



MORPHOMETRIC DIFFERENTIATION AND DISTRIBUTIONAL NOTES
OF THREE SPECIES OF *AKODON* (MURIDAE, SIGMODONTINAE, AKODONTINI)
IN THE ATLANTIC COASTAL AREA OF BRAZIL ¹

(With 3 figures)

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ABSTRACT: Twenty cranial measurements and three body variables were compared among samples of three species of the genus *Akodon* previously identified by karyotype, using univariate (ANOVAs) and multivariate (Discriminant analyses) methods. A geographic analysis for *A. montensis* and *A. cursor* from localities in the State of Rio de Janeiro and adjacent areas was also performed. *Akodon montensis* presented smaller values for most cranial measurements, whereas *A. aff. cursor* showed larger values, with *A. cursor* showing intermediate cranial size. The discriminant analysis revealed a clear separation of *A. aff. cursor* from *A. cursor*, while all other pair of species presented partial overlap. All *A. aff. cursor* and most *A. cursor* were correctly classified, but classification of the *A. montensis* sample was less successful, probably due to the greater size or to the size-related variation in cranial shape of some older specimens. In the studied area, *A. montensis* was exclusively collected in altitudes higher than 800m above sea level, whereas *A. cursor* was found from sea level to altitudes above 1000m. ANOVAs showed one significantly different climatic variable, suggesting some segregation between these two species. Correct classification based solely on the discriminant function extracted on the basis of the present samples could not be fully achieved, although our results suggest that larger samples of karyotypically identified specimens will allow more conclusive patterns on the morphometric differentiation of these taxa.

Key words: Rodentia, biogeography, Atlantic Forest, morphometrics, distribution.

RESUMO: Diferenciação morfológica e notas sobre a distribuição de três espécies de *Akodon* (Muridae, Sigmodontinae, Akodontini) na área costeira atlântica do Brasil.

Vinte medidas cranianas e três variáveis corpóreas foram comparadas entre amostras de três espécies do gênero *Akodon* previamente identificadas por cariótipo, através de análises de variância e análise discriminante. Uma análise geográfica para *A. montensis* e *A. cursor* foi conduzida para amostras de localidades do Estado do Rio de Janeiro e adjacências. *Akodon montensis* apresentou valores menores para a maioria das medidas cranianas e *A. aff. cursor* as maiores medidas, com *A. cursor* apresentando um tamanho craniano intermediário. A análise discriminante mostrou uma separação clara de *A. aff. cursor* e *A. cursor*, enquanto que os demais pares de espécies se sobrepuseram parcialmente. Todos os exemplares de *A. aff. cursor* e a maioria dos de *A. cursor* foram corretamente classificados, mas a classificação da amostra de *A. montensis* apresentou resultados menos satisfatórios, possivelmente relacionados ao tamanho maior ou à variação na forma craniana relacionada ao tamanho em alguns espécimens mais velhos. Na área estudada, *A. montensis* foi coletado exclusivamente em altitudes superiores a 800m acima do nível do mar, ao passo que *A. cursor* foi encontrado do nível do mar até altitudes acima de 1000m. As ANOVAs evidenciaram uma variável climática significativamente diferente, sugerindo alguma segregação entre estas duas espécies. Uma classificação correta baseada somente na função discriminante revelada pelas amostras analisadas aqui não pôde ser obtida, mas as tendências na estruturação da variação morfológica entre as amostras de espécimens sugerem que com amostras maiores será possível obter padrões mais conclusivos sobre a diferenciação morfológica destes táxons.

Palavras-chave: Rodentia, biogeografia, Floresta Atlântica, morfometria, distribuição.

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INTRODUCTION

Among the highly diverse sigmodontine rodents, some genera in the Atlantic Forest include cryptic species, whose correct identification can only be assessed with the use of genetic techniques. For example, specimens of *Brucepattersonius* Hershkovitz, 1998 (a recently described akodont genus including several cryptic species) with similar morphological and karyological features could only be differentiated through the analysis of mitochondrial DNA (SMITH & PATTON, 1993). Similarly, the genus *Akodon* Meyen, 1833, also does not present well defined species boundaries as determined by classical morphological characters, although it represents one of the most speciose genera within the Akodontini tribe (SMITH & PATTON, 1993), with 45 recognized species (MUSSEY & CARLETON, 1993). Such morphological similarity between two or more congeneric species reduce the usefulness of previously collected specimens that did not happen to be identified by genetic tools.

Among species of the genus *Akodon* usually trapped in the Atlantic coastal area of Brazil, three of them, *Akodon montensis* (Thomas, 1913), *A. cursor* (Winge, 1888), and *A. aff. cursor* are morphologically so similar that a precise diagnosis based solely on morphometric characters is not always possible (GEISE, WEKSLER & BONVICINO, 2004). The two former species were grouped together in the so-called *cursor* complex (LIASCOVICH & REIG, 1989), in which GEISE, SMITH & PATTON (2001) also include *A. aff. cursor* and another yet undescribed species studied by SILVA & YONENAGA-YASSUDA (1998). Maximum parsimony and neighbor joining analyses of mtDNA sequences with bootstrap values of 62% and 79% respectively showed that *A. aff. cursor* form a distinct monophyletic clade (GEISE, SMITH & PATTON, 2001).

The specific status of these species is well defined on a genetic basis, based both on karyological (GEISE, CANAVEZ & SEUÁNEZ, 1998; CHRISTOFF, 1997) and molecular (mitochondrial DNA) data (D'ÉLIA, GONZÁLEZ & PARDIÑAS, 2003; GEISE, SMITH & PATTON, 2001). An analysis of the occurrence of the gall bladder performed among 15 Akodontini species allowed a complete discrimination of two of those species, *A. cursor* and *A. montensis* (GEISE, WEKSLER & BONVICINO, 2004).

