

Héctor E. Ramírez-Chaves*, Andrés Felipe Suárez-Castro, Darwin M. Morales-Martínez and María Camila Vallejo-Pareja

Richness and distribution of porcupines (Erethizontidae: *Coendou*) from Colombia

Abstract: In spite of previous reviews, there is still no consensus on the information associated to the richness of the genus *Coendou* in Colombia. To clarify some issues concerning the distribution and the taxonomic identity of the species of *Coendou* in the country, we reviewed specimens from five natural history collections. We introduce the first record of *Coendou ichillus* from the Orinoco river basin of the country, extending the distribution of the species by more than 600 km to the north from previous known localities in Ecuador and Peru. Additionally, we present new records of *C. pruinus* and *C. quichua* from the Amazonia and inter-Andean valleys, respectively. Only one skull presents the diagnostic characters of *C. bicolor*; thus, previous records of this species for the country were based on misidentifications. *Coendou* is distributed in seven of the nine geographic provinces of Colombia. *Coendou prehensilis* was found in five provinces and is expected to be present in the Amazonia, whereas *C. pruinus* was documented in three provinces (North Andean, Orinoco and Guyana). The rest of the species of *Coendou* were distributed in one or two provinces. The richest provinces were North Andean and Orinoco with six and four *Coendou* species, respectively. The elevational ranges of *C. prehensilis* and *C. pruinus* are revised to 0–1975 and 90–2200 m, respectively.

Keywords: Amazonas region; distribution; Hystricomorpha; morphology; range extension.

*Corresponding author: Héctor E. Ramírez-Chaves, Weisbecker Lab, School of Biological Sciences, University of Queensland, Goddard Building 8, St. Lucia 4072, Brisbane, Australia, e-mail: hera.chaves@gmail.com

Andrés Felipe Suárez-Castro: Rhodes Conservation Lab, School of Geography, Planning and Environmental Management, University of Queensland, Steele Building 3, St. Lucia 4072, Brisbane, Australia

Darwin M. Morales-Martínez: Grupo de Mastozoología, and Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Carrera 45 No 26-85, Bogotá, Colombia

María Camila Vallejo-Pareja: Smithsonian Tropical Research Institute, Panama, Republic of Panama, P.O. Box 0843-03092, Panama

DOI 10.1515/mammalia-2014-0158

Received October 22, 2014; accepted December 23, 2014

Introduction

The genus *Coendou* is composed of 15 species, two of which have just been recently described (see Voss 2011, Feijó and Langguth 2013, Mendes-Pontes et al. 2013). In Colombia, between five (Voss 2011) and 10 species (Alberico et al. 2000) have been listed. For the country, Solari et al. (2013) recently included nine taxa, namely, *C. bicolor* (Tschudi, 1844), *C. melanurus* (Wagner, 1842), *C. prehensilis* (Linnaeus, 1758), *C. pruinus* Thomas, 1905, *C. quichua* Thomas, 1899, *C. rothschildi* Thomas, 1902, *C. rufescens* (Gray, 1865), *C. sanctaemartae* J.A. Allen, 1904, and *C. vestitus* Thomas, 1899. Although Solari et al. (2013) reported *C. sanctaemartae* and *C. rothschildi* as valid species, Voss (2011) and Voss et al. (2013) considered these taxa as junior synonym of *C. prehensilis* and *C. quichua*, respectively, on the basis of morphological and cytochrome *b* analyses.

The inclusion of *Coendou bicolor* and *C. melanurus* in different regions of Colombia (see Solari et al. 2013) is believed to be based on misidentifications, and is therefore inaccurate (Voss 2011). *Coendou bicolor* has been reported from several localities at altitudes ranging from 300 to 1000 m (Solari et al. 2013) in the Caribbean (Santa Marta – Department of Magdalena; Tolú – Department of Sucre) and Andean (Provincia – Department of Santander; Department of Norte de Santander; southwestern Colombia) regions (Cuervo-Díaz et al. 1986, Alberico et al. 2000, Solari et al. 2013). Nonetheless, Voss (2011) considered that the specimen from Provincia could represent a melanistic example of *C. prehensilis*, and the one from Tolú an unusually large specimen of *C. quichua*.

For the departments of Amazonas and Vichada, Solari et al. (2013) expanded the altitudinal range of *Coendou melanurus* to 0–500 m on the basis of previous works (Alberico et al. 2000, Woods and Kilpatrick 2005, Voss 2011). However, only Woods and Kilpatrick (2005) included this taxon for the country, whereas Voss (2011) suggested that these records are in fact *C. pruinus*.

In spite of previous reviews, there are still gaps in the information on the richness and distribution of the genus in the country. To address the issues concerning the presence of certain taxa and the distribution of the genus *Coendou* in Colombia, we reviewed specimens deposited in five natural history collections. Moreover, we analyzed the composition of species among different geographic regions, and contrasted the richness of the genus in Colombia with that reported in previous studies (Alberico et al. 2000, Solari et al. 2013). We also introduce new locality records for *C. pruinus* and *C. quichua*, the first record of *C. ichillus* for Colombia, and discuss previous records of *C. bicolor* and *C. prehensilis*.

Materials and methods

We reviewed specimens deposited at the following collections: Escuela de Biología, Universidad Industrial de Santander (UIS), Bucaramanga; Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN), Bogotá; Instituto de Investigaciones Biológicas, Alexander von Humboldt (IAvH), Villa de Leyva; Museo de Historia Natural, Universidad del Cauca (MHNUC), Popayán; and Zoologische Staatssammlung Muenchen (ZSM), Munich. In addition, we reviewed photographs of the skin and skull of two specimens deposited at the collections of Universidad del Valle (UV) in Cali, identified as *Coendou bicolor* (UIS 04, now at UV collections), and *C. rothschildi* (UV VRD 160) by Alberico et al. (2000).

Following Voss (2011), we took the following cranial measurements: condyle-incisive length (CIL), length of diastema (LD), length of maxillary tooth row (MTR), length of molars (LM), breadth of P4 (BP4), breadth of M1 (BM1), anterior palatal breadth (APB), posterior palatal breadth (PPB), posterior zygomatic breadth (PZB), height of the infraorbital foramen (HIF), zygomatic length (ZL), length

of nasals (LN), breadth of nasal aperture (BNA), breadth of braincase (BB), depth of incisor (DI), and breadth of the incisor tips (BIT). External measurements were taken from the labels and included the following: total length (TL), head-and-body length (HBL), length of tail (LT), and length of hind foot (HF).

