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Uncovering species boundaries through qualitative and quantitative morphology in the genus *Dasyprocta* (Rodentia, Caviomorpha), with emphasis in *D. punctata* and *D. variegata*

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The genus *Dasyprocta* Illiger, 1811 includes at least 13 species of medium-sized caviomorph rodents, widely distributed from Mexico to northern Argentina. Despite being abundant, largely diurnal, and easily identifiable by their external traits, the taxonomy of this genus remains poorly understood. In this work, we reviewed the taxonomy of *Dasyprocta* along the Andes and adjoining lowland areas of the western Neotropics, including samples from Mexico to northern Argentina, with emphasis on two species largely confounded—sometimes considered as synonyms—during the last century: *D. punctata* Gray, 1842 and *D. variegata* Tschudi, 1845. In the construction of our taxonomic hypotheses, we use a purely morphological approach, emphasizing qualitative and quantitative cranial features and external traits (color patterns). The results of multivariate statistical analysis and differences in color patterns support the species-level validity of *D. punctata* and *D. variegata*. Within this latter nominal form, we also include those populations from northern Argentina and eastern Bolivia that recently were referred to *D. azarae*. Based on our results, *D. punctata* (including *bellula*, *callida*, *candelensis*, *chiapensis*, *chocoensis*, *colombiana*, *dariensis*, *isthmica*, *nuchalis*, *richmondi*, *underwoodi*, *yucatanica*, and *zuliae*) extends from southern Mexico to Colombia, Ecuador, northernmost Peru, and western Venezuela, while *D. variegata* (including *azarae*, *boliviae*, and *yungarum*) is distributed from south–central Peru and southwestern Brazil to Bolivia and northwestern Argentina.

Key words: agouti, Cavioidea, Caviomorpha, *Dasyprocta*, Dasyproctidae, taxonomy

El género *Dasyprocta* Illiger, 1811 incluye al menos 13 especies de roedores caviomorfos de tamaño mediano, ampliamente distribuidas desde México hasta el norte de Argentina. A pesar de ser abundantes, mayormente diurnas y fácilmente identificables por sus rasgos externos, la taxonomía de este género sigue siendo poco clara. En este trabajo, revisamos la taxonomía de *Dasyprocta* a lo largo de los Andes y tierras bajas adyacentes del Noeotrópico occidental, incluyendo muestras desde México hasta el norte de Argentina, con énfasis en dos especies largamente confundidas (a veces consideradas sinónimos) durante el siglo pasado: *D. punctata* Gray, 1842 y *D. variegata* Tschudi, 1845. En generar nuestra hipótesis taxonómica utilizamos exclusivamente métodos morfológicos, enfatizando características craneales cualitativas y cuantitativas, así como rasgos externos (patrones de color). Los resultados del análisis estadístico multivariado y las diferencias en los patrones de color respaldan la distinción a nivel de especie entre *D. punctata* y *D. variegata*. Dentro de esta última forma nominal incluimos las poblaciones del norte de Argentina y este de Bolivia que fueron referidas recientemente como *D. azarae*. Según nuestros resultados, *D. punctata* (incluyendo *bellula*, *callida*, *candelensis*, *chiapensis*, *chocoensis*, *colombiana*, *dariensis*, *isthmica*, *nuchalis*, *richmondi*, *underwoodi*, *yucatanica* y *zuliae*) se extiende desde el sur de México hasta Colombia, Ecuador, norte de Perú y oeste de Venezuela, mientras que *D. variegata* (incluyendo *azarae*, *boliviae* y *yungarum*) se distribuye desde el centro-sur de Perú y el suroeste de Brasil hasta Bolivia y el noroeste de Argentina.

Palabras clave: agouti, Cavioidea, Caviomorpha, *Dasyprocta*, Dasyproctidae, taxonomía

The genus *Dasyprocta* Illiger, 1811 includes at least 13 species of medium-sized (2–6 kg) cursorial caviomorph rodents commonly known as agoutis (Gilbert and Lacher 2016). In spite of being abundant, widely distributed mammals in the Neotropics, and easily identifiable by their external traits, the taxonomic situation of most of their nominal forms remains poorly understood (Emmons and Feer 1997; Patton and Emmons 2015). In his enlightening treatise about the order Rodentia, Ellerman (1940) wrote: "How many species [of *Dasyprocta*] should be recognized I am not prepared to say, but it seems clear that far too many are at present standing, and many could be reduced to the rank of subspecies. It is to be hoped that someone will attempt a revision of this genus, which is much needed." More than 70 years later, the situation remains mostly unchanged: despite some revisionary and geographically restricted contributions (e.g., Ojasti 1972; Voss et al. 2001; Teta and Lucero 2016; Ramírez-Chaves et al. 2018), the taxonomy of the genus *Dasyprocta* still is somewhat chaotic (Patton and Emmons 2015). At least partially, this situation is the result of the almost nonexistent differences in cranial anatomy between species and our lack of knowledge about intra- and interspecific variability (e.g., Ojasti 1972; Matson and Shump 1980; Voss et al. 2001; Feijó and Langguth 2013).

Two species of *Dasyprocta*, *D. punctata* Gray, 1842 and *D. variegata* Tschudi, 1845, largely were confounded during most of the 20th century (Patton and Emmons 2015). For some authors, *D. punctata* includes *D. variegata* in its synonymy, being distributed throughout Central America and western South America (e.g., Cabrera 1961; Woods and Kilpatrick 2005), while others restrict the name *punctata* to the Central American populations and use the name *variegata* for those in South America (e.g., Allen 1915; Tate 1935; Ellerman 1940). A third group of researchers employed *punctata* to encompass the agoutis of Central America and northwestern South America and *variegata* for those of southern Perú, eastern Bolivia, southwestern Brazil, and northwestern Argentina (e.g., Emmons and Feer 1997). More recently, Patton and Emmons (2015) restricted the concept of *variegata* even more, using this name only for Peruvian and adjoining Bolivian and Brazilian populations, referring animals from eastern Bolivia and northwestern Argentina to *D. azarae* Lichtenstein, 1823. Any case, none of these taxonomic hypotheses has been tested within the framework of a quantitative morphological study of large samples of individuals and with an extensive geographic coverage. To further complicate this scenario, there are a plethora of nominal forms, sometimes recognized as valid under a trinomial classification, alternatively included as synonyms of *D. punctata* or *D. variegata* (see Table 1 for a synthesis). The case of *D. punctata* is paradigmatic in this sense because up to 10 subspecies were recognized by Hall (1981) for Central America alone.

In the absence of other kinds of evidence (e.g., molecular markers), we hypothesize that a careful study of a large series of individuals using multivariate statistical analyses could contribute to solve, at least partially, some of the taxonomic uncertainties that surround this genus. In this contribution, we evaluate the taxonomic status of *D. punctata* and *D. variegata*, two taxa widely distributed in the Neotropical region. Our approach was based both in the study of qualitative and quantitative skull characters and, to lesser extent, color patterns. This study includes one of the largest samples analyzed to date, in terms of both specimen number and geographic coverage, encompassing several holotypes and topotypes of most nominal forms.

Materials and Methods

Species definition.—Qualitative and quantitative morphological approaches in search of both morphological discontinuities and diagnosability remain as a common procedure for species delimitation (e.g., Pacheco et al. 2014; Woodman and Timm 2016; Ruedas 2017; Teta et al. 2017). The three main reasons for this assumption are as follows: (i) morphological variability usually is more reduced within samples of a same species than among samples of different species; (ii) qualitative and quantitative discontinuities in morphological traits frequently are the result of population isolation; and (iii) because morphological discontinuities are at least partially genetically defined, they imply distinct genetic pools and as such, the existence of independent lineages (see do Prado and Percequillo 2017).

Specimens.—We examined 391 individuals assigned to the genus *Dasyprocta*, although only 264 individuals were measured (see Supplementary Data SD1 for details). Specimens document 140 localities of occurrence in 12 countries (Fig. 1) and are housed in the following museums and biological collections: AMNH, American Museum of Natural History (New York, USA); CML, Colección de Mamíferos de la Facultad de Ciencias Naturales e Instituto Miguel Lillo (Tucumán, Argentina); ICN, Colección de Mamíferos Alberto Cadena García, Instituto de Ciencias Naturales, Universidad Nacional de Colombia (Bogotá, Colombia); FMNH, Field Museum of Natural History (Chicago, USA); MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina); MNHNP, Museo Nacional de Historia Natural del Paraguay (Asunción, Paraguay); MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima, Perú); and USNM, United States National Museum of Natural History (Washington, DC, USA).

Features of pelage.—Adult specimens of each recognized geographical group (see definition below, under "Geographic variation") were analyzed qualitatively for the following pelage characters: (i) overall color pattern; (ii) color and

Table 1.—Main taxonomic hypothesis for *Dasyprocta punctata* Gray 1842 and *D. variegata* Tschudi 1845, including the arrangement of subspecies proposed by different authors. *Dasyprocta punctata zuliae* Ojasti 1972, not included in this table, was considered into the synonymy of *D. punctata* by Emmons and Feer (1997) and Patton and Emmons (2015). *Dasyprocta p. candelensis* J. A. Allen 1915 was originally described as a subspecies of *D. fuliginosa* Wagler 1832.

