – João Pessoa (7°09'S, 34°51'W). MZUSP 8456 – Mamanguape, Uruba (6°50'S, 35°08'W). UFPB 10896 – SEMA 1, REBio Guaribas (6°41'29.54"S, 35° 7'25.63"W), UFPB 7299, UFPB 9516, UFPB 9790, UFPB 10689 –

Mamanguape, SEMA 2, REBio Guaribas (6°42'S, 35°10'W). UFPB 7301 – Mataraca, Millenium Miner (6°35'S, 34°58'W). UFPB 9517, UFPB 9785, UFPB 9787, UFPB (FHM 30) – Santa Rita, RPPN Engenho Gargaú (6°59'52"S, 34°57'30"W). UFPB 6762 – Sapé, RPPN Pacatuba (7°02'S, 35°09'W). UFPB 9791 – Rio Tinto, Mata do Oiteiro (69°50'15.6"S, 34°55'21.2"W). UFPB 9590, UFPB 9592, UFPB (FHM 23) – Rio Tinto, SEMA 3, REBio Guaribas (6°48'S, 35°5'W). **Pernambuco:** UFPB 10688 – Aldeia dos Camarás, Camaragibe (7°56'03.6"S 35°01'11.1"W). UFPE 1770 – Igarassu (7°52'18.67"S, 34°54'46.02"W). MNRJ 73383† – Sinharém, Usina Trapiche, Mata Gindai (8°38'50"S, 35°10'15"W). **Unknown localities:** UFPB s/n 1.

Coendou quichua

COLOMBIA **Cundinamarca:** AMNH 73679 – San Juan de Rioseco (4°50'N, 74°37'W). ECUADOR **Esmeraldas:** AMNH 33242 – Esmeraldas (0°58'N, 79°39'W). **Pichincha:** AMNH 46539 – Quito (0°10'S, 78°28'W).

Coendou speratus

BRAZIL **Alagoas:** MNRJ 81600 – Viçosa (9°21'S, 36°13'W). **Pernambuco:** MNRJ 72045† – Sinharém, Usina Trapiche, Mata Gindai (8°38'50"S, 35°10'15"W).

Coendou spinosus

BRAZIL **Espirito Santo:** MNRJ 78937† – Santa Tereza, Várzea Alegre, Fazenda Dora Francisca Loss (19°49'S, 40°40'W). **Minas Gerais:** MNRJ 1365 – Viçosa (20°45'S, 42°52'W). MNRJ 69781 – Além Paraíba, Fazenda Cachoeirão (21°51'S, 42°42'W). UFPB 1618, UFPB 2014, UFPB 2999, UFPB 3000, UFPB 3002, UFPB 3003, UFPB 3004 – Nova Ponte, UHE Nova Ponte, Araguari River (19°07'S, 47°41'W). **Rio de Janeiro:** MNRJ 19327 – Petrópolis (22°30'S, 43°10'W). MNRJ 59613 – Carmo, Providência Farm (21°36'S, 42°36'W). MNRJ 75961 – Sumidouro, Vale do Encanto (22°02'S, 42°40'W). MNRJ 7260 – Teresópolis (22°25'S, 42°56'W). **São Paulo:** MZUSP 1177 – Franca (20°31'S, 47°25'W). MZUSP 327 – Osasco (23°31'S, 46°48'W). UFPB 9593 – São João da Boa Vista, Sítio Mamonal, Pico do Gavião (21°58'S, 46°47'W). MZUSP 2342 – São Paulo (23°38'S, 46°37'W). MZUSP 1816, MZUSP 1817, MZUSP 1819 – Ubatuba (23°25'S, 45°05'W). **Santa Catarina:** MPEG 22198, MPEG

22227 – Campos Novos, Rio Marombas (27°29'S, 51°12'W). MPEG 22225 – Concórdia, B. Jacutinga (27°14'S, 52° 1'W). **Unknown localities:** MZUSP (w/number)

Acronym of Collections of Mammals of the sequenced specimens

AMNH – American Museum of Natural History, New York, USA.

ASNHC – Angelo State Natural History Collection, San Angelo, USA.

EBRG – Estación Biológica de Rancho Grande, Maracay, Venezuela.

FMNH – Field Museum of Natural History, Chicago, USA.

IAvH – Instituto Alexander von Humboldt, Bogota, Colombia.

INPA – Instituto Nacional de Pesquisas da Amazônica, Manaus, Brazil.

KU – Biodiversity Research Center da Universidade do Kansas, Lawrence, USA.

LACM – Los Angeles Country Museum, Los Angeles, USA.

MCNU – Museu de Ciências Naturais da Universidade Luterana do Brasil, Canoas, Brazil.

MNHN – Muséum National d'Histoire Naturelle, Paris, França.

MHNLS – Museo de Historia Natural La Salle, Caracas, Venezuela.

MNRJ – Museu Nacional, Rio de Janeiro, Brazil.

MUFAL – Coleção de Mamíferos da Universidade Federal de Alagoas, Maceió, Brazil.

MUSM – Museo de Historia Natural de La Universidad Nacional Mayor de San Marcos, Lima, Peru.

MVZ – Museum of Vertebrate Zoology da Universidade da Califórnia, Berkeley, USA.

MZUSP – Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

TTU – Museum of Texas Tech University, Lubbock, USA.

UFES – Coleção da Universidade Federal do Espírito Santo, Vitória, Brazil.

UFMG – Coleção da Universidade Federal de Minas Gerais, Belo Horizonte, Brazil.

UFPB – Coleção da Universidade Federal da Paraíba, João Pessoa, Brazil.

UFPE – Coleção da Universidade Federal de Pernambuco, Recife, Brazil.

UnB – Coleção da Universidade de Brasília, Distrito Federal, Brazil

UMMZ – University of Michigan Museum of Zoology, Ann Arbor, USA.

USNM – National Museum of Natural History, Washington, USA.

ZINAS – Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

Manso – Mammals Collected in Manso Hydroelectric Dam, Chapada dos Guimarães, Mato Grosso, Brazil.

FHM – Field Number of F.H. Menezes.

MNFS – Field Number of M.N.F. da Silva (see Lara et al., 1996).

3.7 Appendix 2 - Table A1. Erethizontid sequences utilized in phylogenetic analyses.

GenBank Accession number	Species	Voucher	Sequence Size (bp)	Locality	Source
KY784123	<i>Coendou baturitensis</i>	UFPB 9391	827	Mulungu, Ceará, Brazil	This work
KY784124	<i>Coendou baturitensis</i>	UFPB 9780	1140	Mulungu, Ceará, Brazil	This work
KY784125	<i>Coendou baturitensis</i>	UFPB 9781	1140	Mulungu, Ceará, Brazil	This work
KC463857	<i>Coendou bicolor</i>	AMNH 214612	682	Rio Mamoré, Beni, Bolivia	Voss, Hubbard, and Jansa 2013
KC463858	<i>Coendou bicolor</i>	KU 144560	1140	Cajamarca, Peru	Voss et al. 2013
KC463859	<i>Coendou bicolor</i>	MUSM 9398	1140	Madre de Dios, Peru	Voss et al. 2013
KC463860	<i>Coendou bicolor</i>	FMNH 203679	1140	San Martín, Peru	Voss et al. 2013
KC463861	<i>Coendou ichillus</i>	TTU 115491	1027	Loreto, Peru	Voss et al. 2013
KC261591	<i>Coendou insidiosus</i>	UFES 136	801	Nova Viçosa, Bahia, Brazil	Mendes Pontes et al. 2013
NC_021387	<i>Coendou insidiosus</i> †	–	**	–	Voloch et al. 2013
AF411581	<i>Coendou longicaudatus boliviensis</i>	UnB 1757 (Manso 212)	1132	UHE Manso, Mato Grosso, Brazil	Bonvicino, Penna-Firme, and Braggio 2002
AF411582	<i>Coendou longicaudatus boliviensis</i>	UnB 1758 (Manso 138)	1113	UHE Manso, Mato Grosso, Brazil	Bonvicino et al. 2002
AF411584	<i>Coendou longicaudatus boliviensis</i>	Manso 849	1123	UHE Manso, Mato Grosso, Brazil	Bonvicino et al. 2002
KC463873	<i>Coendou longicaudatus boliviensis</i>	AMNH 262274	1140	San Ramon, Bolivia	Voss et al. 2013
U34851	<i>Coendou longicaudatus longicaudatus</i>	INPA 3919 (MNFS 1016)	1140	Fazenda Santa Fé, Acre, Brazil	Lara, Patton, and da Silva 1996

U34852	<i>Coendou longicaudatus longicaudatus</i>	MVZ 195088 (MNFS 439)	1140	Eirunepé, Amazonas, Brazil	Lara et al. 1996
KC463866	<i>Coendou longicaudatus longicaudatus</i>	USNM 560869	802	Cerro Neblina Base Camp, Amazonas, Venezuela	Voss et al. 2013
KC463867	<i>Coendou longicaudatus longicaudatus</i>	AMNH 273130	762	Nuevo San Juan, Loreto, Peru	Voss et al. 2013
KC463868	<i>Coendou longicaudatus longicaudatus</i>	MUSM 15324	762	Nuevo San Juan, Loreto, Peru	Voss et al. 2013
KC463869	<i>Coendou longicaudatus longicaudatus</i>	MVZ 155200	768	Huampami, Amazonas, Peru	Voss et al. 2013
KC463870	<i>Coendou longicaudatus longicaudatus</i>	MVZ 155201	772	Huampami, Amazonas, Peru	Voss et al. 2013
KC463871	<i>Coendou longicaudatus longicaudatus</i>	MVZ 191349	772	Rio Juruá, Ocidente, Acre, Brazil	Voss et al. 2013
KC463872	<i>Coendou longicaudatus longicaudatus</i>	INPA 2875	788	Eirunepé, Amazonas, Brazil	Voss et al. 2013
KC463874	<i>Coendou longicaudatus longicaudatus</i>	MNHN 1997.643	795	Petit Saut, French Guiana	Voss et al. 2013
KC463875	<i>Coendou longicaudatus longicaudatus</i>	EBRG 23415	798	Río Caroní, Bolívar, Venezuela	Voss et al. 2013
KC463876	<i>Coendou longicaudatus longicaudatus</i>	USNM 281898	802	Valledupar, Cesar, Colombia	Voss et al. 2013
KC463877	<i>Coendou longicaudatus longicaudatus</i>	USNM 281904	678	Valledupar, Cesar, Colombia	Voss et al. 2013
KC463878	<i>Coendou longicaudatus longicaudatus</i>	USNM 443409	802	Las Mesas, Táchira, Venezuela	Voss et al. 2013
KC463879	<i>Coendou longicaudatus longicaudatus</i>	USNM 528360	1140	Limoncocha, Sucumbios, Ecuador	Voss et al. 2013
MG775435	<i>Coendou longicaudatus longicaudatus</i>	IAvH 123	1140	Toledo, Norte de Santander, Colombia	Torres-Martínez et al. 2019

