

A GEOMETRIC MORPHOMETRIC APPROACH TO THE STUDY OF MANDIBLE VARIATION AMONG POPULATIONS OF *CAPROMYS PILORIDES* (RODENTIA: CAPROMYIDAE)Carlos A. MANCINA^{1*}, Jorge VILLEGAS MARTÍN² y Lisbeth BARBÁN ÁLVAREZ¹

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ABSTRACT: *Capromys pilorides* (Say, 1822) (Rodentia, Capromyidae) is the most widely distributed and abundant endemic rodent of the Cuban archipelago. This study aims to quantify and analyze morphological variation in mandible size and shape among populations of this rodent, and to evaluate the reliability of mandible shape as a taxonomic predictor. 2D landmarks and semi-landmarks were used to describe 188 mandibles of adult *C. pilorides*; seven populations were analyzed, including the five recognized subspecies. Size and shape were compared between sexes and localities, using landmark-based geometric morphometric methods. Male-biased sexual size dimorphism was observed, although sexual size and shape differences were moderate compared to differences between populations. Significant differences between populations were found for mandible size and shape. Two extreme shape morphotypes can be observed associated with the general robustness of the mandible: (1) subspecies that inhabit small keys (*C. p. gundlachianus* and *C. p. doceleguas*) possess a short coronoid process, long condylar process, and narrow horizontal ramus; (2) *C. p. pilorides* has long coronoid and angular processes, a short and robust condylar process, and a broad horizontal ramus. Similarity in mandible shape is not correlated with minimal geographic distances between populations. Mandible shape variation probably reflects adaptation to exploiting different resources available in different habitats (e.g. more omnivorous diet associated with terrestrial habitats; phytophagous diet associated with mangroves). Our results support most previously established subspecific designations; however, the Zapata Swamp population display greater variation than expected.

KEYWORDS: Cuba, geometric morphometrics, hutia, intraspecific variation, mandible size/shape.

RESUMEN: ESTUDIO DE LA VARIACIÓN DE LA MANDÍBULA ENTRE POBLACIONES DE *CAPROMYS PILORIDES* (RODENTIA: CAPROMYIDAE): UN ACERCAMIENTO MEDIANTE MORFOMETRÍA GEOMÉTRICA. *Capromys pilorides* (Say, 1822) (Rodentia, Capromyidae) es el roedor endémico de más amplia distribución en el archipiélago cubano. En este estudio se analiza la variación morfológica de la forma y el tamaño de la mandíbula de esta especie, y se evalúa la confiabilidad de esta estructura como predictor taxonómico. Se emplearon puntos anatómicos de referencia y puntos

deslizantes bidimensionales para describir la forma de la mandíbula de 188 individuos adultos, estos incluían siete poblaciones y las cinco subespecies reconocidas. Se comparó el tamaño y la forma entre sexos y localidades usando métodos de morfometría geométrica. Se observó dimorfismo sexual en tamaño sesgado hacia los machos; aunque las diferencias entre los sexos fueron moderadas comparadas con las diferencias entre las poblaciones. Existen diferencias significativas en la forma y el tamaño de la mandíbula entre poblaciones. Se aprecian dos morfotipos extremos asociados a la robustez general de la mandíbula: 1) subespecies que habitan los pequeños cayos (*C. p. gundlachianus* y *C. p. doceleguas*), con un proceso coronoides corto, proceso condilar largo y la rama horizontal estrecha y 2) poblaciones de *C. p. pilorides* con los procesos coronoides y angular largos, proceso condilar corto y robusto, y rama horizontal amplia. La similitud en la forma de la mandíbula no está correlacionada con la distancia geográfica mínima entre las poblaciones. La forma de la mandíbula probablemente esté reflejando adaptaciones locales a explotar los recursos disponibles en los diferentes hábitats (ej. dieta más omnívora en aquellas de hábitats terrestres, dieta fitófaga asociada a los ecosistemas de manglar). Nuestros resultados soportan la mayoría de las designaciones subespecíficas establecidas; sin embargo, la población de Ciénaga de Zapata muestra mayor variación que la esperada.

PALABRAS CLAVE: Cuba, forma/tamaño de la mandíbula, jutía, morfometría geométrica, variación intraespecífica.

INTRODUCTION

The mammalian mandible is a complex structure that consists of two symmetrical dentary bones. Each bone is comprised of four semi-independent modules: the mandibular ramus and the coronoid, condylar and angular processes. These modules are integrated developmentally and structurally to ensure organismal coherence (Winther, 2001; Klingenberg *et al.*, 2003). The mandibular shape in adult mammals is determined by cell processes that are influenced by genetic or environmental factors to produce evolutionary shape changes (Atchley and Hall, 1991; Klingenberg *et al.*, 2003; Renaud *et al.*, 2007). The mammal mandible is therefore a suitable model for the evaluation of patterns and processes of morphological

evolution (e.g. Barrow and Macleod, 2008; Zelditch *et al.*, 2008; Monteiro and Nogueira, 2009; Hautier *et al.*, 2011).

Shape analysis through morphometric geometric techniques has been a revolutionary framework for the statistical study of variation and covariation of the shapes of biological structures (Rohlf, 2000). These techniques allow the description and quantification of changes and variations of shapes, on the basis of the analysis of anatomical point (*landmark*) configurations or shapes of outlines, providing a graphical representation of localized morphometric variation (Bookstein, 1991; Zelditch *et al.*, 2004). These methods allow an understanding of patterns of intra- and interspecific morphological evolution in response to different environmental pressures and ontogenetic processes, as well as an exploration of the relationship between morphology and molecular phylogeny (Adams *et al.*, 2004; Couette *et al.*, 2005; Renaud *et al.*, 2007; Sanfelice and Freitas, 2008; Hautier *et al.*, 2011).

