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CRANIAL MORPHOMETRIC ANALYSES OF THE CRYPTIC RODENT SPECIES *AKODON CURSOR* AND *AKODON MONTENSIS* (RODENTIA, SIGMODONTINAE)

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ABSTRACT

Akodon cursor and *A. montensis* are two morphologically cryptic species of Akodontini rodents, undistinguishable by external, skin or qualitative cranial characters, and they can only be separated based on the presence or absence of a gall bladder or by genetic data. The purpose of our study was to assess whether geometric morphometrics of the skull and mandible could identify and separate specimens of *A. cursor* from those of *A. montensis*. We used 74 adult specimens (48 - *A. cursor* e 25 - *A. montensis*) previously identified by their karyotypes, from Southeastern Brazil. We digitized 24, 22, 25, 13 landmarks on images of their skulls (in dorsal, ventral, and lateral views) and mandible, respectively. We assessed size variation (sexual dimorphism and species differences) through t-tests and ANOVAs of centroid sizes of each structure and view, and shape variation through Goodall tests, MANOVAs and Canonical Variates Analyses on Procrustes coordinates. We found significant sexual size dimorphism ($p<0.001$) as well as size differences between species for all four views ($p<0.001$), with males larger and *A. cursor* larger than *A. montensis*, with an overlap between female *A. cursor* and male *A. montensis* specimens. We found significant sexual shape dimorphism in *A. cursor* (all views) and *A. montensis* (lateral view of the skull only), while the two species were completely separated in shape in all four views. Part of the observed variation in shape of the skull and mandible of the two species are likely related to size (allometry), while the lack of adequate ecological information hinders any evaluation of whether skull differences are related to feeding habits.

Keywords: geometric morphometrics; Rodentia; sexual dimorphism; skull, taxonomy

INTRODUCTION

Geometric morphometric constitute a well-established mathematical framework of tools developed since the 1990s that allow the description and representation of the geometry of the studied shape. While in “traditional” (=linear) morphometrics form (understood as shape + size) variation is studied through the analysis of variance and covariance of pairs of linear measurements (Marcus 1990), geometric morphometrics tools describe and locate the areas of shape changes more clearly and represent graphically such changes (Rohlf and Marcus 1993). The use of geometric morphometrics as a tool in mammalogy is now widespread, and employed in systematics, evolution, biogeography and morphology analyses (Adams *et al.* 2004, Kryštufek *et al.* 2012, Sebastião and Marroig 2013).

Several groups of small mammal species, including the Neotropical rodent cricetid subfamily Sigmodontinae, which is the most diverse mammal group in South America, are widely distributed (Reig 1986). Craniodental characteristics define the Sigmodontinae tribes proposed by Vorontsov (1959, apud Weksler 2006), with some support of DNA sequences (Salazar-Bravo *et al.* 2013). The Akodontini, one of the most diverse tribes, is also one of the most widespread groups of Sigmodontinae, occurring in most South American habitats (Reig 1986). Despite the large geographic distribution and habitat utilization, morphology between and within genera shows a high degree of similarities and overlap. Species boundaries can be established with the use of karyotypic data, mainly in the *Akodon* genus (Ventura *et al.* 2012).

The genus *Akodon*, now with 38 recognized species, still presents a complex and unstable taxonomy, including cryptic and sympatric species, in spite of being genetically defined. This genus possesses a wide distribution in South America, with several species being described recently, such as *A. polopi* Jayat, Ortiz, Salazar-Bravo, Pardiñas & D'Elía, 2010 and *A. philipmyersi* Pardiñas, D´Elía, Cirignoli and Suarez, 2005. Species of *Akodon* can be found in several biomes of Eastern South America (Savanna, Caatinga, Atlantic forest and Paraguayan Chaco), characterized by a wide variation of diploid numbers, of 2n = 9 or 10 up to 2n = 52, with most of the members being nevertheless characterized by a low diploid number (Pardiñas *et al.* 2015).

There are species groups defined according to phylogenetic analysis (for a complete review, see Jayat *et al.* 2010 and Pardiñas *et al.* 2015). The only widespread species group at the Eastern part of South America is the *Akodon cursor* group, which includes five cryptic species, one with the broader latitudinal distribution – *A. cursor* (Geise 2012). Both *A. montensis* and *A. cursor*, besides being cryptic in their external and craniodental morphology are found in sympatry in some localities (Geise *et al.* 2005). The non-described third species, with a diploid number of 2n = 10 (Silva and Yonenaga Yassuda 1998) has a disjunct distribution (Silva *et al.* 2006). The karyotype of *A. cursor* has a diploid number that varies from 14 to 16 (Fagundes *et al.* 1998) and *A. montensis* presents diploid numbers equal to 24 or 25 (Rieger *et al.* 1995). Internal characters, such as the absence or presence of the gall bladder can also be used to distinguish them (Geise *et al.* 2005), or through molecular (Geise *et al.* 2001) and traditional morphometric analyses (Geise *et al.* 2005).