AF411583	<i>Coendou melanurus</i>	UFPB 3001	786	São João da Baliza, Roraima, Brazil	Bonvicino et al. 2002
KC463862	<i>Coendou melanurus</i>	MNHN 1997.641	1140	Barragem Petit Saut, French Guiana	Voss et al. 2013
KC463863	<i>Coendou mexicanus</i>	ASNHC 6407	1140	Campeche, Mexico	Voss et al. 2013
KC261597	<i>Coendou nycthemera</i>	UFES 2079	801	UHE Estreito, Tocantins, Brazil	Mendes Pontes et al. 2013
KC463864	<i>Coendou nycthemera</i>	USNM 519690	795	Ilha de Marajó, Pará, Brazil	Voss et al. 2013
KC463865	<i>Coendou nycthemera</i>	USNM 519692	794	Ilha de Marajó, Pará, Brazil	Voss et al. 2013
KY784126	<i>Coendou prehensilis</i>	UFPB 9412	1119	João Pessoa, Paraíba, Brazil	This work
HM462243	<i>Coendou prehensilis</i>	MNRJ 73383‡	801	Usina Trapiche, Pernambuco, Brazil	Leite et al. 2011
KC463880	<i>Coendou pruinosus</i>	MHNLS 7692	259♣	Zulia, Venezuela	Voss et al. 2013
KC463881	<i>Coendou quichua</i>	KMH 2218	1114	Cotopaxi, Ecuador	Voss et al. 2013
KC463882	<i>Coendou quichua</i>	LACM 27376	1140	Cesar, Colombia	Voss et al. 2013
KC463883	<i>Coendou quichua</i>	USNM 296308	682	Zona Canal, Panama	Voss et al. 2013
KC463884	<i>Coendou rufescens</i>	AMNH 181483	814	Cauca, Colombia	Voss et al. 2013
KC261592	<i>Coendou speratus</i>	UFPE 1708	801	Usina Trapiche, Pernambuco, Brazil	Mendes Pontes et al. 2013
KC261593	<i>Coendou speratus</i>	UFPE 1709	801	Usina Trapiche, Pernambuco, Brazil	Mendes Pontes et al. 2013
KC261594	<i>Coendou speratus</i>	MNRJ 72046	801	Usina Trapiche, Pernambuco, Brazil	Mendes Pontes et al. 2013
KC261595	<i>Coendou speratus</i>	MNRJ 72045♦	801	Usina Trapiche, Pernambuco, Brazil	Mendes Pontes et al. 2013
KC261596	<i>Coendou speratus</i>	UFES 1184	801	Usina Trapiche, Pernambuco, Brazil	Mendes Pontes et al. 2013
KC463885	<i>Coendou spinosus</i>	UNMZ (GD 252)	1112	Itapúa, Paraguay	Voss et al. 2013

KC463886	<i>Coendou spinosus</i>	UMMZ 174975	1112	Caazapá, Paraguay	Voss et al. 2013
KC463887	<i>Coendou spinosus</i>	UFMG 3043	1140	Sorocaba, São Paulo, Brazil	Voss et al. 2013
AF407277	<i>Coendou spinosus</i>	MNRJ 46938	1071	Rio das Ostras, Rio de Janeiro, Brazil	Bonvicino et al. 2002
AF411580	<i>Coendou spinosus</i>	MNRJ 46937	1106	Sumidouro, Rio de Janeiro, Brazil	Bonvicino et al. 2002
EU544661	<i>Coendou spinosus</i>	CIT1326	1140	UHE Rosal, Espírito Santo, Brazil	Vilela et al. 2009
EU544662	<i>Coendou spinosus</i>	MZUSP 35142	1140	Biritiba Mirim, São Paulo, Brazil	Vilela et al. 2009
JX312693	<i>Coendou spinosus</i> †	MNRJ 78937	**	Santa Tereza, Espírito Santo, Brazil	Voloch et al. 2013
KC463888	<i>Coendou vestitus</i>	AMNH 70596	682	Cundinamarca, Colombia	Voss et al. 2013
MG383643	<i>Coendou vestitus</i>	IAvH 7956	1121	Villa de Leyva, Colombia	Ramírez- Chaves et al. 2019
FJ357428	<i>Erethizon dorsatum</i>	–	1140	–	Vilela et al. 2009
KC463889	<i>Erethizon dorsatum</i>	USNM 568658	1140	–	Voss et al. 2013
EU544660	<i>Chaetomys subspinosus</i>	MCNU 918	1140	Salvador, Bahia, Brazil	Vilela et al. 2009

† The sequences from Voloch *et al.* (2013): NC_021387 has no information about its collection locality and the identification of MNRJ 78937 (JX312693) was corrected after examination of the specimen (only skin available). Both sequences are identical, probably due duplicate in GenBank. The sequence NC_021387 is not cited in the work of Voloch *et al.* (2013), what reinforces the hypothesis of duplicate.

‡ Neotype of *Coendou prehensilis*.

◆ Holotype of *Coendou speratus*.

** The authors sequenced the complete mitochondrial genome, but we used only 1140bp of the cytochrome *b* gene.

♣ not used due small sequence size.

References of the cytochrome *b* sequences

- Bonvicino, C. R., Penna-Firme, V., & Braggio, E. (2002). Molecular and Karyologic Evidence of the Taxonomic Status of *Coendou* and *Sphiggurus* (Rodentia: Hystricognathi). *Journal of Mammalogy*, 83(4), 1071–1076.
- Lara, M. C., Patton, J. L., & da Silva, M. N. F. (1996). The simultaneous diversification of South American echimyid rodents (Hystricognathi) based on complete cytochrome b sequences. *Molecular Phylogenetics and Evolution*, 5(2), 403–413. <https://doi.org/10.1006/mpev.1996.0035>
- Mendes Pontes, A. R., Gadelha, J. R., Melo, É. R. A., de Sá, F. B., Loss, A. C., Caldara Jr, V., Costa, L. P., & Leite, Y. L. R. (2013). A new species of porcupine, genus *Coendou* (Rodentia: Erethizontidae) from the Atlantic forest of northeastern Brazil. *Zootaxa*, 3636(3), 421.

- <https://doi.org/10.11646/zootaxa.3636.3.2>
- Ramírez-Chaves, H. E., Torres-Martínez, M. M., Noguera-Urbano, E. A., Passos, F. C., & Colmenares-Pinzón, J. E. (2019). State of knowledge and potential distribution of the Colombian endemic brown hairy dwarf porcupine *Coendou vestitus* (Rodentia). *Mammalian Biology*, 99, 1–11. <https://doi.org/10.1016/j.mambio.2019.09.012>
- Torres-Martínez, M. M., Ramírez-Chaves, H. E., Noguera-Urbano, E. A., Colmenares-Pinzón, J. E., Passos, F. C., & García, J. (2019). On the distribution of the Brazilian porcupine *Coendou prehensilis* (Erethizontidae) in Colombia. *Mammalia*, 83(3), 290–297. <https://doi.org/10.1515/mammalia-2018-0043>
- Vilela, R. V., Machado, T., Ventura, K., Fagundes, V., Silva, M. J. de J., & Yonenaga-Yassuda, Y. (2009). The taxonomic status of the endangered thin-spined porcupine, *Chaetomys subspinosus* (Olfers, 1818), based on molecular and karyologic data. *BMC Evolutionary Biology*, 9(29), 1–17. <https://doi.org/10.1186/1471-2148-9-29>
- Voloch, C. M., Vilela, J. F., Loss-Oliveira, L., & Schrago, C. G. (2013). Phylogeny and chronology of the major lineages of New World hystricognath rodents: insights on the biogeography of the Eocene/Oligocene arrival of mammals in South America. *BMC Research Notes*, 6, 160. <https://doi.org/10.1186/1756-0500-6-160>
- Voss, R. S., Hubbard, C., & Jansa, S. A. (2013). Phylogenetic relationships of New World porcupines (Rodentia, Erethizontidae): implications for taxonomy, morphological evolution, and biogeography. *American Museum Novitates*, 3769, 1–36. <https://doi.org/10.1206/3769.2>

3.8 Supporting Information

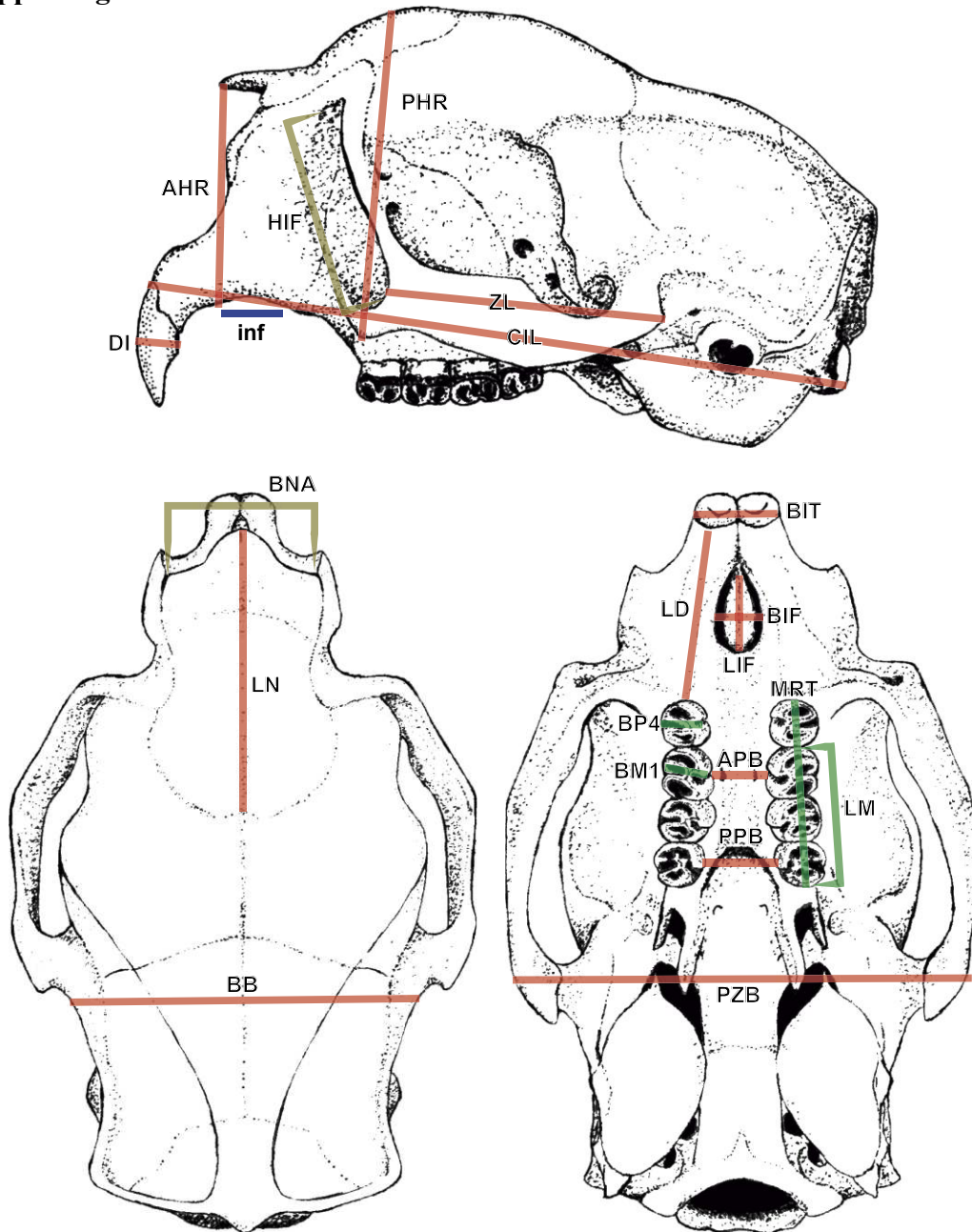


Figure S1. Cranial measurements taken for morphometric analysis.

