

**REASSESSMENT OF THE TAXONOMIC STATUS  
OF THE COTTON MOUSE  
(*Peromyscus gossypinus anastasae*)  
ON CUMBERLAND ISLAND, GEORGIA,  
AND IMPLICATIONS OF THIS INFORMATION  
FOR CONSERVATION.**

*CPSU Technical Report No. 60*

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Cooperative Studies Unit  
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CONSERVATION

by

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B.S., Humboldt State University, 1986

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**DEDICATION**

For my loving wife,  
Liz LaRue,  
who made this all possible.

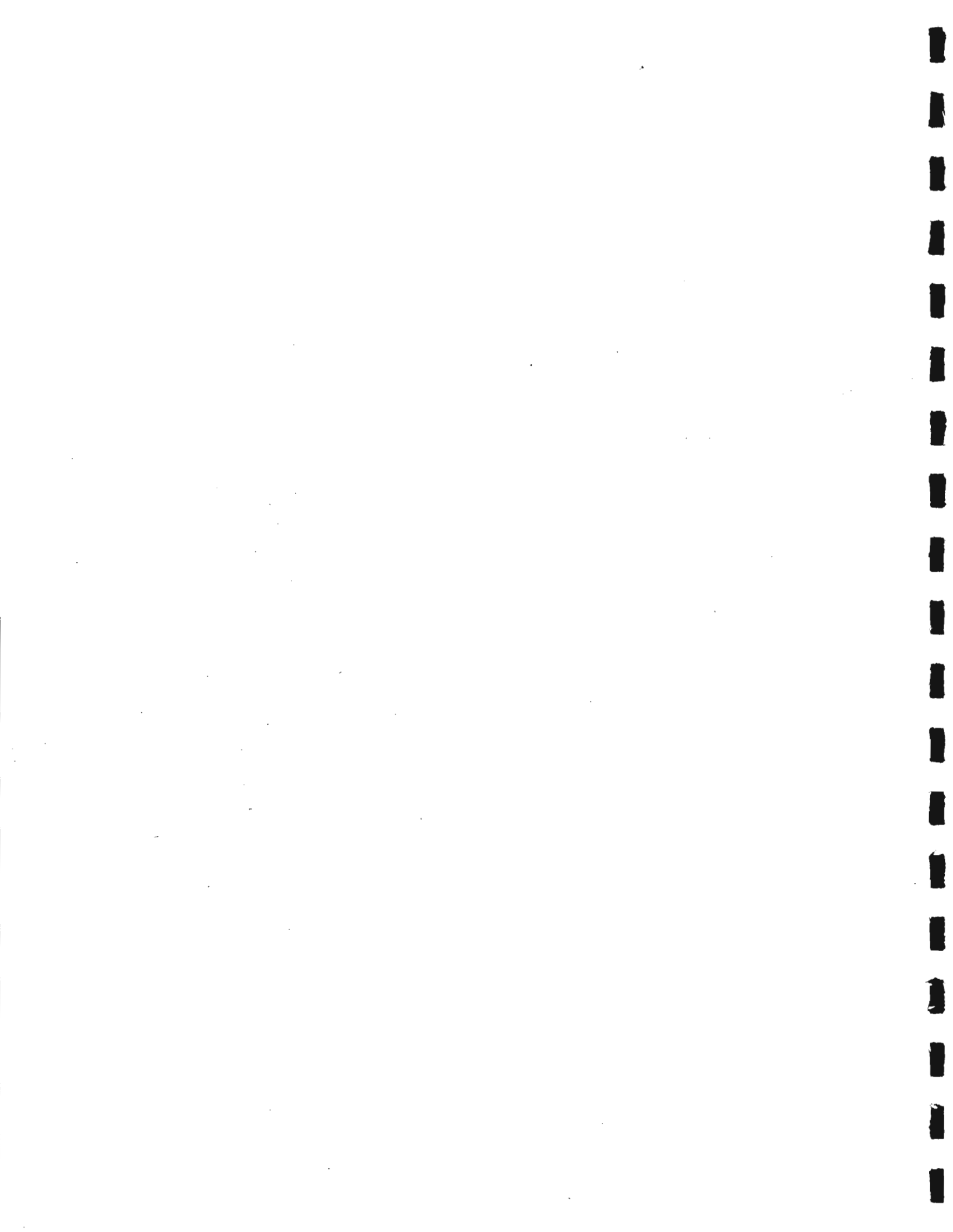


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This project has been a collaborative effort of many people and organizations, and I wish to thank them all. In particular, I wish to thank Dr. David Webster and Dr. Susan Bratton for inspiring me to return to graduate school to work on an island-evolution-conservation question. Many thanks are due to my committee, Drs. Michael Smith, Joshua Laerm, and Walter Cook for ideas, direction, and assistance.

Several organizations contributed financial and logistical support to this project. I thank the Savannah River Ecology Laboratory for supporting the genetic analysis under contract DE-AC09-76SR00819 between the U. S. Department of Energy and the University of Georgia's Institute of Ecology. I also thank the University of Georgia Museum of Natural History, the National Park Service at Cumberland Island National Seashore, the National Park Service's Cooperative Park Studies Unit at the University of Georgia, the University of Georgia School of Forest Resources, and the Little Cumberland Island Association.

For personal assistance, I thank Dr. Joshua Laerm, Liz McGhee, and the many University of Georgia students who assisted in collection and preparation of specimens, in particular, Bruce Humphries, Todd Kunts, Mike Vines, and Brad Wilson. Thanks to Dr. Jim Oliver and his graduate student, Joel Hutcheson, for providing specimens from Merritt Island, Florida. Many thanks to Michael H. Smith and Paul Johns for access to, and assistance in, their electrophoretic laboratory. I thank Dr. Joshua Laerm for the monumental efforts in making all morphological measurements. I thank the many private landowners who allowed me to trap on their property, especially the Jekyll Island Authority and the



Little Cumberland Island Association. I also appreciate the assistance extended by curatorial staffs of the following museums: American Museum of Natural History (AMNH), Academy of Natural Sciences, Philadelphia (ANSP), Charleston Museum (CH), Carnegie Museum of Natural History (CMNH), Delaware Museum of Natural History (DMNH), Field Museum of Natural History (FMNH), Florida Museum of Natural History (UF), Joseph Moore Museum (JMM), University of Kansas Museum of Natural History (KU), Louisiana State University Museum of Zoology (LSUMZ), Harvard University Museum of Comparative Zoology (MCZ), University of Alabama Museum of Natural History (UAL), University of Georgia Museum of Natural History (UGAMNH), University of Illinois Museum of Natural History (UI), and the United States National Museum (USNM).

Most of all, I thank my loving wife, Liz LaRue, for making this endeavor possible in so many ways, not the least of which was entering tens of thousands of morphometric data points into the computer.



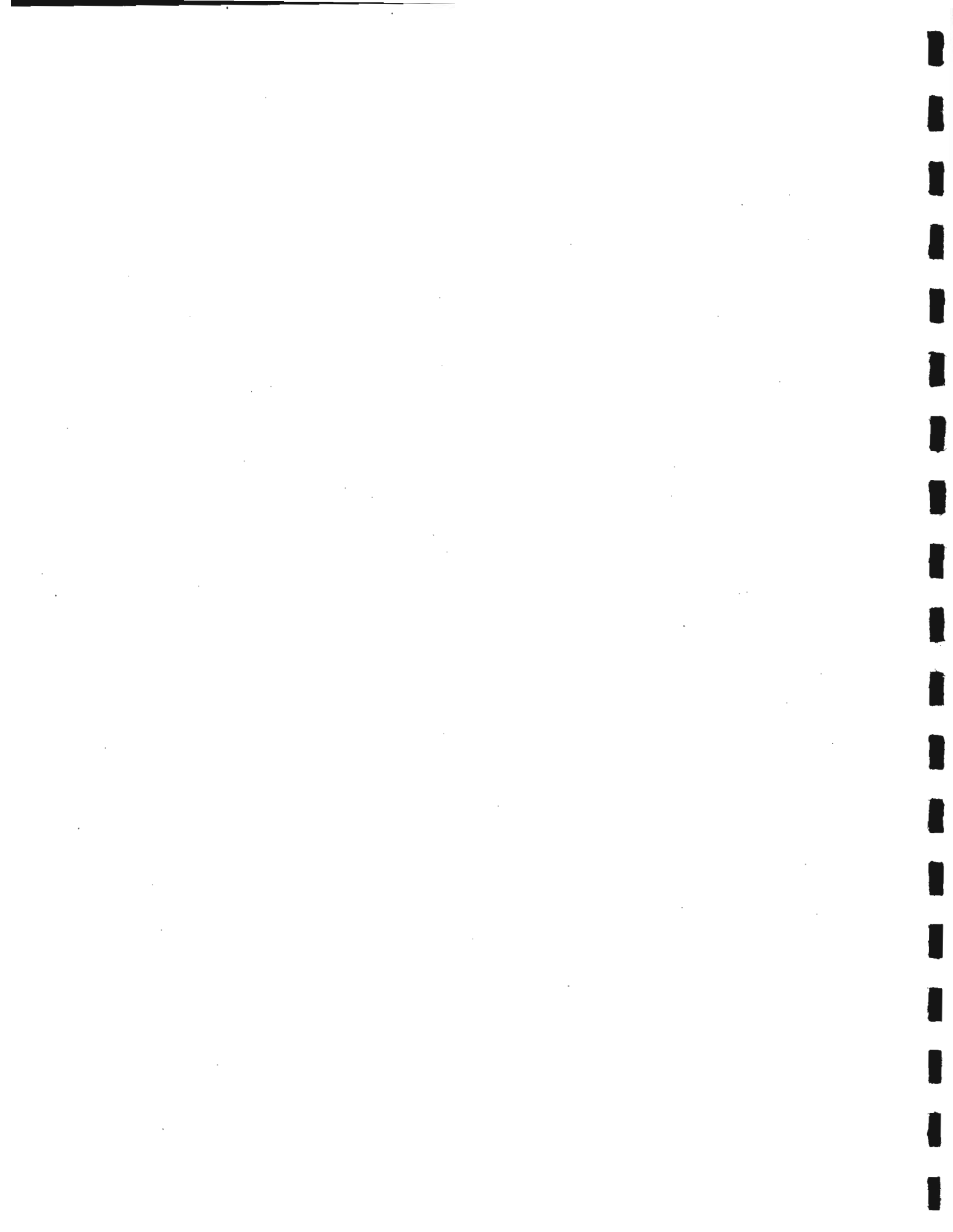


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Reassessment of the Taxonomic Status of the Cotton Mouse  
(*Peromyscus gossypinus anastasae*)  
on Cumberland Island, Georgia,  
and Implications of this Information for Conservation<sup>1</sup>

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<sup>1</sup>Boone, J. L., J. Laerm, and M. H. Smith. 1990. To be submitted to the Journal of Mammalogy.

