

A SYSTEMATIC REVISION OF GENUS *ISTHMOMYS* (RODENTIA: CRICETIDAE)

by

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ABSTRACT

This study provides data on morphometric variation among allopatric populations of two species of *Isthmomys* (Hooper and Musser 1964). Cranio-dental measurements and landmark point coordinate data were collected from dorsal, lateral and ventral views of the crania of 126 museum specimens representing the majority of available specimens in the genus. Morphometric techniques were used to examine secondary sexual dimorphism and geographic variation in size and shape within and among OTUs. Statistical analyses revealed negligible sexual dimorphism; therefore both males and females were pooled in the subsequent analyses. A multivariate analysis of variance (MANOVA) of the linear measurements show significant differences ($p \leq .05$) between allopatric populations and their respective type localities; corresponding canonical variates and principal component analyses show that the groups are well differentiated. After removing the component of size from the landmark data, principal component analyses of shape and canonical variates analysis showed patterns of shape variation within *I. flavidus* and *I. pirrensis* revealing the possibility of polytypic species. Additionally, evaluation of 5 qualitative characters showed unique morphologies for each OTU. Within the context of a systematic revision, these indicate strong possibilities of polytypic species.

Key words: Allopatric, *Isthmomys*, morphometrics, morphometric variation, size, shape analysis, Panama.

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CHAPTER I

INTRODUCTION

The yellow deer mouse (*Isthmomys flavidus*) and the Mt. Pirre deer mouse (*I. pirrensis*) are neotomine-peromyscine Panama endemics that have been recorded from disjunct localities of montane cloud forests at elevations ranging from 900-1500m. Although Panama has been the subject of numerous faunal surveys and ecological studies (Aldrich and Bole 1937; Anthony 1916; Bangs 1902; Fleming 1970; Goldman 1912, 1920; Handley 1966; Mendez 1993; Wenzel and Tipton 1966), museum records indicate that there appears to be no suitable habitats for members of this genus in the low-lying intermediate elevations. Thus, the occurrence of this genus and its population ranges have a propensity to be highly localized and dependent on unknown ecological factors.

Isthmomys flavidus, described by Bangs (1902), was discovered by W. W. Brown, Jr. on the southern slope of Volcan de Chiriqui (8° 49' N, 82° 32' W). He found it common in the upland forest from 1000 to 1500m, but no specimens were taken above or below these elevations (Bangs 1902; Goldman 1920; Goodwin 1946). Museum records specify two isolated populations in western Panama, one at Cerro Colorado where R. Pine *et al.* collected in 1980 (8° 31' 60N, 81° 49' 0W) and at Cerro Hoya on the Azuero Peninsula by C. Handley in 1962 (7° 23' N, 80° 38' W). The presence of *I. flavidus* or a closely allied form in Costa Rica is probable (Goodwin 1946), however, no specimens have been reported. There are no currently known fossil records of *Isthmomys* (McKenna and Bell 1997)

I. pirrensis was described by Goldman (1912) and at the time it was considered as the “most common rat of southeastern Panama” (Anthony 1916). Found only in the eastern region of Darien, *I. pirrensis* appears to be a relic species confined to the Panamanian side of the Serrania del Darien (Herskovitz 1966). Its occurrence on the Colombian side of the Serrania has been suggested without documentation of specimens (Alberico et al. 2000; Cuartas-Calle and Muñoz-Arango 2003; Hall and Kelson 1958; Herskovitz 1966). Localities for *I. pirrensis* indicated by museum records are in the eastern Panama state of Darien throughout the areas surrounding Mt. Pirre (=Pirri, 7° 51' 8" N, 77° 46' 24" W), Mt. Tacarcuna and the Tacarcuna Village (8° 10' 58" N, 77° 17' 3.5" W); however, no specimens are recorded from the low lying areas (<800m) that bisect these two ranges. Although neotomine-peromyscine rodents have historically been the subject of systematic research, studies involving *Isthmomys* have generally excluded *I. flavidus* due to its rarity in museum collections and the unavailability of tissue samples for molecular analysis (Bradley et al. 2007; Bradley et al. 2004; Carleton 1973; Engel et al. 1998; Hill 1975; Stangl and Baker 1984). In addition, morphological and physiological studies involving *I. flavidus* (Carleton 1973, 1980; Hill 1975; Hooper and Musser 1964; Linzey and Layne 1974; Linzey and Layne 1969; Voss and Linzey 1981) utilized specimens from the Cerro Hoya locality which was originally proposed as a geographic race of *I. pirrensis* (Handley 1966).

To date, there have been no studies evaluating geographic and non-geographic variation within the genus or species limits, considering the isolated nature of known populations. A few cranio-dental traits have been used to discriminate the two species.

Most notable is the tendency of a 6-tuberculate condition in the first upper molar of *I. flavidus* (vs. the 5-tuberculate condition in *I. pirrensis*) (Goldman 1920) and the presence of a subsquamosal fenestra in *I. pirrensis* which generally is absent in *I. flavidus* (Carleton 1980, 1989).

The objective of this study was to evaluate the morphometric variation within *Isthmomys* from five allopatric populations distributed throughout Panama. By employing traditional (linear) and geometric morphometric techniques, analyses to identify morphological variation in size and shape of the crania were compared to results from analyses of qualitative characters. Results from the analyses were used to evaluate the taxonomic status of the allopatric populations within the context of a systematic revision of *Isthmomys*.

CHAPTER II

MATERIALS AND METHODS

Isthmomys specimens (A total of 143 individuals) were assigned to one of three age classes (juvenile, sub-adult, and adult) based on eruption of the third upper molar, degree of tooth wear, and pelage color. Specimens classified as adults were further subdivided by degree of tooth wear as young, middle aged adults and old adults (A-IV) (Koh and Peterson 1983). This study is limited to middle-aged adult specimens in order to avoid variation due to pre- and old-adult growth trajectories, thus, specimens reported herein (n=126; 50 *I. flavidus*, 76 *I. pirrensis*) consist principally of skins with their associated skulls (Appendix I) and are housed in the following museums and institutions: American Museum of Natural History, New York City (AMNH); Museum of Natural History, University of Kansas, Lawrence (KU); National Museum of Natural History, Smithsonian Institution, Washington, D.C (USNM); Michigan State University Museum, East Lansing (MSUM); Louisiana Museum of Natural History, Louisiana State University, Baton Rouge (LSU) and Museum of Comparative Zoology, Harvard University (MCZ). A full list of specimens is listed in Appendix B.

Operational Taxonomic Units. — Each of the five individual localities, which according to museum records appear to be isolated, are each regarded as a separate entity. Each operational taxonomic unit (OTU) is assigned in reference to date of discovery and shall be referred as such throughout the remainder of the paper: OTU 1: *I. flavidus* type locality Volcan de Chiriqui (1901); OTU 2: Cerro Hoya (1962); OTU 3: Cerro Colorado (1980); OTU 4: *I. pirrensis* type locality Mt. Pirre and surrounding areas (=Cerro Pirre,

Cana, 1912); OTU 5: Mt. Tacarcuna and surrounding areas (=Cerro Tacarcuna, Cerro Mali, Tacarcuna Village, 1914) (see Fig. 1).

Morphological Characters. — Character states for 5 discrete morphological characters were recorded for 93 individuals (42 *I. flavidus*: 20 males, 22 females; 51 *I. pirrensis*: 32 males, 19 females) from the five OTUs in accordance to observations of *Isthmomys* specimens. The following characters are treated in the analysis and the defined character states are indicated by numbers in parentheses.

Character 1. Bifurcation of the anterior cusp (anteromedian flexus) of first upper molar.

- (0)-absent;
- (1)-present, but only slightly;
- (2)-deep, but not extending completely through the cusp;
- (3)-very deep extending completely through the cusp.

Character 2. Shape of the mesopterygoid fossa

- (0)-lateral borders slightly rounded, anterior border smooth, medial portions extended slightly towards posterior (as in *Peromyscus eva*);
- (1)-lateral borders squared, anterior border jagged or uneven, medial portions of anterior border extended towards palatine;
- (2)-lateral borders squared, anterior border smooth, not extended towards palatine;
- (3)-lateral and anterior borders rounded slightly, medial portions of anterior border extended towards palatine;
- (4)- lateral and anterior borders rounded slightly, not extended towards palatine;
- (5)- lateral and anterior borders completely rounded, medial portions of anterior border extended towards palatine).

Character 3. Shape and size of the post-glenoid fossa compared to the optic canal.

- (0)-absent;
- (1)-small, round or oval-shaped;
- (2)-small, elongated and narrow;
- (3)-large, round or oval-shaped;
- (4)-large, elongated, narrow with pointed or sharp anterior terminus.

Character 4. Size and shape of the subsquamosal fenestra compared to optic canal.

- (0)-absent;
- (1)-tiny, round;
- (2)-small, oddly shaped or oval;
- (3)-large, oddly shaped or oval;
- (4)-large and round;

Character 5. Size and shape of the lacerate (=petrotympanic) foramen compared to m1.

- (0)-absent or tiny;
- (1)-small, narrow;
- (2)-small, rounded or oval;
- (3)-large, narrow and elongated laterally;
- (4)-very large, rounded, size almost that of m1;
- (5)-very large, oddly shaped, extended laterally size almost that of m1.

Characters 1 and 4 historically have been utilized to distinguish between *I. flavidus* and *I. pirrensis* (Carleton 1980, 1989; Goldman 1920), however, insufficient sampling indicated the need for review; characters 2, 3, and 5 were chosen *a priori*. Modal tendencies for each OTU were estimated and hypotheses of phenetic relationships were generated using cluster analysis of Euclidean distances with 500 bootstrapping replicates.

Morphometric variables. — Nineteen cranio-dental measurements following Carleton *et al.* (2002) were measured to 0.01mm using hand-held digital calipers while viewing crania under a stereomicroscope (Carleton, Sanchez, and Vidales 2002): occipitonasal length (ONL); zygomatic breadth (ZB); breadth of zygomatic plate (BZP); interorbital breadth (IOB); breadth of braincase (BBC); breadth of occipital condyles (BOC); height of braincase (HBC); length of rostrum (LR); width of rostrum (WR); length of diastema (LD); length of incisive foramina (LIF); breadth of incisive foramina (BIF); length of bony palate (LBP); breadth of palate between first upper molars (BM1); width of Mesopterygoid fossa (WMF); post-palatal length (PPL); coronal length of

maxillary tooth row (CLM); width of the first upper molar (WM1); breadth of incisor tips (BIT) (Appendix 2). Homologous points of measurement were identified and in order to reduce experimental error, each measurement was taken three times with the value recorded for analysis being equal to the mean. Because multivariate morphometric procedures generally require complete data matrices with all characters present for all specimens, this study applied the expectation-maximization (EM) algorithm for replacing missing values for those samples with 9 or fewer missing values (Strauss, Atanassov, and Oliveira 2003). EM offers an accurate and precise value replacement method when dealing with a small number of variables when the deletion of specimens with missing data could be detrimental to multivariate statistical analyses (Strauss and Atanassov 2006). Definition of the measurements are listed in Appendix C.

A total of 126 individuals (74 males, 52 females) from 5 OTUs were analyzed to determine variation between sexes and between populations. Standard descriptive statistics (mean, range, standard deviation, coefficient of variation) were estimated for each OTU (Table 1). In order to determine the presence of sexual dimorphism in the sample, variation between sexes was evaluated using analyses of variance (ANOVA) on the 19 measurements, all of which were first log-transformed. Multivariate analysis of variance (MANOVA) of the log-transformed data was used to estimate *p*-values to determine if significant differences in multivariate space were present. Post-hoc Hotelling's T^2 -test, the multivariate generalization of the Student's *t* statistic, was used to estimate the level of statistical significance between the OTUs. A principal component analysis using the variance-covariance matrix of log-transformed measurements was used

to summarize the direction of greatest variation within the genus. Canonical variate analysis (CVA) was then conducted to order the populations along maximization differentiation axes. Centroid coordinates of each OTU, calculated as the means of individual canonical scores, were used to determine Euclidean distances between OTUs. Using UPGMA cluster analysis with 500 bootstrapping replicates, a classification tree was constructed to illustrate phenetic similarities. Statistical analyses were performed in the statistical packages R (www.r-project.org) and PAST v1.68 (Hammer, Harper, and Ryan 2001)

Geometric Landmarks. — Digital images of *Isthmomys* skulls were taken and imported into the digitizing software program TPSDig2 (F. J. Rohlf, <http://life.bio.sunysb.edu/morph/>). A set of 73 2-dimensional landmarks (Fig. 2), assumed to be homologous from individual to individual, were identified from dorsal, ventral and lateral views. Landmark configurations for all specimens in each view of the skull were separately superimposed and aligned by a generalized Procrustes superimposition, a least-squares fitting procedure that allows the elimination of non-shape variation and generates a true size-free dataset by removing isometric size variation (Adams, Rohlf, and Slice 2004; Rohlf 1990). For each view, principal component analysis of shape was conducted on the Procrustes rotated landmarks to establish the variance in landmark position. In geometric shape analysis, the principal components reveal patterns of variation of the individual landmarks in relation to one another. PCA is an effective method of data reduction for a large number of coordinates because a small subset of PCs can reveal the majority of total variation in shape (Klingenberg and Zaklan

2000). A MANOVA was conducted for the entire dataset of Procrustes rotated landmarks to determine significant differences between groups. Insufficient sample size prohibited post-hoc Hotelling's pairwise comparisons; therefore mean shape differences were evaluated between OTUs using Goodall's F -statistic which utilizes eigenanalysis and iterative generalized Procrustes analysis for 2-dimensions to estimate p -values. Differences in shape were then summarized using canonical variate analysis to order the populations of *Isthmomys* along axes of maximum differentiation by maximizing between-population variance with respect to within-population variance (Lorenzo et al. 2006; Zelditch et al. 2004). Analyses were performed using statistical packages R and PAST v1.68.

CHAPTER III

RESULTS

Non-geographic Variation. — Results of the ANOVA found no significant differences ($p \leq .05$) between males and females from all OTUs in the majority of the 19 cranio-dental variables. Exceptions were 1 variable (IOB) in OTU 1, and 3 variables (BOC, WM1, WR) in OTU 4. Therefore, sexual dimorphism was found to be negligible and both males and females were pooled in the subsequent analyses.

Morphological Characters. — Carleton (1980) reviewed characters 1 and 4 and reported 2 distinct differences in skull morphology within *Isthmomys*; the presence of a presence of a bifurcated anterior cusp of m1 (character 1) in both species and the absence of the subsquamosal fenestra (character 4) in *I. flavidus* (Carleton 1989). His report concerning character 1 is inconsistent with Goldman (1920) who stated that the bifurcation is present in *I. flavidus* but is absent or slight in *I. pirrensis*. In a review of the 5 characters for all OTUs, which were not all available to prior researchers, cluster analysis using UPGMA of Euclidean distances grouped OTUs of both species separately and show 100% nodal support for this interspecific separation (cophenetic correlation = .8614). Intraspecific OTUs were all clustered together, demonstrating morphological differences between each species. Euclidean distances show high morphological similarity between OTU 1 and OTU 3, and between OTU 4 and OTU 5. OTU 2 was the most distinct from OTUs 4 and 5, which conflicts with Handley's (1966) original conclusion that these populations appear to be geographic races; OTU 2 was most similar to OTU 3. Although this analysis reveals high similarity between certain populations,

each possessed distinct morphological differences from the type specimens; a description of the morphology of each is given here:

OTU 1. Specimens from the type locality of *I. flavidus* have a prominent anteromedian flexus which generally bifurcates completely through the cusp; the lateral borders of the mesopterygoid fossa are squared, the anterior border jagged, or uneven, with the medial portions extended slightly towards the palatine. Post-glenoid fossa is large and rounded towards the anterior. Subsquamosal fenestra is generally present, tiny and round; lacerate foramen (in comparison to m1) is large, rounded and elongated laterally in the majority of the specimens.

OTU 2. *I. flavidus* specimens from Cerro Hoya possess an anteromedian flexus which generally bifurcates completely through the cusp. It differs from the type locality by a rounded mesopterygoid fossa in which the medial portions of the anterior border slightly extend toward the palatine; post-glenoid fossa is large, elongated and narrow with a sharp or pointed anterior terminus. Subsquamosal fenestra is almost always absent and the lacerate foramen is very large (size almost that of m1) and is rounded or oval.

OTU 3. The Cerro Colorado specimens of *I. flavidus* are similar to the type locality in the presence of a deeply bifurcated anteromedian flexus, a large, rounded and laterally elongated lacerate foramen and the majority of specimens possess a mesopterygoid fossa that is squared and an anterior border that is jagged with the medial portions extended slightly towards the palatine. They differ from the type locality in the absence of the

subsquamosal fenestra, a post-glenoid fossa that is large, elongated and narrow with a sharp or pointed anterior terminus.

OTU 4. The type locality of *I. pirrensis* is characterized by the presence of a slight anteromedian flexus which is absent or indistinguishable in some specimens; mesopterygoid fossa is rounded and not extended towards the palatine. Post-glenoid fossa is small with the anterior border rounded; subsquamosal fenestra is generally large and oval-shaped, lacerate foramen is small and narrow.

