Pablo Teta*

Geographic variation in quantitative skull traits in the genus *Myoprocta* Thomas, 1903 (Rodentia, Dasyproctidae) and its taxonomic implications

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Abstract: The genus *Myoprocta* Thomas, 1903 includes two living species of medium-sized caviomorph rodents of the family Dasyproctidae, the red acouchi, *Myoprocta acouchy* (Erxleben 1777), and the green acouchi, *Myoprocta pratti* Pocock 1913. Whereas some recent revisionary work has considered both species to be allopatrically distributed, other reports suggest that both taxa co-occur in eastern Colombia. In this contribution, I revaluate some qualitative and quantitative skull traits within *Myoprocta* to clarify its taxonomy and distribution. Multivariate analyses of quantitative skull characters support the distinction between *M. acouchy* and *M. pratti*, contradicting the findings of some previous authors. Based on these results and the examination of ~100 skins, I concur with the hypothesis that the two species are allopatrically distributed.

Keywords: cavioidea; caviomorpha; hystricognathi; taxonomy.

Introduction

The genus *Myoprocta* Thomas, 1903, includes two living species, *Myoprocta acouchy* (Erxleben 1777) (including *acuschi* E. Geoffroy St.- Hilaire, 1803; *exilis* Wagler, 1831; *leptura* Wagner, 1844; *acuchy* Liais, 1872; and *demararae* Tate, 1939) and *Myoprocta pratti* Pocock, 1913 (including *milleri* J. A. Allen, 1913; *limanus* Thomas, 1920; *parva* Lönnberg, 1921; *archidonae* Lönnberg, 1925; *caymanum* Thomas, 1926; and *puralis* Thomas, 1926), of medium-sized rodents belonging to the family Dasyproctidae (Patton and Emmons 2015). The red acouchi, *M. acouchy*, is distributed from Guyana, French Guiana and Surinam to the northern bank of the Amazon River, while the green acouchi, *M. pratti*, occurs in the western portion of the Amazonia, from Colombia and Venezuela to Peru and northern Bolivia (Patton and Emmons 2015). As their common names indicate, the main feature that distinguishes these taxa is the overall appearance of the coat coloration (cf. Voss et al. 2001). By contrast, the skulls of both species are remarkably similar in their morphology, with minor variations in size and in a few qualitative traits (e.g. size and shape of sphenopalatine vacuities). Red acouchies are, on average, larger than green acouchies (cf. Voss et al. 2001); however, a recent multivariate analysis of quantitative skull traits indicated no morphological separation between samples attributed to each species (cf. Ramírez-Chaves et al. 2014).

The taxonomic status of both species of *Myoprocta* and their corresponding names were controversial during most of the 20th century (reviewed by Voss et al. 2001). Part of the confusion had its origin in the nature of the description provided by Erxleben (1777), which referred a greenish animal to an area today occupied by reddish ones. Consequently, different authors used the name *acouchy* to variably refer both to the reddish (e.g. Thomas 1926, Voss et al. 2001) or the greenish (e.g. Tate 1939) forms. Voss et al. (2001) resolved this situation by designating a neotype for *Cavia acouchy*, attaching this specific epithet to the reddish form, and reviewing its morphological differences with the greenish one. According to Voss et al. (2001), *Myoprocta acouchy* and *Myoprocta pratti* have non-overlapping distributions, a conclusion that has been accepted by most subsequent authors (e.g. Patton and Emmons 2015). Other researchers, however, have suggested that both the reddish and greenish forms are sympatric in eastern Colombia (e.g. Emmons and Feer 1997, Ramírez-Chaves et al. 2014) and eastern Ecuador (Lönnberg 1921, 1925).

In this article, I present a comprehensive analysis of morphometric variability within *Myoprocta*, discussing several issues related both to its taxonomy and distribution. This study includes the largest sample considered in any published multivariate analysis to date, encompassing almost entirely the known geographic range of this genus. In addition, I offer some comments about the taxonomy of "reddish" acouchies from central and southern Colombia.