We contrasted the specimens with the diagnostic characters provided by Alberico et al. (2000), Leite et al. (2011), Voss (2011), Voss and Angermann (1997), Voss and Da Silva (2001), and Voss et al. (2001, 2013). For age classification we followed Voss (2011). We also analyzed the composition of species among the different geographic regions and provinces of the country (Table 1) proposed by Hernández Camacho et al. (1992) based on the presence or absence of records for these areas.

Results

We reviewed a total of 57 specimens from Colombia belonging to seven taxa (Supplemental Appendix 1): *Coendou* cf. *bicolor*, *C. ichillus* Voss and Da Silva, 2001, *C. prehensilis*, *C. pruinus*, *C. quichua* (*sensu* Voss 2011), *C. rufescens*, and *C. vestitus*.

Coendou rufescens was the best represented species in Colombian collections with 22 specimens from seven localities in the Andean region and two from the foothills of Eastern Llanos of the Orinoco region (Table 1 and Supplemental Appendix 1). All specimens reviewed exhibit the diagnostic characters for the species: bi- and tricolored quills, short tail (LT/HBL ca. 40%), and cranial measurements within the ranges proposed for the species (Table 2). In contrast, *C. vestitus* was represented by only one specimen (ICN 3505, skin; also reported by Alberico et al. 2000) from the Orinoco region (Figure 1A). No external measurements were available.

Table 1 Distribution of the genus *Coendou* in seven geographical provinces of Colombia.

Taxa/Province	AM	CA	CH-MG	GU	SN	NA	OR	Total	E
<i>Coendou</i> cf. <i>bicolor</i>	0	0	0	0	0	1	0	1	1300
<i>Coendou ichillus</i>	?	0	0	?	0	0	1	1	582
<i>Coendou prehensilis</i>	?	1	0	1	1	1	1	5	0–1975
<i>Coendou pruinus</i>	0	0	0	1	0	1	1	3	90–2200
<i>Coendou quichua</i>	0	0	1	0	0	1	0	2	0–2200
<i>Coendou rufescens</i>	0	0	0	0	0	1	1	2	360–2900
<i>Coendou vestitus</i>	0	0	0	0	0	1	1	2	610–1440
Total	0	1	1	2	1	6	5		

AM, Amazonia; CA, Peri-Caribbean arid belt; CH-MG, Chocó-Magdalena; GU, Guyana; SN, Sierra Nevada de Santa Marta, NA, North Andean, OR, Orinoco. Question marks denote the expected presence of the species based on records from neighboring countries. Elevation range (E) in meters.

Table 2 Measurements (mm) of the specimens of *Coendou rufescens* from Colombia.

Sex/ Collection	Western		Eastern	Western and Central Cordilleras	Ecuador	Bolivia	
	Cordillera	Cordillera	Cordillera	Cordillera			
	Males/ICN	Females/ICN	Male/AMNH 73678	?/USNM 236908	2 males, 8 females/ AMNH, FMNH	Male/MCZ 36327	Female/CM 5255
CIL	68.7 (65.4–71.4) 8	71.7 (69.9–72.1) 4	72.4	66.0	73.1 (67.1–78.0) 9	73.3	65.9
LD	18.7 (16.2–21.4) 8	19.2 (18.9–19.6) 4	18.8	16.5	19.5 (16.9–21.6) 9	20.3	16.3
MTR	16.8 (15.9–17.6) 8	17.4 (16.5–18.5) 4	16.7	17.4	17.7 (16.7–19.2) 9	17.4	17.3
LM	12.2 (11.5–12.4) 8	12.4 (12.0–12.9) 4	12.0	12.9	12.8 (11.8–14.2) 9	12.7	12.7
BP4	4.7 (4.0–5.3) 8	5.1 (4.6–5.8) 4	4.9	5.6	5.3 (5.1–5.6) 9	5.2	5.0
BM1	4.4 (4.2–4.7) 8	4.6 (4.2–5.2) 4	4.2	4.4	4.7 (4.4–5.1) 9	4.4	4.5
APB	4.3 (3.6–5.8) 8	3.8 (3.7–3.8) 4	3.5	3.8	4.8 (4.1–5.7) 9	5.3	4.8
PPB	6.8 (6.6–7.4) 8	6.5 (5.8–7.3) 4	5.3	6.2	7.3 (6.1–8.8) 8	7.8	7.1
PZB	43.4 (42.6–45.3) 7	43.3 (42.3–44.7) 4	44.0	39.5	43.8 (41.8–45.2) 9	44.4	–
HIF	10.5 (8.7–12.2) 8	11.0 (10.7–11.3) 4	10.6	10.1	10.8 (9.9–12.2) 10	12.8	9.5
ZL	28.6 (27.7–30.0) 8	28.1 (27.7–28.5) 4	27.0	26.2	29.1 (27.5–31.2) 10	29.1	27.1
LN	21.7 (18.7–23.3) 8	23.8 (21.9–25.6) 2	23.4	21.0	24.1 (22.5–27.2) 6	24.2	–
BNA	12.5 (10.4–20.2) 7	11.4 (10.9–11.8) 4	11.4	10.8	11.9 (10.6–12.9) 10	10.9	–
BB	29.9 (28.8–31.0) 8	28.9 (28.0–29.8) 4	30.1	29.9	30.6 (28.8–33.1) 9	30.7	31.6
DI	3.7 (3.3–4.1) 8	3.6 (3.3–3.7) 4	3.0	3.1	3.6 (3.2–3.7) 10	4.0	3.2
BIT	6.8 (6.3–6.8) 8	6.9 (6.7–7.1) 4	4.6	4.4	5.2 (4.7–5.7) 9	5.0	5.2

Western Cordillera (Department of Cauca, Southwestern Colombia): males (ICN 10030–10031, ICN 10034–10035, ICN 10037, ICN 10039, ICN 10041–10042); females (ICN 10032–10033, ICN 10036, ICN 10038). Measurements of AMNH 73678, the National Museum of Natural History, Washington (USNM 236908), the Museum of Comparative Zoology at Harvard University, Cambridge (MCZ 36327), Carnegie Museum, Pittsburgh (CM 5255), and Western and Central Cordillera specimens, taken from Voss (2011). Sample means, the observed range (in parentheses), and the sample size.

We also introduce the first record of *Coendou ichillus* from Colombia (ICN 1772, skin), collected from the Orinoco region (Figure 1B). ICN 1772 exhibits the following diagnostic morphological characters (Voss and Da Silva 2001): presence of blackish and short dorsal fur that not conceals any quills; bi-colored (more extensively black-tipped) quills; tri-colored (pale-tipped) bristle-quills; spiny ventral pelage. External measurements (mm) are as follows: HBL 295, LT 210, HF 55, TL/HBL 71%. ICN 1772 presents differences in external measurements in contrast with those of Voss and Da Silva (2001), especially in the TL/HBL [71% in ICN 1772 vs. ca 85% according to Voss (2011)].

