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# Morphometric and chromosomal variation in populations of *Oryzomys albigularis* (Muridae: Sigmodontinae) from Venezuela: multivariate aspects

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## Abstract

The composite nature of the species *Oryzomys albigularis* Tomes, 1860 has long been recognized from the karyological heterogeneity of diploid and fundamental numbers, with at least two sets of populations in the eastern and northern Andes with 2n = 66 and 2n = 80, respectively. The aim of this study was to test for differences among populations within the species using cranial morphometrics. Populations for the multivariate analyses were defined according to differences in autosomal arm numbers within a single modal diploid number from six locations in two mountain systems of Venezuela, in northern South America. Principal component and canonical variate analyses clearly discriminated among the karyomorphs, the variation at the interorbital, palatal, and incisive foramen regions being the most informative. These traits explained most of the total variance, after adjusting for size effects. We found no evidence for congruence between the patterns of morphometric variation and geographical distance among karyomorphs, but similarity patterns among samples resulted in congruence when morphometric and karyological data were considered. Since variation of these last two datasets can be considered independent of each other, the observed congruence is suggestive of a phylogenetic structure in the data. Our results are consistent with a composite nature for the species, as most of the observed cranial variation appears to be associated with major karyotypic differences. Given the theoretical relevance of the implied karyotypic changes as a means of reproductive isolation, morphometric evidence is used to support the splitting of the "*albigularis*" form in at least two distinct species.

Key words: *Oryzomys albigularis*, morphometrics, karyosystematics, congruence, composite species

## Introduction

A major issue in Rodent systematics has been the instability of the taxonomy of the South American cricetids, or Sigmodontinae. Although there is a moderate level of agreement in the definition of genera and subgenera, this is not so at the specific or subspecific levels (Reig 1986). The genus *Oryzomys* Baird, 1858 exemplifies much of the observed taxonomic confusion, being one of the most diverse genera in the family (Musser and Carleton 1993). Its widespread geographical distribution covers locations in North America, Central America, and northern through southeastern South America (Musser and Carleton 1993). Several authors have recognized the need for more detailed systematic studies within this genus (Honacki et al. 1982; Musser and Carleton 1993).

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Most of the revisions of the species *Oryzomys albigularis* Tomes, 1860 do not agree at the subspecific level. Tate (1932) recognized two subspecies, *albigularis* and *moerex* Thomas, 1914, both from Ecuador, whereas Gyldenstolpe (1932) and Ellerman (1941) included also *maculiventer* Allen, 1899, with the type locality in northern Colombia. Cabrera (1961) included 11 subspecies, while Hershkovitz (1966) used the phallic morphology to include two subspecies previously defined as *O. devius* Bangs, 1902. More recently, Honacki et al. (1982) excluded two subspecies, while Musser and Carleton (1993) listed as synonyms the subspecific names *caracolus* Thomas, 1914, *childi* Thomas, 1895, *maculiventer*, *moerex*, *meridensis* Thomas, 1894, *oconnelli* Allen, 1913, *pectoralis* Allen, 1912, *pirrensis* Goldman, 1913, and *villosus* Allen, 1899. The current *O. albigularis* includes populations from eastern Panama through northern Peru; the holotype is from the Chimborazo Province in Ecuador (Patallanga, 1 509 m, Musser and Carleton 1993).

Gardner and Patton (1976) first recognized the composite nature of the species based on the karyological evidence. They found Andean populations with different diploid numbers (2n = 88 and 66 from Peru, and Colombia and Venezuela, respectively), and they suggested to keep *albigularis* for the 2n = 66 populations. Working with populations from Venezuela, Aguilera et al. (1995) recently found further support for the supraspecific nature of *O. albigularis*. They found differences in the number of autosomal arms or fundamental number (FN) and in the morphology of the sexual pair among several populations from two main mountain systems in the country (Fig. 1). G banding was used to support the status of reproductive isolation between the populations with the extreme FN 90 and 104. Differences in 7 out of 33 chromosome pairs resulted from pericentric inversions. These rearrangements are currently considered as causing hybrid sterility, i.e. postmating reproductive isolation (King 1993). Thus, Aguilera et al. (1995) suggested to keep *O. caracolus* and *O. meridensis* for the populations with FN = 90 and 104, respectively, while a third population with FN = 92 was provisionally assigned to *Oryzomys* sp.

In this study, we use multivariate morphometrics to analyse the cranial variation of the karyomorphs defined by Aguilera et al. (1995). Our aim is to assess the morphological evidence associated to the variation of the "*Oryzomys albigularis* complex", as given by the karyological results. A detailed description of the morphological variants is accomplished through the interpretation of multivariate results.

The joint interpretation of the variation patterns showed by independent data sets from the same populations may reveal important information for inferring the relationships among these populations. We compare karyotype (Aguilera et al. 1995; Gardner and Patton 1976) and morphometric similarity patterns among *O. albigularis* populations to study the extent of congruence between these independent datasets.

## Material and methods

### Population sample

Samples were assembled to represent karyomorphs, and thus individuals were sorted out by their karyotypes. However, sample size limitations led us to pool several localities for some karyomorphs, whereas some were represented by a single locality. Five samples were defined altogether, comprising several localities in Venezuela (Fig. 1):

Avi: El Ávila National Park, Distrito Federal (6 females, 14 males, and 1 of unknown sex); FN = 90; 1 470 m asl. Approx. 10°33′ N, 66°52′ W.

Mac: Macarao National Park and surroundings, Miranda y Aragua states (1 female, 13 males); FN = 90; 1 845 m asl. Approx. 10°25′ N, 67°17′ W.

HPi: Henri Pittier National Park, Aragua state (28 females, 54 males, and 1 of unknown sex); FN = 90; 1 280 m asl. Approx. 10°21′ N, 67°40′ W.