	Ellerman (1940)	Tate (1935)	Cabrera (1961)[a]	Hall (1981)[b]	Emmons and Feer (1997)	Patton and Emmons (2015)
Central America	*D. p. punctata*	*D. p. punctata*		*D. p. punctata*	*D. punctata*	*D. punctata*
	D. p. chiapensis	*D. p. chiapensis*		*D. p. chiapensis*	*D. punctata*	*D. punctata*
	D. p. dariensis	*D. p. dariensis*		*D. p. dariensis*	*D. punctata*	*D. punctata*
	D. p. isthmica	*D. p. isthmica*		*D. p. isthmica*	*D. punctata*	*D. punctata*
	D. p. nuchalis	*D. p. nuchalis*		*D. p. nuchalis*	*D. punctata*	*D. punctata*
				D. p. pallidiventris	*D. punctata*	*D. punctata*
	D. p. richmondi	*D. p. richmondi*		*D. p. richmondi*	*D. punctata*	*D. punctata*
	D. p. underwoodi	*D. p. underwoodi*		*D. p. underwoodi*	*D. punctata*	*D. punctata*
	D. p. yucatanica	*D. p. yucatanica*		*D. p. yucatanica*	*D. punctata*	*D. punctata*
	D. callida	*D. callida*		*D. p. callida*	*D. punctata*	*D. punctata*
	D. ruatanica	*D. p. ruatanica*		*D. ruatanica*	*D. punctata*	*D. punctata*
				D. p. bellula	*D. punctata*	*D. punctata*
South America	*D. v. boliviae*	*D. v. boliviae*	*D. p. boliviae*		*D. variegata*	*D. azarae*
	D. v. chocoensis	*D. v. chocoensis*	*D. p. chocoensis*		*D. punctata*	*D. punctata*
	D. v. colombiana	*D. colombiana*	*D. p. colombiana*		*D. punctata*	*D. punctata*
	D. v. urucuma	*D. v. urucuma*	*D. p. urucuma*		*D. variegata*	*D. azarae*
	D. v. variegata	*D. v. variegata*	*D. p. variegata*		*D. variegata*	*D. variegata*
	D. v. yungarum	*D. v. yungarum*	*D. p. yungarum*		*D. variegata*	*D. azarae*
	D. v. zamorae	*D. v. zamorae*	*D. p. zamorae*		*D. punctata*	*D. punctata*
	D. f. candelensis	*D. f. candelensis*	*D. f. candelensis*		*D. punctata*	*D. punctata*
	D. pandora	*D. pandora*	*D. p. pandora*		*D. punctata*	*D. punctata*

[a]This author provides a list of synonymies only for South American nominal forms.
[b]This author provides a list of synonymies only for Central American nominal forms.

relative length of rump hairs. To facilitate descriptions and comparisons among samples, most pelage traits were analyzed by indexing the gradations in color patterns, following a procedure similar to that of Musser (1968). Because we do not use any objective method to measure the differences in coloration, we restrict our observations mostly to color patterns.

Skull anatomy and measurements.—Anatomical terminology follows Ojasti (1972), Cherem and Ferigolo (2012), and Feijó and Langguth (2013). To find diagnostic traits among populations, cranial characters in adult individuals that showed variation among samples were coded and compared on the basis of their range of variation.

Sixteen craniodental measurements were recorded from each specimen using a digital caliper to the nearest 0.01 mm: total length of the skull (TLS); condylo–incisive length (CIL); interorbital constriction (IOC); greatest zygomatic breadth (ZB); breadth across paraorbitary process (BP); length of nasals (NL); width of nasals (NW); length of frontals (FL); width of upper incisors (IW); length of upper diastema (DL); length of upper toothrow (TRL); length of palate (PL); breadth of palate at the level of the upper premolar (BPPM); breadth across the paraoccipital processes (BPP); and length of tympanic bullae (TBL). In the definition of these measurements, we follow Teta and Lucero (2016; Fig. 2).

Geographic variation.—Geographic variation was described over a distance of about 8,500 km: from México southeastward through Central America to Panamá, and western South America, including Colombia, Venezuela, Ecuador, Peru, Bolivia, eastern Paraguay, and northern Argentina. Studied specimens were pooled into 31 major groups (Fig. 1), based on their geographical proximity, absence of geographical barriers among localities, environmental continuity among samples, and lack of obvious differences in overall size or shape of the skull or external coloration among individuals (for a similar procedure, see Musser 1968; Brennand et al. 2013; Chiquito et al. 2014; Libardi and Percequillo 2016). Because several nominal forms were involved within this study, we did not construct groups including samples previously referred to different subspecies. Based on this rationale, the following groups were defined: arnw, northwestern Argentina (*n* = 3); boce, central Bolivia (*n* = 12); bone, northeastern Bolivia (*n* = 13); coce, central Colombia (*n* = 3); coch, Choco, Colombia (*n* = 5); conc, north–central Colombia (*n* = 8); cone, northeastern Colombia (*n* = 21); conw, northwestern Colombia (*n* = 8); cosc, south–central Colombia (*n* = 3); cosw, southwestern Colombia (*n* = 4); crpa, Pacific slope, Costa Rica (*n* = 8); ecua, western Ecuador (*n* = 13); hnpa, Pacific slope, Honduras–Nicaragua (*n* = 5); hond, Atlantic slope, Honduras (*n* = 5); mexa, Atlantic slope, México (*n* = 6); mexc, Isla de Cozumel, México (n = 1); mexp, Pacific slope México (*n* = 2); nica, Atlantic slope, Nicaragua (*n* = 9); paaz, Península del Azuero, Panamá (*n* = 1); pabt, Isla Colón, Bocas del Toro, Panamá (*n* = 12); pace, central Panamá (*n* = 14); paic, Isla Cébaco, Panamá (*n* = 2); pane, northeastern Panamá (*n* = 3); panw, northwestern Panamá (*n* = 15); pase, southeastern Panamá (*n* = 24); pasm, San Miguel, Isla del Rey, Archipiélago de las Perlas, Panamá (*n* = 1); pasj, Isla San José, Archipiélago de las Perlas, Panamá (*n* = 5); pasw, southwestern Panamá (*n* = 4); pere, southeastern Peru (*n* = 25); perw, southwestern Perú (*n* = 6); vewe, western Venezuela (*n* = 10). Correspondence among geographical groups and subspecies is provided in Table 2. Finally, we also include a sample of *D. azarae* (azar, *n* = 13) from northeastern Argentina

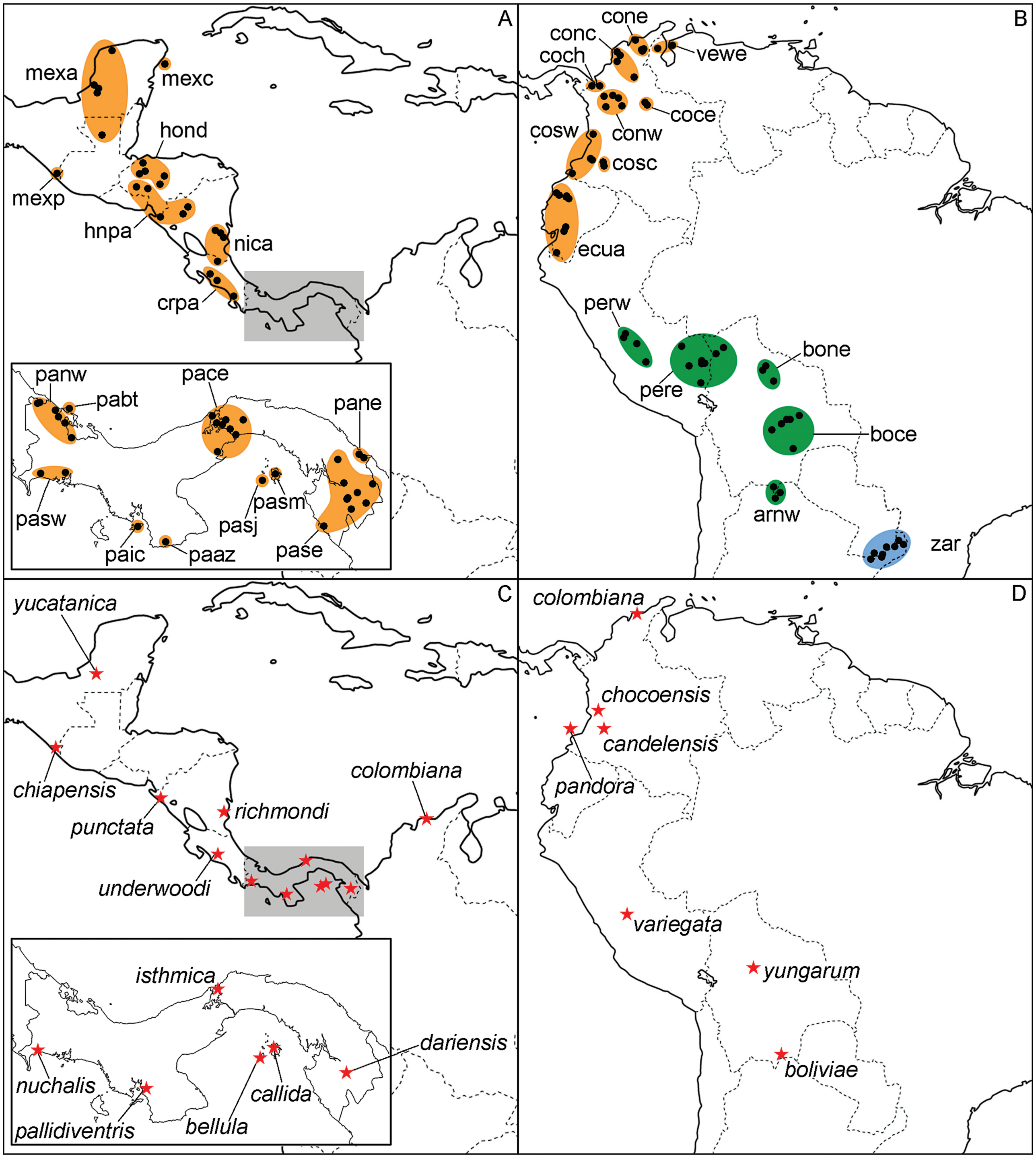

Fig. 1.—Map of Central America (A, C) and northern and central South America (B, D), indicating the collecting localities of the examined specimens of *Dasyprocta* (A, B) and type localities of the nominal forms currently included in *D. punctata* and *D. variegata* (depicted with stars; C, D). Shaded areas in (A) and (B) shown the groupings of localities that constitute the geographical samples analyzed; colors as follows: light blue ellipse, *D. azarae*; orange ellipses, *D. punctata*; green ellipses, *D. variegata*. See Materials and Methods for an explanation of the abbreviations.

and eastern Paraguay to corroborate the quantitative distinction of this species from those populations at arnw, boce, and bone (see also Teta and Lucero 2016).