The difficulty to identify specimens of these two species that do not have data on gall bladder or genetics raised questions about the correct identification of individuals included in ecological studies or the analysis of specimens deposited in collections. To increase the knowledge on the diversification and differentiation of these two species, we analyzed size and shape variation within and between *Akodon* *cursor* and *Akodon montensis* using geometric morphometrics tools, in order to assess whether a geometric morphometrics approach results in a better discrimination than a traditional morphometric analysis.

MATERIAL AND METHODS

Sample

We only used specimens identified through their karyotypes, in order to avoid misidentification. Specimens are housed in the collection of Laboratório de Mastozoologia, Universidade do Estado do Rio de Janeiro, and will be deposited in the Mammal Collection of the Museu Nacional, Rio de Janeiro. Only adults were included, based on patterns of dental eruption following Voss (1991). Specimens were collected in southeastern Brazil (Appendix). For all specimens, we recorded digital images of the skull in dorsal, ventral and lateral view, and of the mandible in lateral view, using the same orientation protocol for all specimens.

Landmarks

Landmark coordinates for all views of skull and jaw were captured using TPSDig2 (Rohlf 2006). Two-dimensional homologous landmarks were digitized on both sides of the skull to facilitate visualization in the graphic representations of deformations grids. For statistical analyses an average of the homologous landmarks after reflection on the symmetry axis was used, to avoid the redundancy of the data (inflation of degrees freedom). Twenty-four landmarks were established for dorsal, 22 for ventral and 25 for lateral of skull views. For mandibles, 13 landmarks were established. Landmarks are illustrated in Figure 1 and are defined as follows. In bilateral views, pairs of numbers refer to right and left

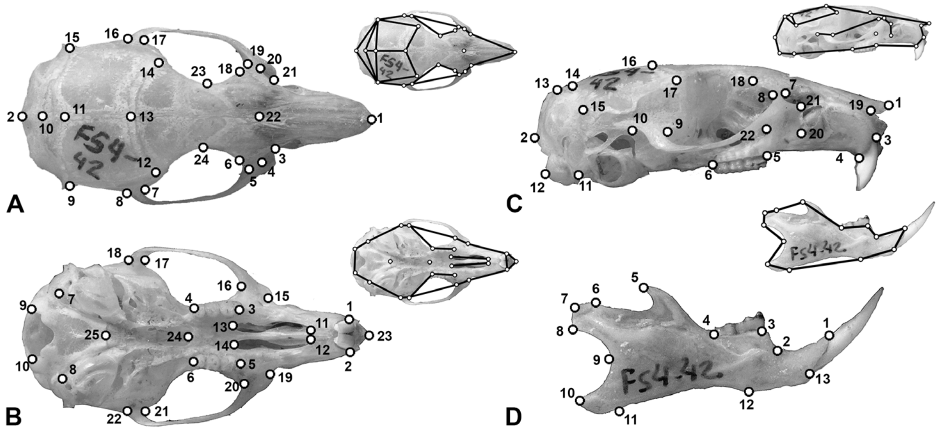

Figure 1. Landmarks used on the dorsal, ventral and lateral views of the skull and on the lateral view of the mandible. Refer to text for precise description of landmark locations. For each view, a scheme with lines linking landmarks, as used in subsequent graphs for clarity and visualization, is presented.

landmarks, respectively (dorsal view) or to left and right landmarks, respectively (ventral view).

Dorsal view of the skull: (1) frontal tip of internasal suture, (2) posterior border of supraoccipital, at the nuchal crest, (3, 21) external border of maxillary at the most anterior curvature of zygomatic arch, (4, 20) more concave curve point of zygomatic notch, (5, 19) internal border of maxillary, at the most anterior curvature of zygomatic arch, (6, 18) most anterior point of maxillary and frontal suture, (7, 17) more concave curve point of squamosal root of zygomatic arch, (8, 16) external posterior border of squamosal root of zygomatic bar, (9, 15) intersection (lateral margin) of parietal and interparietal suture, (10) suture between interparietal and supraoccipital at he nuchal crest, (11) suture interception of both right and left parietal and interparietal in the sagittal plane, (12, 14) intersection of squamosal, parietal and frontal sutures, (13) sagittal suture between frontals and parietals, (22) sagittal suture between frontals and nasals, (23, 24) smaller frontal width (interorbital width).

Ventral view of the skull: (1, 2) lateral margins of incisor alveoli at premaxillary, (3, 5) anterior alveolar margin of the upper molar row, at maxillary, (4, 6) posterior alveolar margin of the upper molar row at palatines, (7, 8) posterior border of ectotympanic part of auditory bulla, (9, 10) most posterior point of occipital condyles, (11, 12) anterior border of incisive foramen, (13, 14) posterior border of incisive foramen, (15, 19) external border of maxillary root of zygomatic arch, (16, 20) internal more concave curve point of maxillary root of zygomatic arch, (17, 21) internal more concave curve point of inner extreme curvature of squamosal root of zygomatic arch, (18, 22) posterior inferior tip of squamosal root of zygomatic bar, (23) tip of nasals at their anterior suture in front of the gnathic process, (24) posterior midline suture of palatines, (25) midpoint of suture between basisphenoid and basioccipital.