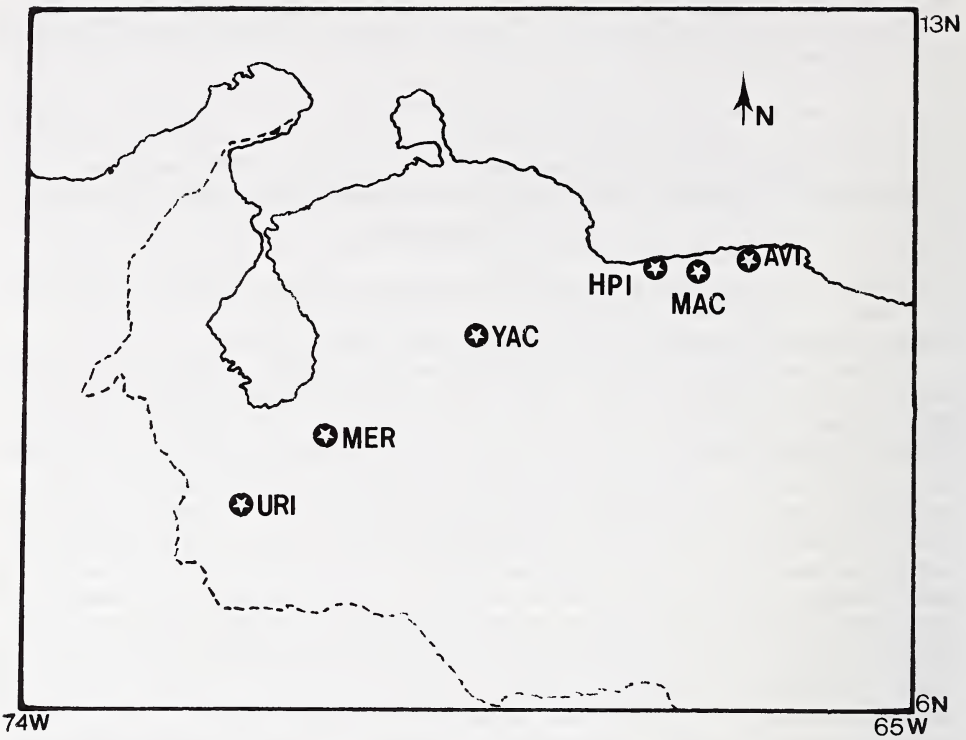


**Fig. 1.** Map showing the *Oryzomys albigularis* population sample locations in the present study. Morphometric samples: Avi: El Ávila N. P., HPi: Rancho Grande Henri Pittier N. P., Mac: Macarao N. P., Yac: Yacambú N. P., Mer: Monte Zerpa, and Uri: La Trampita. Avi, HPi, and Mac represent karyomorphs with FN = 90, Yac and Mer, karyomorphs with FN = 104, and Uri, the karyomorph with FN = 92. Modified from Aguilera et al. (1995).

Mer: Monte Zerpa, Mérida state, and related localities (5 females, 15 males); FN = 104, X chromosome metacentric; 2 140 m asl. Approx. 9°21′ N, 70°18′ W.

Yac: Yacambú National Park, Lara state (18 females, 33 males); FN = 104, X chromosome acrocentric; 1 645 m asl. Approx. 9°40′ N, 69°37′ W.

Uri: La Trampita, Siberia, sector Uribante, Táchira state (7 females, 6 males); FN = 92; 1 100 m asl. Approx. 7°50′ N, 71°57′ W.

Sex, general body measurements, taxonomic status, and locality were read from the museum labels.

## Measurements

Criteria for the selection of multivariate morphometric characters can be found elsewhere (Steppan 1997 a; Voss 1988). These criteria include: homology of landmarks across individuals; uniform bone sampling; preference of measurements on single bones and avoidance of redundancy; and non-coincidence of end landmarks over two or more measurements. We selected 21 cranial and 3 mandible measurements to match those criteria where possible (Tab. 1), but we chose some that might aid comparisons with other studies. An additional consideration was to maximize the sample size, since in a considerable portion of the material several traits were missing. All measurements were taken using a Digimatic caliper Mitutoyo (MTI Corp., Aurora IL, USA) to the next 0.01 mm. In order to reduce the sampling errors due to cranial asymmetries, measurements on symmetric duplicated structures were taken twice on each specimen, and we used the mean in statistical analyses.

**Table 1.** Description of the measurements taken from the *Oryzomys albigularis* skulls.

| Name of variable, Acronym | | Description |
|---|---|---|
| Total length of skull | TL | From the most anterior portion of nasal to posterior-most portion of occipital |
| Nasal length | NL | From anterior-most to posterior-most portions of nasals |
| Nasal-maxillary suture length | NMSL | Limited by both extreme points at the dorsally posterior-most portions of nasals |
| Least interorbital breadth | LIB | Least distance among the orbits in dorsal surface |
| Fronto-parietal suture length | FPSL | Dorsal distance of suture among parietal and temporal bones |
| Maximum breadth of braincase | MB | Greatest width of skull, among temporal bones |
| Maximum rostral height | MRH | Greatest height of rostrum, among frontal bones and parapterigoid plates |
| Braincase height | BH | Greatest height of skull, among parietal and basisphenoid bones |
| Basilar length | BL | From posterior-most edge of incisive alveoli to anterior-most edge of foramen magnum |
| Upper alveolar length | UAL | Greatest length of the upper molar alveolus |
| Length of palate bone | PBL | From posterior-most margin of maxillary to posterior-most margin of palate |
| Breadth of palate bone | PBB | Limited by both lingual alveolar margins |
| Palatilar length | PL | From posterior edge of incisive alveolus to posterior-most margin of palate |
| Upper diastema length | UDL | From posterior edge of incisive alveolus to anterior edge of molar alveolus |
| Premaxillary-maxillary suture length | PMSL | Ventral distance along posterior-most margin of premaxillary |
| Incisive foramen breadth | IFB | Distance at the middle of both incisive foramina |
| Incisive foramen length | IFL | From anterior-most to posterior-most margins of incisive foramina |
| Tympanic bulla length | TBL | Greatest distance along the meatus-bullar tube axis of tympanic bulla |
| Tympanic bulla breadth | TBB | Greatest distance perpendicular to the meatus-bullar tube axis of tympanic bulla |
| Incisive-maxillary length | IML | Lateral distance between anterior-most incisive edge of premaxillary and posterior-most margin of capsular projection for upper incisive |
| Incisive-zygomatic length | IZL | From incisive edge of premaxillary to posterior-most portion of zygomatic arch |
| Mandible length | ML | Greatest length of mandible, excluding incisive teeth |
| Mandibular diastema length | MDL | From posterior edge of lower incisive alveolus to anterior edge of lower molar alveolus |
| Lower alveolar length | LAL | Greatest length of mandible molar alveolus |

## Age criteria

A common problem when defining age classes is to find an age criterion that applies to all of the samples. Size and weight are poor age indices across several independent populations, because the variation in these parameters may be a result of evolutionary divergence. On the other hand, molar toothwear criteria do not necessarily relate to developmental events (e. g. weaning, sexual maturity). These events are the obvious choices to define age classes independently in populations, but they are usually not available for collection-based surveys.

