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## Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae). 2. A Review of the *Coendou vestitus* Group with Descriptions of Two New Species from Amazonia

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## ABSTRACT

Neotropical porcupines of the *Coendou vestitus* group consist of four small-bodied species from northwestern South America that are hypothesized to form a clade on the basis of their unique dorsal pelage composition. In addition to soft wool and barbed quills—hair types widely shared by other erethizontids—the dorsal pelage of *vestitus*-group porcupines includes what may be called bristle-quills: long, thin, unbarbed quills with flexible tips. The group includes *Coendou vestitus* Thomas, 1899; *C. pruinosus* Thomas, 1905; and two new species. The latter provide the first documented records of small porcupines from western Amazonia, where only large porcupines (*C. prehensilis* and *C. bicolor*) were previously known. Other small porcupines probably remain to be discovered in Amazonia, where hydroelectric dam projects offer unique (if unfortunate) faunal-sampling opportunities.

## RESUMEN

El grupo de puercoespines neotropicales *Coendou vestitus* consiste en cuatro especies pequeñas del noroeste de América del Sur, consideradas parte de un clado con base en la composición particular de su pelaje dorsal. Además de lana suave y espinas con púas—tipos de pelo compartidos ampliamente con otros eretizóntidos—el pelaje dorsal de los puercoespines del grupo *vestitus* tiene lo que podría llamarse cerda-espinas: espinas largas, delgadas y ralas, con puntas flexibles. Este grupo incluye a *Coendou vestitus* Thomas, 1899; *C. pruinosus* Thomas, 1905; y dos nuevas especies. Estas últimas constituyen los primeros registros documentados de puercoespines pequeños en la Amazonia occidental, donde previamente sólo se conocían puercoespines grandes (*C. prehensilis* y *C. bicolor*). Se discute la posibilidad de que otros puercoespines pequeños estén por descubrirse en la Amazonia y se enfatizan las oportunidades únicas de muestreo de fauna provistas por la construcción de represas hidroeléctricas.

## RESUMO

Porcos-espinhos neotropicais do grupo *Coendou vestitus* são representados por quatro espécies de pequeno porte, que hipotizamos formar um clado, tendo por base a composição única de sua pelagem. Além da pelagem lanosa e dos espinhos farpados—tipos de pêlos amplamente compartilhados por outros eretizontídeos—a pelagem dorsal dos porcos-espinhos do grupo *vestitus* incluem o que podemos chamar de cerdas espinhosas: longos, finos, espinhos não-farpados de pontas flexíveis. O grupo inclui *Coendou vestitus* Thomas, 1899; *C. pruinosus* Thomas, 1905; e duas novas espécies. Estas fornecem o primeiro registro documentado de porcos-espinhos de pequeno porte no oeste da Amazônia, onde apenas porcos-espinhos de grande porte (*C. prehensilis* e *C. bicolor*) eram anteriormente conhecidos. Discutimos a probabilidade de que outras espécies de porcos-espinhos de pequeno porte sejam descobertas no oeste amazônico, e enfatizamos a importância única de amostragens faunísticas criadas pela construção de barragens hidroeléctricas.

## INTRODUCTION

Conspicuous among the Neotropical prehensile-tailed porcupines currently referred to the genus *Coendou* (including *Sphiggurus*; Handley and Pine, 1992) is a group of small-bodied species whose dorsal pelage contains three intermingled but distinctly different structural types: soft fur, quills (defensive spines with hard, sharp, barbed tips), and an unusual structural type that may be called

bristle-quills (fig. 1). The latter are much longer and thinner than conventional quills, but have the same distinctive root morphology (described and illustrated by Chapman and Roze, 1997), round cross section, stiff cortex, and spongy internal matrix; unlike regular quills, however, the tips of bristle-quills are attenuated, flexible, wire-like filaments, and they are not provided with microscopic barbs.



Fig. 1. Three structural types found in the dorsal pelage of members of the *Coendou vestitus* species group: **a**, soft wool hairs; **b**, quills; **c**, bristle-quills. Approximately life size (drawn from pelage of AMNH 126171, holotype of *C. ichillus*).

Although some species of *Coendou* have been incorrectly described as covered by quills only (e.g., *C. prehensilis*, *C. bicolor*; Ellerman, 1940), a sparse underfur of short wool hairs is always present among the quill bases of such forms. Other species of *Coendou* are superficially covered by long fur, but these taxa always possess an underlying defensive coat of sharp quills. In fact, all *Coendou* species possess both soft fur and quills; the distinctive feature of the species treated in this report consists in the additional presence of thin bristle-quills. Because the latter are not known to occur among any other erethizontids, the simplest explanation for their taxonomic distribution is that they evolved uniquely in the common ancestor of the group of species described below.

The oldest name for any Neotropical porcupine with thin bristle-quills is *Coendou ves-*

*titus* Thomas (1899), originally described on the basis of a single specimen from Colombia purchased by the British Museum in 1854. Thereafter, the species remained unknown from additional material until the early 1920s, when Hermano Nicéforo María obtained seven specimens in the western foothills of the eastern Andes near Bogotá. Unfortunately, no other records of this obviously uncommon (or elusive) porcupine have been reported in the last 75 years, and it is not known whether or not the species is still extant.

A second taxon, closely resembling *Coendou vestitus* but diagnosably different in coloration and craniodental characters, was described as *C. pruinosus* by Thomas (1905). Thomas's type series consisted of five specimens obtained between 2500 and 2600 m elevation in the Venezuelan Andes near Mérida, and most subsequently collected material assignable to *pruinosus* is likewise from montane or foothill habitats in Venezuela and Colombia. Although some authors (e.g., Cabrera, 1961; Honacki et al., 1982; Concepción and Molinari, 1991; Woods, 1993; Soriano and Ochoa, 1997) have regarded *pruinosus* as a subspecies or junior synonym of *vestitus*, others (e.g., Handley, 1976; Handley and Pine, 1992; Linares, 1998; Alberico et al., 1999) have treated these taxa as valid species. However, no substantive discussion of character data has been provided to support either usage.

Herein we redescribe *Coendou vestitus* and *C. pruinosus* based on our examination of types and other specimens in North American and European museums. Clarifying the diagnostic characteristics of *vestitus* and *pruinosus* is necessary in order to diagnose two new species that significantly extend the ecogeographic distribution of *vestitus*-like porcupines into the lowland rainforests of Amazonia. Unanswered questions concerning erethizontid distributions in Amazonia are briefly considered in a concluding discussion. This paper is the second in a series of preliminary reports (initiated by Voss and Angermann, 1997) with the object of resolving key taxonomic problems in advance of a comprehensive revision of Neotropical porcupines currently in preparation.

## MATERIALS AND METHODS

**SPECIMENS:** Specimens that we examined and measured for this study—and others referred to in the text—are in the American Museum of Natural History, New York (AMNH); the Natural History Museum, London (BMNH); the Colección de Vertebrados de la Universidad de los Andes, Mérida (CVULA); the Museo de la Estación Biológica de Rancho Grande, Maracay (EBRG); the Departamento de Biología de la Escuela Politécnica Nacional, Quito (EPN); the Field Museum of Natural History, Chicago (FMNH); the Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA); the Museo de Biología de la Universidad Central de Venezuela, Caracas (MBUCV); the Museum of Comparative Zoology of Harvard University, Cambridge (MCZ); the Museo de Historia Natural La Salle, Caracas (MHNLS); the Muséum National d'Histoire Naturelle, Paris (MNHN); the National Museum of Natural History, Washington, D.C. (USNM); and the Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB).

**MEASUREMENTS:** All reported measurements are in millimeters (mm) and all reported weights are in grams (g). Because head-and-body length (HBL) and length of tail (LT) were seldom recorded by collectors for the specimens treated in this report, we obtained approximate values (prefixed by "ca.") for these dimensions by measuring dried skins to the nearest 5 mm with a flexible rule. Length of the hindfoot (HF), recorded to the nearest millimeter, includes the claws (c.u.) and was either measured by collectors in the field and/or remeasured by us on dried skins (only minimally distorted dried hindfeet containing the intact pedal skeleton were remeasured). Measurements of the skull and dentition, taken with dial or digital calipers and recorded to the nearest 0.1 mm, are abbreviated and defined as follows (see fig. 2):

**CIL, Condylar-incisive Length:** Measured from the articular surface of one occipital condyle to the greater curvature of the ipsilateral upper incisor.

**LD, Length of Diastema:** Measured from the lesser curvature of an upper incisor at the

alveolar margin to the crown of the ipsilateral P4 [dP4 of subadults].

**LIF, Length of Incisive Foramen:** Inside length of one incisive foramen (or both, if the foramina are recessed in a common fossa).

**BIF, Breadth of Incisive Foramina:** Inside breadth across both incisive foramina.

**MTR, Maxillary Tooth Row:** Greatest crown length from P4 [dP4 of subadults] to M3.

**LM, Length of Molars:** Greatest crown length of the upper molar series (M1–M3).

**BP4, Breadth of P4:** Greatest crown breadth of the permanent upper premolar.

**BM1, Breadth of M1:** Greatest crown breadth of the first upper molar.

**APB, Anterior Palatal Breadth:** Measured between the crowns of the first upper molars.

**PPB, Posterior Palatal Breadth:** Measured between the crowns of the third upper molars.

**PZB, Posterior Zygomatic Breadth:** Greatest breadth across the zygomatic arches behind the orbits.

**HIF, Height of the Infraorbital Foramen:** Measured as the greatest inside diameter, usually at an angle of about 30–40° from the midsagittal plane.

**ZL, Zygomatic Length:** Measured from the posterior margin of the infraorbital foramen to the posterolateral corner of the zygomatic arch.

**LN, Length of Nasals:** Greatest length of one nasal bone (the longest if right and left elements are unequal).

**BNA, Breadth of Nasal Aperture:** Greatest transverse dimension of the nasal orifice, always at or near the nasal/premaxillary sutures.

**BB, Breadth of Braincase:** Transverse dimension of the braincase, measured by placing the caliper jaws just above the squamosal zygomatic root on each side.

**DI, Depth of Incisor:** Distance between the greater and lesser curvatures of an upper tooth.

**BIT, Breadth of the Incisor Tips:** Measured across the enameled tips of both upper teeth.

**AGE CLASSIFICATION:** We used maxillary tooth eruption, cranial suture closure, and pelage maturation to define a heuristic age

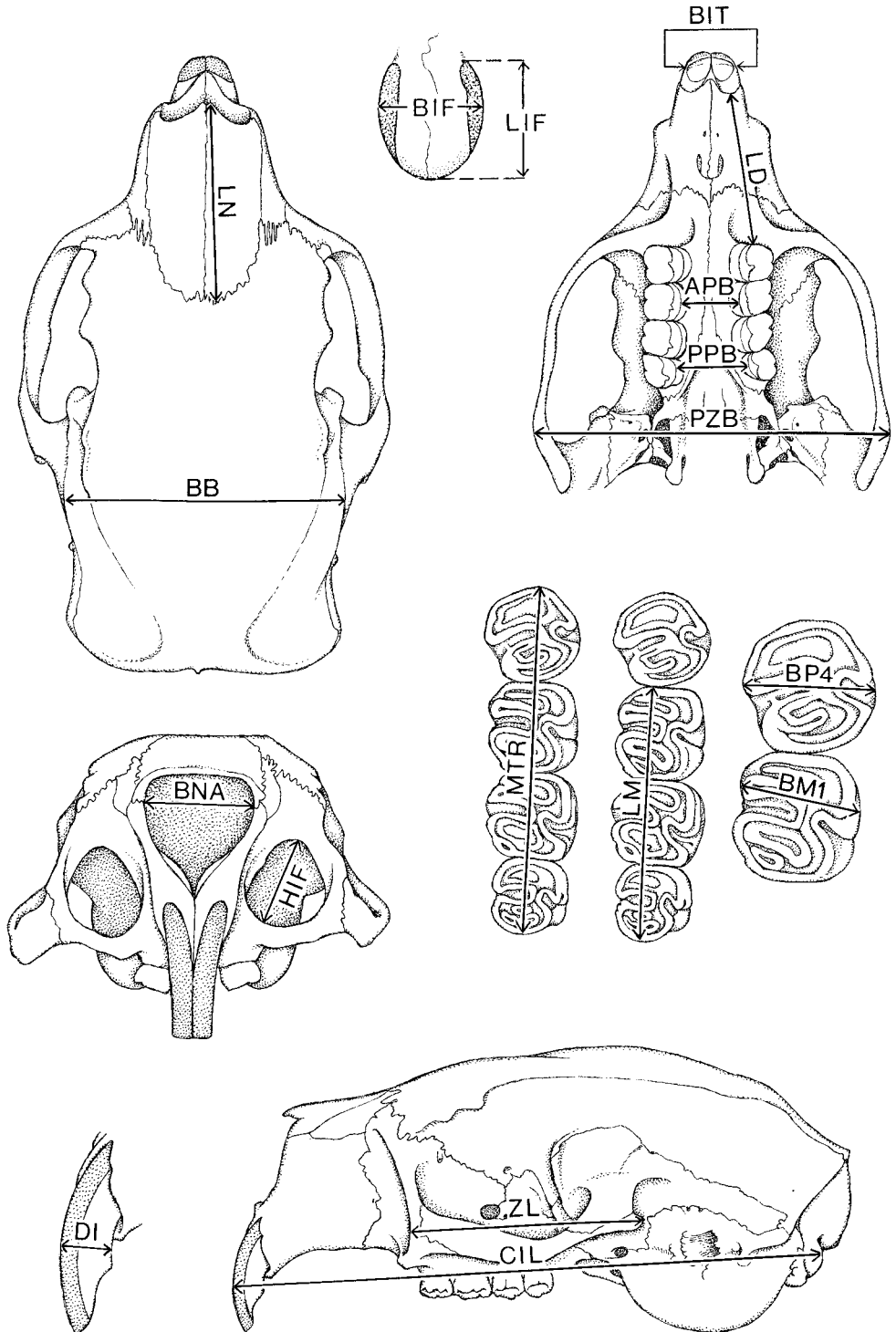


Fig. 2. Anatomical limits of 18 craniodental measurements defined in the text.

classification as follows (after Voss and Angermann, 1997).