Lateral view of the skull: (1) anterior tip of the nasals, (2) skull most posterior border, at supraoccipital bone, above the foramen magnum, (3) labial upper junction of incisors and maxillary, (4) lingual upper junction of incisors and maxillary, (5) anterior border of upper molar row at the alveolar process of maxillary, (6) posterior border of upper molar row at maxillary, (7) most anterior point of the zygomatic arch, at the nasolacrimal foramen, (8) inner extreme point of squamosal root of zygomatic arch, (9) internal more concave curve point of squamosal root of zygomatic arch, (10) posterior superior tip of squamosal root of zygomatic arch, (11) posterior base of ectotympanic part of auditory bulla, (12) most posterior border of occipital condyle, (13) junction of parietal and interparietal sutures, (14) suture between the interparietal and supraoccipital, (15) intersection (lateral margin) of parietal and interparietal suture, (16) suture between frontals and parietals, (17) intersection of squamosal, parietal and frontal sutures, (18) anterior junction of maxillary and the frontal sutures, (19) anterior border of suture between nasal and premaxillaries, (20) anterior external border of zygomatic notch, (21) anterior border of zygomatic plate, (22) point of larger inflection of the subsequent curvature of the zygomatic plate.

Mandible: (1) lingual upper junction of lower incisors and dentary, (2) posterior lower border of diastema and lower molar row, (3) anterior edge of toothrow, at colon of m1, (4) posterior border of m2, at contact with anterior border of m3, (5) tip of coronoid process, (6) anterior edge of articular surface of condylar process, (7) posterior edge of articular surface of condylar process, (8) most posterior point of condylar process, (9) internal more concave curve point of posterior boundary of the mandible, (10) tip of angular process, (11) point of maximum external curvature on inferior border of angular process, (12) inferior end of mandibular symphysis and (13) labial lower junction of lower incisors and dentary.

We assessed repeatability of each (x and y) coordinate of each landmark by setting landmarks twice, in different days and different order, in a subset of 30 specimens. Afterwards, repeatability is calculated as the intraclass correlation coefficient, following Falconer & Mackay (1996). Repeatability for each coordinate of each landmark in all four views varied from 98.96% to 99.99%.

Statistical analyses

Isometric size effects were removed by equaling centroid sizes to 1, and landmark configurations were submitted to a generalized Procrustes analysis - GPA (Rohlf and Slice 1990) to remove information contained in landmarks unrelated to shape, thus generating a matrix of shape variables independent of size.

Sexual Size Dimorphism (SSD) was analyzed comparing centroid sizes of males and females for each view of both species using *t*-tests. To evaluate size differentiation between species and sexes, an analysis of variance (ANOVA) on centroid sizes was performed, comparing between four groups (males of *A. cursor*, females of *A. cursor*, males of *A. montensis* and females of *A. montensis*), followed by Tukey post-hoc comparisons tests (Zar 1996). Sexual dimorphism in shape was investigated with Goodall´s F-test for each view of both species. Shape differentiation in species and sexes was assessed with a Multivariate Analysis of Variance (MANOVA), followed by Canonical Variate Analysis (CVA). Shape variables were regressed onto the first two canonical axes, and deformation grids for the most the ends of the deformations along each axis were show to illustrate shape variation along these axes.

All geometric morphometrics statistical analyses were performed using programs of the TPS series (Rohlf 2006) and IMP (Sheets 2004).

RESULTS

Examined material

We examined 74 specimens of *A. cursor* and *A. montensis*. Sample sizes for each species and sex are presented in Table 1. A full list of specimens examined with respective collecting localities is presented in Appendix 1.

Size differentiation

Both species were significantly sexually dimorphic in size ($p < 0.001$) in all views (Table 2), with males being larger. The ANOVA on centroid size showed significant differences between the four groups ($p < 0.001$) for all views. The Tukey tests indicated significant differences between species and sex for all views. Almost all compared pairs of species and sexes were significantly different in size for all views and structures, except for males and females of *A. montensis*, which showed no difference in mandible size, and for males of *A. montensis* and females of *A. cursor*, which were not different in skull size, but only in mandible size (Table 3).

Shape differentiation

Goodall´s F-tests showed significant sexual dimorphism in shape in *A. cursor* for all views ($p < 0.001$) and all but the lateral view of the skull in *A. montensis* ($p < 0.01$) (Table 4). Differences between species were also significant. The first canonical axis obtained in the CVA explained 71.5% (skull, dorsal view), 71.7% (skull, lateral view), 67.4% (skull, ventral view) and 80.8% (mandible) of the total observed variation. In all analyses, the first axis

Table 1. Numbers of images of the skull and mandible of *Akodon cursor* and *Akodon montensis*, by sex, used in this study.

	Akodon montensis		***Akodon cursor***		**Total**
	♂	♀	♂	♀	
Skull	13	12	24	24	73
Mandible	12	13	25	24	74

Table 2: Descriptive statistics of the centroid size, in mm (Mean, Standard Deviation – SD - and sample size - n), for each structure and analyzed view, and result of the t-tests between the sexes. * p<0.01, ** p<0.001.