In order to define the age classes, we devised a method that incorporates developmental and toothwear information. Starting from a sample of 41 individuals that were brought alive from the Yacambú N. P. (Yac) and reared under laboratory conditions (R. Moscarella, unpubl. data), each speci-

men was labelled as immature or mature, depending upon the developmental stage of its genitalia (vagina open or closed, testes descended or not). A "juvenile" stage was defined when all the individuals were immature, and an "adult" stage when all were mature animals. The intermediate stage was defined as "sub-adult". Sexes were pooled since no differences were detected between them before adulthood. The end points of weight and body length of each stage were recorded, and then used to classify a sample of 51 museum specimens from the same locality whose skulls were available. For each specimen, molar toothwear was observed and related to the corresponding stage. We employed the resulting descriptions as the criteria for classifying the individuals from the remaining populations. The three defined age classes were characterized as follows:

Juveniles: upper M3 unerupted or partially erupted; incipient wear of all molars.

Sub-adults: occlusal surface of upper M3 with intermediate wear. Labial cusps of upper M1 slightly worn. Lingual cusps of upper M1–M2 partially worn.

Adults: upper M3 totally worn. Labial cusps of upper M1 with intermediate to advanced wear. Lingual cusps of upper M1–M2 with intermediate to advanced wear. This class includes senile individuals, which had lost most of their enamel components.

As all toothwear-based age criteria, this method assumes a monotonic wear of the enamel components of the molar teeth, which is also positively correlated with time (Voss et al. 1990). Since the method involves schedules of events related to the development, the homogeneity of these schedules throughout the populations is also assumed.

## Sex dimorphism

A population by sex two-way Type I analysis of variance (ANOVA) was performed on each measurement, excluding specimens with unknown sex and those from Macarao N. P., where only one female was available. The significance of interactions was taken as evidence of sexual dimorphism, which led us to perform separate analysis with each sex.

## Analysis of geographic variation

Evolutionary divergence and ontogenetic variation are usually taken as the main sources of variation of measurement data between and within populations, respectively. In order to minimize the ontogenetic component of the variation, we used only adult specimens in the morphometric analyses. However, allometric variation may be expected to remain in an adult sample (Patton and Rogers 1983). There are several commonly used methods for excluding this effect from the data. In the present study, the preferred method was the shearing of principal components (Humpries et al. 1981; Rohlf and Bookstein 1987), which is based on an explicit causal model of the covariation among characters.

We used multivariate techniques to evaluate the extent of differentiation among population samples. A covariance matrix was constructed by pooling the log-transformed data from the six samples, and principal components were extracted. Resulting eigenvectors were employed to interpret the patterns of among-sample variation. To study the degree of support of the observed eigenstructure to the hypothesis of differentiation between the karyomorphs, we performed univariate analyses of variance (ANOVA) on the principal component scores. Multiple comparisons among pairs of samples were performed by using GT2 tests at a level of significance of $\alpha = 0.05$ (Sokal and Rohlf 1995). According to the aims of our study, only those components that showed significant between-sample differences were taken into account for interpretation.

We estimated the standard errors of eigenvalues as the standard deviations of $n = 1\,000$ bootstrap replicates of the log-transformed data (Klingenberg 1996). In order to support the interpretation of a principal component, its associated variance must not represent merely measurement error (Anderson 1963). Given that this error is supposed to be the same for all measurements, Anderson (1963) provided a criterion to test for the equality of the last $q_r$ eigenvalues. We applied this criterion to the principal component analysis results to support the choice of components to be interpreted.

Canonical structure of between-group data was further examined using canonical variate analysis, and a discriminant function was extracted to verify the percentages of correct re-substitution classification of specimens. These analyses were performed based on the initial 24 measurements, and also removing specific ones, which were shown as the dominant sources of between-sample variation by previous analyses. The purpose of these extra analyses was to assess the degree of generalization supported by the data to the observed differentiation of the karyomorphs.

In order to check the adequacy of the least sample sizes employed in the present study (Mac and Uri samples), we compared the re-substitution classification of those specimens with the results of a cross-validation procedure. Unlike re-substitution, the linear discriminant function employed in cross-validation for classifying each specimen is estimated from the data after excluding this individual. Although a slight increase of error rates can be expected, it should not affect overall results if sample sizes are representative of population variability.

Statistical analyses were performed on the Version 6.08 for the PC of the Statistical Analysis System (SAS Institute 1993). Computational tasks were programmed using combinations of procedures IML, CANDISC, DISCRIM, GLM, and others. The program for shearing was based on Rohlf and Bookstein (1987) algorithm.

## Results

### Sex dimorphism

Analyses of variance showed all measurements to have a highly significant population effect, whereas most characters did not evince a significant sex effect. Only the maximum rostral height and the braincase height showed the sex effect to be marginally significant at a level of $\alpha = 0.05$. The interaction effect resulted significantly only in three measurements (total length, and upper and lower alveolar length), but two of them had P-values above 0.04. These differences were not considered sufficient to separate sexes in multivariate analyses. Sex dimorphism usually is not detected in morphometric studies with sigmodontine rodents (Voss et al. 1990). The differences observed in the present study may reflect a slight body size dimorphism, which has been previously detected in adults of *O. albigularis* raised under laboratory conditions (R. Moscarella, unpubl. data).

### Analysis of geographic variation

Univariate statistics calculated for the population samples (Tab. 2) show a roughly consistent pattern of between-measurement variation across the samples. Means and standard deviations are correlated in all cases, but are not correlated to coefficients of variation. It can be noted that measurements with the highest coefficients of variation are located on the interorbital, palatal, and sub-facial regions, whereas upper and lower alveolar length, and neurocranial measurements bear the lowest ones. Facial skull and total length measurements show intermediate values.

Eigenvalues of the total-sample principal component analysis (Tab. 4) demonstrate the first axis to account for 39–44% of the total variance. Ten axes were needed to extract 90% of the total variance. However, the first three axes attain a 69%, whereas the fourth falls to 4%, then decreasing steadily.

Principal components above the first were sheared for removing the common within-sample allometric variation from the total-sample covariance matrix. The first principal component of the pooled within-group covariance matrix (W1) was taken as the best representation of this common latent factor, sometimes regarded as size.

When contrasted with the first principal component of the total-sample covariance matrix (PC1; Tab. 3), the W1 coefficients of measurements situated on localized cranial regions have lower values, whereas measurements on the facial and neural regions and total-length measurements (total skull and basilar length) have consistently higher values. On the other hand, a comparison between the sheared (H2; Tab. 3) and non-sheared (PC2) second principal components shows the former to have lower coefficients for measurements that are often related to allometric variation (e. g. nasal length, maximum rostral height, basilar length, mandibular diastema length). Thus, W1 appears to be a good choice for representing a common size factor.