As is also the case for other groups of Antillean terrestrial mammals, Antillean rodents have shown high rates of evolutionary radiation and recent extinction (Woods *et al.*, 2001; MacPhee, 2009; Fabre *et al.*, 2014). The hutias (Capromyidae) are hystricognath rodents that are found today on Cuba, Hispaniola, Jamaica, and several small islands in the Caribbean Sea (Woods and Kilpatrick, 2005). Capromyidae is the only family of Antillean rodents that retains living species in the region; however, with the exception of two species, the extant hutias are all listed as threatened (IUCN, 2018). *Capromys pilorides*, locally known as the Conga hutia, is the most widely distributed and abundant endemic rodent of the Cuban archipelago; its body mass is greater than 3 kg, and it is the largest extant capromyid (Borroto-Páez, 2011). Five subspecies, distributed on the main island of Cuba, Isla de la Juventud (formerly Isla de Pinos), and adjacent small keys, have been described: *Capromys pilorides doceleguas* Varona, 1980, from small keys in the Jardines de la Reina archipelago off the coast of southern Cuba; *C. p. gundlachianus* Varona, 1983, from the Sabana archipelago off the northern coast; *C. p. relictus* Allen, 1911, and *C. p. ciprianoi* Borroto *et al.*, 1992, from the north and south of Isla de la Juventud, respectively; and *C. p. pilorides* (Say, 1822) from many localities across the main island of Cuba (Silva *et al.*, 2007; Borroto-Páez, 2011).

These subspecies have been recognized mainly according to external features as body size and pelage coloration (Silva *et al.*, 2007). However, many of these characters are highly variable and overlapping among subspecies, and few molecular studies (Woods *et al.*, 2001) have tried to verify the validity of these subspecific designations. In the absence of adequate molecular data, morphometric study of geographic variation may provide indirect information about genetic structure and the degree of isolation of mammal populations (Elton *et al.*, 2010). The exploration of patterns of subspecific and interpopulation variation could therefore be essential for understanding evolutionary diversification in Antillean rodents, and could supply essential information about biological responses to ecological change. Skull or mandible shape variation, and the ecological and phylogenetic factors related to this variation, have previously been assessed in several mammal species, including hystricognath rodents (Cardini, 2003; Monteiro *et al.*, 2003; Barciová, 2009; Milenkovic *et al.*, 2010; Álvarez *et al.*, 2011).

Capromys pilorides is particularly appropriate for exploring interpopulation ecological effects because it exploits a broad variety of habitats, resulting in a large degree of variation in food resources and environmental conditions that could affect its morphology. Although hutias are phytophagous, some populations consume food of animal origin (Frias and Hernández, 1985). Different populations also show differing degrees of arboreality; some populations on the main island are largely terrestrial, whereas others have an arboreal lifestyle associated with mangroves (Berovides *et al.*, 1990a). This study aims to quantify and analyze patterns of local variation in mandible size and shape between populations of *Capromys pilorides*, to explore the relationship between patterns of morphological variation and geographic distribution of hutia populations, and to evaluate the accuracy of mandible shape as a taxonomic predictor. To achieve these aims, we analyzed a sample of mandibles from adult specimens of *C. pilorides* from all known subspecies, applying *landmark*-based geometric morphometric methods.

MATERIALS AND METHODS

SPECIMENS

This study is based on 188 mandibles of adult individuals of *Capromys pilorides*. The specimens were clustered at subspecies level based on geographic distribution (Silva *et*

TABLE 1. Specimens of *Capromys pilorides* examined.
TABLA 1. Individuos examinados de *Capromys pilorides*.

Subspecies or populations	Acronyms	Localities ¹	Males	Females	Total
<i>Capromys p. pilorides</i> (Western)	Cpp-W	1,2,3,4,5	22	21	43
<i>Capromys p. pilorides</i> (Zapata Swamp)	Cpp-Z	6,7,8,9,10	11	6	17
<i>Capromys p. pilorides</i> (Central)	Cpp-C	11,12,13,14	11	12	23
<i>Capromys p. gundlachianus</i>	Cp gun	15, 16, 17, 18, 19, 20, 21, 22	7	4	18 ²
<i>Capromys p. doceleguas</i>	Cp doc	23, 24, 25, 26, 27	3	3	7 ²
<i>Capromys p. relictus</i>	Cp rel	28, 29	15	13	28
<i>Capromys p. ciprianoi</i>	Cp cip	30, 31, 32, 33, 34	16	36	52

1. Numbers corresponding to localities are indicated in Figure 1.

2. Including specimens of unknown sex.

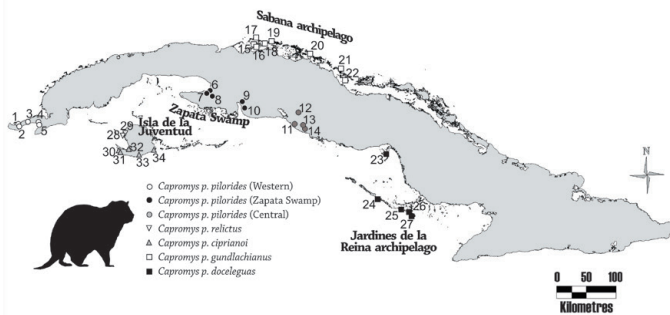


FIGURE 1. Geographic distribution of specimens of *Capromys pilorides* included in this study. Different symbols represent different subspecies or populations studied. FIGURA 1. Distribución geográfica de los especímenes de *Capromys pilorides* incluidos en este estudio. Los símbolos diferentes representan las diferentes subspecies o poblaciones estudiadas.

al., 2007; Borroto-Páez, 2011). The sample of *Capromys pilorides pilorides* was classified into three sub-samples according to their distribution (Table 1, Fig. 1). All specimens examined are housed in the mammal collection of the Instituto de Ecología y Sistemática, La Habana, Cuba. The list of specimens with their catalogue number and geographic origin is given in Appendix 1.

GEOMETRIC MORPHOMETRIC ANALYSIS

Following previous studies on rodents (Duarte *et al.*, 2000; Cardini, 2003; Álvarez *et al.*, 2011) we analyzed mandible shape variation in lateral view. Two-dimensional coordinates were captured on digital images of the left hemi-mandible in lateral view; the mandible rested on the lingual side of the horizontal ramus and the labial side was photographed. We took photographs using a digital SLR camera (Nikon D100, Japan) with a Micro-Nikkor 28–105 mm lens. The camera was positioned directly above the hemi-mandible and parallel to the horizontal ramus. All photographs were taken with a scale bar and a focal distance of 0.25 m.

We chose a set of nine *landmarks* and five *semi-landmarks* (points of maximum curvature) on the labial side of the mandible to represent the mandibular outline in more detail (Fig. 2). The *landmarks* and *semi-landmarks* are defined as follows: 1) antero-dorsal edge of incisor alveolus; 2) lowest point on curve of diastema; 3) anterior edge of tooth-row; 4) intersection of tooth-row with base of coronoid process; 5) tip of coronoid process; 6) lowest point on curve between coronoid and condyloid processes; 7) anterior-most edge of condyle; 8) tip of condyle; 9) posterior-most edge of condyle; 10) anterior-most point on curve between condyloid and angular processes; 11) tip of angular process; 12) dorsal-most point on ventral border of horizontal ramus; 13) ventral-most point of horizontal ramus; 14) antero-ventral edge of incisor alveolus. The x,y coordinates for each *landmark* and *semi-landmark* were digitized using TpsDig 2.12 (Rohlf, 2008).