*Juveniles*—Maxillary toothrow incomplete (three or fewer teeth erupted); all cranial sutures open; pelage often conspicuously immature, including long fur even in species that lack visible fur as adults.

*Subadults*—Immature maxillary dentition (dP4–M3) completely erupted, or dP4 shed and P4 incompletely erupted; all cranial sutures still visible; pelage always appears mature.

*Adults*—Permanent maxillary dentition (P4–M3) fully erupted, with light to moderate wear (teeth usually not worn below widest part of crown and almost always with at least some occlusal detail remaining); some cranial sutures usually obliterated.

*Old adults*—Cheekteeth worn below widest part of crown (and therefore not measurable), with little or no occlusal detail remaining on M1 and M2; only nasal sutures (if any) usually visible.

#### SPECIES ACCOUNTS

The specimens examined for this report can be sorted into four distinct groups on the basis of external and osteological characters. Whereas two of these groups have available names based on extant holotypes, the others are unnamed. The two named forms are re-described below in chronological order of their publication, followed by accounts of the new species. Specimen records are mapped and documented by geographic coordinates in the appendix.

##### *Coendou vestitus* Thomas

Figures 3, 4, 5A, 6A

*Coendou vestitus* Thomas, 1899: 284 (original description).

*Coendou (Sphiggurus) vestitus*: Tate, 1935: 307 (new name combination).

*Coendou (Sphiggurus) vestitus vestitus*: Cabrera, 1961: 603 (new name combination).

*Sphiggurus vestitus*: Honacki et al., 1982: 572 (new name combination).

**TYPE MATERIAL:** The holotype only, BMNH 54.6.26.1, consisting of the skin, skull, and mandibles of a subadult animal of unknown sex. The skin, much faded with age, is understuffed and lacks the left fore-

foot; the left hindfoot is detached but intact. The skull lacks the occiput, a common consequence of early to mid-19th century specimen preparation methods. The original label gives the place of origin only as "N[ouvel]le Grenade" (= Colombia). According to Thomas (1899), the specimen was purchased in 1854.

**GEOGRAPHIC DISTRIBUTION:** *Coendou vestitus* is only known from two definite localities, both of which are in the western foothills of the eastern Andean cordillera of Colombia. The first, where Hermano Nicéforo María collected six specimens from 1923 to 1925, is San Juan de Río Seco, a small village located about 60 km WNW of Bogotá at ca. 1300 m elevation. The second, where the same collector took a single specimen in 1925, is Quipile, a village only about 15 km SSE of San Juan and at approximately the same altitude.

**DESCRIPTION:** *External*—The dorsal fur, soft in texture and dull in appearance, is uniformly blackish brown and averages about 50–60 mm middorsally; the fur is shorter and sparser along the flanks, but it is long enough to conceal most of the quills except on the face. The quills (ranging in length from about 25 to 35 mm middorsally) are bicolored, pale yellow or ivory-white basally and dark-brown or blackish distally; usually only the distalmost 1/3 or less of each quill is dark, so the pale quill bases are exposed when the fur is parted or ruffled. None of the quills anywhere on the body is pale-tipped. Scattered abundantly but inconspicuously throughout most of the dorsal pelage are long (to 70–80 mm) polished bristle-quills that emerge from the fur like fine wires; these are yellowish basally, but the emergent tips are dark. No bristle-quills occur over the rump, however, which is clothed only by short, sharp quills and fur. The ventral surface of the body is densely covered with soft and uniformly dark-brown fur from chin to anus. Two classes of hairs can be distinguished in the ventral fur (fine, wavy wool hairs and coarser, straighter guard hairs), but there are no conspicuously thickened spinous hairs grouped in triads or other clusters.

The tail is short, apparently averaging about half the length of the combined head-





Fig. 3. Dorsal view of the skin of *Coendou vestitus* (BMNH 24.2.21.2). Approximately  $\times 0.4$ .

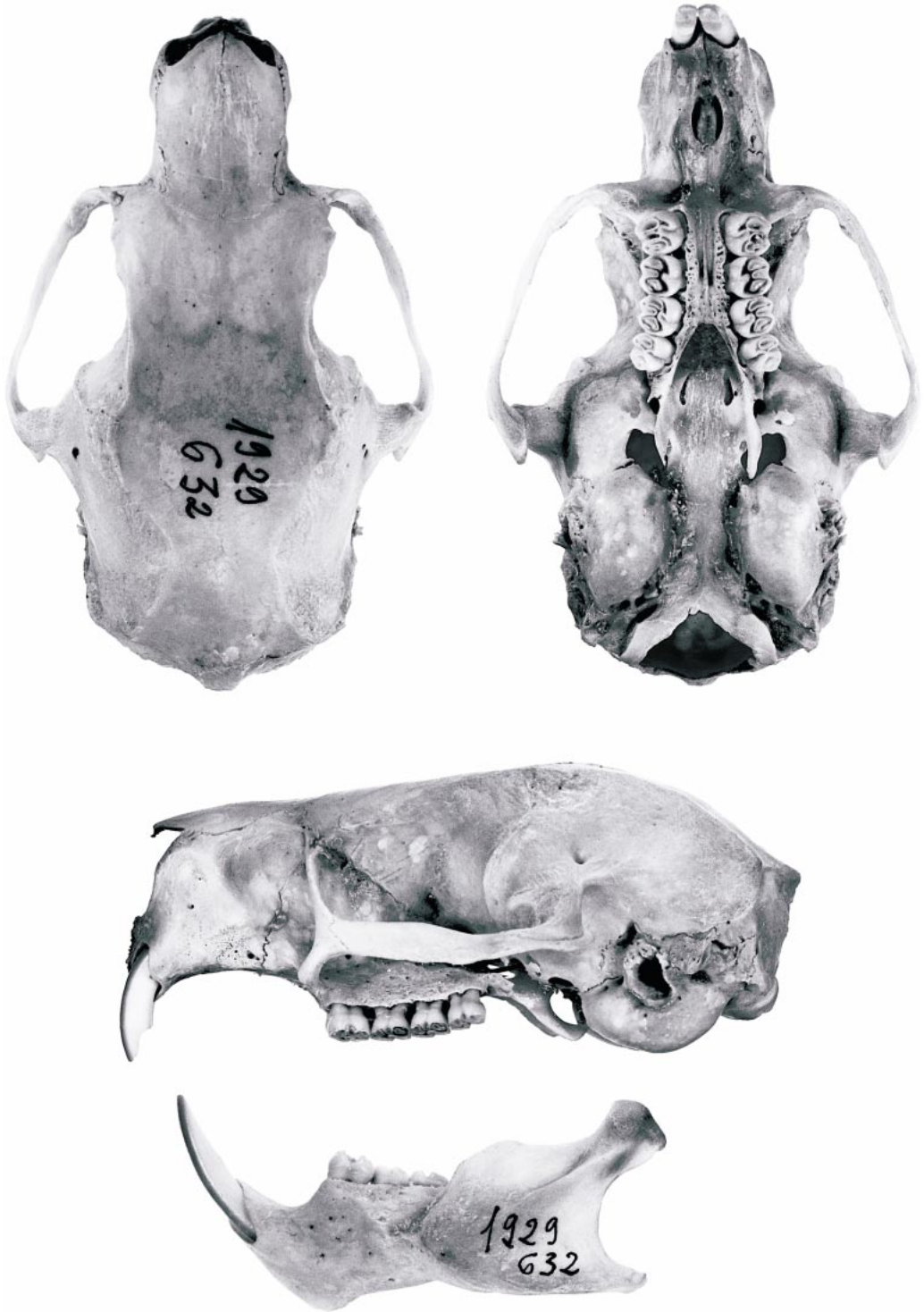


Fig. 4. Dorsal, ventral, and lateral cranial views of *Coendou vestitus* (MNHN 1929–632). All views approximately  $\times 1.5$ .



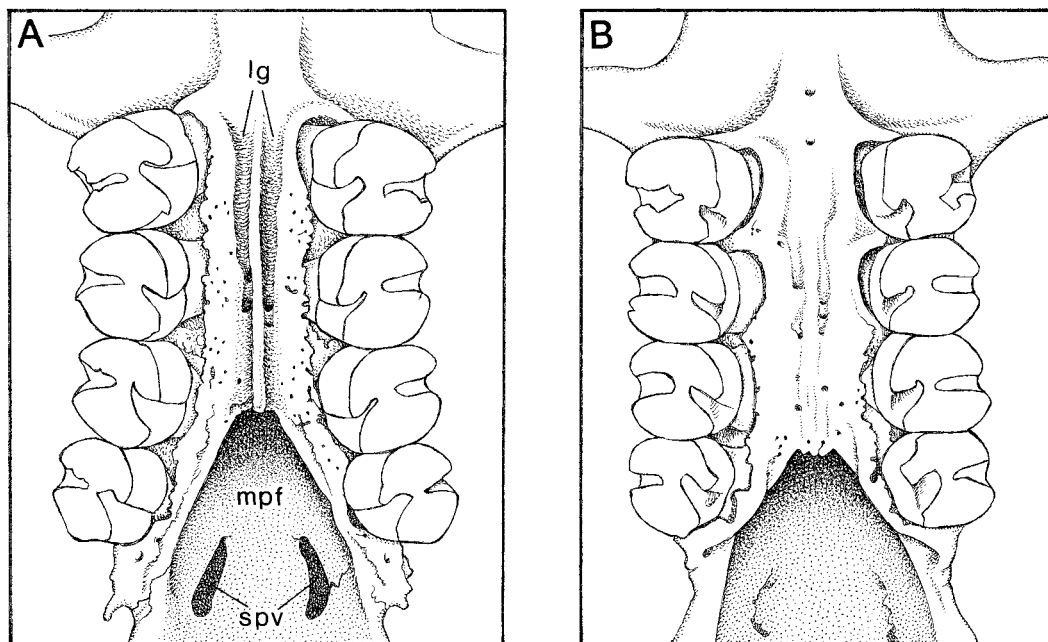


Fig. 5. Ventral cranial views of *Coendou vestitus* (A, MNHN 1929–632) and *C. pruinus* (B, MCZ 18738) showing species differences in palatal morphology. In *Coendou vestitus*, the bony palate between the toothrows is marked by a high median keel that is flanked by deep lateral grooves or gutters (**lg**); in addition, the mesopterygoid fossa (**mpf**) extends anteriorly between the second molars, and the roof of the fossa is perforated by large sphenopalatine vacuities (**spv**). In *C. pruinus*, the palate is sometimes weakly keeled but never has deep lateral gutters; also, the mesopterygoid fossa extends anteriorly only between the third molars, and the roof of the fossa is not perforated by distinct sphenopalatine vacuities.

and-body (see measurements in table 1). The proximal half of the tail is clothed dorsally with quills and woolly fur like the rump, and the tip has a naked, calloused dorsal prehensile surface, but the rest of the tail is covered above and below with blackish bristles; the bristles under the base of the tail are much stiffer and denser than those on the lateral and dorsal surfaces. The dorsal surface of the hands and feet are densely covered with coarse brownish hairs.