### ABSTRACT

Four subspecies of cotton mice (*Peromyscus gossypinus gossypinus*, *P. g. megacephalus*, *P. g. palmarius*, and *P. g. anastasae*) were examined for genetic (14 populations,  $n = 379$ , no. loci = 44) and morphological variation (20 populations,  $n = 683$ , no. characters = 27) to assess the taxonomic validity of *P. g. anastasae* and the affinities of *P. gossypinus* on Cumberland Island.

This species is highly variable within and among populations. Polymorphic loci and heterozygosity per population averaged 40% and 10%, respectively. There was no reduction of genetic variability on the islands, but island mice were generally smaller than mainland mice. Genetic similarity among populations, averaging 0.915, was relatively low for conspecific populations.

Essentially every population was significantly different, genetically and morphologically, from all others when tested in pairwise comparisons. When all of the populations were examined simultaneously, the pairwise interpopulation differences became trivial and were not significant.

While each population was unique, no population was unusually distinct, and neither the Cumberland Island nor Amelia Island populations of *P. g. anastasae* were sufficiently different from other populations to warrant recognition as separate subspecies, and should be designated *P. g. gossypinus*. Despite this, the Cumberland Island and other populations continue to represent unique genetic stocks that deserve further study and conservation. The implications for the management and conservation of these mice are discussed.

### INTRODUCTION

In 1898, Outram Bangs described *Peromyscus insulanus* from Cumberland Island, Georgia, based on its relatively small size, short tail, large hind foot, and light color. Bangs (1898) also described *P. anastasae* from Anastasia Island, Florida, based on its

small size and light colored pelage. Osgood (1909) synonymized *P. insulanus* with *P. anastasae*, a form that it was "absolutely alike", and reduced *P. anastasae* to a subspecies of *P. gossypinus*. Osgood (1909) described *P. g. anastasae* as being about the same size as other Florida *P. gossypinus*, but with paler pelage. Since then, *P. g. anastasae* has become extinct on Anastasia Island, its type locality, and the last known specimen was collected by Surber in 1901 (Elliott, 1901). This leaves Cumberland and Little Cumberland Islands with the only extant populations (Neuhauser, 1979; Pournelle and Barrington, 1953).

Between 1980 and 1987 alone, over 1500 papers were published on members of the genus *Peromyscus* (Butler, 1987). The genus has been the focus of considerable systematic and distributional research (Avisé et al., 1974, 1979; Greenbaum and Baker, 1978; Greenbaum et al., 1978; Hooper, 1968; Osgood, 1909; Price and Kennedy, 1980; Selander et al., 1971; Smith et al., 1973; Stangle and Baker, 1984; Zimmerman et al., 1978), and the results are summarized in Hall and Kelson (1959) and Hall (1981). Several authors have examined the systematic relationships between *P. gossypinus* and other *Peromyscus* species (Avisé et al., 1979; Dice, 1937, 1940; Price and Kennedy, 1980; Robbins et al., 1985), but the only systematic studies within *P. gossypinus* since Osgood (1909) are those of Howell (1939) and Schwartz (1952) describing three new subspecies of *P. gossypinus* from South Florida based largely on pelage color.

No revisionary work has been conducted on this species since Osgood (1909), despite unresolved questions raised by Osgood himself about the validity of *P. g. anastasae* because they...

"are not different from certain aberrant (intermediate?) specimens from the mainland. Moreover, the mainland specimens most similar to them are not from localities immediately adjacent to the islands in question, specimens from St. Mary's, Ga., and Brunside, Fla., etc., being typical *gossypinus*" (Osgood, 1909, p. 141),

where "typical *gossypinus*" refers to *P. g. gossypinus*. Others have also questioned the validity of this subspecies (Neuhauser, 1979; Laerm, 1981a). However, hypotheses based on island biogeography (MacArthur and Wilson, 1967), sea level changes and island formation (Cooke, 1939, 1945; Hoffmeister, 1974), evidence of differentiation in coastal and insular populations of old-field mice (*P. polionotus*) in Georgia and Florida (Selander et al., 1971), ecological differences between islands and the mainland (Blair, 1950), and the possibility of repeated population bottlenecks, genetic drift, and selection suggest that this mouse could be distinct at the subspecies level, and possibly at the species level.

The limited distribution and uncertain population size of *P. g. anastasae* on Anastasia Island in the 1970's lead to the consideration of this population for protection under the Florida endangered species program, but its legal status was listed as "undetermined" because of uncertain taxonomy (Neuhauser, 1979). The Anastasia Island population was also considered for protection under the Federal Endangered Species Act of 1973. However, because of pervasive evidence of extinction on Anastasia Island, it was not protected and is no longer under consideration for protection. This subspecies has not been considered for legal protection in Georgia, but its entire remaining range is protected under the jurisdiction of the U. S. National Park Service on Cumberland and Little Cumberland Islands. If, in fact, the population on Cumberland Island represents the sole remaining population of *P. g. anastasae*, it would warrant protection.

Because of the National Park Service's changing management practices on Cumberland Island National Seashore and potential legal requirements under the Federal Endangered Species Act, resource managers charged with preserving the Cumberland Island ecosystem need to know if this mouse is distinct so that it can be managed appropriately. Additionally, authorized and unauthorized reintroductions of Cumberland Island mice onto Anastasia Island have been considered, but reintroductions have been discouraged due to the uncertain systematic affinities between the two insular forms (Neuhauser, 1979).



The primary purpose of this study is to assess the taxonomic validity of the cotton mouse population on Cumberland Island, Georgia. To do this, the Cumberland Island population will be compared, genetically and morphometrically, to other island and mainland populations throughout Georgia, Florida, and Alabama to test the hypothesis that the Cumberland Island population is different from other populations of *P. gossypinus*. In addition, this study examines, through morphometric analysis, the validity of the population on Anastasia Island, by testing the hypothesis that the subspecies *P. g. anastasiae*, itself, is different from other subspecies. Finally, hypotheses concerning whether this potential distinctiveness is due to general differences between island and mainland populations will be tested using the genetic and morphometric sets.

## METHODS

### *Sampling Methods*

*Collection sites.*—Sample sites were selected to compare insular populations with mainland populations opposite those islands, and to assess the degree of regional variation among populations within the species. Fourteen samples from six islands and eight mainland sites were collected for the genetic analyses (Fig. 1). Islands included in this study are typical barrier islands of the U. S. southeastern coasts. All support old-growth oak-palmetto (*Quercus* sp. and *Serenoa repens*) forests, the apparent preferred habitat of the insular cotton mouse populations. These islands are separated from the mainland by 10 to 12 km of tidal salt marshes and open water. Minimum widths of open water are a few hundred meters, the narrowest being approximately 0.25 km, the width of the intercoastal waterway. Amelia, Jekyll, St. Simons, and Merritt Islands are connected to the mainland by highway bridges. Island sizes, estimated by maximum dimensions, are approximately: Merritt, 29 by 12 km; Amelia, 21 by 5 km; Cumberland, 25 by 9 km; Jekyll, 12 by 3 km; St. Simons, 18 by 10 km; and Sapelo, 17 by 5 km. Portions of the islands date to 25,000 - 50,000 years before present, although receding seas during the late Pleistocene connected

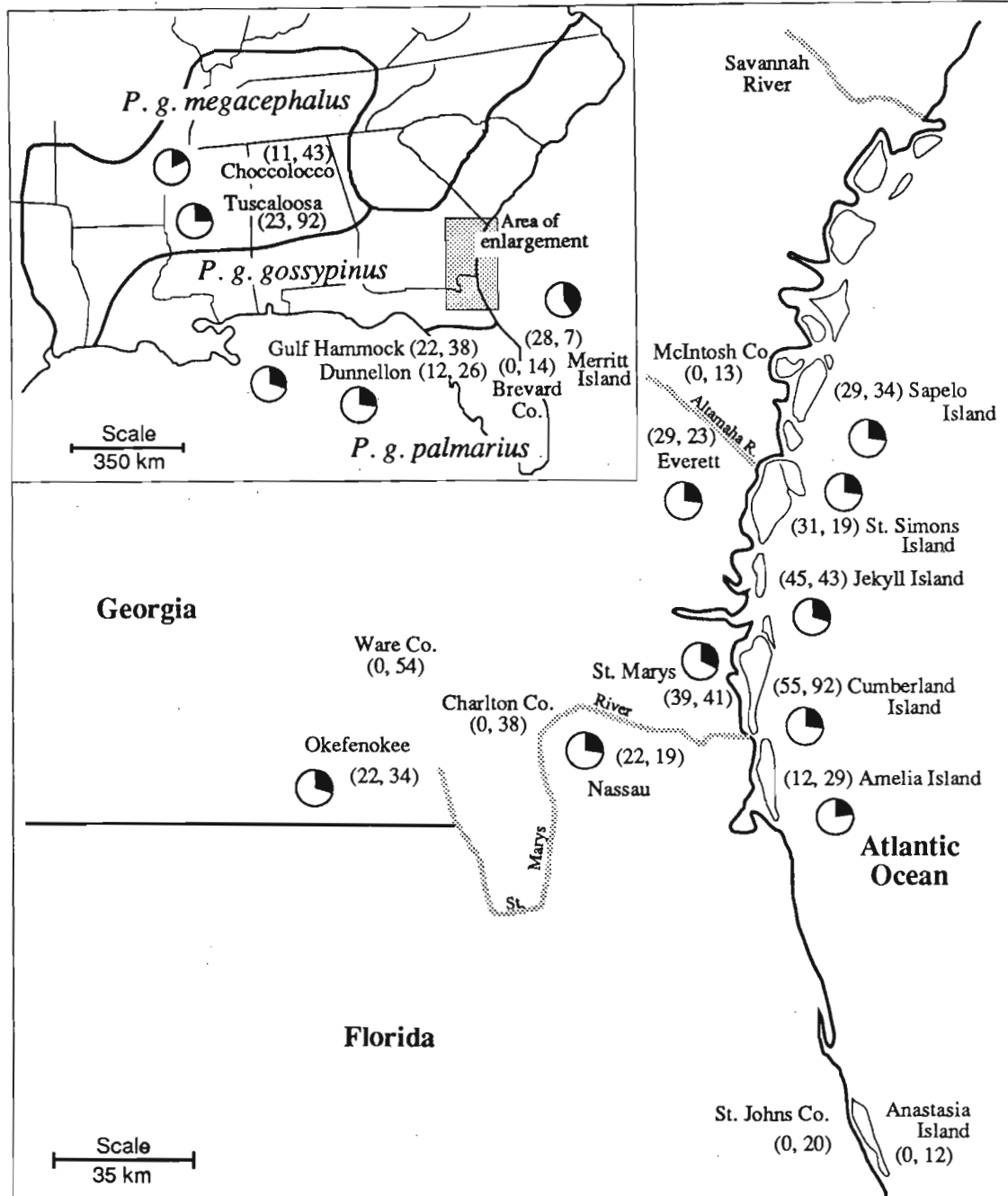


Fig. 1. Southeastern United States (inset) showing range and principle subspecies boundaries of *Peromyscus gossypinus*. Sample sites are indicated by the placement of sample sizes (genetic, morphometric). For the sites from which genetic data were collected, pie diagrams show the percentage of polymorphic loci within each population.

the islands with the mainland for long periods of time. The most recent rise in sea levels is thought to have isolated the islands 5,000-7,000 years ago (Hillestad et al., 1975; Laerm, 1981b).