OTU 5. Cerro Tacarcuna specimens possess the most variability in character states thus their description is highly generalized. Anteromedian flexus of m1 is present in almost all specimens observed, it is generally slight and does not bifurcate completely through the cusp; in some specimens it is almost indistinguishable. Mesopterygoid fossa is rounded and not extended towards the palatine; a few specimens possessed the squared and smooth character state (2). Post-glenoid fossa is generally small with rounded anterior border, lacerate foramen is small and narrow. Subsquamosal foramen, when present, is generally large and round; this character was absent in 34% of specimens observed.

Linear Morphometric Analyses: Intrageneric Variation. — Males and females of age classes A-2 and A-3 from each OTU were pooled for multivariate analysis, treating each as an individual entity. MANOVA of the 19 variables showed significant overall

differences between groups (Wilk's $\Lambda = .03977$, $df1 = 76$, $df2 = 400.2$, $F = 6.375$, $p = < .0001$), however, post-hoc Hotelling's pairwise comparisons revealed no significant differences ($p > .05$) between OTUs 2 and 3. Employment of both principal component and canonical variate analyses allows maximum exploration of patterns of cranio-dental differentiation between each OTU as revealed by MANOVA (Carleton and Byrne 2006). The first three PC's account for 68.01% of the total variation between specimens from the 5 OTUs. Component 1 explained 50.42% of the total intrageneric variation, component 2 explained 9.74% and component 3 explained 7.85% (Fig 3). Component 1 possessed all negative (or equally positive depending on algorithm of statistical package) and similar loading values and are mostly correlated to the component of size. OTUs were most effectively separated along PC 2 in which size is not a major contributing factor; variables that contributed most significantly to this separation were WMF (-.6077), BZP (.416) and BM1 (-.403) (Table 2).

The canonical variate analysis discriminated individuals of different populations within the genus by the first 2 axes; axis 1 (53.44%), in which LBP (.531), WM1 (.581), ONL (.304) and WR (-.335) were the most influential characters in discriminating between the OTUs and axis 2 (27.26%) which was most strongly influenced by BIT (.482), WMF (.395), BM1 (.369) and BBC (.374). Cumulatively, axis 1 and axis 2 effectively discriminate type from allopatric populations, the CVA did not, however, discriminate between the OTUs 2 and 3 as shown by the MANOVA post-hoc pairwise comparisons (Table 6).

Geometric Morphometric Analyses. — A shape PCA of the genus was performed on 73 landmarks in the dorsal, lateral and ventral views and revealed specific patterns of variation as geography progresses west to east within each species; all views were informative and each align the OTUs in a longitudinal gradient of variation from west to east along PC 1. In the dorsal view, the first 3 principal components accounted 59.14% of the total intrageneric variation. This view separates the allopatric populations for both species from their type localities along PC 1 (31.32%) based upon an anterior progression of the intersection of the nasal sutures, a slight narrowing of the braincase and a posterior migration of the coronal suture along the mid-sagittal plane (Fig. 5). The first 3 PC's in the lateral view represent 48.14% (PC 1: 29.21%, PC 2: 10.13%) of the cumulative variation and show a gradual flattening of the dorsal aspect of the braincase as well as a flattening of the posterior margins of the skull (Fig. 6). The ventral view supports the results from the dorsal and lateral analyses by illustrating narrowing of the braincase and flattening of the posterior margins of the skull in which PC 1 possesses 20.2% of the variation and PC 2 represents 13.3% (Fig. 7).

Dispersion of populations for the first 3 canonical axes is shown for the 3 views which were all informative. Supplementary axes were largely uninformative and embody an insignificant value of discriminatory power; all three views clearly separate OTU 1 from all other OTUs. In the dorsal view, discriminatory power by canonical axis 1 is 61.89% and 22.06% in axis 2; a corresponding MANOVA of the Procrustes rotated landmarks revealed significant differences between groups (Wilk's $\Lambda = .001673$, $df1. = 176$, $df2. = 222.1$, $F = 5.007$, $p < .0001$). Axis 1 and 2 in the lateral view represent 54.9%

and 23.9% respectively; canonical axis 1 in the ventral view accounts for 51.70% with axis two at 28.8%. The main pattern of discrimination in all 3 views is characterized by no significant overlap between populations of the same species (Fig. 8). The dorsal view illustrates clear discrimination of type populations from the allopatric populations and aligns OTU 3 with OTU 5 and OTU 2 with OTU 4. This view differs from the lateral view which groups OTUs 2, 3, and 4 together with a significant amount of overlap (Fig. 9). The ventral view supports the separation of the type locality of *I. flavidus* from other populations mostly on canonical axis 2; this view does not notably group any OTUs together (Fig. 10). Results from Goodall's *F* test for mean shape differences reveal significant differences ($p < .05$) in mean shape between all OTUs; the only exception is between OTUs 2 and 4 in the lateral view.

CHAPTER IV

DISCUSSION

This paper presents the first analysis of geographic and non-geographic variation within the genus *Isthmomys*. The mixed-methods approach utilizing morphometric and morphological character analyses identified discriminatory anatomical characteristics that helped to understand the morphological limits between individual OTUs. The results discussed herein include suggestions for a combined methodological approach in the application of morphometric analyses in systematics, suggestions for the taxonomic revision of the genus based on those methods, speculations into the evolutionary history and biogeography of the genus based on the geological history of the region and conservation implications for *I. flavidus*.

Methodological Approaches. — The roots of morphometrics (both traditional and geometric) are embedded in the pursuit to reveal variation in size and shape between specified groups (Adams, Rohlf, and Slice 2004; Rohlf and Marcus 1993; Rohlf 1990; Zelditch et al. 2004). Unfortunately, the use of these two sets of multivariate techniques rarely occurs simultaneously and the attempts to interpret results beyond the scope of the analysis may sometimes be misleading or inaccurate. Attempts to reveal changes in shape by maximizing the number of linear measurements can be problematic and very time consuming without using landmark data. Using a set of linear measurements to generate graphical representations of shape is usually not possible because the geometric relationships among the variables are not preserved. Taking measurements with calipers

requires they be taken from homologous points and any information concerning movement of those points (synonymous with shape changes) is lost (Adams, Rohlf, and Slice 2004). Even when dealing with measurements that theoretically give the best information on shape (zygomatic breadth, breadth of braincase, etc...), the component of allometry is still an issue. Much effort has been spent in designing methods to remove the component of size from linear measurements, but there is little agreement on which method is the best to use (Adams, Rohlf, and Slice 2004). The interpretation of shape differences using linear measurements is then solely dependent on the ability of the researcher to interpret the dimensions of individual measurements and apply them to a shape space.

To accurately interpret changes in shape from linear measurements, a triangulation method (box truss, Delaunay triangulation, etc) is necessary. The main advantages of using these methods is that original shapes can be reconstructed from the data, actual changes in shape and theoretical shapes can be calculated and viewed in the principal components. Utilizing triangulation methods can be problematic for some researchers, however, because it generally requires analysis of landmark data using sophisticated statistical packages or programming languages that may not be easily mastered (i.e.; MATLAB or R). In the same context, superimposed (i.e.; Procrustes) landmark configurations lose the component of allometry and its potential effects on clinal and intrageneric shape variation. Size and shape are important factors in defining limits since two species rarely have the same size or shape dimensions. Interpreting the results of size or shape analyses separately with disregard for the other essentially

produces only assumptions of specific limits. Significant differences in shape between groups of the same species can be the result of environmental pressures, character displacement or simple clinal variation; similarly, differences in size can also arise due to extraneous pressures as well as ecological factors (diet, competition, etc...). With this in mind, translating the results of both size and shape analysis simultaneously is most likely to be the best method to answer any questions concerning systematics using morphometric techniques.

There is debate concerning what the terms “character” and “variable” imply and there appears to be no clear definition of either (Zelditch *et al.* 2004). Herein, the term “character” is defined as an anatomical trait that is measured qualitatively, whereas the term “variable” is considered to be an anatomical trait that is measured quantitatively. The use of linear measurements, or “variables”, as qualitative characters has been suggested, using scaling techniques to transform the continuous variables into qualitative characters for phylogenetic analysis. One major problem that has been associated with methods of discretization of continuous data is that algorithms can classify different states to values that do not differ significantly (Goloboff, Mattoni, and Quinteros 2006). It has been suggested that linear variables can be informative in phylogenetic inferences in an optimization based algorithm, however, Goloboff *et al.* (2006) states that “when characters that seem to be of taxonomic importance appear as continuous, they should be coded as such, instead of simply ignored or discretized” (p. 600).

Definition of Species Limits. — Rarely do researchers define their criteria for identifying species limits in morphometric space. Although the literature applying morphometric analyses in systematics is robust, these techniques offer no clear method to identify discriminatory variables that prove to be useful to researchers in the field, especially when dealing with slight, yet statistically significant, differences in shape and size. The combination of three methods, character analysis, linear morphometrics and geometric morphometrics comprises the best scenario for defining species limits beyond statistical significance. In this paper, species limits are based upon the fulfillment of three specific criteria:

- 1.) OTUs must be significantly distinct from the specimens of the type localities (OTUs) in the linear analysis (MANOVA post-hoc Hotelling's T^2);
- 2.) OTUs must be significantly distinct from the specimens of the type localities in all three views of the geometric morphometric analyses (Goodall's F -statistic);
- 3.) OTUs must possess unique morphological characteristics based upon evaluation of character states and linear measurements. This can be illustrated by the Euclidean distances between groups based upon the centroids of the linear measurements and the modal tendency of morphological characters. To be regarded as distinct or separate, allopatric populations should possess as comparable a phenetic distance from their type locality as exists between the two type localities of the currently recognized species (OTU 1 and OTU 4) (Marriog and Cheverud 2004).

Taxonomic Implications of Study. — Based upon the results of the morphometric analyses, a revision of the taxonomic status within the genus is necessary. The disjunct distributions of the genus prompted Hooper (1968) to suggest that the two species have the aspect of geographic races of the same species (Carleton 1989). This hypothesis would seem logical in the context of the Biological Species Concept (sensu Mayr 1942) as potential zones of sympatry appear non-existent. This study utilizes the Morphological species concept in defining species limits and recognition criteria outlined in Baker & Bradley (2006). This is the most logical approach because there is little or no molecular data available evaluating intrageneric diversity. Evaluation of each individual OTU, based on the combined results of the three methods, is given below as a prelude for taxonomic recommendations:

1. The type localities of both species (OTUs 1 and 4) are indeed recognized as separate entities. Historically, the type localities for *I. flavidus* and *I. pirrensis* have been compared morphologically and defined as separate species by only one author, Goldman (1920); as stated in the introduction, all other comparisons between the species have been made using the Cerro Hoya population of “*I. flavidus*” (OTU 2). With no other option, this paper defines these two groups as separate species based on fulfillment of the first two limiting criteria and thus considers their position concerning the third criterion as the baseline for all other pairwise comparisons.

2. OTU 5 (Tacarcuna) is very similar in morphology and shape to the type locality of *I. pirrensis* (OTU 4). Although significant differences exist in size and shape, this population does not fulfill all three criteria. This group possesses the most phenetic similarity to the type locality of *I. pirrensis* based on Euclidean distances (range = .0134 - .0402) of the linear measurements than any other group. In addition, pairwise comparisons show that specimens from Tacarcuna have a high phenetic similarity in qualitative characters to specimens from the type locality (Fig 11). Given these results, there is no rationale (either morphometric, morphological or geographic) for suggesting separation of Tacarcuna specimens from the type of *I. pirrensis*. The two localities are very close together geographically and are only separated by a thin low-lying valley. This valley, though well below the elevational range of *I. pirrensis*, may not be a significant barrier in the restriction of gene flow between the populations or has not existed long enough to promote genetic drift.
3. OTU 3 (Cerro Colorado) is very similar to the type locality of *I. flavidus*. Similar to OTU 5, significant differences from specimens of the type locality exist in size and shape (Table 6, Fig 3), but this population also does not fulfill all three criteria. Cerro Colorado specimens have a very high phenetic similarity to those from the type locality of *I. flavidus* in both linear measurements and character analysis. Pairwise comparisons of Euclidean Distances show the highest phenetic similarity to type locality in the analysis of character states, differing primarily on the absence of the subsquamosal fenestrated. Shape analyses show that Cerro

Colorado specimens actually have a cranial shape most similar to the type locality of *I. pirrensis*; primarily being less rounded, with an elongated posterior braincase when compared to type specimens of *I. flavidus*. There is an evident possibility of this population being positioned at the extreme of large cline that includes the type locality of *I. flavidus*, Cerro Colorado, and unidentified localities in the intermediate regions. There seems to be no apparent or potential geographic barriers that would isolate this population, nor does there appear to be any rationale for suggesting one. The variation in size and shape is considered to be a result of clinal variation throughout one population. One specimen identified as *I. flavidus* from an intermediate locality is housed in a Panama museum collection and has the potential to establish some idea of a morphological gradient, but was unable to be acquired for analysis.

4. Although all of the OTUs fulfill at least two of the above criteria, only OTU 2 (*I. flavidus* Cerro Hoya) fundamentally meets all three. As noted above, this population tends to have a slightly, yet not significantly, smaller skull (ONL = $37.73 \pm 1.54\text{mm}$) than the type locality of *I. flavidus* (ONL = $38.25 \pm 1.36\text{mm}$), yet possesses a skull that is flatter with a rounded mesopterygoid fossa in which the medial portions of the anterior border slightly extend toward the palatine. Other differences from the type specimens in morphology and shape include the absence of a subsquamosal fenestra, a very large and round lacerate foramen and a post-glenoid fossa that has a pointed anterior terminus. Shape analyses show that Cerro Hoya specimens also have a cranial shape most similar to the type

locality of *I. pirrensis*, generally being less rounded when compared to type specimens of *I. flavidus*. Cluster analyses of Euclidean distances from both linear variables and qualitative character states placed this group at the periphery of what comprises *I. flavidus* (Fig. 11). Contradictory to Handley's (1966) hypothesis that "the large *Peromyscus* inhabiting the higher elevations of Azuero Peninsula may be this species (*I. pirrensis*)," this group is most phenetically different from the type locality of *I. pirrensis* (OTU 4) based on Euclidean distance although the cranial shapes are the most similar. Furthermore, a clear geographic barrier exists in the Santiago Plains which unquestionably isolates Cerro Hoya from any other locality. Based upon these findings and the indisputable isolation of this population, it seems logical to suggest recognition as a taxonomic entity. However, the extent of separation, as outlined in the criteria for delimiting specific boundaries, does not indicate or warrant recognition of specific status. This is a result of the Euclidean distance of this locality from the type locality of *I. flavidus* not exceeding the distance between the type localities of *I. flavidus* and *I. pirrensis*. Nevertheless, as outlined in the third criterion, the distances are comparable and thus acknowledgment as a possible subspecies is suggested.

Recently the effects of sample size on the results of multiple comparisons (i.e.; UPGMA cluster analysis) has suggested that samples with small sizes will lie relatively far from the populations they are supposed to represent (such as those from the Cerro

Hoya population). This is a result of variation within characters and the likelihood that a “small sample will have an outlying mean for one of them” (Strauss, Bradley, and Owen 2002). As a result, assumptions that these populations are not representative may appear to be premature and inaccurate. In addressing this issue and defending the results of this paper, I emphasize the robustness of the analyses and the support each analysis gives to another. In suggesting the recognition of the Cerro Hoya population as separate, all three analyses support one another. The shape analysis in all three views as well as the linear analysis clearly discriminates between this group and its respective type locality. In addition, the pairwise comparisons revealed significant differences between Cerro Hoya and the type locality of *I. flavidus*. The isolated nature of this group also adds to the strength of the results as well as the suggestion of subspecific recognition, of which the name shall be addressed in a future publication.

Biogeographical History of Isthmomys. — The late Pliocene uplift of the Isthmus of Panama connecting North and South America gave rise to the massive exchange of fauna termed the Great American Biotic Interchange (Beu 2001; Hershkovitz 1966; Smith and Bermingham 2005). Geological information dates the collision of the Panamanian arc with present day Colombia as early as 12 million years ago (Beu 2001; Coates *et al.* 2004; Webb 2006) and evidence indicates a gradual uplift of the isthmus until its completion around 3-2.5 million years ago (Beu 2001; Boer *et al.* 1991; Coates *et al.* 2004; Hooghiemstra, Wijninga, and Cleef 2006; Pascual 2006). These authors point toward an independent development and uplift of the central cordillera, Azuero

Peninsula, the Mt. Pirre and Cerro Tacarcuna regions (see Coates fig. 8 and Pascual fig. 12). This gives rise to two possible hypotheses concerning the biogeographical history of *Isthmomys*. Consistent with the theory that rodents habitually crossed water barriers to reach islands (Hershkovitz 1966), there is the possibility that the ancestor to modern *Isthmomys* was able to colonize the land masses that would eventually form into the current localities prior to the completion of the isthmus by “island hopping.” Upon arrival, these animals progressively adapted to the individual habitats and became localized.

Subsequent genetic drift accumulated and divergence between the populations progressed through time. This would necessarily begin the divergence timeline within *Isthmomys* at around 1.5-2 million years ago. The second hypothesis is dependent on climatic fluctuations during the last Glacial Maximum around 18,000 years before present. The climate of Neotropical lowlands during the late Pleistocene is accepted as being much cooler and dryer, thus the disjunct montane localities indicate an isolation to high elevation refugia from aridity (Bush *et al.* 1992; Pascual 2006; Piperno 2006).