**Table 2.** Univariate statistics for the six population samples of *Oryzomys albigularis* analysed in this study. For each sample, first columns are means in mm, second columns are standard deviations, and third columns are coefficients of variation. See Tab. 1 for character acronyms. Avi: El Ávila N. P.; HPi: Rancho Grande, Henri Pittier N. P.; Mac: Macarao N. P.; Mer: Monte Zerpa; Uri: La Trampita; Yac: Yacambú N. P.

| Variables | Population Samples | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Avi | | | HPi | | | Mac | | | Mer | | | Uri | | | Yac | | |
| TL | 34.2 | 1.63 | 4.77 | 35.5 | 1.14 | 3.21 | 35.1 | 1.10 | 3.14 | 35 | 1.37 | 3.92 | 35.3 | 1.15 | 3.27 | 34.2 | 0.86 | 2.52 |
| NL | 13.2 | 1.04 | 7.87 | 13.5 | 0.70 | 5.20 | 13.5 | 0.45 | 3.34 | 13.2 | 0.69 | 5.25 | 13.5 | 0.82 | 6.07 | 12.8 | 0.56 | 4.37 |
| NMSL | 7.3 | 0.46 | 6.24 | 7.8 | 0.38 | 4.93 | 7.4 | 0.39 | 5.25 | 7.5 | 0.35 | 4.72 | 7.7 | 0.37 | 4.85 | 7.5 | 0.36 | 4.82 |
| LIB | 4.9 | 0.25 | 5.20 | 5.2 | 0.27 | 5.18 | 5 | 0.27 | 5.29 | 4.7 | 0.36 | 7.64 | 5.2 | 0.19 | 3.56 | 4.8 | 0.28 | 5.72 |
| FPSL | 6.2 | 0.51 | 8.17 | 6.5 | 0.48 | 7.37 | 6.3 | 0.40 | 6.26 | 5.1 | 0.44 | 8.50 | 6.2 | 0.34 | 5.56 | 5.4 | 0.38 | 6.96 |
| MBB | 13.6 | 0.39 | 2.87 | 13.9 | 0.36 | 2.63 | 13.9 | 0.39 | 2.79 | 14 | 0.37 | 2.66 | 13.6 | 0.24 | 1.72 | 13.9 | 0.31 | 2.24 |
| MRH | 8.2 | 0.52 | 6.37 | 8.7 | 0.36 | 4.16 | 8.6 | 0.23 | 2.69 | 8.5 | 0.40 | 4.66 | 8.6 | 0.45 | 5.16 | 8.5 | 0.27 | 3.13 |
| BH | 10 | 0.32 | 3.20 | 10.49 | 0.34 | 3.29 | 10.26 | 0.34 | 3.29 | 10.39 | 0.32 | 3.07 | 10.46 | 0.37 | 3.54 | 10.30 | 0.26 | 2.48 |
| BL | 26.2 | 1.30 | 4.95 | 27.2 | 1.02 | 3.74 | 26.7 | 0.95 | 3.55 | 26.9 | 1.12 | 4.18 | 27.3 | 1.07 | 3.93 | 26.4 | 0.82 | 3.09 |
| UAL | 5.6 | 0.20 | 3.54 | 5.7 | 0.19 | 3.28 | 5.8 | 0.19 | 3.24 | 5.7 | 0.25 | 4.43 | 5.6 | 0.23 | 4.10 | 5.4 | 0.15 | 2.81 |
| PBL | 6.4 | 0.39 | 6.10 | 6.7 | 0.39 | 5.82 | 6.7 | 0.34 | 5.05 | 7.1 | 0.37 | 5.25 | 6.4 | 0.30 | 4.60 | 6.7 | 0.34 | 4.99 |
| PBB | 1.9 | 0.16 | 8.36 | 1.9 | 0.15 | 7.72 | 2 | 0.11 | 5.26 | 1.8 | 0.12 | 6.40 | 2 | 0.14 | 7.08 | 1.7 | 0.14 | 7.85 |
| PL | 14.1 | 0.69 | 4.87 | 14.6 | 0.53 | 3.66 | 14.3 | 0.59 | 4.11 | 14.7 | 0.78 | 5.26 | 14.4 | 0.49 | 3.42 | 14.3 | 0.51 | 3.56 |
| UDL | 9.2 | 0.58 | 6.30 | 9.5 | 0.50 | 5.25 | 9.4 | 0.34 | 3.61 | 9.4 | 0.57 | 6.11 | 9.5 | 0.47 | 5.00 | 9.1 | 0.35 | 3.87 |
| PMSL | 5.5 | 0.41 | 7.47 | 5.8 | 0.27 | 4.74 | 5.7 | 0.51 | 8.89 | 5.4 | 0.22 | 4.12 | 5.6 | 0.27 | 4.85 | 5.5 | 0.24 | 4.32 |
| IFB | 2.5 | 0.15 | 5.96 | 2.4 | 0.17 | 7.07 | 2.5 | 0.12 | 4.70 | 2.3 | 0.18 | 7.74 | 2.6 | 0.21 | 8.26 | 2.3 | 0.17 | 7.46 |
| IFL | 6.1 | 0.43 | 7.11 | 6.1 | 0.37 | 6.09 | 6 | 0.50 | 8.27 | 5.6 | 0.35 | 6.21 | 6 | 0.34 | 5.63 | 5.4 | 0.37 | 6.73 |
| TBL | 6.9 | 0.34 | 4.91 | 7.2 | 0.44 | 6.11 | 7 | 0.38 | 5.50 | 7.1 | 0.29 | 4.12 | 7.2 | 0.25 | 3.55 | 7 | 0.25 | 3.63 |
| TBB | 5 | 0.18 | 3.53 | 5.2 | 0.18 | 3.40 | 5.1 | 0.17 | 3.33 | 5.2 | 0.18 | 3.46 | 5.4 | 0.13 | 2.50 | 5.1 | 0.16 | 3.07 |
| IML | 6.2 | 0.60 | 9.71 | 6.7 | 0.48 | 7.14 | 6.5 | 0.42 | 6.39 | 6.3 | 0.38 | 5.97 | 6.7 | 0.42 | 6.19 | 6.2 | 0.29 | 4.71 |
| IZL | 23 | 1.15 | 5.02 | 24 | 0.92 | 3.84 | 23.5 | 0.88 | 3.74 | 23 | 1.01 | 4.39 | 23 | 0.90 | 3.93 | 22.6 | 0.50 | 2.22 |
| ML | 17.3 | 0.81 | 4.67 | 18 | 0.72 | 4.02 | 17.6 | 0.63 | 3.59 | 17.7 | 0.54 | 3.05 | 18 | 0.68 | 3.77 | 17.7 | 0.59 | 3.31 |
| MDL | 4.5 | 0.31 | 6.90 | 4.6 | 0.33 | 7.11 | 4.5 | 0.32 | 7.23 | 4.5 | 0.28 | 6.29 | 4.6 | 0.28 | 5.98 | 4.4 | 0.25 | 5.57 |
| LAL | 5.7 | 0.18 | 3.22 | 5.8 | 0.20 | 3.43 | 5.8 | 0.23 | 4.05 | 5.8 | 0.23 | 3.96 | 5.7 | 0.24 | 4.20 | 5.5 | 0.19 | 3.43 |

The main between-sample differentiation is obtained with the H2 scores by itself (Fig. 3 b), whereas both the first and second non-sheared principal components are required to depict this pattern (Fig. 2), possibly indicating the presence of size-related variation in the non-sheared vectors.