We found three specimens of *Coendou pruinus* (Figure 1C) in Colombian collections: one from the Andean region (ICN 10980), and two from the Orinoco (ICN 13939, IAvH 3963). All specimens present the diagnostic characters proposed by Voss and Da Silva (2001): frontal sinuses not inflated, roof of the external auditory meatus weakly keeled, mesopterygoid fossa not perforated by sphenopalatine vacuities and extended anteriorly only until the third molars (Voss and Da Silva 2001, Voss 2011; Figure 2). Measurements of the skull of ICN 13939 (Table 3) are within the range proposed for the species (Voss and Da Silva 2001, Voss 2011), except for LD, APB, PPB, PZB and

HIF, which are slightly smaller, but this discrepancy is probably because the individual is a sub-adult. ICN 10980 presents cranial measurements within the range proposed for other specimens by Voss and Da Silva (2001), except for the MTR and ZL, which are larger (Table 3). IAvH 3963 presents cranial measurements similar to those suggested by Voss and Da Silva (2001), except for the MTR, LM and ZL, which are smaller, and BIT, BB and BP4, which are larger (Table 3).

Coendou quichua is represented by five specimens: three from the Andean region (ICN 2015, ICN 16185, UIS 001), one from the Pacific region (IAvH 3083), and one without locality data (UIS 027). All the reviewed skins present bi- and tri-colored quills and do not have long fur (Figure 1D). For the only specimen with available external measurements (IAvH 3083), we found a LT/HBL ratio (105%) larger than that reported for the species (55%–90%) by Voss (2011). In addition, ICN 16185, IAvH 3083, and UIS 001 match the cranial measurements (Table 4) and diagnostic characters proposed for the species by Voss (2011): frontal sinuses not inflated and the roof of the external auditory meatus strongly keeled (Figure 2). UIS 001 exhibits MTR smaller than that of the other specimens reviewed (Table 4) and we consider it as a small adult. The



Figure 1 Skins of *Coendou* spp. from Colombia. (A) *C. vestitus* (ICN 3505); (B) *C. ichillus* (ICN 1772); (C) *C. pruinus* (ICN 10980); (D) *C. quichua* (ICN 2015); (E) *C. prehensilis* (ICN 1419); (F) *C. prehensilis* (IAvH 6786).

dental measurements of UIS 027 are slightly smaller than the species range. In contrast, IAvH 3083 presents larger skull dimensions than the other specimens from Colombia, but they are within the range of specimens from the Canal Zone in Panama (Voss 2011).

Coendou prehensilis (Figure 1E, F) is represented by 17 specimens (Supplemental Appendix 1), of which 10 are from northern Colombia, three from the Eastern Llanos of the Orinoco, and the remaining from the Andean region. Most specimens from northern Colombia are slightly smaller than the specimens from Eastern Colombia, Brazil and Bolivia (Voss 2011; Tables 5 and 6).

We found one specimen (ICN 123) from the Andes that match the cranial characters of *Coendou bicolor* proposed by Voss (2011): frontal sinuses not inflated and roof of the

external auditory meatus smooth (Figure 3). However, the lack of skin does not allow us to make further conclusions. Although the skull of ICN 123 is broken, some cranial measurements (mm) compared with those of Voss (2011, in parentheses) include the following: BP4: 5.59 (5.4–6.0); BM1: 5.75 (5.2–5.7); APB: 6.09 (5.7–7.4); HIF 13.77 (12.6–16.1); ZL: 36.93 (32.9–35.8); LN 32.41 (27.6–30.9); BNA 20.87 (17.0–20.8); BB: 39.31 (37.6–40.8). We assigned ICN 123 as *C. cf. bicolor*, subject to confirmation through genetic analyses. One specimen misidentified as *C. bicolor* (IAvH 6786; Figure 1F), is a melanistic *C. prehensilis*, with bi- and tri-colored darker quills and cranial diagnostic characters typical of this species (frontal sinuses inflated, roof of the external auditory meatus weakly keeled, mesopterygoid fossa extends anteriorly only between the third molars). We also found a marked melanistic case in the sides of the body of one uncatalogued specimen housed at ICN from northern Colombia collected by A. Cadena at the department of Magdalena, Santa Marta, Minca, Finca El Recuerdo.

Coendou species were recorded in four natural regions (Andean, Caribbean, Orinoco and Pacific), and in seven of the nine geographic provinces of Colombia (Hernández Camacho et al. 1992), namely, Peri-Caribbean arid belt, Sierra Nevada de Santa Marta, Chocó-Magdalena, Orinoco, Guyana, Amazonia, and North Andean (Figure 4). We also expect the presence of the genus in the Amazonia, but currently there are no specimens available for that region. *Coendou prehensilis* was found in five provinces (except in Chocó-Magdalena and Amazonia, although it is expected in the latter). *Coendou pruinus* was found in three provinces (North Andean, Orinoco and Guyana), whereas the rest of the species were only observed in up to two provinces (Table 1). The richest provinces were North Andean and Orinoco with six and four species, respectively. In the Chocó-Magdalena, Peri-arid Caribbean belt and Sierra Nevada de Santa Marta provinces, only one species was registered (Table 1).

Discussion

Our review clarifies some of the issues surrounding the distribution and the taxonomic identity of some species of the genus *Coendou* in Colombia. Seemingly, misidentifications were due to the absence of revisionary works prior to 2011 that include external and cranial characters to identify species. We present the first record of *C. ichillus* for the country (ICN 1772), which extends the distribution of the species by more than 600 km to the north (Figure 4).