		Akodon montensis			***Akodon cursor***		
		Mean	**(SD)**	**n**	**Mean**	**(SD)**	**n**
Dorsal view of the skull	♂	64.51	3.08	13	69.65	6.34	24
	♀	61.15	9.01	12**	66.41	5.59	24**
Lateral view of the skull	♂	88.95	8.93	12	95.93	12.57	24
	♀	83.41	23.69	12**	90.77	11.11	24**
Ventral view of the skull	♂	62.82	5.43	13	67.98	6.59	24
	♀	58.68	12.42	12**	64.41	6.74	23**
Mandible	♂	40.35	3.68	13	45.85	5.27	25
	♀	38.07	7.83	12**	43.10	4.59	24*

clearly separates the two species. The second canonical axis explained 28.5% (skull, dorsal view), 14.6% (skull, lateral view), 32.6% (skull, ventral view) and 19.2% (mandible) of the total observed variation. In all analyses, the second axis separates, to a greater or lesser extent, sexes within the two species, except for the lateral view of the skull, in which a third canonical axis separates sexes of *A. montensis* better than on the second axis. The results of the CVAs along with the deformation grids representing the shapes associated with the higher and lower scores for each axis are presented in Figures 2 to 6.

For the dorsal view (Figure 2) CV1 separates the studied species almost completely. *Akodon cursor* specimens have relatively shorter skulls, shorter rostra, shorter nasals and relatively longer zygomatic arches, while the opposite features are found in *A. montensis.* Additionally, CV2 separates almost completely males and females of *A. cursor*, but differences are much

Table 3: Results of the Tukey post-hoc tests for centroid size of the skull and mandible of *Akodon cursor* and *Akodon montensis*, following the ANOVA on centroid size (p < 0.001). The letters indicate significant differences between the groups in line and column headings for the indicated views (p < 0.01). D. view dorsal of the skull; V. view ventral of the skull, L. view lateral of the skull; M. Mandible. -. Not significant.

		***A. montensis* ♂**	***A. montensis* ♀**	***A. cursor* ♂**	***A. cursor* ♀**
A. montensis	♂	-	DVL	DVLM	M
A. montensis	♀		-	DVLM	DVLM
A. cursor	♂			-	DVLM
A. cursor	♀				-

Table 4: Results of the Goodall´s F-tests for sexual dimorphism in shape in each of the analyzed structures in *Akodon cursor* and *Akodon montensis*. df. Degrees of freedom. n.s. Non significant.

View		**F**	***df***	**p**
Dorsal view of the skull	*A. cursor*	3.07	26; 1196	< 0.001
	A. montensis	1.67	26; 598	< 0.02
Lateral view of the skull	*A. cursor*	3.15	40; 1840	< 0.002
	A. montensis	1.56	40; 920	< 0.01
Ventral view of the skull	*A. cursor*	4.16	24; 1080	< 0.001
	A. montensis	1.35	24; 552	n.s.
Mandible	*A. cursor*	3.76	22; 1034	< 0.001
	A. montensis	1.71	22; 506	< 0.02

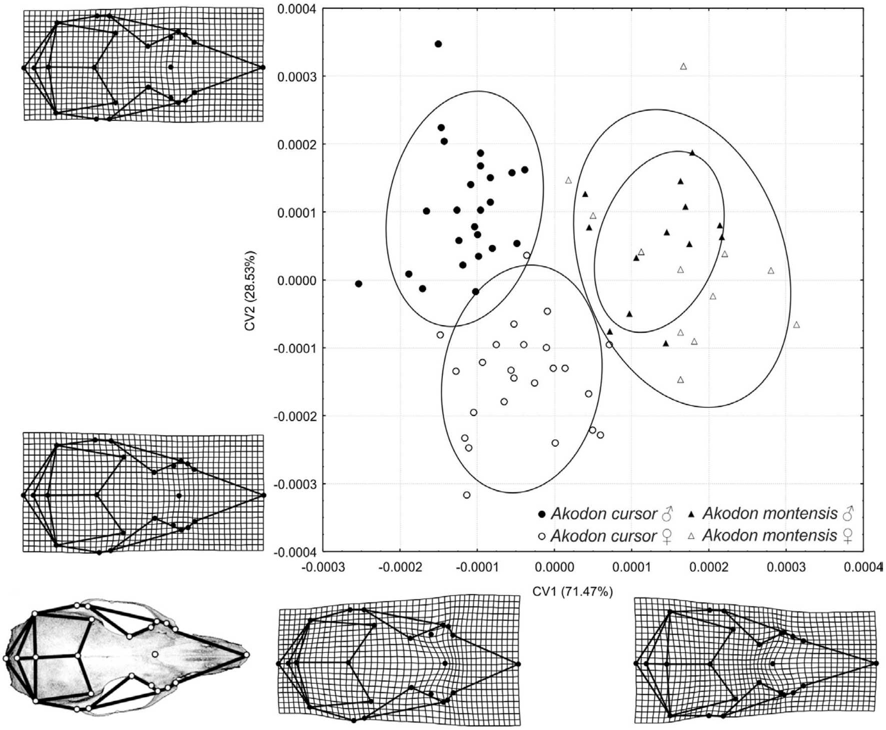

Figure 2. Canonical variates (CV) analysis of shape variables (partial warps + uniform components) of the skull in dorsal view of the studied sample of *Akodon cursor* and *Akodon montensis*. Grids indicate deformation for shapes associated with the extremes of each CV (x3), from a multivariate regression of shape variables onto CV scores for each axis.