The arrangement of specimens on the ordination plots (Figs. 2, 3 b) displays the formation of two clusters, including the Avi, HPi, Mac, and Uri samples, and the Mer and Yac samples, respectively. While the former includes individuals from three coast cordillera

**Table 3.** Measurement coefficients of the first principal component of the pooled within-group covariance matrix (W1), first and second principal components (PC1 and PC2, respectively) and first principal component (H2) of the sheared total-sample covariance matrix. See Tab. 1 for character acronyms.

| Character | W1 | PC1 | PC2 | H2 | Character | W1 | PC1 | PC2 | H2 |
|---|---|---|---|---|---|---|---|---|---|
| TL | 0.196 | 0.167 | 0.117 | 0.035 | PL | 0.215 | 0.144 | 0.188 | 0.103 |
| NL | 0.265 | 0.226 | 0.147 | 0.038 | UDL | 0.283 | 0.218 | 0.184 | 0.072 |
| NMSL | 0.185 | 0.186 | 0.034 | –0.042 | PMSL | 0.244 | 0.231 | 0.086 | –0.014 |
| LIB | 0.082 | 0.196 | –0.256 | –0.287 | IFB | 0.257 | 0.237 | 0.003 | –0.086 |
| FPSL | 0.034 | 0.367 | –0.735 | –0.750 | IFL | 0.276 | 0.331 | –0.069 | –0.182 |
| MBB | 0.064 | 0.039 | 0.053 | 0.030 | TBL | 0.158 | 0.135 | 0.108 | 0.039 |
| MRH | 0.234 | 0.182 | 0.152 | 0.059 | TBB | 0.102 | 0.078 | 0.106 | 0.060 |
| BH | 0.104 | 0.076 | 0.087 | 0.044 | IML | 0.345 | 0.309 | 0.180 | 0.034 |
| BL | 0.223 | 0.174 | 0.151 | 0.061 | IZL | 0.216 | 0.206 | 0.082 | –0.009 |
| UAL | 0.073 | 0.113 | –0.006 | –0.047 | ML | 0.193 | 0.144 | 0.142 | 0.065 |
| PBL | 0.176 | 0.063 | 0.293 | 0.221 | MDL | 0.281 | 0.221 | 0.184 | 0.071 |
| PBB | 0.213 | 0.316 | –0.133 | –0.229 | LAL | 0.060 | 0.088 | 0.003 | –0.031 |

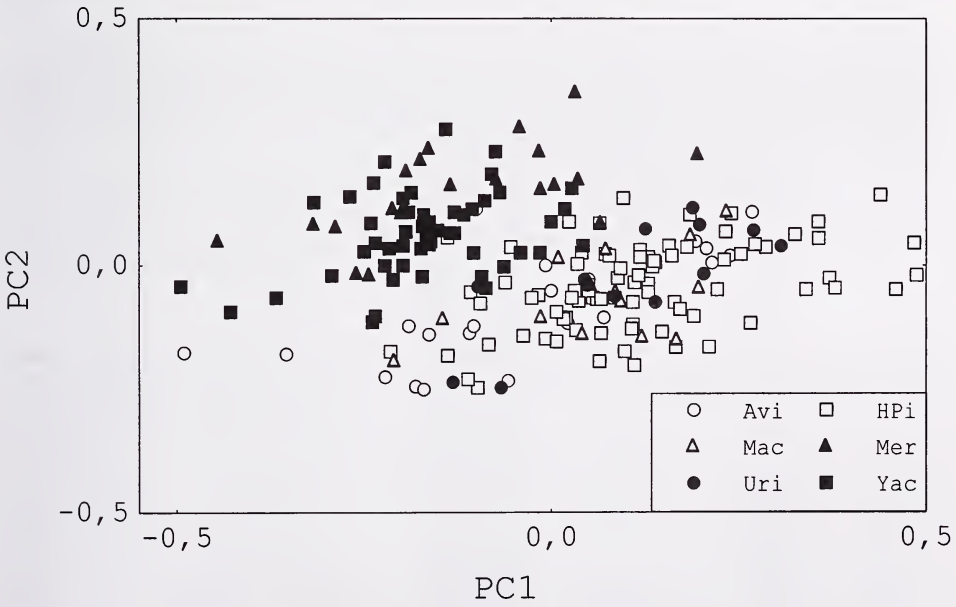


**Fig. 2.** Scores for the *Oryzomys albigularis* individuals from the six population samples on the first and second principal component of the total covariance matrix. Open marks represent samples from the coastal cordillera, and closed ones from the Andean cordillera.

and one Andean cordillera populations, the latter only incorporates specimens from Andean populations. The respective FNs (Fig. 1) are 90, 90, 90, 92, 104 and 104. Thus, it is evident that some extent of correspondence exists between morphometric variation and karyomorph similarity patterns, irrespective of the geographical location of the samples. The eigenvector coefficients (Tab. 3) of the axes that best represent this pattern demonstrate that contrasts among measurements located on the interorbital, palatal, and incisive foramen regions are the responsible ones for the karyomorph separation. Specimens with FN = 104 seem to have a long and narrow palate bone, whereas the coastal and Uri specimens seem to have wider interorbital bones. There seems to be a slight difference between samples, related to the length of incisive foramen, which covaries positively with the interorbital region, and negatively with the length of the palate bone.

Analyses of variance on the specimen scores resulted in significant between-population mean differences ($\alpha = 0.05$) in 1st through 5th, 7th, 8th, 10th, 11th, and 14th principal components (Tab. 4). Application of the Anderson's (1963) criterion to test for the differences of 14th through 24th eigenvalues produced significant results ($X^2 = 473.26$, d. f. = 65); thus the remaining eigenvalues (1st through 13th) are considered relevant for interpretation.

Vectors W1 and H2 were used instead of PC1 and PC2 for projecting the morphometric data, since the latter are probably confounding size and size-independent variation. GT2 test on W1 scores (ANOVA $F = 14.47$, $P < 0.001$) arranged four overlapped groups, with the HPi and Mac samples in the upper extreme, and the Avi and Yac samples in the lower one (Fig. 3 a). This result could be revealing an East-West size gradient along the coastal cordillera populations.

