

Rethinking the living diversity of the *Abrocoma cinerea* Thomas, 1919 species complex (Rodentia, Abrocomidae)

Repensando a diversidade atual do complexo de espécies de *Abrocoma cinerea* Thomas, 1919 (Rodentia, Abrocomidae)

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Abstract: The genus *Abrocoma* Waterhouse includes eight living species of medium-sized rats with long, soft, and dense fur, large ears, and moderate to short tails. Six of these species are included within the informally called *A. cinerea* species complex (*A. cinerea* Thomas, *A. budini* Thomas, *A. famatina* Thomas, *A. schistacea* Thomas, *A. vaccarum* Thomas, and *A. uspallata* Braun and Mares). Based both on the study of specimens housed in biological collections and the reinterpretation of previous morphological evidence, I suggest that the current recognized species richness of the genus could be overestimated. Both qualitative and quantitative morphological approaches are consistent with the recognition of no more than two morphotypes within the *A. cinerea* species complex. However, additional lines of evidence and approaches are needed to disentangle the complex taxonomy of this genus (e.g., phylogenetic analysis of DNA sequences). Until then, I prefer to not make changes in the current classification of *Abrocoma*, especially taking into account that any taxonomic change could have undesirable consequences in the conservation of these rodents.

Keywords: Hystricognathi. Caviomorpha. Octodontoidea. Chinchilla rat.

Resumo: O gênero *Abrocoma* Waterhouse inclui oito espécies viventes de ratos de tamanho médio, com pêlos longos, macios e densos, orelhas grandes e caudas moderadas a curtas. Seis dessas espécies estão incluídas informalmente no complexo de espécies de *A. cinerea* (*A. cinerea* Thomas, *A. budini* Thomas, *A. famatina* Thomas, *A. schistacea* Thomas, *A. vaccarum* Thomas, and *A. uspallata* Braun and Mares). Os estudos de espécimes alojados em coleções biológicas e na reinterpretação de evidências morfológicas anteriores sugerem que a atual riqueza de espécies reconhecida do gênero possa ser superestimada. As abordagens morfológicas qualitativas e quantitativas são consistentes com o reconhecimento de não mais que dois morfotipos no complexo de espécies de *A. cinerea*. Contudo, linhas adicionais de evidência e abordagens são necessárias para desembaraçar a complexa taxonomia deste gênero (por exemplo, análise filogenética de sequências de DNA). Até então, prefiro não fazer alterações na classificação atual da *Abrocoma*, especialmente levando em consideração que qualquer alteração taxonômica pode ter consequências indesejáveis na conservação desses roedores.

Palavras-chave: Hystricognathi. Caviomorpha. Octodontoidea. Rato chinchila.

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INTRODUCTION

The genus *Abrocoma* Waterhouse, 1837 includes eight living species of medium-sized rats (164–196 g) of rotund bodies with long, soft, and dense fur; large ears; and moderate to short tails (Emmons, 1999). Based on their external and cranial features, three main species groups can be recognized within this genus (Glanz & Anderson, 1990; Braun & Mares, 2002; Patton & Emmons, 2015). Two of these contain a single species each, *A. bennettii* Waterhouse 1837, and *A. boliviensis* Glanz and Anderson 1990, while the third one, the informally called *A. cinerea* species complex, includes the other six species (*A. cinerea* Thomas, 1919; *A. budini* Thomas, 1920; *A. famatina* Thomas, 1920; *A. schistacea* Thomas, 1921; *A. vaccarum* Thomas, 1921; and *A. uspallata* Braun and Mares, 2002). Species of the *A. cinerea* complex are specialized for a saxicolous life, inhabiting mostly in stonewalls and rock crevices above 1800 m (Patton & Emmons, 2015; Emmons, 2016).

Five of the six species currently included within the *A. cinerea* complex were described by Thomas (1919, 1920a, 1920b, 1921a, 1921b) under the paradigm of the typological species concept. Subsequently, all these taxa were considered by Ellerman (1940) as subspecies of *A. cinerea*, a view followed during most of the XX century (e.g., Cabrera, 1961). More recently, Braun & Mares (2002) reviewed this group based on morphological evidences, reinstalling the specific status of *A. budini*, *A. famatina*, *A. schistacea*, and *A. vaccarum* and describing an additional nominal form of species level, *A. uspallata*. Species delimitation within the *A. cinerea* species complex was mostly based on geography and subtle differences in both qualitative and quantitative morphological traits (Braun & Mares, 2002; Patton & Emmons, 2015). In fact, even when recognized as distinct species, the multivariate statistical analysis presented by Braun & Mares (2002) do not allow for a complete separation between *A. budini*, *A. famatina*, *A. schistacea*, *A. vaccarum*, and *A. uspallata*.