subtler than between species: females possess relatively smaller nasals, wider braincases and shorter zygomatic arches when compared to males. Males and females of *A. montensis* overlap completely in shape of the skull in dorsal view.

For the lateral view (Figure 3) CV1 completely separates species, and additionally provides and almost complete separation of sexes in *A. cursor*. *Akodon montensis* of both sexes are clearly separated from *A. cursor* by possessing a more bulbous braincase, nasals anterior tips less protruded, relatively shorter parietals, and a greater angle of the zygomatic plate. The same features that distinguish *A. montensis* from *A. cursor* further separate females from males of the latter species, with males showing the extreme opposite features of those of *A. montensis* and females presenting and intermediate phenotype. Sexes of *A. cursor* are also partially separated along CV2, with males presenting a more elongated skull and with the anterior end of the zygomatic arch located more anteriorly

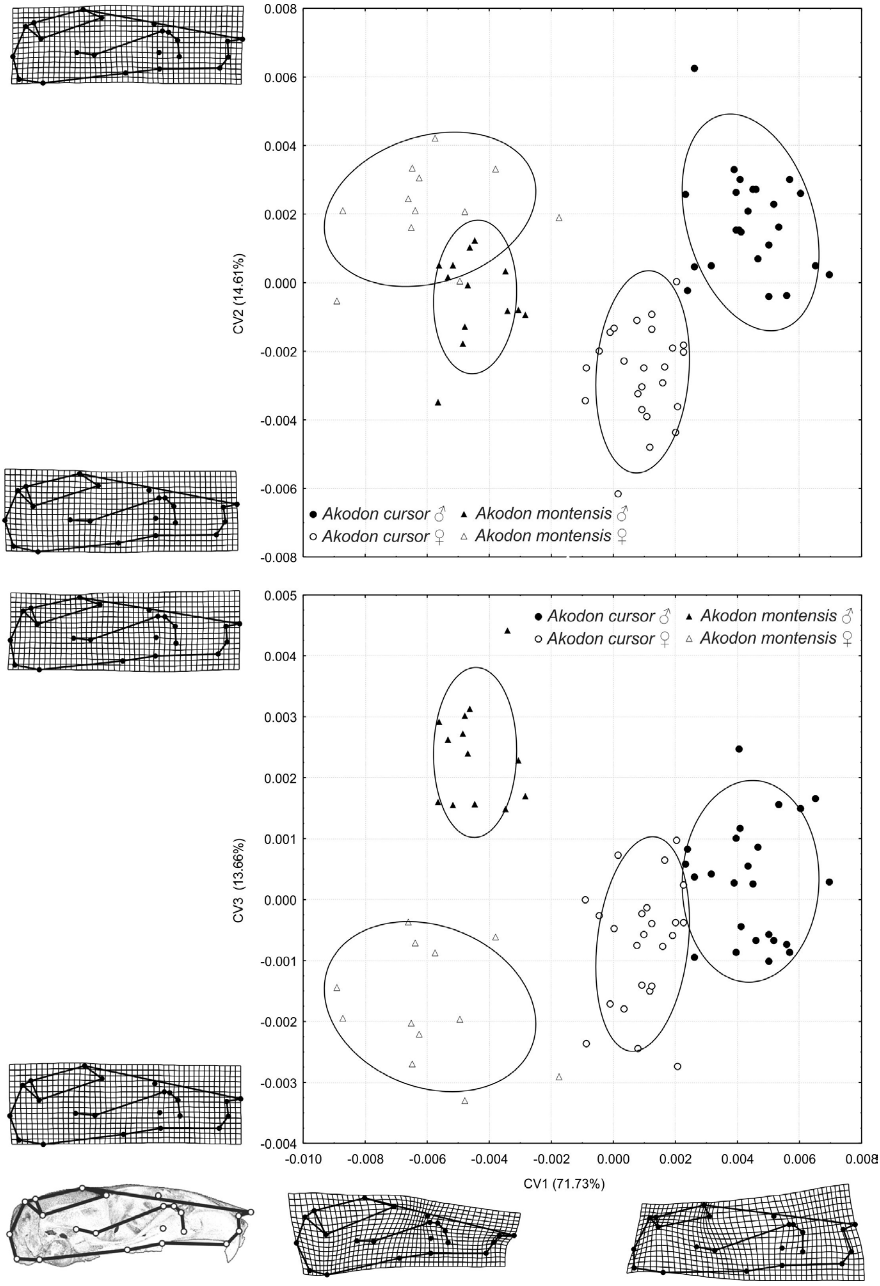

Figure 3. Canonical variates (CV) analysis of shape variables (partial warps + uniform components) of the skull in lateral view of the studied sample of *Akodon cursor* and *Akodon montensis*. Grids indicate deformation for shapes associated with the extremes of each CV (x3), from a multivariate regression of shape variables onto CV scores for each axis.

as compared to that of females. Sexes of *A. montensis* are completely separated along CV3, with females possessing a skull that is more arched ventrally than that of males.