The *landmarks* and *semi-landmarks* were converted to shape coordinates by procrustes generalized least-squares superimposition (Rohlf and Slice, 1990; Bookstein, 1991; Zelditch *et al.*, 2004). *Semi-landmarks* were slid

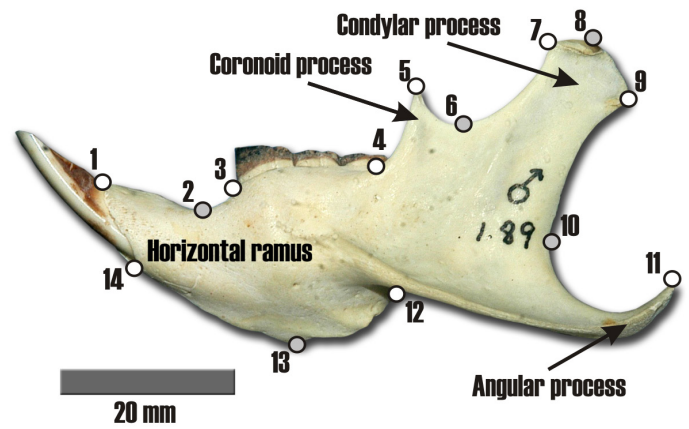


Figure 2. Morphological *landmarks* (white points) and *semi-landmarks* (grey points) defined on the labial side of the mandible of *Capromys pilorides* (for description see Materials and Methods).

FIGURA 2. Puntos anatómicos (blancos) y puntos deslizantes (grises) definidos sobre el lado labial de la mandíbula de *Capromys pilorides*.

along vectors tangential to the respective curves using the minimum bending energy criterion (Bookstein, 1997). Procrustes superimpositions remove all information unrelated to shape (location, rotation, and size), and convert specimens into shape variables and centroid sizes. Landmark superimpositions provide a mean shape for each sample (i.e. sex, subspecies or population); the average configurations were superimposed to obtain the grand mean that was used as a tangent configuration (reference configuration) to calculate partial warps. The partial warps represent localized changes of shape and may be used to depict shape variation. A more detailed description of geometric shape variables can be found elsewhere (Rohlf and Bookstein, 1990; Rohlf, 1996; Zelditch *et al.*, 2004). Superimposition of *landmarks* and *semi-landmarks* was performed using TpsRelw 1.45 (Rohlf, 2007).

Measurement error in *landmark* acquisition was assessed by digitizing ten different individuals of the same population (western population) and sex (males) on five times. The within-sample error was quantified as a percent measurement error (% ME) (Bailey and Byrnes, 1990). A one-way ANOVA on the residuals of Procrustes distances was used to compare within- and among individual components of shape variance. Measurement error was calculated as $\%ME = [(S^2_{within}) / (S^2_{within} + S^2_{among})] \times 100\%$. The % ME to assess digitizing error was 0.65%; this indicates that measurement error thus is negligibly small as compared to the variation among individuals. Measurement error of less than 15% could be within the reliable variation range for establishing biological trends (Bailey and Byrnes 1990).

MULTIVARIATE ANALYSIS

Principal components analysis (PCA) was carried out using the covariance matrix of the Partial Warp Scores. Due to the small size of some samples, it was impossible to use the matrix of partial warp scores as dependent shape variables; therefore, we used a subset of the first ten PCs (relative warps) obtained through a PCA of the partial warps matrix as new shape variables. This reduces

RESULTS

the dimensionality of the data set and summarizes trends in mandible shape variation among taxa (Rohlf, 1993). Our subset of relative warps (RW) explained approximately 90 % of total shape variance. We calculated the RW scores including the uniform component using TpsRelw 1.45 (Rohlf, 2007).

We used centroid size as a measure of size; this is a measure of overall size that is computed as the square root of the sum of squared distances from each landmark from the centre of the form (Zelditch *et al.*, 2004). Two-way ANOVA (sex and locality) was used to analyze sexual dimorphism in size. Size variation between sexes and localities was summarized using box-plots. The relationships between body mass and body length, and mandible size were examined through linear regression; data on mass and body length were obtained from specimen collection tags.

Multivariate two-way analysis of variance (MANOVA) was performed to test the effect of sexual dimorphism and locality on mandible shape. We performed a multivariate covariate analysis (MANCOVA) to control the effect of size on mandible shape using \log_{10} centroid size as a covariate. A lack of significant differences in the interaction between groups (sex and locality) would suggest similar allometric trajectories. To explore the effect of small sample sizes (i.e. *Capromys pilorides doceleguas* and *C. p. gundlachianus*, which have $n < 5$ specimens of either sex) on the results, all tests were repeated after removing the smallest samples. These tests showed similar levels of statistical significance, and so the results are not shown. Because sexual dimorphism and the interaction term of sex-locality for mandibular shape was small compared to the variation between localities, the sexes were pooled in subsequent analyses. Discriminant analysis (DA) was also employed for testing shape differences between sexes and populations, and for graphical illustrations of the MANOVA results. We used squared Mahalanobis distances between sexes and populations as a measure of morphological similarity. Statistica 6.1 (StatSoft, Inc., 2003) was used for statistical analyses.

To depict shape variation associated with two first canonical variates (CV), shape variables were regressed onto the CV scores and deformation grids were determined and visualized using TpsRegr 1.34 (Rohlf, 2007). The scores of the first two CVs were regressed onto the logarithm of centroid size to explore the influence of size in each ordination axis. In order to visualize mandibular shape affinities at the population level, populations were clustered using a Neighbour-joining tree computed on the matrix of Euclidian distances obtained from PCA. Neighbour-joining tree was computed using PAST (Hammer *et al.*, 2001). To estimate the degree of correspondence between mandible shape variation and geographic distance, we used a test of matrix correlation. We compared the matrices of Mahalanobis and geographic distances (minimal distance between populations) with a Mantel's test with 5 000 permutations, using MANTEL for Windows 1.19 (Cavalcanti, 2008).