In this contribution, based on a moderately large sample from Salta (*A. cinerea*) and few additional individuals from Mendoza (here referred to *A. cf. A. uspallata*) and San Juan (*A. schistacea*), I put the emphasis in the intraspecific

variability of some external and cranial characters. In addition, I present a reinterpretation of previous qualitative and quantitative morphological evidences, suggesting that the current diversity in *Abrocoma* could be overestimated.

MATERIALS AND METHODS

Studied specimens, consisting of skins and skulls, are housed in the following biological collections (see Appendix 1 for a detail): American Museum of Natural History (AMNH) (New York, USA); *Instituto Argentino de Investigaciones de Zonas Áridas* (CMI) (Mendoza, Argentina); *Facultad de Ciencias Naturales e Instituto Miguel Lillo* (CML) (Tucumán, Argentina); Field Museum of Natural History (FMNH) (Chicago, USA); *Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”* (MACN) (Buenos Aires, Argentina); *Universidad Austral de Chile* (UACH) (Valdivia, Chile).

Anatomical terminology follows Braun & Mares (2002) and Verzi *et al.* (2016). Fifteen skull measurements were recorded with digital calipers (accurate to 0.01 mm), including: total length of the skull (TLS); condyle-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); incisive foramina length (IFL); incisive foramina width (IFW); maxillary toothrow (MTR); palatal length (PL); breadth of palatal bridge across upper fourth premolars (BP4); and tympanic bullae length (TBL).

Skull measurements, all of which were first transformed to logarithms (base 10), were analyzed to summarize patterns of variation within and between the sampled populations, using between group principal component analyses. Multivariate statistical procedures were restricted to adult specimens and made with software PAST v. 2.17 (Hammer *et al.*, 2001).

Age classes were based on size, craniodental morphology and fusion of cranial sutures (see Braun & Mares, 2002). Both females and males were pooled together in order to obtain more robust samples for its inclusion in the statistical analyses (for a similar procedure, see Braun & Mares 2002).



RESULTS

Studied specimens of the species of the *A. cinerea* species complex were relatively uniform in its skull morphology, depicting some minor variation in some cranial measurements and in the shape of the interorbital constriction (see the Results below). Craniums are moderately delicate, with a narrowed and elongated rostrum and a bowed dorsal profile; nasals are narrow for most of their length, tapering to a point posteriorly; frontals are not constricted posterior to the postorbital process; braincase is rounded, without well developed parietal ridges or supraoccipital crests; mastoid islands are medium to large in size and are enclosed between the occipitals and parietals; paroccipital processes are short, broad, and adhered to the posterior surface of the tympanic bullae; incisors are narrow; maxillary tooththrows are slightly convergent anteriorly; molar teeth are hypselodont, flat-crowned, and have a 8-shaped occlusal pattern. Shape and size of nasals, shape of the anterior border of the mesopterygoid fossa, size of mastoid islands, orientation of zygomata, and procumbency of the upper incisors vary moderately between individuals. For example, some specimens ($n = 2$) from Chorrillos and San Antonio de Los Cobres (northwestern Salta, Argentina) have their nasals wider at their proximal third (Figure 1A), while in other specimens of this same locality ($n = 3$) are wider towards their middle portion (Figure 1B). In that same population, mastoid islands varied between large ($n = 3$; Figure 1C) to medium ($n = 3$; Figure 1D) and the anterior border of the mesopterygoid fossa from pointed ($n = 4$; Figure 1E) to nearly rounded ($n = 2$; Figure 1F, 1G). Additional specimens from Mendoza (*A. cf. A. uspallata*) and San Juan (*A. schistacea*) also presented some degree of morphological variation, departing from the diagnosis provided by Braun & Mares (2002) for *A. uspallata* and *A. schistacea* or other closely distributed species such as *A. vaccarum*. For example, I recorded either a rounded (FMNH 46157) or V-shaped mesopterygoid fossa (MACN-Ma 18828) within samples referred to *A. schistacea*, while