Consistency with the Refugia Hypothesis would require the historical distribution of *Isthmomys* to be much greater than the present, expanding throughout all of Panama and possibly throughout Costa Rica and Colombia. As temperatures became cooler and aridity increased, flora and fauna were forced to seek refuge at higher elevations at which time the populations became isolated and speciation due to genetic drift occurred. This would propose a much more recent time of evolutionary divergence which appears to be more amenable considering the high overall intrageneric similarity.

There are no fossils that would allow us to establish a geographic origin or the evolutionary history of *Isthmomys* throughout geological time (McKenna and Bell 1997; Mendez 1993) and recent molecular data of *I. pirrensis* suggests that this genus may not be as closely associated with *Peromyscus* as previously thought (Bradley *et al.* 2007). This factors increase the difficulty of assessing the biogeographical and evolutionary history of this genus. The lack of fossil records and lack of sufficient molecular data for the genus makes establishing an evolutionary timeline with any accuracy very complicated.

Conservation Implications. —The recognition of the Cerro Hoya population as unique brings the question of the conservation status of *I. flavidus*. In 1996, the UICN classified *I. flavidus* as Lower Risk/least concern, but in the last ten years deforestation, human interactions and other extraneous pressures have increased dramatically. Despite several attempts since the original trappings at the type locality (> 100 years), only one specimen has been trapped in the local vicinity and its identification has yet to be confirmed. To date there have no additional specimens found other than those by Handley (1962) at Cerro Hoya, and by Pine (1980) at Cerro Colorado. These areas are also under extreme pressures by human interaction such as forest clearing in Cerro Hoya and the development of copper mining in Cerro Colorado. With these variables taken into consideration, the conservation status of localities currently allocated to *I. flavidus* needs to be re-evaluated.

Conclusions. -- This paper presents the first analysis of geographic variation and secondary sexual dimorphism within the genus *Isthmomys* as well as an exploration of mixed methodological approaches in the use of phenetic and morphometrics analyses and their application to the systematics of this genus. In addition, specific criteria for defining species limits using these three methods are also provided. Based on the results of this analysis and the fulfillment of the limiting criteria, within the context of a systematic revision of *Isthmomys*, specimens of the Cerro Hoya population of *I. flavidus* are suggested as deserving at least subspecific rank. The results of this paper suggest the need for future research concerning the OTUs that were not regarded as distinct. With adequate sampling, molecular analyses are almost always able to resolve geographic limits for cryptic species (Baker and Bradley 2006); however, the lack of molecular data for *I. flavidus* proves to be the limiting factor in addressing this issue.

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APPENDIX A TABLES AND FIGURES

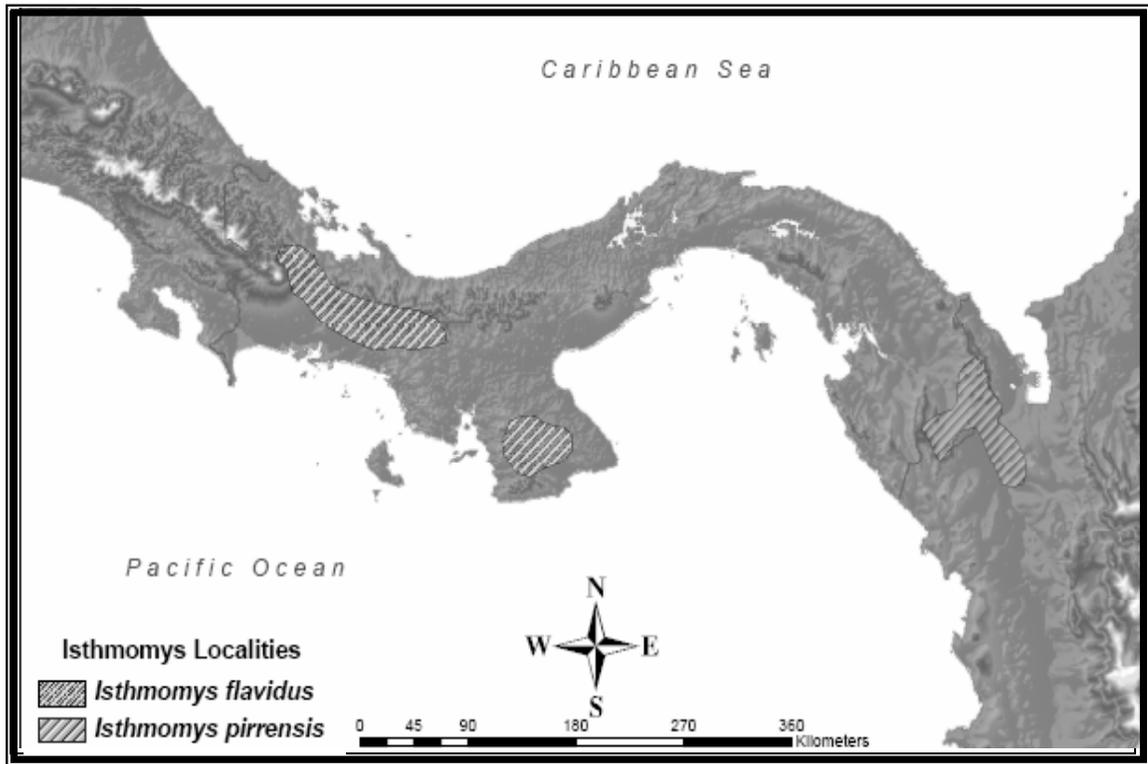


Fig 1. Trapping localities and theoretical distributions map *Isthmomys*; OTU 1: Volcan de Chiriqui; OTU 2: Cerro Hoya; OTU 3: Cerro Colorado; OTU 4: Cerro Pirre; OTU 5: Cerro Tacarcuna. Distributions downloaded from INFONATURA (www.infonatura.org).

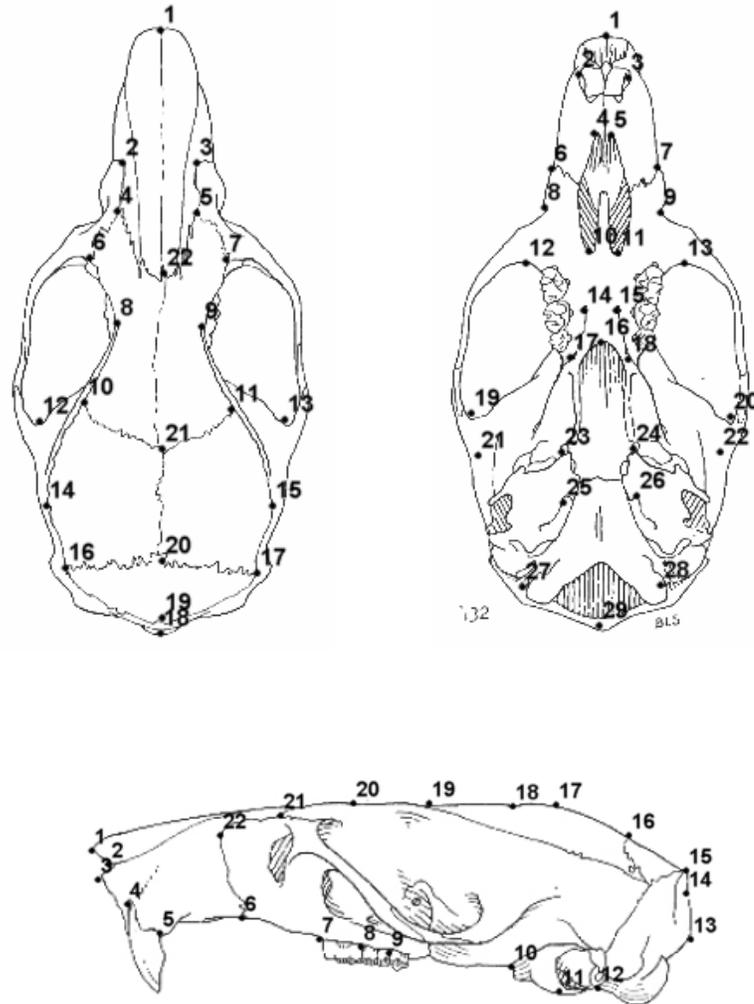


Fig 2. 72 landmarks in dorsal, lateral and ventral views, illustration from Hall (1981)

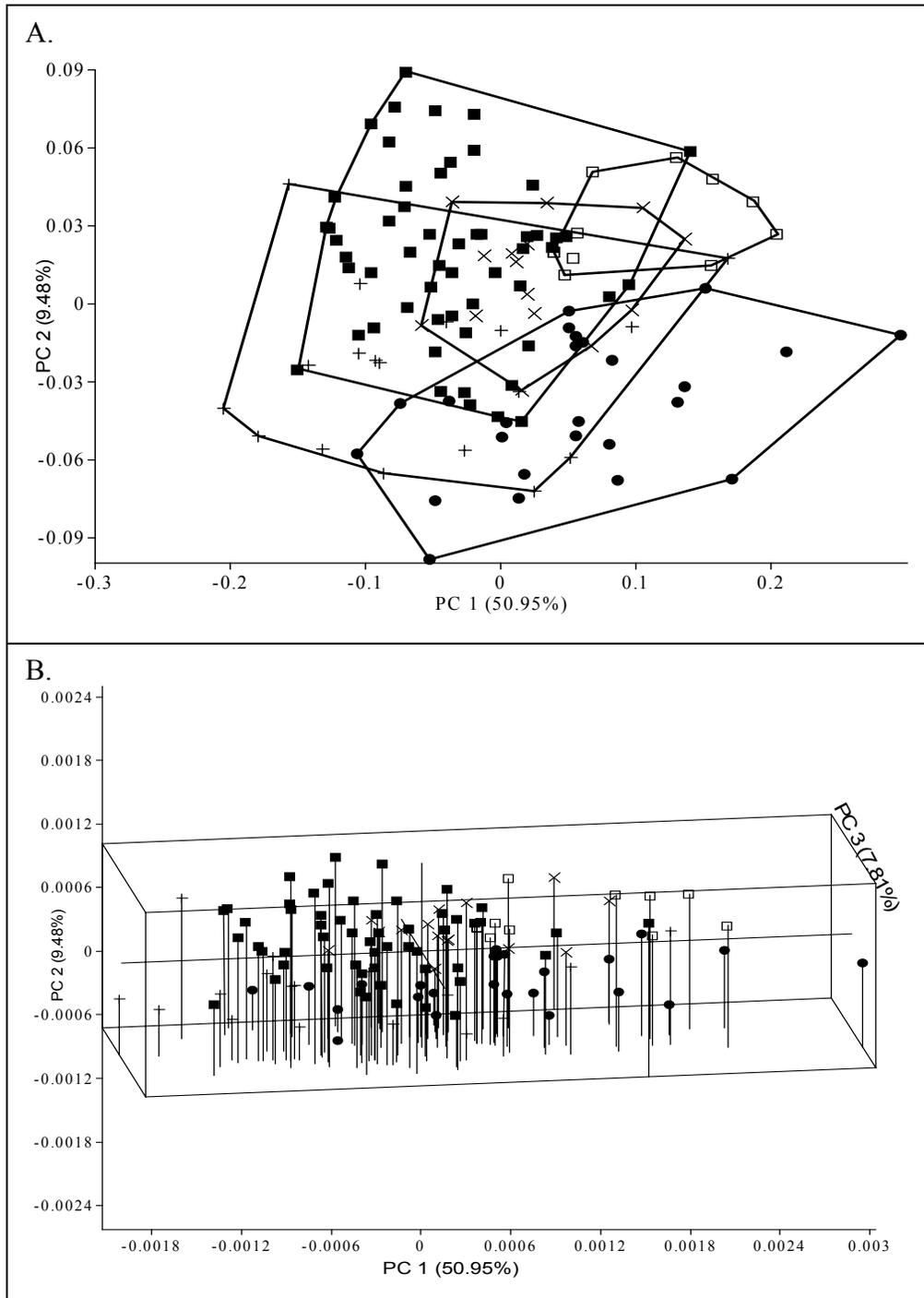
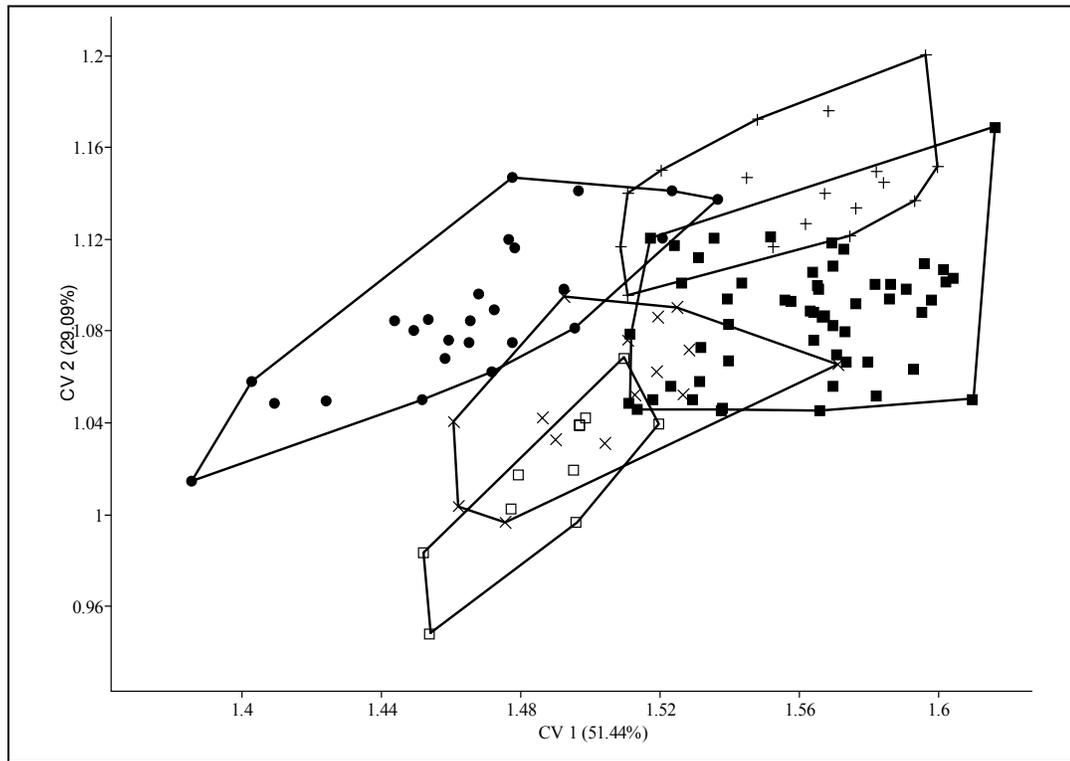


Fig 3. a.) First 2 principal components of linear measurements of 5 populations of *Isthmomys* from Panama: *I. flavidus* type (●); *I. flavidus* Cerro Colorado (x); *I. flavidus* Cerro Hoya (□); *I. pirrensis* type (+); *I. pirrensis* Tacarcuna (■). Loadings for the first 3 components are indicated below. b.) 3-dimensional plot of specimen scores the first 3 principal components.



Population (OTU)	OTU 1	OTU 2	OTU 3	OTU 4	OTU 5	Total % correct	% correct within species
<i>I. flavidus</i> (OUT 1)	23	0	0	1	0	96%	88%
<i>I. flavidus</i> (OTU 2)	0	6	5	0	1	50%	
<i>I. flavidus</i> (OTU 3)	0	2	9	1	3	64%	
<i>I. pirrensis</i> (OTU 4)	2	1	0	10	5	55%	92%
<i>I. pirrensis</i> (OTU 5)	1	0	2	3	48	89%	

Fig 4. (Top) Linear measurement Canonical Variates Analysis of 5 populations of *Isthmomys* from Panama: *I. flavidus* type (●); *I. flavidus* Cerro Colorado (x); *I. flavidus* Cerro Hoya (□); *I. pirrensis* type (+); *I. pirrensis* Tacarcuna (■). (Bottom) Cross validation from discriminant functions.