SEXUAL SIZE AND SHAPE DIMORPHISM

The ANOVA of (sex x locality) on centroid size showed that differences between populations are highly significant (Table 2). The hutias from the western main island of Cuba and the south of Isla de la Juventud are significantly larger than those from Zapata Swamp and the north of Isla de la Juventud (Tukey test, $p < 0.001$). Male hutias are larger on average than females ($p > 0.005$). Sexual dimorphism in mandible size is greater in the westernmost population of *C. p. pilorides*; however, the highest degree of intra-population variation between sexes was not significant ($p > 0.05$). Centroid size variation for each population, including sizes of both sexes, is shown in Fig. 3.

TABLE 2. Two-way ANOVA for centroid size in populations of *Capromys pilorides*. Centroid size was logarithmically (\log_{10}) transformed to homogenize the variances and improve normality of the data.

TABLA 2. ANOVA de dos factores para el tamaño del centroide para poblaciones de *Capromys pilorides*. El tamaño del centroide fue transformado a logaritmo (\log_{10}) para homogenizar las varianzas y mejorar la normalidad de los datos.

Effect	Sum of squares	df	F	P
Sex	0.0078	1	7.8	0.0058
Localities	0.0553	5	11.0	< 0.00001
Sex x Locality	0.0017	5	0.3	0.892
Error	0.1644	179		

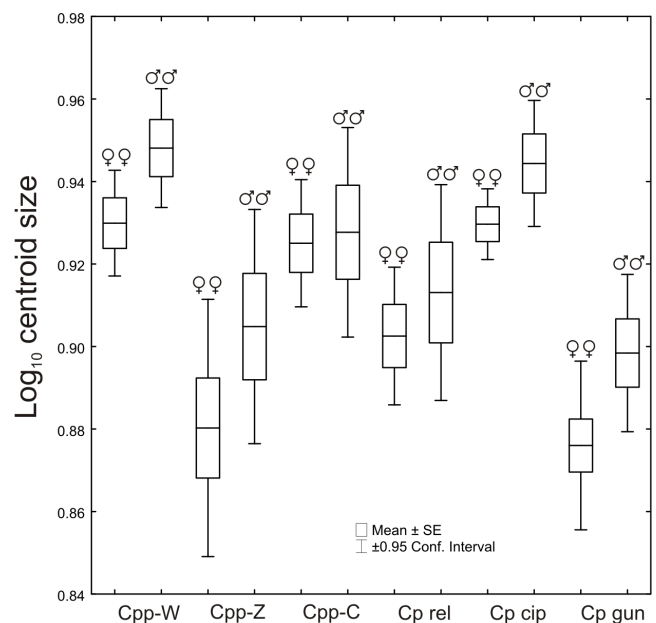


FIGURE 3. Box-plots of mandibular \log_{10} centroid size between sexes in six populations of *Capromys pilorides* (see Materials and Methods for acronyms and sample size of each sex).

FIGURA 3. Gráfico de caja del \log_{10} del tamaño del centroide entre sexos en seis poblaciones de *Capromys pilorides* (ver Materiales y Métodos para acrónimos y tamaño de muestra).

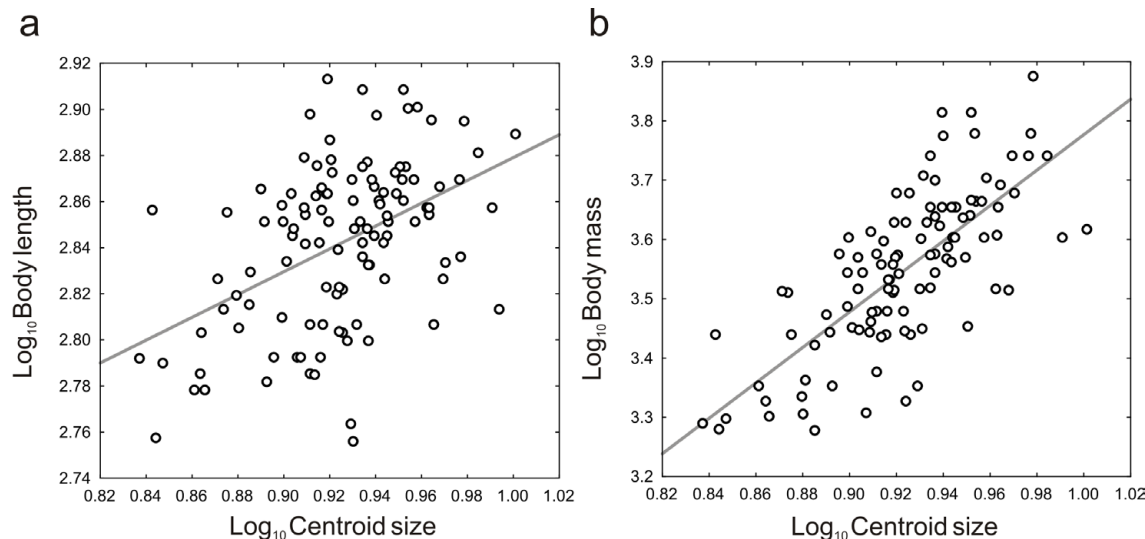


FIGURE 4. Linear regression of body length (A) and body mass (B) onto centroid size (all variables \log_{10} transformed) in *Capromys pilorides*.

FIGURA 4. Regresión lineal entre la longitud del cuerpo (a) y la masa corporal (b) sobre el tamaño del centroide (todas las variables transformadas a \log_{10}) en *Capromys pilorides*.

\log_{10} transformed centroids were highly correlated with \log_{10} body length ($F_{1,111} = 30.3$, $p < 0.0001$) and \log_{10} body mass ($F_{1,106} = 126.5$, $p < 0.0001$). Centroid size explained only 21 % of body length variance, but explained 54 % of body mass variance (Fig. 4). The test for homogeneity of slopes using sexes as a predictor was not significant (body length: $F_{1,109} = 0.263$, $p = 0.61$; body mass: $F_{1,104} = 0.87$, $p = 0.35$), suggesting similar linear trends in mandible size between sexes for both variables.

The results of the multivariate analysis of variance are shown in Table 3. Mandibular shape differed significantly between sexes and localities. As with size, populations of *C. pilorides* in western Cuba and Zapata Swamp had the most pronounced sexual dimorphism in shape; Mahalanobis distances between sexes were only significant in these populations ($p < 0.02$). After size-related shape differences were removed using a multivariate analysis of covariance with \log_{10} centroid size as a covariate, shape remained significantly different between localities, but the sexual dimorphism was no statistically significant (Table 3).