Each island was assumed to contain a single panmictic breeding unit, and insular mice were collected from as wide an area as possible on each island. Individual collection sites (i.e. specific trap lines) on each island were generally less than 10 km apart. Within each mainland collection area, distances between individual trap lines were generally comparable with the distances between island trap lines. Mainland mice were collected from as small an area as possible to minimize Wahlund effects, that is, to reduce the possibility of inadvertently sampling more than one gene pool and increasing within-population genetic variance (Hartl and Clark, 1989). The Dunnellon sample had the greatest distances between trap sites, with a maximum distance of approximately 25 km. (Appendix 1). The Alabama *P. g. megacephalus* and Florida *P. g. palmarius* populations were included as outgroups.

Museum specimens from six populations were included in the morphometric analysis that were not included in the genetic analysis (Fig. 1). Except as noted, specimens used for morphometric analysis were grouped by county to form populations or operational taxonomic units. The population designated Choccolocco included specimens from DeKalb, Jackson, and Marshall Counties, Alabama, and the population designated Dunnellon included specimens from Citrus, Marion, and Sumter Counties, Florida. Specimens from Anastasia Island were included to assess the taxonomic validity of the subspecies *P. g. anastasiae* itself, not simply an assessment of whether the Cumberland Island population was a member of that subspecies.

*Collection of individuals.*—Determination of the appropriate sample size for genetic surveys has been examined by Sarich (1977), Nei (1978), and Gorman and Renzi (1979). They suggest that when a species has a low degree of heterozygosity, few individuals per population are needed for accurate estimates of heterozygosity and genetic distance if many

loci are examined. Pooling these three papers, it appears that samples of 12 or more individuals per population and 50 or more loci should provide very good estimates of genomic level heterozygosity and genetic distances. Using few individuals is acceptable for heterozygosity estimates because rare alleles have little effect on this estimate (Gorman and Renzi, 1979). Very accurate estimates of allele frequencies, however, require 50 or more individuals (Nei, 1978).

Price and Kennedy (1980) found a heterozygosity value of 0.029 in *P. gossypinus*. Relative to other mammals, this value was low (Awise and Aquadro, 1982). However, Robbins et al. (1985) found a more typical mammalian value of 0.05. As a consequence of these heterozygosity values, a conservative approach was taken in determining the number of mice to collect per population. Samples of greater than 25 individuals per population, twice the minimum number of 12, were considered adequate. In two cases, Amelia Island and Choccolocco Game Management Area, fewer than this number were collected. Sample sizes for morphological analysis were the maximum number obtainable. Sample sizes are given in Figure 1, and specimens examined for genetic and morphometric analyses are listed in Appendices 2 and 3, respectively (more detailed collection information for the genetic specimens is listed in Appendix 1).

Mice were caught between March 1988 and June 1989 using Sherman box traps baited with oats. Typically, 400 traps per night were placed in groups of 25 or 50 in preferred habitat, old-growth oak-palmetto on islands and bottomland hardwoods on the mainland. A sufficient number of mice generally collected in 600 - 1000 trap-nights.

*Tissue collection.*—Mice were removed from traps each morning, and tissues were typically taken the same day. Mice were euthanized, and blood, liver, and muscle were immediately collected. Blood, collected in heparinized micro-hematocrits, was immediately centrifuged, and the plasma and red blood cell portions were stored separately, using techniques similar to Selander et al. (1971). Liver and abdominal muscle were stored together.

Samples were frozen in liquid nitrogen or dry ice prior to storage at  $-70^{\circ}\text{C}$ . Carcasses were saved to supplement the museum specimens used in the morphological analysis.

### *Genetic Methods*

*Electrophoresis.*—Electrophoretic analysis was performed in July and August, 1989, using standard horizontal starch gel electrophoretic and protein staining techniques (Clayton and Tretiak, 1972; Harris and Hopkins, 1976; Richardson et al., 1986; Selander et al., 1971; Shaw and Prasad, 1970). In the preliminary genetic survey, approximately 80 enzymatic and nonenzymatic protein systems (presumptive gene loci) were examined. Of these 80 systems, approximately 60 were scorable. However, only 44 systems were included in this analysis; the remaining systems were excluded because of inconsistent staining across all populations or interpretation problems. Many of the excluded systems were variable, and a few (e.g., Phosphoglucomutase-2 and Adenosine Deaminase) were extremely variable.  $\beta$ -Hemoglobin was excluded because the banding patterns within individuals were found to change over time while the samples were in storage. Proteins, buffers, and tissues included in this analysis are listed in the results section as Table 2.

Samples from a single old-field mouse (*P. polionotus*) were run on all gels as a standard to aid in scoring and for comparative purposes with previous studies (Selander et al., 1971). For systems where this *P. polionotus* did not aid in scoring, selected individuals from each gel were run side-by-side to insure consistency across gels. Alleles were designated by their frequency and relative mobility of their protein products (allozymes). The most common allele was designated as 100, and the other alleles were designated according to the mobility of their allozymes relative to that of the most common allele. Purine Nucleoside Phosphorylase had allozymes which moved cathodally when the most common one moved anodally; these were indicated with a negative (-) sign.

*Statistical procedures.*—Electrophoretic data were analyzed using BIOSYS-1 (Swofford and Selander, 1981). Levels of heterozygosity and polymorphism were

determined by the direct-count of individuals heterozygous per locus and number of polymorphic loci within populations. Goodness of fit of allelic frequencies to Hardy-Weinberg expectations was tested according to the procedure of Swofford and Selander (1981) which avoids statistical problems associated with low frequency expectations. This was accomplished by considering only three groups: homozygotes for the most common allele, all other homozygotes, and heterozygotes consisting of the most common allele and any other allele.

Population subdivision was measured with Wright's F-statistics (Wright, 1978). These are procedures that partition observed genetic variance according to various hierarchical arrangements, and then compare observed with expected values. Typically, the variance is partitioned into  $F_{(it)}$ , the variance among individuals (i) within the total (t) sample; into  $F_{(is)}$ , the variance among individuals within populations (s, where "s" comes from Wright's use of the term "subpopulations"); and into  $F_{(st)}$ , the variance among populations within the total.  $F_{(is)}$  and  $F_{(it)}$  can also be defined as measures of the deviation of the observed allele frequencies from Hardy-Weinberg expectations under panmixia. Values of  $F_{(is)}$  or  $F_{(it)}$  greater than zero indicate that fewer than the expected number of heterozygotes were found. These deviations can be caused by many factors, including Wahlund effects, inbreeding, selection, and population structure.  $F_{(st)}$  can also be defined as the ratio of variance among populations to the total amount of variation, where, for example, an  $F_{(st)}$  value of 0.10 would indicate that 10% of the variation in allele frequencies is attributable to differences among populations.

Using the methods of Cockerham (1969, 1973),  $F_{(st)}$  can be defined in terms of the familiar analysis of variance (ANOVA) and used to determine whether there are significant differences among various groups. The total variance can be partitioned into variance among and within groups, and significance of the differentiation among populations, (variance among groups,  $F_{(st)}$ ), depends on the amount of variation among populations relative to the amount within populations.

Genetic variance can be more finely partitioned. For example, in a nested analysis of variance, the total variance can be partitioned among regions, among populations within regions, and within populations. In this study, a test of genetic differences among subspecies involved partitioning variance in this manner. Significance of variance among subspecies, therefore, generally depends on the presence of significantly more variation among subspecies than among populations within subspecies. Additionally, there can be significant differences among populations within subspecies, while at the same time nonsignificant differences among the subspecies.

This study will use pairwise and hierarchical  $F_{(st)}$  analyses. Pairwise  $F_{(st)}$  analysis is equivalent to the simple ANOVA with only two groups, and will be used to test the significance of genetic differences between pairs of populations. Hierarchical  $F_{(st)}$  analysis is equivalent to the nested ANOVA, and will be used to test the significance of genetic differences among subspecies and among geographic regions.

Genetic similarities, where genetic similarity (S) is related to genetic distance (D) by  $S = 1 - D$ , were calculated according to Rogers (1972), and cluster analyses were performed on these matrices using the unweighted pairs grouping method with arithmetic means (UPGMA) of Sneath and Sokal (1973). Nei's (1972, 1978) genetic distances and identity are presented in the appendices for comparative purposes. Correlation between genetic and geographic distances was tested with Mantel analysis (Mantel, 1967).