The long mystacial vibrissae are uniformly blackish and extend behind the pinnae when laid back alongside the head. Supraorbital (superciliary), genal, submental, and postcranial vibrissae are also present. The postcranial vibrissae occur on the forelimb between the elbow and wrist, on the hindlimb between the knee and ankle, and along the ventral surface of the body between the forelimb and hindlimb.

*Skull*—The frontal and nasal sinuses are uninflated, resulting in a flat dorsal profile from the nasal tips to the midparietal region in all the specimens examined. The rostrum is short and tapering in younger animals, but old adults have proportionately longer rostrums with prominent lateral excavations for the origin of the infraorbital muscle. The nasal bones are more-or-less parallel-sided, neither increasing nor decreasing posteriorly in breadth, with rounded posterior margins that extend well behind the premaxillae. Viewed from above, the zygomatic arches converge anteriorly from their widest point at the level of the squamosal roots with only a slight lateral deflection at the level of the orbits. The jugals are slender elements, lacking any conspicuous postorbital expansion. The dorso-lateral contours of the braincase are strongly sculpted by the origin of the temporalis muscle, but the left and right temporal scars are

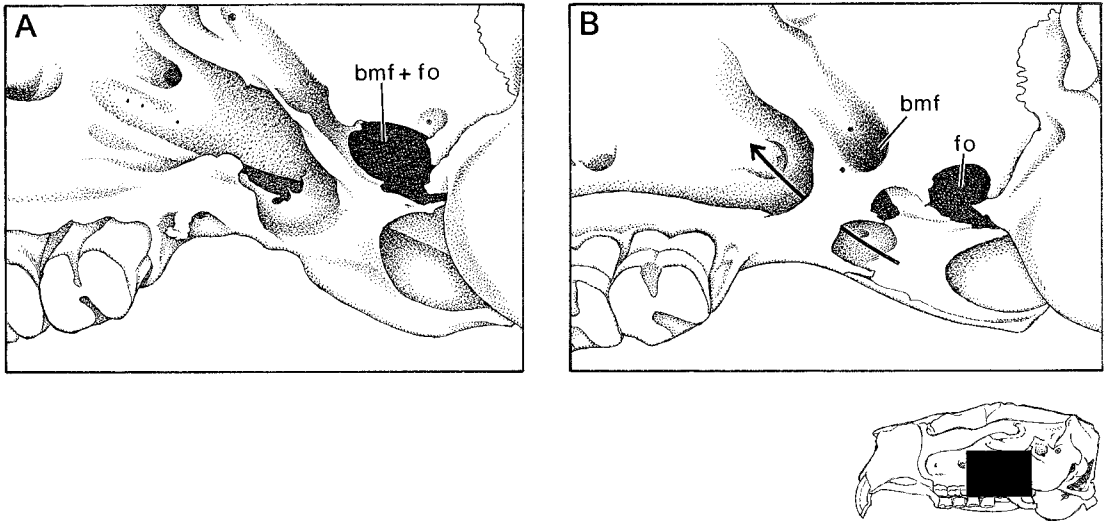


Fig. 6. Ventrolateral cranial views of *Coendou vestitus* (A, AMNH 71360) and *C. pruinosus* (B, MCZ 18738) showing species differences in alisphenoid morphology. In *Coendou vestitus*, the alisphenoid is incompletely ossified, resulting in an open sphenopterygoid canal and a buccinator-masticatory foramen (**bmf**) that is confluent with the foramen ovale (**fo**). By contrast, the alisphenoid is fully ossified in *C. pruinosus*, whose sphenopterygoid canal (arrow) is laterally enclosed and whose buccinator-masticatory and oval foramina are separate.

widely separated and do not join middorsally to form a sagittal crest.

The small incisive foramina are completely contained in the premaxillae (e.g., BMNH 24.2.21.2) or shallowly contact the maxillae (e.g., AMNH 71359), but do not deeply penetrate between the latter bones; the left and right foramina are incompletely separated and are recessed in a common fossa in some specimens, but in others they are completely separated and are not recessed together. The posterior diastema is marked by shallow and widely separated lateral sulci. In all of the specimens examined, the palatal bridge (between the tooththrows) has a well developed central keel and deep lateral gutters (fig. 5A). The mesopterygoid fossa penetrates anteriorly to or between the second molars, and the bony roof of the fossa is perforated by well-formed sphenopalatine vacuities (>1 mm in diameter) in all of the specimens at hand. The alisphenoid is incompletely ossified, with the result that the sphenopterygoid canal is open laterally and the buccinator-masticatory foramen is confluent with the foramen ovale (fig. 6A). The auditory bullae

are small (ca. 14–15 mm) rounded capsules that are well separated from the base of the paroccipital process on each side. The dorsal roof of the external auditory meatus has an indistinct bony ridge that is less well developed than that seen in some congeneric taxa (e.g., *Coendou melanurus*; Voss et al., 2001: fig. 70A).

The mandible is distinctive in the absence of a well-defined coronoid process, which is represented only as a rounded convexity at the base of the ascending ramus in all specimens examined.

*Dentition*—The upper incisors have pale yellow-orange enamel bands and are moderately procumbent. The cheekteeth essentially resemble those of other erethizontids (except *Chaetomys*) in occlusal morphology, and the tooththrows are subparallel to weakly convergent. The permanent fourth upper premolar is only slightly larger than the first molar in some specimens (e.g., AMNH 70529), but P4 is conspicuously larger than M1 in others (e.g., USNM 240035).

COMPARISONS: See the accounts for *Coen-*

TABLE 1  
Measurements (mm) of All Known Specimens  
of *Coendou vestitus*

	BMNH 54.6.26.1 <sup>a</sup>	Adults <sup>b</sup>
Sex	unknown	5 females, 3 unknown
HBL	—	346 (330–370) 6
LT	—	179 (170–195) 6
HF	57	60 (56–63) 6
CIL	—	66.8 (65.4–68.3) 6
LD	[15.2] <sup>c</sup>	17.4 (16.9–17.9) 7
LIF	3.9	4.2 (3.6–4.9) 7
BIF	2.5	2.9 (2.7–3.1) 7
MTR	[14.8] <sup>c</sup>	15.5 (14.7–16.4) 7
LM	11.3	11.3 (10.8–12.0) 7
BP4[dP4]	[3.6]	4.5 (4.1–4.9) 7
BM1	3.8	4.0 (3.8–4.3) 7
APB	4.1	4.9 (4.2–5.6) 7
PPB	5.5	6.2 (5.1–7.2) 7
PZB	40.3	42.9 (42.1–43.5) 6
HIF	8.0	10.4 (9.8–11.0) 7
ZL	24.9	27.2 (26.2–28.1) 7
LN	18.6	20.2 (18.9–21.8) 5
BNA	9.0	10.7 (10.4–11.2) 7
BB	29.1	29.8 (27.8–30.6) 7
DI	3.1	3.3 (3.1–3.5) 7
BIT	4.1	4.6 (4.2–4.8) 7

<sup>a</sup>The subadult holotype.

<sup>b</sup>The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 70529, 70596, 71359, 71360; BMNH 24.2.21.2; MNHN 1929.631, 1929.632; USNM 240035.

<sup>c</sup>One or both endpoints include dP4 (not P4).

*Coendou pruinosus* and the new species described below.

**NATURAL HISTORY AND CONSERVATION STATUS:** Nothing has apparently been recorded about the habitats or behavior of this species, but the natural vegetation at the two localities where specimens are definitely known to have been collected was probably lower montane moist forest (bosque húmedo subtropical; Espinal and Montenegro, 1963). Unfortunately, habitat destruction is virtually complete in this part of Colombia (IAVH, 1998), and it is possible that the species has been extirpated. Apparently, no specimens or sightings have been recorded since 1925.

**SPECIMENS EXAMINED:** **Colombia**—*Cundinamarca*, Quipile (AMNH 70529), San Juan

de Río Seco (AMNH 70596, 71359; BMNH 24.2.21.2; MNHN 1929.631, 1929.632; USNM 240035); “Colombia” (no other locality data, AMNH 71360); “N[ouvel]le Grenade” (BMNH 54.6.26.1 [holotype]).

### *Coendou pruinosus* Thomas

Figures 5B, 6B, 7, 8

*Coendou pruinosus* Thomas, 1905: 310.

*Coendou (Sphiggurus) pruinosus*: Tate, 1935: 307 (new name combination).

*Coendou (Sphiggurus) vestitus pruinosus*: Cabrera, 1961: 602 (new name combination).

*Sphiggurus vestitus*: Honacki et al., 1982: 572 (part; *pruinosus* treated as a junior synonym).

**TYPE MATERIAL:** The holotype, BMNH 5.7.5.9, consisting of the skin, skull, and mandibles of an adult male collected by S. Briceño Gabaldón e hijos at 2500 m elevation in the Montañas de la Pedregosa near Mérida, Venezuela, on 14 January 1905. In addition, Thomas (1905) examined four paratypes, of which three retain original labels with Briceño’s commercial imprint: two of these are from “Montaña del Valle 2600 m”, and were collected on 16 November 1903 (BMNH 5.7.5.8, 5.7.5.11); the other is from “Montañas del Tabay 2600 m”, and was collected on 28 January 1904 (BMNH 5.7.5.12). The fourth paratype (BMNH 5.7.5.10) has a museum label in Thomas’s hand with the locality given as “Merida, Venezuela”, and the collection date as 14 June 1904. Details of skin preparation suggest that the entire type series came from Briceño e hijos, well-known commercial collectors and taxidermists active at Mérida around the turn of the last century.

**GEOGRAPHIC DISTRIBUTION:** Referred specimens are from the foothills and crest of the Cordillera Oriental of Colombia, from the adjacent but disjunct Serranía de la Macarena, and from western and northern Venezuela. The known range of this species in Venezuela includes the foothills of the Serranía de Perijá, the lowlands of the western Maracaibo Basin, the Cordillera de Mérida, and the Cordillera de la Costa. Recorded elevations on specimen tags range from 54 to 2600 m above sea level.

**DESCRIPTION:** *External*—The pelage of *Coendou pruinosus* is morphologically sim-



Fig. 7. Dorsal view of the skin of *Coendou prinosus* (BMNH 10.12.3.5). Approximately  $\times 0.4$ .