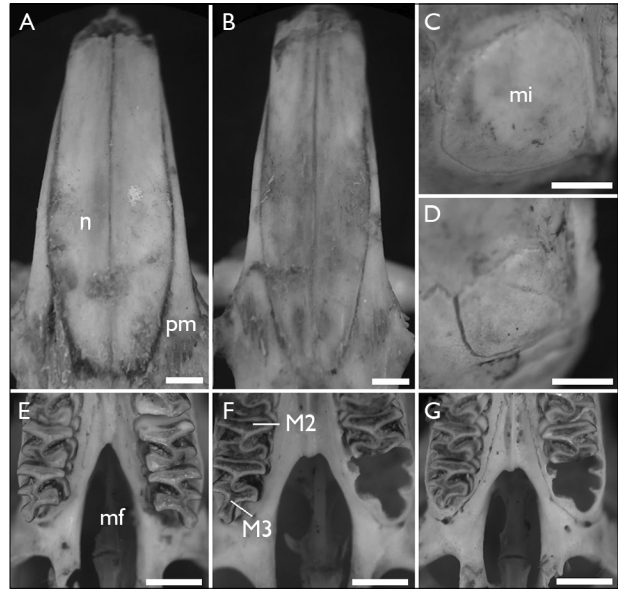


Figure 1. Selected anatomical traits for *Abrocoma cinerea* (= morphotype 1) from northwestern Salta, Argentina. A, B: nasals (n) (A, MACN-Ma 26117; B, MACN-Ma 30.61); C, D: mastoid islands (mi) (C, MACN-Ma 30.61; D, MACN-Ma 30.62); E-G: mesopterygoid fossa (mf) (E, MACN-Ma 30.118; F, MACN-Ma 30.61; G, MACN-Ma G30.62). Other abbreviations: pm = premaxillary; M2 = upper second molar; M3 = upper third molar. Scales = 2 mm.

Braun & Mares (2002) mentions a rounded mesopterygoid fossa as diagnostic for this species.

Despite the morphological variation and the overall similarity among populations, two main morphotypes were recognized on the base of differences in tail length, shape of the interorbital region, and skull size (see the Discussion below). Morphotype 1 is characterized by a short tail (~63 mm), having a proportionally broader interorbital region with divergent and slightly beaded supraorbital borders and moderately developed postorbital processes (Figure 2A). Within this group are included those samples from northwestern Argentina in the provinces of Salta and Tucumán, Bolivia and Chile. Morphotype 2 is represented by samples from the Argentinean provinces of Catamarca, Mendoza, and San Juan and has moderately long to large tails (94-144 mm), proportionally narrow and elongated interorbital regions, with almost parallel outer borders and conspicuous postorbital processes (Figure 2B).

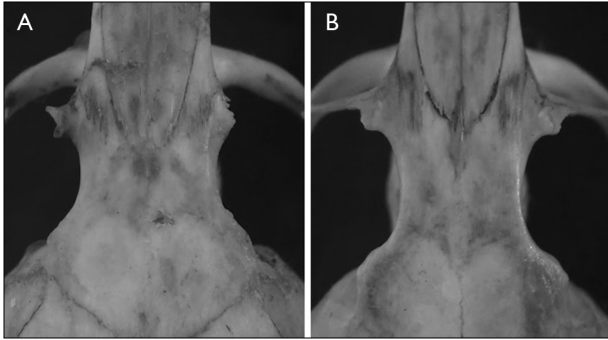


Figure 2. Interorbital region in *Abrocoma*, showing the shape differences between the (A) morphotype 1 (MACN-Ma 30.61; least interorbital breadth = 7.92 mm), and (B) morphotype 2 (MACN-Ma 18828; least interorbital breadth = 6.82 mm) populations.

Results from the principal component analysis showed that plots of individual scores are segregate in two main clusters along the second PC, which are coincident with the morphotypes described above. On PC1, the highest loadings corresponded to BP4 and FL towards positive values and IFL towards the negative ones; on PC2 the largest positive loading corresponds to the LIB (Figure 3; Table 1). Regarding the additional individuals from Mendoza and San Juan, the multivariate space of *A. schistacea* was completely overlapped with those of *A. cf. A. uspollata*.