***Corresponding author: Pablo Teta,** División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Avenida Ángel Gallardo 470, C1405DJR, Buenos Aires, Argentina, e-mail: antheca@yahoo.com.ar

Materials and methods

Studied specimens (see Appendix 1 for a detail) consist primarily of skins with their associated skulls and are housed in the following museums: AMNH, American Museum of Natural History (New York, USA); FMNH, Field Museum of Natural History (Chicago, USA); MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina); USNM, United States National Museum of Natural History (Washington, DC, USA).

Fifteen skull measurements were recorded with digital calipers (accurate to 0.01 mm) and analyzed to summarize patterns of variation within and between the populations sampled. Cranial dimensions were measured as described by Voss et al. (2001) and Teta and Lucero (2016): total length of the skull (TLS); condylo-incisive length (CIL); least interorbital breadth (LIB); zygomatic breadth (ZB); braincase breadth (BB); nasal length (NL); nasal width (NW); frontal length (FL); upper diastema length (DL); maxillary toothrow (MTR); palatal length (PL); breadth across paraoccipital processes (BPP); breadth of palatal bridge across upper fourth premolars (BP4); breadth of palatal bridge across upper third molars (BP3); tympanic bulla length (TBL).

To explore the geographic patterns of morphological variation within *Myoprocta*, specimens of both *Myoprocta acouchy* and *Myoprocta pratti* were grouped according to geographical proximity, absence of geographical barriers among localities, and lack of obvious differences in size or shape of the skull or external coloration among different samples (see Musser 1968, Teta and Lucero 2016). Based on these procedures, the following operational groups were defined (Figure 1): *M. acouchy*, **ama** = northern bank of the Amazon River (n = 13); **gui** = Guyana, Surinam and French Guiana (n = 16); *M. pratti*, **col** = eastern Colombia (n = 6); **ecu** = eastern Ecuador (n = 23); **pec** = central and southern Peru (n = 10); **pen** = northern Peru and western Brazil (n = 21); **ven** = Venezuela (n = 5).

Multivariate computations were restricted to 95 adult specimens (those with complete maxillary tooth eruption). Principal component analysis (PCA) and discriminant function analysis (DFA) were conducted using craniodental measurements, all of which were first transformed to logarithms (base 10). Principal components were extracted from the variance-covariance matrix.

All statistical procedures were performed using software PAST v. 2.17 (Hammer et al. 2001).

Results

The studied specimens were remarkably uniform in skull morphology, but with some minor variation in overall size

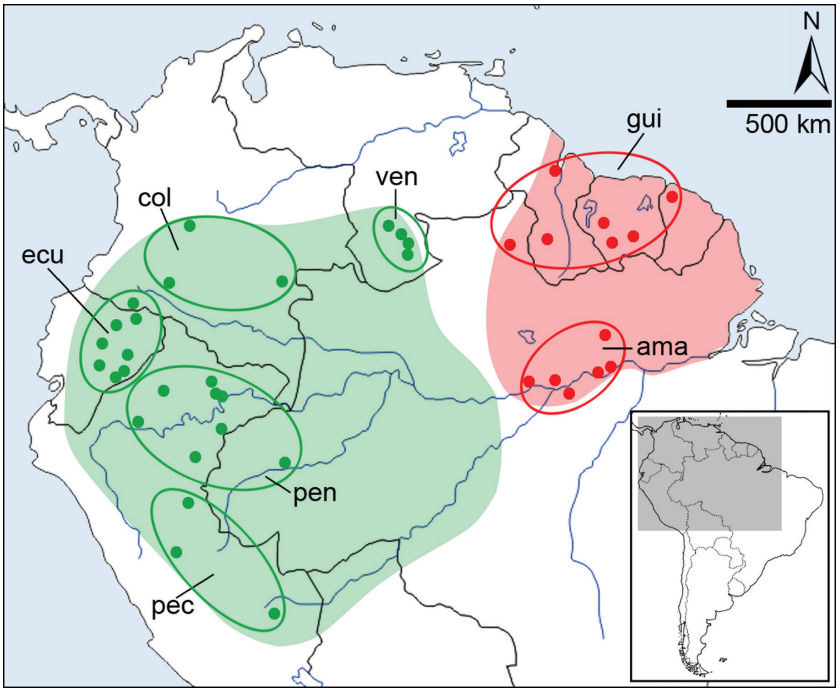

Figure 1: Map of northwestern South America, depicting the studied samples. Red and green dots correspond to *Myoprocta acouchy* and *Myoprocta pratti*, respectively (shadow areas represent the known distribution of each species). See Materials and methods section for explanation of the abbreviations.