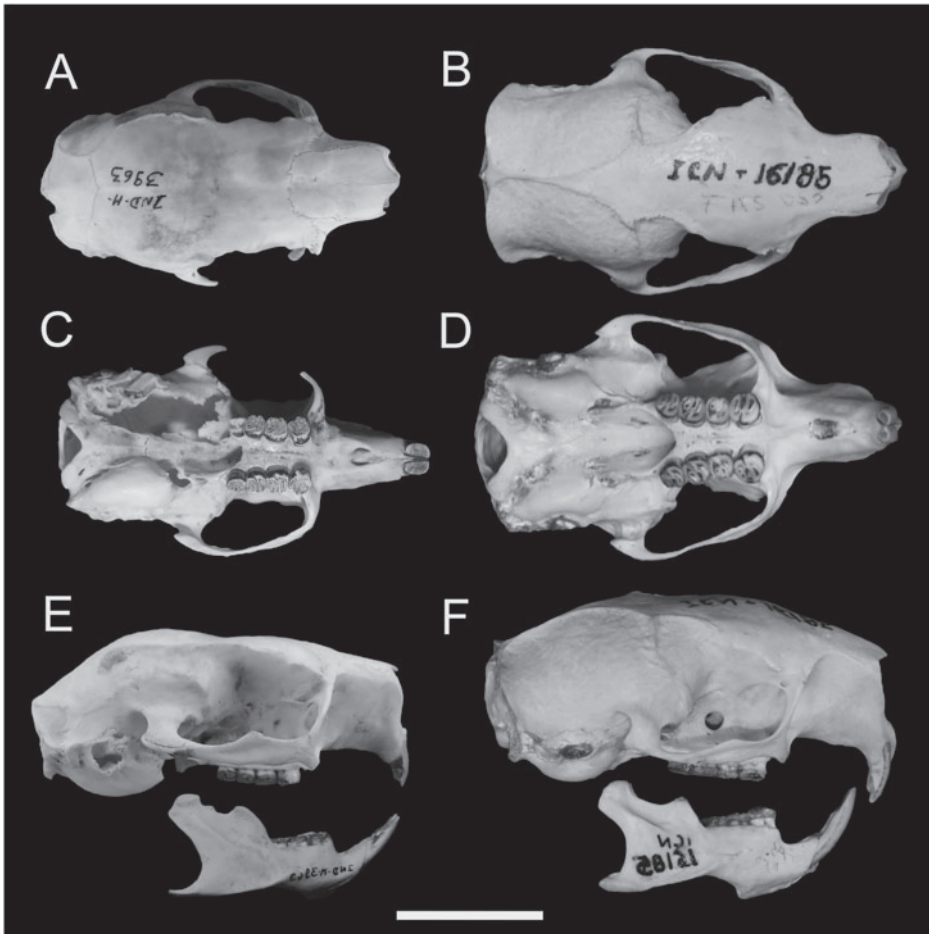


Figure 2 Dorsal, ventral and lateral view of the cranium of *Coendou pruinosus* (A, C, E; IAvH 3963), and *C. quichua* (B, D, F; ICN 16185), Scale bar: 20 mm.

Table 3 Measurements (mm) of the specimens of *Coendou pruinosus* from Colombia.

	FMNH 140260	FMNH 140261	ICN 10980	ICN 13939	IAvH 3963
Sex	Male	Female	Female	Unknown	Female
HBL	350	350	320	–	320
LT	185	160	180	–	235
HF	–	63	50	–	53
CIL	64.9	–	–	–	63.1
LD	17.1	19.1	16.5	15.4	17.7
MTR	15.8	15.3	16.1	15.4	14.3
LM	11.9	11.5	11.6	10.9	10.3
BP4	4.6	4.6	4.8	4.2	4.8
BM1	4.5	4.2	4.3	4.2	4.3
APB	4.6	4.7	4.3	4.1	5.2
PPB	6.4	6.0	5.1	4.6	6.1
PZB	42.0	40.1	40.5	37.9	–
HIF	8.5	9.7	9.3	8.1	8.7
ZL	25.6	26.5	28.1	27.8	24.7
LN	17.8	–	18.7	17.9	18.6
BNA	10.1	11.4	10.2	10.8	11.1
BB	29.9	28.1	28.6	–	30.3
DI	3.2	3.5	3.6	2.8	1.9 ^a
BIT	4.7	5.1	5.3	–	6.0

Measurements of specimens FMNH 140260 and FMNH 140261 taken from Voss and Da Silva (2001). ^aOutlier.

Table 4 Measurements (mm) of the specimens of *Coendou quichua* from Colombia.

Sex	ICN 2015		ICN 16185	UIS 001	UIS 027	LACM 27376	IAVH 3083	Chiriquí, Panama	Canal Zone, Panama	Ecuador
	Male	Female	Male	Male	Female	Female	5 males, 6 females, 1 unknown	1 male, 6 females, 3 unknown	1 male, 6 females, 3 unknown	1 male, 6 unknown
HBL	264.0	-	-	-	-	-	-	391±24 (360-420) 10	379 (332-438) 6	367 (345-395) 6
LT	204.0	-	-	-	-	-	-	324±41 (270-420) 10	349 (300-413) 6	208 (120-245) 6
HF	60.0	-	-	-	66.0	66.0	-	69 (67-71) 3	74 (70-78) 6	64 (60-68) 5
CIL	-	70.1	-	72.1	70.4	70.4	80.2	77.5±3.2 (73.2-83.0) 12	78.5±3.9 (73.8-86.9)	1072.0 (69.2-78.9) 5
LD	-	19.3	-	19.8	18.0	18.0	24.8	22.9±1.7 (19.6-25.6) 12	22.6±2.1 (20.3-27.0) 10	18.9 (15.7-22.2) 7
MTR	-	17.7	-	16.4	17.5	17.5	18.7	17.5±0.6 (16.8-18.5) 12	18.1±0.3 (17.6-18.6) 10	18.0 (17.4-18.5) 7
LM	-	12.6	-	12.8	12.9	12.9	14.0	12.8±0.4 (12.2-13.6) 12	13.2±0.3 (12.6-13.7) 10	13.3 (12.9-13.7) 7
BP4	-	5.6	-	3.8	5.2	5.2	5.8	5.3±0.3 (4.9-5.8)	5.4±0.2 (5.0-5.7) 10	125.3 (4.9-5.6) 7
BM1	-	4.7	-	4.5	4.9	4.9	4.9	4.9±0.2 (4.4-5.2) 12	4.9±0.2 (4.6-5.3) 10	4.8 (4.3-5.2) 7
APB	-	3.9	-	4.8	5.1	5.1	5.3	5.0±0.5 (4.2-5.7) 12	5.2±0.7 (4.2-6.5) 10	5.1 (4.2-6.2) 7
PPB	-	4.5	-	7.15	7.7	7.7	6.6	6.8±0.6 (5.7-7.7) 12	7.1±0.6 (6.3-8.4) 10	7.4 (6.1-8.5) 6
PZB	-	42.2	-	41.75	42.1	-	46.7	44.6±1.0 (43.3-46.3) 10	46.0±2.0 (42.1-48.4) 10	44.3 (42.3-46.2) 5
HIF	-	10.8	-	11.3	10.7	10.5	11.0	11.4±0.8 (10.6-13.3) 12	11.4±1.3 (9.7-13.6) 10	10.6 (9.3-12.4) 7
ZL	-	31.1	-	27.4	26.4	26.4	30.6	31.0±1.0 (29.8-33.3) 11	30.6±1.6 (27.2-33.2) 10	29.0 (27.6-30.9) 5
LN	-	-	-	-	-	-	25.5	25.2 (22.8-27.6) 2	24.3 (22.5-26.5) 7	24.7 (22.9-27.3) 3
BNA	-	10.8	-	13.2	11.1	11.1	14.5	14.8±1.0 (13.0-16.8) 11	14.3±0.9 (12.5-15.7) 10	11.7 (10.4-12.8) 4
BB	-	30.7	-	32.4	30.6	30.6	33.9	33.7±1.1 (31.5-35.4) 12	34.6±1.1 (32.7-36.4) 10	34.0 (32.6-35.7) 6
DI	-	3.6	-	3.7	3.9	3.9	3.2	4.0±0.3 (3.6-4.4) 123.9	3.9±0.2 (3.6-4.2) 10	(3.4-4.3) 7
BIT	-	6.0	-	5.9	5.2	5.2	6.9	5.1±0.4 (4.6-5.8) 10	5.2±0.3 (4.7-5.7) 10	5.4 (5.2-5.6) 4