For the ventral view (Figure 4) CV1 separates the two species completely. *Akodon cursor* specimens have shorter rostra, tips of the nasals protruding farther anteriorly in relation to the incisives, relatively shorter and more divergent palatine foramina, wider braincases and relatively longer molar series. For this view, CV2 separates almost completely males and females of both species, with similar features found on males and females of both taxa. In both species, the tip of the nasals of females protrude more anteriorly ahead of the incisives than those of males.

For the mandible (Figure 5) CV1 separates the studied species completely. *Akodon cursor* specimens have relatively higher coronoid processes and narrower angular processes, as well as shorter and stouter incisive alveoli. Additionally, CV2 separates completely males and females of *A. montensis* and

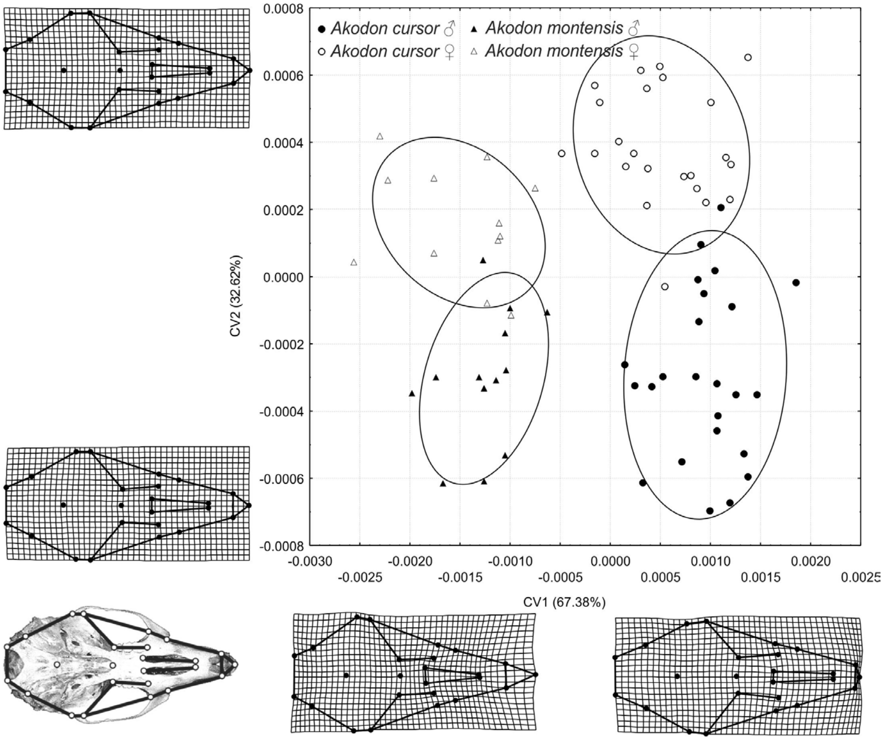

Figure 4. Canonical variates (CV) analysis of shape variables (partial warps + uniform components) of the skull in ventral view of the studied sample of *Akodon cursor* and *Akodon montensis*. Grids indicate deformation for shapes associated with the extremes of each CV (x3), from a multivariate regression of shape variables onto CV scores for each axis.