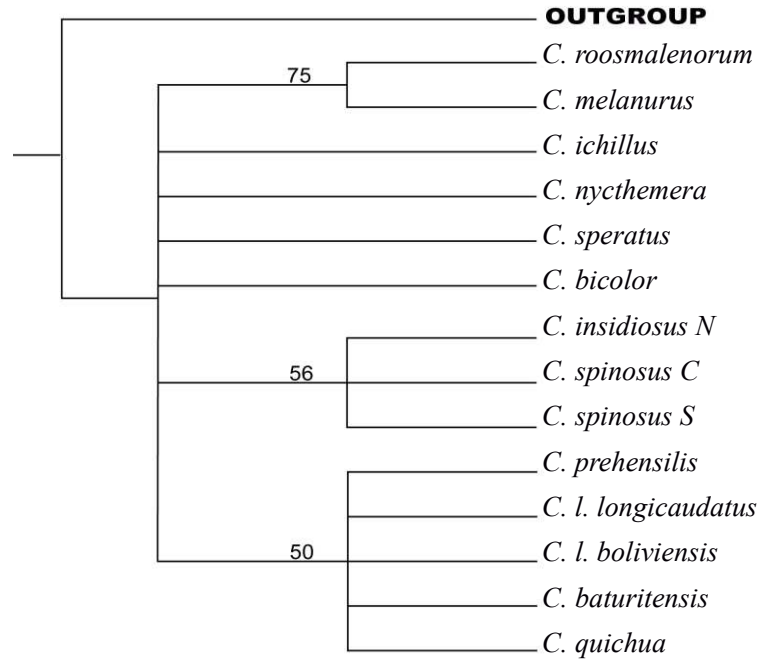


Figure S2. Erethizontid's phylogenetic tree obtained by Maximum Parsimony with morphological data.

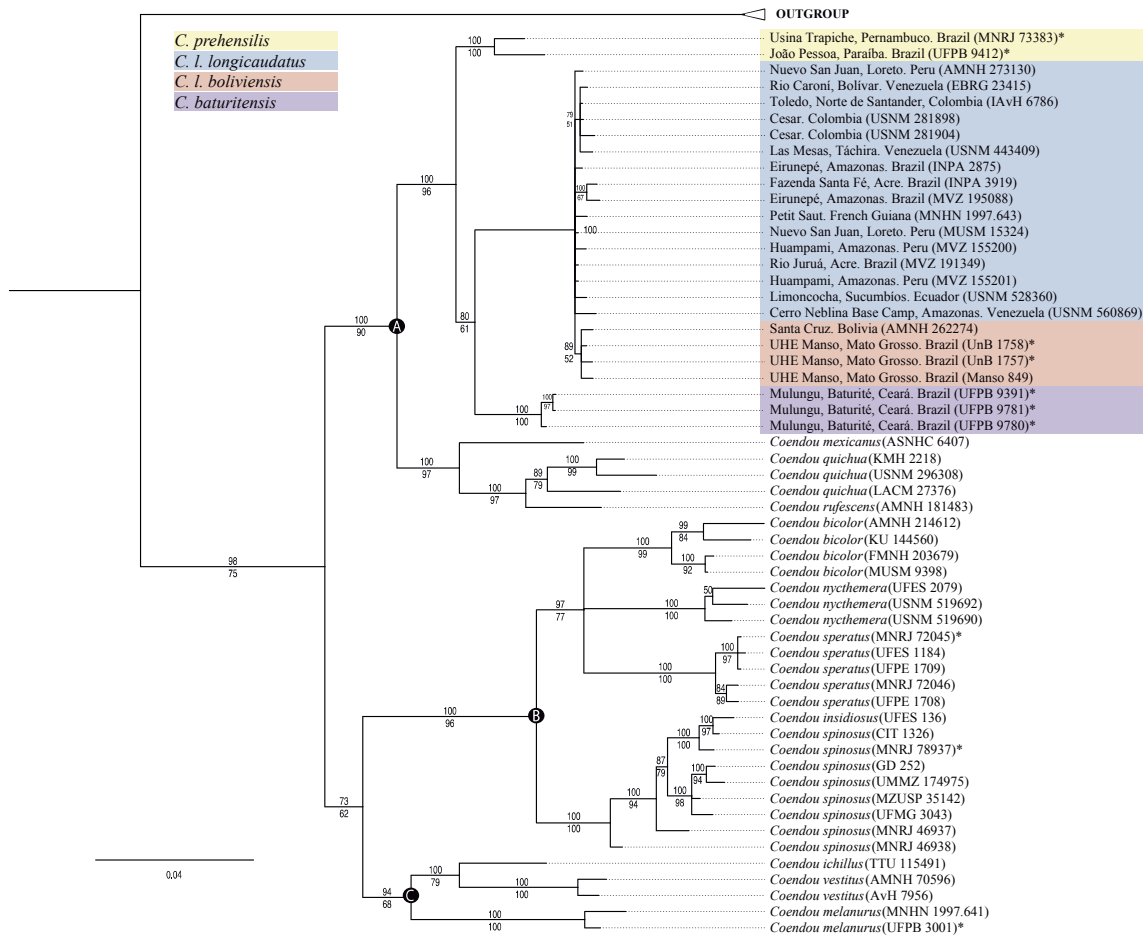


Figure S3. Erethizontid's phylogenetic tree obtained by Bayesian Inference (BI) and Maximum Likelihood (ML) with *cyt b* sequences.



Figure S4. Holotype (UFPB 6809) of *Coendou baturitensis*.

4 Capítulo 3: Phylogenetic relationships, distribution, and conservation of Roosmalens' dwarf porcupine *Coendou roosmalenorum* (Rodentia: Erethizontidae)

Fernando Heberon Menezes¹, Thiago Borges Fernandes Semedo³, Juliane Saldanha, Guilherme Siniciato Terra Garbino, Hugo Fernandes-Ferreira, Pedro Cordeiro-Estrela, Itayguara Ribeiro da Costa

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Abstract

The New World porcupines of genus *Coendou* comprise 16 species of arboreal nocturnal rodents. Some of these porcupines are poorly known and have not been included in phylogenetic analyses. Based on recently collected specimens with associated tissue from the Brazilian Amazonia we investigate the distribution and phylogenetic position of the Roosmalens' dwarf porcupine *Coendou roosmalenorum* using an integrative based on mitochondrial *cyt b* gene and morphological data from new specimens and localities. Our results recovered *C. roosmalenorum* in the subgenus *Caaporamys*. However the molecular and combined datasets provided distinct topologies. The new record shows the presence of *C. roosmalenorum* 480 km to the southeast of the Rio Madeira and 95 km away from Rio Juruena in Mato Grosso State, indicating a wider distribution in southern Amazonia as suspected. All the known records of *C. roosmalenorum* are in the Madeira Province. Therefore, based on our results we consider the possibility that this porcupine species is endemic of the Madeira Province as other arboreal species of mammals.

Keywords

Amazonia; Brazil; Madeira Province; cytochrome *b*; Neotropical porcupines.

4.1 Introduction

The New World porcupines are arboreal, herbivorous, and nocturnal rodents of the family Erethizontidae, which can be found along tropical and subtropical regions of the Americas (Eisenberg and Redford 1999). Erethizontids are characterized mainly by having their fur modified into quills, a bulbous snout and a long dorsally prehensile tail, which is an exclusive trait among prehensile-tailed mammals (Emmons 1997, Voss 2015). Currently the 18 species of erethizontids are classified in three genera, with the genus *Coendou* Lácepède, 1799 comprising 16 species (Menezes et al. 2021).

Since the early 1990s, studies have clarified the taxonomic status and phylogenetic relationships among species of the genus *Coendou* (e.g., Handley and Pine 1992, Voss and Angermann 1997, Voss and da Silva 2001, Voss 2011, Feijó and Langguth 2013, Mendes Pontes et al. 2013, Voss et al. 2013), as well as its subgeneric classification (e.g., Bonvicino et al. 2002, Menezes et al. 2021). Additionally, there have also been advances on the knowledge about the distribution and natural history of *Coendou* species (e.g., Freitas et al. 2013, Gregory et al. 2015, Menezes et al. 2020, Ramírez-Chaves et al. 2020a).

Most of the knowledge about the *Coendou* porcupines are restricted to species that occur close to urban centers (see Voss 2015). In the Amazonia, most of the records are from the margins of the main rivers. Neotropical porcupines are usually hard to record, because they are not captured by usual live-trapping sampling methods, and have cryptic behavior (Kays and Allison 2001, Gregory et al. 2015, Kaizer et al. 2022). Nevertheless, species of *Coendou* may be locally abundant in some areas, such as *Coendou melanurus* (Wagner, 1842) in French

Guiana (Vié 1999). Hence, information on species distributed along the Amazonian rainforest or at the Andean foothills are mostly scarce, with the exceptions of *Coendou rufescens* (Gray, 1865) (e.g., More and Crespo 2017, Acosta et al. 2018, Narváez-Romero et al. 2018, Ramírez-Chaves et al. 2020b, 2021a) and *Coendou vestitus* Thomas, 1899 (e.g., Ramírez-Chaves et al. 2019, Torres-Martínez et al. 2021b, 2021a). Out of the 16 *Coendou* species that have undergone an extinction risk assessment by the IUCN Red List, one is classified as Endangered and six are Data Deficient, among which *Coendou roosmalenorum* Voss and da Silva, 2001 (IUCN, Roach and Naylor 2016).

The dwarf porcupine *Coendou roosmalenorum* is one of the least known species of New World porcupines. It was originally known to occur only in the Brazilian Amazon from both banks of the Madeira River, and only anecdotal information is available on its natural history (Voss and da Silva 2001). Since the description of the species, no novel data was published on its biology, natural history, or distribution. An exception is a morphological phylogeny that included *C. roosmalenorum*, placing it in the subgenus *Caaporamys* Menezes, Feijó, Fernandes-Ferreira, da Costa & Cordeiro-Estrela, 2021 (Menezes et al. 2021).

Due to the scarcity of information, and the lack of fresh tissue samples, its phylogenetic position remains uncertain. Here, based on a recently collected specimen with associated tissue, from Aripuanã, Mato Grosso, we investigate the phylogenetic position and distribution of *Coendou roosmalenorum*. We assess the phylogenetic position of *C. roosmalenorum* in the *Coendou* and discuss the distribution and conservation of the species based on the new record.

4.2 Material and Methods

4.2.1 Specimens Examined

The examined specimens are deposited in two collections (abbreviations in parentheses): Coleção de Mamíferos da Universidade Federal de Mato Grosso (UFMT), Cuiabá and Coleção de Mamíferos da Universidade Federal da Paraíba (UFPB), João Pessoa (Figures 1 and 2). The holotype and paratype of *C. roosmalenorum* are deposited in the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus (see Voss & Silva 2001). The recently collected specimen from which we obtained the tissue sample was accidentally killed by a bulldozer during a forest suppression activity in a mining site in Serra do Expedito, Aripuanã, Mato Grosso (10° 40'S, 59° 30'W). It is preserved in fluid, and a muscle sample was obtained and preserved in ethanol 70°. The skull is severely damaged but external characters of the pelage and quills allowed us to identify the specimen as *C. roosmalenorum*.

The nomenclature of the soft hairs and quills of the porcupines used here follows Menezes et al. (2021). Skull characters follow Menezes et al. (2021) and the original description of *C. roosmalenorum* (Voss and da Silva 2001, Voss 2015).