Los Angeles County Museum (LACM) specimen measurements provided by R.S. Voss. Measurements of the specimens from Panama and Ecuador from Voss (2011).

Table 5 Measurements (mm) of the specimens of *Coendou prehensilis* from Northern and Eastern Andes of Colombia.

Measurement	Northern Colombia at ZSM (Ramírez-Chaves 2014)	Northern Colombia (Voss 2011)	ICN 14932 (Eastern Andes)	ICN 3033 (Eastern Andes)
HBL	393.3 (370–430) 3	451 (403–508) 15	–	–
LT	461 (420–528) 3	453 (365–487) 15	–	–
HF	72.6 (68–75) 3	90 (82–97) 15	–	–
CIL	82.9 (78.8–85.5) 7	84.5 (77.8–91.8) 16	–	–
LD	20.9 (18.4–22.8) 7	22.0 (20.0–24.6) 16	–	19.4
MTR	19.3 (18.2–20.8) 6	19.4 (18.6–20.4) 15	20.4	20.4
LM	14.3 (13.5–15.3) 6	14.3 (13.3–14.8) 15	15.2	14.8
BP4	5.4 (4.8–6.0) 7	5.7 (5.3–6.1) 16	5.7	5.8
BM1	5.3 (4.7–5.7) 7	5.4 (5.1–5.7) 15	5.8	5.9
APB	6.7 (5.8–7.8) 7	6.5 (5.2–7.5) 16	6.9	5.6
PPB	8.4 (8.0–9.1) 6	8.7 (7.7–10.0) 14	10.2	8.5
PZB	50.5 (46.7–53.2) 6	50.1 (46.8–53.3) 14	57.9	52.5
HIF	12.7 (12.0–14.7) 7	12.2 (10.2–13.5) 16	16.1 ^a	11.7
ZL	33.2 (31.2–35.7) 6	32.9 (30.7–35.8) 16	38.9	33.8
LN	32.2 (28.0–35.0) 4	30.0 (27.5–32.0) 11	–	–
BNA	18.6 (15.3–20.5) 7	19.0 (17.3–20.3) 13	24.4	–
BB	36.1 (34.3–38.0) 7	37.0 (35.2–39.2) 16	39.3	–
DI	4.0 (3.1–4.4) 7	4.2 (3.8–4.5) 16	–	5.6
BIT	8.8 (7.5–10.7) 7	6.1 (5.6–7.4) 15	–	7.8

Sample means, the observed range (in parentheses), and the sample size. ^aOutlier.

Table 6 Cranial measurements of three specimens (ICN 18567, ICN 18568, ICN 21448) that match the discrete cranial characters proposed by Voss (2011) for *Coendou prehensilis*, but the measurements are smaller.

Measurement	ICN 18567 Serranía del Perijá	ICN 18568 Serranía del Perijá	ICN 21448 Norte de Santander	Northern Colombia (Voss 2011)
CIL	75.1	–	–	84.5 (77.8–91.8) 16
LD	18.2	–	–	22.0 (20.0–24.6) 16
MTR	18.2	17.9	15.8	19.4 (18.6–20.4) 15
LM	14.1	12.8	–	14.3 (13.3–14.8) 15
BP4	4.6	6.7	4.9	5.7 (5.3–6.1) 16
BM1	5.5	5.7	–	5.4 (5.1–5.7) 15
APB	5.8	4.6	–	6.5 (5.2–7.5) 16
PPB	8.8	8.1	8.5	8.7 (7.7–10.0) 14
PZB	49.6	47.6	50.9	50.1 (46.8–53.3) 14
HIF	8.6 ^a	12.3	15.6 ^a	12.2 (10.2–13.5) 16
ZL	31.1	31.6	33.9	32.9 (30.7–35.8) 16
LN	27.6	–	–	30.0 (27.5–32.0) 11
BNA	16.6	18.3	20.7	19.0 (17.3–20.3) 13
BB	36.0	34.5	35.4	37.0 (35.2–39.2) 16
DI	4.0	–	–	4.2 (3.8–4.5) 16
BIT	7.4	–	–	6.1 (5.6–7.4) 15

^aOutlier.

This species was previously known only from records from the Amazonas region of Ecuador and Peru (Voss 2011). Moreover, we extend the distribution of *C. pruinosus* to the Orinoco region of Colombia. One of the specimens (ICN 13939) constitutes the southernmost known record for the species (Figure 4).