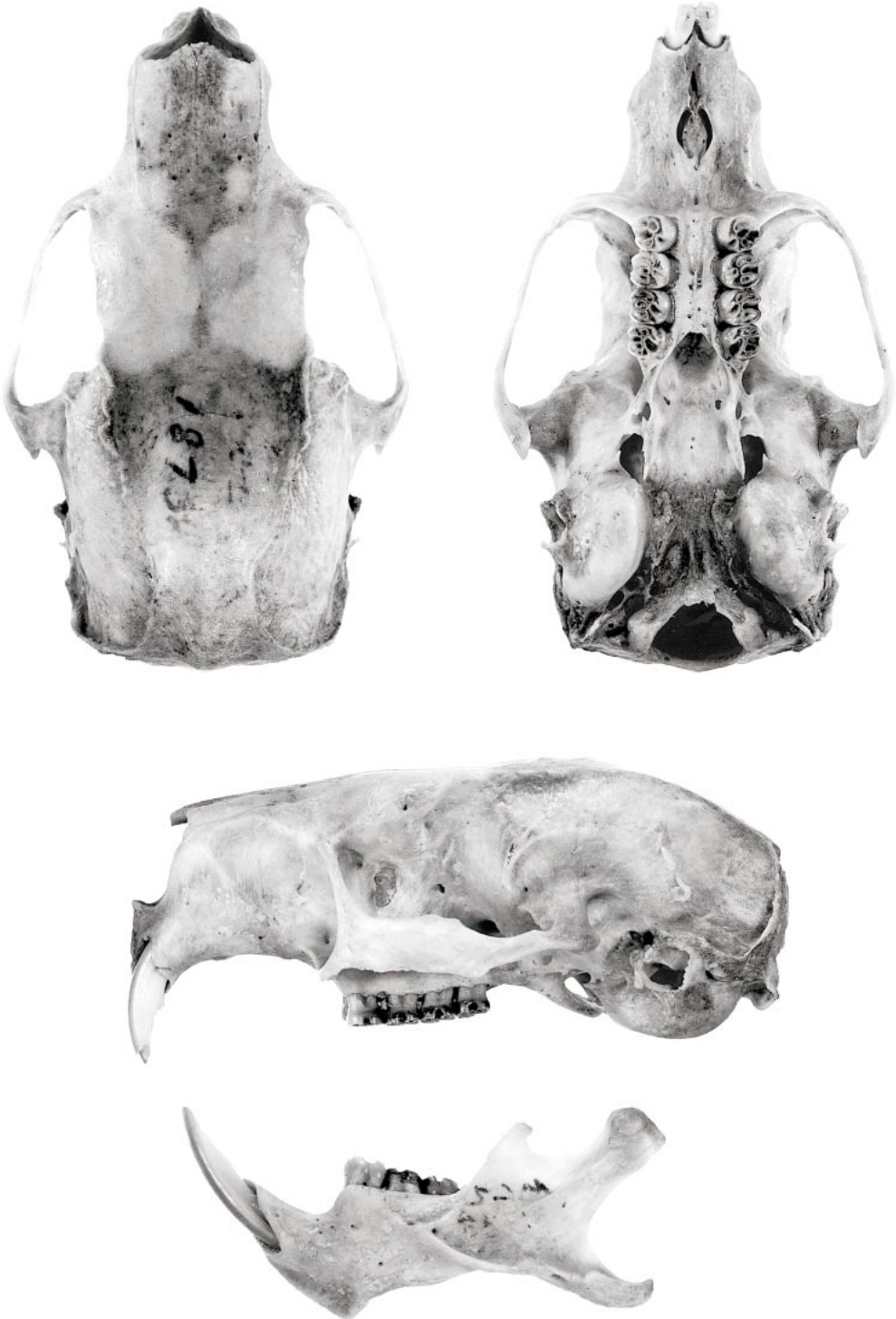


Fig. 8. Dorsal, ventral, and lateral cranial views of *Coendou pruinosus* (MCZ 18738). All views approximately  $\times 1.5$ .



ilar to that of *C. vestitus* but differs in coloration. Although the dorsal fur is predominantly blackish (Thomas, 1905) or dark brown, the hair tips are pale (grayish or silvery), producing a frosted effect that is more pronounced in some individuals (e.g., BMNH 10.12.3.5) than in others (e.g., BMNH 26.11.4.11). The fur is long (50–70 mm midorsally) and dense enough to conceal most of the underlying quills except on the head. All of the body quills (30–40 mm long middorsally) are bicolored (yellowish or ivory-white basally with the extreme tips dark brown), but some of the quills on the crown of the head and on the cheeks are tricolored (with white bases and tips separated by a broad dark middle band). Scattered throughout the dorsal pelage—except over the rump—are many long (to 80–100 mm) wire-like bristle-quills, the pale (usually ivory-white or yellowish) tips of which are conspicuous against the dark background of the fur; most of the bristle-quills are actually tricolored (with pale bases and tips separated by a single dark middle band), but some are entirely pale. The ventral body pelage consists of soft frosted-brown fur from chin to anus. Longer, straighter, coarser guard hairs can be distinguished from finer, shorter, wavy wool hairs in the ventral pelage, but there are no conspicuously thickened spinous hairs rooted in obvious clusters.

The tail is short, averaging slightly more than half the combined length of the head-and-body in specimens from montane habitats (e.g., the Alturas de Pamplona and Mérida series in table 2), but specimens from the Maracaibo lowlands (e.g., MHNLS 7692) and Caracas (BMNH 26.11.4.11) appear to have relatively and absolutely longer tails. Whereas the dorsal surface of the proximal half of the tail is covered by a mixture of quills and soft fur like that on the rump, pale-tipped bristles occur along the sides of the tail and converge posteriorly onto the caudal dorsum forming a conspicuous pale (yellowish or whitish) chevron. The prehensile tail tip is naked and calloused dorsally, but the rest of the tail is covered by blackish bristles; the bristles under the base of the tail are much stiffer and denser than those on the lateral and dorsal surfaces. The dorsal surface

of the hands and feet are covered with coarse frosted-brownish hairs.

The cranial and postcranial vibrissae have the same morphology, coloration, and anatomical distribution as previously described for *Coendou vestitus*.

*Skull*—The frontal and nasal sinuses are uninflated in most specimens, resulting in a dorsal profile that is nearly flat from the nasal tips to the midparietal region; a single specimen (MHNLS 7692), however, has slightly inflated dorsal sinuses that produce a small but distinct swelling over the maxillary zygomatic roots. The rostrum is short and tapering in subadults and young adults, but lengthens in older animals, some of which develop shallow lateral excavations for the infraorbital muscle. The nasal bones are approximately parallel-sided in some specimens and taper slightly posteriorly in others, but always have rounded posterior margins that extend well behind the premaxillae. Viewed from above, the zygomatic arches converge anteriorly from the squamosal roots without a well-developed secondary widening at the orbits; some specimens (e.g., FMNH 140260), however, have more rounded (less angular) zygomatic outlines than others (e.g., MCZ 18738; fig. 8). The jugals are moderately deep (dorsoventrally expanded), with some specimens (e.g., BMNH 10.12.3.5, USNM 172985) exhibiting a distinct postorbital swelling. The bony crests and scars associated with the origin of the temporalis muscle are strongly developed in some specimens, but a sagittal crest is not developed in any of the material examined.

The incisive foramina are moderately long and usually bordered posteriorly by the maxillae, but they do not penetrate deeply between those bones; in most specimens, the left and right foramina are completely separated by a bony septum and are not recessed in a common fossa. (A single specimen among those we examined, USNM 496172, is an exception: the foramina are contained within the premaxillae, and are incompletely separated and recessed in a common fossa.) The posterior diastema is marked by shallow and widely separated lateral sulci. The palatal bridge between the tooththrows is smooth (e.g., AMNH 21350) or weakly keeled (USNM 172985), but lacks deep lateral gut-

TABLE 2  
Measurements (mm) of Adult Specimens of *Coendou pruinosus*

	Venezuela				
	Colombia <sup>a</sup>		Vicinity of Mérida <sup>b</sup>	Maracaibo Basin	
	FMNH 140260	FMNH 140261		USNM 496172	MHNLS 7692
Sex	male	female	5 males, 2 females, 1 unk.	male	male
HBL	350	350	360 (325–380) 5	—	331
LT	185	160	199 (180–215) 5	—	235
HF	—	63	59 (58–60) 6	58	60
CIL	64.9	—	64.8 (61.5–67.2) 6	65.7	70.5
LD	17.1	19.1	18.1 (16.3–19.0) 8	18.4	19.8
LIF	5.9	5.9	5.6 (4.9–6.0) 8	5.5	4.2
BIF	3.2	3.5	3.3 (2.9–4.0) 8	2.7	3.4
MTR	15.8	15.3	15.0 (14.3–15.8) 8	14.8	15.0
LM	11.9	11.5	11.0 (10.5–11.6) 8	11.3	11.0
BP4	4.6	4.6	4.5 (4.1–4.8) 8	4.3	4.4
BM1	4.5	4.2	4.0 (3.8–4.2) 8	4.2	4.1
APB	4.6	4.7	4.7 (4.2–5.1) 8	4.9	4.1
PPB	6.4	6.0	5.7 (5.4–6.2) 8	6.3	5.7
PZB	42.0	40.1	40.4 (38.8–41.2) 6	39.4	40.4
HIF	8.5	9.7	9.5 (8.2–10.4) 8	9.2	9.6
ZL	25.6	26.5	25.4 (24.1–26.8) 8	24.9	27.3
LN	17.8	—	19.8 (17.9–21.0) 4	20.7	—
BNA	10.1	11.4	11.1 (10.0–11.6) 8	10.7	12.0
BB	29.9	28.1	29.1 (28.2–30.4) 8	29.3	29.1
DI	3.2	3.5	3.2 (3.0–3.5) 8	3.1	3.3
BIT	4.7	5.1	4.4 (4.1–4.8) 8	4.5	4.5

<sup>a</sup>From Alturas de Pamplona, Norte de Santander.

<sup>b</sup>The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 21350; BMNH 5.7.5.9 [holotype], 5.7.5.10–5.7.5.12, 10.12.3.5; MCZ 18738; USNM 172985. Not all of the specimens are actually labeled as from the vicinity of Mérida, but uniform details of skin preparation together with collection dates clustered in the interval 1900–1905 suggest that all are originally from the Mérida-based collecting firm of Briceño and Sons.

ters (fig. 5B). The mesopterygoid fossa is shallow in most specimens (penetrating only between the third molars) and the bony roof of the fossa is perforated by tiny nutrient foramina or by small irregular holes that do not have the aspect of distinct sphenopalatine vacuities. The alisphenoid is completely ossified in all specimens examined, such that the sphenopterygoid canal is enclosed laterally and the buccinator-masticatory foramen is not confluent with the foramen ovale (fig. 6B). The auditory bullae are small (ca. 14–15 mm) rounded capsules that are well separated from the paroccipital processes in most specimens, but three skulls (BMNH 26.11.4.11; FMNH 140261; MHNLS 7692)

have unusually large (16–18 mm) bullae. The dorsal roof of the external auditory meatus has an indistinct bony ridge in most adult specimens, but two specimens (MHNLS 7692, USNM 496172) have distinct auditory ridges.

The mandible bears a small but distinct coronoid process in all specimens examined.

*Dentition*—The dentition of *Coendou pruinosus* is similar to that of *C. vestitus*, apparently without any distinctive features.

*COMPARISONS*: *Coendou pruinosus* and *C. vestitus* are similar in many points of comparison, yet each is morphologically distinctive. Externally, *pruinosus* differs from *vestitus* by its frosted (versus unicolored-dark)

dorsal and ventral fur, tricolored (versus bicolor) head quills, pale-tipped (versus dark-tipped) bristle-quills, and chevron of pale-tipped caudal bristles (versus caudal chevron absent). Cranially, the two species are clearly distinguishable by palatal morphology (the bony palate between the toothrows is more distinctly ridged and grooved in *vestitus* than in *pruinus*), mesopterygoid perforation (distinct sphenopalatine vacuities are present in *vestitus* versus absent in *pruinus*), alisphenoid ossification (the sphenopterygoid canal is laterally open in *vestitus* versus closed in *pruinus*), and mandibular morphology (a distinct coronoid process is absent in *vestitus* but present in *pruinus*). In addition, other modal differences support the hypothesis that these are genetically differentiated taxa: (1) rostral morphology (the sides of the rostrum appear to be more deeply excavated for the origin of the infraorbital muscle in *vestitus* than in like-aged *pruinus*); (2) depth of the jugal (more dorsoventrally expanded below the orbit in *pruinus* than in *vestitus*); (3) morphology of the incisive foramina (short, incompletely separated, and contained entirely by the premaxillae in most *vestitus* versus longer, completely separated, and bordered by the maxillae in most *pruinus*); and (4) depth of the mesopterygoid fossa (penetrating to or between the second molars in *vestitus* versus shallower in most *pruinus*). Although only small samples are currently available for taxonomic comparisons, these differences permit unambiguous identifications and seem more than sufficient to recognize *C. vestitus* and *C. pruinus* as valid species.

**VARIATION:** Consistent with its larger eogeographic range, *Coendou pruinus* is more morphologically variable than *C. vestitus*, but all of the referred material shares a common aspect and we provisionally regard it as representing conspecific populations. Nevertheless, a few specimens from geographically peripheral localities are notably atypical. In particular, AMNH 136312 (from the foothills of the Cordillera Oriental in Departamento Meta, Colombia) has unusually sparse fur, a deep mesopterygoid fossa (extending between the second molars), and small toothrows (MTR, 13.3 mm); its bullae are relatively longer (approaching the base of

the paroccipital process on each side) and more laterally compressed than those seen in topotypical material. Likewise, MHNLS 7692 (from the foothills of the Serranía de Perijá) has uniquely swollen frontal sinuses, dorsal bristles tipped with pale orange (instead of white or pale yellow), and very large bullae. Finally, the single specimen examined from the Cordillera de la Costa (BMNH 26.11.4.11, a subadult) has unusually short incisive foramina, small teeth, and large bullae. The possibility that such outliers represent distinct taxa merits testing when more material becomes available from these areas.