Application of the GT2 test on the H2 scores (ANOVA $F = 87.95$, $P < 0.001$) confirmed the pattern depicted by the plots (Fig. 3 b). Analysis of the scores of principal components above the second, further discriminated the samples initially grouped in two clusters. Sample 95% confidence intervals of third principal component scores seemed to

**Table 4.** Eigenvalues (and SE) of the first 14 principal components of the total-sample covariance matrix, cumulative variance extracted, and results from the ANOVA on principal component scores to test for population effects. Eigenvalues and their SE are multiplied by 100. Standard errors calculated as bootstrap standard deviations with n = 1 000 replicates.

| Principal Component | Eigenvalue | % Cumulative variance |
|---|---|---|
| 1*** | 3.533 (0.350) | 41.78 (2.49) |
| 2*** | 1.337 (0.128) | 57.59 (1.81) |
| 3*** | 0.929 (0.089) | 68.58 (1.61) |
| 4*** | 0.417 (0.036) | 73.51 (1.38) |
| 5*** | 0.350 (0.027) | 77.65 (1.16) |
| 6 | 0.285 (0.023) | 81.01 (0.96) |
| 7* | 0.242 (0.019) | 83.87 (0.80) |
| 8*** | 0.211 (0.015) | 86.37 (0.66) |
| 9 | 0.207 (0.014) | 88.81 (0.54) |
| 10** | 0.151 (0.011) | 90.60 (0.45) |
| 11*** | 0.139 (0.009) | 92.24 (0.37) |
| 12 | 0.134 (0.008) | 93.82 (0.30) |
| 13 | 0.104 (0.007) | 95.06 (0.25) |
| 14** | 0.090 (0.006) | 96.12 (0.21) |
| Total variance | 8.458 (0.408) | |

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

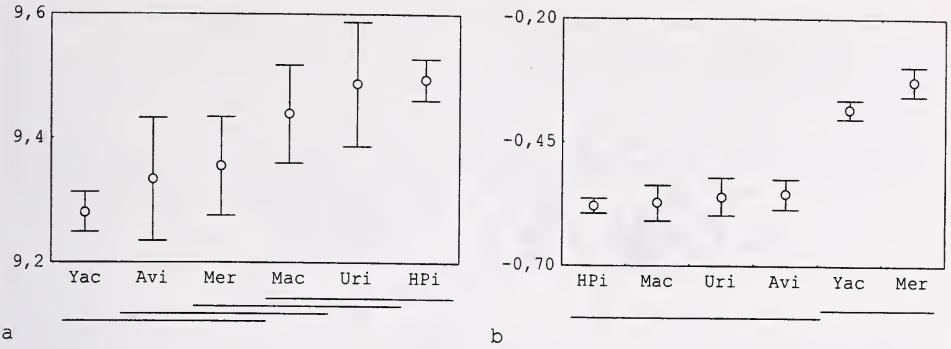


**Fig. 3.** Sample means and 95% confidence intervals of the scores of *Oryzomys albigularis* log-transformed data projected on the (a) first eigenvector of the pooled within-group covariance matrix, and (b) first eigenvector of the sheared total-sample covariance matrix. Lines under plots represent results of multiple comparison tests (GT2) to test for mean differences among samples.

differentiate the HPi sample from the Mac, Avi, and Uri ones, but the GT2 test did not support these observations. Eigenvector coefficients of the third axis (11% of total variance) contrasted the length of palate bone and interorbital measurements, with the length and breadth of the incisive foramen and breadth of the palate bone. Tests of between-sample differences and observations of the confidence intervals supported the discrimination of the Yac and Mer samples on the eighth axis (2.5% of total variance), due to a contrast between the alveolar, palate, and tympanic bulla lengths. On the other hand, Uri is not separated from the coastal samples until the 11th principal component (1.6% of total variance). The remaining significant principal components showed no further differentiation of the groups of karyomorphs evinced in the second sheared principal component.

Mahalanobis distances among karyomorphs showed the same similarity pattern described by previous analyses (Tab. 5). The coastal cordillera samples yielded the least D values, which were correlated with geographic distance; the Yac and Mer D value was also low. Mahalanobis distances between Uri and remaining samples were intermediate; however, these specimens were closer to coastal samples than to Andean ones. Hotelling $T^2$ tests significantly differentiated almost every pair of samples. Only the Avi-Mac distance resulted in a non-significant P value at $\alpha = 0.05$. When the significance value was adjusted for 15 non-independent comparisons (Dunn-Šidák $\alpha' = 0.0034$), the HPi-Mac distance was non-significant as well.

**Table 5.** Mahalanobis distances (above diagonal) among the six population samples of *Oryzomys albigularis*, and F-values of the Hotelling's $T^2$ statistic for pairwise comparisons of centroids (below diagonal). See text for population acronyms.

| Samples | Avi | HPi | Mac | Mer | Uri | Yac |
|---|---|---|---|---|---|---|
| Avi | | 2.41 | 2.25 | 4.92 | 4.41 | 4.80 |
| HPi | 3.58*** | | 2.06 | 4.77 | 3.69 | 4.40 |
| Mac | 1.57 | 1.87* | | 4.89 | 4.20 | 4.96 |
| Mer | 9.11*** | 13.49*** | 7.25*** | | 5.37 | 2.70 |
| Uri | 5.74*** | 5.62*** | 4.38*** | 8.36*** | | 4.71 |
| Yac | 12.60*** | 22.51*** | 9.96*** | 3.85*** | 8.45*** | |

* $P < 0.05$, *** $P < 0.001$.