(Figure 2; Supplementary Table 1). The cranium is elongate and smooth, without heavy ridging, except for a slight sagittal crest over the posterior portion of the braincase in adult individuals; the rostrum is deep and heavy; the nasals are broad and surpass, together with the premaxillae, the anterior surface of the upper incisors; the zygomatic arches are short and weak; the anterior margin of mesopterygoyd fossa is rounded and reaches nearly to the posterior margin of the second upper molar; the auditory bullae are moderately inflated; the paroccipital processes are very small; the maxillary toothrows are nearly parallel; and the strongly hypsodont molariform teeth are semirooted, with flattened occlusal surfaces (Figure 2).

Results from the PCA (Figure 3A; Table 1) show that individual scores tend to segregate into two main clusters, one including those samples from **ama** and **gui** (=*Myoprocta acouchy*) and another encompassing those from **col**, **ecu**, **pec**, **pen** and **ven** (=*Myoprocta pratti*). Specimens corresponding to both clusters overlapped moderately along both PC1 and PC2, which account for 52.3% and 9.5% of the total variance, respectively (Figure 3A; Table 1). All variables contribute positively to PC1, suggesting that this component is a size vector. On PC1, the highest positive loadings corresponded to (in order) NL, PL, NW, BP3 and DL. On PC2, the largest positive loadings were FL, BP3, TBL and MTR and the lowest negative were NL, BPP, DL and NW.

The DFA revealed a major separation among the first axis (48.9% of the total variance) between **ama** and **gui** on one side and **col**, **ecu**, **pec**, **pen** and **ven** on the other (Figure 3B; Table 1). Within each of these clusters, the second axis (18.9% of the total variance) contributes to separate **ama** from **gui** and **col**, **ecu**, **pen** and **ven** from **pec.** Cranial dimensions related to PL, NW, BP3 and DL were relevant for discrimination on the first axis and FL, BP3, TBL and MTR on the second. A second discriminant function analysis, considering only two groups, *Myoprocta acouchy* and *Myoprocta pratti*, correctly classified 94% of the individuals.