**REMARKS:** A specimen collected ca. 75 km SW of the type locality was karyotyped by Concepción and Molinari (1991), who reported a diploid number of 42 and a fundamental number of 76. Their morphological description of the karyotyped animal is consistent with that given above for *Coendou pruinus*, with only minor differences. The reported external dimensions and weight of this specimen (CVULA I-3030, an adult male) are the only such data obtained to date from positively identified fresh material near the type locality: 300 mm (HBL)  $\times$  220 mm (Tail)  $\times$  55 mm (HF, c.u.)  $\times$  22 (Ear) = 1010 g.

Specimens currently labeled as "*Sphigurus vestitus*" in Venezuelan museums are presumably referable to *Coendou pruinus* as herein recognized, but the following material should be examined for diagnostic attributes to confirm this identification: EBRG 126 (*Aragua*, Rancho Grande), EBRG 4350 (*Mérida*, 2 km E Jají), EBRG 10281 (*Miranda*, Parque Nacional El Ávila), EBRG 20243 (*Aragua*, Colonia Tovar), MBUCV 1472 (*Distrito Federal*, Carayaca), MBUCV 4155 (*Miranda*, Estación Experimental de Río Negro), MHNLS 58 (*Miranda*, Turgua), MHNLS 3879 (*Distrito Federal*, Caracas), MHNLS 8480 (*Zulia*, Hacienda La Ceiba).

**NATURAL HISTORY:** All known specimens of *Coendou pruinus* have been collected in regions where the original (non-anthropogenic) vegetation is (or was) humid forest. At elevations below 1000 m, the species inhabits lowland rainforest, but at higher elevations the typical habitat is probably cloud forest (Lower Montane or Upper Montane Rainforest; Grubb, 1977). To the best of our knowledge, no specimens have been taken in

unforested (e.g., savanna or páramo) landscapes.

Published natural history information can be associated with only three positively identifiable records of *Coendou pruinosus*. Handley (1976: 55) reported that one individual (USNM 496172, an adult male) was “found in a tree in an upland area in mature evergreen forest” near El Rosario (54 m elevation; Estado Zulia, Venezuela), where the local vegetation was further characterized as “[m]ature evergreen forest 18–30 m high, with many palms and vines” (op. cit.: 69). Concepción and Molinari (1991: 238) subsequently reported another specimen (CVULA 1–3030, also an adult male) that was captured “in an area dominated by cloud forest” at an elevation of 1500 m near the town of Zea (Estado Mérida, Venezuela).

On the night of 6 July 1986, Voss shot another adult male specimen (MHNLS 7692) that was perched about 20 m above the ground on the trunk of a large buttressed tree festooned with lianas and epiphytes near Misión Tukuko (ca. 300 m elevation; Estado Zulia, Venezuela). The tree was part of the original rainforest canopy at this site, but most of the surrounding undergrowth had been cleared for cacao cultivation (for a detailed description of local habitats, see Voss, 1991: 68–70). The freshly dissected stomach was full of brownish paste, possibly consisting of chewed bark; no insect parts, seeds, or other identifiable food fragments were observed.

**SPECIMENS EXAMINED:** **Colombia**—*Meta*, Villavicencio (AMNH 136312), Pico Rengifo (FMNH 87896); *Norte de Santander*, Alturas de Pamplona (FMNH 140260, 140261). **Venezuela**—*Distrito Federal*, Caracas (BMNH 26.11.4.11); *Mérida*, Mérida (AMNH 21350, BMNH 5.7.5.10, 10.12.3.5), Montañas de la Pedregosa (BMNH 5.7.5.9), “Montaña de la Sierra” (MCZ 18738, ZMB 33377), Montañas de Tabay (BMNH 5.7.5.12), “Montaña del Valle” (BMNH 5.7.5.8, 5.7.5.11); *Zulia*, El Rosario (USNM 496172), Misión Tukuko (MHNLS 7692). **“South America”** (USNM 172985).

### *Coendou ichillus*, new species

Figures 9–12

**TYPE MATERIAL:** The holotype, AMNH 126171, consists of the skin, skull, and man-

dibles of a young adult of unknown sex collected by the von Baumann-Roosevelt Expedition in July 1936 on the Río Pastaza, Ecuador.<sup>3</sup> The stuffed skin (fig. 9) appears to be slightly faded, but is in otherwise perfect condition with no missing elements. The skull (fig. 10) lacks part of both nasal bones together with most of the right premaxilla, but is otherwise complete. Two paratypes are from unknown localities on the Río Comambo (EPN 806, an adult female) and the Río Yana Rumi (FMNH 43289, an adult male), both in Provincia Pastaza, Ecuador.

**GEOGRAPHIC DISTRIBUTION:** All unambiguous records of *Coendou ichillus* are from the Amazonian lowlands of eastern Ecuador, but a referred juvenile specimen purchased near Iquitos (see Variation, below) suggests that the species is more widely distributed.

**ETYMOLOGY:** From *ichilla*, meaning “small” (Orr, 1978) in the dialect of the lowland Quichua, within whose tribal territory the new species occurs.

**DIAGNOSIS:** A member of the *Coendou vestitus* group distinguished from other species by its long tail, lack of visible fur in the adult pelage, more extensively black-tipped quills, tricolored (pale-tipped) bristle-quills, spiny ventral pelage, and a unique combination of cranial traits.

**DESCRIPTION:** *External*—No soft fur is apparent in the dorsal pelage except by close examination because the blackish wool hairs are sparse and hidden among the quills and bristles; a few dorsal wool hairs plucked from two specimens were about 40 mm in length. All of the quills (30–40 mm long middorsally) are bicolored (yellowish basally with the terminal 1/3 to 1/2 dark-brown or

<sup>3</sup> The original specimen label gives the locality as “Río Pastaza” only, but the entire von Baumann-Roosevelt collection (including 10 other mammals and 25 birds variously labeled “Río Tigre”, “Río Bobonaza”, “Río Blanco”, “Río Pastaza”, and “Río Napo”) was known to have been obtained in Ecuador, so the lower (Peruvian) course of this river can be ruled out. Unfortunately, the exact route traveled by the von Baumann-Roosevelt Expedition is unknown, and no archival record of the purpose or staffing of this mysterious outfit appears to exist. Filed correspondence with its director, Cyril von Baumann, consists only of an AMNH accession receipt dated 23 January 1937, together with a curt acknowledgment from von Baumann dated 1 February.





Fig. 9. Dorsal view of the skin of *Coendou ichillus* (AMNH 126171, holotype). Approximately  $\times 0.4$ .



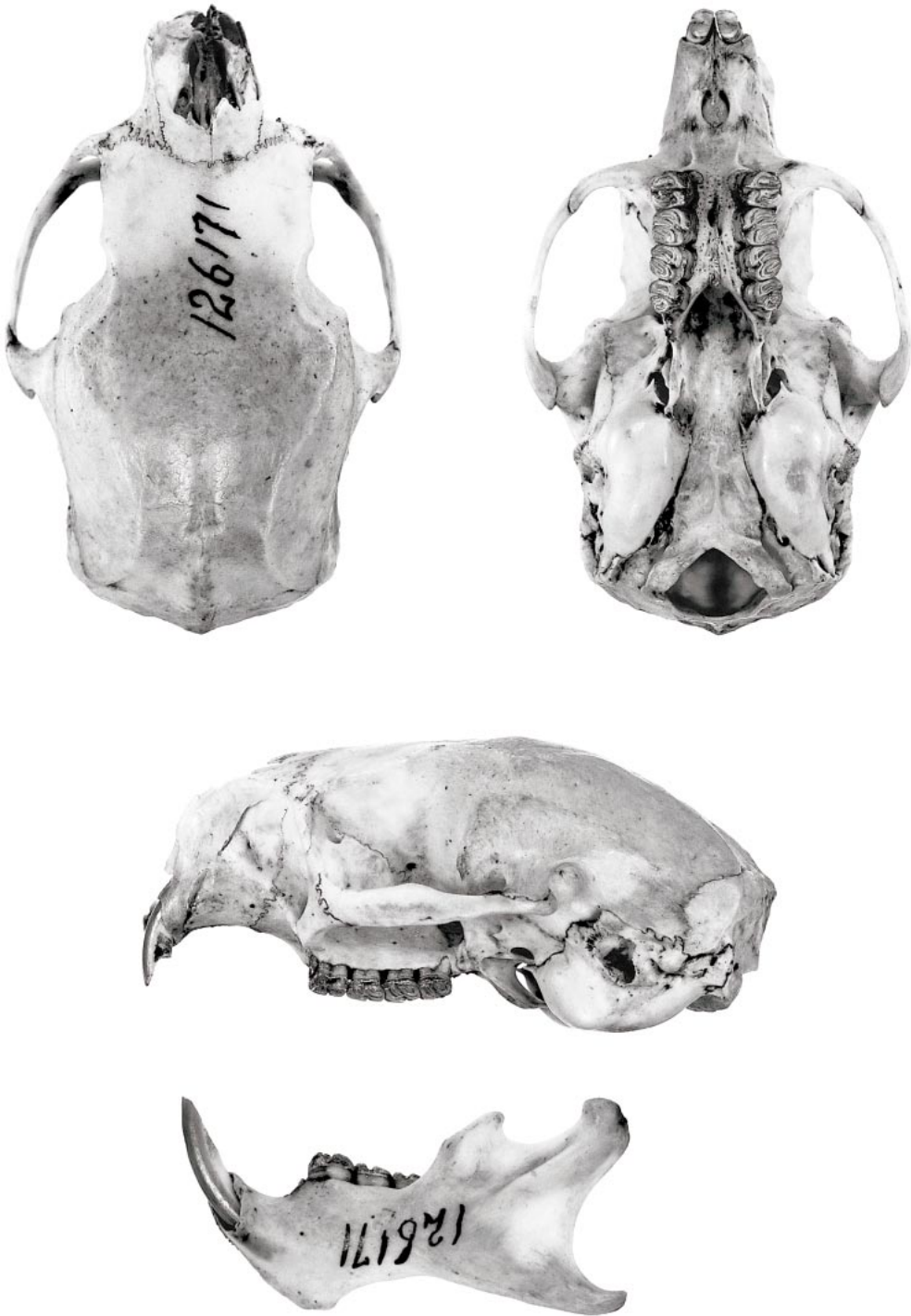


Fig. 10. Dorsal, ventral, and lateral cranial views of *Coendou ichillus* (AMNH 126171, holotype). All views approximately  $\times 1.5$ .



Fig. 11. Dorsal, ventral, and lateral cranial views of *Coendou ichillus* (FMNH 43289, paratype). All views approximately  $\times 1.5$ .



Fig. 12. An adult female *Coendou ichillus* eating bananas suspended from the rafters of a building at La Selva Jungle Lodge, Provincia Sucumbíos, Ecuador, on 9 July 1996 (photo courtesy of P. J. DeVries).

blackish), except on the head, where some quills are tricolored (with ivory-white bases and tips separated by a dark middle band). Densely scattered among the quills are many long (to ca. 80 mm) thin bristle-quills with yellowish bases and tips separated by a broad dark-brown or blackish middle band; the pale tips of the bristle-quills produce a character-

istically streaked effect over the whole dorsum with the exception of the rump (which is covered only with short bicolored quills and a few wool hairs). The ventral body pelage consists of very coarse bicolored or tricolored hairs (ca. 0.30–0.40 mm in diameter and 15 mm long) that are usually rooted in triplets but occasionally in groups of two or

TABLE 3  
Measurements (mm) of All Known  
Adult Specimens of *Coendou ichillus*

	AMNH 126171 <sup>a</sup>	EPN 807	FMNH 43289
Sex	unknown	female	male
HBL	ca. 290	—	ca. 260
LT	ca. 250	—	ca. 210
HF	—	59	58
CIL	58.8	64.2	64.4
LD	14.0	15.8	16.9
LIF	3.7	—	3.7
BIF	2.7	—	3.1
MTR	14.1	15.2	14.0
LM	10.3	11.4	10.5
BP4	4.1	4.5	3.9
BM1	3.8	4.2	3.8
APB	4.4	4.5	4.1
PPB	5.9	6.2	6.5
PZB	39.2	39.1	39.0
HIF	8.6	8.3	9.8
ZL	24.0	25.7	26.2
LN	—	18.8	—
BNA	—	9.9	—
BB	29.3	31.3	28.9
DI	2.9	2.9	—
BIT	4.7	4.0	—

<sup>a</sup>The holotype.

four; a few short wool hairs are almost invisibly scattered among this harsh covering.