The presence of *Coendou melanurus* in Colombia does not seem to have any support at the moment. Although Solari et al. (2013) considered *C. insidiosus* as a synonym of *C. melanurus*, the differences between these two species have been widely documented (Voss and Angermann 1997, Voss et al. 2001, Voss 2011). The only specimen (IAVH 3963)

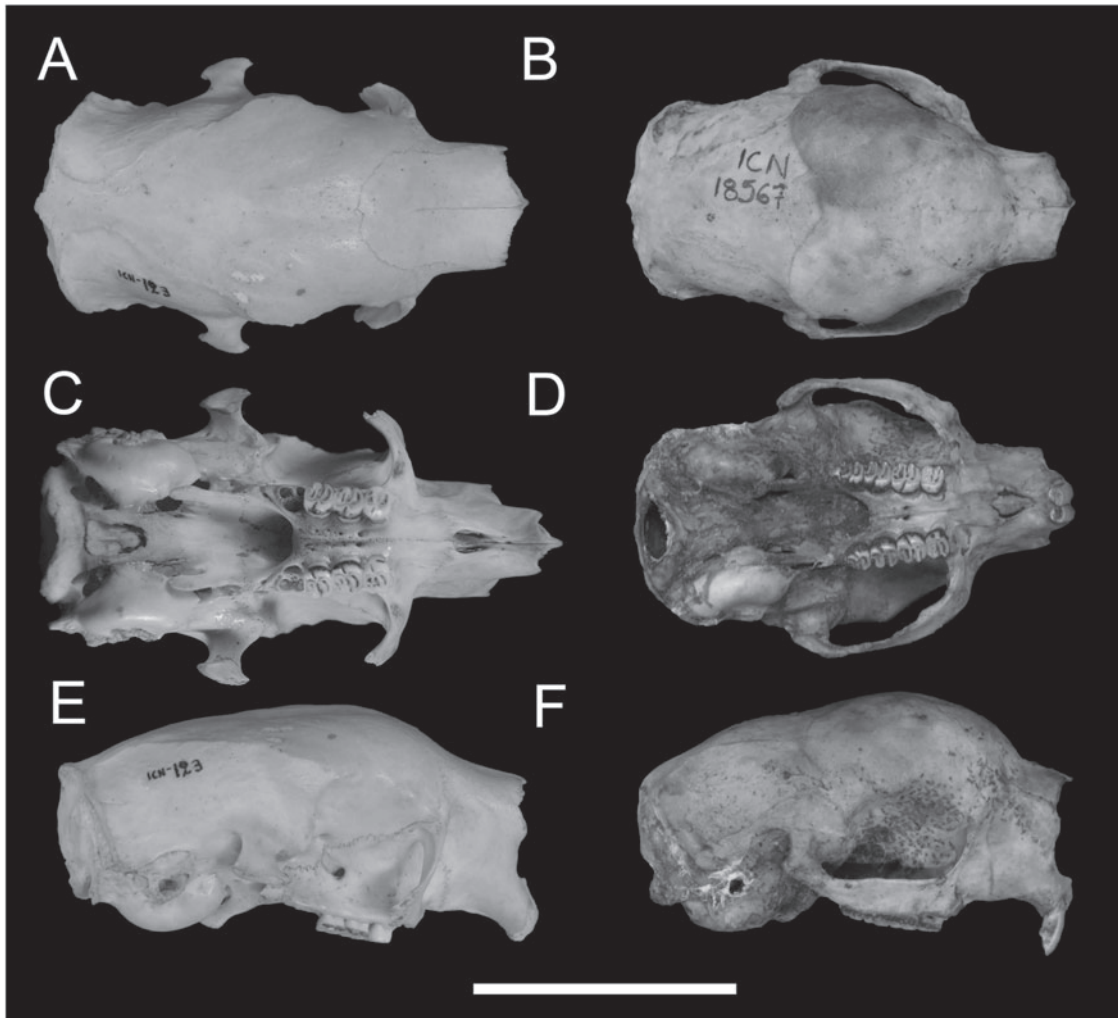


Figure 3 Dorsal, ventral and lateral view of the cranium of *Coendou* cf. *bicolor* (A, C, E; ICN 123), and *C. prehensilis* (B, D, F; ICN 18567), Scale bar: 40 mm.

previously identified as *C. insidiosus* corresponds to *C. pruinosus* (Figure 2), and none of the reviewed specimens match the characteristics of *C. melanurus*. Therefore, we confirmed Voss' (2011) suggestion that previous reports of *C. insidiosus* (see Cuervo-Díaz et al. 1986, Rodríguez-Mahecha et al. 1995) and *C. melanurus* (Solari et al. 2013) from the country are misidentifications.

Aside from several accounts of the presence of *Coendou bicolor* in Colombia (Cuervo-Díaz et al. 1986, Alberico et al. 2000, Muñoz-Saba 2010), we found no specimens associated to these records except for ICN 123, which we tentatively assign to this species but one that needs further corroboration using genetic data. Alberico et al. (2000) suggested that one specimen of this taxon (UIS 04, skin and skull) was housed at UIS collection. However, at the time of our visit, UIS 04 had been sent out on loan to UV (J.G. Moreno pers. comm.). UIS 04, now

deposited at UV collections (UV 13294), exhibit the cranial and external characters (except for darker coloration of the quills, especially the tips that are black, followed by brown and white) of *C. prehensilis* and likely represents a melanistic form of *C. prehensilis* as previously suggested by Voss (2011).

We discarded two records attributed to *Coendou bicolor* from Perijá, Serranía de Ibérico (ICN 18567, ICN 18568) by Muñoz-Saba (2010). These specimens exhibit the discrete cranial characters of *C. prehensilis* (frontal sinuses inflated, and roof of the external auditory meatus weakly keeled) (Figure 3), and most measurements are in the range of available specimens of *C. prehensilis* from northern Colombia (Table 6). An additional record of *C. bicolor* from Sucre, Tolú (IAvH 4097; Alberico et al. 2000) also represents *C. prehensilis* and not a large specimen of *C. quichua* as suggested by Voss (2011). The