SIZE AND SHAPE VARIATION AMONG POPULATIONS

The ANOVA of \log_{10} centroid size showed that subspecies-level or population-level differences are highly

significant ($F_{6,181} = 11.7$, $p < 0.0001$). The results of post hoc tests showed that the western and central populations of *Capromys p. pilorides* and *Capromys p. ciprianoi* are significantly ($p < 0.0001$) larger than *C. p. doceleguas*, *C. p. gundlachianus* and *C. p. pilorides* from Zapata Swamp (Fig. 5). Because shape variation did not show marked sexual dimorphism compared with variation between populations, the DA was performed with pooled sexes.

The difference in mandible shape between populations was highly significant (Wilks' Lambda = 0.105, $F_{90,945.7} = 4.96$, $p < 0.00001$). Many pairwise comparisons of squared Mahalanobis distances were significantly different ($p < 0.0001$) (Table 4). According to the Neighbour-joining tree, based on pairwise Euclidian distances, two main phenetic clusters are observed (Fig. 6); one comprising *C. p. doceleguas* and *C. p. gundlachianus*, and the other comprising the remaining subspecies and populations. In the latter cluster, the sample from Zapata Swamp shows higher morphological similarity with those of *C. p. pilorides* from Isla de la Juventud than with those of *C. p. pilorides*. The two subspecies found on Isla de la Juventud (*C. p. relictus* and *C. p. ciprianoi*) showed the highest morphological similarity among all samples. However, the Mantel test did not show a statistically significant correlation between

TABLE 3. Multivariate analysis of variance of sex x locality for mandible shape in four populations of *Capromys pilorides*. The dependent variables were the first ten relative warps (including uniform and non-uniform components) that represented 90% of total shape variation.

TABLA 3. Análisis de varianza múltiple de dos factores (sexo y localidad) para la forma de la mandíbula en cuatro poblaciones de *Capromys pilorides*. Las variables dependientes fueron los primeros diez componentes principales "relative warps" (incluyendo los componentes uniformes y no uniformes) que representan 90 % de la variación total de la forma.

Effect	MANOVA				MANCOVA (\log_{10} CS as covariate)			
	Wilks' λ	F	df	P	Wilks' λ	F	df	P
Sex	0.864	2.004	10,128	0.0379	0.888	1.591	10,127	0.1162
Locality	0.294	6.484	30,376.4	< 0.00001	0.319	5.915	30,373.4	< 0.00001
Sex x Locality	0.665	1.864	30,376.4	0.0045	0.664	1.859	30,373.4	0.0047

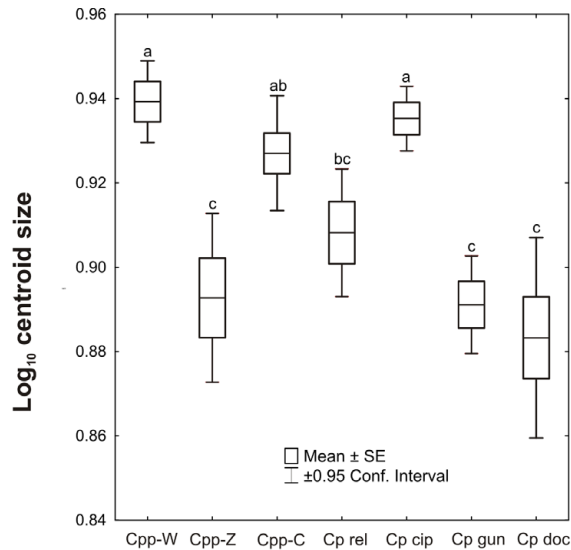


FIGURE 5. Box plots of centroid size (data log-transformed) for seven populations (sexes pooled) of *Capromys pilorides* (see Materials and Methods for acronyms); same letters indicate that mean not are significantly different from each other (Tukey test, $p < 0.05$).

FIGURA 5. Gráfico de caja del tamaño del centroide (datos transformados en \log_{10}) para siete poblaciones (sexos combinados) de *Capromys pilorides* (ver Materiales y Métodos para acrónimos y tamaño de muestra); letras iguales significa que las medias no difieren significativamente (prueba de Tukey, $p < 0,05$).

morphological and minimal geographic distances among samples ($r = -0.19$, $p = 0.78$).

The linear regression of shape variables onto \log_{10} centroid size was highly significant (Wilks' Lambda = 0.559, $F_{24,1163} = 5.34$, $p < 0.0001$), although only 2.7 % of the mandible shape variation was related to size changes. In a test of homogeneity of slopes, the interaction between centroid size and locality was significant (Wilks' Lambda = 0.304, $F_{144,890.3} = 1.394$, $p = 0.003$), suggesting different allometric trends among populations.

The first two CVs account for 67.7 % of all variance (CV1 = 43.9 %, CV2 = 23.8 %). CV1 is significantly correlated

with size ($F_{1,186} = 4.87$; $p < 0.02$), but size explains less than 3 % of the variation along this component. CV2 also is correlated with size ($F_{1,186} = 27.15$; $p < 0.0001$) and size explains 12.7% of the variation along this component. Shape changes occurring along CV1 and CV2 are illustrated with TPS grids obtained by regressing shape variables onto the first two canonical axes (Fig. 7). We observed a large overlap among samples (Fig. 7). The most important shape deformations associated with the highest values of CV1 are a markedly narrower mandible, long condylar process, and short coronoid processes (individuals from Isla de la Juventud and Zapata Swamp); samples with negative scores have a high horizontal ramus, short condylar process, and long and wide coronoid and angular processes. CV2 describes more localized effects, such as the forward or backward movement of the coronoid and condilar processes and the compression of the horizontal ramus or alveolar region; this axis separates individuals from *C. p. doceleguas* and *C. p. gundlachianus* from the rest of the samples.

DISCUSSION

The present study shows that mandible morphology in *Capromys pilorides* is highly variable in size and shape across the Cuban archipelago. As with other mammal species (Cardini, 2003; Frost *et al.*, 2003), we found a strongly positive relationship between mandibular centroid size and body mass and length; this geometric variable can therefore be used as an accurate indicator of these two measures of body size. Morphological variation between populations of this species has been observed in previous studies (Berovides *et al.*, 1990a; Borroto *et al.*, 1992; Silva *et al.*, 2007), and could reflect adaptations to different local environments and biotic factors (Berovides *et al.*, 1990b; Ricklefs and Miles, 1994). Other studies have also shown the presence of population-level differentiation in size and shape of the skull and mandible in other rodents (e.g. Renaud and Millien, 2001; dos Reis *et al.*, 2002; Cardini, 2003; Lalis *et al.*, 2009). In particular, the western population of *C. p. pilorides* and *C. p. ciprianoi* (from the south of Isla de la Juventud) are conspicuously larger than *C. p. doceleguas* and *C. p. gundlachianus*, which are both restricted to small mangrove keys off the coast of the main island of Cuba. Terrestrial habits in some populations of

TABLE 4. Matrix for pairwise comparisons of mandible shape in populations of *Capromys pilorides* (see Materials and Methods for acronyms). Values above the diagonal correspond to squared Mahalanobis distances; values under the diagonal are p values (determined by the sequential Bonferroni procedure), significant results are in bold.