The tail is moderately long, averaging rather more than  $\frac{3}{4}$  of head-and-body length on the two skins from which approximate measurements could be obtained (table 3); in life, the extended tail of one individual (only partly visible in fig. 12) seemed to be almost as long as the head and body, but no accurate measurement could be taken from this unrestrained animal (see Natural History, below). The dorsal part of the base of the tail is densely covered with short bicolored quills like those of the rump, but tricolored bristles extend along the lateral caudal surfaces and converge dorsally to form an indistinct whitish or yellowish chevron near the middle of the tail. The prehensile tail-tip is calloused and naked dorsally, but the rest of the tail is densely covered by blackish bristles; the caudal bristles are conspicuously stiffer and

denser under the base of the tail than elsewhere. The hands and feet are covered dorsally with coarse blackish hairs.

The cranial and postcranial vibrissae of this species have the same morphology, coloration, and distribution as previously described for *Coendou vestitus*.

*Skull*—The frontal and nasal sinuses are uninflated, resulting in a flat dorsal profile from the nasal tips to the midparietal region. In dorsal view, the rostrum is short and moderately broad, lacking obvious lateral emarginations for the origin of the infraorbital muscle. The nasal bones are damaged in two of the three specimens at hand, but appear to taper gently from front to back; the posterior nasal margins are rounded and extend behind the premaxillae (much more so in FMNH 43289 than in AMNH 126171). Viewed from above, the zygomatic arches are rounded (AMNH 126171) or biconcave (EPN 807, FMNH 43289) because they are anteriorly deflected to accommodate relatively larger orbits than those of either *Coendou vestitus* or typical *C. pruinus*. The jugals have either a small postorbital expansion (AMNH 126171, EPN 807) or taper more-or-less evenly from front to back (FMNH 43289). The dorsolateral contours of the braincase show only slight to moderate sculpting for the origin of the temporalis muscle; the right and left temporalis scars are widely separated in all three specimens examined.

The small incisive foramina are incompletely separated and recessed in a common fossa that is contained entirely by the premaxillae (EPN 807) or bordered narrowly by the maxillae behind. The posterior diastema is marked by shallow and widely separated lateral sulci. The palatal bridge between the toothrows does not have a distinct median keel or deep lateral gutters in any of the specimens examined. The mesopterygoid fossa extends anteriorly just beyond the point of contact between M2 and M3, and the bony roof of the fossa (in AMNH 126171 and EPN 807) is not perforated by distinct sphenopalatine vacuities. The alisphenoid is completely ossified such that the sphenopterygoid canal is enclosed laterally and the buccinator-masticatory and oval foramina are separate. The auditory bullae are large (ca.



16–17 mm) inflated capsules that contact the base of the paroccipital process on each side. The dorsal roof of the external auditory meatus lacks a distinct bony keel in both specimens at hand (AMNH 126171, FMNH 43289).

The mandible is provided with a small but well-developed coronoid process.

*Dentition*—The dentition is qualitatively similar to that of *Coendou vestitus* and *C. pruinus*, but measurements suggest that the incisors are relatively broader than in those species, and they appear to be more deeply pigmented as well.

*COMPARISONS*: No other species of the *Coendou vestitus* group lacks a visible coat of long fur, and this trait together with its relatively long tail and spiny ventral pelage make *C. ichillus* externally unmistakable. Additionally, the pigmented tips of the defensive quills are much longer in *ichillus* than in either *vestitus* or *pruinus*; as a result, when the long fur of the latter two species is shed or parted, the exposed quills and bristles produce the effect of a pale (yellowish or whitish) animal streaked and stippled with dark brown, whereas the permanently exposed quills and bristles of *ichillus* produce the effect of a blackish animal streaked with white or yellow.

Cranially, *Coendou ichillus* is distinguished from *C. vestitus* and from typical examples of *C. pruinus* by its proportionately smaller and less laterally excavated rostrum, more rounded (or biconcave) zygomatic arches, and proportionately larger bullae. From *vestitus*, the new species additionally differs by its less strongly muscle-scarred braincase, less strongly keeled and grooved palatal bridge, unperforated mesopterygoid fossa, and distinct mandibular coronoid process. From *pruinus*, the new species additionally differs by its smaller incisive foramina and more anterior mesopterygoid penetration.

External and cranial comparisons with the second new species are provided in the following account.

*VARIATION*: Cranial differences among the three available adult specimens of *Coendou ichillus* do not exceed the range of osteological variation routinely observed within local populations of other Neotropical porcupines.

However, the skin of the holotype appears to be faded by comparison with the more vividly colored paratypes. The latter closely resemble living examples (fig. 12), whose dark pelage markings are distinctly blackish. By contrast, the corresponding pigmentation on AMNH 126171 is brownish (near Smithe's [1975] Sepia or Raw Umber), a chromatic difference that might have resulted from inadequate specimen storage (e.g., exposure to light or bleaching agents) at some point in the past.

An immature specimen (FMNH 112565) purchased by Pekka Soini in 1971 near Iquitos is mounted for display with the skull inside and has painted seeds for eyes; obviously intended for the tourist trade, it is unaccompanied by records of sex, measurements, or habitat. The dorsal body pelage consists of bicolored quills, tricolored bristle-quills, and long reddish fur; the ventral pelage consists mostly of reddish fur, but a few clusters of soft spines are emerging along the midline. Measurements made with a flexible rule suggest that the tail in life was more than three-quarters of the combined length of head and body; the estimated length of the dried hind foot is ca. 48 mm.

Long reddish juvenile fur appears to be a taxonomically widespread trait among Neotropical porcupines, occurring even in those species that lack visible fur as adults (Roberts et al., 1985; Handley and Pine, 1992). We identify FMNH 112565 as *Coendou ichillus* because its long tail, boldly black-tipped quills, tricolored bristle-quills, and emerging ventral spines suggest a similar external phenotype at maturity. Although this identification is biogeographically plausible (other eastern Ecuadorean taxa have ranges that extend southeastward into Peru, e.g., *Saguinus nigricollis graellsii*; Hershkovitz, 1977: fig. X.21), the exact provenance of FMNH 112565 is uncertain because tourist items sold near Iquitos might have originated far from the city.

*NATURAL HISTORY*: Although no useful ecological association can be inferred from the type locality, "Río Pastaza", a river that traverses a considerable range of habitats in its descent from the Andes to the Amazon, both paratypes are from densely rainforested catchments below 500 m elevation. The orig-



inal skin tag attached to FMNH 43289 includes the notation "Col[ectado]: con cerbatana y beneno" (collected with blowgun and poisoned dart), suggesting that the animal was taken from a tree by a native hunter, probably belonging to one of the lowland Quichua groups described by Whitten (1976). No other natural history information is available from any of the specimens at hand.

Fortunately, field observations of *Coendou ichillus* are available from at least one definite locality: La Selva Jungle Lodge, an ecotourist facility and biological station at ca. 300 m elevation on the left (north) bank of the Río Napo in Provincia Sucumbíos, Ecuador. Situated between the oxbow lakes of Garza Cocha and Mandi Cocha, the lodge and its surrounding trail system occupy the typical ridge-and-swale landscape created by meandering white-water rivers, with tall forest on the high ground and swamps in the valley bottoms. Balslev et al. (1987) provided a detailed description of the local vegetation based on their study of flooded and unflooded forest at nearby Añangu (on the opposite bank of the Napo). Several years of weather records from La Selva suggest that this region receives between 3500 and 4000 mm of annual rainfall (DeVries et al., 1999).

An adult female porcupine, unambiguously identifiable as *Coendou ichillus*, was briefly observed at La Selva (by J. E. Cadle, P. J. DeVries, L. H. Emmons, and R. S. Voss) on the night of 9 July 1996 as it ate ripe bananas suspended by a cord from the rafters of a building surrounded by gardens and secondary vegetation (fig. 12). Several days later, another adult *C. ichillus* was observed at night (by J. E. Cadle and L. H. Emmons) in adjacent primary floodplain forest, where it was perched on a liana about 8 m above the ground. At least two individuals were said by lodge employees to inhabit holes in hollow palm trunks that were used as upright supports for the kitchen and other buildings at La Selva.

**SPECIMENS EXAMINED:** **Ecuador**—*Pastaza*, Río Conambo (EPN 807), Río Yana Rumi (FMNH 43289); *Río Pastaza* (AMNH 126171 [holotype]). **Peru**—*Loreto*, Iquitos region (FMNH 112565).

*Coendou roosmalenorum*, new species

Figures 13, 14

**TYPE MATERIAL:** The holotype, INPA 2586 (original number CCM 58), consists of the well-preserved skin, skull, and mandibles of an adult female collected by M.G.M. and T. van Roosmalen on 23 November 1996 at the caboclo settlement of Novo Jerusalem near the left bank of the middle Rio Madeira in the Brazilian state of Amazonas. One paratype (INPA 2587) is from the nearby village of Santa Maria on the same side of the Madeira, but the other (INPA 677) is from 49 km E Porto Velho on the opposite bank in the Brazilian state of Rondônia.

**GEOGRAPHIC DISTRIBUTION:** Known from both banks of the middle Rio Madeira in Brazil between 5 and 9° S latitude.

**ETYMOLOGY:** For Marc van Roosmalen and his son Tomas, whose collections from the middle Madeira included this distinctive porcupine together with other previously undescribed mammalian taxa (Roosmalen et al., 1998, 2000).

**DIAGNOSIS:** A member of the *Coendou vestitus* group distinguished from other member species by its small size, long tail, long adult fur, minutely black-tipped quills, nonspinous ventral fur, and unique combination of craniodental traits.

**DESCRIPTION:** *External*—The dorsal fur of soft wool hairs is dull in appearance and apparently variable in coloration, pale grayish-brown in one specimen (INPA 2586) but dark brown in the other two (INPA 677, 2587); in the specimens with brownish dorsal fur, the hair tips are pale (grayish or silvery) but these do not produce a distinctly frosted mass effect. The dorsal fur is long (50–70 mm) and dense enough over the back and rump to partly (INPA 2586, 2587) or completely (INPA 677) conceal the underlying quills. All of the quills (ranging in length from about 25 to 35 mm middorsally) are bicolored (yellowish basally with the extreme tips dark brown) over the entire dorsum, including the head. Scattered abundantly throughout most of the dorsal pelage (except the rump) are long (40–70 mm) wire-like bristle-quills; almost all of these are tricolored—with pale (yellowish or ivory-white) bases and tips separated by a single



Fig. 13. Holotype of *Coendou roosmalenorum* (INPA 2586) in life. Photos courtesy of M.G.M. van Roosmalen.



Fig. 14. Dorsal, ventral and cranial views of *Coendou roosmalenorum* (INPA 2586 [original number CCM 58], holotype). All views approximately  $\times 1.5$ .



TABLE 4  
Measurements (mm) of All Known Specimens  
of *Coendou roosmalenorum*

	Subadult		Adults	
	INPA 2587	INPA 2586 <sup>a</sup>	INPA 677	INPA 677
Sex	female	female	female	female
HBL	290	290	—	—
LT	245	260	—	—
HF	53	53	—	—
CIL	59.9	59.4	64.4	64.4
LD	[15.4] <sup>b</sup>	16.0	17.2	17.2
LIF	5.0	3.9	4.9	4.9
BIF	3.0	2.4	2.9	2.9
MTR	[14.1] <sup>b</sup>	13.4	12.6	12.6
LM	10.7	10.1	9.5	9.5
BP4[dP4]	[3.8]	4.0	4.0	4.0
BM1	3.8	3.8	3.8	3.8
APB	4.3	4.2	5.4	5.4
PPB	—	6.6	7.4	7.4
PZB	38.5	36.9	39.1	39.1
HIF	7.2	8.5	8.5	8.5
ZL	24.5	25.2	24.9	24.9
LN	18.5	17.9	—	—
BNA	9.2	9.3	10.0	10.0
BB	29.8	29.0	29.1	29.1
DI	2.8	2.5	2.9	2.9
BIT	3.7	3.9	4.7	4.7

<sup>a</sup>The holotype.

<sup>b</sup>One or both endpoints include dP4 (not P4).

dark-brown middle band of variable width—but a few bristles are bicolored (with pale bases and dark tips). The ventral surface of the body is densely covered with a mixture of fine, soft, brownish wool and coarser, banded (tricolored or bicolored) hairs from chin to anus; the banded hairs (0.20–0.25 mm in diameter and 15–20 mm long) are rooted in clusters, usually triplets but occasionally groups of two or four.