Among the newly studied specimens, the dorsal coloration of three individuals of *A. cf. A. uspollata* varies between grayish brown (e.g., CMI 7012, CMI 3769) to grayish drab (e.g., CMI 7011). The ventral hairs are dark gray for about three-fourths of their length and with creamy tips. The specimen CMI 7012 was the only in to have a drab throat patch. Hairs of sternal gland are white to base, forming (e.g., CMI 7012) or not (e.g., CMI 7011, CMI 3769) a distinctive patch on mid-venter. The area surrounding the perianal region is covered with hairs white to creamy to base and not contrasting with the overall ventral coloration. The forefeet and hindfeet are covered with white (e.g., CMI 7012) to creamy hairs (e.g., CMI 7011, CMI 3769). The tail was bicolored, grayish brown above and creamy below. Unfortunately, no skins are available for new specimens here referred to *A. schistacea*.

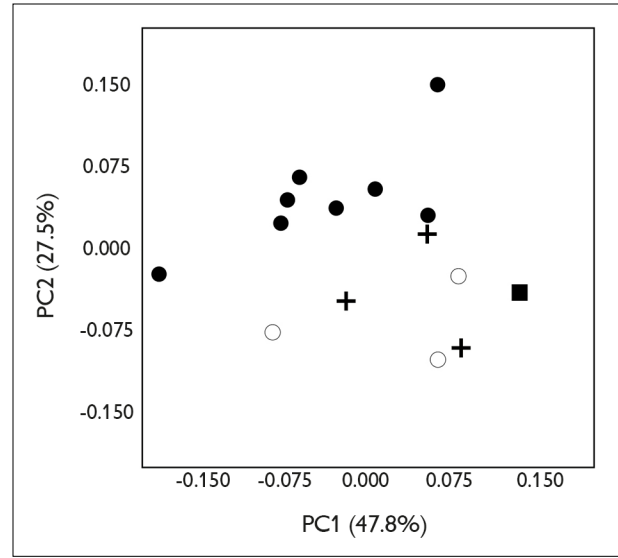


Figure 3. Specimen scores of adult individuals of *Abrocoma* ($n = 15$) for principal components 1 and 2. Symbols are as follow: black circles = *A. cinerea*; black square = *A. budini*; crosses = *A. schistacea*; hollow circles = *A. cf. A. uspollata*.

Table 1. Results of principal components analyses performed on young adult and adult individuals of *Abrocoma* ($N = 15$). See Materials and Methods for explanation of the abbreviations.

	PC1	PC2
TLS	0.2406	0.1449
CIL	0.2369	0.1878
LIB	-0.2027	0.6537
ZB	0.2549	-0.0034
BB	0.1919	0.1800
NL	0.2704	0.2222
NW	0.0963	0.3184
FL	0.3583	-0.1549
DL	0.1897	0.2527
IFL	-0.3328	0.0985
IFW	0.2588	-0.1368
MTR	0.2434	0.0816
PL	0.2071	0.1878
BP4	0.4095	-0.2878
TBL	0.1646	0.2777
Eigenvalue	0.0089	0.00514
% variance	47.79	27.49

DISCUSSION

Qualitative and quantitative external and cranial features have allowed me to recognize two main morphotypes within the *Abrocoma cinerea* species complex. One of these (morphotype 1) coincides with the concept of *A. cinerea* s.s., as had been defined by Braun & Mares (2002). This species is distributed from southern Peru, western Bolivia and northern Chile to northwestern Argentina (with documented records for the provinces of Catamarca, Jujuy, Salta, and Tucumán; Figure 4A). Externally, this species is characterized by a weakly bicolored, short tail (35-42% of head and body length; Patton & Emmons, 2015) and an overall grayish coloration. *A. cinerea* s.s. has an interorbital constriction that is significantly greater than that of the other nominal forms within this species group (> 7.5 mm; Braun & Mares, 2002; Figure 2A); in addition, the supraorbital borders are posteriorly divergent and beaded, with moderately developed postorbital process (Figure 2A). The second morphotype distributes in central-western Argentina, from southern Catamarca province to northwestern Mendoza (Figure 4B). At least five nominal forms can be linked with this morphotype, including *A. budini*, *A. famatina*, *A. schistacea*, *A. uspillata*, and *A. vaccarum*; all these taxa are characterized by grayish to brownish dorsal colorations and moderately long to large and sometimes strongly bicolored tails (53-68% head and body length; Patton & Emmons, 2015; Figure 4B). The interorbital regions of these samples are narrow and elongated, with almost parallel outer borders and conspicuous postorbital processes (Figure 2B).