Statistical analyses.—Standard descriptive statistics (mean, minimum and maximum values, standard deviation) were provided for each geographical group (Appendix 1). Multivariate statistical procedures were restricted to adult individuals ($N = 264$; age classes IV–VII, sensu Matson and Shump 1980). Principal component analysis (PCA) and discriminant function analysis (DFA) were computed using the previously defined 16 craniodental variables. PCA was undertaken using log10-transformed data to normalize the contribution of each

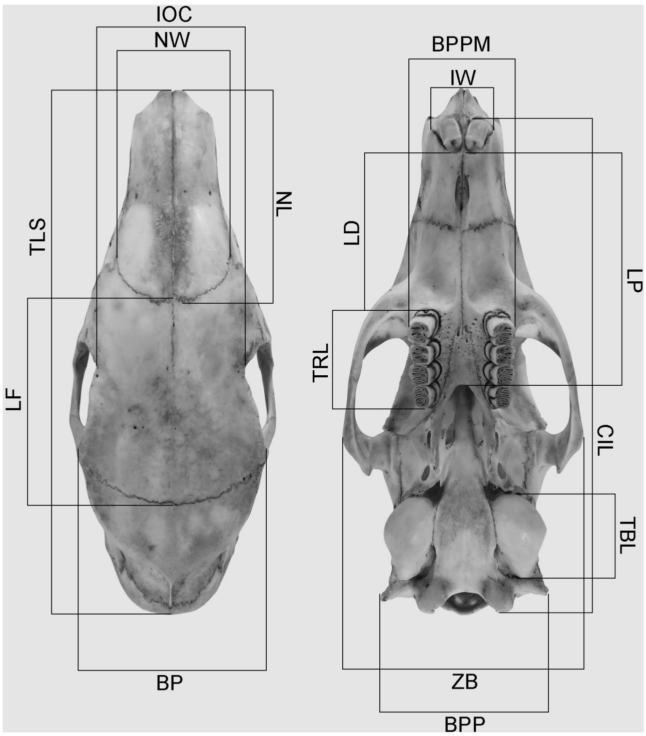

Fig. 2.—Skull of *Dasyprocta* indicating the measurements used in this study. Refer to Materials and Methods for measurement acronyms.

measurement to the total variance. Only groups with $n > 3$ were used. Principal components (PCs) were extracted from the variance–covariance matrix (Strauss 2010). DFA was used to determine which variables contribute to differentiate between geographical groups (Strauss 2010). Multivariate analysis of variance (MANOVA) was carried out to test the statistical significance of differences between *D. azarae* ($n = 13$), *D. punctata* (Central America; $n = 115$), *D. punctata* (northwestern South America; $n = 75$), and *D. variegata* ($n = 61$). Samples of *D. punctata* from Central and northwestern South America were considered separately, to test previous hypotheses about the taxonomy of these agoutis (cf. Tate 1935). Because previous authors did not detect differences between sexes (e.g., Ojasti 1972), males and females were combined for subsequent morphometric analyses. All statistical analyses were carried out using the software PAST v. 2.17 (Hammer et al. 2001).

Results

Features of pelage.—Two main types of color patterns were defined (here identified as "A" and "B"), with a large variation in coat color within each of them (Fig. 3). Populations from Central America in Guatemala, Honduras, México, and the Atlantic slope of Costa Rica and northwestern Panamá, as well as those of South America in northwestern Argentina, Bolivia, Peru, and parts of Colombia (e.g., north–central, northwest) are almost uniformly colored (pattern "A"; Fig. 3 [see also Supplementary Data SD2: Fig. S1]). In these animals, coloration varies from reddish brown (northeastern Costa Rica, Honduras, Pacific slope of México, northwestern Panamá, some individuals in north–central Colombia), to orangish (southeastern Perú, central and northeastern Bolivia, northwestern Argentina), yellowish-brown to gray-yellow (Atlantic slope of México, Guatemala, some individuals in northeastern Bolivia), or brownish (e.g., south–central Colombia, southwestern Peru, south–central Panamá). In this pattern, dorsal fur is finely grizzled with black throughout when viewed closely; nape and rump hairs do not differ from remainder of upper parts; hairs of rump are scarcely or not elongated into an overhanging fringe; and chin, throat, midline of venter, and inguinal region, usually are lighter than dorsum (Fig. 3 [see also Supplementary Data SD2: Fig. S1]). Populations from northwestern Argentina, Bolivia, and Perú have the head, midline of back, and sometimes the rump usually darker than the sides. Finally, some animals from Perú (e.g., Junín) are blackish frosted with white and yellow (Fig. 3).

Table 2.—Correspondence between the geographical groups defined in this study and the subspecies traditionally recognized within *Dasyprocta punctata* Gray 1842 and *D. variegata* Tschudi 1845.

Geographical group	Species/subspecies
azar	*D. azarae*
coce	*D. p. zuliae*
coch	*D. v. chocoensis*
conc	*D. v. colombiana*
cone	*D. v. colombiana*
conw	*D. v. colombiana*
cosc	*D. p. candelensis*
cosw	*D. v. chocoensis*
crpa	*D. p. underwoodi*
ecua	Not determined
hnpa	*D. p. punctata*
hond	*D. p. richmondi*
mexa	*D. p. yucatanica*
mexc	*D. p. yucatanica*
mexp	*D. p.chiapensis*
nica	*D. p. richmondi*
paaz	*D. p. pallidiventris*
pabt	Not determined
pace	*D. p. isthmica*
paic	Not determined
pane	*D. p. dariensis*
panw	*D. p. isthmica*
pasw	*D. p. dariensis*
pasm	*D. p. callida*
pasj	*D. p. bellula*
vewe	*D. p. zuliae*
arnw	*D. v. yungarum*
boce	*D. v. boliviae*
bone	*D. v. boliviae*
pere	*D. v. variegata*
perw	*D. v. variegata*

In contrast, populations from the Pacific slope of Costa Rica, southwestern and southeastern Panamá, central, central–eastern and southwestern Colombia, western Ecuador, and western Venezuela, have a more colorful pelage pattern, usually with large, overhanging rump hairs (pattern "B"; Fig. 3). These animals have brown to blackish heads and foreparts, finely grizzled with yellow or olivaceous; the midbody forward of rump is covered by a band of more or less bright orangish to yellowish banded hairs in some populations (e.g., Pacific

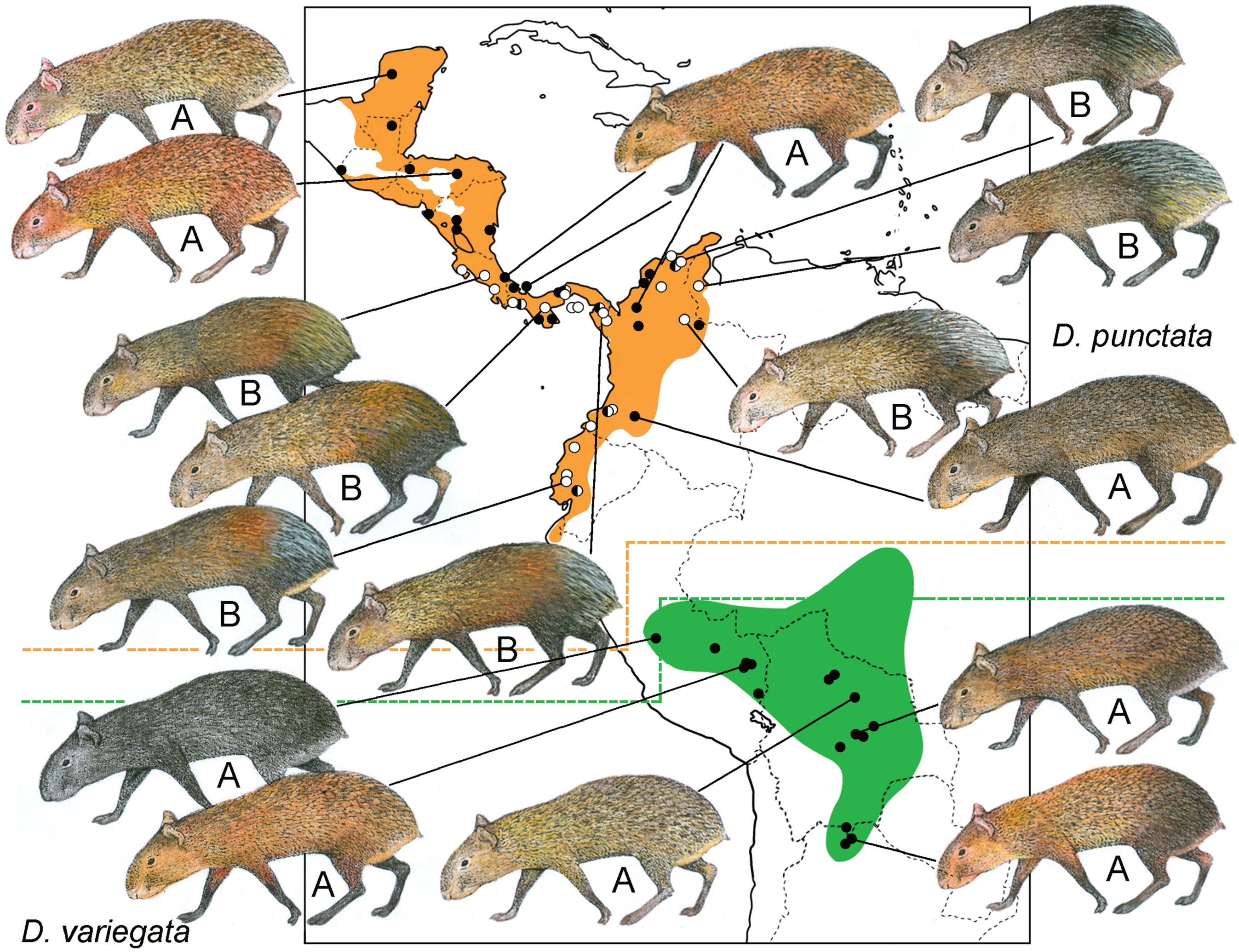

Fig. 3.—Geographic variation of coat color and color pattern of some studied samples of *Dasyprocta* (based on specimens housed at AMNH, FMNH, and USNM). Patterns "A" (black circles) and "B" (white circles) are described in the Results section. Individuals with an intermediate pattern between "A" and "B" are depicted on the map by a black/white circle.

slope of Costa Rica, central and southeastern Panamá), while in others the entire midbody forward of rump is similar to the foreparts or blackish (e.g., central and northeastern Colombia, western Venezuela) (Fig. 3). The chin and inguinal region usually are whitish and the belly is brown. As a characteristic of this pattern, rump hairs are long and black, with long yellow to white tips in some individuals, forming a conspicuous fringe that overhangs the rump (Fig. 3).

Individuals with intermediate color patterns and with more or less differentiated overhanging rump hairs were found through central, southwestern and southeastern Panamá, northeastern and southwestern Colombia and western Ecuador (Fig. 3 [see also Supplementary Data SD2: Fig. S1]).