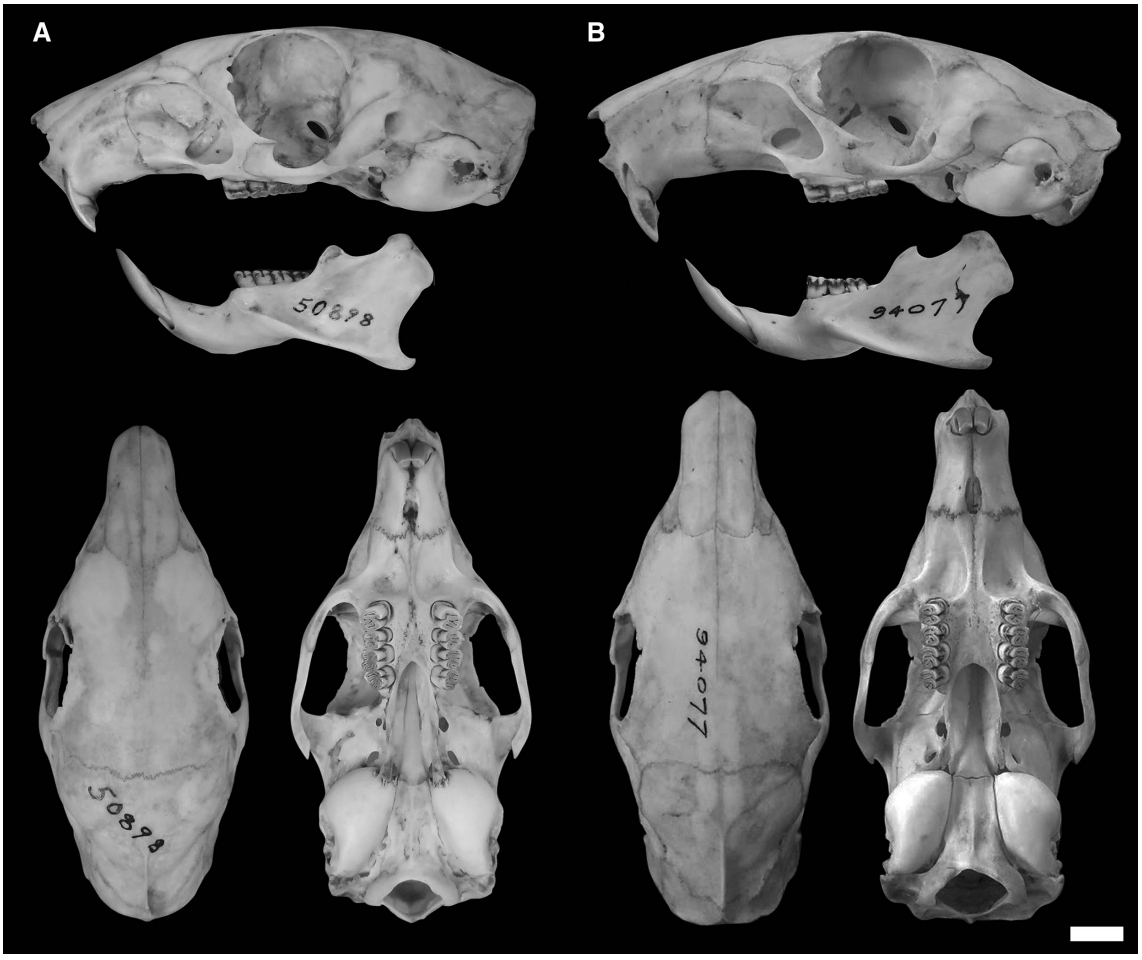

Figure 2: Cranial anatomy in species of the genus *Myoprocta*.
Lateral, dorsal and ventral views of the skulls and labial views of the mandibles of *Myoprocta acouchy* (A) and *Myoprocta pratti* (B). Scale = 10 mm.

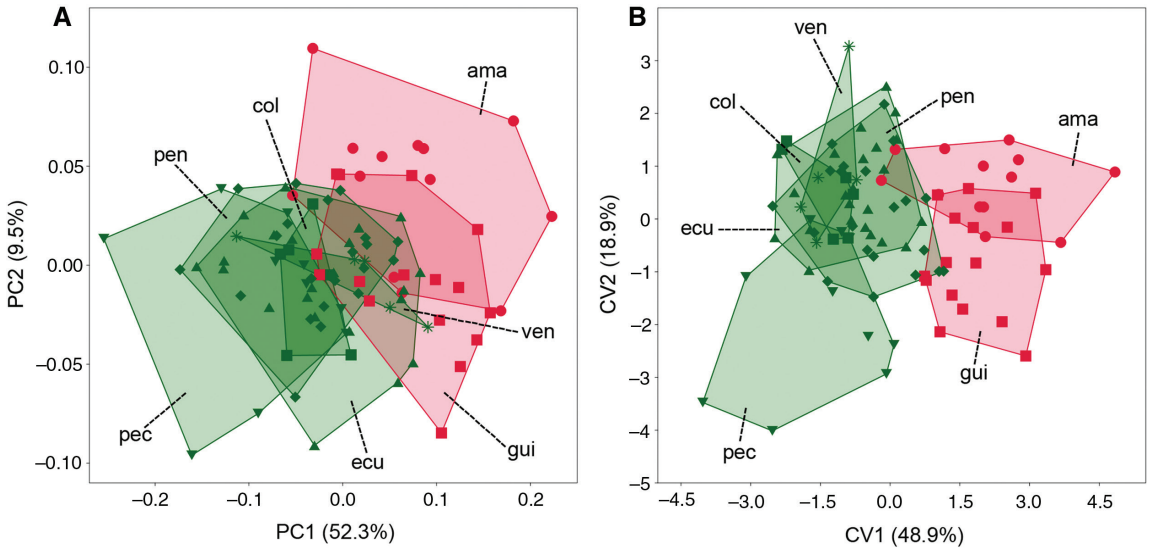

Figure 3: Multivariate statistics for *Myoprocta* populations.
Projections of specimen scores on the first two principal components (A) and the first two canonical variates (B) from analyses of craniodental measurements of adult specimens of *Myoprocta acouchy* (red polygons) and *Myoprocta pratti* (green polygons). For the acronyms of the geographical operational groups see the Materials and methods section.