The species studied here range from Argentina (D'ÉLIA, GONZÁLEZ & PARDIÑAS, 2003) to the

Northeastern coastal area of Brazil (MAIA & LANGGUTH, 1981). Empirical collecting data using only specimens identified through complementary techniques shows differentiation in the geographic range and preference of habitats, with *A. cursor* occurring between 15°17'S to 25°28'S and 39°00'W to 48°49'W, and *A. montensis* from 19°38'S to 30°14'S and 42°08'W to 59°18'W (SILVA, 2001). Some altitudinal differentiation was suggested in part of their geographic distribution (Rio de Janeiro State), where *A. cursor* was observed from sea level to localities upon ca. 800m. In altitudes greater than that only *A. montensis* was collected, together with other species, such as *A. reigi* González, Langguth & Oliveira, 1998 and *A. serrensis* Thomas, 1902 (GEISE, 1995; GEISE, WEKSLER & BONVICINO, 2004).

In this paper we analyze the morphometric differentiation between the cryptic species *Akodon montensis*, *A. cursor* and *A. aff. cursor*, using individuals captured in a wide range of their known distribution. The purpose of this analysis was to determine if these three cryptic species could be diagnosed on morphometric grounds, using only specimens which had their identification confirmed by karyotypic data. Since some altitudinal differentiation among *A. montensis* and *A. cursor* was formerly observed by GEISE (1995), a detailed analysis of collecting localities was also performed in order to elucidate how these species segregate according to climatological and altitudinal data. Our study is aimed to clarify the identities and altitudinal distributions of these three species.

MATERIAL AND METHODS

Specimens were collected with live-traps. Chromosomes were obtained directly from bone marrow as described by FORD & HAMERTON (1956) or obtained from bone marrow cultures with cells cultured in MEM Dulbecco's medium. Skins and skulls for all specimens were prepared following standard procedures (*e.g.* WILSON *et al.*, 1996). The data set was complemented with specimens deposited in museums only when karyological information was available (Appendix). Twenty cranial measurements were obtained with a digital caliper: condylo-incisive length (CIL), breadth between occipital condyles (BOC), length of diastema (LDI), length of palatal bridge (LPB), length (LIF) and breadth of incisive foramina (BIF), length of maxillary molar row (LMR), breadth of upper first molar (BFM), breadth

across molars (BAM), length of bulla (LBU), height of skull, measured posteriorly to the border of third molar and orthogonal to skull length (HSK), length of the rostrum, measured from the internal border of the anteorbital bridge of maxillary to the nasal tip (LRO), rostrum width (ROW), least interorbital width (LIW), orbital internal length, measured between the internal borders of the anteorbital bridge of maxillary and of the squamosal process of zygomatic arch (OIL), zygomatic breadth (ZIB), breadth of braincase (BBR), breadth of zygomatic plate (BZP), height of mandible, measured across the angular and condyloid processes (HMA), length of mandible, measured from the incisive basis to the condyloid process (LMA) (Fig.1). Age classes were determined according to molar teeth wear (CERQUEIRA *et al.*, 1989), and only adult specimens were considered for statistical analyses. Additionally, body length (BL), tail length (TL) and body weight (W) were also compared between taxa.

Sexual dimorphism within each species was assessed through t-tests for each measurement, using Bonferroni corrected p-values ($\alpha = 0.05/20 = 0.0025$). In order to evaluate whether specific traits could be used as morphometric diagnostic characters, all measurements were compared among the three species through Analyses of Variance (ANOVAs), using the same Bonferroni corrected p-values as above, and followed by Tukey post-hoc comparisons tests. Finally, a Discriminant Analysis was conducted to determine the amount of multivariate differentiation among the three species.

Collecting localities for *A. montensis* and *A. cursor* in the State of Rio de Janeiro and in adjacent regions in the states of São Paulo and Minas Gerais were analyzed with respect to altitude and nine climatic variables: annual mean temperature (AMT), annual minimum mean temperature (MMT), annual maximum mean temperature (MXT), annual minimum absolute temperature (MBT), annual maximum absolute temperature (MAT), annual total precipitation (PRC), annual total cloudiness (CLD), annual relative humidity (HUM), and annual rainy days (RAI), to investigate the existence of patterns of altitudinal and climatic segregation in the distribution of these taxa. Climatic variables among collecting localities were compared with Analyses of Variance (ANOVAs) for each variable, using Bonferroni corrected p-values ($\alpha = 0.05/9 = 0.006$).

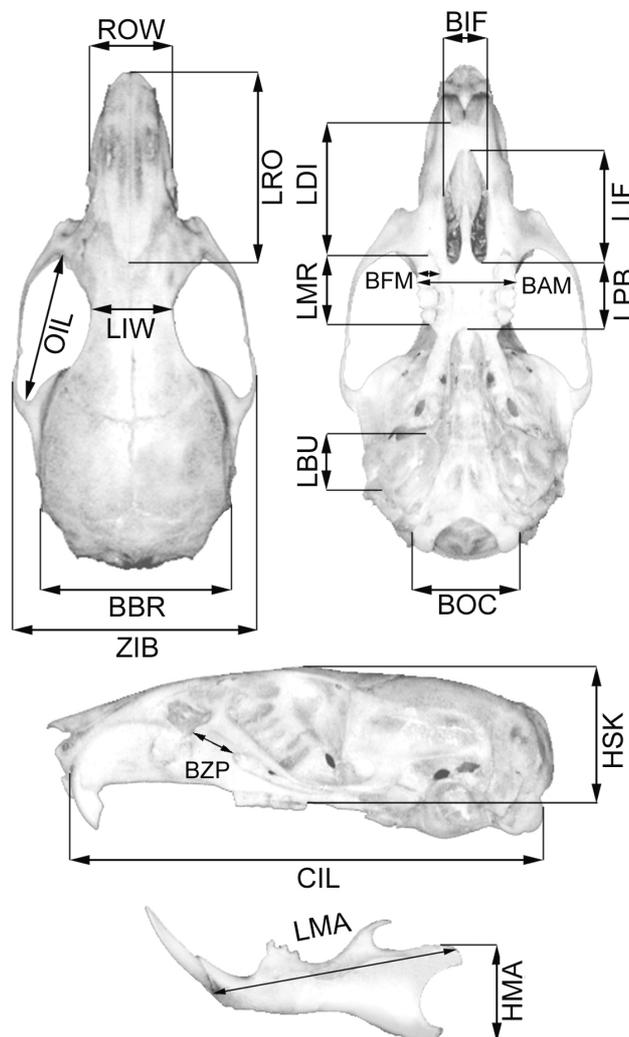


Fig.1- Cranial measurements used in this study. Refer to text for measurement definitions and acronyms.