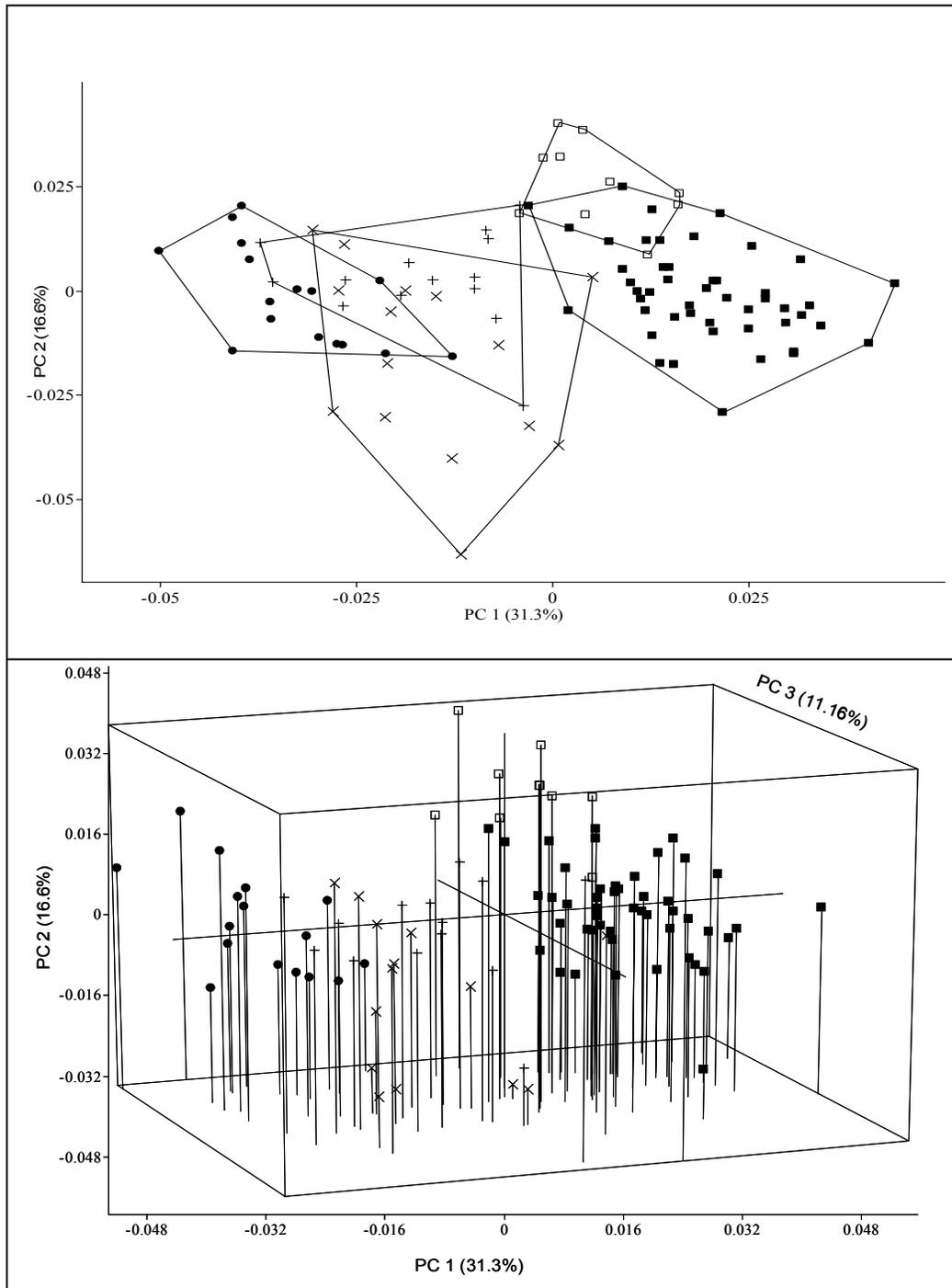


Fig 5. (Top) Shape PCA of dorsal landmarks: *I. flavidus* type (●); *I. flavidus* Cerro Colorado (x); *I. flavidus* Cerro Hoya (□); *I. pirrensis* type (+); *I. flavidus* Tacarcuna (■). (Bottom) 3-dimensional plot of specimen PC scores for the first 3 principal components.

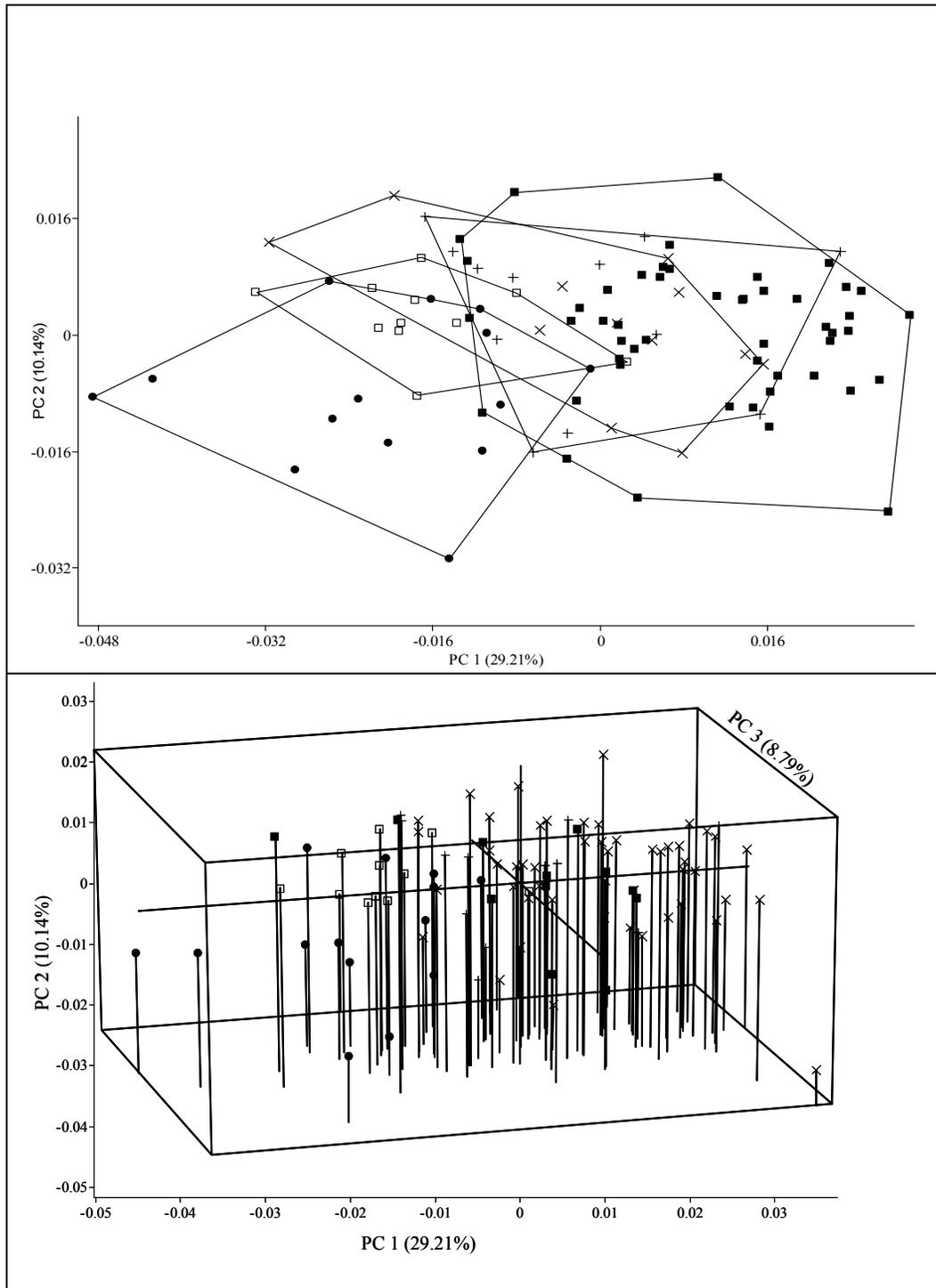


Fig. 6. Shape PCA of lateral landmarks: *I. flavidus* type (●); *I. flavidus* Cerro Colorado (●); *I. flavidus* Cerro Hoya (□); *I. pirrensis* type (+); *I. pirrensis* Tacarcuna (■). B.) 3-dimensional plot of specimen PC scores for the first 3 principal components.

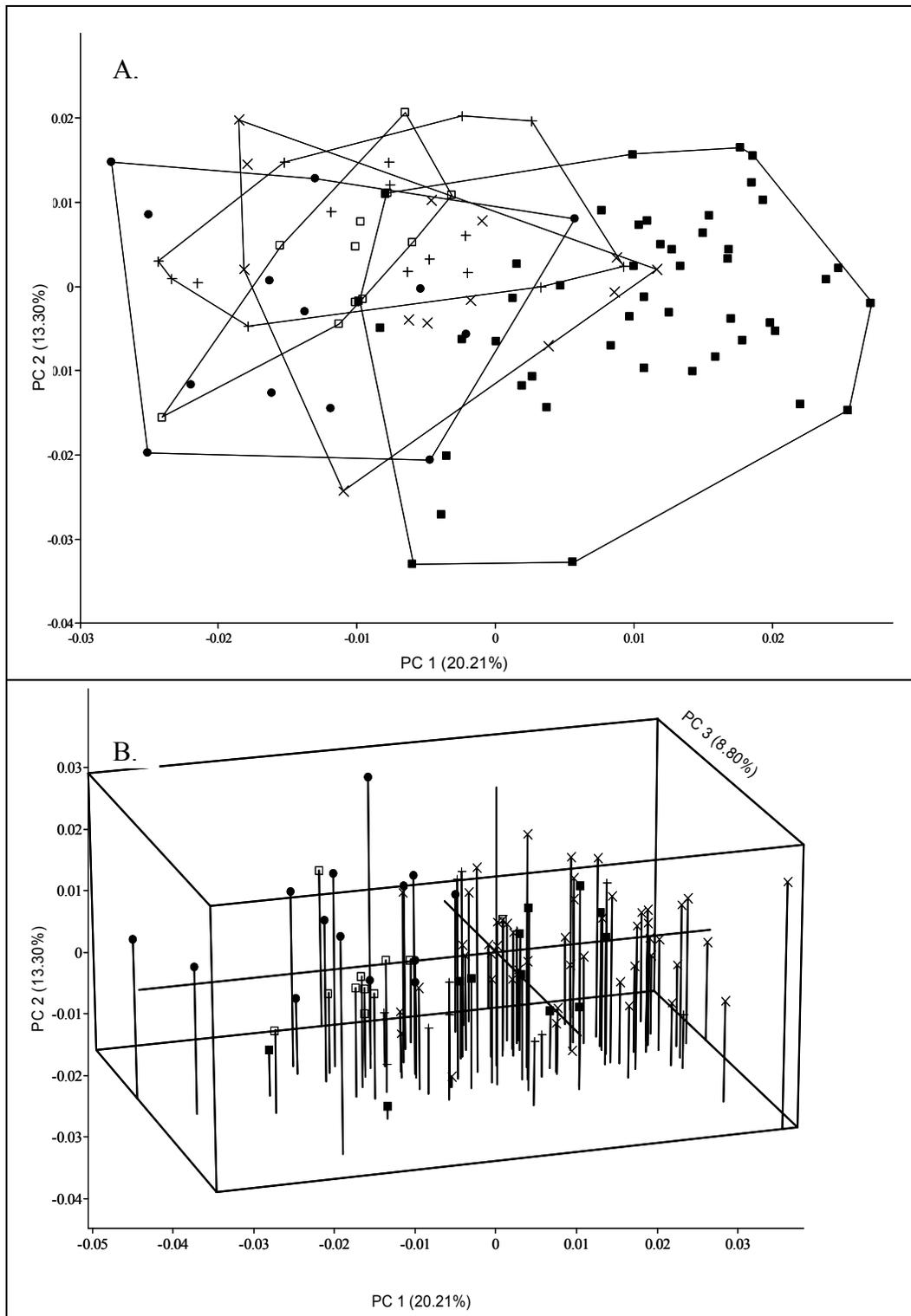


Fig. 7. Shape PCA of ventral landmarks: *I. flavidus* type (●); *I. flavidus* Cerro Colorado (x); *I. flavidus* Cerro Hoya (□); *I. pirrensis* type (+); *I. pirrensis* Tacarcuna (■). B.) 3-dimensional plot of specimen PC scores for the first 3 principal components.

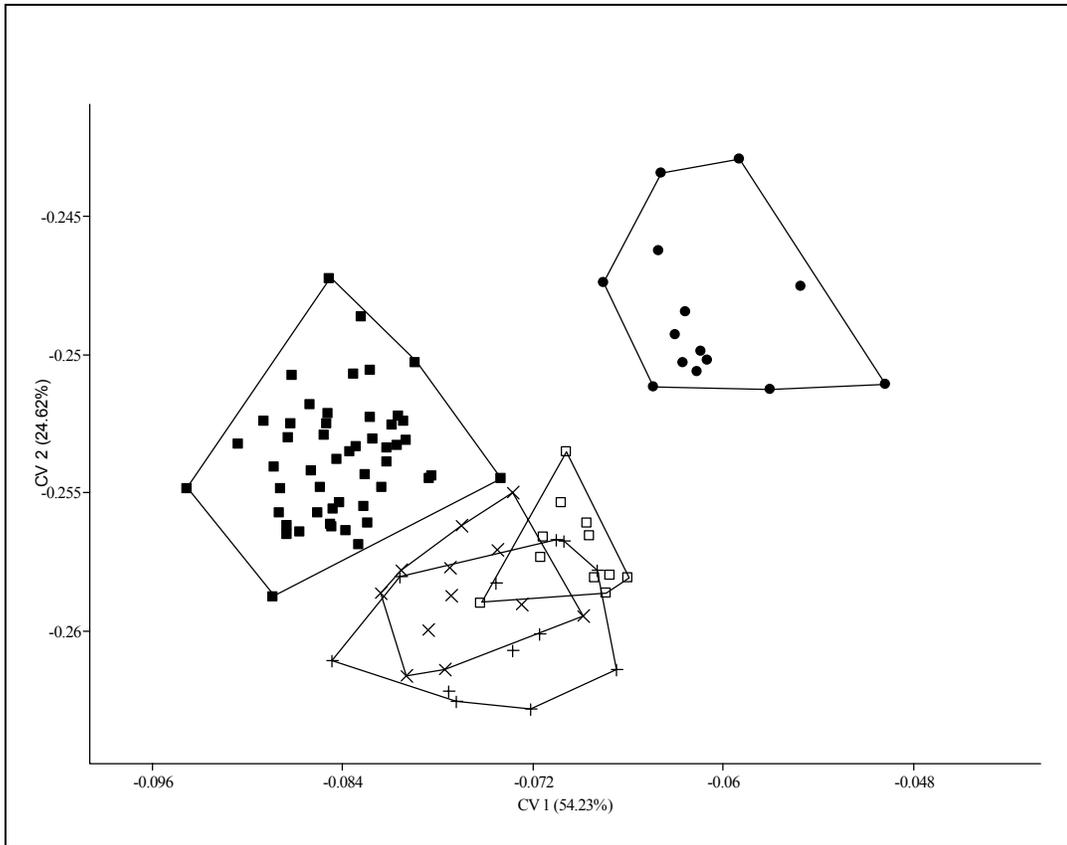


Fig. 8. CVA of dorsal view: *I. flavidus* type (●); *I. flavidus* Cerro Colorado (x); *I. flavidus* Cerro Hoya (□); *I. pirrensis* type (+); *I. pirrensis* Tacarcuna (■).

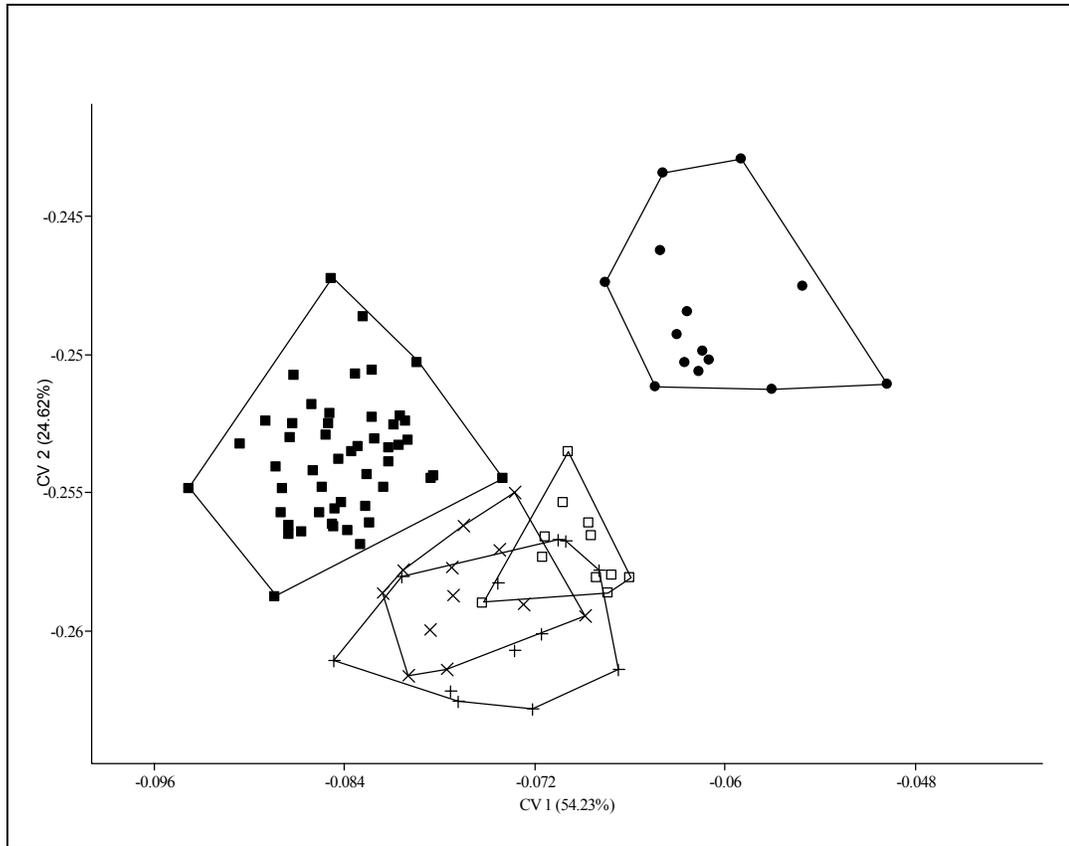


Fig. 9. CVA of lateral view: *I. flavidus* type (●); *I. flavidus* Cerro Colorado (x); *I. flavidus* Cerro Hoya (□); *I. pirrensis* type (+); *I. pirrensis* Tacarcuna (■).