Table 1: Results of principal components analyses and discriminant function analyses performed on adult individuals of *Myoprocta* (n = 94).

	PC1	PC2	PC3	CV1	CV2	CV3
TLS	0.237	0.002	0.069	0.010	0.001	0.000
CIL	0.259	−0.015	0.037	0.010	0.002	−0.001
LIB	0.274	−0.011	−0.004	0.013	0.000	−0.001
ZB	0.195	−0.096	−0.002	0.006	0.003	−0.006
BB	0.121	0.011	0.045	0.006	0.002	−0.004
NL	0.311	−0.243	0.760	0.015	−0.005	−0.005
NW	0.342	−0.178	−0.267	0.011	0.001	0.002
FL	0.165	0.186	−0.483	0.004	0.008	0.006
DL	0.357	−0.211	−0.214	0.009	0.009	−0.003
MTR	0.089	0.760	0.222	0.012	0.008	0.009
PL	0.324	0.024	−0.095	0.011	0.012	−0.002
BPP	0.221	−0.215	−0.021	0.004	0.002	−0.006
BP4	0.235	0.087	−0.063	0.009	0.007	−0.006
BP3	0.345	0.226	0.013	0.011	0.003	−0.005
TBL	0.213	0.371	0.037	0.009	0.003	0.011
Eigenvalue	0.007	0.001	0.001	1.897	0.731	0.550
% Variance	52.27	9.50	7.30	48.91	18.86	14.19

See Materials and methods section for explanation of the abbreviations.

Discussion

Our results confirm that reddish (=*Myoprocta acouchy*) and greenish (=*Myoprocta pratti*) acouchies can be safely separated by quantitative skull traits, contradicting the recent findings of Ramírez-Chaves et al. (2014). Overall, the skull of *M. acouchy* is characterized by larger toothrows and bullae, broader interorbits and longer nasals than most specimens of *M. pratti* (see also Voss et al. 2001). That the samples I measured are not quite completely separated even by DFA, is not unexpected, as previous researchers have documented that Dasyproctid are remarkably conservative in cranial anatomy, at least in terms of qualitative traits, with some minor variation in quantitative features (e.g. Patton and Emmons 2015, Teta and Lucero 2016). This fact strongly contrasts with the coat color patterns exhibited by these same animals, which include substantial intra- and interpopulational variation (cf. Patton and Emmons 2015). Most samples of *M. acouchy* are characterized by a reddish dorsal coloration, with uniformly orange to reddish underparts and by a distinct rump patch of very long (60–80 m) and highly glossy, brownish to blackish hairs, extending to the base of the tail (Voss et al. 2001, Patton and Emmons 2015). On the contrary, *M. pratti* has a much more variable dorsal coloration (see the discussion below), ranging from drab yellowish to grayish-brown, sometimes washed with reddish; ventrally, most *M. pratti* skins are orangish to yellowish, usually with a distinct white midventral streak. Additionally, *M. pratti* lack the distinctive patch of glossy rump hairs seen in *M. acouchy* (Emmons and Feer 1997, Voss et al. 2001, Patton and Emmons 2015).

Individuals of *Myoprocta acouchy* from the Guianas (=**gui**) and those from the northern bank of the Amazon River (=**ama**) occupy two, slightly overlapping, multivariate spaces in these results. Specimens from the Guianas are characterized by larger maxillary toothrows and

tympanic bullae and wider palatal bridges across upper third molars, whereas those from the northen bank of the Amazon River have larger diastemas and larger and wider nasals. Externally, the former have generally less saturated pigments and darker rump hairs than the latter (cf Voss et al. 2001). Additional samples and new sources of data (e.g. molecular markers) are needed to determine the biological meaning, if any, of these geographical differences. *Cavia exilis* Wagler, 1813, with type locality restricted to "near the mouth of Rio Negro" (Allen 1916:205), might be an available name for samples from the northern bank of the Amazon River if any taxonomic distinction from Guiana material seems justified by future research.