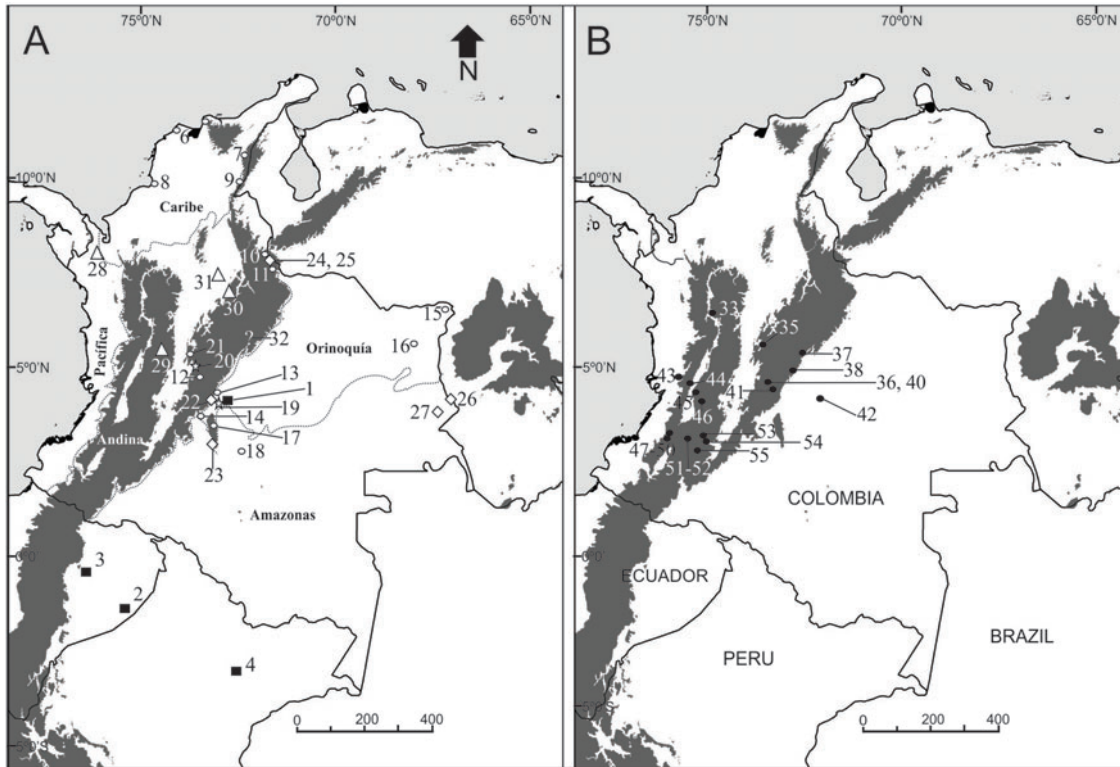


Figure 4 Distribution of the genus *Coendou* in Colombia. (A) Black squares: *C. ichillus* in Colombia, Ecuador and Peru. White circles: *C. prehensilis*. White stars: *C. vestitus*. White diamonds: *C. pruinosis*. White triangles: *C. quichua*. Question mark: *C. cf. bicolor*. (B) Records of *C. rufescens* from Colombia. Shaded area represents the Andean region. There are no records for the Amazonia region. Localities are summarized in Supplemental Appendix 2.

inclusion of *C. bicolor* in the department of Norte de Santander by Solari et al. (2013) is not supported by evidence, as the only specimen from that region previously identified with that name (IAvH 6786) belongs to *C. prehensilis* based on external and cranial characters: long tri-colored quills over the entire dorsal surface, no distinct mantle of longer quills over the nape, shoulders, and upper back, inflated frontal sinuses, and the mesopterygoid fossa penetrates between M2/M3 commissure.

With regard to the taxonomic status of *Coendou rothschildi* and *C. sanctaemartae*, we follow Voss (2011) in considering these taxa as junior synonyms of *C. quichua* and *C. prehensilis*, respectively, because of the lack of morphological characters that support their separation. Although the morphological characters are constant within the evaluated taxa, we found some variation in size when specimens from different populations were compared. Although the low number of specimens of these populations allows no further comparison, we found that *C. quichua* from the Biogeographic Chocó (IAvH 3083 reported as *C. rothschildi* by Alberico et al. 2000) presents larger external and cranial measurements than

those of specimens from the Andes region (inter-Andean valleys) of Colombia (ICN 16185, ICN 2015, UIS 001), but similar to those of specimens from the geographically closer Canal Zone in Panama (Table 4). A comparison of the evolutionary divergence between cytochrome *b* sequences of *C. quichua* (Voss et al., 2013) performed using MEGA6 (Tamura et al. 2013) of one specimen from Panama (National Museum of Natural History, Washington, USNM 296308) and one from Cesar, Colombia (LACM 27376) showed a high value (4.8%) of divergence. This value is within the range (4%–11%) found in sister-species of mammals (Bradley and Baker 2001) and has been used to show the presence of cryptic diversity within the genus *Coendou* (Leite et al. 2011). Therefore, it is highly possible that two species comprise *C. quichua* in Colombia, and the application of the available name *C. rothschildi* for the Biogeographic Chocó specimens needs to be reassessed.

We also observed this size variation in the specimens of *Coendou prehensilis* from northern Colombia. Although three specimens from Serranía del Perijá (ICN 18567, ICN 18568, ICN 21448) match the cranial characters proposed by Voss (2011), the measurements are smaller (Table 6)

than those of species in other localities in the Caribbean region of Colombia (Voss 2011, Ramírez-Chaves 2014). Unfortunately, there are no skins associated with these skulls to perform additional comparisons. It is possible that the intraspecific variation of *C. prehensilis* is not well documented or perhaps there is cryptic diversity enclosed in this species from Colombia, as it has been found in Brazil (Leite et al. 2011). As currently understood, *C. prehensilis* is wide ranging and polytypic, and has eight junior synonyms (Woods and Kilpatrick 2005). Recently, Leite et al. (2011) restricted typical *C. prehensilis* to north-eastern Brazil, and there is a possibility that other populations of *C. prehensilis* from the eastern part of north-eastern Brazil need nomenclatural reclassification (Voss 2011, Voss et al. 2013). Additional material and genetic data of *C. prehensilis* (*sensu lato*) in different areas of northern South America is needed to clarify these issues.

Our analysis of distribution has reduced the number of records of *Coendou* in Colombia, especially in the Amazonia province, where at least two species (*C. ichillus* and *C. prehensilis*) are expected to occur. These species have been recorded in the Orinoco region of Colombia and in the Amazonia region of adjacent countries (Brazil, Ecuador, and Peru; see Voss 2011, de Freitas et al. 2013). In the Orinoco region of Colombia, *C. ichillus* is also in virtual sympatry with three other species (*C. pruinusosus*, *C. rufescens*, and *C. vestitus*) previously considered as allopatrically distributed by Voss et al. (2013). Our data also suggest that *C. quichua* presents some narrow sympatry in the northern Andes of Colombia with the latter four species, and fills the geographic relationships suggested by Voss et al. (2013). Aside from the differences in the number of species listed in the country and the extension of distribution in comparison with previous checklists (Solari et al. 2013), the elevational distribution of some species is revised (Table 1). The most remarkable differences are for *C. prehensilis*, occurring from sea level up to 1975 m (0–500 m in Solari et al. 2013), and for *C. pruinusosus*, found in elevations ranging from 90 to 2200 m (1800–2500 m in Solari et al. 2013).

The North Andean province presents the highest richness because it encloses one of the largest area of the country and a wide range of different ecosystems. This is not surprising considering that this region, and in general the tropical Andes, are recognized as areas of high diversity and abundant endemism (Myers et al. 2000). However, it is also possible that the presence of the main cities and roads in the Andes of Colombia allows for higher levels of sampling effort in this region, leading to bias in the results. More information on the presence of species of

Coendou in Colombia is necessary to delimit their elevational and geographical distributions.