The long tail is almost 90% of head-and-body length in both of the specimens from which measurement data are available (table 4). The basal third of the tail is covered dorsally with bicolored quills and woolly fur, and the prehensile tail-tip is bare and calloused dorsally, but the rest of the tail (above and below) is uniformly covered with blackish bristles; the caudal bristles under the base of the tail are stiffer and denser than those occurring elsewhere. The dorsal surfaces of

the hands and feet are densely covered with coarse dark-brown or blackish hairs.

The cranial and postcranial vibrissae have essentially the same morphology, coloration, and anatomical distribution as previously described for other *vestitus*-group porcupines.

*Skull*—The frontal and nasal sinuses are slightly inflated in the younger left-bank specimens (INPA 2586, 2587), producing a slightly swollen dorsal profile above the orbits; the sinuses of the older right-bank specimen (INPA 677) are uninflated, however, resulting in a flat dorsal profile from the nasal tips to the midparietal region. The rostrum is short and tapering in our younger examples but moderately broad in INPA 677; however, there are no well-developed lateral emarginations for the origin of the infraorbital muscle in any specimen. The nasal bones taper gently from front to back, with rounded posterior margins that extend well behind the premaxillae. Viewed from above, the zygomatic arches converge anteriorly from the squamosal roots without a conspicuous widening at the level of the orbits. The jugals are moderately deep with distinct postorbital processes in all examined material. The dorsolateral contours of the braincase are only slightly (INPA 2587) to moderately (INPA 2586 and 677) sculpted by the origin of the temporalis muscles. The left and right temporalis scars are widely separated and are not joined middorsally to form a sagittal crest in any specimen.

The incisive foramina are short and almost completely contained in the premaxillae (INPA 2586), or longer and penetrating between the maxillae posteriorly (INPA 2587, 677); the left and right foramina are completely separated by a bony septum in INPA 2586, but the septum is incomplete and both foramina are recessed in a common fossa in the other two specimens. The posterior diastema is marked by shallow and widely separated lateral sulci. Although the palatal bridge between the toothrows has a weakly developed central keel and shallow lateral gutters anterior to M1, the posterior palate is more-or-less smooth. The mesopterygoid fossa extends slightly anterior to the point of contact between M2 and M3 in the holotype, but not in either paratype. Small sphenopalatine vacuities (ca. 1 mm in diameter) per-

forate the bony roof of the mesopterygoid fossa in INPA 677, but not in INPA 2586 (the mesopterygoid region of INPA 2587 is too damaged to score confidently for this trait). The alisphenoid is completely ossified, such that the sphenopterygoid canal is enclosed laterally and the buccinator-masticatory foramen and the foramen ovale are separate. The auditory bullae are large (ca. 17 mm) inflated capsules that contact the base of the paroccipital process on each side. The dorsal roof of the external auditory meatus has a weakly developed bony ridge in two specimens (INPA 677 and 2587) but not in INPA 2586.

The coronoid process of the mandible is well-developed in all examined specimens.

*Dentition*—The dentition is qualitatively similar to that of the remaining species of the *vestitus* group, but the toothrows of INPA 2586 and INPA 677 are remarkably small (table 4). The upper incisors are strongly procumbent and deeply pigmented (orange).

COMPARISONS: *Coendou roosmalenorum* can be distinguished unambiguously from other species of the *vestitus* group by a unique combination of characters, the most salient of which are tabulated for easy reference (table 5). Externally, *roosmalenorum* resembles *vestitus* and *pruinus* by its long, dense dorsal fur and nonspinous ventral pelage, but it differs from both of those species in details of fur coloration (grayish or brownish versus blackish), in body size (much smaller, as indicated by hindfoot measurements), and by its conspicuously longer tail. Other external characters provide different patterns of taxonomic contrasts. Like *vestitus*, *roosmalenorum* has only bicolored cranial quills, whereas at least some cranial quills are tricolored in all examined specimens of *pruinus*. Like *pruinus*, however, *roosmalenorum* has tricolored bristle-quills, whereas the bristle-quills of *vestitus* are bicolored. In craniodental traits, *roosmalenorum* differs from *vestitus* in palatal sculpturing, alisphenoid ossification, bullar size, mandibular morphology, and in many additional (but subtler) details. From *pruinus*, *roosmalenorum* differs craniodentally by its relatively much larger bullae, but other osteological contrasts between these taxa are harder to assess due to the wide range of var-

iation among referred specimens. For example, the contrast in rostral morphology between some exemplar crania of *pruinus* (e.g., MCZ 18738; fig. 8) and *roosmalenorum* (e.g., INPA 2586; fig. 14) is striking, but other specimens that we could have chosen to represent each species (e.g., FMNH 140260 [*pruinus*] and INPA 677 [*roosmalenorum*]) are much more similar in this character. Average (or modal) character differences between *roosmalenorum* and *pruinus*, however, include dental size (*roosmalenorum* has smaller molars), mesopterygoid penetration between the tooththrows (deeper in *roosmalenorum*), mesopterygoid fenestration (sphenopalatine vacuities are better developed in *roosmalenorum*), and nasal/frontal sinus inflation (perhaps more frequent in *roosmalenorum*).

Although *Coendou roosmalenorum* and *C. ichillus* are both long-tailed species, they differ markedly in external appearance, most notably in dorsal fur length (long versus short, respectively), density (dense versus sparse), and color (gray or brown versus blackish); in addition, whereas the quills of *roosmalenorum* are only dark at the extreme tips, those of *ichillus* are much more extensively pigmented. Other trenchant external differences include size (*roosmalenorum* is smaller, as evidenced by hindfoot measurements), and ventral pelage composition (coarse banded hairs in *ichillus*, woollier in *roosmalenorum*). The sum of such contrasts is sufficiently striking that it is unlikely that these species could be confused in the field by competent observers. By contrast, cranial differences between *roosmalenorum* and *ichillus* are harder to identify given the small samples at hand. Although it is possible that the morphology of the nasal/frontal sinuses (perhaps more frequently inflated in *roosmalenorum*), zygomatic arches (perhaps more rounded in *ichillus*), and the mesopterygoid roof (perhaps more frequently fenestrated in *roosmalenorum*) might have some diagnostic value alone or in combination, larger samples are clearly needed to assess such modal differences.

Body weight data suggest that *Coendou roosmalenorum* is one of the smallest living erethizontids, but the adult holotype (INPA 2586, 600 g) may have been emaciated (see



TABLE 5  
Morphological Comparisons Among Four Species of the *Coendou vestitus* Group<sup>a</sup>

<i>vestitus</i>	<i>pruinus</i>	<i>ichillus</i>	<i>rosmalenorum</i>
Hindfoot 56–63 mm.	Hindfoot 58–63 mm.	Hindfoot 58–59 mm.	Hindfoot 53 mm.
Tail very short (ca. 50% of head-and-body length).	Tail short (ca. 60% of head-and-body length). <sup>b</sup>	Tail long (ca. 80% of head-and-body length).	Tail long (ca. 90% of head-and-body length).
Dorsal fur blackish, long and dense, concealing most quills.	Dorsal fur frosted-blackish; long and dense, concealing most quills.	Dorsal fur blackish; short and very sparse, not concealing any quills.	Dorsal fur grayish or brownish; long and dense, concealing most quills.
All quills bicolored on head and body; body quills with short dark tips.	Some quills tricolored on head; body quills with short dark tips.	Some quills tricolored on head; body quills one-third to one-half dark.	All quills bicolored on head and body; body quills with very short dark tips.
Bristle-quills bicolored, with long dark tips.	Bristle-quills tricolored, with long pale tips.	Bristle-quills tricolored, with long pale tips.	Bristle-quills tricolored, with long pale tips.
Ventral pelage consisting of dense wool and guard hairs.	Ventral pelage consisting of dense wool and guard hairs.	Ventral pelage consisting of clustered spinous hairs and sparse wool.	Ventral pelage consisting of sparse wool and guard hairs.
Palatal bridge with strong median keel and deep lateral gutters.	Palatal bridge without strong median keel or deep lateral gutters.	Palatal bridge without strong median keel or deep lateral gutters.	Palatal bridge without strong median keel or deep lateral gutters.
Mesopterygoid fossa usually penetrates between M2s; sphenopalatine vacuities present.	Mesopterygoid fossa usually penetrates between M3s; sphenopterygoid vacuities absent.	Mesopterygoid fossa penetrates to M2/M3 contact; sphenopalatine vacuities absent.	Mesopterygoid fossa penetrates to M2/M3 contact; sphenopalatine vacuities variable.
Alisphenoid incompletely ossified (sphenopterygoid canal unenclosed, buccinator-masticatory and oval foramina confluent).	Alisphenoid completely ossified (sphenopterygoid canal enclosed, buccinator-masticatory and oval foramina separate).	Alisphenoid completely ossified (sphenopterygoid canal enclosed, buccinator-masticatory and oval foramina separate).	Alisphenoid completely ossified (sphenopterygoid canal enclosed, buccinator-masticatory and oval foramina separate).
Auditory bullae small, uninflated, not contacting paroccipital processes.	Auditory bullae small, uninflated, not contacting paroccipital processes. <sup>b</sup>	Auditory bullae large, inflated, contacting paroccipital processes.	Auditory bullae large, inflated, contacting paroccipital processes.
Coronoid process of mandible absent.	Coronoid process of mandible well-developed.	Coronoid process of mandible well-developed.	Coronoid process of mandible well-developed.

<sup>a</sup>Tabulated character information simplified and condensed from text accounts, which should be consulted for additional information.

<sup>b</sup>Tabulated descriptors apply to the typical morphology of montane populations; other referred material may differ (see text).

below), and the other weighed specimen (INPA 2587, 800 g) is a subadult. By comparison, 42 postjuvenile<sup>4</sup> specimens of *C. melanurus* weighed by Richard-Hansen et al. (1999) ranged from 1500 to 2600 g, and 70 specimens of *C. prehensilis* weighed by the same authors ranged from 1800 to 5800 g.

VARIATION: With only three specimens in hand, the possible significance of observed character variation in *Coendou roosmalenorum* is hard to evaluate. Although certain differences observed in our material are plausibly attributable to ontogeny, others are not. An example of the former is the rostrum of INPA 677 (an old adult), which is relatively and absolutely larger than the rostrums of INPA 2587 (a subadult) and INPA 2586 (a young adult). An example of the latter is the grayish dorsal fur of INPA 2586 versus the brownish fur of the other two skins.

Although we examined specimens from both banks of the Rio Madeira, a major Amazonian tributary and one of the largest rivers in the world, the similarities uniting our material as a taxon diagnosable from other forms of *Coendou* are more persuasive than the few differences that segregate our left-bank examples (INPA 2586, 2587) from our right-bank singleton (INPA 677). However, the more inflated sinuses of the former specimens are perhaps noteworthy in this context, as is the extremely small tooththrow of the latter. Future studies based on larger samples from both populations will doubtless contribute to a more informed judgement about their taxonomic status.

NATURAL HISTORY: According to information kindly summarized for us by Marc van Roosmalen, the holotype was captured by caboclos at Novo Jerusalem when it emerged from a felled tree. Kept alive as a pet, the animal was released every evening to roam freely in the surrounding terra firme forest, returning at dawn to sleep throughout the day in a box underneath its owners' house. This individual subsequently lived for several months in captivity at Manaus, where it maintained its nocturnal habits (sleeping in

a tree hole by day), and ate a variety of seeds and fruit. It died of unknown causes while seeming perfectly healthy.

The paratype from Santa Maria was shot at night by a caboclo boy who mistook its eyeshine for that of a paca (*Cuniculus paca*) as it was walking on the ground no more than 100 m from the shore of Lago Matupiri, a blackwater lake. The local vegetation was tall "seringal" forest growing on terra firme with abundant rubber trees (*Hevea brasiliensis*), Brazil nuts (*Bertholletia excelsa*), ingas (*Inga* spp.), and other trees known locally as orelha de macaco (*Enterolobium schomburgkii*), bacuri (*Rheedia macrophylla*), and taperebá (*Spondias mombin*).

The paratype from 49 km E Porto Velho was taken in the course of faunal rescue efforts at the Samuel hydroelectric dam site, but the ecological circumstances of its capture are unknown.