### *Morphometric Methods*

*Data collection.*—Twenty-four cranial measurements were measured on 683 specimens to the nearest 0.1 mm using dial calipers. These included: greatest length of skull, basonasal length, basilar length, rostral length, greatest rostral breadth, nasal length, interorbital constriction, zygomatic breadth, greatest cranial breadth, bony palate length, palatal foramen length, posterior palatal length, maxillary tooth row length, total tooth row length, maxillary diastema, palatal width, pterygoid breadth, bullar length, bullar width,

bullar depth (depth of skull), mandibular tooth row length, coronoid depth, condylar depth, and mandibular diastema as defined in Appendix 4. Three standard body measurements, (total, tail, and hind-foot lengths) and sex were recorded from specimen tags. Body length was calculated as the difference between total and tail lengths. Age class was estimated from pelage characteristics, tooth wear, and cranial suture ossification according to Schmidly's (1973) six age-group classification. Juveniles (age classes 1 and 2) were not included in the morphological analyses. Ten percent of the specimens did not have sex recorded on the specimen label; of the remaining specimens, the proportion of each sex was 60% female and 40% male. The proportion in each age class was: 1% subadults, 58% young adults, 28% adults, and 13% old adults. The joint frequency distribution of sex and age did not differ from random expectations ( $p < 0.80$ ).

*Statistical procedures.*—Morphological data were analyzed using various univariate and multivariate statistical procedures and programs including BioStat II (Pimentel and Smith, 1986), SYSTAT (Wilkinson, 1986), and SAS (SAS Institute Inc., 1985). Univariate analyses were performed using analysis of variance, and simultaneous post-hoc comparisons were made using Fisher's least significant difference (Fisher's LSD), a test that is robust to sample size differences. Multivariate data were summarized using principal components and cluster analyses, and differences among groups were tested with discriminant analysis. In multivariate analyses, missing values were replaced with the within-population mean for the character in question. This method allowed for including all specimens in multivariate procedures that did not permit missing values without affecting within-group means.

Analyses were performed on raw data and on data transformed according to Burnaby's method of sheared principal components analysis to remove the effects of size (Bookstein et al., 1985; Burnaby, 1966; Rohlf and Bookstein, 1987). Under certain conditions, the first principle component of log-transformed morphological data is assumed to be "size", and Burnaby's method removes the variance associated with this component



from the data set. However, these data did not match the assumptions, very little of the variance was removed, and therefore, results based on this transformation are not presented. A SAS program which correctly performs this transformation, tested on data from Rohlf and Bookstein (1987), is presented in Appendix 5.

The significance of univariate differences among populations was tested with analysis of variance, and the significance of multivariate differences among populations was tested with discriminant analysis. Relationships among populations were inferred using principle components and cluster analysis. Significance of the correlation between geographic and morphometric distance, and between morphometric distance and genetic distance was tested with Mantel analysis (Mantel, 1967). Statistical differences were considered significant when the probability of making a type-1 error was less than 5%, and highly significant when less than 1%.

## RESULTS

### *Genetic Results*

*Descriptive Statistics.*—This species was found to be highly variable within and among populations. The frequency of polymorphic loci ranged from 0.27 to 0.54 at the 99% criterion and averaged 0.40 (Fig. 1, Table 1). Direct-count heterozygosity ranged from 0.07 to 0.12 and averaged 0.099. Genetic distances, sample size per locus, mean number of alleles, percent polymorphic loci, and direct-count heterozygosities are listed in Table 1. Of the 44 loci examined, 34 were polymorphic in at least one population, and 28 had not previously been reported polymorphic in this species (Table 2).

Population differentiation, as measured with Wright's  $F_{(st)}$  ranged from 0.010 to 0.542 per locus, and averaged 0.219 across all loci (Table 2, Appendix 6). Major shifts in allele frequencies at three loci, Albumin, General Protein 1, and Peptidase 1, contributed most heavily to this high average value. The most common Albumin allele occurred in frequencies ranging from 0.60 to 0.96 in all except the *P. g. megacephalus* populations,

Table 1. Genetic variability of 44 loci in 14 populations summarized for all populations, for island populations, and for mainland populations. Standard errors in parentheses.

Population	Mean sample size per locus <sup>1</sup>	Mean no. of alleles per locus	Percentage of loci polymorphic <sup>2</sup>	Mean direct-count heterozygosity	Mean Rogers' similarity
Merritt Island	26.0	1.9 (0.2)	50.0	0.115 (0.027)	0.917
Amelia Island	12.0	1.4 (0.1)	31.8	0.116 (0.035)	0.896
Cumberland	54.2	1.7 (0.2)	38.6	0.089 (0.025)	0.901
Jekyll Island	44.9	1.9 (0.2)	54.5	0.106 (0.025)	0.911
St. Simons	30.6	1.6 (0.2)	38.6	0.092 (0.027)	0.902
Sapelo Island	28.8	1.5 (0.1)	34.1	0.078 (0.022)	0.903
Dunnellon	11.9	1.5 (0.2)	27.3	0.100 (0.030)	0.932
Gulf Hammock	21.9	1.7 (0.2)	38.6	0.123 (0.031)	0.914
Nassau	21.9	1.7 (0.2)	45.5	0.092 (0.024)	0.930
Okefenokee	22.0	1.9 (0.2)	47.7	0.102 (0.025)	0.932
St. Marys	38.7	1.9 (0.2)	40.9	0.108 (0.029)	0.918
Everett	28.9	1.8 (0.2)	45.5	0.092 (0.024)	0.920
Tuscaloosa	23.0	1.7 (0.2)	38.6	0.112 (0.031)	0.929
Choccolocco	11.0	1.3 (0.1)	27.3	0.066 (0.023)	0.901
Overall	Average	1.7	39.9	0.099	0.915
Islands	Maximum	1.9	54.5	0.116	0.917
	Minimum	1.4	31.8	0.078	0.896
	Average	1.7	41.3	0.099	0.905
Mainland	Maximum	1.9	47.7	0.123	0.932
	Minimum	1.3	27.3	0.066	0.901
	Average	1.7	38.9	0.099	0.922

<sup>1</sup> Deviation from integers in sample sizes reflect inability to score all individuals at all loci.

<sup>2</sup> A locus is considered polymorphic if the frequency of the common allele did not exceed 99%.

Table 2. Variable protein systems, buffers, tissues, number of alleles, average heterozygosity ( $h$ ), Wright's F-statistics ( $F_{(is)}$ ,  $F_{(it)}$ , and  $F_{(st)}$ ), and the significance of  $F_{(st)}$  given as the probability of the associated Chi-square value (n.s. = not significant at  $p > 0.05$ ).

Name (substrate)	Buffer	no.	$h$	$F_{(is)}$	$F_{(it)}$	$F_{(st)}$	$p$
	Tissue	alleles					
Aconitase-2*	1-L	6	0.086	0.07	0.15	0.081	0.001
Aconitase-3*	1-L	2	0.093	-0.12	0.03	0.133	0.001
Albumin	1-M	5	0.280	0.09	0.34	0.336	0.001
Alcohol Dehydrogenase*	1-L	3	0.004	-0.02	0.00	0.014	n.s.
Aspartate Aminotransferase 1*	4-M	2	0.003	-0.02	0.00	0.021	n.s.
Aspartate Aminotransferase 2*	4-M	2	0.079	-0.01	0.06	0.064	0.001
Carbonic Anhydrase 1*	1-B	5	0.226	-0.01	0.07	0.080	0.001
Carbonic Anhydrase 2*	1-B	2	0.019	-0.10	-0.01	0.086	0.001
Esterase 1 (Naphthyl-AS-Acetate)	3-L	12	0.682	0.00	0.13	0.130	0.001
Esterase 7 ( $\alpha$ -Naphthyl Propionate)*	5-M	5	0.366	0.13	0.29	0.182	0.001
Esterase $\beta$ NP ( $\beta$ -Naphthyl Acetate)*	3-L	5	0.368	0.08	0.27	0.205	0.001
Esterase M ( $\alpha$ -Naphthyl Propionate)*	5-M	6	0.266	0.42	0.58	0.283	0.001
Fumarate Hydratase 2*	1-L	3	0.019	-0.05	-0.01	0.038	0.001
General Plasma Protein 1*	2-P	4	0.188	0.17	0.62	0.542	0.001
Glucose Phosphate Isomerase	1-M	2	0.003	-0.02	0.00	0.021	n.s.
Glucose-6-Phosphate Dehydrogenase*	5-M	4	0.002	-0.01	0.00	0.010	n.s.
Glutamate Dehydrogenase*	3-L	3	0.016	-0.03	-0.01	0.018	n.s.
Glyceraldehyde Phosphate Dehydrogenase*	1-M	2	0.000	1.00	1.00	0.032	0.05
$\alpha$ -Glycerophosphate Dehydrogenase*	1-M	4	0.018	-0.04	-0.01	0.034	0.001
Isocitrate Dehydrogenase 1	4-M	4	0.060	0.00	0.11	0.113	0.001
Lactate Dehydrogenase 1*	4-M	4	0.072	-0.03	0.02	0.054	0.001
Malic Enzyme*	5-M	3	0.031	0.10	0.13	0.041	0.001
Peptidase 1 (Leucyl-alanine)*	2-M	4	0.326	0.06	0.39	0.355	0.001
Peptidase 2 (Leucyl-alanine)*	2-M	4	0.137	-0.24	0.10	0.117	0.001
Peptidase 3 (Leucyl-glycyl-glycine)*	2-M	5	0.113	-0.04	0.07	0.103	0.001
Peptidase 4 (Leucyl-alanine)*	2-M	4	0.044	0.02	0.21	0.193	0.001
Phosphoglucomutase 1	3-L	3	0.353	-0.02	0.17	0.182	0.001
Phosphoglucomutase 3*	3-L	2	0.008	-0.03	0.00	0.026	n.s.
6-Phosphogluconate Dehydrogenase*	1-M	4	0.044	0.15	0.19	0.050	0.001
Post Albumin Protein*	2-P	4	0.122	-0.03	0.02	0.051	0.001
Purine Nucleoside Phosphorylase*	1-L	5	0.301	-0.01	0.12	0.126	0.001
Sorbitol Dehydrogenase*	1-L	2	0.003	-0.02	0.00	0.020	n.s.
Superoxide Dismutase 2*	1-L	2	0.006	-0.02	0.00	0.020	n.s.
Transferrin	2-P	3	0.030	-0.09	-0.01	0.068	0.001
Means:			0.099	0.07	0.28	0.219	0.001

Buffers: 1 = AC = N-(3-Amino propyl) morphine-Citrate; 2 = Lithium Hydroxide; 3 = Tris-Citrate pH 8.0; 4 = Tris-Citrate pH 6.7; 5 = Tris-Maleate. Tissues: L = Liver; P = Blood Plasma; M = Muscle; B = Red Blood Cells.