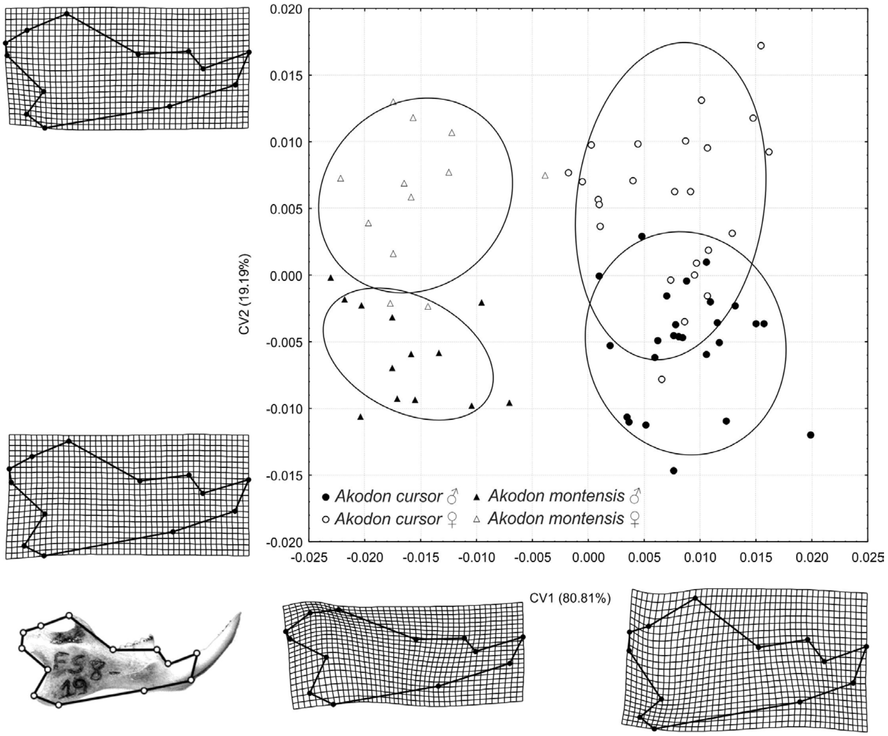

Figure 5. Canonical variates (CV) analysis of shape variables (partial warps + uniform components) of the mandible of the studied sample of *Akodon cursor* and *Akodon montensis*. Grids indicate deformation for shapes associated with the extremes of each CV (x3), from a multivariate regression of shape variables onto CV scores for each axis.

partially those of *A. cursor*, with females having condylar processes that are more displaced caudally.

DISCUSSION

Previous results using traditional (linear) morphometrics had shown the presence of sexual dimorphism in both species, as well as some level of morphometric divergence between them (Geise *et al*. 2005). However, geometric morphometric results provided a clearer distinction between these two taxa, both in size and shape. Geise *et al*. (2005) found some levels of overlap between their whole sample of *A. cursor* and *A. montensis*. In their study, sexes were pooled after a correction in size for each linear measurement, and as multivariate analyses of linear measurements address both size and shape simultaneously, it is possible that such correction might have removed effects of sex differences in each measurement individually, yet did not address differences in shape between sexes in each species, and this resulted in the observed overlap. This hypothesis could be tested using other methods of removing size or allometry effects (as sexes are shown here to be sexually dimorphic in both size and shape), such as the multivariate allometric size-scaling (Lleonart *et al*. 2000). When size and shape are analyzed separately, females are smaller than males in both species, and *A. montensis* are smaller than *A. cursor* (as traditional morphometric had shown, Geise *et al*. 2005). This leads to a potential overlap in size between larger *A. montensis* males, and smaller *A. cursor* females. However, differences in shape were also found here between sexes and species, and as shape differences between closely related taxa are frequently allometric, due to shared static and/or ontogenetic trajectories (Marroig 2007, Sebastião and Marroig 2013), it is very likely that the overlap in size between females *A. cursor* and males *A. montensis* results in a similar overlap in shape, thus leading to the observed overlap in the traditional morphometrics approach. Procrustes superimposition removes isometric size effects, but shape information that is allometrically related to size remains after this step. The fact that a clear separation in shape is obtained in some views (e.g. ventral view of the skull, Figure 4, and mandible, Figure 5) suggests that there is part of the shape variation of these structures that is not directly related to size. However, in the dorsal and lateral views of the skull, females *A. cursor* are in an intermediate position between males of the two species along CV1 (Figures 2 and 3), thus suggesting that in these views, the shape variation observed is allometric. As a whole, however, it seems that a geometric morphometric approach allowed for a clearer distinction between the sexes and species, both in size and shape (mostly due to the fact that they are formally separated and analyzed as such), as has occurred in other mammal groups, in which geometric morphometric approaches allowed for a clear distinction between taxa where traditional approaches had failed to do so (Monteiro-Filho *et al.* 2002).

A proper evaluation of the diversity of any given region can be frequentely understimated because of the occurrence of cryptic (and thus unaccounted for) species. Although cryptic species are more frequent in invertebrates, the use of genetic tools in the study of diversity in some vertebrate species have provided enough additional evidence to separate them into species groups, based on their evolutionary history (Oliver *et al.* 2009). The genus *Akodon* is known to present low diversity in the external and craniodental morphology (Reig 1986, Pardiñas *et al.* 2015). Geise *et al*. (2004), however, showed that the study of the soft anatomy might reveal additional taxonomically informative characters, as some differentiation between *Akodon* species can be related to the presence or absence of the gall bladder.

Some species with a high chromosomal diversity between and within population, with a sympatric or partially overlapping geographic distribution pattern may indicate scenarios with similar histories as those seen in the South American Atlantic Forest with *A. cursor* and *A. montensis*. The *Akodon aerosus* (*A. aerosus* (2n=22, 38 and 40) and *A. torques* (2n=22, 24 and 26)) and *A. dolores* species groups

(*A. toba* (2n=40, 42, 43)) have a high diploid number variation. The three different karyotypes observed in *A. aeorosus* occurs in three different and non-sympatric areas in Peru (Ayacucho, Puno and Cusco), but with overlap of their distributions with *A. siberiae* (with 2n=38) in Cochabamba, Bolivia, with *A. surdus* in Machu Picchu, Peru and with *A. torques* in some localities in Peru. *Akodon toba* can be found in sympatry with *A. dayi* (Pardiñas *et al*. 2015). It is probable that morphometric analyses, and particularly those using geometric morphometric techniques, will be able to identify craniodental differentiation indicating strong geographic variation or possible different species, as phylogenetic analyses using DNA sequences have already shown (Jayat *et al*. 2010).