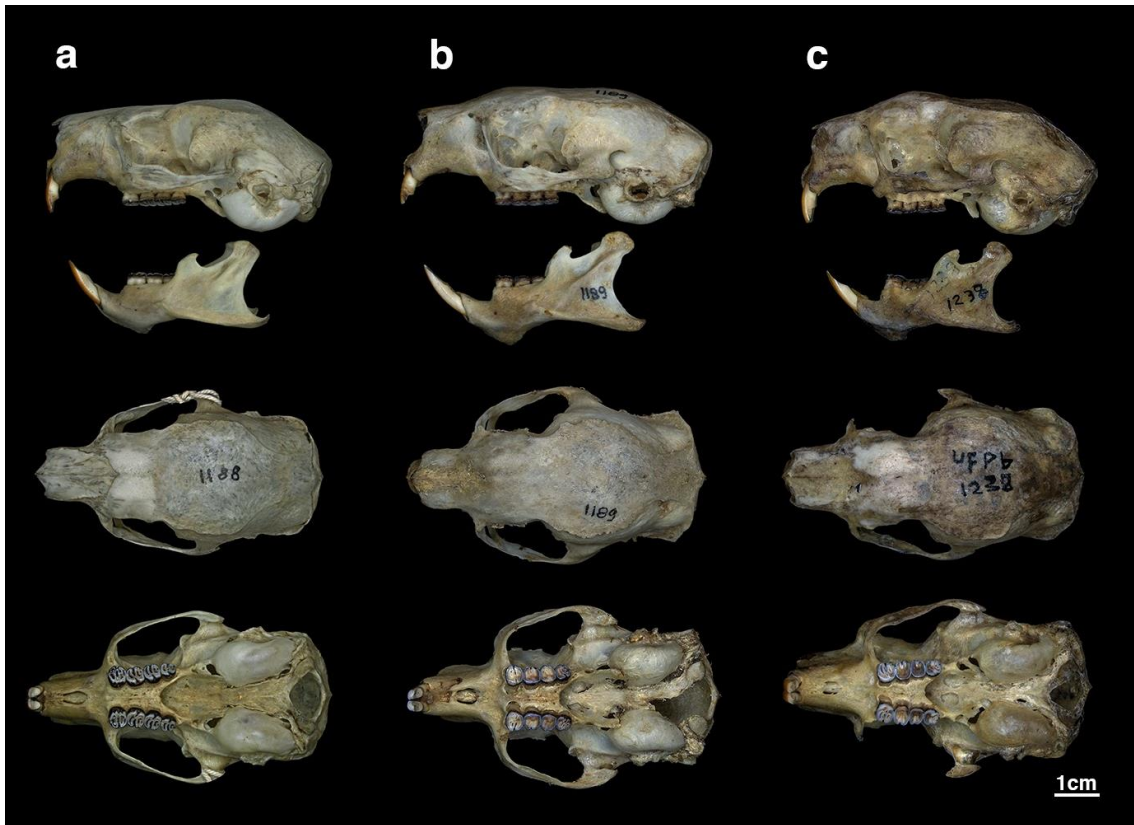


Figure 1: Skulls and mandibles of *Coendou roosmalenorum* specimens deposited in Coleção de Mamíferos da Universidade Federal da Paraíba (UFPB): a) UFPB 1188, b) UFPB 1189 and c) UFPB 1238.



Figure 2: Stuffed skins (a, b and c) and entire fluid-preserved specimen (d) of dwarf porcupines, *Coendou roosmalenorum*: a) UFPB 1188, b) UFPB 1189, c) UFPB 1238 and d) UFMT 4930.

4.2.2 DNA purification and sequencing

The genomic DNA of the *C. roosmalenorum* individual was obtained from ethanol-preserved tissues using a saline extraction protocol (Aljanabi and Martinez 1997), with modifications. We used the MVZ05 and MVZ16 primers (Smith and Patton 1993) for amplification of the mitochondrial Cytochrome *b* gene (*cyt b*), following the protocol described in Saldanha et al. (2019). Purification and sequencing were obtained by the Sanger method, in both directions with the amplification primers on ABI3730xl Genetic Analyzer at the “Biotecnologia, Pesquisa e Inovação – BPI, SP, Brazil”. We obtained a partial cytochrome *b* sequence with 821 nucleotide length. The sequence was aligned to assemble the consensus in the software Geneious v. 7.1.3, Biomatters, available at <http://www.geneious.com> (Kearse et al. 2012), and deposited in GenBank under the accession number xxxxxx.[*number will be provided in the proof*]

4.2.3 Phylogenetic analyses

To investigate the phylogenetic position of *C. roosmalenorum* we used two approaches: 1) a molecular approach, and 2) a combined approach.

Only cytochrome *b* (*cyt b*) sequences were available for the molecular analysis, where we used the molecular dataset previously published by Menezes et al. (2021), with the additional new sequence of *C. roosmalenorum* (Table S1), totaling 60 sequences aligned by MUSCLE algorithm in MEGA 11 (Tamura et al. 2021). We did not trim the final alignment and treated the gaps as missing data, resulting in an alignment size of 1140 nucleotides. Before the phylogenetic analyses, we tested the best substitution model using the ModelFinder plugin (Kalyaanamoorthy et al. 2017) in the PhyloSuite environment (Zhang et al. 2020). The best-fit model selected according to the Bayesian Information Criterion (BIC) (see Sullivan and Joyce 2005) was the HKY (Hasegawa et al. 1985) with gamma distribution (+G). The HKY+G model was used in all phylogenetic analyses. After model selection, we ran a Maximum Likelihood (ML) and a Bayesian Inference (BI1) using *Chaetomys subspinosus* (Olfers), 1818 and *Erethizon dorsatum* (Linnaeus, 1758) as outgroups.

Maximum likelihood (ML) consensus tree was inferred using IQ-TREE (Nguyen et al. 2015) plugin of the PhyloSuite environment under 5000 ultrafast (Minh et al. 2013) bootstraps, as well as the Shimodaira–Hasegawa–like approximate likelihood-ratio test (Guindon et al. 2010), an initial BioNJ tree method (Guindon and Gascuel 2003) and four categories of gamma distribution (Gamma=0.258). Estimated nucleotide frequencies are $f(A)=0.304$, $f(C)=0.265$, $f(G)=0.124$, $f(T)=0.307$. Bayesian Inference (IB1) phylogenies were inferred using MrBayes 3.2.6 (Ronquist et al. 2012) plugin of PhyloSuite environment with eight chains over 10 million generations sampled every 100, in which the initial 25000 sampled data were discarded as burn-in to estimate consensus trees and evolutionary parameter.

The dataset used in the combined approach contains the same *cyt b* sequences combined with morphological characters from the character matrix of Menezes et al. (2021). The coding of morphological characters and the combination with molecular sequences were made in the nexus file following Maddison et al. (1997). To detect the autapomorphies of *C. roosmalenorum*, we performed a maximum parsimony (MP) analysis with 1000 bootstrap replicates in PAUP4 (Swofford 2002, Wilgenbusch and Swofford 2003). Gaps were treated as "additional states." Starting tree(s) obtained via stepwise addition and the tree–bisection–reconnection (TBR) algorithm with reconnection limit of 8. Branches collapse (creating

polytomies) if maximum branch length is zero. The consensus tree used a 50% majority-rule consensus rule. After MP, we ran Bayesian Inference (IB2) with combined characters through the use of partitioned models in MrBayes plugin of PhyloSuite environment. We used the same model and parameters of IB1 for the *cyt b* partition and the parsimonious model of Lewis (2001) for the morphological partition.

The genetic distances were calculated for the *cyt b* dataset in MEGA 11 (Tamura et al. 2021) using the Kimura's 2-parameter model (K2P, Kimura 1980) considering no gamma distribution or invariant sites following previous studies (e.g., Mendes Pontes et al. 2013, Torres-Martínez et al. 2019). All ambiguous positions were removed for each sequence pair (pairwise deletion option).

4.2.4 Distribution and conservation data

In order to provide an updated distribution map of *C. roosmalenorum*, we used published records that were based on museum specimens (Voss and da Silva 2001, Voss 2015), and new records obtained by us (Table 1). The map was made considering geopolitical boundaries of the South American countries, Brazilian states and the biogeographical regionalization of the Neotropical region following Morrone et al. (2022).

Table 1: List of the known localities of the Brazilian endemic *Coendou roosmalenorum*. The “locality” column refers to the numbers on the map of Figure 5.

Locality	Latitude	Longitude	Reference
1. Serra do Expedito, Aripuanã, Mato Grosso	10°40'S	59°30'W	This study
2. 2. Samuel Hydroelectric Dam, Rio Jamari, Rondônia	8°45'S	63°27'W	This study
3. 3. BR 364, 49 km E from Porto Velho, Rondônia*	8°45'S	63°30'W	Voss and da Silva 2001
4. 4. Novo Jerusalém on Lago Matupirizinho, Amazonas	5°33'S	61°07'W	Voss and da Silva 2001
5. 5. Santa Maria on Lago Matupiri, Amazonas	5°33'S	61°15'W	Voss and da Silva 2001

*coordinates estimated in this study.

We calculated the Extent of Occurrence (EOO) which is the area contained within the smallest continuous boundary that can be drawn to encompass all known, inferred or projected points of the current presence of a taxon (IUCN 2012). Based on IUCN recommendations, we estimated the EOO using the Minimum Convex Polygon (MCP). This method consists of the smallest polygon in which no interior angle exceeds 180° and which contains all occurrence points recorded (Burgman and Fox 2003). The Area of Occupancy (AOO) is defined as the area inside the EOO occupied by the species (IUCN 2012). Because it is an arboreal mammal, we assumed as the AOO the forest cover currently available based on Projeto Mapbiomas (Souza et al. 2020). This same database was used to estimate the deforestation in the polygon between 1987 and 2020. The analyzes were performed using the QGIS software version 3.32.

4.3 Results

The specimens examined have the diagnostic characters of *Coendou roosmalenorum* (Figure 3): brownish dorsal fur covering the quills; bristle-quills with strong yellowish B1, blackish B2 and light yellowish B3 on the dorsal crest; bicolored short quills with long yellowish B1 and very short blackish B2; blackish unicolored bristles on tail; small sizes when compared to other porcupine species; no nasofrontal inflation on the skull; and tail length subequal to body length (Voss and da Silva 2001, Menezes et al. 2020).

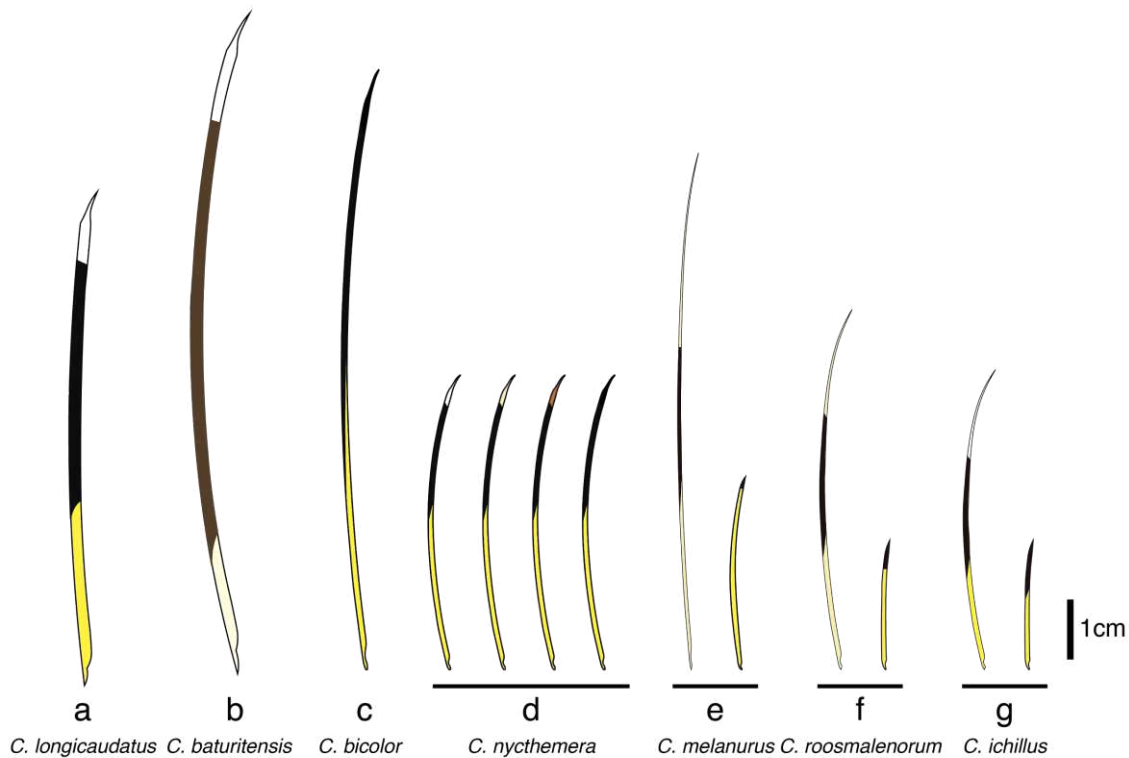


Figure 3: Quills and bristle-quills of selected species of Brazilian porcupines. a) Amazonian *C. longicaudatus* long tricolored quill, b) *C. baturitensis* long tricolored quill, c) *C. bicolor* long bicolored quill, d) *C. nycthemera* long quills with different distal band colors, e) *C. melanurus* tricolored guard hair and bicolored quill, f) *C. roosmalenorum* tricolored bristle-quill and bicolored quill, and g) *C. ichillus* tricolored bristle-quill and bicolored quill (adapted from Menezes et al. 2020).