Qualitative cranial characters.—The samples studied were remarkably uniform in skull anatomy, but with some variation in their overall size (see below), and in shape and size of the incisive foramina (Figs. 4 and 5). With respect to this feature, two main types could be recognized within the samples referred to *D. punctata* and *D. variegata* (Fig. 5). First, specimens from Central America and northwestern South America (= *D. punctata*) have small and relatively short, posteriorly divergent openings that do not reach the maxillo-premaxillary suture and usually lacks posterolateral flanges (sensu Patton 1987). In contrast, those animals from Peru, Bolivia, and northwestern Argentina (= *D. variegata*) have relatively larger openings, usually reaching the maxillo-premaxillary suture, parallel sided, and frequently with prominent posterolateral flanges. Despite the presence of some variation in this feature across individuals and populations, this character was useful to sort the studied specimens in two main groups.

Quantitative cranial characters.—Craniodental measurements, including mean, *SD*, and range, are summarized in Appendix 1. PCA revealed that all variables were positively correlated with the 1st PC (PC1 = 47.5%), suggesting that size is an important source of variation among individuals (Fig. 6A and B; Table 3). Despite a marked overlap of specimens from different samples in the first three PCs, four main morphometric groups can be recognized along them. The first group is composed of samples from Central America (= *D. punctata*, in part), including crpa, hnpa, hond, mexa, nica, pabt, pace,

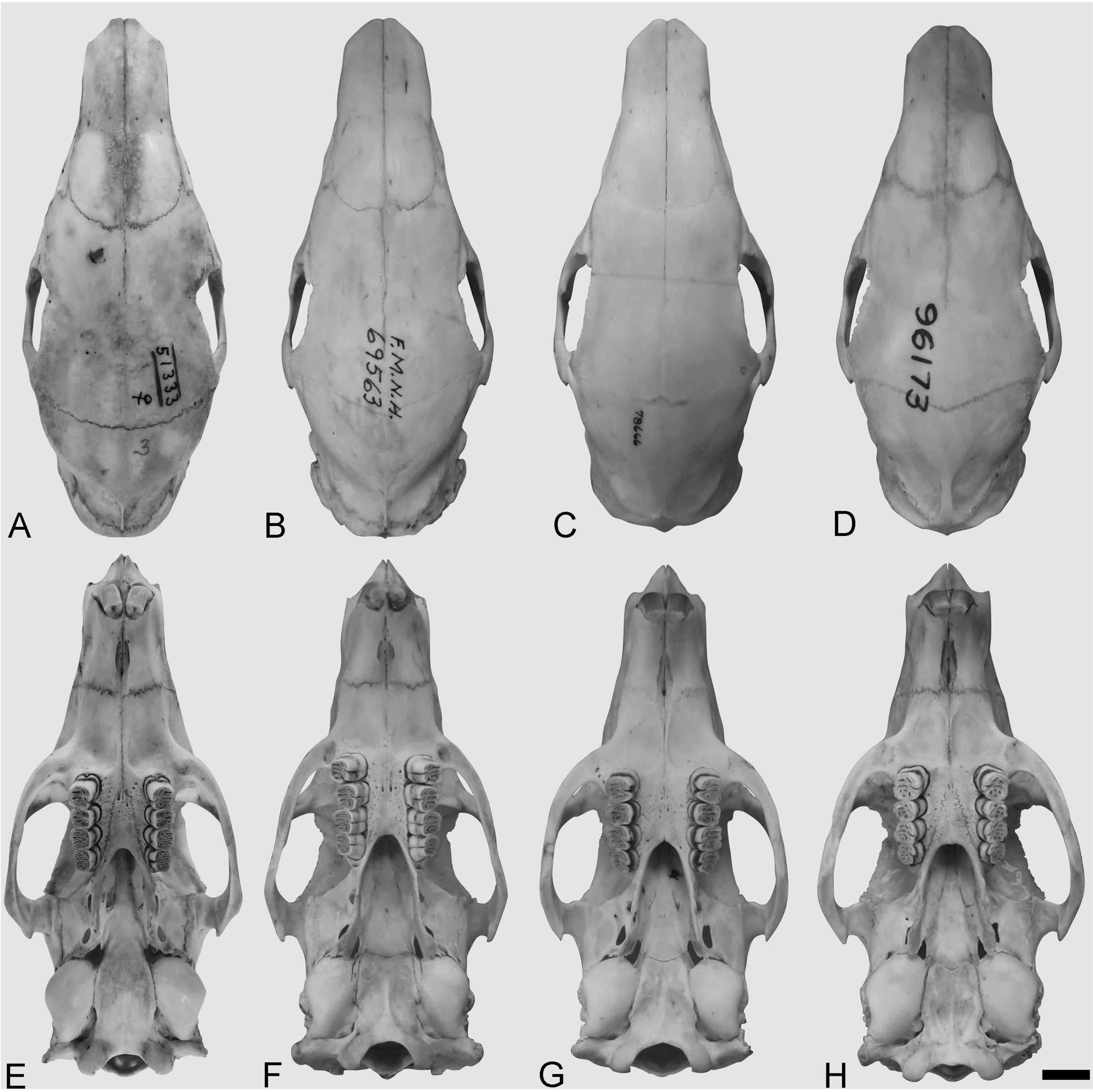

Fig. 4.—Dorsal (A–D) and ventral (E–H) views of the skulls of selected individuals of *Dasyprocta punctata* (A, E; USNM 51333, holotype of *D. p. richmondi* [Nicaragua]; B, F; FMNH 69563 [Colombia]) and *D. variegata* (C, G; FMNH 78666 [Peru]; D, H; FMNH 96173 [Bolivia]). Specimens are not to scale to facilitate comparisons.

panw, pase, pane, pasj, and pasw; the second corresponds to northwestern South America (= *D. punctata*, in part), including coce, coch, conc, cone, conw, cosc, cosw, ecua, and vewe; the third corresponds to west–central South America and encompasses arnw, boce, bone, pere, and perw (= *D. variegata*); and the fourth is only represented by azar (= *D. azarae*). The first PC primarily contributes to separate the first and fourth groups from the second and third groups, while the PC2 (12.6%) segregates the first group from the fourth group and PC3 (7.5%) separates the second group from the third group. PC1 was strongly related to NL and BPP; the highest positive loading in PC2 and PC3 correspond to IW and BPP and NW and NL, respectively.

Results of DFA (Fig. 6C and D; Table 3) depict a size gradient along the first discriminant function (38.1%), in which samples from Central America on the one hand (crpa, hnpa, hond, mexa, nica, pabt, pace, panw, pase, pasj, and pasw) and northwestern South America on the other (coce, coch, conc, cone,

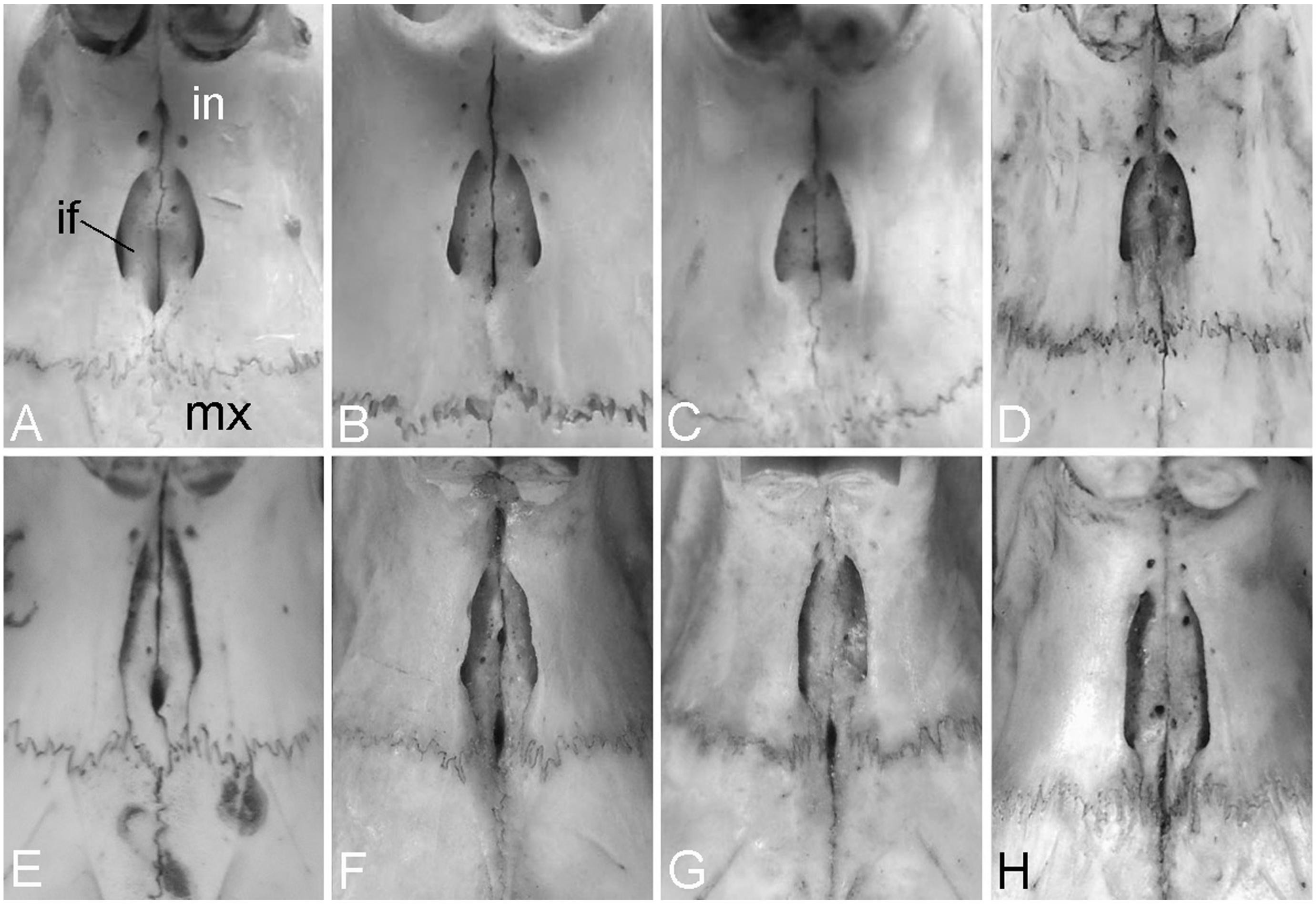

Fig. 5.—Representative incisive foramina (if) in *Dasyprocta punctata* (above; from left to right: (A) AMNH 36470 [Ecuador]; (B) AMNH 66725 [Ecuador]; (C) AMNH 36584 [Ecuador]; (D) USNM 179076 [Panamá]) and *D. variegata* (below; from left to right: (E) MUSM 15736 [Perú]; (F) MACN–Ma 33.149 [Bolivia]; (G) MACN–Ma 33.148 [Bolivia]; (H) MACN–Ma 15600 [Argentina]). The incisive (in) and maxillary (mx) bones are identified.

conw, cosc, cosw, ecua, and vewe), are placed at the extremes of the morphospace, while those of arnw, boce, bone, pere, and perw are intermediate. The sample referred as azar is separated from the others along the CV2 (17.4%). Plot of individual scores along the CV1 and CV3 repeated this pattern, although azar mostly was superimposed with Central American samples. Highest positive loadings on CV1 correspond to NL and NF. On CV2, most loadings were negative, with BPP reaching the lowest negative value. Finally, highest absolute scores on CV3 correspond to ZB and BPPM, being both negative.