The following were invariant: Adenylate Kinase, 2-M; Aldolase, 1-M; Creatine Kinase-1, -3, 2-M; Lactate Dehydrogenase-2, 4-M; Leucine Amino Peptidase, 2-M; Malate Dehydrogenase-1, -2, 4-M; Plasma Protein B, 2-P; Superoxide Dismutase-3, 1-L.

Asterisks (\*) indicate proteins that have not previously been reported polymorphic in this species, although some confusion may exist for the esterase loci.

The names of Esterase M and Esterase 7 follow Teska et al. (in press).

where it was absent. The most common General Protein 1 allele was found in frequencies greater than 0.70 in nine populations, but in frequencies of less than 0.50 in the remaining populations, and the common allele was absent in the Amelia Island and Choccolocco populations. The frequencies of Peptidase 1 alleles showed similar differences. The most common allele was fixed in the Sapelo Island and Gulf Hammock populations, but was found in frequencies of less than 0.20 in the Jekyll Island, St. Simons Island, and St. Marys populations.

Of the 34 polymorphic loci, 25 had associated  $F_{(st)}$  values that were highly significant, one was significant, and eight were not significant. Excluding Glyceraldehyde Phosphate Dehydrogenase,  $F_{(is)}$  values ranged from 0.42 to -0.24, and the frequency distribution of positive and negative values did not differ from random expectations. Assuming no selection, this pattern indicates that there was no significant inbreeding within populations and that the sampling scheme achieved the goal of avoiding Wahlund effects. At the Glyceraldehyde Phosphate Dehydrogenase locus, an anomalous  $F_{(is)}$  value of 1.0 was observed because all except one individual was homozygous for the common allele, and the remaining individual was homozygous for an alternate allele. As might be expected from the large  $F_{(st)}$  values,  $F_{(it)}$  values were generally positive, indicating a significant overall deficiency of heterozygotes.  $F_{(st)}$ ,  $F_{(it)}$ , and  $F_{(is)}$  values are listed in Table 2.

At each variable locus, the within-population frequency distribution of alleles was tested for goodness of fit to Hardy-Weinberg expectations. In a matrix of 14 populations by 34 variable loci (476 potential cases), there were 246 cases in which a locus was variable within a population. In 229 (93.1 %) of these cases, the allele frequency distribution did not differ from Hardy-Weinberg expectations. Ten of 34 loci had allele frequency distributions that differed significantly from Hardy-Weinberg expectations in at least one population. In 11 of 14 populations, the allele frequency distribution differed significantly from Hardy-Weinberg expectations at one or more loci. Allele frequency distributions at the Esterase-M locus showed the most consistent deviations from Hardy-Weinberg

expectations with an excess of homozygotes in eight populations. Allele frequencies and relative mobilities are listed by population in Appendix 6.

Genetic similarities among most populations were relatively low for conspecific populations, ranging from 0.866 to 0.963. The greatest genetic differentiation was found between populations from sites with the least geographical separation; Cumberland and Amelia Islands, separated by less than 1 km, had a similarity of only 0.866. The Dunnellon and Okefenokee populations, representing different subspecies (*P. g. palmarius* and *P. g. gossypinus*, respectively) and moderate geographical separation (175 km), were genetically most similar (0.963). Similarities between Cumberland Island and its nearest neighbors of St. Marys, Jekyll Island, and Amelia Island were 0.917, 0.894, and 0.866, respectively. The genetic similarity between populations from Cumberland Island and St. Marys, 0.917, was virtually identical to the overall mean similarity of 0.915. Mean similarities between each population and all others are listed in Table 1, and genetic similarities between populations are summarized in Figure 2 as a dendrogram.

Rogers' similarity is not the only common measure of genetic similarity. Therefore, for comparison with existing literature, Nei's (1972) genetic distance ranged from 0.004 to 0.082, and Nei's (1978) unbiased genetic distance ranged from 0.000 to 0.079. Nei's (1982) distance between Cumberland Island and St. Marys was 0.028, 0.009 less than the average of 0.035. Nei's (1972, 1978) and Rogers' distance and similarity matrices, and dendrograms derived from these matrices, are presented in Appendices 7 and 8).

*Tests of significance.*—In pairwise comparisons of populations using  $F_{(st)}$  analysis, all pairs of populations except Dunnellon and Okefenokee were highly significantly different. Given the possibility of type-1 error problems, this indicates that essentially every population was distinct and different from most others. Furthermore, the Dunnellon and Okefenokee populations were geographically separated by the Gulf Hammock population, from which both were significantly different.

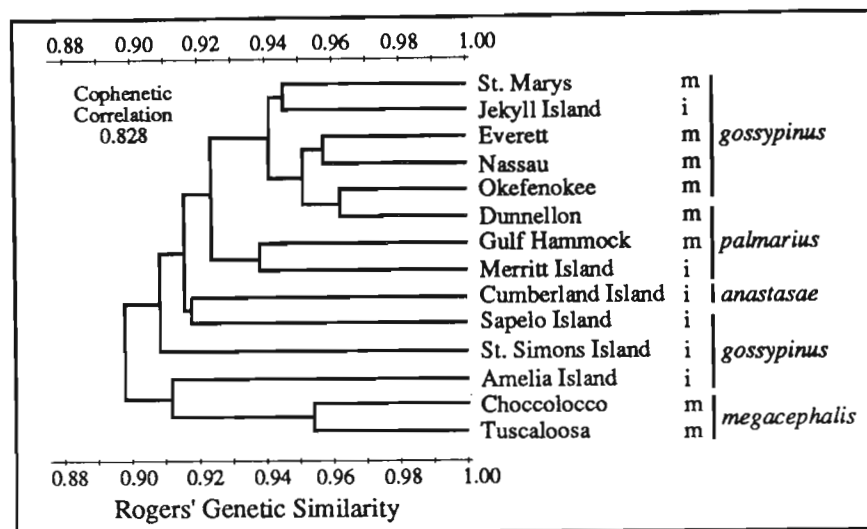


Fig. 2. Dendrogram showing relationships among 14 populations of *Peromyscus gossypinus* derived from UPGMA clustering of Rogers' genetic similarity coefficients. Branches were rotated to simplify grouping by subspecies and location; i = island, and m = mainland.

Thus, when genetic differences were tested using pairwise comparisons, the Cumberland Island population was highly significantly different from all other populations. For paired comparisons between the Cumberland Island population and its neighbor populations,  $F_{(st)}$  values were as follows: Cumberland Island vs St. Marys, 0.106; Cumberland Island vs Jekyll Island, 0.174; and Cumberland Island vs Amelia Island, 0.276. In a paired comparison of the Cumberland Island population vs all other populations as a single group, the difference was highly significant ( $F_{(st)} = 0.092$ ). However, when genetic differences were tested in hierarchical analysis, where the difference between the Cumberland Island population and other populations were examined in the context of variation within the species, the Cumberland Island population was not significantly different from the other populations ( $F_{(st)} \approx 0.00$ ). This indicates that while most populations are different, the Cumberland Island population is not unusually different and does not stand out from the other populations (Fig. 2). To determine whether the *P. g. megacephalus* populations were

the cause of the significance of the former tests and the nonsignificance of the latter, the data for *P. g. megacephalus* were deleted, and the tests were performed again. Again, the pairwise difference between the Cumberland Island population vs the Georgia and Florida populations considered as one unit was highly significant ( $F_{(st)} = 0.095$ ), but results of the hierarchical analysis were not significant ( $F_{(st)} \approx 0.00$ ).

Differences between island populations were tested in pairwise comparisons among nearest neighbors. As above, all differences were highly significant, which is many more than would be expected by chance alone.  $F_{(st)}$  values for island neighbors excluding Cumberland Island were as follows: Merritt Island vs Amelia Island, 0.143; Jekyll Island vs St. Simons Island, 0.081; and St. Simons Island vs Sapelo Island, 0.242. Differences among mainland populations excluding *P. g. megacephalus* were slightly lower. For example,  $F_{(st)}$  values among pairs of nearby populations were as follows: Gulf Hammock vs Okefenokee, 0.068; St. Marys vs Everett, 0.060; Okefenokee vs St. Marys, 0.057; and Dunnellon vs Gulf Hammock, 0.094. Genetic differentiation on the islands vs the mainland (including *P. g. megacephalus*) was tested in hierarchical analysis and found to be not significantly different ( $F_{(st)} \approx 0.00$ ). Results of the hierarchical analysis of island vs mainland populations without the *P. g. megacephalus* data were also not significant ( $F_{(st)} \approx 0.00$ ). Additionally, pairwise comparisons of all island populations considered as one group vs Florida and Georgia mainland populations as a group were not significant ( $F_{(st)} = 0.007$ ).

The distribution of genetic variance among subspecies, as measured by hierarchical  $F_{(st)}$  analysis, shows that most of the genetic variance within the species is distributed among individuals within populations. Of the total genetic variance, only 24.8% was explained by differences among subspecies, however, this 24.8% was highly significant. Inspection of the dendrograms suggested that *P. g. megacephalus* populations may be different from the Georgia and Florida populations. This was found to be justified, and a

highly significant proportion of the variance (56%) attributed to differences among subspecies was accounted for by *P. g. megacephalus* vs the other subspecies.

To determine whether genetic differentiation was greater among the island populations than among mainland populations, single-locus  $F_{(st)}$  values were calculated among populations in each region. The average of these  $F_{(st)}$  values among island and mainland populations was 0.257 and 0.107, respectively. Individually, these values were highly significant, but they were not significantly different from one another. However, the trend towards greater differentiation on the islands was significant (paired t-test), as more of the single-locus  $F_{(st)}$  values were larger among island populations.

For the species as a whole, the overall  $F_{(st)}$  of 0.219 indicates that 21.9% of the total genetic variation is explained by population differentiation, and that 88% of the variance was found within populations. Within island and mainland regions, however, on average only 74% and 89% of the total variation in those regions, respectively, is contained within populations.

A moderate, but nonsignificant, correlation was found between the matrices of Rogers' genetic distance and geographic distance ( $r = 0.33$ ,  $p = 0.068$ ).

### *Morphometric Results*

*Univariate tests.*—One-way and two-way analysis of variance was used to test each character for differences between sexes and age classes. No significant sexual differences were found for any character, but significant differences between age classes were found for every character. Despite these differences, tests were performed on all available adults to increase sample sizes. Restricting the analyses to individual age classes would have reduced the total sample size by at least 42%, and would have eliminated some populations from consideration because of an insufficient number of individuals. Restricting the



analysis to adults reduced the problem of high within-group variance, but incorporating age-related variation in the data did reduce discriminatory power of statistical tests.