The Maximum Parsimony analysis with combined data has the following indices: Tree length = 1206 steps, Consistency index (CI) = 0.4934, Homoplasy index (HI) = 0.5066, CI excluding uninformative characters = 0.4337, HI excluding uninformative characters = 0.5663, Retention index (RI) = 0.8231, Rescaled consistency index (RC) = 0.4061, f value = 53305, f-ratio = 0.3722. The values of the indices indicate a dataset with a lot of homoplasies.

Both datasets recovered *C. roosmalenorum* in *Caaporamys* subgenus, as expected based on morphological traits. But the molecular dataset (ML and IB1) and combined dataset (MP and IB2) had two distinct topologies (Figure 4). The molecular dataset recovered *C. roosmalenorum* as the sister taxon of *C. vestitus* while the combined dataset suggests that *C. roosmalenorum* is the sister species of *C. melanurus*. The internal relationships among the four species of subgenus *Caaporamys* differ using both datasets. Additionally, the species with lowest genetic distance value of *C. roosmalenorum* is *C. vestitus* (Table 2).

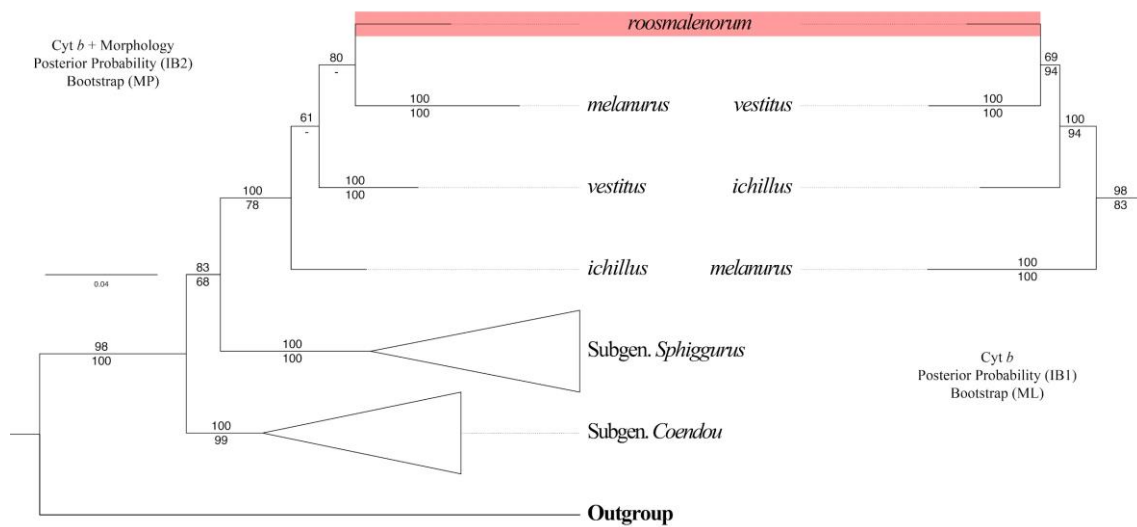


Figure 4: Phylogenetic hypotheses of *Coendou*, focused on the species of subgenus *Caaporamys* based on two distinct datasets. Left: combined morphological and *cyt b* datasets, the values above the branches represent the posterior probabilities of IB2 and values below represent the bootstrap supports of MP. Right: *cyt b*, the values above the branches represent the posterior probabilities of IB1 and values below represent the bootstrap proportions of ML. Branches of subgenera other than *Caaporamys* are collapsed.

Table 2: Estimates of evolutionary divergence over cytochrome *b* sequence pairs between species of subgenus *Caaporamys*, calculated using K2P model.

	<i>C. ichillus</i>	<i>C. melanurus</i>	<i>C. roosmalenorum</i>
<i>C. melanurus</i>	8.2%		
<i>C. roosmalenorum</i>	5.3%	7.8%	
<i>C. vestitus</i>	5.7%	8.4%	5.1%

The Maximum Parsimony analysis with combined data revealed a single morphological apomorphy of *C. roosmalenorum*, which is a weakly developed Lambdoidal ridge (Char25:1, CI 0.4, Table 3). There is no morphological synapomorphy for the *C. melanurus* + *C. roosmalenorum* hypothesis, as the MP analysis resulted in a polytomy for the relationships among the *Caaporamys* species.

Table 3: List of morphological apomorphies of *Caaporamys* species obtained in Maximum Parsimony of combined data.

Subgenus <i>Caaporamys</i>	Character	Steps	CI	State Change	Description
<i>C. ichillus</i>	Char1	1	0.250	1 → 0	Fur is not covering quills on the dorsal crest
	Char2	1	0.500	1 → 0	Absence of dorsal fur
	Char11	1	0.500	2 → 0	B3 of bristle-quills is whitish
	Char21	1	0.400	0 → 1	Medial masseter scar is oval and wide
	Char24	1	0.667	0 → 1	Temporal crests drawing in dorsal view is V-shaped
	Char26	1	0.333	0 → 1	Palatal keel conspicuous

	Char31	1	0.200	1 → 0	The dorsal roof of the external auditory meatus is not keeled
	Char33	1	0.500	1 → 0	Orbito temporal fossa is shallow
<i>C. melanurus</i>	Char12	1	0.429	0 → 1	B2 is about the same length of B1
	Char13	1	0.500	2 → 1	B3 is about the same length of B2
<i>C. vestitus</i>					Only molecular apomorphies available
<i>C. roosmalenorum</i>	Char25	1	0.400	0 → 1	Lambdoidal ridge weakly developed

All the records of *C. roosmalenorum* are in the Madeira Province (Figure 5). The new record (locality 1) is 480 km east from Samuel Hydroelectric Dam (localities 2 and 3) and 590 km south from the Matupiri lake region (localities 4 and 5). The Extent of Occurrence (EOO) estimated is 108,049.87 km² and the Area of Occupancy (AOO) is 107,763.84 km².

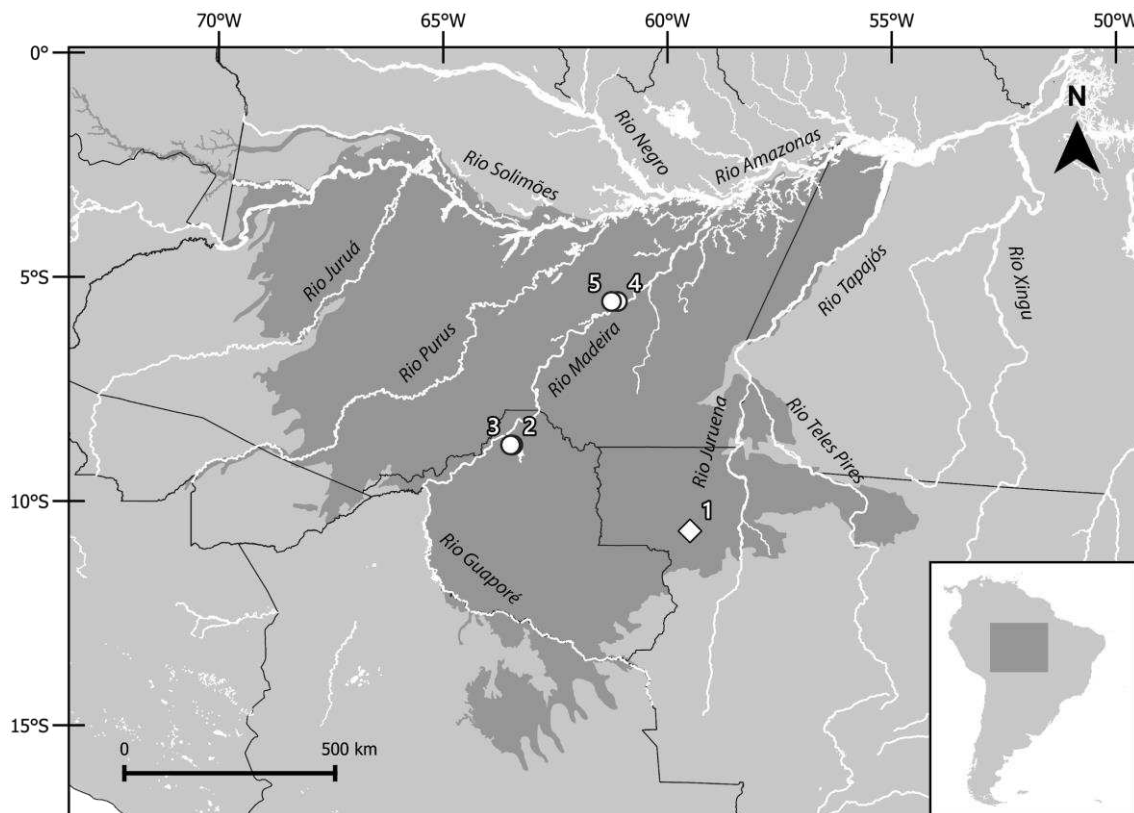


Figure 5: Distribution of *C. roosmalenorum* in Brazilian Amazonia. The numbered localities are detailed in Table 1. The new record (locality 1) is the most southeastern record for the species, from the State of Mato Grosso, Brazil. The darker gray area represents the Madeira Province *sensu* Morrone et al. (2022). The main rivers are white colored and their names are above.

4.4 Discussion

4.4.1 Phylogenetic position of *C. roosmalenorum*

The molecular and combined datasets recovered *Coendou roosmalenorum* as a member of *Caaporamys* subgenus, as expected based on the morphological characters. The species has the diagnostic morphological traits of the subgenus, such as the presence of bristle-quills on the

dorsal crest, soft ventral pelage and unicolored quills on the tail (Menezes et al. 2021). The new information we obtained agrees with the only phylogeny that included the species (Menezes et al. 2021), which reinforces the importance of external characters to subgeneric classification of the genus *Coendou*.