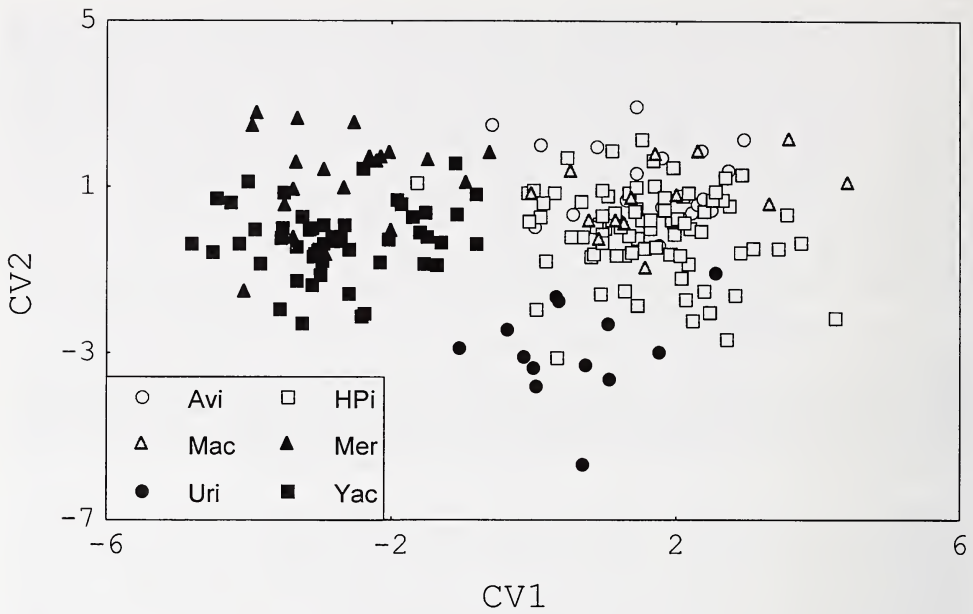


**Fig. 4.** Scores for *Oryzomys albigularis* individuals from the six population samples on the first two canonical variates computed from 24 morphometric variables.

Canonical variate analysis also resulted in a similar pattern (Fig. 4); the main between-sample separation occurred at the first canonical variate (67.73% of total extracted variance). This analysis discriminated the Uri sample and the three coastal ones at the second canonical axis (14.29% of total variance). The utilization of a linear discriminant function for classifying by re-substitution yielded error rates from 0.077 to 0.357; incorrect a posteriori classifications occurred within the same cluster (coast cordillera or Mer-Yac samples), bearing the Uri sample the least error rate.

As expected, the classification of specimens by a cross-validated discriminant analysis resulted in a slight increase of error rates in almost every sample. However, the overall pattern of results was not altered, and almost every misclassified specimen was assigned to a locality with an identical karyotype. Exceptions to this pattern were the same seen in previous classifications and no exception was found in the Macarao N. P. (Mac) sample, despite bearing the highest increase in error rate (+ 28.57%). The cross-validation of Uribante (Uri) data resulted in the same percentage of correct classification as with re-substitution; the same individual was misclassified in both procedures. This coherence was also evident when different character sets were used to classify the data. The overall patterns observed for the Uri and Mac samples may be used as an indicative of within-sample cohesion, what might be a consequence of representative sample sizes.

Results from principal component and canonical variate analyses show a pattern in which the Uri sample lies closer to the coast than to the remaining Andean ones. Coefficients of total-sample eigenvectors and the canonical structure indicate this pattern to be mainly due to measurements on interorbital bones, palate bone, and incisive foramen. Standardized loadings on the second canonical axis associate the separation of the Uri and coastal samples with a contrast between the incisive foramen, incisive-zygomatic, palate bone lengths, and tympanic bulla breadth, mandible, and incisive-maxillary lengths.

Recalculation of canonical variates and Mahalanobis distances after removing measurements on interorbital, palatal, and incisive foramén regions yielded similar results.

However, the Uri specimens were arranged closer to the remaining Andean than the coastal ones. When only these characters were used to calculate the canonical variates and Mahalanobis distances, a unique sample discrimination was observed in the first axis (83.31% of the total variance), depicting the same pattern that had been observed with the complete set of characters. This result reveals that the similarity of the Uri and coastal cordillera populations could be a consequence of the covariation pattern among the implied six measurements.

## Discussion

Previous investigators (Aguilera et al. 1995; Gardner and Patton 1976) have documented the relatively high karyological diversity of northern South America populations of *O. albigularis*. Northernmost Venezuelan populations (the Avi, Mac, and HPi samples herein, FN = 90) have been shown to be more similar to those located at the southern Venezuelan Andes (the Uri sample, FN = 92), and at the southern Colombian Andes (FN = 94; Gardner and Patton 1976), whereas populations from northern Venezuelan Andes (the Yac and Mer samples, FN = 104) resemble those from northern Colombia (FN = 112; Gardner and Patton 1976). These results have been employed to argue that *O. albigularis* is as a supraspecific complex, by considering also that pericentric inversions have played a major role in the differentiation of the karyotypes (Aguilera et al. 1995).

The main objective of the present study was to elucidate the systematic relationships among several karyotypic variants of *O. albigularis* using multivariate skull morphometrics. Although this kind of data may not be suitable for reconstructing phylogenetic relationships (Bookstein 1991), phenotypic differentiation of forms can be expected when evolutionary divergence has caused the gene flow among populations to stop (Lande 1980). The pattern of morphometric variation observed in the present study showed a clear relationship with the karyological and geographical patterns of the analysed populations, in addition to allowing the craniometric characterization of the karyomorphs.

Multivariate ordinations clustered specimens with identical or nearly identical karyotypes. Single factors, such as the first eigenvectors of both total-sample and pooled within-group covariance matrices, produced the best within-karyomorph discrimination of population samples with FN = 90 and 104. This pattern suggests allometry as a major factor in the evolutionary divergence of the closest related forms, perhaps through the intervention of heterochronic processes (Klingenberg 1998). This result allowed us to disregard size as being important for karyomorph distinction, in accordance with the traditional approach, which considers "shape" as a more relevant factor for the study of evolutionary morphometric divergence (Rohlf and Bookstein 1987).

The present analyses give morphological support to the proposal of defining Venezuelan populations of *O. albigularis* as a species complex instead of a single nominal species (Aguilera et al. 1995). Following early classifications (Ellerman 1941; Gyldenstolpe 1932; Tate 1932), the terms *O. meridensis* and *O. caracolus* should be retained for populations from the northern Andean range (i. e. Yac and Mer samples), and from the coast cordillera. For the Uribante (Uri) population, Aguilera et al. (1995) have preferred the provisional denomination of *Oryzomys* sp.

An important finding emerging from our results is the observed coincidence of the patterns of karyomorph similarity when either karyotypic or morphometric data are considered. Discrimination of the three karyomorphs with different FN resulted in two clusters, constituted by coastal cordillera and Uri samples, and Mer and Yac ones, respectively. This pattern was kept almost the same even when a different combination of characters was employed, with the exception of the Uri sample, whose relationship with

remaining samples relied on the set of traits employed. Measurements related to interorbital breadth, palatal breadth and length, and incisive foramen dimensions caused the Uri to resemble the coastal samples, whose karyotypes are probably closely related. Removal of those characters bridged morphometric similarity with geographical distance, disregarding karyotype similarity as being important in establishing relationships.

The congruence of patterns derived from independent data sets has been regarded elsewhere as evidence of a common causal factor affecting variation in both sets (Thorpe et al. 1991). Since independent portions of organisms are unlikely to diverge in the same way by means of selection after population isolation, phylogeny has been invoked as the most probable common causal factor for the actual patterns (Thorpe 1996; Thorpe et al. 1991).