The MANOVA showed an overall significant intergroup variation (λ = 0.3206, df = 30, 474, $P < 0.001$). Posterior pairwise comparisons using Bonferroni corrected *P* values showed that all groups (*D. azarae*, *D. punctata* [Central America], *D. punctata* [northwestern South America], and *D. variegata*) differed significantly from each other.

Discussion

Characters of the skin and skull for many years have served as the foundation of mammalian classification. However, as has been demonstrated by different authors, species of *Dasyprocta* have a large intraspecific variation in coat color and color patterns and are remarkably similar in their skull architecture (e.g., Ojasti 1972; Emmons and Feer 1997). Based on the morphological (qualitative and quantitative) and geographical evidence presented in this contribution, we recognize *D. punctata* Gray, 1842 (including the groups coce, coch, conc, cone, conw, cosc, cosw, crpa, ecua, hnpa, hond, mexa, nica, pabt, pace, panw, pase, pane pasj, and pasw; and vewe) and *D. variegata* Tschudi, 1845 (i.e., arnw, boce, bone, pere, and perw) as two valid taxa without geographic overlap between them (Fig. 7). Despite some variation in external coloration and quantitative cranial traits, both species display discrete morphological differences in the size and shape of their incisive foramina (Figs. 4 and 5). That the samples we measured are not quite completely separated in our multivariate procedures is not unexpected because previous contributions have documented that dasyproctids are remarkably conservative in their cranial anatomy (e.g. Teta and Lucero 2016; Teta 2019; Campo et al. 2020). Quantitative variation is especially large within *D. punctata* (Figs. 3 and 6; Appendix 1), suggesting that this taxon could represent a species complex. However, because most of that variation is clinally structured, with a moderate

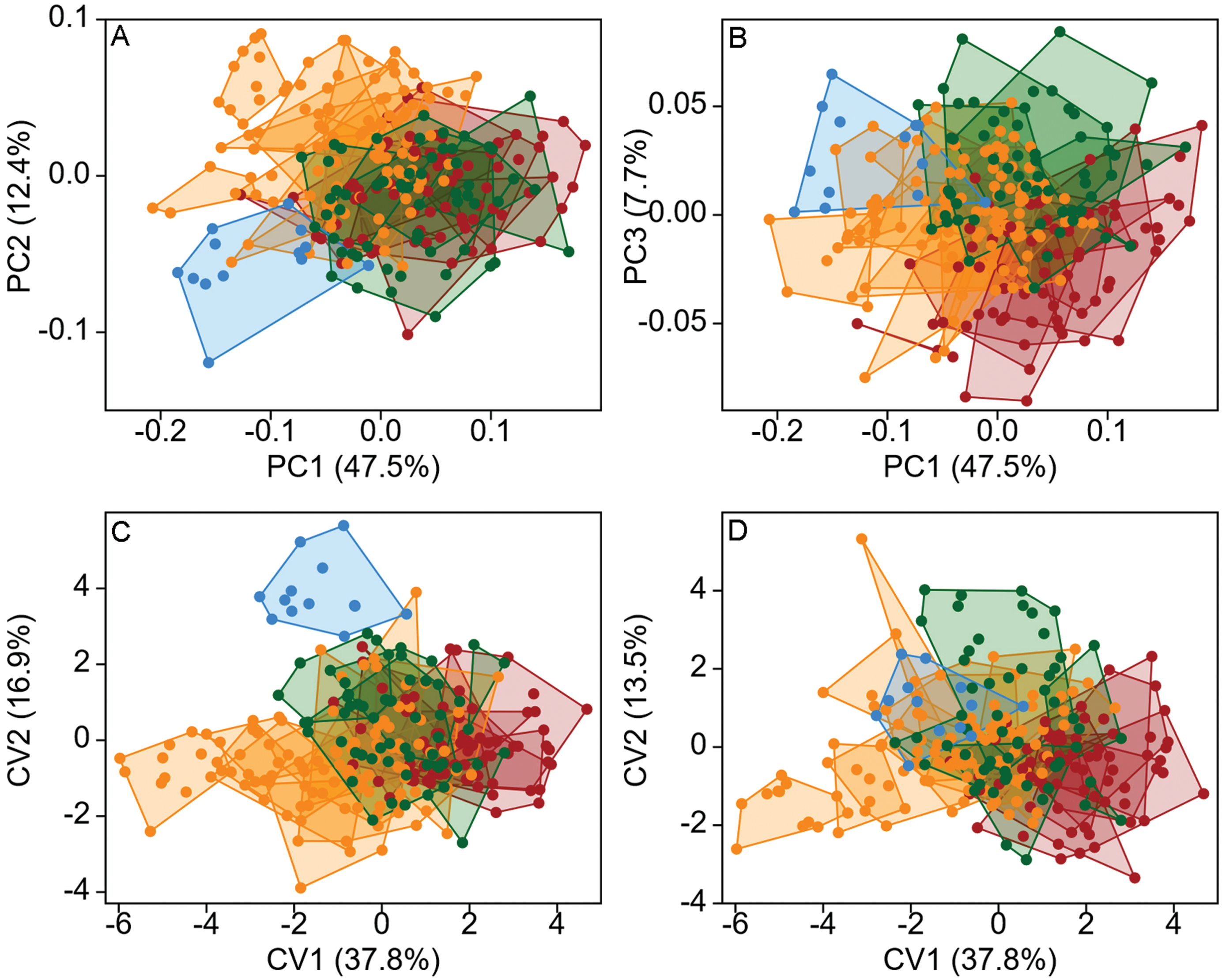

Fig. 6.—Projections of specimen scores of adult specimens of *Dasyprocta* for principal components 1 and 2 (A) and 1 and 3 (B) and canonical variates 1 and 2 (C) and 1 and 3 (D) extracted from the discriminant function analyses of 27 geographical groups. Colors as follows: light blue dots, *D. azarae*; orange dots, *D. punctata* (Central America); red dots, *D. punctata* (northwestern South America); green dots, *D. variegata*.

Table 3.—Results of principal component analyses (first, second, and third rows) and discriminant function analysis (fourth, fifth, and sixth rows) performed on 27 geographical groups of adult specimens of *Dasyprocta*. See Materials and Methods for explanation of variable abbreviations.

	PC 1	PC 2	PC 3	CV1	CV2	CV3
TLS	0.24784	0.12164	0.08213	0.00676	−0.00668	0.00084
CIL	0.23126	0.09956	0.03585	0.00651	−0.00470	−0.00031
IOC	0.22092	0.13777	0.03638	0.00415	−0.00479	−0.00392
ZB	0.22488	0.03795	0.035207	0.00616	−0.00193	−0,17567
BP	0.20254	0.16545	−0.00936	0.00412	−0.00680	−0.00155
BPP	0.34376	0.39684	−0.33076	0.00850	−0.01730	−0.00663
NL	0.45381	−0.54454	−0.41023	0.01957	0.00477	−0.00300
NW	0.17014	−0.00696	0.55214	0.00343	−0.00132	0.00826
LF	0.30581	−0.18958	−0.01553	0.01091	−0.00528	0.00703
IW	0.24876	0.44618	−0.06071	0.00551	−0.00504	−0.01247
LP	0.22107	−0.42058	0.09878	0.01116	0.00056	0.00602
LD	0.23971	0.19936	0.19109	0.00536	−0.00282	−0.00254
BPPM	0.23104	−0.04138	0.03169	0.00505	−0.00308	−0,08482
TRL	0.22983	0.03888	0.07419	0.00671	−0.00282	−0.00265
TBL	0.15391	−0.13626	0.59165	0.00169	0.00568	−0.00104
Eigenvalue	0.00577	0.00151	0.00093	3.4531	1.5474	12.375
% variance	47.54	12.39	76.77	37.81	16.95	13.55

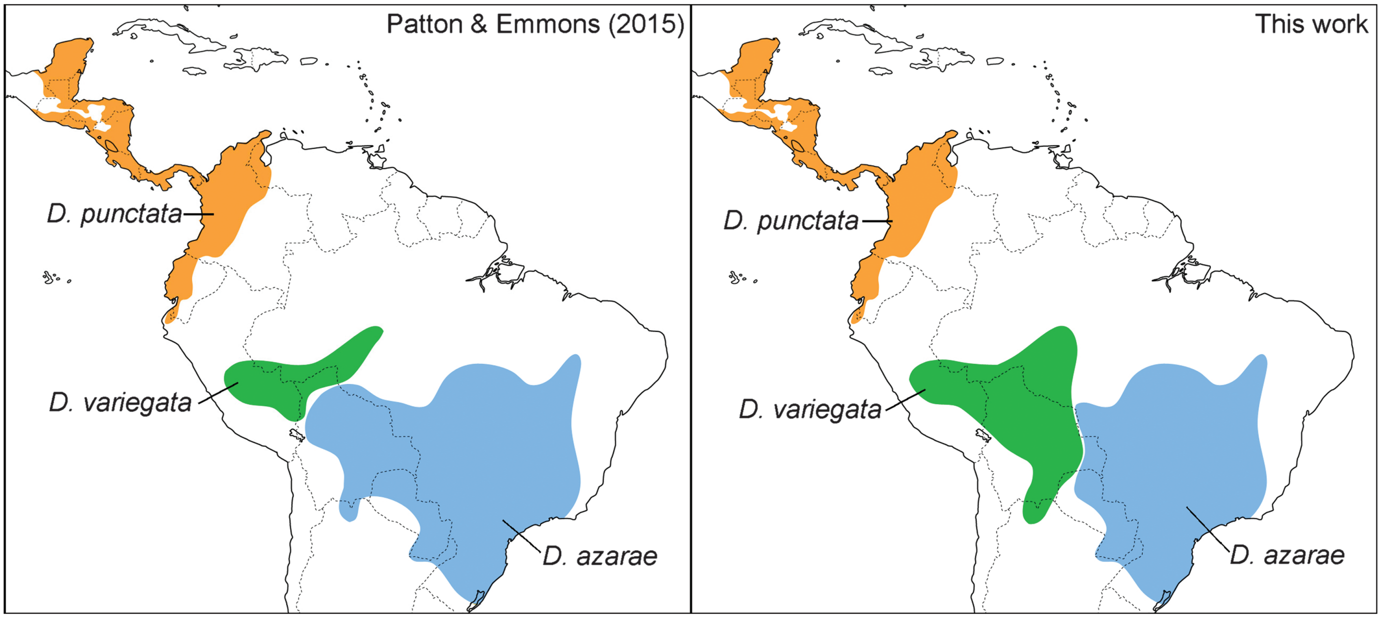

Fig. 7.—Approximate distributional limits of *Dasyprocta azarae*, *D. punctata*, and *D. variegata*, based on Patton and Emmons (2015) and this work.

and gradual increase in skull size from north to south (Fig. 6; Supplementary Data SD2: Fig. S2), we prefer to be conservative, maintaining all populations from Central America and northwestern South America within a polytypic *D. punctata*. Finally, we corroborate the findings of Teta and Lucero (2016) who, using a much smaller sample, referred populations from northwestern Argentina (arnw) and Bolivia (boce, bone) to a same morphotype, morphologically closer to *D. variegata* and distinguishable from *D. azarae*.