Most of qualitative morphological traits mentioned as diagnostic for those taxa within the *A. cinerea* species complex (e.g., shape and size of nasals, shape of the anterior border of the mesopterygoid fossa, size of mastoid islands, orientation of zygomata, and procumbency of the upper incisors) prove to be even within populations. This situation diminishes their value as diagnostic traits, at least within this species group, suggesting the need to carry out detailed studies of intraspecific variability to construct robust

morphology-based taxonomic hypotheses (Bezerra & De Oliveira, 2010; Teta *et al.*, 2017).

Despite the fact that the number of specimens included in my multivariate analysis is much smaller than those used by Braun & Mares (2002), results of both studies are fully congruent. The principal component analysis conducted by Braun & Mares (2002) also recovers two main groups within the *Abrocoma cinerea* species complex (Braun & Mares, 2002, fig. 2; see also Figure 5), which correspond with the morphotypes recognized here. In accordance with my data, the specimens studied by Braun & Mares (2002) segregates mostly along the second component, corresponding also to the interorbital constriction the highest absolute loading on this axis.

The overall similarity among the different putative species of *Abrocoma* was firstly noted by Thomas (1921b, p. 217), which stated that "All these Argentine species of *Abrocoma* are nearly allied and very similar to each other, but the characters used, slight as they are, seem to be locally constant, while the respective mountain habitats are well separated and often completely isolated". Partly based on this assertion, Braun & Mares (2002) recommend to regard as distinct species the forms described by Thomas (1919, 1920a, 1920b, 1921a, 1921b), indicating that isolated distribution in patches of rocky habitat along the Precordillera and Sierra Pampeanas chains of the various members of the *cinerea* species complex (excluding *A. cinerea*) would be indicative of a pattern of allopatric speciation. Despite that some records correspond to nearly isolated localities, additional trapping effort suggests that at least in some areas, populations of *Abrocoma* are much widely distributed than previously envisioned (e.g., *A. schistacea* in San Juan; Taraborelli *et al.*, 2015). In addition, rocky environments are almost nearly continuous along western Argentina, suggesting that some level of connectivity among populations is highly likely. Another caviomorph rodent with saxicolous adaptations, the mountain vizcachas of the genus *Lagidium* Meyen, 1833,

present a similar distributional pattern, with more or less phenotypically differentiated populations along this same general area (Teta & Lucero, 2017). As in the case of *Abrocoma*, these rodents have a moderate variability in their dorsal coloration, which has resulted in the description of several subspecies (Teta & Lucero, 2017).

My results are consistent with the recognition of no more than two morphotypes among the *Abrocoma cinerea* species complex, for which the names *cinerea* and *budini* are available for nomenclatorial purposes. Saying that, I cannot rule out that some minor variation in qualitative (e.g., external coloration) and quantitative traits (e.g., tail