However, the two datasets suggest two different topologies in *Caaporamys* subgenus, with *C. roosmalenorum* placed either as the sister species of *C. melanurus* or *C. vestitus*. The distinct hypotheses may be the result of the availability of morphological data for *Caaporamys* species. The available morphological dataset for phylogenetic analyses lacks cranial characters for *Coendou melanurus* and includes only molecular characters for *Coendou vestitus*. Because of this character combination, external characters with the same states appear to have a major contribution to the combined data, such as the colors and length of the quill bands, in the absence of cranial characters.

The color and length of quill bands of the neotropical porcupines have a high level of homoplasy (Table 3 and Menezes et al. 2021). Homoplasy is known to have negative effects on phylogenetic inference, such as the reduction of branch supports, artificial grouping (Simpson 2010, Radel et al. 2013), and long-branch attraction (Bergsten 2005). Therefore, we understand the topology of the combined dataset as a case of grouping by homoplasy and consider *C. vestitus* as sister species of *C. roosmalenorum* until new data arise.

4.4.2 Distribution and conservation of *C. roosmalenorum*

Previously, the distribution of *C. roosmalenorum* was associated with the Rio Madeira margins, as the species was known from only two localities along that river or its tributary, Rio Jamari, in Brazil (Voss and da Silva 2001). The new record shows the presence of *C. roosmalenorum* 480 km to the southeast of the Rio Madeira and 95 km away from Rio Juruena in Mato Grosso State, indicating a wider distribution in southern Amazonia, as suspected (Voss 2015). The area the new record was made is in an Amazon rainforest region that is not subject to seasonal flooding.

All the known records of *C. roosmalenorum* are in the Madeira Province *sensu* Morrone et al. (2022). Therefore, based on our results we consider the possibility of this porcupine species be distributed along the Madeira Province or even more restricted as other arboreal species of mammals, such as the following primates: *Callicebus cinerascens*, *C. ornatus*, *C. stephennashi*, *C. brunneus*, *C. cupreus* (see the map in Carneiro et al. 2016), *Mico humeralifer*, *M. humilis*, *M. chrysoleucos*, *M. marcai*, *M. rondoni* (Garbino 2014, Garbino and Nascimento 2014) and *Chiropotes albinasus* (Ferrari et al. 1999).

Distribution patterns suggest that *Coendou* species can occur in sympatry with species of different porcupine subgenera and only be allopatric with species of the same subgenus. *Coendou roosmalenorum* occurs in sympatry with *Coendou longicaudatus* Daudin, 1802, the largest porcupine species of subgenus *Coendou*, and is allopatric with other *Caaporamys* species. *Coendou ichillus* Voss and da Silva 2001 is the *Caaporamys* species that occurs nearer to *C. roosmalenorum*, with records on north of the Solimões and Amazonas rivers (Menezes et al. 2020). A similar pattern occurs with *Coendou nycthemera* (Olfers, 1818), of the subgenus *Sphiggurus* F. Cuvier, 1823, which is sympatric with the larger *Coendou baturitensis* Feijó and Langguth 2013 through most of its distribution and is allopatric with other *Sphiggurus* species, such as *Coendou bicolor* (Tschudi, 1844) or *Coendou speratus* Mendes Pontes et al. 2013 (Freitas et al. 2013, Leal et al. 2017, Menezes et al. 2020) which are the closely related to *C. nycthemera* (Mendes Pontes et al. 2013, Menezes et al. 2021). Also the species of subgenus *Coendou* are allopatric, but sympatric with species of different subgenera, as *Coendou*

prehensilis (Linnaeus 1758) is sympatric with *C. speratus* (Menezes et al. 2021) and *C. rufescens* is sympatric with *Coendou ichillus* (Ramírez-Chaves et al. 2016).

Coendou roosmalenorum is classified as Data Deficient (DD) by the IUCN Red List due the absence of recent information on its status and ecological requirements (Roach and Naylor 2016). The EOO and AOO here documented are certainly underestimated (because of the sampling gaps) but much larger than the maximum required by the IUCN distribution criteria for the first threat category (Vulnerable) (IUCN 2012). However, this polygon has lost 9.34% of forest cover since 1987, almost completely replaced by pasture (9.13%) (Souza et al. 2020). Considering Madeira Province, most of this territory is in the Amazonas and Rondônia states, which have lost approximately 15,400 and 15,500 km² respectively between 2008 and 2022. Aripuanã (Mato Grosso state), municipality of the new distribution record of *C. roosmalenorum*, faced 1,226 km² of deforestation in the same period (INPE 2023). In addition to habitat loss, *Coendou* species face other threats in South America such as hunting for subsistence, predation by domestic dogs, and roadkills (Ramírez-Chaves et al. 2020b, 2021b). Moreover, a recent infection by Brazilian porcupine poxvirus was described (Hora et al. 2021) and recorded in two *Coendou* species of different subgenera, *Coendou spinosus* (F. Cuvier, 1823) (Guerra et al. 2022) of the subgenus *Sphiggurus* and *Coendou longicaudatus* (Silva et al. 2023) of the subgenus *Coendou*.

Therefore, it is necessary to investigate population size and decline to assess a more accurate conservation status of *C. roosmalenorum* based on IUCN criteria. In addition to standard ecological approaches focused on erethizontids such as visual census, radiotelemetry, and arboreal camera traps (e.g. Giné et al. 2015, Bowler et al. 2017, Melo-Dias et al. 2023), we suggest that alternative sampling methods may yield new records of this poorly known species. Citizen science data, mainly animals photographed by the community, may provide new records, as attested by recent publications on the genus (e.g., Ramírez-Chaves et al. 2020b).

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Bibliography

- Acosta LH, Urey JLP, Azurduy H (2018) Nuevos registros del Puerco Espín Cola Corta (*Coendou rufescens* Gray 1865) en Bosques Nublados de Bolivia. *Kempffiana* 14: 22–31.
- Aljanabi SM, Martinez I (1997) Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Research* 25: 4692–4693. <https://doi.org/10.1093/nar/25.22.4692>
- Bergsten J (2005) A review of long-branch attraction. *Cladistics* 21: 163–193.

<https://doi.org/10.1111/j.1096-0031.2005.00059.x>

- Bonvicino CR, Penna-Firme V, Braggio E (2002) Molecular and Karyologic Evidence of the Taxonomic Status of *Coendou* and *Sphiggurus* (Rodentia: Hystricognathi). *Journal of Mammalogy* 83: 1071–1076.
- Bowler MT, Tobler MW, Endress BA, Gilmore MP, Anderson MJ (2017) Estimating mammalian species richness and occupancy in tropical forest canopies with arboreal camera traps. *Remote Sensing in Ecology and Conservation* 3: 146–157. <https://doi.org/10.1002/rse2.35>
- Burgman MA, Fox JC (2003) Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. *Animal Conservation* 6: 19–28. <https://doi.org/10.1017/S1367943003003044>
- Carneiro J, De Sousa E Silva J, Sampaio I, Pissinatti A, Hrbek T, Rezende Messias M, Rohe F, Farias I, Boubli J, Schneider H (2016) Phylogeny of the titi monkeys of the *Callicebus moloch* group (Pitheciidae, Primates). *American Journal of Primatology* 78: 904–913. <https://doi.org/10.1002/ajp.22559>
- Eisenberg JF, Redford KH (1999) *Mammals of the Neotropics (Volume 3): The Central Neotropics: Ecuador, Peru, Bolivia, Brazil*. 1st ed. University of Chicago Press, Chicago.
- Emmons LH (1997) *Neotropical Rainforest Mammals: A field guide*. The University of Chicago Press, Chicago.
- Feijó A, Langguth A (2013) Mamíferos de médio e grande porte do Nordeste do Brasil: Distribuição e taxonomia, com descrição de novas espécies. *Revista Nordestina de Biologia* 22: 3–225.
- Ferrari SF, Iwanaga S, Coutinho PEG, Messias MR, Neto EH, Ramos EM, Ramos PCS (1999) Zoogeography of *Chiropotes albinasus* (Platyrrhini, Atelidae) in Southwestern Amazonia. *International Journal of Primatology* 20: 995–1004.
- Freitas MA de F, França DPF de, Veríssimo D (2013) First record of the Bicoloured-spined Porcupine *Coendou bicolor* (Tschudi, 1844) for Brazil. *Check List* 9: 94. <https://doi.org/10.15560/9.1.94>
- Garbino GST (2014) The Taxonomic Status of *Mico marcai* (Alperin 1993) and *Mico manicorensis* (van Roosmalen et al. 2000) (Cebidae, Callitrichinae) from Southwestern Brazilian Amazonia. *International Journal of Primatology* 35: 529–546. <https://doi.org/10.1007/s10764-014-9766-4>
- Garbino GST, Nascimento FO (2014) *Mico humeralifer* (Primates: Callitrichidae). *Mammalian Species* 911: 40–47. <https://doi.org/10.1644/911.1>
- Giné GAF, de Barros EH, Duarte JMB, Faria D (2015) Home range and multiscale habitat selection of threatened thin-spined porcupine in the Brazilian Atlantic Forest. *Journal of Mammalogy* 96: 1095–1105. <https://doi.org/10.1093/jmammal/gyv117>
- Gregory T, Lunde D, Zamora-Meza HT, Carrasco-Rueda F (2015) Records of *Coendou ichillus*

- (Rodentia, Erethizontidae) from the Lower Urubamba Region of Peru. *ZooKeys*: 109–121. <https://doi.org/10.3897/zookeys.509.9821>
- Guerra JM, Navas-Suárez PE, Ferreira-Machado E, Ervedosa TB, Figueiredo KB, de Carvalho ACSR, Silva ML, Caiaffa MG, da Costa ALM, Teixeira RHF, Buti TEM, Luchs A, Namiyama GM, de Lima LB, Taniwaki NN, Matsumoto PSS, de Azevedo Fernandes NCC (2022) Diagnosis and successful treatment of Brazilian porcupine poxvirus infection in a free-ranging hairy dwarf porcupine (*Coendu spinosus*). *Brazilian Journal of Microbiology* 53: 2321–2327. <https://doi.org/10.1007/s42770-022-00804-3>
- Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52: 696–704. <https://doi.org/10.1080/10635150390235520>
- Guindon S, Dufayard J-F, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* 59: 307–321. <https://doi.org/10.1093/sysbio/syq010>
- Handley CO, Pine RH (1992) A new species of prehensile-tailed porcupine, genus *Coendou* Lacépède, from Brazil. *Mammalia* 56. <https://doi.org/10.1515/mamm-1992-0207>
- Hasegawa M, Kishino H, Yano T (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution* 22: 160–174. <https://doi.org/10.1007/BF02101694>
- Hora AS, Taniwaki SA, Martins NB, Pinto NNR, Schlemper AE, Santos ALQ, Szabó MPJ, Brandão PE (2021) Genomic analysis of novel poxvirus brazilian porcupinepox virus, Brazil, 2019. *Emerging Infectious Diseases* 27: 1177–1180. <https://doi.org/10.3201/eid2704.203818>
- INPE (2023) Programa de monitoramento da Amazônia e demais biomas. Available from: <http://terrabrasilis.dpi.inpe.br/downloads/> (June 27, 2023).
- IUCN (Ed.) (2012) IUCN Red List Categories and Criteria: Version 3.1. Second edition. IUCN, Gland, Switzerland and Cambridge, UK. Available from: <https://portals.iucn.org/library/node/10315> (June 26, 2023).
- Kaizer MC, Alvim THG, Novaes CL, McDevitt AD, Young RJ (2022) Snapshot of the Atlantic Forest canopy: surveying arboreal mammals in a biodiversity hotspot. *Oryx* 56: 825–836. <https://doi.org/10.1017/S0030605321001563>
- Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermini LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589. <https://doi.org/10.1038/nmeth.4285>
- Kays R, Allison A (2001) Arboreal tropical forest vertebrates: current knowledge and research trends. In: Linsenmair KE, Davis AJ, Fiala B, Speight MR (Eds), *Tropical forest canopies: ecology and management*. Forestry Sciences. Springer Netherlands, Dordrecht, 109–120. https://doi.org/10.1007/978-94-017-3606-0_9

- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649. <https://doi.org/10.1093/bioinformatics/bts199>
- Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111–120. <https://doi.org/10.1007/BF01731581>
- Leal ESB, Gomes-Silva FF, de Lyra-Neves RM, Telino-Júnior WR (2017) Range extension and first record of *Coendou speratus* Mendes Pontes et al., 2013 (Rodentia, Erethizontidae) from a cloud forest enclave in northeastern Brazil. *Check List* 13: 951–957. <https://doi.org/10.15560/13.6.951>
- Lewis PO (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology* 50: 913–925. <https://doi.org/10.1080/106351501753462876>
- Maddison DR, Swofford DL, Maddison WP (1997) NEXUS: an extensible file format for systematic information. *Systematic Biology* 46: 590–621. <https://doi.org/10.1093/sysbio/46.4.590>
- Melo-Dias M, Rocha MF, Dalfior ICD, Bissa L, Marcial T, Secco H, Passamani M, Rosa C (2023) Translocation and long-term monitoring of threatened thin-spined porcupines (*Chaetomys subspinosus*) on the Brazilian coast. *Journal for Nature Conservation* 74: 126434. <https://doi.org/10.1016/j.jnc.2023.126434>
- Mendes Pontes AR, Gadelha JR, Melo ÉRA, de Sá FB, Loss AC, Caldara Junior V, Costa LP, Leite YLR (2013) A new species of porcupine, genus *Coendou* (Rodentia: Erethizontidae) from the Atlantic forest of northeastern Brazil. *Zootaxa* 3636: 421–438. <https://doi.org/10.11646/zootaxa.3636.3.2>
- Menezes FH, Feijó A, Fernandes-Ferreira H, da Costa IR, Cordeiro-Estrela P (2021) Integrative systematics of Neotropical porcupines of *Coendou prehensilis* complex (Rodentia: Erethizontidae). *Journal of Zoological Systematics and Evolutionary Research* 59: 2410–2439. <https://doi.org/10.1111/jzs.12529>
- Menezes FH, Garbino GST, Semedo TBF, Lima M, Feijó A, Cordeiro-Estrela P, Costa IR da (2020) Major range extensions for three species of porcupines (Rodentia: Erethizontidae: *Coendou*) from the Brazilian Amazon. *Biota Neotropica* 20. <https://doi.org/10.1590/1676-0611-bn-2020-1030>
- Minh BQ, Nguyen MAT, von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* 30: 1188–1195. <https://doi.org/10.1093/molbev/mst024>
- More A, Crespo S (2017) Registros documentados del puerco espín de cola corta *Coendou rufescens* (Erethizontidae, Rodentia) en el Noroeste de Perú. *The Biologist* 14. <https://doi.org/10.24039/rtb2016142113>

- Morrone JJ, Escalante T, Rodríguez-Tapia G, Carmona A, Arana M, Mercado-Gómez JD (2022) Biogeographic regionalization of the Neotropical region: New map and shapefile. *Anais da Academia Brasileira de Ciências* 94: e20211167. <https://doi.org/10.1590/0001-3765202220211167>
- Narváez-Romero C, Reyes-Puig C, Valle D, Brito J (2018) New records and estimation of the potential distribution of the stump-tailed porcupine *Coendou rufescens*. *Therya* 9: 137–146. <https://doi.org/10.12933/therya-18-581>
- Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274. <https://doi.org/10.1093/molbev/msu300>
- Radel D, Sand A, Steel M (2013) Hide and seek: placing and finding an optimal tree for thousands of homoplasy-rich sequences. *Molecular Phylogenetics and Evolution* 69: 1186–1189. <https://doi.org/10.1016/j.ympev.2013.08.001>
- Ramírez-Chaves HE, Suárez-Castro AF, Morales-Martínez DM, Vallejo-Pareja MC (2016) Richness and distribution of porcupines (Erethizontidae: *Coendou*) from Colombia. *Mammalia* 80. <https://doi.org/10.1515/mammalia-2014-0158>
- Ramírez-Chaves HE, Caranton-Ayala D, Morales-Martínez DM, Rosero E (2020a) Filling distribution gaps: first record of the Western Amazonian Dwarf Porcupine, *Coendou ichillus* Voss & da Silva, 2001 (Mammalia, Rodentia), in the Napo Moist Forests ecoregion of Colombia. *Check List* 16: 1627–1631. <https://doi.org/10.15560/16.6.1627>
- Ramírez-Chaves HE, Torres-Martínez MM, Noguera-Urbano EA, Passos FC, Colmenares-Pinzón JE (2019) State of knowledge and potential distribution of the Colombian endemic brown hairy dwarf porcupine *Coendou vestitus* (Rodentia). *Mammalian Biology* 99: 1–11. <https://doi.org/10.1016/j.mambio.2019.09.012>
- Ramírez-Chaves HE, Romero-Ríos C, Henao-Osorio JJ, Franco-Herrera JP, Ramírez-Padilla BR (2020b) Notes on the natural history of the Stump-tailed Porcupine, *Coendou rufescens* (Rodentia, Erethizontidae), in Colombia. *Neotropical Biology and Conservation* 15: 471–478. <https://doi.org/10.3897/neotropical.15.e56926>
- Ramírez-Chaves HE, Torres-Martínez MM, Henao-Osorio JJ, Osbahr K, Concha-Osbahr C, Passos FC, Noguera-Urbano E (2021a) Distribution update, male genitalia, natural history, and conservation of the stump-tailed porcupine *Coendou rufescens* in South America. *Mammalia* 86: 160–170. <https://doi.org/10.1515/mammalia-2021-0025>
- Ramírez-Chaves HE, Torres-Martínez MM, Henao-Osorio JJ, Osbahr K, Concha-Osbahr C, Passos FC, Noguera-Urbano E (2021b) Distribution update, male genitalia, natural history, and conservation of the stump-tailed porcupine *Coendou rufescens* in South America. *Mammalia* 86: 160–170. <https://doi.org/10.1515/mammalia-2021-0025>
- Roach N, Naylor L (2016) *Coendou roosmalenorum*. IUCN Red List of Threatened Species: e.T136518A22214051.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L,

- Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Saldanha J, Ferreira DC, da Silva VF, Santos-Filho M, Mendes-Oliveira AC, Rossi RV (2019) Genetic diversity of *Oecomys* (Rodentia, Sigmodontinae) from the Tapajós River basin and the role of rivers as barriers for the genus in the region. *Mammalian Biology* 97: 41–49. <https://doi.org/10.1016/j.mambio.2019.04.009>
- Silva DJF, Moreira JMAR, Ribeiro M, Maruyama FH, Morgado TO, Nakazato L, Dutra V, Souza MA, Colodel EM (2023) Brazilian porcupinepox virus infection in a free-ranging neotropical porcupine in Mato Grosso, Brazil. *Journal of Veterinary Diagnostic Investigation* 35: 304–306. <https://doi.org/10.1177/10406387231161340>
- Simpson MG (2010) Phylogenetic Systematics. In: *Plant Systematics*. Elsevier, 17–52. <https://doi.org/10.1016/B978-0-12-374380-0.50002-6>
- Smith MF, Patton JL (1993) The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. *Biological Journal of the Linnean Society* 50: 149–177. <https://doi.org/10.1111/j.1095-8312.1993.tb00924.x>
- Souza CM, Z. Shimbo J, Rosa MR, Parente LL, A. Alencar A, Rudorff BFT, Hasenack H, Matsumoto M, G. Ferreira L, Souza-Filho PWM, de Oliveira SW, Rocha WF, Fonseca AV, Marques CB, Diniz CG, Costa D, Monteiro D, Rosa ER, Vélez-Martin E, Weber EJ, Azevedo T (2020) Reconstructing Three Decades of Land Use and Land Cover Changes in Brazilian Biomes with Landsat Archive and Earth Engine. *Remote Sensing* 12: 2735. <https://doi.org/10.3390/rs12172735>
- Sullivan J, Joyce P (2005) Model selection in phylogenetics. *Annual Review of Ecology, Evolution, and Systematics* 36: 445–466. <https://doi.org/10.1146/annurev.ecolsys.36.102003.152633>
- Swofford DL (2002) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis version 11. *Molecular Biology and Evolution* 38: 3022–3027. <https://doi.org/10.1093/molbev/msab120>
- Torres-Martínez MM, Ramírez-Chaves HE, Noguera-Urbano EA, Passos FC (2021a) Assessment of the rarity and conservation status of the Colombian endemic brown hairy dwarf porcupine *Coendou vestitus*. *Oryx* 55: 765–770. <https://doi.org/10.1017/S0030605319001029>
- Torres-Martínez MM, Aya-Cuero CA, Noguera-Urbano EA, Passos FC, Ramírez-Chaves HE (2021b) *Coendou vestitus* (Rodentia: Erethizontidae). *Mammalian Species* 53: 43–50. <https://doi.org/10.1093/mspecies/seab005>
- Torres-Martínez MM, Ramírez-Chaves HE, Noguera-Urbano EA, Colmenares-Pinzón JE, Passos FC, García J (2019) On the distribution of the Brazilian porcupine *Coendou*

- prehensilis* (Erethizontidae) in Colombia. *Mammalia* 83: 290–297. <https://doi.org/10.1515/mammalia-2018-0043>
- Vié J-C (1999) Wildlife rescues—the case of the Petit Saut hydroelectric dam in French Guiana. *Oryx* 33: 115–126. <https://doi.org/10.1046/j.1365-3008.1999.00037.x>
- Voss RS (2011) Revisionary notes on neotropical porcupines (Rodentia: Erethizontidae) 3. An annotated checklist of the species of *Coendou* Lacépède, 1799. *American Museum Novitates* 3720: 1–36. <https://doi.org/10.1206/3720.2>
- Voss RS (2015) Superfamily Erethizontoidea Bonaparte, 1845. In: Patton JL, Pardiñas UFJ, D’Elía G (Eds), *Mammals of South America, Volume 2: Rodents*. The University of Chicago Press, Chicago, 786–805.
- Voss RS, Angermann R (1997) Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae). 1. Type material described by Olfers (1818) and Kuhl (1820) in the Berlin Zoological Museum. *American Museum Novitates*: 1–44.
- Voss RS, da Silva MNF (2001) Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae). 2. A Review of the *Coendou vestitus* Group with Descriptions of Two New Species from Amazonia. *American Museum Novitates* 3351: 1–36. [https://doi.org/10.1206/0003-0082\(2001\)351<0001:RNONPR>2.0.CO;2](https://doi.org/10.1206/0003-0082(2001)351<0001:RNONPR>2.0.CO;2)
- Voss RS, Hubbard C, Jansa SA (2013) Phylogenetic Relationships of New World Porcupines (Rodentia, Erethizontidae): Implications for Taxonomy, Morphological Evolution, and Biogeography. *American Museum Novitates* 3769: 1–36. <https://doi.org/10.1206/3769.2>
- Wilgenbusch JC, Swofford D (2003) Inferring evolutionary trees with PAUP*. *Current Protocols in Bioinformatics* Chapter 6: Unit 6.4. <https://doi.org/10.1002/0471250953.bi0604s00>
- Zhang D, Gao F, Jakovlić I, Zou H, Zhang J, Li WX, Wang GT (2020) PhyloSuite: An integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. *Molecular Ecology Resources* 20: 348–355. <https://doi.org/10.1111/1755-0998.13096>