Following Emmons (1990), Emmons and Feer (1997), and Patton and Emmons (2015), we restrict the name *punctata* Gray to agoutis of Central America and northwestern South America, including populations of cis-Andean distribution on the Pacific coast of Colombia, Ecuador, and northernmost Peru, the Caribbean coast of Colombia and northwestern Venezuela, and the inter-Andean valleys west of the Cordillera Oriental of Colombia. In this sense, our concept of *punctata* is equal to the group of "Central American agouties" of Tate (1935), including in its synonymy the names *bellula* Kellogg, 1946; *callida* Bangs, 1901; *candelensis* J.A. Allen, 1915; *chiapensis* Goldman, 1913; *chocoensis* J. A. Allen, 1915; *colombiana* Bangs, 1898; *dariensis* Goldman, 1913; *isthmica* Alston, 1876; *nuchalis* Goldman, 1917; *richmondi* Goldman, 1917; *underwoodi* Goldman, 1931; *yucatanica* Goldman, 1913; and *zuliae* Ojasti, 1972 (see Appendix 2). Although *D. punctata* exhibit two main color patterns (Fig. 3 [see also Supplementary Data SD2, Fig. S1]), no definite geographic trends were detected in these traits and some individuals and populations could be considered intermediate between the extremes (see Results; Fig. 3). According to Emmons and Feer (1997) and Patton and Emmons (2015), populations from the Pacific slope from southern Mexico to Panamá, Colombia, and Ecuador mostly correspond to the pattern "A," while those along Atlantic slope from Costa Rica, Panamá, and northern Colombia correspond to the pattern "B". However, we also found pattern "A" along the Atlantic coast of northeastern Costa Rica, northwestern Panamá, and north–central Colombia, and pattern "B" in several localities along the Pacific slope of Costa Rica, Panamá, Colombia, and Ecuador (Supplementary Data SD2: Fig. S1).

As do Emmons and Feer (1997), we restrict the name *variegata* Tschudi (including *boliviae* Thomas, 1917 and *yungarum* Thomas, 1910; see Appendix 2) to agoutis that inhabit the lowland rainforests of southern Peru, western Brazil, eastern Bolivia, and northwestern Argentina. This view partially differs from the hypothesis of Patton and Emmons (2015), who excluded from *variegata* populations from eastern Bolivia and northwestern Argentina, instead referring them to *D. azarae*. However, as documented by Teta and Lucero (2016), *D. azarae* clearly is distinguishable from Argentinian (northwest) and Bolivian populations, both in terms of qualitative and quantitative morphological traits. The eastern limits of *D. variegata* and the western boundary of *D. azarae* are unclear; additional specimens are much needed to more accurately delineate the distributional range of both nominal forms, especially from Chacoan areas in eastern Bolivia and western Paraguay (cf. Tabilo et al. 2020). *Dasyprocta variegata* is nearly sympatric with *D. kalinowskii* Thomas, 1897, a poorly known montane species. Thomas (1897) described this species from southern Peru (type locality "Idma, Valley of Santa Ana, Cuzco, Peru. Alt. 4600 feet."), highlighting the peculiar coloration of its long rump hairs, which are white with black tips (vs. black basally and yellowish to whitish tipped in Peruvian *variegata*). However, we examined at least one specimen of *variegata* from Bolivia (MACN–Ma 50.3003), in which the rump hairs are similar to those supposedly diagnostic of *kalinowskii* (i.e., white basally and blackish distally). A small sample of five individuals collected in the general area of the type locality of *kalinowskii* housed at the AMNH (AMNH 75961, 75963, 75964, 76617, 76619) has both types of color patterns of rump hairs, being in most other characters indistinguishable from other Peruvian representatives of *variegata*. In sum, an adequate characterization of *D. kalinowskii* is much needed, especially to compare it with *D. variegata* and, following Patton and Emmons (2015), with *D. fuliginosa*.

As in the case of other Neotropical rodents described during 1850–1950, most nominal forms of *Dasyprocta* were defined on the basis of few specimens under a limited knowledge of its intra- and interspecific variability. In fact, most nominal taxa currently included within *punctata* were described between 1850 and 1950, under the paradigm of the "trinomial revolution in zoology" (see Mallet 2007), resulting in a profusion of multiple subspecific forms mostly based on subtle differences in coat color or size (Alston 1876; Bangs 1898, 1901; Goldman 1913, 1917, 1931; Allen 1915; Bole and Aldrich 1937; Kellogg 1946). Additional samples still are much needed, particularly for some geographic areas (e.g., northern Central America; northern Bolivia, western Paraguay). A major obstacle to illuminating the taxonomy of *Dasyprocta* is the almost complete absence of molecular data (cf. Upham and Patterson 2015). The inclusion of DNA sequences could play an important role by providing and independent source of information to test the hypothesis advanced here and, more generally, the suggested allopatry between species of *Dasyprocta* (Ramírez-Chaves et al. 2018). Unfortunately, medium- to large-sized rodents are scarcely represented by recent specimens (i.e., collected in the last 10–20 years) in biological collections, perhaps as a result of requiring difficult to handle methods of capture (e.g., firearms). In addition, medium- to large-sized rodents, such as agouties, pacas, or maras, are more charismatic than the smaller ones (mice and rats), generating a fiercer public opposition and criticism aimed at biological collecting (Patterson 2002). At least preliminarily, "ancient" DNA sequences obtained from dried skins could be a promising option to seek for cryptic diversity within *Dasyprocta*. Because this genus has a wide distribution, occurring in forested areas at low to middle elevations from México to northern Argentina, it represents a good model to understand the historical biogeography of some endangered ecoregions, such as those that are part of the Amazonia or the Atlantic forest.

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Supplementary Materials

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Table S1. List of the specimens examined in this study and their localities. See materials and methods for a reference of the acronyms.

Supplementary Data SD2.—Supplementary figures.

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Appendix 1.—Summary statistics (mean, SD, range) of cranial measurements (in mm) of adult samples (*n*) of *Dasyprocta*. See Materials and Methods for explanation of the abbreviations of geographical groups and cranial measurements

	arnw					boce					bone					coce				
	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.
TLS	3	111.55	2.91	109.35	114.85	13	110.57	4.05	101.82	117.31	14	107.81	2.92	102.55	111.61	3	106.41	1.85	104.28	107.65
CIL	3	96.32	1.48	94.74	97.67	13	94.46	3.57	88.23	99	14	92.7	2.59	87.53	96.1	3	90.15	0.66	89.45	90.77
IOC	3	32.85	3.29	30.58	36.63	13	30.93	2.04	25.98	33.68	14	29.2	1.75	26.54	32.89	3	28.3	2.49	25.44	29.98
ZB	3	52.59	2.36	50.31	55.02	13	51.19	2.19	47.53	54.3	14	49.53	2.05	47.09	53.87	3	46.45	1.65	44.55	47.5
BP	3	41.65	2.73	39.49	44.72	13	41.58	1.78	38.39	44.34	14	40.34	1.5	38.14	43.21	3	39.49	2.04	37.32	41.38
BPP	3	35.94	1.39	34.35	36.9	13	37.25	2.28	31.3	40.32	14	35.76	1.3	33.21	37.43	3	35.87	1.23	34.88	37.25
NL	3	42.72	1.12	41.5	43.7	13	41.15	4.07	32.91	46.97	14	40.13	1.52	37.32	42.34	3	40.96	0.92	39.9	41.55
NW	3	23.31	0.23	23.07	23.52	13	21.45	1.48	18.47	23.45	14	19.91	1.33	17.29	21.58	3	20.2	1.28	18.78	21.26
LF	3	39.67	0.13	39.54	39.8	13	41.4	2.74	37.24	46.72	14	40.41	1.52	37.08	43.55	3	36.17	1.08	35.39	37.4
IW	3	12.2	0.06	12.14	12.25	13	11.97	0.5	11.07	12.75	14	11.57	0.58	10.7	12.35	3	11.42	0.57	10.76	11.76
LP	3	43.8	1.7	41.93	45.26	13	42.04	2.12	38.18	44.35	14	41.63	1.44	38.37	44.48	3	38.13	0.76	37.25	38.6
LD	3	29.79	0.9	28.91	30.71	13	28.77	1.69	26.56	31.62	14	27.98	1.34	25.24	30.37	3	25.74	0.49	25.2	26.15
BPPM	3	21.69	0.87	20.85	22.59	13	20.47	1.57	16.95	22.96	14	19.7	0.85	17.78	21.13	3	19.42	0.68	18.96	20.21
TRL	3	21.33	0.38	21.01	21.75	13	19.1	0.84	17.32	20.08	14	18.57	0.94	16.59	19.82	3	18.61	1.12	17.45	19.68
TBL	3	18.01	0.92	16.97	18.69	13	18.28	1.08	16.56	19.83	14	17.67	0.77	16.37	19.05	3	15.17	0.51	14.59	15.47