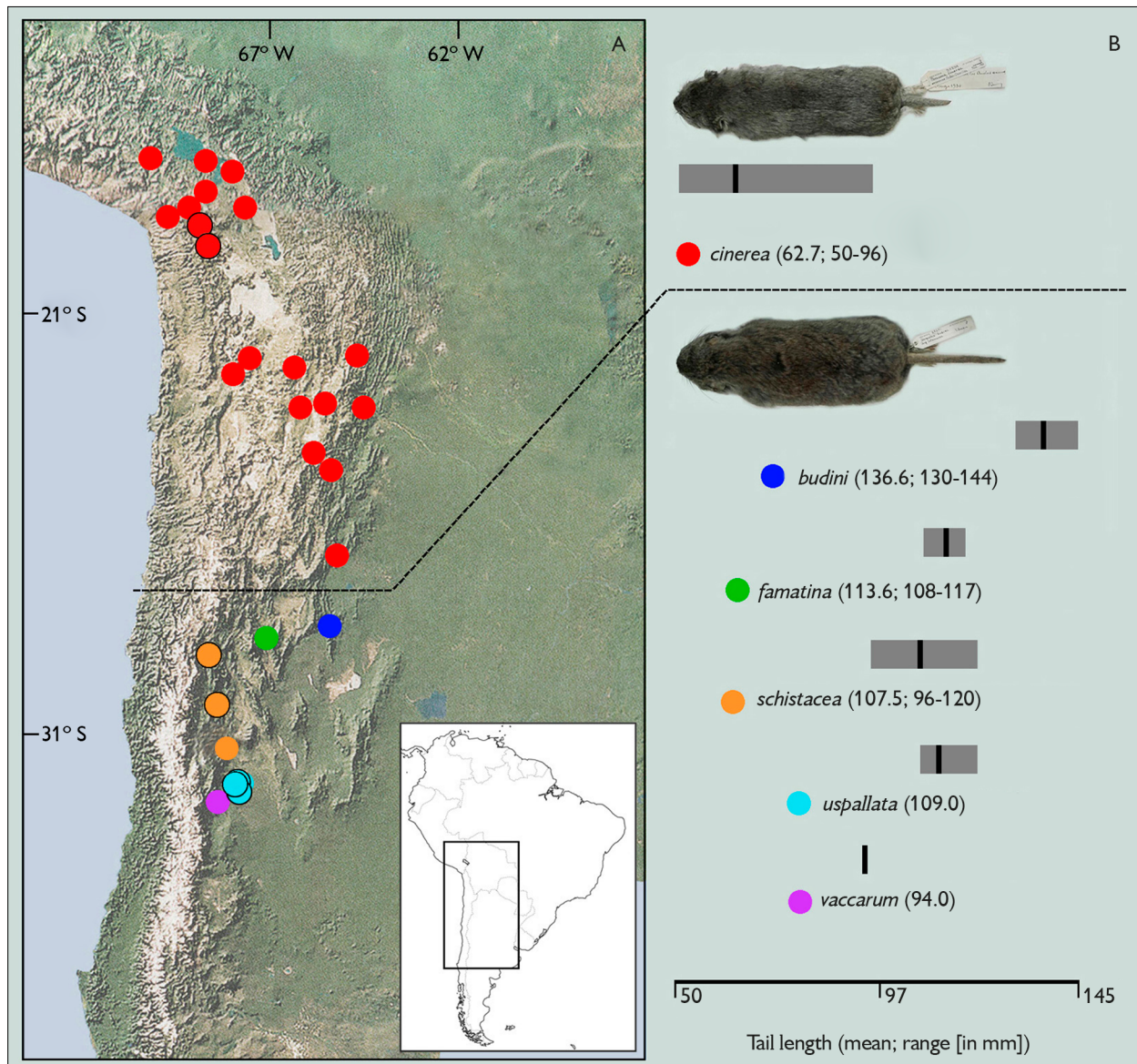


Figure 4. (A) Localities for *Abrocoma* specimens (taken from Braun & Mares, 2002; localities not reviewed by these authors are encircled with black) and (B) differences in tail length between different species; mean values are indicated by black vertical lines, while the gray areas depict the ranges (cf. Braun & Mares, 2002; this work).