Specimens from different geographical groups of *Myoprocta pratti* broadly overlap in multivariate space, with the exception of the sample from central and southern Peru (=**pec**), which seem moderately differentiated from the others in size. Dorsal pelage coloration, by contrast, is strongly variable among individuals, with some geographical component, but also within the same population (cf. Voss et al. 2001, Patton and Emmons 2015). For example, most specimens from Venezuela are grayish brown grizzled with white hairs dorsally (e.g. USNM 388222, USNM 406522, USNM 406797), whereas specimens with reddish dorsal tones and orangish underparts (e.g. FMNH 24793, 24794, 88908-88911) frequently occur in eastern Colombia (=**col**; see the discussion below) and in northern Peru/western Brazil (=**pen**). With the evidence at hand, we prefer to maintain the current taxonomic arrangement, including all greenish acouchies under the concept of *M. pratti*. However, the limited available molecular evidences (Rowe and Honeycutt 2002) plus the geographic morphological variation noted above, suggest that *M. pratti* might be a complex of closely related species (cf. Voss et al. 2001, Ramírez-Chaves et al. 2014). Populations from central and southern Peru, for which no name is available, deserve special attention, as they exhibit moderate differences from other greenish acouchies in quantitative morphological traits.

Although some researchers have reported that *Myoprocta acouchy* and *Myoprocta pratti* occur sympatrically in eastern Ecuador (Lönnberg 1921, 1925) or eastern Colombia (Emmons and Feer 1997), the data at hand suggest that these species are allopatrically distributed. In a recent study, Ramírez-Chaves et al. (2014) illustrated some possible examples of reddish acouchies from eastern Colombia, returning to the idea that both species co-occur in some parts of this country. However, a close examination of the photographs provided by these authors (cf. Ramirez-Chávez et al. 2016: Figure 2) led us to arrive at a different conclusion. Despite its overall reddish coloration, both the specimens IAvH 1856 and IAvH 2542 fall well within the variability observed for other populations of *M. pratti* (e.g. those from northern Peru and western Brazil). In addition, both individuals apparently lack the patch of glossy rump hair that characterized *M. acouchy*. Likewise, the specimen IAvH 1856 has a distinct white midventral streak, a marking typical of *M. pratti*. Finally, it is noteworthy that both of these animals were included within the multivariate space of *M. pratti* in the morphometric analyses presented by these authors (cf. Ramirez-Chávez et al. 2016: Figure 4).

Despite the cranial similarity of these species, some minor qualitative differences have been documented (Tate 1939, Voss et al. 2001). According to Voss et al. (2001), the most constant traits that distinguish *Myoprocta acouchy* and *Myoprocta pratti* are the shape and size of the sphenopalatine vacuities. These openings are reduced to very narrow slits (<1 mm wide) in most specimens of *M. acouchy*, whereas they are wider (>1 mm) and teardrop-shaped in most specimens of *M. pratti*. Most of the specimens for this study conform to this diagnosis, although some noteworthy variability was found among samples [e.g. some individuals of *M. pratti* from western Brazil have large sphenopalatine vacuities; FMNH 50898, FMNH 50899; see also Ramírez-Chaves et al. (2014), who reached similar results in a previous contribution and discussed the diagnostic value of this character].

Dasyproctid are conspicuous faunal elements found in the forested areas of South America. However, despite their abundance, ubiquity and diagnosability, agoutis and acouchies are among the least known mammals of the Neotropics, at least from a taxonomical perspective (Patton and Emmons 2015). This situation is partially explained by the lack of diagnostic qualitative skull traits (Patton and Emmons 2015) and because, unlike many Neotropical rodent genera, there is no data on molecular markers for most species of *Dasyprocta* or *Myoprocta* (Upham and Patterson 2015). Integrative studies, including large samples of individuals from different geographical areas, are much needed, to better clarify the systematics of this taxa.

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Appendix

List of studied specimens and their collection localities. Specimens consist primarily of skins and associated skulls and are housed in the following museums: AMNH, American Museum of Natural History (New York, USA); FMNH, Field Museum of Natural History (Chicago, USA); MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina); USNM, United States National Museum of Natural History (Washington, DC, USA).