RESULTS

The total sample sizes for each species and sex, along with their respective means and standard deviations are presented in table 1. Sexual dimorphism was found in 14 out of 20 measurements for both *A. cursor* and *A. montensis* (Tab.1), with males larger than females for all skull traits, while no sexual dimorphism could be detected for *A. aff. cursor*. The interaction between sex and species was evaluated in a Multivariate Analysis of Variance with all measurements, testing for sex, species, and sex*species effects. Since no significant sex*species effect was detected (*i.e.*, the direction of the dimorphism is the same in all species and

measurements), the effect of sex differences was removed by adding the mean difference for each measurement to the females values. Sexes were then pooled for all subsequent analyses, which were carried out on these transformed values.

The ANOVAs revealed significant differences among species in all of the 20 cranial and mandibular measurements (Tab.2), as well as in body measurements and weight. In all cases *A. montensis* was significantly smaller than either *A. cursor* or

Table 1. Descriptive statistics – mean \pm standard deviation (sample size) – of the 20 cranial measurement for each species and sex separately.

	<i>A. aff. cursor</i>		<i>A. cursor</i>		<i>A. montensis</i>	
	♂	♀	♂	♀	♂	♀
CCBA	28.57 \pm 0.93 (5)	27.66 \pm 1.43 (15)	28.20 \pm 1.20 (114)*	27.18 \pm 1.17 (94)	27.15 \pm 1.06 (52) *	25.71 \pm 1.21 (39)
LCON	6.90 \pm 0.16 (5)	6.69 \pm 0.31 (15)	6.89 \pm 0.24 (118)	6.82 \pm 0.27 (94)	6.49 \pm 0.22 (50)	6.35 \pm 0.21 (39)
DIAS	8.40 \pm 0.51 (6)	8.07 \pm 0.54 (15)	8.26 \pm 0.52 (117) *	7.92 \pm 0.50 (95)	7.98 \pm 0.49 (52) *	7.52 \pm 0.53 (40)
PPAL	4.08 \pm 0.15 (6)	4.08 \pm 0.37 (15)	4.25 \pm 0.28 (117)	4.18 \pm 0.31 (95)	3.79 \pm 0.30 (52) *	3.61 \pm 0.24 (39)
CFIN	6.96 \pm 0.58 (6)	6.60 \pm 0.57 (15)	6.46 \pm 0.41 (117) *	6.27 \pm 0.39 (95)	6.42 \pm 0.43 (52)	6.13 \pm 0.51 (39)
LFIN	2.28 \pm 0.18 (6)	2.24 \pm 0.19 (15)	2.41 \pm 0.20 (118) *	2.28 \pm 0.17 (95)	2.30 \pm 0.18 (52) *	2.17 \pm 0.14 (40)
SMOS	4.66 \pm 0.20 (6)	4.64 \pm 0.13 (15)	4.46 \pm 0.16 (119)	4.45 \pm 0.18 (95)	4.25 \pm 0.16 (51)	4.21 \pm 0.20 (40)
LM01	1.31 \pm 0.06 (6)	1.33 \pm 0.06 (15)	1.30 \pm 0.08 (118)	1.29 \pm 0.07 (95)	1.23 \pm 0.07 (52)	1.20 \pm 0.06 (40)
M1M1	6.02 \pm 0.32 (6)	5.93 \pm 0.27 (15)	5.97 \pm 0.34 (118)	5.87 \pm 0.31 (95)	5.67 \pm 0.29 (52) *	5.42 \pm 0.27 (40)
CBUL	5.12 \pm 0.24 (6)	5.10 \pm 0.26 (15)	4.69 \pm 0.27 (114)	4.70 \pm 0.27 (90)	4.89 \pm 0.30 (52)	4.83 \pm 0.23 (40)
ACRA	8.61 \pm 0.36 (6)	8.41 \pm 0.32 (15)	8.68 \pm 0.26 (119) *	8.49 \pm 0.29 (95)	8.26 \pm 0.32 (52) *	7.99 \pm 0.26 (40)
CROS	12.45 \pm 0.57 (6)	11.72 \pm 0.88 (15)	11.55 \pm 0.56 (118) *	11.20 \pm 0.57 (93)	11.49 \pm 0.58 (52) *	10.99 \pm 0.67 (39)
LROS	5.56 \pm 0.17 (6)	5.26 \pm 0.27 (15)	5.61 \pm 0.38 (117) *	5.28 \pm 0.37 (93)	5.24 \pm 0.40 (52) *	4.87 \pm 0.31 (39)
LCIN	5.30 \pm 0.21 (6)	5.22 \pm 0.23 (15)	5.40 \pm 0.19 (119) *	5.30 \pm 0.19 (95)	5.08 \pm 0.24 (52)	4.95 \pm 0.19 (40)
CORB	9.78 \pm 0.62 (6)	9.53 \pm 0.49 (15)	9.79 \pm 0.43 (119) *	9.44 \pm 0.41 (94)	9.28 \pm 0.34 (52) *	8.86 \pm 0.31 (39)
LZIG	15.49 \pm 0.54 (5)	15.07 \pm 0.45 (11)	15.69 \pm 0.56 (108) *	15.11 \pm 0.64 (85)	14.48 \pm 0.66 (44) *	13.82 \pm 0.51 (32)
LCCR	12.29 \pm 0.46 (6)	11.93 \pm 0.33 (15)	12.30 \pm 0.45 (111) *	12.07 \pm 0.49 (92)	11.89 \pm 0.41 (51) *	11.48 \pm 0.39 (40)
LPZI	2.94 \pm 0.14 (6)	3.01 \pm 0.32 (15)	3.06 \pm 0.25 (119) *	2.92 \pm 0.28 (94)	2.72 \pm 0.26 (52) *	2.55 \pm 0.22 (40)
AMAN	6.97 \pm 0.34 (6)	6.62 \pm 0.43 (15)	6.73 \pm 0.39 (114) *	6.53 \pm 0.33 (89)	6.27 \pm 0.37 (52) *	5.97 \pm 0.40 (39)
CMAN	15.45 \pm 0.82 (6)	15.12 \pm 0.89 (14)	15.19 \pm 0.73 (116) *	14.73 \pm 0.66 (93)	14.38 \pm 0.71 (52) *	13.67 \pm 0.69 (39)
BL	122.83 \pm 6.05 (6)	117.80 \pm 11.77 (15)	121.60 \pm 9.29 (106)	117.33 \pm 9.04 (91)	115.21 \pm 8.13 (46)	108.83 \pm 11.10 (38)
TL	101.83 \pm 7.28 (6)	93.87 \pm 10.29 (15)	93.53 \pm 10.62 (99)	90.44 \pm 7.56 (82)	93.01 \pm 10.13 (48)	88.41 \pm 8.44 (35)
W	57.00 \pm 6.16 (6)	45.67 \pm 12.09 (15)	53.19 \pm 11.45 (105)	45.23 \pm 10.64 (84)	43.31 \pm 11.14 (48)	36.43 \pm 12.83 (35)