Using univariate statistics on Bangs' (1898) original criteria of body length, tail length, foot length, and total length, Cumberland Island mice were significantly smaller than St. Marys mice. However, using these characters, Anastasia Island mice were not significantly different from St. Johns Co. mice. Additionally, Cumberland Island mice were not significantly different from Anastasia Island mice. These two populations were, however, smaller than most other populations.

Although highly significant differences among the 20 populations were found for the external body measurements that Bangs examined, results of post-hoc simultaneous comparisons of all population means showed that neither the Cumberland Island nor the Anastasia Island populations were significantly different from most other island or mainland populations (Table 3). Using Fisher's post-hoc test for tail length, the Cumberland Island population was not different from eight, and the Anastasia Island population was not different from 12 other populations; additionally, the Cumberland and Anastasia Island populations were not different from one another. Similar results were found for comparisons of body, total, and hind-foot lengths (Table 3, Appendix 9).

Results of univariate analyses of cranial characters showed patterns among populations that were similar to those of the external body characters. For example, highly significant differences in skull length were observed among populations. The Anastasia Island population was highly significantly different from the St. Johns Co. population, but the Cumberland Island population was not significantly different from the St. Marys Co. population (Appendix 9). The Anastasia Island population had the shortest average skull length, and was significantly smaller than 18 other populations. However, Cumberland Island mice ranked fourteenth smallest, and were virtually identical to those from St. Marys. The Cumberland Island population was significantly different from the Anastasia Island population for skull length and most other cranial characters. Although all possible comparisons

Table 3. Results of analysis of variance and post-hoc tests for body and tail lengths (mm) among 20 populations of *Peromyscus gossypinus*. Populations are arrayed in order of increasing mean. Vertical lines beside the table indicate sets of means that are not significantly different from one another as determined by Fisher's least significant difference (LSD) test using alpha of 0.05. Symbols are as follows: 1 = subspecies: *P. g. anastasiae* (a), *P. g. gossypinus* (g), *P. g. palmarius* (p), and *P. g. megacephalus* (m); 2 = island (i) or mainland (m).

Source	df	F-Value	P-Value	Source	df	F-Value	P-Value
Population	19	5.33	0.0001	Population	19	10.21	0.0001
Residual	565			Residual	566		

Dependent: body length (mm)

Dependent: tail length (mm)

	1	2	Mean	Fisher's LSD		1	2	Mean	Fisher's LSD
Sapelo	g	i	92.2		Sapelo	g	i	63.0	
St. Simons	g	i	92.7		Jekyll	g	i	64.0	
Ware	g	m	94.2		Cumberland	a	i	64.6	
Anastasia	a	i	94.2		Anastasia	a	i	65.3	
Everett	g	m	94.6		St. Simons	g	i	66.8	
Tuscaloosa	m	m	95.2		Amelia	g	i	66.9	
Jekyll	g	i	95.5		Everett	g	m	66.9	
Amelia	g	i	96.1		Nassau	g	m	67.7	
Merritt	p	i	96.3		St. Johns	p	m	68.0	
Cumberland	a	i	96.4		Gulf Ham.	p	m	68.4	
St. Johns	p	m	96.9		Dunnellon	p	m	69.1	
Gulf Ham.	p	m	97.3		St. Marys	g	m	69.2	
Okefenokee	g	m	97.9		Ware	g	m	69.2	
McIntosh	g	m	98.9		McIntosh	g	m	71.1	
Brevard	g	m	99.8		Merritt	p	i	71.2	
St. Marys	g	m	100.2		Okefenokee	g	m	71.2	
Nassau	p	m	101.0		Tuscaloosa	m	m	71.9	
Choccolocco	m	m	102.0		Charlton	g	m	74.7	
Dunnellon	p	m	102.3		Choccolocco	m	m	76.7	
Charlton	g	m	103.4		Brevard	p	m	78.4	

were not made (to avoid type-1 error problems), it is likely that each population is significantly different from each other population in at least one character. For each population, the mean, range, standard error, and sample size of each character are presented in Appendix 10.

*Multivariate tests.*—Principle components analysis, a descriptive technique for summarizing the variance in a data matrix, was performed on the covariance matrix. Distributions of the 20 populations plotted on the first two principle components were virtually identical (Fig. 3). The distribution of populations in two-dimensional principle component space for sheared data showed even less variation among populations, suggesting that what little variation was present in the raw data was due to differences in size but not shape. Unusually low correlations among variables were found. Correlation and covariance matrices are presented in Appendix 11.

Discriminant analysis, a powerful technique for testing the difference among groups, has three aspects. The first aspect develops an algorithm (the discriminant function) for maximally separating groups based on an *a priori* grouping criterion, the second uses the algorithm for *a posteriori* prediction of the group to which each data point belongs, and the third tests the significance of differences among the groups. Discriminant analysis was performed on the 20 populations simultaneously. Highly significant separation of group centroids was achieved, but classification of individuals based on the discriminant function was only 50.7% successful. Discriminant analysis was also performed with populations grouped according to the boundaries of the four subspecies. Again, highly significant separation of group centroids was achieved, but classification of individuals based on the discriminant function was only 68% successful (467 of 683), and only 59% of *P. g. anastasiae* were correctly classified (57 of 97). Plotting the four subspecies in two dimensional canonical space showed little separation of groups (Fig. 4). Discrimination of *P. g. anastasiae* from the other three subspecies as a group was highly significant with an overall successful classification rate of 91% (631 of 683), but of the *P. g. anastasiae*, only

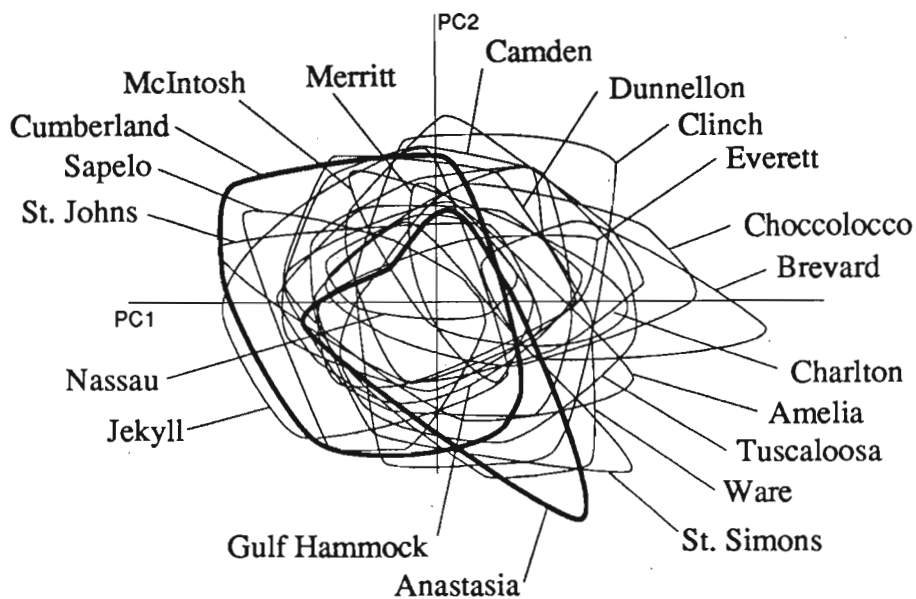


Fig. 3. Distributions of 20 populations of *Peromyscus gossypinus* on the first two principle component axes extracted from the 27 character covariance matrix of raw data .

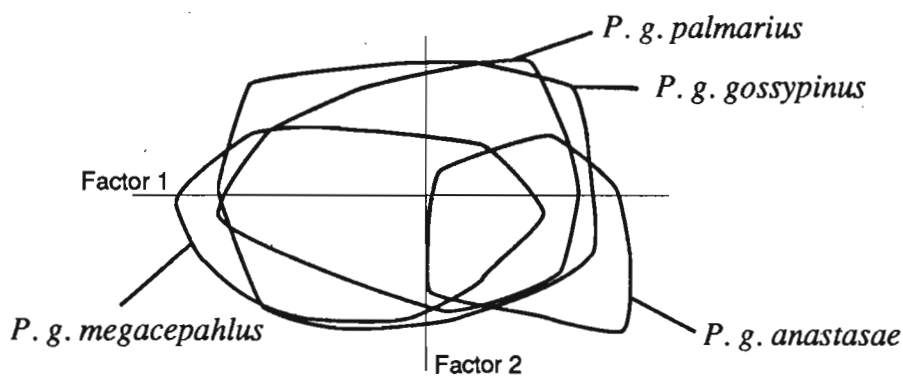


Fig. 4. Distribution of four subspecies of *Peromyscus gossypinus* plotted on the first two canonical axes extracted from the 27 character covariance matrix of raw data.

47% (46 of 97) were correctly classified. These tests indicate that while the populations are significantly different, there is a large degree of overlap among populations.

For all characters except basonasal, basilar, and posterior palatal lengths, island mice as a group had smaller average lengths than mainland mice as a group, and in 16 of 24 cases, this difference was significant. Discrimination of island from mainland mice was highly significant with an overall successful classification rate of 80% (544 of 683), but of the island mice, only 57% (130 of 228) were correctly classified.

A slight negative, nonsignificant correlation was found between morphometric distance, calculated as the Euclidian distance between population centroids in 27 dimensional morphometric space, and geographic distance ( $r = -0.166$ ). A slight positive, but nonsignificant, correlation was also found between genetic distance and morphometric distance ( $r = 0.167$ ).

## DISCUSSION

### *Systematics and Taxonomy*

Bangs' (1898) original descriptions of *P. insulanus* and *P. anastasiae* were based on small size and light coat color. In this study, tail, foot, and body lengths were found to be highly variable both within and among populations (Table 3). While mice from the insular populations tended to have shorter tails, this was not consistent, and mice from several mainland populations had similar short tails. There was no clinal or other geographic association with tail length; mice in the northern most Choccolocco and southern most Brevard County populations had the longest tails. Insular mice also tended to have shorter bodies and hind feet, but as with tail length, this was not consistent. As with tail lengths, hind foot and body lengths showed no evidence of clinal variation among island or mainland populations, and the three populations with the longest body lengths (all mainland) were from a northern, a central, and a southern area.