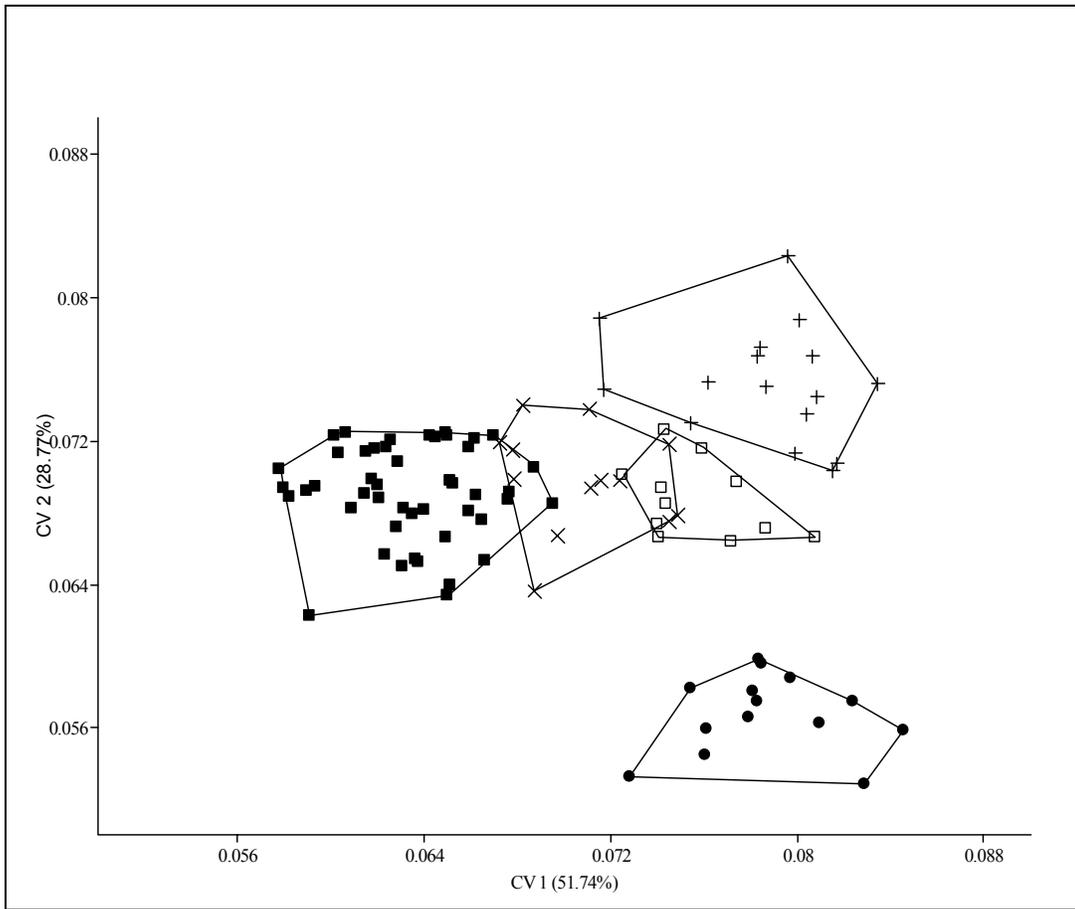


Fig. 10. CVA of ventral view: *I. flavidus* type (●); *I. flavidus* Cerro Colorado (x); *I. flavidus* Cerro Hoya (□); *I. pirrensis* type (+); *I. pirrensis* Tacarcuna (■).

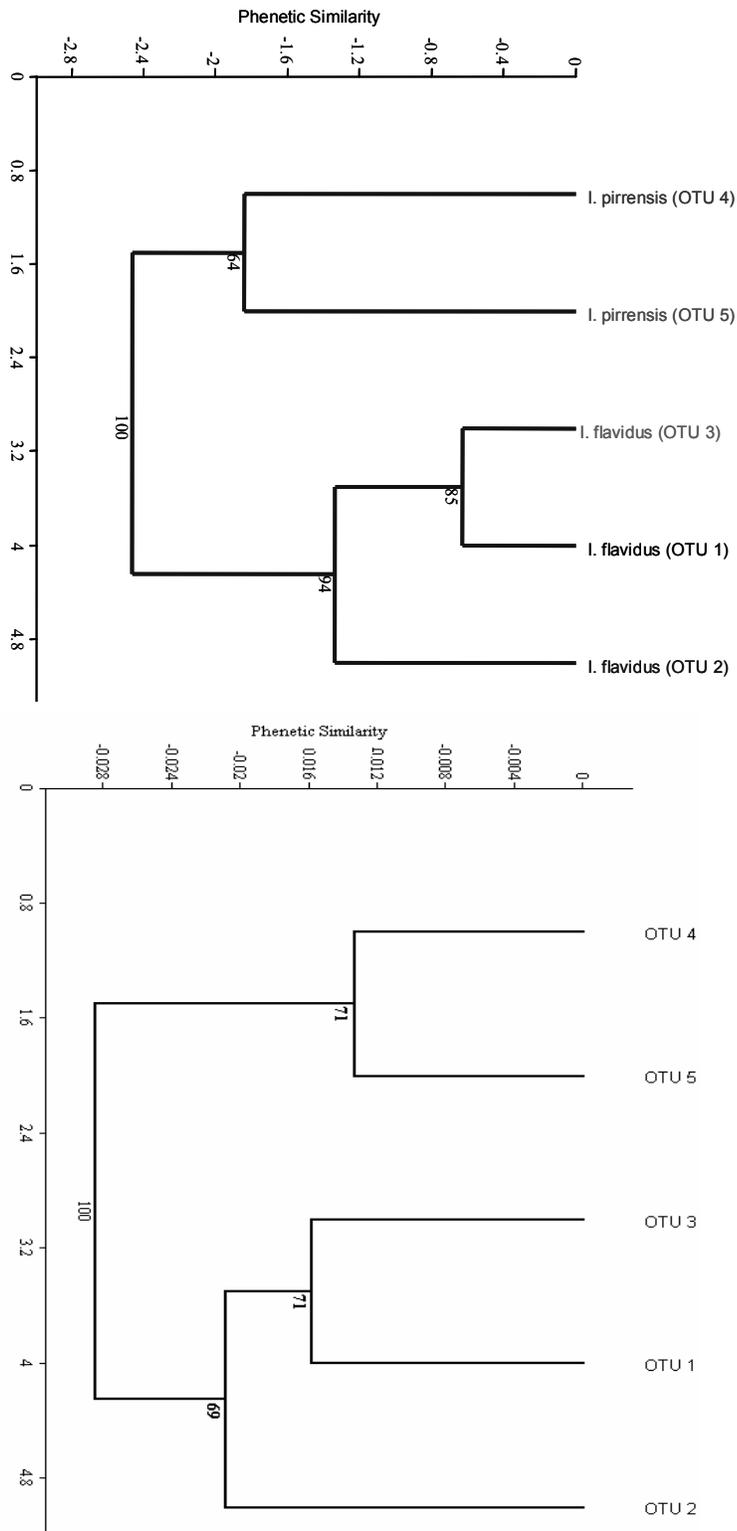


Fig 11. Comparisons of UPGMA cluster analysis of Euclidean distances for morphological characters (top) and linear measurements (bottom).

Table 1. Standard descriptive statistics for each OTU with expectation-maximization imputation for missing values.

I. flavidus Type Locality																			
	ONL	ZB	BZP	IOB	BBC	BOC	HBC	LR	WR	LD	LIF	BIF	LBP	BM1	WMF	PPL	CLM	WM1	BIT
N	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25
Min	35.39	16.44	2.31	5.43	13.28	8.39	9.81	11.63	6.44	9.58	6.44	2.68	5.77	3.51	2.37	12.17	5.29	1.55	1.90
Max	40.74	19.50	3.18	5.96	14.25	9.27	10.60	14.26	7.86	11.28	7.98	3.75	6.92	4.25	3.01	15.14	5.78	1.81	2.47
Mean	38.25	18.20	2.63	5.75	13.70	8.70	10.30	13.08	7.04	10.46	7.20	3.26	6.45	3.88	2.66	13.91	5.59	1.68	2.18
Std. error	0.28	0.15	0.04	0.03	0.06	0.04	0.06	0.14	0.08	0.11	0.09	0.05	0.08	0.04	0.03	0.12	0.03	0.02	0.03
Variance	1.85	0.55	0.04	0.02	0.07	0.04	0.08	0.47	0.13	0.25	0.19	0.07	0.14	0.03	0.03	0.36	0.02	0.01	0.02
Stand. dev	1.36	0.74	0.20	0.15	0.27	0.19	0.28	0.69	0.36	0.50	0.44	0.26	0.38	0.19	0.16	0.60	0.13	0.08	0.16
Median	38.15	18.24	2.66	5.75	13.71	8.67	10.36	13.28	6.97	10.54	7.21	3.28	6.42	3.90	2.60	14.05	5.62	1.68	2.18
Skewness	-0.22	-0.41	0.58	-0.46	0.61	1.09	-0.47	-0.44	0.63	-0.24	0.00	-0.21	-0.26	-0.09	0.50	-0.48	-0.52	0.01	-0.04
Kurtosis	-0.64	-0.45	0.61	-0.76	-0.42	1.54	-1.36	-0.87	-0.47	-1.01	-1.06	-0.60	-1.30	-0.54	-0.55	1.54	-0.70	-1.30	-1.09
Geom. mean	38.22	18.18	2.63	5.75	13.69	8.70	10.29	13.06	7.03	10.45	7.19	3.25	6.44	3.88	2.65	13.89	5.59	1.68	2.18
I. flavidus (Cerro Hoya)																			
	ONL	ZB	BZP	IOB	BBC	BOC	HBC	LR	WR	LD	LIF	BIF	LBP	BM1	WMF	PPL	CLM	WM1	BIT
N	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
Min	35.70	16.92	2.13	5.40	12.50	7.79	9.95	12.09	5.85	9.66	6.09	2.72	6.22	3.38	2.19	12.29	5.33	1.57	1.62
Max	41.00	19.75	3.07	6.03	13.99	8.92	11.00	14.27	7.70	11.42	7.32	3.39	7.35	4.14	2.78	14.78	5.87	1.77	2.38
Mean	37.73	17.72	2.74	5.63	13.29	8.41	10.35	13.09	6.53	10.30	6.74	2.99	6.63	3.63	2.50	13.27	5.54	1.68	1.98
Std. error	0.46	0.23	0.08	0.07	0.15	0.10	0.10	0.21	0.15	0.15	0.13	0.06	0.10	0.06	0.06	0.21	0.05	0.02	0.07
Variance	2.36	0.61	0.07	0.05	0.24	0.11	0.11	0.49	0.25	0.23	0.18	0.05	0.11	0.04	0.04	0.50	0.03	0.00	0.05
Stand. dev	1.54	0.78	0.27	0.23	0.49	0.33	0.34	0.70	0.50	0.48	0.42	0.21	0.33	0.21	0.20	0.71	0.17	0.06	0.22
Median	37.79	17.62	2.77	5.60	13.23	8.51	10.23	13.19	6.37	10.30	6.78	2.92	6.55	3.60	2.46	13.22	5.50	1.69	1.90
Skewness	0.56	1.39	-0.76	0.54	-0.07	-0.49	0.63	0.11	0.85	0.78	-0.07	0.49	0.78	1.08	0.04	0.60	0.44	-0.06	0.20
Kurtosis	-0.64	1.43	-0.24	-1.42	-1.62	-0.92	-1.08	-1.47	0.04	0.07	-1.60	-1.01	-0.48	0.41	-1.53	-0.41	-1.14	-1.17	-1.07
Geom. mean	37.70	17.71	2.72	5.63	13.28	8.41	10.34	13.08	6.51	10.29	6.73	2.99	6.62	3.62	2.49	13.25	5.54	1.68	1.97
I. flavidus (Cerro Colorado)																			
	ONL	ZB	BZP	IOB	BBC	BOC	HBC	LR	WR	LD	LIF	BIF	LBP	BM1	WMF	PPL	CLM	WM1	BIT
N	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15
Min	36.61	17.22	2.52	4.60	12.12	8.03	10.09	12.44	6.29	9.73	6.62	2.87	5.89	3.48	2.32	12.75	5.00	1.55	1.88
Max	40.90	19.08	3.09	5.98	14.28	8.88	11.10	14.25	7.57	11.85	7.74	3.46	7.51	4.00	2.80	14.93	5.67	1.79	2.40
Mean	39.20	18.27	2.85	5.54	13.13	8.50	10.61	13.58	6.82	10.74	7.16	3.18	6.54	3.71	2.58	13.91	5.41	1.70	2.20
Std. error	0.33	0.15	0.04	0.09	0.13	0.06	0.09	0.14	0.09	0.16	0.09	0.04	0.10	0.04	0.04	0.18	0.04	0.02	0.05
Variance	1.59	0.32	0.02	0.13	0.27	0.05	0.11	0.32	0.13	0.37	0.13	0.03	0.15	0.02	0.03	0.50	0.03	0.00	0.03
Stand. dev	1.26	0.56	0.14	0.36	0.52	0.23	0.34	0.56	0.35	0.61	0.37	0.17	0.39	0.15	0.16	0.71	0.16	0.06	0.18
Median	39.27	18.41	2.86	5.61	13.13	8.52	10.60	13.58	6.89	10.69	7.17	3.16	6.55	3.72	2.62	14.05	5.42	1.70	2.23
Skewness	-0.30	-0.20	-0.38	-1.01	0.34	-0.27	-0.01	-0.44	0.25	0.31	0.13	0.12	0.60	0.34	-0.11	-0.26	-0.79	-0.78	-0.56
Kurtosis	-0.98	-1.25	0.04	0.68	-0.07	-0.72	-1.45	-1.03	-0.68	-1.04	-1.46	-0.99	0.27	-0.62	-1.54	-1.35	0.38	0.37	-1.29
Geom. mean	39.19	18.27	2.84	5.53	13.12	8.49	10.61	13.57	6.82	10.73	7.15	3.17	6.53	3.71	2.57	13.89	5.41	1.70	2.19
Ipirrensis Type locality																			
	ONL	ZB	BZP	IOB	BBC	BOC	HBC	LR	WR	LD	LIF	BIF	LBP	BM1	WMF	PPL	CLM	WM1	BIT
N	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18
Min	36.11	16.75	2.35	5.41	13.39	8.29	10.33	12.63	6.09	9.47	6.29	2.89	6.19	3.42	2.43	11.93	5.51	1.66	1.92
Max	44.05	21.02	3.62	6.05	15.35	9.60	11.81	15.55	8.50	12.06	8.84	3.47	8.08	4.58	3.08	16.03	6.22	1.95	2.88
Mean	40.64	19.42	2.85	5.73	14.12	8.75	10.86	14.06	7.21	10.98	7.31	3.23	7.19	4.02	2.75	14.45	5.83	1.83	2.36
Std. error	0.55	0.31	0.07	0.05	0.12	0.08	0.09	0.22	0.15	0.16	0.16	0.04	0.10	0.07	0.04	0.27	0.04	0.02	0.05
Variance	5.44	1.74	0.10	0.04	0.25	0.11	0.15	0.90	0.40	0.49	0.47	0.03	0.19	0.08	0.03	1.31	0.03	0.01	0.04
Stand. dev	2.33	1.32	0.32	0.20	0.50	0.34	0.39	0.95	0.64	0.70	0.68	0.16	0.44	0.28	0.17	1.14	0.17	0.08	0.19
Median	41.09	19.69	2.85	5.72	14.07	8.67	10.91	13.96	7.21	11.01	7.20	3.24	7.27	4.00	2.74	14.45	5.81	1.82	2.36
Skewness	-0.45	-0.47	0.52	0.06	0.66	0.83	0.50	0.19	0.18	-0.67	0.54	-0.37	-0.21	-0.01	0.24	-0.69	0.21	-0.08	0.40
Kurtosis	-0.87	-1.14	-0.30	-1.21	-0.22	-0.05	-0.36	-1.23	-0.85	-0.35	-0.52	-0.97	-0.10	-0.52	-0.64	-0.42	-0.27	-0.69	1.60
Geom. mean	40.57	19.37	2.84	5.73	14.11	8.74	10.85	14.03	7.19	10.95	7.28	3.22	7.17	4.01	2.75	14.41	5.83	1.83	2.36
Ipirrensis (Cerro Tacarcuna)																			
	ONL	ZB	BZP	IOB	BBC	BOC	HBC	LR	WR	LD	LIF	BIF	LBP	BM1	WMF	PPL	CLM	WM1	BIT
N	57	57	57	57	57	57	57	57	57	57	57	57	57	57	57	57	57	57	57
Min	37.04	16.83	2.32	5.03	11.03	8.08	9.79	12.06	6.08	10.05	5.99	2.62	6.37	3.24	2.10	12.15	5.05	1.65	2.00
Max	42.98	21.23	3.54	6.43	15.91	9.47	13.94	15.68	7.81	14.16	8.32	3.52	7.96	4.39	2.86	15.61	6.10	2.09	2.56
Mean	40.40	19.00	2.89	5.75	13.84	8.74	10.64	14.00	6.88	11.38	7.35	3.17	7.17	3.83	2.56	14.35	5.65	1.82	2.29
Std. error	0.17	0.10	0.03	0.04	0.08	0.04	0.09	0.12	0.05	0.09	0.06	0.02	0.05	0.03	0.02	0.09	0.03	0.01	0.02
Variance	1.73	0.61	0.07	0.11	0.39	0.09	0.43	0.84	0.15	0.50	0.20	0.03	0.16	0.06	0.03	0.42	0.04	0.01	0.02
Stand. dev	1.32	0.78	0.26	0.32	0.62	0.30	0.66	0.92	0.39	0.71	0.45	0.18	0.40	0.25	0.16	0.65	0.20	0.08	0.13
Median	40.41	18.85	2.85	5.80	13.76	8.67	10.57	13.90	6.89	11.33	7.34	3.18	7.23	3.87	2.57	14.23	5.63	1.82	2.28
Skewness	-0.16	0.19	0.10	-0.31	-0.75	0.26	2.47	-0.02	0.02	0.98	-0.27	-0.44	-0.04	-0.25	-0.23	-0.54	-0.44	0.42	0.04
Kurtosis	-0.44	0.53	-0.21	-0.59	7.04	0.29	9.54	-0.96	-0.27	2.33	0.29	0.27	-0.77	-0.40	-0.03	1.13	0.53	1.07	-0.61
Geom. mean	40.38	18.98	2.88	5.74	13.82	8.73	10.62	13.97	6.87	11.36	7.34	3.17	7.16	3.82	2.55	14.33	5.65	1.82	2.29

Table 2. A.) Loadings for first 3 principal component coefficients of linear measurements, B.) Principal Component Correlations, C.) Loadings for first 3 Canonical Variates of linear measurements.