TABLA 4. Matriz de comparaciones pareadas de la forma de la mandíbula en poblaciones de *Capromys pilorides*. Los valores por encima de la diagonal corresponden a la distancia de Mahalanobis y por debajo la significación (corregida por el método de Bonferroni); las comparaciones significativas se indican en negritas.

	Cpp-W	Cpp-Z	Cpp-C	Cp cip	Cp rel	Cp gun	Cp doc
Cpp-W	0	12.230	2.599	7.785	6.733	10.225	14.947
Cpp-Z	< 0.0001	0	8.963	7.610	5.662	9.635	20.077
Cpp-C	0.0316	0.0022	0	6.293	4.955	6.835	11.800
Cp cip	< 0.0001	0.0041	< 0.0001	0	1.226	6.857	18.417
Cp rel	< 0.0001	0.0107	0.0038	0.2804	0	4.732	13.191
Cp gun	< 0.0001	0.0087	0.0081	< 0.0001	0.0222	0	12.330
Cp doc	0.0002	0.1052	0.0853	< 0.0001	0.0171	0.2344	0

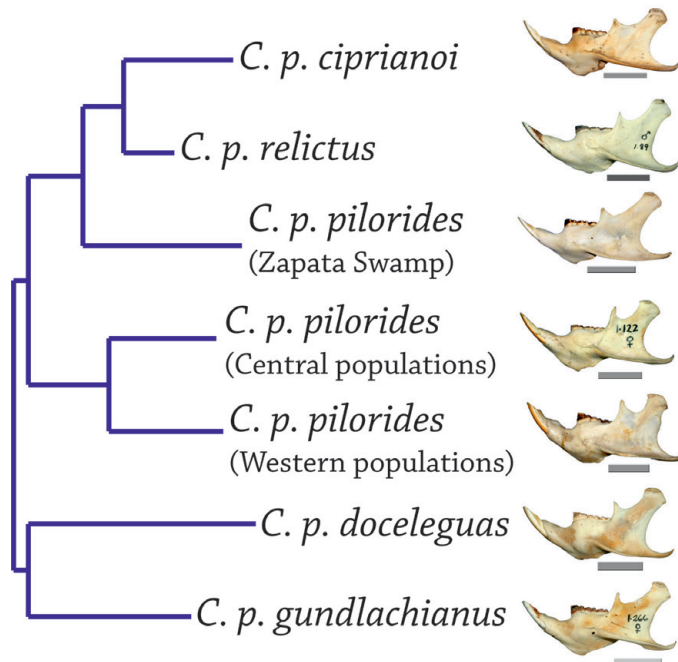


FIGURE 6. Dendrograms showing similarities of mean shape of labial side of the mandible for populations of *Capromys pilorides*. The populations were clustered using a Neighbour-joining tree computed on the matrix of Euclidian distances obtained from PCA on shape variables. The pictures show mandibular shapes for each subspecies or population. Scale bar = 20 mm.

FIGURA 6. Dendrograma mostrando la similitud en la forma de la mandíbula en vista labial de poblaciones de *Capromys pilorides*. Las poblaciones o subespecies se agruparon por el método de Neighbour-joining tree sobre la matriz de distancia euclidiana obtenida del análisis de componentes principales de las variables de forma. Se muestran las formas mandibulares de cada una de las subespecies o poblaciones; la barra de escala = 20 mm.

C. p. pilorides and *C. p. ciprianoi* (Borrito-Páez *et al.*, 1992; Silva *et al.*, 2007), as well as a higher abundance of food resources on the largest Cuban islands, may have promoted larger body sizes in these populations (Berovides *et al.*, 1990b).

Male mandibles are larger than those of females in all analyzed populations. This result contrasts with previous studies using traditional morphometric approaches that have found little evidence of sexual size dimorphism in hutias (for review see Silva *et al.*, 2007). This discrepancy probably results from the higher resolution of geometric over traditional morphometric methods to detect differences between sexes (Hood, 2000). Geographic variation in degree of sexual dimorphism was not uniform across the distributional range of this species. We observed marked size dimorphism in the western populations of *C. p. pilorides* and in *C. p. ciprianoi*, although these significant differences in both populations could be related to the fact that these populations had the largest sample sizes. The male-biased sexual size dimorphism detected at all localities suggests that similar selection pressures are acting to a greater or lesser degree across the range of the species or that sexual dimorphism represents an

ancestral characteristic for the species. The differences in mandible size and shape in *C. pilorides* seem to be related to growth patterns (Isaac, 2005) or behavioural differences between sexes. Resource partitioning between sexes could be higher in seasonal and terrestrial habitats (e.g. in semideciduous forests) than in arboreal habitats (e.g. mangrove forests) where food availability is more homogenous around the year (Silva *et al.*, 2007). Berovides *et al.* (1990a) found that morphometric differences between sexes in hutias are strongly related to degree of arboreality, whereas differences in mass and body size are greater in terrestrial than in arboreal populations.

As with size, mandible shape shows significant variation between sexes and populations, although sexual dimorphism in mandible shape was small compared with inter-population differences. Similar allometric relationships between mandible shape and size were observed in all populations, and only 3% of shape variation in the sample was explained by size changes. Two extreme shape morphotypes can be observed associated with general robustness of the mandible, corresponding to populations from small keys (*C. p. gundlachianus* and *C. p. doceleguas*), which have a short coronoid process, a long condylar process and a narrow horizontal ramus, and to populations from the main island, which have a long coronoid and angular process, a short and robust condylar process, and a broad horizontal ramus.