	coch					conc					cone					conw				
	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.
TLS	5	112.5	4.61	106.72	119.42	8	115.06	1.92	111.47	117.24	21	114.23	5.73	101.87	123.87	8	121.49	17.39	109.67	163.37
CIL	5	96.08	3.65	92.97	101.44	8	98.17	1.51	95.37	100.27	21	98.48	4.67	88.07	106.83	8	98.62	2.78	94.39	103.17
IOC	5	30.44	2.2	28.77	34.25	8	30.6	1.23	29.09	32.03	21	31.68	1.65	29.03	34.15	8	31.11	0.94	29.29	32.25
ZB	5	49.94	2.17	47.28	52.29	8	50.84	1.66	48.91	52.9	21	51.41	1.85	47.74	54.82	8	50.68	2.04	46.85	53.08
BP	5	41.55	1.59	39.45	43.78	8	41.43	0.72	40.34	42.38	21	41.88	2.26	37.15	46.55	8	42.59	1.28	40.14	44.7
BPP	5	37.2	2.82	34.83	41.69	8	38.46	1.38	36.65	40.74	21	38.19	1.64	34.75	41.09	8	37.44	0.91	36.55	39.3
NL	5	42.93	2.08	40.65	45.46	8	45.61	1.34	43.86	47.63	21	44.93	2.65	39.11	48.25	8	45.89	2.44	42.2	50.45
NW	5	22.04	2.24	20.24	25.23	8	21.78	1.19	20.12	23.21	21	22.34	1.64	20.11	25.54	8	22.57	1.95	19.72	24.6
LF	5	40.95	2.04	38.59	44.11	8	39.86	1.85	36.87	42.37	21	40.63	3.32	34.41	47.64	8	41.36	1.96	38.23	44.33
IW	5	11.97	1.19	10.75	13.69	8	12.37	0.49	11.63	13.01	21	12.33	0.83	10.93	14.42	8	12.39	0.73	11.42	13.65
LP	5	41.8	2.75	39.2	45.99	8	42.91	1.06	41.19	44.36	21	44.36	2.26	38.83	47.95	8	43.14	1.53	41.28	45.5
LD	5	27.92	2.3	25.6	31.67	8	29	0.77	28.2	30.4	21	30.01	1.81	26.79	33.57	8	29.45	1.55	27	31.7
BPPM	5	20	0.8	18.97	20.86	8	20.74	0.89	19.43	21.66	21	20.95	1.08	18.84	23.34	8	20.36	1.12	19.23	22.05
TRL	5	20.47	1.17	19.49	22.18	8	20.55	1.53	18.08	22.97	21	20.46	1.21	18.1	23.14	8	19.79	1.4	18.14	21.96
TBL	5	16.76	0.8	16.22	18.18	8	17.03	1.11	15.42	18.36	21	16.87	1.02	15.19	19.16	8	16.71	1.06	14.71	18.09

	cosc					cosw					crpa					ecua				
	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	v	Mean	SD	Min.	Max.
TLS	3	110.64	1.14	109.67	111.9	4	114.1	7.31	106.61	121.3	8	110.77	5.32	101.4	116.16	13	109.58	3.52	104.61	113.93
CIL	3	94.86	0.93	94.2	95.92	4	97.7	4.55	93.42	102.2	8	94.02	4.74	85.53	98.84	13	94.21	2.92	90	98.66
IOC	3	31.8	0.91	31.16	32.84	4	30.66	1.18	29.56	31.99	8	30.3	1.36	28.78	32.71	13	30.79	1.54	28.79	34.14
ZB	3	50.22	0.46	49.87	50.74	4	50.14	2.09	47.43	52.51	8	49.38	3.59	42.94	52.63	13	49.73	1.98	46.51	52.24
BP	3	41.24	1.99	38.97	42.68	4	41.97	1.61	39.73	43.26	8	41.27	1.56	38.32	43.64	13	41.3	1.24	38.5	43.31
BPP	3	36.99	0.7	36.47	37.78	4	36.97	1.49	35.22	38.62	8	37.22	2.13	33.59	39.73	13	36.25	1.94	33.2	40.28
NL	3	41.41	0.82	40.47	41.92	4	42.8	4	37.53	46.57	8	41.53	3.71	35.11	45.33	13	42.07	2.16	38.09	44.8
NW	3	22.52	0.46	22.23	23.05	4	22.17	1.67	20.65	24.36	8	19.35	0.99	17.87	20.76	13	21.44	0.93	20.16	22.88
LF	3	40.29	1.39	38.79	41.52	4	41.54	3.14	37.94	45	8	41.27	2.16	37.87	43.8	13	38.5	2.04	35.28	42.17
IW	3	12.36	0.85	11.78	13.33	4	11.87	0.28	11.52	12.2	8	11.38	0.6	10.7	12.52	13	12.19	0.8	10.63	13.43
LP	3	42.3	1.31	41.12	43.71	4	42.89	3.02	40.1	46.44	8	42.65	2.53	38.16	45.86	13	40.56	2.87	33.4	45.42
LD	3	27.78	0.8	26.93	28.53	4	29.6	2.37	26.74	32.05	8	28.86	2.24	25.15	31.11	13	28	3.11	19.91	33.77

Appendix 1.—Continued

BPPM	3	20.4	0.48	19.88	20.83	4	20.73	1.64	19.03	22.77	8	19.49	1.67	17.08	22.52	13	19.67	1.08	18.16	22.06
TRL	3	20.05	0.15	19.92	20.22	4	19.11	1.49	17.5	20.52	8	18.82	0.8	17.64	19.86	13	18.85	1.28	16.23	20.39
TBL	3	16.64	1.04	15.54	17.6	4	17.09	0.47	16.59	17.69	8	16.35	0.53	15.67	17.41	13	16.68	0.94	15.17	17.95

	hnpa					hond					mexa					mexc				
	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n				
TLS	5	111.37	2.39	109.56	114.95	5	107.81	2.99	102.48	109.51	6	107.93	3.2	103.95	111.68	1	106.04			
CIL	5	94.06	1.17	92.18	95.26	5	91.16	2.96	86.04	93.74	6	91.72	2.89	88.62	95.75	1	91.32			
IOC	5	30.58	1.33	29.34	32.55	5	29.62	1.69	26.71	31.12	6	29.56	1.38	27.8	30.92	1	29.59			
ZB	5	49.48	1.61	47.09	51.16	5	48.84	0.99	47.45	50.05	6	47.96	2.91	45.6	53.23	1	45.98			
BP	5	41.55	1.43	39.72	43.14	5	40.02	1.04	38.7	41.15	6	39.39	2.22	37.01	42.71	1	39			
BPP	5	36.34	1.38	34.5	38.14	5	37.06	3.52	33.11	42.36	6	34.66	1.39	32.24	36.37	1	31.61			
NL	5	42.16	2.38	38.1	43.97	5	40.08	2.62	36.29	42.73	6	42.32	1.8	40.24	44.57	1	43.26			
NW	5	20.92	0.56	20.33	21.8	5	20.95	0.47	20.51	21.51	6	17.92	0.62	16.99	18.57	1	17.03			
LF	5	41.49	1.4	39.78	43.58	5	37.73	3.06	34.62	42.27	6	38.32	2.2	35.16	41.92	1	30.84			
IW	5	11.37	0.43	10.69	11.76	5	10.68	0.27	10.31	10.94	6	10.4	0.57	9.45	11.17	1	10.21			
LP	5	42.18	2.34	38.11	43.79	5	40.81	1.64	38.34	42.36	6	41.32	2.05	38.97	44.41	1	39.99			
LD	5	28.78	0.92	27.49	29.75	5	26.56	0.87	25.36	27.63	6	27.68	1.67	25.9	30.34	1	26.13			
BPPM	5	19.9	0.37	19.4	20.4	5	19.09	0.9	17.62	19.9	6	20.04	1.46	18.31	22.37	1	18.19			
TRL	5	19.01	0.81	18.32	20.34	5	19.64	0.68	18.65	20.35	6	17.9	0.56	17.33	18.87	1	18.09			
TBL	5	16.14	1.3	14.72	17.66	5	17.2	1.71	15.05	18.63	6	16.66	0.81	15.8	17.66	1	15.07			

	mexp					nica					paaz					pabt				
	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n					n	Mean	SD	Min.	Max.
TLS	2	105.29	4.21	102.31	108.26	9	110.3	2.06	107.47	113.73	1	104.53				12	103.84	2.33	99.63	107.78
CIL	2	89.92	2.88	87.88	91.96	9	93.38	1.54	91.93	95.99	1	89.68				12	88.83	1.8	85.53	91.33
IOC	2	28.16	0.37	27.89	28.42	9	30.57	1.21	28.26	31.81	1	28.72				12	29.95	0.85	28.31	31.29
ZB	2	48.5	1.25	47.61	49.38	9	49.7	1.36	47.52	51.39	1	47.75				12	46.5	1.23	43.97	48.04
BP	2	40.15	0.42	39.85	40.45	9	41.27	1.21	39.62	42.89	1	39.17				12	40.39	0.87	38.57	41.47
BPP	2	34.42	1.34	33.47	35.37	9	35.34	1.29	33.58	37.31	1	34.15				12	34.63	0.86	33.65	36.48
NL	2	41.03	3.62	38.47	43.59	9	43.58	2.82	40.29	49.86	1	37.19				12	40.57	1.25	38.65	42.2
NW	2	18.86	1.7	17.65	20.06	9	19.11	1.52	17.21	22.24	1	17.85				12	16.61	0.62	15.52	17.61
LF	2	38.29	1.3	37.37	39.21	9	39.56	1.42	37.52	42.56	1	41.32				12	37.58	1.5	35	39.76
IW	2	11.19	0.17	11.07	11.31	9	12.05	0.62	11.01	13.12	1	10.94				12	10.54	0.43	9.6	11.23
LP	2	40.12	2.55	38.32	41.92	9	40.29	4.59	28.32	43.26	1	40.14				12	40.19	1.14	38.24	42.19
LD	2	26.67	1.73	25.45	27.89	9	28.06	0.9	26.86	29.3	1	26.94				12	27.62	0.59	26.39	28.54
BPPM	2	20.28	0.23	20.11	20.44	9	20.43	0.65	19.52	21.54	1	17.94				12	19.04	0.65	18	19.99
TRL	2	18.84	0.08	18.78	18.89	9	18.85	0.97	17.77	20.93	1	19.67				12	16.36	0.76	14.94	17.74
TBL	2	15.28	1.1	14.5	16.06	9	16.37	0.87	15.23	17.63	1	15.67				12	16.74	0.71	15.7	17.85