Morphological differences between closely related species may have an allometric explanation, in those cases where selection, particularly disruptive selection, might have driven species apart mostly along the existing size variation, as a way to avoid niche overlap, for example. In fact, size usually constitutes one of the major axis of existing variation in organisms, as size can be easily changed by either interrupting or extending growth, for example (Alberch *et al.* 1979), and as such, represent lines along which the major amounts of variation exist and therefore the axes along which selection will be acting more easily (called lines of least evolutionary resistance) (Marroig and Cheverud 2005). Alternate explanations for the existing differences in size or shape could be tentatively related to ecological differences. This, however, requires adequate information on the species' ecology, and such information is very often lacking for the vast majority of species of Neotropical small mammals. The presence or absence of the gall bladder in *A. cursor* and *A. montensis* (Geise *et al.* 2004) could be related to different feeding habits, for example, and it is therefore possible that such differences could also be reflected in the skull and mandible size or shape differences.

The amount of existing information on the feeding ecology of these two species is still restricted to a few studies. In *A. cursor*, field studies point to a diet based mostly in invertebrates (Carvalho *et al.* 1999), but laboratory food experiments have more recently pointed to a more diverse diet where fruits and seeds could constitute the major food type (Finotti *et al.* 2012), and *A. cursor* is more likely to be actually an omnivorous species, which is also reflected in a generalized digestive tract. Field studies indicate that *A. montensis* have a diet based on animal and vegetal items, with 1/3 of the items recovered in fecal samples being of animal origin and 2/3 of vegetal material, but they are also considered omnivorous (Vieira *et al.* 2006, Talamoni *et al.* 2008). In fact, the existing amount of field data does not allow a proper distinction of the diet of these two species that could be posteriorly related to craniodental morphology. Standardized laboratory experiments, however, indicate that *A. cursor* is a more generalist species than *A. montensis*, which is apparently more insectivorous (Finotti *et al.* 2012). These data, as informative on the species' basic ecology as they can be, are unfortunately insufficient to relate putative dietary specializations to skull morphology, and such inferences would be highly speculative. As a consequence, a proper appraisal of the existing variation of skull morphology in these species would require both the inclusion of all closely related species, so that the actual effects of phylogeny can be assessed, and still unavailable but strongly needed adequate ecological information.

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Appendix 1. Gazetteer of collecting localities and specimens examined: FS – Field number of the Laboratório de Ecologia de Vertebrados, UFRJ; LG – Field number of Lena Geise. States are listed in bold uppercase, followed by municipalities in bold. In parenthesis coordinates and elevation in meters.

Akodon cursor

RIO DE JANEIRO, **Guapimirim**, Fazenda Chorona (22^{o}33'46"S 42^{o}57'13"W, 100m), Males: FS04 – 2-4, 6, 9, 11, 37, 42, 43, 45, 46, 53-55, 58, 61; Females: FS04 - 10, 14, 19, 33, 36, 41, 48, 71, 75. Fazendas Consorciadas (22^{o}331'4"S, 42*o*54'09"W, 150m), Males: FS05 - 3, 58, 69; Females: FS05-36. Fazenda Chorona (22^{o}33'46"S 42^{o}57'13"W, 100m), Male: FS 07-08; Female: FS07-25. Fazenda Iguaçu (23^{o}31'11"S, 42^{o}53"12"W, 100m), Males: FS08 - 73, 79, 80; Females: FS 08 - 19, 76. **Cachoeiros de Macacú**, Fazenda Pica Pau Amarelo (22^{o}31'01"S, 42^{o}45'16"W, 200m). Males: FS17 - 3, 13, 35; Females: FS17 - 1, 2, 8, 14, 17. **BAHIA, Joaíma**, Fazenda Anga Pehy (16^{o}43'7.6"S, 41^{o}14'57.6"W, 820m), Males: LG477, 485, 524, 527; Females:LG 474, 497, 500, 501, 503, 506, 526. **Pau Brasil**, Fazenda Água Santa (15^{o}27'S, 39^{o}37'W, 90m). Male: LG196; Females: LG190, LG200.

Akodon montensis

SÃO PAULO, Bananal, Estação Ecológica do Bananal (22^{o}48'22"S, 44^{o}22'22"W, 1119m), Males: EEB695, 703, 713; Females: EEB563, 651, 676, 678, 680. **São João da Boa Vista** (21^{o}58"S, 46^{o}47'W, 767m). Female: HGB-DB01. **RIO DE JANEIRO, Teresópolis**, Parque Nacional da Serra dos Órgãos, Abrigo Paquequer (22^{o}27'S, 42^{o}59"W, 1200m). Males: FS10 - 3, 14, 26, 31, 43, 44, 52, 53, 61, 84, 87, 89, 94; Females: FS10 - 27, 28, 30, 33, 45, 65, 77, 96.