(*) significant differences between sexes from t-tests, at the Bonferroni-corrected p level of 0.0025. Refer to text for measurements acronyms. Cranial and body measurements in mm, weight in g.

A. aff. cursor, or than both. In those cases in which significant differences were found between *A. cursor* and *A. aff. cursor*, the former presented larger values. Therefore, an overall size gradient exists between these three species, with *A. aff. cursor* being the largest (*A. aff. cursor* is larger than *A. cursor* in seven out of 20 cranial variables and tail length, and larger than *A. montensis* in 19 out of 20 cranial and all body variables), followed by *A. cursor* (which is larger than *A. montensis* in 17 out of 20 variables, and in body length and weight), and finally by *A. montensis* (Tabs. 1 and 2).

The Discriminant Function was significant (Wilks' lambda = 0.1338, $p < 0.001$). Ordination of the specimens along the two Canonical Axes is shown in

figure 2, and both the Standard and Jackknifed classification matrices are presented in tables 3-4. None of the two canonical axes provide complete separation between any of the three groups (Fig. 2). However, there is no overlap between specimens of *A. aff. cursor* and *A. cursor* along a combination of the two functions, while the former overlap with the *A. montensis* sample along both axes. Samples of *A. cursor* and *A. montensis* overlap partially, indicating that there is some morphometric differentiation between these two species, as could be seen in the univariate analyses. Most of the overlap observed between the *A. montensis* and the two other samples is due to a few *A. montensis* specimens, most of them misclassified, which consisted of old specimens (age class 6).

Table 2. Results of the Analyses of Variance among the three species. All ANOVAs were found significant at the Bonferroni-corrected p level of 0.0025.

MEASUREMENT	SIGNIFICANT PAIRWISE DIFFERENCES		
	TUKEY POST-HOC TESTS		
CIL		afc-mon	cur-mon
BOC		afc-mon	cur-mon
LDI		afc-mon	cur-mon
LPB	afc-cur	afc-mon	cur-mon
LIF	afc-cur	afc-mon	
BIF	afc-cur		
LMR	afc-cur	afc-mon	cur-mon
BFM		afc-mon	cur-mon
BAM		afc-mon	cur-mon
LBU	afc-cur	afc-mon	cur-mon
HSK		afc-mon	cur-mon
LRO	afc-cur	afc-mon	
ROW		afc-mon	cur-mon
LIL		afc-mon	cur-mon
OIL		afc-mon	cur-mon
ZIB		afc-mon	cur-mon
BBR		afc-mon	cur-mon
BZP	afc-cur	afc-mon	cur-mon
HMA		afc-mon	cur-mon
LMA		afc-mon	cur-mon
BL		afc-mon	cur-mon
TL	afc-cur	afc-mon	
W		afc-mon	cur-mon

Significantly different pairs of species (as determined by the Tukey post-hoc tests) are indicated (afc) *Akodon aff. cursor*; (cur) *A. cursor*; (mon) *A. montensis*. Refer to text for measurements acronyms.

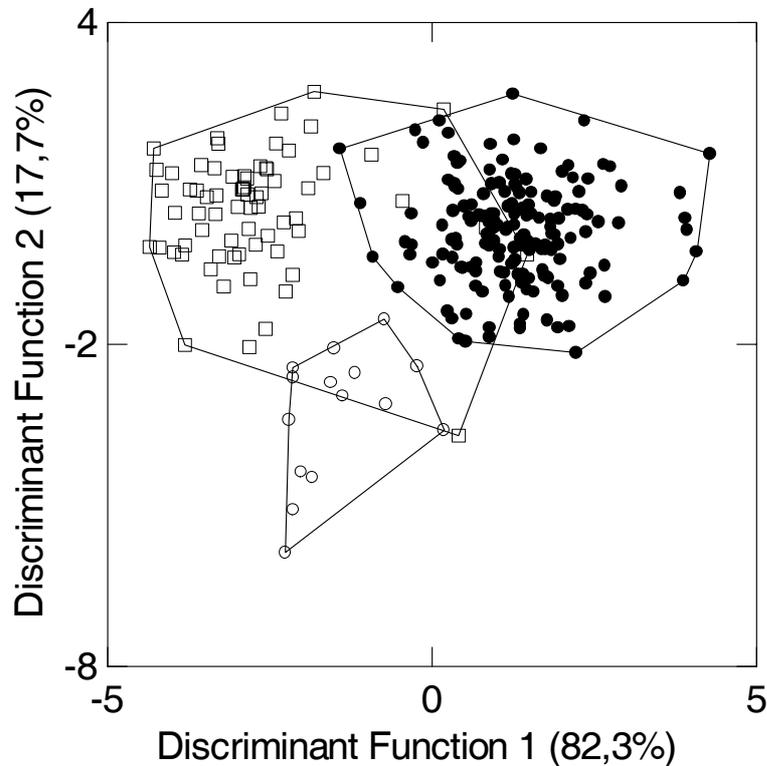


Fig.2- Plot of the Canonical scores extracted from the discriminant analyses, and percentages of total variance explained by the two functions. (○) *Akodon aff. cursor*, (●) *Akodon cursor*, (□) *Akodon montensis*.