	pace					paic					pane					panw				
	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.
TLS	14	109.54	4.31	101.12	114.83	2	101.89	0.81	101.32	102.46	3	111.9	1.86	110.01	113.72	15	110.99	2.51	105.2	114.71
CIL	14	92.84	3.24	86.57	96.17	2	87.33	1.06	86.58	88.08	3	94.32	0.97	93.21	95.03	15	93.88	2.54	86.22	97.24
IOC	14	30.71	1.33	27.27	32.82	2	29.08	0	29.08	29.08	3	29.65	0.17	29.45	29.76	15	30.55	1.55	28.24	34.27
ZB	14	48.71	1.75	45.64	51.2	2	48.43	0.04	48.4	48.46	3	48.68	1.74	46.73	50.08	15	49.03	2.05	46.2	53.03
BP	14	41.14	1.67	37.86	43.5	2	40.25	1.03	39.52	40.98	3	40.61	0.03	40.59	40.64	15	40.99	1.84	38.06	44.55
BPP	14	35.28	1.29	32.96	37.19	2	33.89	1.01	33.17	34.6	3	35.3	0.94	34.22	35.97	15	36.14	1.34	33.54	39.23
NL	14	41.53	2.09	37.92	44.94	2	38.21	0.21	38.06	38.36	3	42.95	0.69	42.18	43.51	15	43.02	1.94	39.66	46.91
NW	14	19.04	1.23	17.53	21.93	2	16.63	0.27	16.44	16.82	3	18.84	1.3	17.51	20.11	15	18.02	1.12	16.34	19.49
LF	14	40.74	2.19	37.81	44.76	2	38.96	0.05	38.92	38.99	3	39.73	1.83	37.65	41.07	15	41.22	2.67	36.99	45.61
IW	14	11.92	0.88	10.46	13.63	2	10.41	0.66	9.94	10.88	3	10.84	0.59	10.17	11.28	15	11.08	0.56	10.19	12.13

Appendix 1.—Continued

LP	14	40.77	1.8	37.04	42.86	2	38.98	0.15	38.87	39.08	3	41.39	0.65	40.81	42.1	15	42.85	1.32	39.71	44.39
LD	14	27.96	1.52	25.3	30.49	2	26.5	0.33	26.27	26.73	3	25.21	4.49	20.05	28.22	15	28.99	1.15	26.12	30.59
BPPM	14	19.89	1.14	18.21	22.06	2	18.41	0.54	18.03	18.79	3	20.44	0.49	20.1	21	15	19.83	0.54	18.96	21
TRL	14	18.88	0.97	17.22	20.65	2	15.86	0.88	15.24	16.48	3	19.24	0.91	18.28	20.09	15	18.57	0.79	16.6	19.46
TBL	14	16.15	0.67	14.82	17.33	2	14.74	0.34	14.5	14.98	3	16.34	0.76	15.5	16.99	15	16.56	0.79	15.37	17.61

	pase					pasj					pasm					pasw				
	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n					n	Mean	SD	Min.	Max.
TLS	24	113.51	3.55	106.04	119.14	5	100.08	2.52	96.87	103.06	1	96.67				4	111.41	4.1	105.94	115.52
CIL	24	95.75	2.95	89.83	101.41	5	86.58	2.41	83.03	88.95	1	82.47				4	95	3.25	91.13	97.9
IOC	24	29.91	1.9	26.92	36.44	5	28.57	1.15	27.24	30.27	1	27.05				4	30.88	1.27	29.65	32.6
ZB	24	49.82	2.53	45.17	54.84	5	46.1	0.93	44.61	47.08	1	45.71				4	49.23	1.19	48.01	50.6
BP	24	41.24	1.87	38.17	45.33	5	37.98	0.39	37.57	38.4	1	37.95				4	40.89	1.09	40.07	42.41
BPP	24	35.4	1.67	32.56	38.76	5	33.75	1.11	32.72	35.39	1	32.12				4	36.39	1.96	35.01	39.3
NL	24	43.33	2.23	39.38	47.49	5	37.3	2.48	34.47	40.52	1	33				4	41.73	2.98	39.31	46.06
NW	24	19.66	1.47	16.8	23.31	5	16.99	1.13	15.72	18.22	1	17.63				4	19.97	0.75	19.27	21
LF	24	41.52	2.1	37.16	45.56	5	38.28	0.92	36.68	38.87	1	41.63				4	41.67	3.42	37.42	45.24
IW	24	11.77	1.03	8.33	13.36	5	11.26	0.57	10.72	12.09	1	10.89				4	12.55	0.76	11.68	13.21
LP	24	42.04	2.03	38.52	46.49	5	36.83	0.94	35.63	37.97	1	36.08				4	42.13	0.82	41.21	43.19
LD	24	28.63	1.35	26.9	31.76	5	25	1.02	23.75	26.01	1	24.02				4	27.95	0.78	27.24	29.05
BPPM	24	19.5	1.22	17.44	22.13	5	18.57	0.71	17.53	19.25	1	17.87				4	19.5	0.69	18.71	20.29
TRL	24	19.26	0.89	17.18	20.33	5	18.01	0.55	17.13	18.61	1	17.34				4	19.37	1.84	16.63	20.6
TBL	24	16.19	0.83	14.69	17.49	5	14.6	0.97	13.45	16.15	1	14.85				4	15.76	1.23	13.94	16.56

	pere					perw					vewe				
	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.
TLS	25	112.38	3.54	105.16	120.6	6	120.12	3.06	115.97	124.6	10	111.69	3.05	105.94	117.06
CIL	25	95.39	3.23	90.34	103.24	6	99.06	2.93	94.59	102.03	10	95.51	2.23	90.91	98.63
IOC	25	30.42	1.59	27.83	33.36	6	31.71	2.47	28.98	35.44	10	29.92	1.21	27.87	32.1
ZB	25	50.64	2.72	40.32	54.9	6	51.97	1.82	48.64	53.51	10	50.41	1.41	48.52	53.33
BP	25	41.72	1.65	39.61	45.89	6	42.46	2.05	40.04	45.93	10	40.99	1.31	39.3	42.94
BPP	25	36.88	1.47	34.51	40.47	6	39.37	2.18	36.51	41.96	10	36.35	1.41	34.21	38.26
NL	25	41.76	2.67	37.85	46.19	6	45.85	1.37	43.94	47.3	10	44.77	2.01	42.04	47.48
NW	25	20.33	1.62	17.36	23.41	6	21.56	2.26	19.2	25.55	10	21.66	1.05	20.11	23.76
LF	25	42.48	2.08	37.61	46	6	44.41	1.87	42.62	46.72	10	39.11	2.15	35.65	41.54
IW	25	12.5	0.74	11.22	13.68	6	12.96	0.58	12.31	13.83	10	12.3	0.45	11.55	13.06
LP	25	42.13	1.81	38.65	46.68	6	44.27	1.35	42.78	46.38	10	41.81	1.49	38.91	43.7
LD	25	26.39	1.86	24.36	30.78	6	28.81	1.13	27.65	30.54	10	28.58	1.26	26.47	30.44
BPPM	25	20.68	0.82	19.2	22.5	6	20.65	0.85	19.66	22.15	10	19.86	0.61	18.56	20.76
TRL	25	20.05	1.02	17.72	22.23	6	20.39	1.03	19.3	21.8	10	19.14	1.03	17.53	20.5
TBL	25	17.46	1.04	15.01	19.48	6	17.45	1.01	16.54	19.2	10	15.71	1.01	14.2	17.74

Appendix 2.—Synonyms of *D. punctata* and *D. variegata*.

Dasyprocta punctata Gray, 1842

Central American Agouti

Synonyms: Dasyprocta punctata Gray, 1842:264: type locality "South America," restricted to [El] Realejo, Nicaragua by Goodwin (1946:417).

Dasyprocta isthmica Alston, 1876:347; type locality "Central America…Colon." [Colón, Panamá].

Dasyprocta colombiana Bangs, 1898:163; type locality "Santa Marta, Colombia."

Dasyprocta fuliginosa candelensis J. A. Allen, 1915:625; type locality "La Candela (altitude 6500 feet), Huila, Colombia."

Dasyprocta callida Bangs, 1901:635: type locality "San Miguel Island…Bay of Panamá…Archipelago de las Perlas" [Isla del Rey, Archipiélago de Las Perlas].

Dasyprocta punctata dariensis Goldman, 1913:11; type locality "near head of Rio Limon (altitude 5.200 feet), Mount Pirri, Eastern Panama."

Dasyprocta punctata yucatanica Goldman, 1913:12; type locality "Apazote (near Yohaltun), Campeche, Mexico."

Dasyprocta punctata chiapensis Goldman, 1913:13; type locality "Huehuetán, southern Chiapas, Mexico."

Dasyprocta variegata chocoensis J. A. Allen, 1915:627; type locality "Los Cisneros (altitude 600 feet), Chocó district, Colombia."

Dasyprocta punctata nuchalis Goldman, 1917:113; type locality "Divala, Chiriqui, Panama."

Dasyprocta punctata richmondi Goldman, 1917:114; type locality "Escondido River, 50 miles above Bluefields, Nicaragua."

Dasyprocta pandora Thomas, 1917:313; type locality "Gorgona Island, off west coast of Colombia."

Dasyprocta punctata underwoodi Goldman, 1931:481; type locality "San Geronimo, Pirris, western Costa Rica."

Dasyprocta punctata pallidiventris Bole, 1937:182; type locality "Paracoté (Plantation headquarters of the Boston Cocoanut Company). 1½ miles south of the mouth of the angulo River, Mariato–Suay Lands, Veraguas Province, Panama. (Altitude: Sea level.)"

Dasyprocta punctata bellula R. Kellogg, 1946:59; type locality "Isla San José, Archipielago de las Perlas, Golfo de Panama, Panama."

Dasyprocta punctata zuliae Ojasti, 1972:190; type locality "Matera Cusaré, Cuenca del río Negro en la Sierra de Perijá, Edo. Zulía, Venezuela."

Dasyprocta variegata Tschudi, 1845

Brown agouti

Synonyms: D[*asyprocta*]. *variegata* Tschudi, 1845:190; type locality "hingegen höher hinauf bis an die Gränze der obern Waldund Ceja–region dis zu 6000' ü. M.," [= "the boundary of the upper forest and Ceja region, 6000 feet."] Chanchamayo region, Junín, Peru.

Dasyprocta variegata yungarum Thomas, 1910:505; type locality "Chimosi [= Chimasi], alt. 1700 m. Yungas, [La Paz,] Bolivia."

Dasyprocta variegata boliviae Thomas, 1917:312; type locality "Yacuiba, [Tarija,] southern Bolivia, on Argentine boundary south of Caiza."