Tail length and body size in house mice (*Mus musculus*) can be influenced by non-genetic factors. Nest temperature, mother's body length, and litter size can effect offspring tail lengths (Falconer, 1981). Additionally, offspring tail and body lengths are not necessarily related to the length of the mother's tail or body (Falconer, 1981; Thompson, 1976; Willham, 1963; Baker and Cockrem, 1970). Nutritional levels have been shown to influence body size, including cranium size, in pocket gophers (*Geomys*; Patton and Brylski, 1987). Because these plastic phenotypic responses may occur in other rodents, body size and tail length should be interpreted carefully in taxonomic surveys among populations within rodent species. Tail length is, however, an extremely valuable character in the discrimination of different *Peromyscus* species in the southeastern United States (Boone and Laerm, in prep).

Coat color, while taxonomically valuable in describing some groups of animals, is not generally informative in these four subspecies, although a possible exception is made for *P. g. telmaphilus*, a south Florida subspecies described by Schwartz (1952) that was not examined here. Personal observations on hundreds of museum specimens from throughout the range of the species reveal that mice in some populations tend towards lighter color, but this is not more pronounced on islands, and all populations have darker and lighter individuals. Batson (1958), working in Alabama, found that coat color in these mice tends to be paler in the spring and summer than in fall and winter. Based on personal observations of captive cotton mice over 1.5 years (current age range of approximately 2 - 3 years), coat color, presence or absence of a dark mid-dorsal stripe, and degree of coarseness of fur seems to vary with age, season, and possibly diet. Most striking was the tendency of a shift to cinnamon-colored pelage with increased age in these captive mice. Both Howell (1939) and Schwartz (1952) noted age related pelage color changes. Thus, the age of the animals and the season of collection may be important determinants of average pelage color in collections. While coat color is of obvious adaptive significance to the survival of these animals, it is dismissed in these four subspecies as a taxonomically useful character.

Based on Bangs' (1898) original morphological and pelage criteria, *P. insulanus* and *P. anastasae* are not sufficiently different from each other or from *P. gossypinus* to warrant species status. In this study, principal components and discriminant analysis indicated essentially no separation of any population or any subspecies from the remaining populations. Thus, neither univariate nor multivariate analysis of a large set of morphological characters supports the taxonomic validity of *P. g. anastasae* on either Cumberland or Anastasia Islands.

The conclusion, based on the morphometric data, that *P. g. anastasae* is not a valid taxon is supported, but not so clearly, by the genetic data. Rogers' genetic similarity between the Cumberland Island population and its nearest neighbors (St. Marys on the mainland, Amelia Island, and Jekyll Island) was 0.92, 0.87, and 0.89, respectively (Appendix 7). These differences are comparable with differences between sibling species of *Peromyscus* (0.88 - 0.91; Zimmerman et al., 1978), where sibling species are recently diverged, morphologically similar, but reproductively isolated. Using a genetic similarity criteria of 0.94, the similarity between the sibling species *P. merriami* and *P. eremicus* (Avice et al., 1974), populations from Everett, Nassau, Dunnellon, and Okefenokee would form one group, while those from Tuscaloosa and Choccolocco would form another group, and all other populations would be distinct (Fig. 2, Appendix 8), clearly an unmanageable situation. Using a more conservative genetic similarity criteria of 0.91, the difference between the sibling species *P. truei* - *P. gentilis* and *P. nasutus* - *P. difficilis* (Zimmerman et al., 1978), there would still be four distinct groups. All of the insular populations except Jekyll Island and Merritt Island have genetic distances of 0.91 - 0.92. For comparison with other literature, Zimmerman et al. (1978) found that the average Nei's (1972) genetic distance between subspecies of *Peromyscus* was 0.052. The genetic distance between the Cumberland Island population and the populations at St. Marys, Amelia Island, and Jekyll Island were 0.028, 0.082, and 0.051, respectively (Appendix 7). Thus, there is a dilemma: either these insular populations are at least separate subspecies based on

genetic differences, or this is simply a highly variable species with little regional association among genetic characters.

Because of the complexity of the genetic and morphometric relationships, there are currently not enough populations in the data sets (genetic or morphometric) to conclusively determine the evolutionary relationships among these populations. However, we may conclude that the Cumberland Island population is not more different from the St. Marys population, and the Anastasia Island population is not more different from the St. Johns Co. population, than would be expected by chance based on differences observed between other pairs of populations. Additionally, the distribution of genetic variation within these populations of the four subspecies shown by hierarchical  $F_{(st)}$  analysis, and the relationships indicated by cluster analysis (Fig. 2, Appendix 7), indicate that the current delineations of subspecies boundaries are dubious. Elucidating these relationships is the focus of an ongoing study.

While differences may be found among populations, it is not generally valid to search for a single character that shows differences among populations and use that character to define taxa, while at the same time ignoring all other similarities. Application of rules based on univariate differences among populations, for instance Amadon's (1949) 75% rule, can lead to conflicting taxonomic descriptions depending on the character used. Taxonomic definitions should be based on a large number of characters which the group holds in common, and that differ from other such groups. This concern, however, does not apply to the creation and use of taxonomic keys for identification of unknown specimens where the goal is to determine the taxonomic group to which a specimen belongs rather than the definition of the taxonomic groups themselves.

#### *Relevance to Existing Literature*

*P. gossypinus* vs other species.—Previous authors have examined the genetics of this species. Smith, et al. (1984) examined the relationship between food availability and



heterozygosity in South Carolina, and found that eight of 23 loci they studied were polymorphic in 223 mice. Four of these, hemoglobin, Esterase-1, Purine Nucleoside Phosphorylase, and another esterase were highly polymorphic, and these contributed to a high heterozygosity of approximately 0.08. Price and Kennedy (1980) working primarily in Tennessee, and Robbins et al. (1985), working throughout the Southeast, examined genetic relationships between *P. gossypinus* and *P. leucopus*. Price and Kennedy (1980) found that three of the 14 loci that they examined, hemoglobin, an esterase, and superoxide dismutase (= indophenol oxidase), were polymorphic in a sample of 47 *P. gossypinus*. Of these three loci, hemoglobin and the esterase are not comparable with this study, and superoxide dismutase was polymorphic here. Of the remaining 11 loci that were monomorphic, six were polymorphic in this study. Because the alternate alleles at all six loci were in very low frequencies, it is possible that Price and Kennedy's (1980) samples were not large enough to detect these alleles. Tennessee is also on the northern edge of this species' range, and these alleles may be absent in those populations. It is typical to find reduced genetic variation in peripheral populations (McClenaghan and Gaines, 1981). Price and Kennedy (1980) found genetic differentiation that was comparable with this study, but their average heterozygosity value of 2.9% differed greatly from the 10% value found here. Robbins et al. (1985) examined 100 mice and 25 loci. They found eight polymorphic loci, and all were polymorphic here. However, except for transferrin, this study found more alleles at each of these loci. Robbins et al. (1985) found genetic differentiation that was less than was found by Price and Kennedy (1980) or this study. Robbins et al. (1985) found a lower heterozygosity value, 4.7%, than was found in this study. The higher heterozygosity, more alleles, and greater differentiation in this study relative to the previous studies is probably due in part to the larger sample size (individuals, populations, and loci) examined here. The average heterozygosity of 0.10 is among the highest reported for vertebrates (Calhoun et al., 1988) and is more than twice the average

for mammals (Awise and Aquadro, 1982). This high level of heterozygosity was also found for the insular populations.

There was significant genetic differentiation among populations that was somewhat higher than observed for many other vertebrates, and approximately 22% of the total genetic variation is due to population differentiation. This degree of differentiation is roughly twice that found for New Mexico prairie dogs (*Cynomys ludovicianus*; Chesser, 1983), in Scandinavian moose (*Alces alces*; Ryman et al., 1980), and in house mice (Nei, 1975), but slightly more than half of that observed in pocket gophers (*Thomomys bottae*, Patton and Yang, 1977).

*Morphological vs genetic differentiation.*—Aquadro and Kilpatrick (1981) examined the correspondence between morphological and biochemical differentiation in insular and mainland deer mice (*Peromyscus maniculatus*) in New England. As in their study, little correlation was found here between the morphological and genetic data sets (Mantel analysis:  $r = 0.167$ , not significant), and conclusions concerning the relationships among populations differed with the two data sets. It is not unreasonable to find that relationships among populations on a local scale differ with the morphological and genetic data sets. Schnell and Selander (1981) state that morphological characters are generally determined by complex interactions between many genes and the environment, thus consistent correlations between the data sets should not generally be expected. Additionally, if phenotypic characters such as tail length can respond plastically to environmental variation and random genetic drift is occurring, then the two should not covary. However, it is troubling that relationships among populations at a gross regional scale do not agree.

*Genetic variation on islands.*—Genetic variation is usually reduced on islands (Aquadro and Kilpatrick, 1981; Browne, 1977; Kilpatrick, 1981). This reduction is generally attributed to smaller population sizes, and therefore higher rates of genetic drift and inbreeding on islands relative to mainland areas (Awise et al., 1974). Kilpatrick (1981, p. 30) states, "An absence or severe reduction of genetic variability has characteristically been

associated with isolated populations.” Kilpatrick (1981) lists many supporting citations and a few exceptions. In these insular populations, genetic variability was not reduced. Insular and mainland populations had identical average numbers of alleles per locus and average direct-count heterozygosities, and the insular populations had a higher average percentage of polymorphic loci (Table 1, Fig. 1). The population with the highest direct-count heterozygosity (Gulf Hammock) was on the mainland, but the population with the lowest heterozygosity (Choccolocco) was also on the mainland. Factors accounting for this unexpected distribution of variation are not clear. It may be that there is an intermediate population size where drift operates to change allele frequencies but does not result in a loss of alleles or heterozygosity.