Differentiation in mandible shape is seen between most of populations of *C. pilorides*. However, patterns of

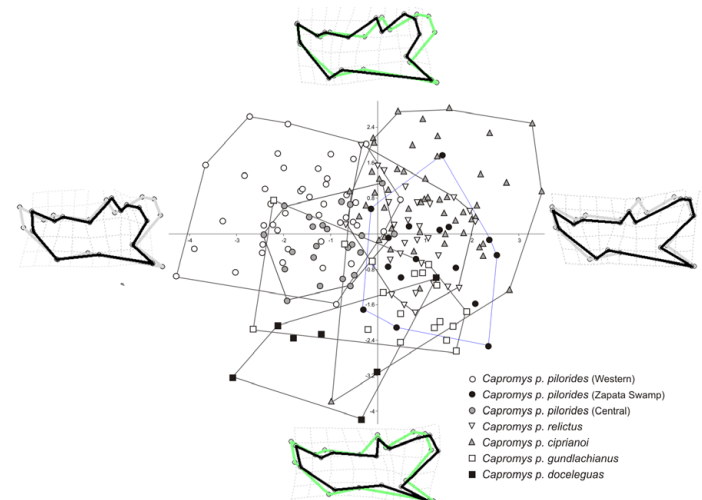


FIGURE 7. Ordination of seven populations of *Capromys pilorides* in the morphospace of the first two canonical axes. The TPS deformation grids show the shape changes at the extremes of both CV axes (the consensus shape is represented by the grey outline); the effects on the grids were amplified by a factor of three to help visualize the shape changes.

FIGURA 7. Ordenación de las siete poblaciones de *Capromys pilorides* en el morfoespacio de los dos primeros ejes canónicos. Las rejillas de deformación muestran los cambios de forma en los extremos de ambos ejes (la forma consenso se muestra en gris); los efectos en las rejillas fueron amplificados por un factor de tres para ayudar a visualizar los cambios de forma.

relationships of similarity between populations and subspecies are not related to geographic proximity. Our results suggest that mandible size and shape in *C. pilorides* could instead be related to morpho-functional modifications associated with different ecological niches. The morphological similarity in mandible shape shown by *C. p. doceleguas* and *C. p. gundlachianus*, which represent isolated populations on small keys off the main island of Cuba, could be evidence of convergent adaptive modifications for exploiting similar habitats, as both subspecies are largely arboreal and feed almost exclusively on mangrove leaves.

Changes of the angle and height of the mandibular process in *C. pilorides* may be related to variation in jaw musculature, and so to variation in mandible movement and muscle force during mastication (Woods and Howland, 1979; Atchley and Hall, 1991). The longer coronoid process and more robust mandible seen in populations of *C. p. pilorides* (excluding the sample from Zapata Swamp) could be associated with an omnivorous diet not seen in hutias that inhabit mangroves (Silva *et al.*, 2007; Borroto-Páez, 2011). Similarly, Monteiro *et al.* (2003) found relatively longer coronoid and angular processes in populations of the echimyid rodent *Thrichomys* occurring in xeric environments, where seeds may have tougher coats. However, some studies suggest that craniomandibular morphological variation in rodents may be more related to habit than to masticatory strategies (Olivares *et al.*, 2004). Hautier *et al.* (2011) found a significant morphological differentiation of the mandible between hystricognathous rodents that are characterized by distinct diets or habitats, with those species living in open areas and feeding on grass having more slender mandibles than those with different ecologies.

Our results support most of the previously recognized subspecific designations in *C. pilorides*. However, the Zapata Swamp population displays unexpected patterns of morphological variation. A highly significant pairwise mean shape difference was found between the Zapata Swamp and other mainland populations of *C. p. pilorides*. The Zapata Swamp population is morphologically nearest to the populations from Isla de la Juventud, and there was no significant shape difference between the Zapata population and *C. p. relictus* from the north of Isla de la Juventud. We suggest that this similarity may reflect a close evolutionary history between these populations. During the Pleistocene-Holocene marine transgression (Curtis *et al.*, 2001), the south-central coast of Cuba was connected to Isla de la Juventud by large areas of mangrove, which may have permitted dispersal of hutias from the main island to Isla de la Juventud. Changes in climate and sea level during the Pleistocene are known to have had a major influence on the distribution of terrestrial vertebrates across the West Indies (Pregill and Olson, 1981).

During their evolutionary history, hutias probably became reproductively isolated in Zapata Swamp and became adapted to the region's distinct and different ecological conditions (seasonally flooded landscapes). Because of its unique geological and biotic characteristics, Zapata's flora and fauna have high endemism, and it is among the most important biodiversity hotspots of the Cuban archipelago (Kirkconnell *et al.*, 2005). In contrast to other

populations of *C. p. pilorides*, the Zapata Swamp population is semi-arboreal and is associated with semi-deciduous and swamp forests that grow on soggy ground (Berovides *et al.*, 1990b). Because its mandible shape is markedly different from those of other populations of *C. p. pilorides*, the Zapata population may well represent an incipient stage in the process of adaptive radiation; future molecular studies will be necessary to assess the taxonomic status of this population.

We found that the two subspecies from Isla de la Juventud show the highest degree of mandible shape similarity among all populations studied. Morphological variation between the northern (*C. p. relictus*) and southern (*C. p. ciprianoi*) populations is effectively related to size. This size variation may be explained by changes in local food availability and habitats. *C. p. ciprianoi* is mainly terrestrial and associated with semi-deciduous forest, whereas *C. p. relictus*, possibly as a result of hunting, is restricted to marshy areas with more limited resources (Borroto *et al.*, 1992). Because of the geographical proximity and absence of effective dispersal barriers between these populations (which are only separated by Lanier Swamp), there may be ongoing gene flow between them. Indeed, our study support a previous genetic analysis of these populations, which documented only a very low degree of genetic divergence (< 0.5%) (Woods *et al.*, 2001). The existence of two subspecies of *C. pilorides* on Isla de la Juventud is therefore questionable.

Geometric morphometrics has been demonstrated to be a highly suitable tool for detecting and quantifying patterns of morphological variation between species and populations. Because it assesses information about spatial relationships between anatomical landmarks, it is more appropriate for analyzing morphometric variation than methods based on distance measurements (Rohlf, 2000; Barciová, 2009). Shape variation may also be used to estimate levels of genetic differentiation, as several studies on rodents have found concordance between morphometric and genetic data at lower taxonomic levels (Fadda and Corti, 2000; Nicola *et al.*, 2003; D'Ánatro and Lessa, 2006; Álvarez *et al.*, 2011). Due to a lack of extensive molecular studies of Cuban mammal species, geometric morphometric studies may therefore be able to provide meaningful information for assessing levels of intraspecific and interspecific variation between different taxa (Mancina and Balseiro, 2005), as well as exploring patterns of morphological differentiation across different geographical scales and ecological environments.