A.

	PC 1	PC 2	PC 3
ONL	-0.2483	0.06045	-0.05424
ZB	-0.2497	-0.07667	-0.1171
BZP	-0.3304	0.416	0.4302
IOB	-0.07525	-0.05115	-0.1924
BBC	-0.1161	-0.0574	-0.2363
BOC	-0.103	-0.01551	0.07349
HBC	-0.1256	0.1229	0.1061
LR	-0.2715	0.1449	-0.2553
WR	-0.2273	-0.2661	0.04062
LD	-0.3092	0.09719	-0.1285
LIF	-0.2832	-0.0123	0.4082
BIF	-0.1929	-0.3384	0.3611
LBP	-0.2839	0.1394	-0.4696
BM1	-0.1943	-0.4034	-0.06108
WMF	-0.06387	-0.6077	-0.02222
PPL	-0.3098	-0.01312	0.1198
CLM	-0.06698	-0.06361	-0.2226
WM1	-0.1437	0.1529	-0.1286
BIT	-0.3733	-0.03437	-0.05632

B.

	PC 1	PC 2	PC 3
ONL	-0.9623	0.1011	-0.0823
ZB	-0.8739	-0.1158	-0.1605
BZP	-0.7095	0.3853	0.3616
IOB	-0.3178	-0.0932	-0.3181
BBC	-0.5016	-0.107	-0.3997
BOC	-0.5992	-0.0389	0.1673
HBC	-0.5056	0.2133	0.1671
LR	-0.7785	0.1792	-0.2865
WR	-0.7109	-0.3589	0.04972
LD	-0.8669	0.1175	-0.141
LIF	-7.53E-01	-0.0141	0.4248
BIF	-0.5732	-0.4338	0.42
LBP	-0.7546	0.1599	-0.4886
BM1	-0.5942	-0.5322	-0.0731
WMF	-0.1808	-0.742	-0.0246
PPL	-0.9159	-0.0167	0.1387
CLM	-0.3609	-0.1479	-0.4695
WM1	-0.5131	0.2356	-0.1798
BIT	-0.8553	-0.034	-0.0505

C.

	CV 1	CV2	CV3
ONL	0.32056	-0.20622	0.39724
ZB	0.11721	0.077442	0.18573
BZP	0.17066	-0.20843	0.13441
IOB	-0.02323	-0.00771	-0.25938
BBC	0.012915	0.3708	-0.16358
BOC	-0.04448	0.13636	-0.45328
HBC	0.11518	-0.02437	0.35853
LR	0.13591	-0.07427	0.15367
WR	-0.3554	0.1002	0.095976
LD	0.24304	-0.06613	-0.36547
LIF	0.011643	0.068712	-0.18307
BIF	-0.13752	0.051694	0.040393
LBP	0.52498	0.070962	-0.07406
BM1	-0.03183	0.35997	0.13241
WMF	-0.14264	0.37835	0.19906
PPL	0.072971	0.10193	-0.17852
CLM	-0.0339	0.31104	0.12835
WM1	0.55786	0.32544	-0.08055
BIT	0.029659	0.48287	0.20634

Table 3. Principal Component correlations for first 3 PC's in geometric analysis in A.) dorsal, B.) lateral, C.) ventral views.

A.

Coordinate	PC 1	PC 2	PC 3
X1	-0.6768	0.3979	-0.1839
Y1	0.05412	-0.01431	-0.2128
X2	-0.4466	0.4544	-0.3265
Y2	-0.05928	-0.06171	0.04158
X3	-0.3758	0.5249	-0.1729
Y3	-0.1854	0.1262	-0.09854
X4	-0.1571	0.1129	-0.5108
Y4	-0.1448	0.2012	-0.1517
X5	-0.08088	0.08156	-0.5389
Y5	0.1444	-0.2584	0.291
X6	0.2496	0.2057	-0.131
Y6	0.2405	-0.00841	-0.006238
X7	0.1718	0.1278	-0.07731
Y7	-0.1185	-0.1771	0.05393
X8	0.871	0.2712	0.3545
Y8	0.6355	0.4279	0.144
X9	0.8808	0.2022	0.3511
Y9	-0.573	-0.4721	-0.06977
X10	0.1821	-0.8567	0.05036
Y10	-0.4002	-0.1224	0.08814
X11	0.1435	-0.8781	0.007638
Y11	0.4423	0.1393	-0.1317
X12	0.3508	-0.2046	-0.2622
Y12	-0.3653	0.4041	0.2088
X13	0.4322	-0.2437	-0.2883
Y13	0.3499	-0.2133	-0.1474
X14	-0.2737	-0.1142	0.2584
Y14	-0.6177	0.5401	0.1624
X15	-0.08164	0.02751	0.1249
Y15	0.5358	-0.5229	-0.166
X16	-0.5454	0.218	-0.3823
Y16	-0.1292	0.5349	0.4325
X17	-0.4986	0.1207	-0.4799
Y17	0.1416	-0.5817	-0.3953
X18	-0.4053	0.3226	-0.3846
Y18	0.09856	0.01062	-0.05778
X19	-0.06312	0.2273	-0.1109
Y19	-0.1355	-0.024	0.02252
X20	-0.1312	0.3514	0.1098
Y20	-0.07897	-0.002292	-0.08368
X21	0.6237	-0.03418	0.08701
Y21	-0.2195	0.02121	0.01029
X22	-0.7538	-0.1675	0.5844
Y22	0.1488	0.04251	-0.1494

B.

Coordinate	PC 1	PC 2	PC 3
X1	-0.6257	0.02818	-0.2624
Y1	0.548	0.1984	-0.5057
X2	-0.2741	0.09929	-0.3244
Y2	0.7264	0.1085	-0.4486
X3	-0.7833	0.01909	-0.1805
Y3	0.6924	0.171	-0.3922
X4	-0.5002	0.2835	-0.1317
Y4	0.39	0.466	-0.09051
X5	-0.654	0.09751	-0.1356
Y5	-0.0001754	0.1989	-0.07497
X6	0.05935	-0.1452	0.03009
Y6	-0.3435	-0.1985	0.231
X7	0.6847	-0.08688	-0.09123
Y7	-0.3622	-0.2044	0.3998
X8	0.6093	-0.1807	-0.1503
Y8	-0.5662	-0.2098	0.3109
X9	0.3368	-0.19	-0.1449
Y9	-0.5411	-0.2295	0.358
X10	0.8191	-0.2566	-0.16
Y10	-0.1087	-0.5403	0.1574
X11	0.553	-0.4495	-0.3543
Y11	0.4237	-0.5912	0.3128
X12	0.603	-0.3692	-0.2836
Y12	0.5513	-0.4579	0.2378
X13	-0.4119	0.4227	-0.2917
Y13	0.6475	0.4784	0.2706
X14	-0.6828	0.05576	-0.3329
Y14	0.5088	0.515	0.08765
X15	-0.6165	0.1631	0.07085
Y15	0.3811	0.3654	-0.3712
X16	-0.5765	-0.2381	0.1753
Y16	-0.4164	0.3675	-0.4669
X17	-0.2569	-0.03111	0.5809
Y17	-0.7724	0.222	-0.2641
X18	0.05326	0.6557	0.4794
Y18	-0.8927	0.04436	-0.1441
X19	0.4928	-0.003889	0.2602
Y19	-0.8283	-0.1483	0.05691
X20	0.3366	0.04841	0.1934
Y20	-0.5229	-0.3557	0.3037
X21	0.3413	-0.001014	0.2451
Y21	0.02954	-0.5009	0.3
X22	-0.237	-0.0659	-0.1318
Y22	-0.111	-0.4851	0.1471

C.

Coordinate	PC 1	PC 2	PC 3
X1	-0.3932	0.1641	-0.2385
Y1	-0.07485	-0.09828	0.08551
X2	-0.361	-0.03552	-0.1801
Y2	0.03021	-0.3039	-0.1574
X3	-0.293	-0.07102	-0.1626
Y3	-0.2605	-0.007871	-0.009395
X4	-0.5447	0.1149	0.2423
Y4	-0.2109	-0.04822	0.01358
X5	-0.5299	0.09423	0.2398
Y5	-0.1785	-0.04962	0.1386
X6	-0.02976	-0.01293	-0.04906
Y6	-0.08977	-0.05136	-0.3162
X7	0.05525	0.0395	-0.09782
Y7	0.3908	0.1398	0.2535
X8	0.01751	0.08936	-0.02817
Y8	-0.6058	0.02586	-0.2656
X9	-0.02853	-0.04492	-0.2356
Y9	0.562	0.07359	0.3242
X10	-0.5671	0.0221	0.1893
Y10	-0.1636	0.1109	-0.3083
X11	-0.5481	0.1112	0.1297
Y11	0.1815	-0.01031	0.07585
X12	0.4378	0.0456	0.2031
Y12	-0.2796	-0.1784	-0.3223
X13	0.3683	-0.1187	0.08586
Y13	0.3957	0.2697	0.2447
X14	-0.2577	-0.235	-0.02267
Y14	-0.2956	0.05159	-0.2099
X15	-0.2867	-0.2124	0.04316
Y15	0.3859	0.1189	0.09707
X16	-0.02393	-0.3614	-0.1237
Y16	-0.3032	0.1016	0.004799
X17	-0.005059	-0.4155	-0.0538
Y17	-0.149	0.0618	-0.02273
X18	-0.1803	-0.4312	-0.1844
Y18	0.2521	0.1142	0.1511
X19	0.6768	0.1688	0.3269
Y19	-0.6398	0.2323	-0.1997
X20	0.5727	0.03003	0.3108
Y20	0.7389	-0.09633	0.3401
X21	0.5666	-0.3447	-0.07133
Y21	-0.04609	-0.38	-0.2977
X22	0.5933	-0.2996	-0.1404
Y22	-0.2279	0.159	0.2839
X23	0.36	0.5826	-0.3401
Y23	-0.6975	0.2145	-0.1926
X24	0.208	0.8979	-0.1546
Y24	0.8647	-0.01841	0.2267
X25	0.3959	-0.5164	-0.4684
Y25	-0.2545	-0.1898	-0.4283
X26	0.3985	-0.5378	-0.4537
Y26	0.1322	0.09193	0.4843
X27	-0.5057	-0.009386	0.5617
Y27	-0.5157	-0.08478	-0.3302
X28	-0.2722	-0.237	0.5927
Y28	0.3181	-0.2026	0.2135
X29	-0.5884	0.1585	0.5009
Y29	0.07362	-0.2197	-0.0802

Table 4. Principal Component coefficients for first 3 PC's in geometric analyses A.) dorsal, B.) lateral, C.) ventral views.

A.				B.				C.			
Coordinate	PC 1	PC 2	PC 3	Coordinate	PC 1	PC 2	PC 3	Coordinate	PC 1	PC 2	PC 3
X1	-0.2605	0.2102	-0.1186	X1	-0.1834	0.01402	-0.1401	X1	-0.1584	0.08147	-0.1514
Y1	0.00623	-0.0023	-0.0411	Y1	0.1514	0.09304	-0.2546	Y1	-0.0139	-0.0225	0.02503
X2	-0.096	0.134	-0.1175	X2	-0.07282	0.04479	-0.1571	X2	-0.08235	-0.01	-0.0647
Y2	-0.0072	-0.0103	0.00848	Y2	0.1802	0.04569	-0.2027	Y2	0.005135	-0.0637	-0.0422
X3	-0.0907	0.1738	-0.0699	X3	-0.1971	0.00816	-0.0828	X3	-0.056	-0.0167	-0.049
Y3	-0.0222	0.02074	-0.0198	Y3	0.2011	0.08429	-0.2076	Y3	-0.03995	-0.0015	-0.0023
X4	-0.0373	0.03683	-0.2034	X4	-0.09738	0.09369	-0.0467	X4	-0.1202	0.03125	0.08427
Y4	-0.0208	0.03971	-0.0366	Y4	0.09894	0.2006	-0.0418	Y4	-0.02086	-0.0059	0.00212
X5	-0.0205	0.02834	-0.2286	X5	-0.1561	0.03951	-0.059	X5	-0.1117	0.02449	0.07967
Y5	0.02136	-0.0525	0.07213	Y5	-2.00E-05	0.05464	-0.0221	Y5	-2.18E-02	-0.0075	0.02663
X6	0.04253	0.04809	-0.0374	X6	0.01128	-0.0468	0.01042	X6	-0.00891	-0.0048	-0.0232
Y6	0.03598	-0.0017	-0.0016	Y6	-0.05161	-0.0506	0.06323	Y6	0.01597	0.01408	-0.0446
X7	0.02815	0.02873	-0.0212	X7	0.1798	-0.0387	-0.0437	Y7	0.08347	0.03681	0.08535
Y7	-0.0183	-0.0376	0.01396	Y7	-0.0648	-0.0621	0.1303	X8	0.003452	0.02172	-0.0088
X8	0.4758	0.2033	0.3245	X8	0.1378	-0.0694	-0.062	Y8	-0.154	0.0081	-0.1064
Y8	0.1494	0.1381	0.05672	Y8	-0.1249	-0.0786	0.125	X9	-0.00674	-0.0131	-0.0878
X9	0.4281	0.1349	0.2859	X9	0.06963	-0.0667	-0.0546	Y9	0.1584	0.02558	0.1441
Y9	-0.1177	-0.1331	-0.024	Y9	-0.1221	-0.0879	0.1472	X10	-0.193	0.00927	0.1015
X10	0.08079	-0.5216	0.03744	X10	0.2843	-0.1512	-0.1012	Y10	-0.02544	0.02126	-0.0756
Y10	-0.1107	-0.0464	0.04084	Y10	-0.02678	-0.2259	0.07064	X11	-0.1908	0.0477	0.07117
X11	0.06354	-0.5336	0.00567	X11	0.1773	-0.2447	-0.207	Y11	0.02541	-0.0018	0.01674
Y11	0.1115	0.04823	-0.0556	Y11	0.1064	-0.2521	0.1432	X12	0.08782	0.01128	0.0642
X12	0.08559	-0.0685	-0.1072	X12	0.1648	-0.1712	-0.1412	Y12	-0.09757	-0.0768	-0.1773
Y12	-0.0761	0.1156	0.07292	Y12	0.1509	-0.2127	0.1186	X13	0.07432	-0.0295	0.02731
X13	0.09821	-0.076	-0.1098	X13	-0.09884	0.1722	-0.1275	Y13	0.1262	0.106	0.123
Y13	0.08143	-0.0681	-0.0575	Y13	0.2534	0.3178	0.1929	X14	-0.05521	-0.0621	-0.0077
X14	-0.0642	-0.0367	0.1015	X14	-0.1771	0.02455	-0.1574	Y14	-0.04446	0.00956	-0.0498
Y14	-0.1428	0.1713	0.06289	Y14	0.1601	0.2751	0.05027	X15	-0.0671	-0.0613	0.01592
X15	-0.0176	0.00816	0.0452	X15	-0.1572	0.07059	0.03292	Y15	0.05116	0.01943	0.02029
Y15	0.1263	-0.1691	-0.0655	Y15	0.08451	0.1376	-0.15	X16	-0.0069	-0.1284	-0.0562
X16	-0.1544	0.08471	-0.1813	X16	-0.2177	-0.1526	0.1206	Y16	-0.08197	0.03387	0.00205
Y16	-0.0353	0.2007	0.1981	Y16	-0.1069	0.1602	-0.2184	X17	-0.00135	-0.1365	-0.0226
X17	-0.1121	0.03725	-0.1807	X17	-0.09589	-0.0197	0.3951	Y17	-0.01906	0.00975	-0.0046
Y17	0.03916	-0.2209	-0.1832	Y17	-0.2669	0.1302	-0.1663	X18	-0.0535	-0.1578	-0.0863
X18	-0.0945	0.1032	-0.1502	X18	0.02311	0.4829	0.379	Y18	0.06373	0.03559	0.06019
Y18	0.00886	0.00131	-0.0087	Y18	-0.2952	0.0249	-0.0868	X19	0.2177	0.06692	0.1657
X19	-0.0118	0.05837	-0.0348	X19	0.1851	-0.0025	0.1781	Y19	-0.194	0.08681	-0.0954
Y19	-0.0101	-0.0025	0.00281	Y19	-0.2049	-0.0623	0.02565	X20	0.1793	0.01159	0.1534
X20	-0.0323	0.1187	0.04528	X20	0.1451	0.03543	0.1519	Y20	0.2398	-0.0385	0.174
Y20	-0.0076	-0.0003	-0.0135	Y20	-0.1011	-0.1168	0.107	X21	0.2038	-0.1529	-0.0404
X21	0.2032	-0.0153	0.04748	X21	0.1211	-0.0006	0.1585	Y21	-0.01412	-0.1435	-0.1437
Y21	-0.0256	0.0034	0.00201	Y21	0.00593	-0.1707	0.1097	X22	0.2135	-0.1329	-0.0797
X22	-0.514	-0.1568	0.6677	X22	-0.04582	-0.0216	-0.0464	Y22	-0.07152	0.06151	0.1404
Y22	0.01422	0.00558	-0.0239	Y22	-0.02756	-0.2045	0.06657	X23	0.1904	0.3798	-0.2834
								Y23	-0.2753	0.1044	-0.1198
								X24	0.1347	0.7171	-0.1578
								Y24	0.4125	-0.01083	0.1705
								X25	0.1477	-0.2374	-0.2754
								Y25	-0.05498	-0.05054	-0.1458
								X26	0.1492	-0.2482	-0.2677
								Y26	0.02506	0.02148	0.1447
								X27	-0.1894	-0.00433	0.3316
								Y27	-0.1444	-0.02927	-0.1458
								X28	-0.08956	-0.09613	0.3074
								Y28	0.08669	-0.06805	0.09171
								X29	-0.2268	0.07532	0.3044
								Y29	0.01298	-0.04774	-0.0223