A phylogenetic hypothesis for explaining morphometric and karyotypic similarity would involve the Uribante and coastal cordillera populations to be more closely related to each other than to the northern Andean ones. Moreover, if we take into account the Gardner and Patton (1976) observations of the karyological similarity among the southern Colombia and coastal cordillera individuals, the Uribante population could be considered as a member of the same clade. The pattern of geographical distances among the populations sampled for the present study does not match with the observed similarity. Thus, acceptance of a phylogenetic hypothesis would require a biogeographic model which explains the actual disjointed distribution of the members of the low FN clade, with the high FN clade in the middle of their range.

Results that these considerations depend on are based on the covariation patterns of a few localized cranial regions. Although a rigorous test of the evolutionary significance of the involved characters is outside the aims of the present study, a thorough inspection of our results can help to assess the validity of a phylogenetic hypothesis. If common history did not cause observed patterns, these would relate to local effects acting independently on current populations (Thorpe et al. 1991), such as directional selection and adaptation. On the other hand, absence of selection would be a strong indicator of phylogeny, but its presence would prevent us from distinguishing phylogeny from chance as the main cause of congruence.

The morphological evolution of the palate bone has been recognized as an important aspect within the radiation of the sigmodontines (Hershkovitz 1962). Its variation has been related to the progressive invasion and adaptation to the diverse habitat types that these rodents actually occupy. In spite of being unable to extrapolate these observations to our study, a selective value of the palate bone cannot be excluded as a possible explanation for the observed variation in *O. albigularis*. Nonetheless, the validity of this reasoning depends on the ecological variability associated with these traits. Characters located on the incisive foramen and interorbital regions have not been explicitly related to sigmodontine diversification, but they received attention in early descriptions of "*caracolus*" and "*meridensis*" forms (Gyldenstolpe 1932) as diagnostic characters.

The observed high covariation between palate bone dimensions and the interorbital region suggests their morphological integration, possibly due to epigenetic factors acting in these traits as a group (Leamy et al. 1999; Riska 1985; Wright 1932). Covariation of palate bone with incisive foramen measurements must be reflecting non-independent variation caused by their proximity. In the case where these regions were evolving as a character complex, an "ecogenetic" explanation could not be ruled out for the observed pattern of variation, based on the convergence or parallelism of the FN = 90 and 92 morphometric trait means for this group of characters. Nevertheless, rejection of a common-cause hypothesis for the observed congruence would imply the acceptance of a high number of chromosomal changes among populations with extreme FN.

A last issue that can be integrated in the interpretation of present results is the extent of variability shown by individual measurements, as given by the coefficients of variation. Those traits associated with the main karyomorph discrimination, with the highest total-

sample variances, were also those with the highest coefficients of variation within the samples. This pattern resembles a series of findings discussed several years ago, the so-called "Kluge and Kerfoot (1973) phenomenon", which consists of high positive correlations among within- and between-sample coefficients of variation. Although the methods employed to detect this pattern were criticized (see Rohlf et al. 1983 and references therein), the question concerning its true existence remained to be documented. Although our results do not account for such a correlation, it seems remarkable that shifting of means over populations is most evident in traits whose variances remained consistently high amongst diversification. Explanations given to this sort of pattern tend to involve considerations on selection and developmental constraints, and commonly assume an inverse relationship between the variation of a trait and its effect upon fitness, or the strength of the constraint (Rohlf et al. 1983). This conclusion favors a phylogenetic hypothesis, because of the implicit reduction of the selective value associated with highly variable characters.

Stability of patterns of variation across evolutionary divergence of means has been demonstrated for variances (Lande 1976) and covariances (Lande 1979; Riska 1985; Steppan 1997 b). This has led authors to hypothesize a long-term stability of variance-covariance patterns caused by constraints on morphology, despite short-term divergence of developmental paths. This stability is not restricted to whole morphological structures, but has been invoked to explain the evolution of groups of traits controlled by their own constraints (Riska 1985; Wright 1932).

Patterns depicted by our data could be the consequence of a non-selective shift of means, as evinced by their congruence with karyology and the high within-population variance; and selective maintenance of variances and covariances, probably by means of stabilizing selection on several correlated characters. These observations, along with the association with "shape", instead of "size" of the discrimination between karyomorphs, led us to propose phylogeny as the most parsimonious hypothesis to explain the observed pattern of similarity. Testing of this hypothesis and analysis of Colombian specimens will help to clarify the taxonomic confusion within the species, through the understanding of the cladistic arrangement of the karyomorphs and populations.

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## Zusammenfassung

***Morphometrische und chromosomale Variation von Oryzomys albigularis (Muridae: Sigmodontinae) aus Venezuela: Multivariate Aspekte***

Der zusammengesetzte Charakter der Art *Oryzomys albigularis* ist aufgrund der karyologischen Heterogenität im Hinblick auf Chromosomenzahl und FN lange bekannt. Aus den östlichen und den nördlichen Anden wurden zwei Gruppen von Populationen mit 2n = 66 bzw. 2n = 80 beschrieben. Das Ziel der vorliegenden Arbeit war die Abschätzung von Unterschieden zwischen Populationen an Hand von metrischen Schädelmerkmalen. Die für multivariate Analysen verwendeten Populationen

wurden auf der Grundlage von Unterschieden in der Zahl autosomaler Chromosomenarme definiert. Hauptkomponentenanalysen und kanonische Varianzanalysen erlaubten eine klare morphologische Unterscheidung zwischen den Karyomorphen. Die meiste Information lieferte dabei die Variation im Interorbitalbereich, im Palatalbereich und im Bereich der Foramina incisivi. Nach einer vorgenommenen Korrektur für Größenunterschiede erklärten diese Merkmale den größten Teil der Gesamtvarianz. Über die einzelnen Gruppen hinweg ergaben sich bemerkenswert ähnliche Varianzen für alle Maße, was auf stabile Muster innerhalb der Gruppen hindeutet. Es wurde kein Hinweis auf eine Kongruenz zwischen den Mustern der morphologischen Variation und dem geographischen Abstand zwischen den Karyomorphen gefunden, aber die Ähnlichkeitsbeziehungen zwischen den Stichproben erwiesen sich für morphologische und chromosomale Merkmale als übereinstimmend. Da die beiden Merkmalsbereiche voneinander unabhängige Information liefern, kann angenommen werden, daß unsere Daten phylogenetische Beziehungen wiedergeben. Unsere Ergebnisse bestätigen den polytypischen Charakter der untersuchten Art, da die meisten morphologischen Unterschiede durchgehend mit den grundlegenden karyologischen Unterschieden zusammenfallen.

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