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APPENDIX 1

This provides locality information for all examined specimens of *Capromys pilorides*. Data include: locality number (see Fig. 1), collection locality name (obtained from collection tags), latitude and longitude (in parentheses; obtained from MapInfo version 10.0), collection catalogue number, and sex of specimen (? =unknown sex). All examined specimens are housed in the mammal collection of the Instituto de Ecología y Sistemática, La Habana, Cuba.

Capromys pilorides pilorides

WESTERN POPULATIONS: 1. El Veral (21°56'N, -84°44'W), 1.095, 1.103, 1.108, 1.109, 1.563 (2 females, 3 males); 2. La Palma (21°55'N, -84°43'W), 1.453, 1.454, 1.456 (3 males); 3. Península de Guanahacabibes (21°57'N, -84°35'W), 1.443, 1.444, 1.445, 1.460, 1.461, 1.464, 1.468, 1.469, 1.470, 1.471, 1.474, 1.475, 1.476 (7 females, 6 males); 4. Laguna Lugones

(21°56'N, -84°24'W), 1.098, 1.101, 1.106, 1.552, 1.555, 1.556 (3 females, 3 males); 5. Limón Chico, 10 km al Norte de La Bajada (21°58'N, -84°24'W), 1.565, 1.567 (1 female, 1 male).

ZAPATA SWAMP: 6. Cayo Corral, 10 km al Noroeste de Maneadero (22°25'N, -81°44'W), 1.353 (1 female); 7. Cayo Laguna del Palmar, 6 km al Oeste de Maneadero (22°23'N, -81°41'W), 1.357 (male); 8. Cayo Gervadero, 5 km al Oeste de Maneadero (22°24'N, -81°41'W), 1.355 (1 female); 9. Molina (22°17'N, -81°09'W), 1.506, 1.507, 1.509, 1.512, 1.529, 1.531, 1.533, 1.535 (1 female, 7 males); 10. Majagua (22°15'N, -81°06'W), 1.500, 1.502, 1.504, 1.505, 1.508, 1.510, 1.528 (5 females, 2 males).

CENTRAL POPULATIONS: 11. Yaguanabo (21°53'N, -80°11'W), 1.134, 1.135, 1.136, 1.138, 1.139, 1.140, 1.142, 1.143, 1.185, 1.186 (6 females, 4 males); 12. Macagua (22°09'N, -80°05'W), 1.513, 1.516, 1.561 (1 female, 2 males); 13. Itabo (21°56'N, -80°02'W), 1.122, 1.124, 1.244 (2 females, 1 male); 14. Arroyo Grande (21°55'N, -80°00'W), 1.112, 1.113, 1.115, 1.116, 1.117 (2 females, 3 males).

Capromys pilorides gundlachianus

ARCHIPIÉLAGO DE SABANA: 15. Cayo Macho (23° 10'N, -80° 59'W), 1.332 (?); 16. Cayo la Pluma (23° 14'N, -80° 55'W), 1.262, 1.264 (1 female, 1?); 17. Cayo Cinco Leguas (23° 07'N, -80° 54'W), 1.276, 1.277, 1.281, 1.285 (1 male, 3 ?); 18. Cayo Boca Rompía (23° 14'N, -80° 52'W), 1.329 (male); 19. Cayo Piñipiñi (23° 12'N, -80° 48'W), 1.265, 1.266, 1.269, 1.304, 1.328 (3 females, 2 males); 20. Cayo Punta Arenas (23° 12'N, -80° 44'W), 1.246 (male); 21. Cayo Fragoso (22° 42'N, -79° 27'W), 1.221, 1.306, 1.322 (?) (1 male, 2 ?); 22. Cayo Jutía (22° 57'N, -79° 50'W), 1.239 (male).

Capromys pilorides doceleguas

ARCHIPIÉLAGO JARDINES DE LA REINA: 23. Júcaro (21°38'N, -78°51'W), 1.292, 1.298, 1.300 (2 females, 1 male); 24. Cayo Anclitas (20°46'N, -78°54'W), 1.241 (female); 25. Cayo Juan Grin (20°37'N, -78°33'W), 1.273, (1 male); 26. Cayo Caguama (20°33'N, -78°23'W), 1.340 (?); 27. Cayo Cabeza del Este (20°33'N, -78°20'W), 1.295 (1 male).

Capromys pilorides relictus

NORTE DE LA ISLA DE LA JUVENTUD: 28. Estero del Soldado (21°46'N, -83°02'W), 1.537, 1.541, 1.542, 1.543, 1.545, 1.546, 1.547, 1.548 (5 females, 3 males); 29. Laguna del Capitán (21°52'N, -83°01'W), 1.082 (female); w/n. Cayo los Monos, 1.081, 1.085, 1.086, 1.087 (2 females, 2 males); w/n. Loma Siberia, 1.064, 1.065, 1.066 (2 female, 1 male); w/n. Pica Pica, 1.072, 1.073, 1.074, 1.075, 1.076, 1.078, 1.079, 1.083 (3 females, 4 males); w/n. Punta la Gorda, 1.088, 1.089, 1.090 (1 female, 2 males).

Capromys pilorides ciprianoi

SUR DE LA ISLA DE LA JUVENTUD: 30. Hato de Milián (21°33'N, -83°07'W), 1.020, 1.031, 1.058 (2 females, 1 male); 31. Cabo Pepe, Cocodrilo (21°28'N, -83°04'W), 1.046, 1.047, 1.053, 1.054, 1.055, 1.057 (3 females, 2 males); 32.

Estero las Piedras (21°34'N, -82°56'W), 1.019, 1.022, 1.023, 1.026, 1.027, 1.028, 1.029, 1.032, 1.033 (3 females, 6 males); 33. Rincón del Guanál (21°28'N, -82°47'W), 1.006, 1.008, 1.009, 1.010, 1.017, 1.030, 1.034, 1.036, 1.037, 1.039, 1.041, 1.048, 1.050, 1.051, 1.056, 1.060, 1.062, 1.318 (13 females, 5 males); 34. Punta del Este (21°33'N, -82°33'W), 1.520, 1.521, 1.522, 1.524, 1.525 (5 females); w/n. Rancho Castor, 1.011, 1.012, 1.014, 1.015, 1.016 (4 females, 1 male); w/n. Sur de Isla de la Juventud (21°31'N, -82°37'W), 1.002, 1.247, 1.327 (2 females, 1 male).