5 CONSIDERAÇÕES FINAIS

Após décadas de impasses taxonômicos, os caracteres diagnósticos de citocromo *b*, crânio, mandíbula e pelagem aqui utilizados permitem a identificação inequívoca de 11 espécies do gênero *Coendou* e na delimitação de subgêneros através de uma abordagem integrativa, demonstrando o conteúdo informativo do uso de caracteres de pelagem para estudos sistemáticos do gênero. Dividimos o gênero *Coendou* em três subgêneros, *Coendou*, *Sphiggurus* e *Caaporamys* com caracteres diagnósticos únicos que também facilitam a identificação e diagnose das espécies incluídas neles. O subgênero *Coendou* apresenta crista dorsal composta por espinhos grossos, longos e flexíveis, o ventre apresenta pelagem rígida e espinhosa e a cauda apresenta seu primeiro terço dorsal com espinhos bicolores e tricolores tais quais o dorso. O subgênero *Sphiggurus* apresenta crista dorsal composta por espinhos finos, longos e flexíveis, o ventre apresenta pelagem majoritariamente macia e a cauda apresenta seu primeiro terço dorsal com espinhos bicolores e tricolores tais quais o dorso, enquanto isso, o subgênero *Caaporamys* apresenta a crista dorsal composta por cerdas-espinhosas, o ventre com pelagem macia e a cauda com espinhos monocores pretos. A distribuição das espécies, em especial das amazônicas, foi alterada, apontando a presença de 11 espécies de *Coendou* no Brasil, com novo registro de *Coendou ichillus* ocorrendo no território brasileiro e consideráveis ampliações de distribuição das espécies *C. bicolor*, *C. nycthemera*, *C. baturitensis* e *C. roosmalenorum*, e demonstrando que espécies de um mesmo subgênero são alopátricas, mas podem ser simpátricas a espécies de outros subgêneros de *Coendou*.

6 PERSPECTIVAS FUTURAS

O gênero *Coendou* representa um desafio em seus estudos taxonômicos, mas também uma oportunidade de investigação e novas descobertas. Todas as espécies do gênero carecem de informações acuradas sobre sua biologia, distribuição e história natural. Mesmo a identidade taxonômica e relações filogenéticas de algumas linhagens permanecem obscuras, em especial das distribuídas pela Amazônia. Otimizar a abordagem integrativa ao adicionar novos marcadores moleculares e morfológicos é a chave para a resolução dessas questões.

O uso de novas tecnologias, como drones, armadilhas fotográficas suspensas e sistemas para ciência cidadã, são o futuro para o estudo de animais de difícil observação e coleta por métodos convencionais. E os porcos-espinhos se apresentam como um modelo fantástico para essas novas abordagens, seja pelo tamanho dos indivíduos que facilita sua detecção pelas tecnologias, ou seja pelo carisma, que desperta curiosidade e atenção pela comunidade não acadêmica.

REFERÊNCIAS

- BONVICINO, C. R.; PENNA-FIRME, V.; BRAGGIO, E. Molecular and Karyologic Evidence of the Taxonomic Status of *Coendou* and *Sphiggurus* (Rodentia: Hystricognathi). **Journal of Mammalogy**, [s. l.], v. 83, n. 4, p. 1071-1076, nov. 2002. [https://doi.org/10.1644/1545-1542\(2002\)083<1071:MAKEOT>2.0.CO;2](https://doi.org/10.1644/1545-1542(2002)083<1071:MAKEOT>2.0.CO;2).
- EISENBERG, J. F.; REDFORD, K. H. **Mammals of the Neotropics (Volume 3): The Central Neotropics: Ecuador, Peru, Bolivia, Brazil**. Chicago: University of Chicago Press, 1999. p. 624.
- ELLERMAN, J. R. **The families and genera of living Rodents**. 2. ed. London: The British Museum (Natural History), 1940. v. 1. p. 689
- EMMONS, L. H. **Neotropical Rainforest Mammals: A field guide**. Chicago: The University of Chicago Press, 1997. p. 396
- FEIJÓ, A.; LANGGUTH, A. Mamíferos de médio e grande porte do Nordeste do Brasil: Distribuição e taxonomia, com descrição de novas espécies. **Revista Nordestina de Biologia**, [s. l.], v. 22, n. 1, p. 3-225, set. 2013.
- FREITAS, M. A. de F.; FRANÇA, D. P. F. de; VERÍSSIMO, D. First record of the Bicoloured-spined Porcupine *Coendou bicolor* (Tschudi, 1844) for Brazil. **Check List**, [s. l.], v. 9, n. 1, p. 94, mar. 2013. <https://doi.org/10.15560/9.1.94>.
- GAUBERT, P.; WOZENCRAFT, W. C.; CORDEIRO-ESTRELA, P.; VERON, G. Mosaics of convergences and noise in morphological phylogenies: what's in a viverrid-like carnivoran? **Systematic Biology**, [s. l.], v. 54, n. 6, p. 865-894, dez. 2005. <https://doi.org/10.1080/10635150500232769>.
- HANDLEY, C. O.; PINE, R. H. A new species of prehensile-tailed porcupine, genus *Coendou* Lacépède, from Brazil. **Mammalia**, [s. l.], v. 56, n. 2, jan. 1992. <https://doi.org/10.1515/mamm-1992-0207>.
- LEWIS, P. O. A likelihood approach to estimating phylogeny from discrete morphological character data. **Systematic Biology**, [s. l.], v. 50, n. 6, p. 913-925, dez. 2001. <https://doi.org/10.1080/106351501753462876>.
- MCKENNA, M. C.; BELL, S. K. **Classification of Mammals above the Species Level**. Nova York: Columbia University Press, 1997. p. 640.
- MENDES PONTES, A. R.; GADELHA, J. R.; MELO, É. R. A.; DE SÁ, F. B.; LOSS, A. C.; CALDARA JUNIOR, V.; COASTA, L. P.; LEITE, Y. L. R. A new species of porcupine, genus *Coendou* (Rodentia: Erethizontidae) from the Atlantic Forest of northeastern Brazil. **Zootaxa**, [s. l.], v. 3636, p. 421-438, abr. 2013. <https://doi.org/10.11646/zootaxa.3636.3.2>.
- VOSS, R. S.; SILVA, M. N. F. da. Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae). 2. A Review of the *Coendou vestitus* Group with Descriptions of Two New Species from Amazonia. **American Museum Novitates**, [s. l.], v. 3351, p. 1-36, out. 2001. [https://doi.org/10.1206/0003-0082\(2001\)351<0001:RNONPR>2.0.CO;2](https://doi.org/10.1206/0003-0082(2001)351<0001:RNONPR>2.0.CO;2).

VOSS, R. S.; HUBBARD, C.; JANSA, S. A. Phylogenetic Relationships of New World Porcupines (Rodentia, Erethizontidae): Implications for Taxonomy, Morphological Evolution, and Biogeography. **American Museum Novitates**, [s. l.], v. 3769, n. 3769, p. 1-36, fev. 2013. <https://doi.org/10.1206/3769.2>.

VOSS, R. S. Revisionary notes on neotropical porcupines (Rodentia: Erethizontidae) 3. An annotated checklist of the species of *Coendou* Lacépède, 1799. **American Museum Novitates**, [s. l.], v. 3720, n. 3720, p. 1-36, jun. 2011. <https://doi.org/10.1206/3720.2>.

VOSS, R. S. Superfamily Erethizontoidea Bonaparte, 1845. *In*: PATTON, J. L.; PARDIÑAS, U. F. J.; D'ELÍA, G. (Eds.). **Mammals of South America**. Chicago: The University of Chicago Press, 2015. v. 2. p. 786–805.

WOODS, C. A.; KILPATRICK, C. W. Infraorder Hystricognathi. *In*: WILSON, D. E.; REEDER, D. M. (Eds.). **Mammal Species of the World: A Taxonomic and Geographic Reference**. 2. ed. [s.l.]: Johns Hopkins University Press, 2005. p. 1538-1600.

APÊNDICE A - SUMÁRIO DE PRODUÇÃO CIENTÍFICA

A seguir, uma lista de publicações produzidas durante o tempo de doutorado.

2020

Artigo: Major range extensions for three species of porcupines (Rodentia: Erethizontidae: *Coendou*) from the Brazilian Amazon

Fernando Heberson Menezes, Guilherme Siniciato Terra Garbino, Thiago Borges Fernandes Semedo, Mendelson Lima, Anderson Feijó, Pedro Cordeiro-Estrela, Itayguara Ribeiro da Costa

Biota Neotropica, 20(2): e20201030. <https://doi.org/10.1590/1676-0611-BN-2020-1030>

2021

Capítulo: Coleção de Mamíferos do Departamento de Biologia da Universidade Federal do Ceará (UFC.M)

Ana Karolina Rodrigues de Almeida, Thiago Sales Lobo Guerra, **Fernando Heberson Menezes**, Vicente Vieira Faria

Livro I Seminário de Museus e Coleções da UFC, 1ª ed, Vol. 2.

Artigo: Integrative systematics of Neotropical porcupines of *Coendou prehensilis* complex (Rodentia: Erethizontidae)

Fernando Heberson Menezes, Anderson Feijó, Hugo Fernandes-Ferreira, Itayguara Ribeiro da Costa, Pedro Cordeiro-Estrela

Journal of Zoological Systematics and Evolutionary Research, 59(8): 2410-2439. <https://doi.org/10.1111/jzs.12529>

2022

Artigo: First record of albinism in a cavy of the genus *Galea* Meyen, 1832 (Rodentia: Caviidae)

Ana K. R. Almeida, **Fernando Heberson Menezes**, Hugo Fernandes-Ferreira

Notas sobre Mamíferos Sudamericanos, 4. <https://doi.org/10.31687/saremNMS.22.3.3>

2023

Artigo: A new species of jupati, genus *Metachirus* Burmeister 1854 (Didelphimorphia, Didelphidae), for the Brazilian Amazon

Cleuton Lima Miranda, Mario Nunes, Arielli Fabrício Machado, Izeni Farias, **Fernando Heberson Menezes**, Natália Ardente, Manoel dos Santos Filho, Yennie Bredin, Maria Nazareth da Silva

Mammalia, 87(2): 172-189. <https://doi.org/10.1515/mammalia-2021-0176>

Artigo: Essential oil constituents as the chemosystematic markers in *Eugenia* L. (Myrtaceae): An evolutionary perspective

Raisa Maria Silveira, **Fernando Heberson Menezes**, Igor Gonçalves Lima, Ana F. F. Urano Carvalho, Maria de Oliveira Bünger, Itayguara Ribeiro da Costa

South African Journal of Botany, 160: 309-318. <https://doi.org/10.1016/j.sajb.2023.07.015>

APÊNDICE B - COORIENTAÇÕES CONCLUÍDAS

2019: Reestruturação da Coleção de Mamíferos da UFC

Ana Karolina Rodrigues de Almeida

Bacharelado em Ciências Biológicas – Universidade Federal do Ceará

2022: Efeito das condições de criação na reprodução e na ontogenia de besouros necrófagos (*Dermestes maculatus*)

João Gabriel Colares Silveira

Bacharelado em Ciências Biológicas – Universidade Federal do Ceará

2023: Análise forense osteológica de crânio regenerado de jaguatirica, *Leopardus pardalis* (Carnivora, Felidae)

Lyandra Maria de Sousa Barbosa

Licenciatura em Ciências Biológicas – Universidade Estadual do Ceará