REMARKS: Three specimens (two males and one female) collected at the Samuel hydroelectric dam site (49 km E of Porto Velho on BR 364) were identified by Naiff et al. (1996) as the "Black dwarf porcupine" of Emmons (1990: 199), a taxon that is technically known as *Coendou nycthemera* Olfers (see Voss and Angermann [1997], who explain that *C. koopmani* Handley and Pine is a junior synonym). One of those specimens (the female, INPA 677) is a paratype of *C. roosmalenorum*, but the whereabouts of the two male specimens is unknown. It is difficult to understand how INPA 677 could possibly have been mistaken for Emmons' black dwarf porcupine, which was clearly described by her as having entirely spiny blackish upperparts. One possible explanation is that the two missing specimens from Naiff's series were, in fact, *C. nycthemera* (which is known to occur on the right bank of the lower Madeira near Borba), and that INPA 677 was mistaken for a conspecific long-furred juvenile. Whether or not this conjecture is correct, future collectors should be alert to the possibility that two small species of *Coendou* may be sympatrically or parapatrically distributed along the right (east) bank of the Madeira.

SPECIMENS EXAMINED: **Brazil**—Amazonas, Novo Jerusalem (INPA 2586), Santa Maria

<sup>4</sup> Richard-Hansen et al. (1999) judged their weighed specimens to be adults, but those authors did not employ dental criteria to assess maturity. Most subadult porcupines are externally indistinguishable from adults.

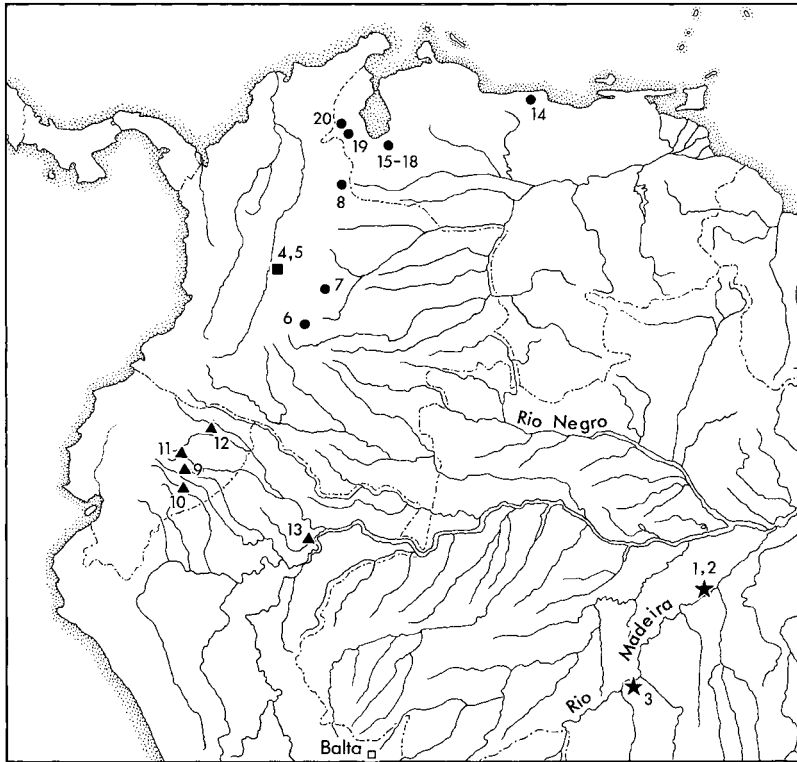


Fig. 15. Collection localities and sight records for members of the *Coendou vestitus* species group. Numbered symbols for *C. vestitus* (■), *C. pruinosis* (●), *C. ichillus* (▲), and *C. roosmalenorum* (★) are keyed to entries in the accompanying gazetteer (appendix). The geographic configuration of localities 9–11 is approximate because specimen labels provide only river names. Western Amazonia (as defined by Voss and Emmons, 1996: 8) is that part of the basin west of the Rio Negro and the Rio Madeira. The Cashinahua Indian village of Balta is the source of an unvouchered record of small porcupines discussed in the text.

(INPA 2587); Rondônia, 49 km E Porto Velho (INPA 677).

#### DISCUSSION

All published inventories of rainforest mammals from western Amazonia (i.e., west of the Negro and Madeira rivers; see fig. 15) have hitherto reported only one species of porcupine at any given site (Patton et al., 1982; Janson and Emmons, 1990; Woodman et al., 1991; Hutterer et al., 1995; Peres, 1999; Fleck and Harder, 2000; Patton et al., 2000). Invariably, the single reported species is a large (3–5 kg) animal that has been identified as either *Coendou prehensilis* or *C. bicolor*. By contrast, small (1–2 kg) porcupines have long been known to occur sympatrically with *C. prehensilis* in eastern Amazonia (Ca-

bani, 1848; Walsh and Gannon, 1967; Pine, 1973; Husson, 1978; George et al., 1988; Handley and Pine, 1992; Vié, 1999; Voss et al., 2001).<sup>5</sup>

This report provides the first definite records of small *Coendou* from western Amazonia, where they are almost certainly sympatric with one or more large (*prehensilis*-like) porcupines. Why these diminutive species, and perhaps others of the same size

<sup>5</sup> The small porcupine that occurs throughout northeastern Amazonia is *Coendou melanurus* (see Voss et al., 2001), but this species has often been misidentified as *C. insidiosus* (e.g., by Husson, 1978). The small species of southeastern Amazonia is *C. nycthemera*, previously known by its junior synonym *C. koopmani* (see Voss and Angermann, 1997). The large porcupines currently known as *C. prehensilis* are unrevised and may represent a complex of closely related species.

class, have remained undetected for so long begs explanation. Two hypotheses merit discussion.

First, it is possible that small porcupines have very restricted distributions in western Amazonia and simply do not occur in regions where most faunal inventory projects have been carried out. By this interpretation, *Coendou ichillus* and *C. roosmalenorum* might survive as relicts of a formerly widespread ancestral taxon that went extinct elsewhere for ecological reasons. Perhaps *vestitus*-like porcupines are narrowly adapted to some particular type of forest that occurs only along the middle Rio Madeira and in eastern Ecuador. Unfortunately, vegetational mapping in this region is currently too coarse to test such ad hoc conjectures.

Alternatively, the absence of other records of small porcupines from western Amazonia could be an artifact of inadequate collecting efforts in this still largely inaccessible region. Although impressive faunal sampling efforts have been made at a few sites, small porcupines appear to be difficult to detect by any known inventory method (e.g., those described by Voss and Emmons, 1996). Instead, most collected specimens appear to have been encountered by chance. To the best of our knowledge, none have ever been taken in traps, and few have been taken by deliberately hunting for them at night.

Only anecdotal evidence is available to support the hypothesis that small porcupines are actually widespread in western Amazonia. For example, Cashinahua hunters at Balta (in Departamento Ucayali, Peru: fig. 15) told A. L. Gardner about a morphologically distinctive small porcupine that occurs sympatrically with *Coendou bicolor* at that locality, but only the latter was collected (see Voss and Emmons, 1996: appendix 9). Because Balta is far from the known range of both *C. ichillus* and *C. roosmalenorum*, it is not surprising that the small porcupine described by the Cashinahua is clearly not referable to either taxon (A. L. Gardner, personal commun.).

We predict that more new species of small *Coendou*, perhaps including some that belong to other clades than the *vestitus* group, will eventually be found in western Amazonia, but opportunities to collect specimens of

these elusive animals are so infrequent that none should be ignored. In particular, faunal rescue operations following hydroelectric dam construction afford unique opportunities for wildlife researchers to examine large numbers of porcupines (Walsh and Gannon, 1967; Mascarenhas and Puerto, 1988; Vié, 1999). Regrettable as such events are from other perspectives, each is a rare chance to gain valuable information about erethizontid diversity.

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## APPENDIX: Gazetteer

Below are listed all localities at which examined specimens referable to the *Coendou vestitus* group have been collected. Italicized place names are those of the largest political divisions (state/department/province) within countries; boldface identifies collection localities as they appear in the text of this report. Unless recorded by the collector, geographic coordinates (degrees and minutes latitude/longitude) and elevation above sea level in meters (m) are provided in square brackets with a cited secondary source for these data. The species name, name(s) of collector(s), and date(s) of collection are separated from the locality entry by a colon. Numbered localities are plotted on the accompanying map (fig. 15).

## BRAZIL

1. *Amazonas*, **Novo Jerusalem** on Lago Matupirizinho (5°33'28"S, 61°07'20"W, <100 m): *Coendou roosmalenorum* (coll. M. G. M. van Roosmalen and T. van Roosmalen, 23 November 1996).
2. *Amazonas*, **Santa Maria** on Lago Matupiri (5°33'15"S, 61°15'47"W, <100 m): *Coendou roosmalenorum* (coll. M.G.M. van Roosmalen and T. van Roosmalen, April 1997).
3. *Rondônia*, **49 km E Porto Velho** [coordinates unknown, ca. 100 m]: *Coendou roosmalenorum* (coll. "Equipe J. Arias," 9 July 1985).

## COLOMBIA

4. *Cundinamarca*, **Quipile** [4°45'N, 74°32'W; DMA, 1988], W of Bogotá: *Coendou vestitus* (coll. Nicéforo María, February 1925).
5. *Cundinamarca*, **San Juan de Río Seco** [4°51'N, 74°38'W, 1303 m; Paynter and Traylor, 1981]: *Coendou vestitus* (coll. Nicéforo María, 1923–1925).
6. *Meta*, [Serranía de] La Macarena, **Pico Rengifo** [ca. 3°06'N, 73°55'W; Paynter and

Traylor, 1981], 4500 ft: *Coendou pruinosus* (coll. K. von Sneider, 2 April 1957).

7. *Meta*, **Villaviciencio** [4°09'N, 73°37'W; Paynter and Traylor, 1981], 500 m: *Coendou pruinosus* (coll. R. M. Gilmore, 15 June 1939).
8. *Norte de Santander*, **Alturas de Pamplona** [7°23'N, 72°39'W, 2340 m; Paynter and Traylor, 1981]: *Coendou pruinosus* (coll. Nicéforo María, July 1950).

## ECUADOR

9. *Pastaza*, **Río Conambo** [ca. 1°52'S, 76°47'W, ca. 300 m at village of Conambo; Paynter and Traylor, 1977]: *Coendou ichillus* (coll. C. Estrella, 18 February 1966).
10. ? *Pastaza*, **Río Pastaza** [no other locality data]: *Coendou ichillus* (coll. von Baumann-Roosevelt Expedition, July 1936).
11. *Pastaza*, **Río Yana Rumi** [presumably the Río Yanarumiyacu, with mouth at 1°38'S, 76°59'W; DMA, 1987]: *Coendou ichillus* (coll. R. Olalla, 19 October 1934).
12. *Sucumbíos*, La Selva Jungle Lodge (0°30'S, 76°22'W): *Coendou ichillus* (unvouchered sightings by J. E. Cadle, P. J. DeVries, L. H. Emmons, and R. S. Voss, July 1996).

## PERU

13. *Loreto*, **Iquitos region** [ca. 3°46'S, 73°15'W; Stephens and Traylor, 1983]: *Coendou ichillus*. (purchased by P. Soini, 1971).

## VENEZUELA

14. *Distrito Federal*, **Caracas** [ca. 10°30'N, 66°55'W, 917 m; Paynter, 1982]: *Coendou pruinosus* (collector unknown, ca. 1926).
15. *Mérida*, **Finca el Cumbe**, 3.5 km SW Zea [8°23'N, 71°47'W; Paynter, 1982], eleva-

- tion 1500 m: *Coendou pruinosus* (see Concepción and Molinari, 1991).
16. *Mérida, Mérida* (and localities presumably near this city including “Montaña Sierra 2100[?] m” and “Montaña del Valle 2600 m”) [ca. 8°36'N, 71°08'W]: *Coendou pruinosus* (coll. S. Briceño Gabaldón e hijos, ca. 1900–1905).
  17. *Mérida, Montañas de la Pedregosa*, elevation 2500 m [ca. 8°36'N, 71°12'W; Paynter, 1982]: *Coendou pruinosus* (coll. S. Briceño Gabaldón e hijos, 14 January 1905).
  18. *Mérida, Montañas de Tabay*, elevation 2600 m [ca. 8°38'N, 71°04'W; Paynter, 1982]: *Coendou pruinosus* (coll. S. Briceño Gabaldón e hijos, 28 January 1904).
  19. *Zulia, El Rosario* [ca. 9°09'N, 72°36'W; Handley, 1976], 48 km WNW Encontrados, 54 m: *Coendou pruinosus* (coll. A. Tuttle et al., 1 March 1968).
  20. *Zulia, Misión Tukuko* [9°50'N, 72°52'W; Voss, 1991], elevation 200 m: *Coendou pruinosus* (coll. R. S. Voss, 7 July 1986).