Table 3. Classification matrix determined by the discriminant function.

Species	Predicted group membership			% correct
	<i>A. aff. cursor</i>	<i>A. cursor</i>	<i>A. montensis</i>	
<i>A. aff. cursor</i>	15	0	0	100
<i>A. cursor</i>	0	163	3	98
<i>A. montensis</i>	4	4	62	89
Total	19	167	65	96

The percentage of overall correctly classified specimens was 96%. The percentage of correctly classified specimens was better for both *A. aff. cursor* and *A. cursor*, with all specimens correctly classified for the former and 98% for the latter (Tab.3). *Akodon montensis* also presented an elevated amount of correctly classified individuals (89%), with a few specimens being erroneously classified. As expected, the amounts of correctly classified specimens are slightly lower in the jackknifed classification matrix (Tab.4), but these results are consistent with the standard matrix, suggesting that the discriminant

function determined is good. The greater reduction observed in the percentage of correctly classified specimens for *A. aff. cursor* is mostly due to its reduced sample size.

In localities from Rio de Janeiro State and its vicinities (Fig.3) *A. montensis* was not found in altitudes below 800m above sea level and *A. cursor* was found from sea level to altitudes above 1000m. The ANOVAs showed that only one climatic variable is significantly different, namely annual mean temperature ($p=0.004$), suggesting some segregation between these two species (Tab.5).

Table 4. Jackknifed classification matrix determined by the discriminant function.

SPECIES	PREDICTED GROUP MEMBERSHIP			% correct
	<i>A. aff. cursor</i>	<i>A. cursor</i>	<i>A. montensis</i>	
<i>A. aff. cursor</i>	12	2	1	80
<i>A. cursor</i>	2	160	4	96
<i>A. montensis</i>	4	4	62	89
Total	18	166	67	93

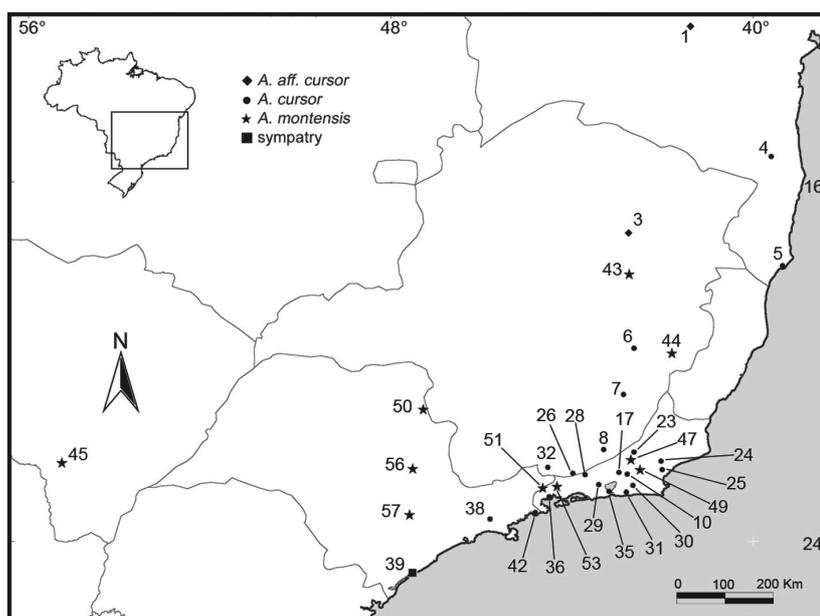


Fig.3- Map with collecting localities numbered according to the appendix. Some localities presented in the map refer to more than one locality listed in the appendix: 1 = 1, 2; 10 = 10 to 16; 17 = 17 to 22, 48; 25 = 25, 27; 32 = 32, 33; 36 = 36, 37; 45 = 45, 56; 53 = 40, 53, 54.

Table 5. ANOVA results for climatic variables between *A. cursor* and *A. montensis*.

VARIABLES	F	p
AMT	9.560	0.004*
MMT	3.510	0.701
MXT	0.192	0.664
MBT	0.637	0.430
MAT	1.393	0.246
PRC	3.788	0.060
CLD	7.764	0.008
HUM	1.357	0.252
RAI	1.067	0.309

Significant values are marked with *. Refer to text for acronyms.

DISCUSSION

The taxonomic status of both *A. cursor* and *A. montensis* is well defined. The first species presents diploid numbers equal to 14, 15 or 16 (CERQUEIRA, FERNANDEZ & QUINTELA, 1990; RIEGER, LANGGUTH & WAIMER, 1995). Specimens with diploid numbers of 24/25 have been referred to as *A. montensis*, in a taxonomic assignment that may need a reevaluation, as specimens with both diploid numbers have been collected in the type locality of *A. cursor* (Lagoa Santa, MG) (GEISE, SMITH & PATTON, 2001). This question could be addressed by including the type material of both species in a morphometric analysis, provided that reliable morphometric discrimination could be established beforehand on the basis of genetically identified samples.