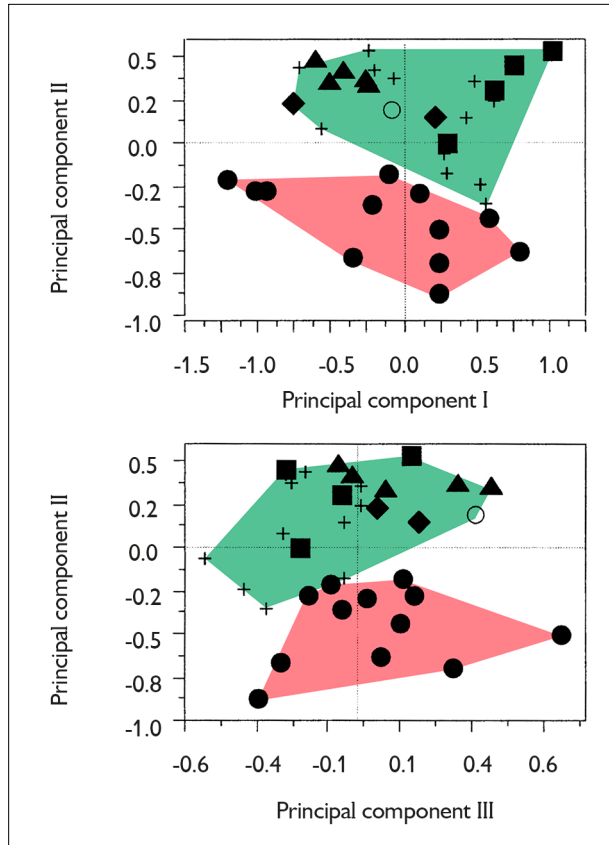


Figure 5. Specimen scores of adult individuals of *Abrocoma* for principal components 1 and 2 (above) and 2 and 3 (below) after Braun & Mares (2002). Symbols are as follow: black squares = *A. budini*; black circles = *A. cinerea*; black triangles = *A. famatina*; crosses = *A. schistacea*; hollow circles = *Abrocoma uspallata*; black diamonds = *A. vaccarum*. Red and green polygons were added by my and correspond to morphotypes 1 (= *A. cinerea*) and 2 recognized in this contribution.

length, *cf.* Braun & Mares, 2002) is indicative of different cryptic species or subspecies within each morphotype. For example, as was noted by Braun & Mares (2002) there are some metric differences between the northern and southern populations of *Abrocoma cinerea* s.s, being those animals from Bolivia and Peru larger than those from northwestern Argentina in some external measurements (e.g., length of head and body, length of hindfoot). In any case, the resolution of these and other questions need the concurrence of additional lines of evidence and approaches, among which phylogenetic analysis of DNA sequences will

be much useful to disentangle the complex taxonomy of these rodents. Until then, I prefer to not make changes in the current classification of this genus, especially taking into account that any taxonomic change could have undesirable consequences in the conservation of these rare rodents.

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Appendix 1. List of studied specimens and their collecting localities. Specimens consist primarily in skins with their associate skulls and are housed in the following institutions: AMNH, American Museum of Natural History (New York, USA); CMI, *Instituto Argentino de Investigaciones de Zonas Áridas* (Mendoza, Argentina); CML, *Facultad de Ciencias Naturales e Instituto Miguel Lillo* (Tucumán, Argentina); FMNH, Field Museum of Natural History (Chicago, USA); MACN, *Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* (Buenos Aires, Argentina); UACH, *Universidad Austral de Chile* (Valdivia, Chile). Specimens not reviewed by Braun & Mares (2002) are indicated with an asterisk.

Abrocoma budini: ARGENTINA: **Catamarca**: Otro Cerro (FMNH 23641; incorrectly referred to the USNM by Braun & Mares, 2002).

Abrocoma cinerea: ARGENTINA: **Salta**: Chorrillos (CML 89, FMNH 35239, MACN-Ma 30.115, MACN-Ma 30.117; MACN-Ma 30.118, MACN-Ma 30.119), San Antonio de los Cobres (MACN-Ma 30.61, MACN-Ma 30.62, MACN 30.63); **Tucumán**: Concepción (CML 91). BOLIVIA: **La Paz**: 8.5 km W of San Andres de Machaca (AMNH 268930). CHILE: **Parinacota**, Chapiquiña, Putre (UACH 3586*); **Camarones**: Salar Surire (UACH 4178*).

Abrocoma famatina: ARGENTINA: **La Rioja**: Sierra de Famatina (MACN-Ma 27.55), without precise locality (MACN 49.247, MACN-Ma 49.248).

Abrocoma schistacea: ARGENTINA: **San Juan**: Reserva Don Carmelo (MACN s/n*), Los Sombreros (FMNH 46157; incorrectly referred to the USNM by Braun & Mares, 2002), Reserva San Guillermo (MACN-Ma 18828), without precise locality (MACN-Ma 39.758).

Abrocoma cf. A. uspillata: ARGENTINA: **Mendoza**: 7 km de Uspallata, on road to Cerro de Siete Colores (CMI 7011*), Arroyo Uspallata, 2000 m (CMI 3769*), Cerro Cacheuta, Agua de Las Avispas (CMI 7080), Villavicencio (CMI 7012*).