Table 5. Character states for individual specimens for *I. flavidus* (left) and *I. pirrensis* (right). Missing values are indicated by a “?”

Specimen ID	m1	MF	PGF	SSF	LF
outgroup	0	0	0	0	0
10328	3	1	?	?	?
18773	3	1	4	1	4
10330	3	1	?	?	4
10332	3	1	3	1	2
10334	3	1	3	1	1
10335	3	1	?	1	?
10337	3	1	?	1	?
10338	3	1	3	1	3
10339	3	1	3	1	3
10341	3	1	?	?	3
10345	3	2	?	?	3
10346	3	1	3	1	3
10347	3	1	3	1	?
10348	3	1	3	1	?
10349	3	1	3	0	3
10350	3	1	3	1	3
10351	3	1	3	1	3
10354	3	1	3	1	1
323925	3	3	4	0	4
323936	3	3	3	2	5
323928	3	2	4	1	5
323929	3	3	3	0	5
323930	3	1	2	0	4
323931	3	4	2	1	5
323932	3	2	4	0	5
323933	3	2	2	0	5
323934	3	3	2	0	1
323935	3	2	1	0	5
323936	3	5	4	0	4
541256	3	3	1	0	1
541257	3	1	4	0	4
541258	3	4	2	0	3
541259	3	1	4	3	3
541260	3	1	4	0	3
541261	3	1	1	0	1
541263	3	3	?	?	3
541264	3	2	2	0	3
541265	3	3	4	0	3
541266	3	1	1	0	3
541267	3	1	2	0	3
541271	3	2	2	0	3

Specimen ID	m1	MF	PGF	SSF	LF
21634	3	2	?	4	?
25440	2	3	2	1	4
25441	0	4	1	2	3
25442	1	4	1	1	1
25443	2	4	1	2	1
178980	1	5	3	1	1
178981	1	5	3	2	3
178984	1	4	3	4	1
178985	1	4	3	4	?
565924	1	2	1	1	1
179572	1	4	4	4	1
38007	1	4	3	3	1
38008	1	4	?	?	1
38011	2	4	3	1	1
38013	2	4	4	1	1
38014	2	3	2	4	3
38015	2	5	2	4	1
38017	1	4	1	0	1
38020	1	5	?	?	1
38022	2	5	1	0	1
38023	2	4	1	0	1
38032	2	5	2	1	1
38040	1	5	1	0	1
38033	2	4	1	1	1
38041	2	4	?	?	1
38045	2	4	2	1	1
38046	2	4	1	0	1
38048	2	4	?	?	1
38049	2	4	1	0	1
38050	2	4	2	2	1
38051	1	4	1	1	1
38052	2	5	2	1	1
38054	2	4	1	1	1
38061	1	5	1	1	1
310609	2	4	1	0	1
310610	2	4	1	3	1
310612	2	1	2	3	1
338269	2	4	1	1	1
338270	1	?	1	0	1
338271	2	2	1	0	1
338272	2	2	1	2	1
338273	1	4	1	0	3
338274	1	4	?	1	3
338285	1	4	1	0	1
338288	1	4	1	2	1
338289	1	2	2	2	1
338290	2	5	1	2	1
338291	1	4	2	2	1
338292	2	4	1	0	1
338293	2	4	2	3	3
338294	2	4	1	0	1
338296	2	2	2	2	1
338297	1	4	2	5	1
338298	1	4	1	4	1
338299	1	4	1	2	1
338300	2	4	1	4	2
338301	2	4	1	4	1
338302	1	4	1	5	1

Table 6. Results from post-hoc pairwise comparisons of: A.) Goodall's *F*-test for mean shape differences for dorsal, lateral and ventral views; B.) Hotelling's *T*² test of linear variables.

A.

	<i>I. flavidus</i> (type)	<i>I. flavidus</i> (Cerro Hoya)	<i>I. flavidus</i> (Cerro Colorado)	<i>I. pirrensis</i> (type)
<i>I. flavidus</i> (type) OTU 1				
<i>I. flavidus</i> (Cerro Hoya) OTU 2	p < .05			
<i>I. flavidus</i> (Cerro Colorado) OTU 3	p < .05	p < .05		
<i>I. pirrensis</i> (type) OTU 4	p < .05	p < .05	*p > .05* (Lateral)	
<i>I. pirrensis</i> (Tacarcuna) OTU 5	p < .05	p < .05	p < .05	p < .05

B.

	<i>I. flavidus</i> (type)	<i>I. flavidus</i> (Cerro Hoya)	<i>I. flavidus</i> (Cerro Colorado)	<i>I. pirrensis</i> (type)
<i>I. flavidus</i> (type) OTU 1				
<i>I. flavidus</i> (Cerro Hoya) OTU 2	p < .05			
<i>I. flavidus</i> (Cerro Colorado) OTU 3	p < .05	p > .05		
<i>I. pirrensis</i> (type) OTU 4	p < .05	p < .05	p < .05	
<i>I. pirrensis</i> (Tacarcuna) OTU 5	p < .05	p < .05	p < .05	p < .05

APPENDIX B LIST OF SPECIMENS

Morphometric analyses.—All specimens examined are listed below by locality and museum acronym.

Isthmomys flavidus— Type locality Panama: Chiriqui; Boquete(=Bajo Boquete) 1000-1500m (MCZ 10327, 10328, 10329, 10330, 10331, 10332, 10333, 10334, 10335, 10336, 10337, 10338, 10339, 10340, 10341, 10342, 10343, 10344, 10345, 10346, 10347, 10348, 10349, 10350, 10351, 10352, 10353, 10354, USNM 156909, AMNH 18770, 18773, 18774).

Panama: Chiriqui; Cerro Colorado 900-1500m (USNM, 541256, 541257, 541258, 541259, 541260, 541261, 541262, 541263, 541264, 541265, 541266, 541267, 541268, 541269, 541270, 541271)

Panama: Los Santos; Cerro Hoya 100-1500m (USNM, 323932, 323930, 323931, 323925, 323933, 323935, 323924, 323926, 323928, 323929, 323934, 323936).

Isthmomys pirrensis—Type locality Panama: Darien; Mount Pirri, Near Head of Rio Limon 1100-1700m (USNM 178979, 178981, 178980, 178986, 179572, 178982, 178983, 178984, 178985, 565924, LSU 25440, 25443, 25441, 25442).

Panama: Darien; Cerro Tacarcuna 1500-1600m (USNM 338269, 338270, 338271, 338272, 338273, 338274, 338288, 338289, 338290, 338291, 338293, 338294, 338295, 338296, 338297, 338298, 338299, 338300, 338301, 338302, 338303, 338304, 338305, 310608, 310609, 310610, 310611, AMNH 38007, 38008, 38009, 38010, 38011, 38012, 38013, 38014, 38015, 38016, 38017, 38019, 38020, 38021, 38022, 38023, 38026, 38028,

38031, 38032, 38037, 38041, 38045, 38047, 38048, 38049, 38050, 38051, 38052, 38054,
38055, 38056, 38057, 38058, 38059, 38060, 38061, 38062).

Panama: Darien; Cerro Nique 1400m (MSUM 21624, 22295, 22357, 22474).

APPENDIX C

DEFINITION OF LINEAR MEASUREMENTS

ONL: Occipitonasal Length: length from the tip of the rostrum to the posterior margin of the occiput.

ZB: Zygomatic breadth: the greatest breadth across the Zygomatic arches.

BZP: Breadth of Zygomatic Plate: distance between the greater and lesser curvatures of the zygomatic plate.

IOB: Interorbital Breadth: the least distance, as viewed dorsally, across the frontals bones across the orbital fossae.

BBC: Breadth of Braincase: Measured immediately posterior to squamosal roots of each zygomatic arch.

BOC: Breadth of Occipital Condyle: the greatest breadth across the distal portions of the condyles.

HBC: Height of Braincase: measured from the top of the braincase to the ventral surface of the basiosphenoid bone.

LR: Length of Rostrum: from the tip of the nasal bones to the posterior margin of the zygomatic notch (the anterior edge of the dorsal maxillary root of the zygomatic plate.)

WR: Width of Rostrum: measured just inside the anteroventral edge of the zygomatic plate.

LD: Length of Diastema: the distance from the anterior alveolar margins of the left first upper molar to the exposed lesser curvature of the upper incisor of the same side.

LIF: Length of Incisive Foramina: the distance from the anterior edge of the left incisive foramen to its posterior edge.

BIF: Breadth of Incisive Foramina: the greatest distance across both foramina.

LBP: Length of the Bony Palate: measured from the posterior edge of the left incisive foramina to the anterior edge of the mesopterygoid fossa.

BM1: Breadth of Palate Between the First Molars: measured between the protocones of the first maxillary molars.

WMF: Width of Mesopterygoid Fossa: distance between the pterygopalatine sutures.

PPL: Post palatal Length: measured from the ventral edge of the foramen magnum to the posterior edge of the mesopterygoid fossa.

CLM: Coronal Length of Maxillary Tooth Row: measured from the crown of the first upper molar to the crown of the third upper molar.

WM1: Width of the First Upper Molar: breadth of the first upper molar across the protocone-paracone cusp pair.

BIT: Breadth of Incisor Tips: distance across tips of upper incisors.

APPENDIX D PROGRAM CODES IN R FOR LINEAR MORPHOMETRICS

Program Codes in R for statistical analysis using morphometric techniques. All programs were written by John Middleton. All programs listed here make use of statistical analyses that complement each other; it is advisable to use these programs in the order that they are listed.

```
data=read.csv("copy_pop_repl.csv")
```

```
#MANOVA between species
```

```
man = manova(cbind(lnonl, lnzb, lnbzp, lniob, lnbbc, lnbc, lnhbc, lnlr, lnwr, lnld, lnlif, lnbit, lnbp, lnbm1, lnwfm, lnpppl, lnclm, lnwm1, lnbit)~species, data)  
summary(man)
```

```
#MANOVA between sexes
```

```
man = manova(cbind(lnonl, lnzb, lnbzp, lniob, lnbbc, lnbc, lnhbc, lnlr, lnwr, lnld, lnlif, lnbit, lnbp, lnbm1, lnwfm, lnpppl, lnclm, lnwm1, lnbit)~sex, data)
```

```
#between population/species (two-way MANOVA)
```

```
man = manova(cbind(lnonl, lnzb, lnbzp, lniob, lnbbc, lnbc, lnhbc, lnlr, lnwr, lnld, lnlif, lnbit, lnbp, lnbm1, lnwfm, lnpppl, lnclm, lnwm1, lnbit)~pop*species, data)  
summary(man)
```

```
##Principal Components for Linear Measurements
```

```
princomp(data, cor = FALSE, scores = TRUE, covmat = NULL, subset = rep(TRUE, nrow(as.matrix(data[c(5:23)])))
```

```
Linear Discriminant Function Analysis (LDA)
```

```
#LDA, you may replace names with whatever variable you need to.
```

```
ldaI=lda(data$pop~data$lnonl + data$lnzb + data$lnbzb + data$lniob + data$lnbbc + data$lnbc + data$lnhbc + data$lnlr + data$lnwr + data$lnld + data$lnlif + data$lnbit + data$lnbp + data$lnbm1 + data$lnwfm + data$lnpppl + data$lnclm + data$lnwm1 + data$lnbit)
```

```
#LDA species
```

```
ldaIsp=lda(data$species~data$lnonl + data$lnzb + data$lnbzb + data$lniob + data$lnbbc + data$lnbc + data$lnhbc + data$lnlr + data$lnwr + data$lnld + data$lnlif + data$lnbit +
```

```
data$lnlbp + data$lnbm1 + data$lnwmf + data$lnppl + data$lnclm + data$lnwm1 +
data$lnbit)
```

```
#plot the LDA, first three DF's
plot(ldaI, col=as.integer(data$pop), pch=16, cex=1)
```

```
##give values in LD a name
LD1<-predict(ldaI)$x[,1]
LD2<-predict(ldaI)$x[,2]
LD3<-predict(ldaI)$x[,3]
```

```
# Group centroid for plotting ld1, ld2
cent.ft=cbind(sum(LD1*(data$pop=="1"))/sum(data$pop=="1"),sum(LD2*(data$pop=="1"))/sum(data$pop=="1"),col=as.integer(data$pop))
cent.colo = cbind(sum(LD1*(data$pop=="2"))/sum(data$pop=="2"),
sum(LD2*(data$pop=="2"))/sum(data$pop=="2"),col=as.integer(data$pop))
cent.fch = cbind(sum(LD1*(data$pop=="3"))/sum(data$pop=="3"),
sum(LD2*(data$pop=="3"))/sum(data$pop=="3"),col=as.integer(data$pop))
cent.pt= cbind(sum(LD1*(data$pop=="4"))/sum(data$pop=="4"),
sum(LD2*(data$pop=="4"))/sum(data$pop=="4"),col=as.integer(data$pop))
cent.tacar=cbind(sum(LD1*(data$pop=="5"))/sum(data$pop=="5"),
sum(LD2*(data$pop=="5"))/sum(data$pop=="5"),col=as.integer(data$pop))
cent.m=cbind(sum(LD1*(data$pop=="6"))/sum(data$pop=="6"),
sum(LD2*(data$pop=="6"))/sum(data$pop=="6"))
```

```
#Centroid for plotting ld2, ld3
cent.ftld2=cbind(sum(LD2*(data$pop=="1"))/sum(data$pop=="1"),sum(LD3*(data$pop=="1"))/sum(data$pop=="1"), col=as.integer(data$pop))
cent.ptld2=cbind(sum(LD2*(data$pop=="2"))/sum(data$pop=="2"),sum(LD3*(data$pop=="2"))/sum(data$pop=="2"),col=as.integer(data$pop))
cent.fchld2=cbind(sum(LD2*(data$pop=="3"))/sum(data$pop=="3"),sum(LD3*(data$pop=="3"))/sum(data$pop=="3"),col=as.integer(data$pop))
cent.pctld2=cbind(sum(LD2*(data$pop=="4"))/sum(data$pop=="4"),sum(LD3*(data$pop=="4"))/sum(data$pop=="4"),col=as.integer(data$pop))
cent.fcld2=cbind(sum(LD2*(data$pop=="5"))/sum(data$pop=="5"),sum(LD3*(data$pop=="5"))/sum(data$pop=="5"),col=as.integer(data$pop))
```

```
#Plot centroid
centroids=rbind(cent.ft, cent.fch,cent.colo, cent.tacar, cent.pct, cent.m)
points(centroids, col=as.integer(data2$pop), pch=16, cex=2)
##centroids for lda2, lda3
centroidsld2=rbind(cent.ftld2, cent.fchld2, cent.fcld2, cent.ptld2, cent.pctld2)
```

```

points(centroidsld2, col="yellow", pch=16, cex=2)

##Plot LDA between species
ld.isth=plot(LD1, LD2, xlab="DF1 (...%)", ylab=DF2(...%), pch=16, cex=1,
col=as.integer(data$species))

ld.isth=plot(LD2, LD3, xlab="DF1 (...%)", ylab=DF2(...%), pch=16, cex=1,
col=as.integer(data$species))

##Between populations
ld.isth=plot(LD1, LD2, xlab="DF1 (52.6%)", ylab="DF2 (27.1%)", pch=16, cex=1,
col=as.integer(data$pop), text(rbind(LD1), labels=(data$pop), col=as.integer(data$pop),
cex=1.5))

ld.isth=plot(LD2, LD3, xlab="DF1 (52.6%)", ylab="DF2 (27.1%)", pch=16, cex=1,
col=as.integer(data$pop), text(rbind(LD2), labels=(data$pop), col=as.integer(data$pop),
cex=1.5))

##plot LD1, LD2 w text
ld.isth=plot(LD1, LD2, xlab="DF1 (56.5%)", ylab="DF 2 (28.5%)", pch=16, cex=1,
col=as.integer(data$pop), text(cbind(LD1,LD2), labels=(data$pop),
col=as.integer(data$pop), cex=1.5))

#plot ld1, ld2 with points instead of id text
ld.isth=plot(LD1, LD2, xlab="DF1 (52.6%)", ylab="DF 2 (27.1%)", pch=16, cex=1,
col=as.integer(data$pop), points(centroids, col="yellow", pch=16, cex=3))

ld.isth=plot(LD2, LD3, xlab="DF1 (52.6%)", ylab="DF 2 (27.1%)", pch=16, cex=1,
col=as.integer(data$pop), points(centroidsld2, col="yellow", pch=16, cex=2))

#center 0,0
abline(h=0)
abline(v=0)

arrows(c(0,0), c(0,0),length = 0.25, ldaI$scaling[,1], ldaI$scaling[,2])

text(rbind(ldaI$scaling), labels=rownames(ldaI$scaling), cex=2, col="blue"))

##Cross-validation
lda.cv = lda(data$pop~data$lnonl + data$lnzb + data$lnbzb + data$lniob + data$lnbbc +
data$lnboc + data$lnhbc + data$lnlr + data$lnwr + data$lnld + data$lnlif + data$lnbif +