Akodon montensis was originally described as a subspecies of *A. arviculoides* (Thomas, 1913), and latter related to *A. cursor* by XIMENEZ & LANGGUTH (1970). Although there are now abundant distributional, chromosomal, molecular, and morphological data supporting their species status (GEISE, 1995; RIEGER, LANGGUTH & WAIMER, 1995; SBALQUEIRO & NASCIMENTO, 1996; CHRISTOFF, 1997; GEISE, CANAVEZ & SEUÁNEZ, 1998; GEISE, SMITH & PATTON, 2001; GEISE, WEKSLER & BONVICINO, 2004), confusion remains, because these two taxonomic entities are difficult to distinguish by external or craniodental characters.

Descriptive statistics (Tab.1) and univariate analyses indicate that *A. montensis* is smaller than the two remaining species, as revealed by significant differences found in all measured traits between this species and either one or both the other species. The analyses also indicate that *A. aff. cursor* is significantly larger than the other two species. These opposite trends in skull size lead to a better separation between *A. montensis* and *A. aff. cursor* than between any of these and *A. cursor* (Tab.2). Nevertheless, the general smaller size in *A. montensis* also leads to significant differences in most measurements when compared to *A. cursor*. The multivariate analysis yielded slightly different results, and did not provide a complete segregation between all of the three species (Fig.2). The greater differences found between *A. aff. cursor* and *A. montensis* in the univariate analyses are partially recovered in the discriminant analysis. Although there is some overlap between the two samples, most of this overlap is due to a single, aged *A. montensis* individual, highly divergent from the rest of the sample. However, while in the univariate analyses *A. cursor* was better distinguished from *A. montensis* than from *A. aff. cursor*, in the multivariate approach it showed no overlap with the latter, while partially overlapping with the former. These results are also recovered in the classification matrices (Tabs.3-4). Again, most of this overlap is related to a few aged *A. montensis* specimens, all of them misclassified in the analysis. These results also indicate that, while the univariate differentiation between *A. cursor* and *A. aff. cursor* was only observed in a few cranial measurements, the multivariate results represent additional evidence for the separation of these two taxa in separate species.

These results suggest that although some specific traits are clearly different between the analyzed groups, overall and precise differentiation between

A. cursor and *A. montensis* cannot be achieved based on morphometric grounds solely. While 98% of all *A. cursor* specimens were correctly identified with the use of the discriminant function, some *A. montensis* were erroneously identified as either *A. cursor* or *A. aff. cursor* (about 10%). It is important to note that most of these specimens are particularly old. Since *A. montensis* appears to be the smallest of the three species analyzed here, it could be expected that larger and older specimens could resemble the other taxa more closely. In a previous analysis comparing only *A. cursor* and *A. montensis*, CHRISTOFF (1997) obtained similar results, although with slightly better classification for *A. montensis* and better discrimination of these two species. His results also indicate that most of the differentiation between these two taxa is allometric. While an evaluation of the allometric relationships among the studied taxa was not the primary goal of this study, this is consistent with our results, in as much as *A. montensis* shows partial multivariate segregation from *A. cursor*, coupled with significantly smaller values recorded for most measured characters. Thus, the lack of a complete segregation noted above in the multivariate analyses between these two taxa are more probably related to smaller specimens of *A. cursor* that end up erroneously classified as *A. montensis* or overlapped with these in figure 2, simultaneously to larger specimens of *A. montensis* being classified as *A. cursor*. This morphometric similarity may be related purely to size (since almost all variables were significantly different between the two taxa), or most probably to size-related (*i.e.* allometric) shape differences in the skull and mandible. CHRISTOFF (1997) also considers *A. aff. cursor* and *A. cursor* to be conspecific, but results presented here indicate a clear morphometric differentiation between these two groups, recovered both in the multivariate and in the univariate analyses. These results are in agreement with all previous genetic results (D'ÉLIA, GONZÁLEZ & PARDIÑAS, 2003; GEISE, SMITH & PATTON, 2001; GEISE, CANAVEZ & SEUÁNEZ, 1998; CHRISTOFF, 1997).

Nevertheless, the sample of *A. aff. cursor* used here is much smaller than the two others, and it cannot be determined whether its separation from the remaining two is an artifact of the variance estimates for this species, since discriminant function analyses depend on within-group variation as related to between-group variation to determine axes orientations, as well as within group

orientation, and both factors are influenced by sample size (PIMENTEL, 1992; MARCUS, 1990). Thus, further morphometric analyses surely need to be carried out when a larger number of karyotyped specimens becomes available. The resolution of the taxonomic issue related to the correct matching of the morphological form represented by the type of *A. cursor* from Lagoa Santa with the karyotypical forms of either $2n=14/15/16$ or $2n=24/25$ is therefore dependent on the availability of better classification functions obtained with greater sample sizes.

GEISE (1995), in a previous geographical analysis, showed that *A. cursor* and *A. montensis* presented completely separated altitudinal distributions, indicating that in the Rio de Janeiro State and surrounding localities they rarely occur in sympatry. In our samples, both species were recorded together only in two localities (Bananal and Iguape; localities #40 and 39). This finding corroborates other results which show that these two species have different geographic distribution patterns (SILVA, GRELE & GEISE, in preparation). Although in Rio de Janeiro State *A. montensis* is not found in altitudes below 800m above sea level, it does occur below this level at higher latitude localities. Climatic variables, such as temperature, can account for such altitudinal distribution of this species, forcing it to higher altitudes (with lower temperatures) in lower latitude localities. GEISE (1995) had showed an altitudinal segregation around 800m, with one species occurring above (*A. montensis*) and other occurring below (*A. cursor*) this altitude, in this same area. However, recently some *A. cursor* specimens were collected above this altitude (reaching 1,227m) in Bananal (Locality #40) and 850m in Serrinha do Alambari (Locality #32). We believe that these specific records of *A. cursor* in an altitude supposedly exclusive to *A. montensis* could be explained by habitat and microclimatic changes caused by deforestation. Both localities show high levels of habitat degradation and deforestation, the former consisting of modified grasslands (where forest was almost completely removed) and the second (Locality # 32) being an area with secondary forest. *Akodon cursor* can present a distinct physiology that allows it to invade open areas more easily, as in the present studied area it is usually found from sea level to the Rio Paraíba Basin in open and quite degraded areas. During the last 10 years, one of the authors (L.Geise) observed that *A. montensis* is more frequently trapped in better preserved

vegetational formations, such as for example those present in Itatiaia (GEISE *et al.*, 2004; GEISE, SMITH & PATTON, 2001), Teresópolis, Nova Friburgo, and Bocaina (Localities # 48, 49 and 51). A study comparing microgeographical ecological differences among these two species, such as the one performed between two populations of *A. cursor* (CERQUEIRA *et al.*, 2003), could possibly lead us to a better understanding of such habitat different usages. The significant differences between species found in annual mean temperature can be an artifact of the low number of analyzed localities of *A. montensis* in the present study.