Unfortunately, the genus *Coendou* is poorly represented in the collections reviewed, and this limits our ability to evaluate intraspecific variation or geographical patterns. It is important to obtain morphological and molecular information of poorly known groups such as Neotropical porcupines, for which basic aspects of taxonomy and species distribution are still largely unresolved (Leite et al. 2011, Voss 2011). As pointed out by de Freitas et al. (2013), the use of less conventional sources of information, such as roadkills or rescue of fauna in hydroelectric dam construction projects, constitutes an important opportunity to obtain important data that help us to increase our knowledge and the mechanisms to protect our biodiversity.

Acknowledgments: We thank Hugo López-Arévalo (ICN), María del Pilar Rivas Pava (MHNUC), Michael Hiermeier (ZSM), Jose Gregorio Moreno and Martha Patricia Ramírez (UIS), and Fabio Forero and Arturo Gonzalez (IAvH) for allowing us to review specimens under their care. Robert S. Voss (AMNH) provided important information and measurements of *Coendou quichua* from Colombia. Juan P. López-Ordoñez provided photographs of one individual of *C. prehensilis* from Guaviare, and Miguel Rodríguez-Posada provided photographs of specimens at UV collections. Payal Bal reviewed an early version of this work. MCVP thanks Carlos Jaramillo (STRI), Christine D. Bacon (University of Gothenburg), Jorge Hernández (UIS), and Manuel Paez-Reyes for their support. This work was partially supported by the UQCent and UQI Scholarships of the University of Queensland (to HER-C), and COLCIENCIAS PhD Scholarships (to AFSC).

References

- Alberico, M., V. Rojas-Díaz and J.G. Moreno. 2000. Aporte sobre la taxonomía y distribución de los puercoespines (Rodentia: Erethizontidae) en Colombia. *Rev. Acad. Colomb. Cienc. Exact. Fis. Nat.* 23 (Supl. especial): 595–612 [Dated 1999, printed 2000].
- Bradley, R.D. and R.J. Baker. 2001. A test of the genetic species concept: cytochrome-*b* sequences and mammals. *J. Mamm.* 82: 960–973.
- Cuervo-Díaz, A., J. Hernández-Camacho and A. Cadena G. 1986. Lista actualizada de los mamíferos de Colombia[:] anotaciones sobre su distribución. *Caldasia* 15: 471–502.
- de Freitas, M.A., D.P.F. de França and D. Veríssimo. 2013. First record of the Bicoloured-spined Porcupine *Coendou bicolor* (Tschudi, 1844) for Brazil. *Check List* 9: 94–96.
- Feijó, A. and A. Langguth. 2013. A new species of porcupine from the Baturité range. *Rev. Nordestina de Biol.* 22: 124–126.

- Hernández Camacho, J.I., A.H. Guerra, R.O. Quijano and T. Walschburger. 1992. Unidades biogeográficas de Colombia. In: (G. Halffter, ed.) La Diversidad Biológica de Iberoamérica. Acta Zoológica Mexicana (n.s.), pp. 105–151.
- Leite, Y., V. Júnior, A. Loss, L. Costa, E.R.A. Melo, J.R. Gadelha and A.R. Pontes. 2011. Designation of a neotype for the Brazilian porcupine, *Coendou prehensilis* (Linnaeus, 1758). Zootaxa 2791: 30–40.
- Mendes-Pontes, A.R., J.R. Gadelha, E.R.A. Melo, F.B. Sá, A.C. Loss, V. Caldara Jr, L.P. Costa and Y.L.R. Leite. 2013. A new species of porcupine, genus *Coendou* (Rodentia: Erethizontidae) from the Atlantic forest of Northeastern Brazil. Zootaxa 3636: 421–438.
- Muñoz-Saba, Y. 2010. Fauna de mamíferos de la Serranía del Perijá, Colombia. In: (O. Rangel-Ch., ed.) Colombia, Diversidad Biológica VIII, Media y baja montaña de la Serranía del Perijá. Instituto de Ciencias Naturales, Arte y Fotolito, Bogotá. pp. 475–488.
- Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.
- Ramírez-Chaves, H.E. 2014. Mammals of Colombia deposited at the Zoologische Staatssammlung Muenchen, Germany. Biota Colombiana 15: 104–114.
- Rodríguez-Mahecha, J.V., J.I. Hernández-Camacho, T.R. Defler, M. Alberico, R.B. Mast, R.A. Mittermeier and A. Cadena. 1995. Mamíferos colombianos: sus nombres comunes e indígenas. Occasional Papers in Conservation Biology, Occasional Paper No. 3. Conservation International 3: 1–56.
- Solari, S., Y. Muñoz-Saba, J. Rodríguez-Mahecha, T.R. Defler, H.E. Ramírez-Chaves and F. Trujillo. 2013. Riqueza, Endemismo y conservación de los mamíferos de Colombia. Mastozool. Neotrop. 20: 301–365.
- Tamura K., G. Stecher, D. Peterson, A. Filipski and S. Kumar. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. Mol. Biol. Evol. 30: 2725–2729.
- Voss, R.S. 2011. Revisionary notes on Neotropical porcupines (Rodentia: Erethizontidae). 3. An annotated checklist of the species of *Coendou* Lacepede, 1799. Am. Mus. Novit. 3720: 1–36.
- Voss, R.S. and R. Angermann. 1997. Revisionary notes on Neotropical porcupines (Rodentia: Erethizontidae). 1. Type material described by Olfers (1818) and Kuhl (1820) in the Berlin Zoological Museum. Am. Mus. Novit. 3214: 1–44.
- Voss, R.S. and M.N.F. Da Silva. 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. Mus. Novit. 3351: 1–36.
- Voss, R.S., D.P. Lunde and N.B. Simmons. 2001. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna. Part 2. Non volant species. Bull. Am. Mus. Nat. Hist. 263: 1–236.
- Voss, R.S., C. Hubbard and S.A. Jansa. 2013. Phylogenetic relationships of New World porcupines (Rodentia, Erethizontidae): implications for taxonomy, morphological evolution, and biogeography. Am. Mus. Novit. 3769: 1–36.
- Woods, C.A. and C.W. Kilpatrick. 2005. Infraorder Hystricognathi Brandt, 1855. In: (D.E. Wilson and D.M. Reeder, eds.) Mammal Species of the World: a taxonomic and geographic reference. 3rd edition. The Johns Hopkins University Press, Baltimore, Maryland, USA, pp: 1538–1600.

Supplemental Material: The online version of this article (DOI: 10.1515/mammalia-2014-0158) offers supplementary material, available to authorized users.