Myoprocta acouchy: **Brazil:** Amazonas, San Antonio de Amatari (AMNH 92888, AMNH 93043); Amazonas, río Amazonas, Lago do Serpa (FMNH 50897); Amazonas, río Amazonas, Lago do Baptista (FMNH 50885); Pará, boca río Paratucu, N bank río Amazonas (AMNH 94074); Pará, N bank of río Amazonas (AMNH 94068, AMNH 94070, AMNH 94071, AMNH 94072); Pará, "Castanhal on Río Jamundá" (AMNH 94076); Pará, Oriximina, Cachoeira Porteira (USNM 546296, USNM 546297); Pará, San José on Río Jamundá (AMNH 94077); Roraima, Serra Grande (FMNH 20019). **French Guiana:** Tamanoir on Mana River (FMNH 21785, FMNH 21786, FMNH 21787). **Guyana:** Cuyuni-Mazaruni, Kartabo (AMNH 70198); Upper Takutu-Upper Essequibo, Dadanawa, 15 mi E, Rupununi Savannah (USNM 338970, USNM 339671); "Kuitaro River", Rupununi Savanna (USNM 339671). **Suriname:** Kaiserberg airstrip, Zuid river (FMNH 93227, FMNH 93273, FMNH 93275, FMNH 93276); Marowijne, Palomeu Camp, Tapahoni river (FMNH 95593, FMNH 95787); Nickerie, Wilhelmina mts.,West River (FMNH 95775, FMNH 95778).

Myoprocta pratti: **Brasil:** Río Jurua, Joao Pessoa (FMNH 50898, FMNH 50899). **Colombia:** Amazonas, Javá, río Vaupes (AMNH 78599); Colombia, Caquetá (AMNH 34352, AMNH 34355); Caquetá, Morelia, Río Bodoquena (AMNH 33659); Meta, La Macarena, Parque, Río Guayapa (FMNH 88023, FMNH 88024); Putumayo, San Antonio, Río Mecaya (FMNH 71133). **Ecuador:** Amazonas, Río Santiago (AMNH 98236); Napo, 12 km NE Lago Agrio (FMNH 125086, FMNH 125085); Napo, San José Nuevo (AMNH 64007, AMNH 64008, AMNH 68228, AMNH 68230, AMNH 68231, AMNH 68232); Napo, río Suno (AMNH 66775, AMNH 68226, AMNH 68227, AMNH 68233, AMNH 68234, AMNH 68236, AMNH 68244, FMNH 31118); Pastaza, Río Capahuari (FMNH 43191); Pastaza, río Pindo Yaco (FMNH 43187); Pastaza, río Yana Rumi (FMNH 43189, FMNH 43190); río Bobonazo, Montalvo (FMNH 41485). **Peru:** Boca río Yaquerana (FMNH 88909); Cuzco, Quince Mil (FMNH 75195, FMNH 75196, FMNH 78667); Loreto, boca río Curaray (AMNH 72169, AMNH 72170, AMNH 72171, AMNH 72172, AMNH 72173); Loreto, Marupo River (AMNH 98242); Loreto, Orasa, rio Amazonas (AMNH 73858, AMNH 73859, AMNH 73861, AMNH 73866, AMNH 74069, AMNH 74070, ANMH 74067); Loreto, Puerto Indiana, río Amazonas (AMNH 73360, AMNH 73361); Loreto, Sarayacu (AMNH 76277); Loreto, Quebrada Pushaga (FMNH 88907); Pucallpa, 59 km W (USNM 461289); Quebrada Esperanza (FMNH 88911); Río Nanay (FMNH 86918, FMNH 86919); Santa Cecília (FMNH 86920); Ucayali, Lagarto, Rio Ucayali (AMNH 76621, AMNH 76622, AMNH 76623). **Venezuela:** 56 km NNW Esmeralda, río Cunucunuma (USNM 388222); Amazonas, Boca Mavaca, 84 km SSE Esmeralda (USNM 372886, USNM 406522); Amazonas, Mount Duida, Valle de los Monos (AMNH 77041); Amazonas, Tamataa, Río Orinoco (USNM 406797).

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