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APPENDIX

Specimens examined: MN – Museu Nacional, Rio de Janeiro; MZUSP – Museu de Zoologia da Universidade de São Paulo; MVZ – Museum of Vertebrate Zoology, University of California, Berkeley. Other acronyms correspond to field number of collectors: EDH (E.Hingst-Zaher), HB, HGB-DB, HGB-REGUA and HGB-CFVC (H.G.Bergallo), JLP (J.L.Patton), RTS (R.T.Santori), LC and LPC (L.P.Costa); YL (Y.Leite), BRP (B.R.Portugal) and CEG (C.E.Grelle). MC, LS, PE, PB, FS, SU – field numbers of collecting localities, collection of the Laboratório de Vertebrados, Depto. Ecologia, Universidade Federal do Rio de Janeiro; EEB – field numbers of MZUSP. U = undetermined sex. Numbers between brackets are localities number in figure 3. To avoid repetition of locality names in the second reference only the number is given.

Akodon aff. cursor – BRAZIL - BAHIA: [1] Morro da TeleBahia, Lençóis (12°32'S, 41°24'W, 560m) (♂ : CD137, 157, 178; ♀ : CD141, 143, 242); [2] Remanso, Lençóis (12°36'S, 41°21'W, 464m) (♂ : CD30, 94, 164; ♀ : CD5, 27, 62, 66, 102-104, 110, 124). MINAS GERAIS: [3] Estação Ecológica Acauã, Turmalina (17°08'S, 42°46'W, 800 m) (♀ : LC74, YL71, 80).

Akodon cursor (Winge, 1887) – BRAZIL - BAHIA: [4] Fazenda Água Santa, Pau Brasil (15°27'S, 39°37'W, 90m) (♂ : LG196; ♀ : LG190, 200); [5] Helvécia, Nova Viçosa (17°53'S, 39°22'W, 52m) (♂ : MN47992). MINAS GERAIS: [6] Parque Estadual do Rio Doce, Marliéria (19°43'S, 42°39'W, 300m) (♂ : LC84, 98; ♀ : LC88, 90, YL87, 88, 96); [7] Mata do Paraíso, Viçosa (20°45'S, 42°53'W, 650m) (♂ : MN35936, 35937, 35939; ♀ : MN35934, 35935); [8] Sítio Maglândia, Simão Pereira (21°58'S, 43°19'W, 500m) (♂ : MN33688, 33691, 33693-95, 33697, 35918; ♀ : MN33690, 33692, 33696, BPR07). RIO DE JANEIRO: Cachoeiras de Macacu Municipality: [9] Reserva de Guapiaçu (no coordinates data) (♂ : HGB-REGUA2; ♀ : HGB-REGUA1, 17); [10] Sítio Rosimary (22°29'S, 42°51'W, 54m) (♂ : FS11-12, 25, 30, 40, 41, FS14-05, 39; ♀ : FS11-23, 47, 83, FS14-41); [11] Fazenda Pica Pau Amarelo (22°30'S, 42°45'W, 200m) (♂ : FS13-27, 32, 91, FS17-15, 20, 43; ♀ : FS17-16, 18, 21, 39, 40, 44-46); [12] Conjunto de Fazendas (ex. Sítio do Rio Doce) (22°31'S, 42°47'W, 100m) (♂ : FS16-24, 25, 40; ♀ : FS12-14, 15, 32, FS16-07, 33); [13] (22°31'S, 42°48'W) (♂ : FS6-9, 13, 30-32); [14] Bairro Quizanga (22°31'S, 42°51'W, 100m) (♂ : FS16-29, 37); [15] (22°34'S, 42°54'W, 150m) (♂ : FS15-41, 43, 58, 80, 81, 86, FS18-4-6; ♀ : FS15-40, 42, 44, 45, 57, FS18-12, 27, 34, 35); [16] (22°35'S, 42°54'W, 150m) (♂ : FS15-13, 50-52, FS18-22; ♀ : FS18-13); Guapimirim Municipality: [17] Garrafão (22°29'S, 43°00'W) (♀ : ORG 46); [18] Parque Nacional da Serra dos Órgãos, sede Guapimirim (22°29'S, 42°59'W, 470m) (♂ : PSS15); [19] Fazenda Iguaçu (22°31'S, 42°53'W) (♂ : FS5-57, 59, FS8-31, 58; ♀ : FS8-28, 77); [20] Fazendas Consorciadas (22°33'S, 42°53'W, 15m) (♂ : FS5-3, 58, 69, FS8-73, 79, 80, FS17-2, 3, 13, 35; ♀ : FS5-22, 36, 37, FS8-19, 76, FS13-28, FS17-1, 8, 14, 17); [21] Fazenda Chorona (22°33'S, 42°57'W, 140m) (U: FS4-71, ♂ : FS4-2, 3, 4, 6, 8, 9, 11, 37, 42, 43, 45, 46, 53-55, 58, 61, 81, FS7-8; ♀ : FS4-10, 14, 19, 33, 36, 41, 48, 56, 75, FS7-25); [22] Centro de Primatologia (22°38'S, 42°58'W, 100m) (♀ : HGB405); [23] Vale do Pamparrão, Sumidouro Municipality (22°02'S, 42°39'W, 300m) (♂ : MN43750, 43754, SU8, 9); [24] Glicério, Macaé Municipality (22°14'S, 42°03'W, 250m) (♂ : MN35928, 35931; ♀ : MN35929, 35930, 35932, 35933); [25] Reserva União, Casimiro de Abreu Municipality (22°25'S; 42°02'W, 50m) (♂ : MN59115; ♀ : MN35941); [26] Pinheiral, Pirai Municipality (22°30'S, 44°00'W, 345m) (♂ : CEG70, 75, 77; ♀ : CEG73, 74, 78); [27] Morro de São João, Casimiro de Abreu Municipality (22°32'S; 42°02'W, 260m) (♀ : MN35940); [28] Fazenda São José das Paineiras, Mendes Municipality (22°32'S, 43°44'W, 610m) (♂ : MN35913); [29] Tinguá, Nova Iguaçu Municipality (22°45'S, 43°26'W, 125m) (♂ : MN26810, 28810, ♀ : 28928); [30] Catimbau Grande, Rio Bonito Municipality (22°46'S; 42°40'W, 200m) (♂ : MN35915, 35917, ♀ : 35916); [31] Restinga de Barra de Maricá, Maricá Municipality (22°55'S; 42°49'W, 3m) (U: MN26839, 28948, 30140, ♂ : MN26791, 26791, 26815, 26844, 27825, 28813, 28833, 28843, 28946; ♀ : MN26853, 28543, MC229); [32] Serrinha do Alambari, Resende Municipality (22°22'S, 44°33'W, 850m) (♂ : MN47988, 47989, 47993, 47994; ♀ : MN47986, 47987, 47990, 47991); Itatiaia Municipality [33] Piscina Maromba, Parque Nacional de Itatiaia (22°26'S, 44°37'W, 620m) (♂ : HGB-DB22; ♀ : HGB-DB21), [34] Parque Nacional de Itatiaia (no coordinates data) (♀ : HGB-CFVC 1, 3, 6); [35] Rio de Janeiro Municipality (22°54'S, 43°12'W, 2m) (♀ : MZUSP24168); [36] Mambucaba, Angra dos Reis Municipality (23°01'S, 44°31'W, 100m) (♂ : MN42760, MAM5; ♀ : MN42762, 42766); [37] Tarituba, Paraty Municipality (23°02'S, 44°35'W, 105m) (♀ : MN62185, 62186).