```

```
data$lnlbp + data$lnbm1 + data$lnwmf + data$lnppl + data$lnclm + data$lnwm1 +  
data$lnbit, CV=T)  
lda.cv=lda(data2$pop~data2$x1=data2$y1  
  
#group membership predictions  
tab=predict(ldaI)  
pred=table(data2$pop,ldaI$class)
```

APPENDIX E

PROGRAM CODES IN R FOR GEOMETRIC MORPHOMETRICS

R program codes for shape analysis in 3 views for a variable number of landmarks.

```

##Dorsal landmarks
data1=read.csv("isthmomys_dorsal.csv")
##set up matrix data set 1
d2=array(as.matrix(data1), dim=c(22, 2, 103))
ds = cbind(data1[1:22,], data1[23:44,], data1[45:66,], data1[67:88,], data1[89:110,],
data1[111:132,], data1[133:154,], data1[155:176,],data1[177:198,], data1[199:220,],
data1[221:242,], data1[243:264,], data1[265:286,], data1[287:308,], data1[309:330,],
data1[331:352,], data1[353:374,], data1[375:396,], data1[397:418,], data1[419:440,],
data1[441:462,], data1[463:484,], data1[485:506,], data1[507:528,], data1[529:550,],
data1[551:572,], data1[573:594,], data1[595:616,], data1[617:638,], data1[639:660,],
data1[661:682,], data1[683:704,], data1[705:726,], data1[727:748,], data1[749:770,],
data1[771:792,], data1[793:814,], data1[815:836,], data1[837:858,], data1[859:880,],
data1[881:902,], data1[903:924,], data1[925:946,], data1[947:968,], data1[969:990,],
data1[991:1012,], data1[1013:1034,], data1[1035:1056,], data1[1057:1078,],
data1[1079:1100,], data1[1101:1122,], data1[1123:1144,], data1[1145:1166,],
data1[1167:1188,], data1[1189:1210,], data1[1211:1232,], data1[1233:1254,],
data1[1255:1276,], data1[1277:1298,], data1[1299:1320,], data1[1321:1342,],
data1[1343:1364,], data1[1365:1386,], data1[1387:1408,], data1[1409:1430,],
data1[1431:1452,], data1[1453:1474,], data1[1475:1496,], data1[1497:1518,],
data1[1519:1540,], data1[1541:1562,], data1[1563:1584,], data1[1585:1606,],
data1[1607:1628,], data1[1629:1650,], data1[1651:1672,], data1[1673:1694,],
data1[1695:1716,], data1[1717:1738,], data1[1739:1760,], data1[1761:1782,],
data1[1783:1804,], data1[1805:1826,], data1[1827:1848,], data1[1849:1870,],
data1[1871:1892,], data1[1893:1914,],data1[1915:1936,], data1[1937:1958,],
data1[1959:1980,], data1[1981:2002,], data1[2003:2024,],data1[2025:2046,],
data1[2047:2068,], data1[2069:2090,], data1[2091:2112,], data1[2113:2134,],
data1[2135:2156,], data1[2157:2178,],data1[2179:2200,], data1[2201:2222,],
data1[2223:2244,], data1[2245:2266,])

all= array(as.matrix(ds), dim = c(22,2,103))

flavidus_type=all[,1:16]
flavidus_colo=all[,17:30]
flavidus_ch=all[,31:40]
pirrensis_type=all[,41:55]
cerro_tacarcuna=all[,56:103]

```

```

#bookstein2d
bookft<-bookstein2d(flavidus_type)
bookfcolo<-bookstein2d(flavidus_colo)
bookfch<-bookstein2d(flavidus_ch)
bookpt<-bookstein2d(pirrensis_type)
bookct<-bookstein2d(cerro_tacarcuna)

###plot mean shapes with joinline
plotshapes(bookft$mshape,bookfch$mshape,joinline=c(1:22:1))

#Generalized Procrustes Analysis
out.procall=procGPA(all)
out.procft<-procGPA(flavidus_type)
out.profcolo<-procGPA(flavidus_colo)
out.procfch<-procGPA(flavidus_ch)
out.procpt<-procGPA(pirrensis_type)
out.procct<-procGPA(cerro_tacarcuna)
plotshapes(out.procfch$rotated,
joinline=c(1,2,4,6,8,10,12,14,16,18:20,1,3,5,7,9,11,13,15,17:20,1))
plotshapes(out.procft$rotated,
joinline=c(1,2,4,6,8,10,12,14,16,18:20,1,3,5,7,9,11,13,15,17:20,1))

tpsgrid(out.procft$mshape, out.procfch$mshape, -0.6,-0.6,1.2,2,0.2,30)

shapepca(out.procall, pcno = c(1, 2), type = "v",mag=2)

shapepca(out.procft, pcno = c(1, 2), type = "v",mag=2)

shapepca(procall, pcno = c(1, 2), type = "v",mag=2)

shapepca(out.procfch, pcno = c(1, 2), type = "v",mag=2)

#Riemenian distance
riemdist(out.procft$mshape,out.procfch$mshape)

#Goodall's F-test for Mean shape Difference
testmeanshapes(flavidus_type, flavidus_colo, Hotelling = FALSE)
testmeanshapes(flavidus_type, flavidus_ch, Hotelling = FALSE)
testmeanshapes(flavidus_type, cerro_tacarcuna, Hotelling = FALSE)
testmeanshapes(flavidus_type, pirrensis_type, Hotelling = FALSE)

testmeanshapes(flavidus_colo, flavidus_ch, Hotelling = FALSE)
testmeanshapes(flavidus_colo, pirrensis_type, Hotelling = FALSE)

```

```
testmeanshapes(flavidus_colo, cerro_tacarcuna, Hotelling = FALSE)
```

```
testmeanshapes(flavidus_ch, cerro_tacarcuna, Hotelling = FALSE)
```

```
testmeanshapes(pirrensis_type, cerro_tacarcuna, Hotelling = FALSE)
```

```
testmeanshapes(pirrensis_type, flavidus_ch, Hotelling = FALSE)
```

```
#Lateral Analysis
```

```
data1=read.csv("isthmomys_lat.csv")
```

```
ds = cbind(data1[1:22,], data1[23:44,], data1[45:66,], data1[67:88,], data1[89:110,],
data1[111:132,], data1[133:154,], data1[155:176,], data1[177:198,], data1[199:220,],
data1[221:242,], data1[243:264,], data1[265:286,], data1[287:308,], data1[309:330,],
data1[331:352,], data1[353:374,], data1[375:396,], data1[397:418,], data1[419:440,],
data1[441:462,], data1[463:484,], data1[485:506,], data1[507:528,], data1[529:550,],
data1[551:572,], data1[573:594,], data1[595:616,], data1[617:638,], data1[639:660,],
data1[661:682,], data1[683:704,], data1[705:726,], data1[727:748,], data1[749:770,],
data1[771:792,], data1[793:814,], data1[815:836,], data1[837:858,], data1[859:880,],
data1[881:902,], data1[903:924,], data1[925:946,], data1[947:968,], data1[969:990,],
data1[991:1012,], data1[1013:1034,], data1[1035:1056,], data1[1057:1078,],
data1[1079:1100,], data1[1101:1122,], data1[1123:1144,], data1[1145:1166,],
data1[1167:1188,], data1[1189:1210,], data1[1211:1232,], data1[1233:1254,],
data1[1255:1276,], data1[1277:1298,], data1[1299:1320,], data1[1321:1342,],
data1[1343:1364,], data1[1365:1386,], data1[1387:1408,], data1[1409:1430,],
data1[1431:1452,], data1[1453:1474,], data1[1475:1496,], data1[1497:1518,],
data1[1519:1540,], data1[1541:1562,], data1[1563:1584,], data1[1585:1606,],
data1[1607:1628,], data1[1629:1650,], data1[1651:1672,], data1[1673:1694,],
data1[1695:1716,], data1[1717:1738,], data1[1739:1760,], data1[1761:1782,],
data1[1783:1804,], data1[1805:1826,], data1[1827:1848,], data1[1849:1870,],
data1[1871:1892,], data1[1893:1914,], data1[1915:1936,], data1[1937:1958,],
data1[1959:1980,], data1[1981:2002,], data1[2003:2024,], data1[2025:2046,],
data1[2047:2068,], data1[2069:2090,], data1[2091:2112,], data1[2113:2134,],
data1[2135:2156,], data1[2157:2178,], data1[2179:2200,])
```

```
all_lat = array(as.matrix(ds), dim = c(22,2,100))
```

```
flavidus_type=all_lat[,1:14]
```

```
flavidus_colo=all_lat[,15:27]
```

```
flavidus_ch=all_lat[,28:38]
```

```
pirrensis_type=all_lat[,39:50]
```

```
cerro_tacarcuna=all_lat[,51:100]
```

```
bookft<-bookstein2d(flavidus_type)
```

```
bookfcolo<-bookstein2d(flavidus_colo)
```

```
bookfch<-bookstein2d(flavidus_ch)
```

```

bookpt<-bookstein2d(pirrensis_type)
bookct<-bookstein2d(cerro_tacarcuna)

out.procall=procGPA(all_lat)
out.procft<-procGPA(flavidus_type)
out.profcfcolo<-procGPA(flavidus_colo)
out.procfch<-procGPA(flavidus_ch)
out.procpt<-procGPA(pirrensis_type)
out.procct<-procGPA(cerro_tacarcuna)

shapepca(out.procall, pcno = c(1, 2), type = "v",mag=2)

#Goodall's F-test for Mean shape Difference
testmeanshapes(flavidus_type, flavidus_colo, Hotelling = FALSE)
testmeanshapes(flavidus_type, flavidus_ch, Hotelling = FALSE)
testmeanshapes(flavidus_type, cerro_tacarcuna, Hotelling = FALSE)
testmeanshapes(flavidus_type, pirrensis_type, Hotelling = FALSE)

testmeanshapes(flavidus_colo, flavidus_ch, Hotelling = FALSE)
testmeanshapes(flavidus_colo, pirrensis_type, Hotelling = FALSE)
testmeanshapes(flavidus_colo, cerro_tacarcuna, Hotelling = FALSE)

testmeanshapes(flavidus_ch, cerro_tacarcuna, Hotelling = FALSE)
testmeanshapes(pirrensis_type, cerro_tacarcuna, Hotelling = FALSE)
testmeanshapes(pirrensis_type, flavidus_ch, Hotelling = FALSE)

#Ventral Analysis
data1=read.csv("ventral.csv")
d2=array(as.matrix(data1), dim=c(29, 2, 101))
ds = cbind(data1[1:29,], data1[30:58,], data1[59:87,], data1[88:116,], data1[117:145,],
data1[146:174,], data1[175:203,], data1[204:232,], data1[233:261,], data1[262:290,],
data1[291:319,], data1[320:348,], data1[349:377,], data1[378:406,], data1[407:435,],
data1[436:464,], data1[465:493,], data1[494:522,], data1[523:551,], data1[552:580,],
data1[581:609,], data1[610:638,], data1[639:667,], data1[668:696,], data1[697:725,],
data1[726:754,], data1[755:783,], data1[784:812,], data1[813:841,], data1[842:870,],
data1[871:899,], data1[900:928,], data1[929:957,], data1[958:986,], data1[987:1015,],
data1[1016:1044,], data1[1045:1073,], data1[1074:1102,], data1[1103:1131,],
data1[1132:1160,], data1[1161:1189,], data1[1190:1218,], data1[1219:1247,],
data1[1248:1276,], data1[1277:1305,], data1[1306:1334,], data1[1335:1363,],
data1[1364:1392,], data1[1393:1421,], data1[1422:1450,], data1[1451:1479,],
data1[1480:1508,], data1[1509:1537,], data1[1538:1566,], data1[1567:1595,],
data1[1596:1624,], data1[1625:1653,], data1[1654:1682,], data1[1683:1711,],
data1[1712:1740,], data1[1741:1769,], data1[1770:1798,], data1[1799:1827,],

```

```
data1[1828:1856,], data1[1857:1885,], data1[1886:1914,], data1[1915:1943,],
data1[1944:1972,], data1[1973:2001,], data1[2002:2030,], data1[2031:2059,],
data1[2060:2088,], data1[2089:2117,], data1[2118:2146,], data1[2147:2175,],
data1[2176:2204,], data1[2205:2233,], data1[2234:2262,], data1[2263:2291,],
data1[2292:2320,], data1[2321:2349,], data1[2350:2378,], data1[2379:2407,],
data1[2408:2436,], data1[2437:2465,], data1[2466:2494,], data1[2495:2523,],
data1[2524:2552,], data1[2553:2581,], data1[2582:2610,], data1[2611:2639,],
data1[2640:2668,], data1[2669:2697,], data1[2698:2726,], data1[2727:2755,],
data1[2756:2784,], data1[2785:2813,], data1[2814:2842,], data1[2843:2871,],
data1[2872:2900,], data1[2901:2929,])
```

```
all_vent = array(as.matrix(ds), dim = c(29,2,101))
```

```
flavidus_type=all_vent[,1:14]
flavidus_colo=all_vent[,15:30]
flavidus_ch=all_vent[,31:41]
pirrensis_type=all_vent[,42:54]
cerro_tacarcuna=all_vent[,55:101]
```

```
bookft<-bookstein2d(flavidus_type)
bookfcolo<-bookstein2d(flavidus_colo)
bookfch<-bookstein2d(flavidus_ch)
bookpt<-bookstein2d(pirrensis_type)
bookct<-bookstein2d(cerro_tacarcuna)
```

```
out.procall=procGPA(all_vent)
out.procft<-procGPA(flavidus_type)
out.procfcolo<-procGPA(flavidus_colo)
out.procfch<-procGPA(flavidus_ch)
out.procpt<-procGPA(pirrensis_type)
out.procct<-procGPA(cerro_tacarcuna)
```

```
#Goodall's F-test for Mean shape Difference
testmeanshapes(flavidus_type, flavidus_colo, Hotelling = FALSE)
testmeanshapes(flavidus_type, flavidus_ch, Hotelling = FALSE)
testmeanshapes(flavidus_type, cerro_tacarcuna, Hotelling = FALSE)
testmeanshapes(flavidus_type, pirrensis_type, Hotelling = FALSE)
```

```
testmeanshapes(flavidus_colo, flavidus_ch, Hotelling = FALSE)
testmeanshapes(flavidus_colo, pirrensis_type, Hotelling = FALSE)
testmeanshapes(flavidus_colo, cerro_tacarcuna, Hotelling = FALSE)
```

```
testmeanshapes(flavidus_ch, cerro_tacarcuna, Hotelling = FALSE)
```

```
testmeanshapes(pirrensis_type, cerro_tacarcuna, Hotelling = FALSE)  
testmeanshapes(pirrensis_type, flavidus_ch, Hotelling = FALSE)
```

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