SÃO PAULO: [38] Salesópolis (23°31'S, 45°50'W, 806m) (♂ : MZUSP27429); [39] Iguape (24°43'S, 47°33'W, 20m) (♂ : MZUSP24169); [40] Trilha das Pedras Vermelhas, Bananal (22°47'S, 44°21'W, 1227m) (♂ : EEB665); [41] Icapara (no coordinates data) (♂ : MZUSP27428), [42] Picinguaba, Ubatuba Municipality (23°22'S, 44°50'W) (♀ : MN98069);

Akodon montensis (Thomas, 1913) – BRAZIL - MINAS GERAIS: [43] Jambreiro, Nova Lima Municipality (18°04'S, 42°46'W, 913m) (♂ : LG207); [44] Fazenda Montes Claros, Estação Biológica de Caratinga, Caratinga Municipality (19°50'S, 41°50'W, 320m) (♂ : MN31450). MATO GROSSO DO SUL: Dourados Municipality [45] Fazenda Maringá, 54km W de Dourados (22°16'S, 55°18'W, 427m) (U: LPC612, 614-621, 663, 671, 673, 680-682; ♂ : LPC622, 633, 635, 640, 656, 661, 662, 676, 678; ♀ : LPC641, 654, 655, 657, 659, 672, 674, 677); [46] Balança Velha, 55km W de Dourados (22°20'S, 55°18'W, 518m) (U: LPC611, ♂ : JLP16989, 16996-98; ♀ : JLP16990-95). RIO DE JANEIRO: [47] Fazenda São José da Serra, Serra do Paqueque, Sumidouro Municipality (22°12'S; 42°44'W, 1033m) (♂ : MCL26, 36; ♀ : MCL28, 33); [48] Sede do Parque Nacional da Serra dos Órgãos, Teresópolis Municipality (22°24'S, 42°59'W, 871m) (U: FS10-45; ♂ : FS10-2, 3, 8, 14, 26, 31, 43, 44, 46, 52, 53, 61, 72, 84, 87, 89, 94, 97; ♀ : FS10-27, 28, 30, 33, 39, 65, 77, 96); [49] Sítio Xitaca, Debossan, Nova Friburgo Municipality (22°26'S; 42°32'W, 1100m) (♂ : MN35925). SÃO PAULO: [50] Clube Náutico de Araraquara, Araraquara Municipality (21°05'S, 47°19'W, 664m) (♂ : RTS13); [51] Parque Nacional da Bocaina, São José do Barreiro Municipality (22°50'S, 44°41'W, 1400m) (♀ : HGB-DB8); Estação Ecológica de Bananal, Bananal Municipality: [52] Trilha da Casa Velha (no coordinates data) (♂ : EEB713); [53] Trilha do Rio das Cobras (22°28'S, 44°22'W, 1164m) (♀ : EEB563, 676); [40] (♂ : EEB695; ♀ : EEB680); [54] Trilha das Sete Quedas (22°48'S, 44°22'W) (♂ : EEB703; ♀ : EEB651); [55] Trilha do Alemão (no coordinates data) (♀ : EEB678); [56] Fazenda São José, Rio Claro Municipality (22°24'S, 47°33'W, 850m) (♀ : SJ1, RTS8); [57] Floresta Nacional de Ipanema, Sorocaba (23°26'S, 47°37'W, 701m) (U: LPC793, ♂ : LPC810, 855, 856, 859, 863, 866-868, 870; ♀ : 799, 858, 860, 862, 869, 872); [39] (♂ : MZUSP24174, 24176, 24178; ♀ : MZUSP24175, 24177).