Population size on the islands appears to fluctuate severely over relatively short time intervals. Ivey (1949), working on an unnamed island in northern Florida (probably in St. Johns Co.), found large numbers of mice between 1939 and 1942, but few in the winter of 1946 - 47 (eight captures in 2,300 trap-nights). Jim Richardson (pers. comm.) on Little Cumberland Island reported that the island was over run with mice in the early 1970's, but in this study, only four were caught in 1,000 trap-nights in July 1988. Almost no mice were caught on Cumberland Island in the early 1980's (2 - 4 per 1,000 trap-nights, L. Logan, pers. comm), but in January 1988, 31 were caught in 500 trap-nights, and later in July, 55 were caught in 1,300 trap-nights. The high level of genetic variation in the insular populations was unexpected because frequent, severe reductions in populations size should result in repeated genetic bottlenecks and a reduction in genetic variation. One would predict that no rare mainland alleles would be present on the islands. However, there is no evidence for the effects of genetic bottlenecks. For instance, the Cumberland Island population ( $n = 55$ ) and the St. Marys population ( $n = 39$ ) on the mainland opposite Cumberland Island share most alleles, but there are several rare mainland alleles that are not represented in the island population, and there are several rare alleles on the island that are not represented in the mainland population (Appendix 6). These mice experience annual fluctuations

in population size (McCarley, 1954; Smith et al., 1974), but this should produce similar average effects in mainland and island populations.

One explanation for this distribution of variation is the possibility that the islands and mainland form a panmictic breeding unit (therefore all genetic measurement parameters are equal), and that the higher percent polymorphic loci on the islands is a result of sampling error. Choccolocco, with the smallest sample size ( $n = 11$ ), also had the smallest percentage of polymorphic loci. However, the observed genetic differences between the island and mainland populations indicate that there has been little gene flow among these populations. Kimura and Maruyama (1971) demonstrated for the island model of migration and neutral alleles, that when the number of migrants is four or greater per generation, two populations will behave as a single panmictic unit. Slatkin (1987), found that as few as one migrant per generation will prevent strong local differentiation. Allendorf (1983) modeled migration and various modes and strengths of selection, and showed that the degree of population differentiation differs under various combinations of these forces. However, under the assumption of neutral alleles, Allendorf (1983) found that one reproductively successful migrant among demes per generation will prevent the loss of alleles in populations due to genetic drift, but that this rate of migration will allow populations to respond to differing local selective forces. Thus, very low migration rates will prevent qualitative changes (all alleles in every population), but not quantitative changes among populations (changes in allele frequencies). The populations in this study do not share all alleles, and therefore they do not appear to be behaving as a single panmictic unit. Thus, the differences are probably not due to sampling error.

*Rodent body size on islands.*--Foster (1964), Lawlor (1982), and others (see Roth and Klein, 1986) have found that small mammals on islands tend to be larger than their mainland counterparts. Roth and Klein (1986) describe this observation as the "island rule", and Van Valen (1973) states that this ecological and evolutionary rule seems to have fewer exceptions than any other ecological rule for mammals. The "island rule" is not

supported by the body size of these mice. Size rankings were variable across populations on the mainland and islands, and the size relationships among populations differed among age classes and among characters. In general, island mice were smaller than mainland mice, and as a group, island mice were significantly smaller than mainland mice for all body characters and 16 of 24 cranial characters. Sapelo Island, Anastasia Island, and Amelia Island mice tended to be smallest, and Okefenokee and Choccolocco mice tended to be largest. Brevard Co. mice, while among the largest for external characters, were among the smallest for cranial characters (Table 3, Appendix 10).

*Clinal variation.*--Wolfe and Linzey (1977) suggest that the size differences used to define the three major mainland subspecies, *P. g. megacephalus* (large), *P. g. gossypinus* (medium), and *P. g. palmarius* (small), may not be taxonomically significant and may simply represent clinal variation within the species. In this study, clustering and ordination of the morphometric data, as well as Mantel analysis, indicated that there was no correlation between morphometric and geographic relationships. To produce an index of size that was not confounded by shape, population means of the morphological characters for adult (age class 5 where presumably allometric growth would have reached a maximum) mice were rank ordered by population, and an index of population size was calculated as the average of the ranks across variables. This produced scores with extreme values of 1 and 20, where a score of 1 would indicate a population that was smallest for all 27 morphological characters, and a score of 20 would be largest for all characters. The Okefenokee population ranked largest with a score of 16.0. While the Choccolocco *P. g. megacephalus* population ranked nineteenth largest, the Tuscaloosa *P. g. megacephalus* population ranked thirteenth, and was exceeded by five *P. g. gossypinus* and *P. g. palmarius* populations from two islands and three mainland populations. Sapelo island ranked smallest with a score of 2.3, followed by the Anastasia and Amelia island populations. Five of seven island population ranked less than or equal to the median. Thus, clinal variation in overall size is not likely.

### *Conservation*

*Reintroductions.*—Suggestions have been made to reintroduce Cumberland Island mice onto Anastasia Island (Neuhauser, 1979; others, pers. comm.). Before this is done, the motives for such an action must be examined, because different motives have different optimal reintroduction strategies. If the objective is to reestablish the original "Anastasia Island" mouse, then this is probably impossible. Based on the observed genetic and morphological differences among extant populations, there is no reason to suspect that Cumberland Island mice were more similar to Anastasia Island mice than Anastasia Island mice were to any other randomly chosen population.

If the motive for a planned reintroduction is to reestablish a population of cotton mice to restore a natural balance or to reintroduce a historically occurring rodent to the ecosystem, then there are several logical strategies which do not necessarily involve the Cumberland Island population. Morphologically, any randomly chosen mouse should be able to survive on the Anastasia Island because all of the mice seem to be structurally similar. There do not appear to be, for example, major structural differences in the feeding apparatus of these mice that might be important adaptations for specific habitats. Genetically, the mouse populations in Georgia and Florida have basically the same set of alleles, suggesting that there are no major genetic differences. A reintroduction program, then, would not need to rely on any particular population for founders, but it would be more likely to succeed if a large number of mice were released. Large numbers would reduce the chances of significant founder effects, and increase the chance that some animals would survive the initial stress of handling.

Perhaps the most natural strategy would be to "assist" potential founders by capturing mice from coastal St. John's Co. and releasing them on Anastasia Island. This strategy has the effect of simply accelerating events that would probably occur naturally. Another strategy, one which minimizes capture effort, would be to capture mice for

reintroduction from anywhere they are abundant. Because all of the populations are unique, this would establish a new population that was similar to only one other population. Mice could also be caught from several areas of high abundance and released on the island as a mixture of genetic stocks. This strategy would probably allow for novel gene complexes to arise, and it would enhance the probability that the new population would, given time, evolve another unique distribution of allelic frequencies. However, this new population would most likely not “re-evolve” into the original Anastasia Island mouse because the outcome of evolution, according to Wright’s shifting balance model (1982a, 1982b), is the result of the interaction of selective forces and chance processes. Thus, even if all original genetic variation were reintroduced, and even if the selective forces operating now were identical to those operating in 1901 when the last collections were made, chance events would probably drive the population to a new adaptive peak. The new population would eventually adapt to the conditions of life on Anastasia Island, but it would probably not be the same as the original population. The strategy of mixing genetic stocks would have the risk of causing outbreeding depression, so the best set of founders would probably be from coastal and insular populations near Anastasia Island. If the motive for reintroduction was to replicate a rare population to enhance its chances of survival, as has been conducted with insular populations of *P. polionotus* in Florida (Holler and Maison, 1987; Holler et al., 1989), then perhaps mice from Amelia Island could be introduced because they appear to be the most genetically divergent insular form (Fig. 2). However, the low cophenetic correlation (0.83) indicates that a relatively large amount of the variance in the genetic similarity matrix has not been explained by the branching pattern shown in the dendrogram, and therefore we have little confidence in the branching pattern. Thus, all populations with a genetic similarity of less than an arbitrary value of, for example, 0.92 or 0.93, should probably be considered equally divergent.

*Spatial variance partitioning.*—Genetic and morphometric variance in this species is finely partitioned, and the distribution patterns of the variance are not correlated with the

geographic distribution patterns of the populations. This degree and pattern of variance partitioning illuminates a potentially very important concept for conservation because it is contrary to the typical view of generally homogeneous populations on a local scale, but with regional differentiation. The degree of differentiation shown by *P. gossypinus* is much more than is usually observed among mammals. In these mice, adjacent populations are generally as different from one another as they are from distant populations. These populations are so divergent that adequately conserving them requires regional strategies that are generally unlike current conservation practices. For example, all populations within a subspecies are usually treated as if they were the same, and efforts to conserve a subspecies such as *P. g. gossypinus* would probably result in the establishment of a refuge and the protection of one, or at most, a few populations. *P. g. gossypinus* would be protected, but a great deal of the variation within the subspecies would not be represented in the refuge. The spatial pattern of genetic differentiation seen here suggests that important genetic combinations will be lost if only one, or even a few, populations are protected. In addition, Smith, et al. (1984) found that allele frequencies change in *P. g. gossypinus* over relatively short time periods. Thus, conserving less than the total amount of genetic diversity would decrease the potential for new allelic combinations to arise and would reduce the capability for dynamic temporal genetic changes. The capability to undergo spatial and temporal genetic changes is necessary for the evolution of a species. A closer examination of variance partitioning in other species is needed to determine the generality of the type of pattern seen in *P. gossypinus*. If this pattern of variance partitioning is general, conservation programs should shift their focus to regional scales where many populations, and their capability for dynamic genetic change, would be conserved.

*Science vs politics.*—Assigning subspecific status to a population or group of populations is scientifically useful when that status aids in understanding the evolutionary history of a species. Subspecific status implies that significant divergence has occurred, and that given time and some degree of continued isolation, the subspecies may continue to



diverge and become distinct species. Subspecific status also implies that the populations so designated are different from other subspecies, and, although incorrectly, that the populations within a subspecies are fairly homogeneous. Removing subspecific status from a population seems scientifically "correct" when that status does not aid in understanding the organism's evolutionary history or when there is no rational way to assign subspecific status. For the taxonomist who is also concerned about conservation, however, there is a dilemma when the organism under study is used as a reason for habitat preservation. Legal protection for organisms is usually granted only to species and subspecies, and the desire to protect habitat often involves searching for threatened or endangered subspecies. Removing subspecific status from a protected organism may also remove protection from its habitat and all of the organisms with which it coexists, possibly resulting in undesirable development and loss of the habitat. This dilemma leads one to suggest that there should be a method of habitat protection where habitat can be protected for its own value and not simply because it provides living space for a protected organism. If habitat was protected in this way, the issues of assigning scientifically informative taxonomic status and political decisions concerning habitat preservation would be separated. Habitat could still be protected because it provided living space for rare biota, but this would not necessarily be the only criteria for habitat protection.

Removing subspecific status from the mice on Cumberland Island, *P. g. anastasiae*, and grouping them with *P. g. gossypinus*, does not imply that the Cumberland Island mice are genetically or morphologically identical, or even similar, to any other population or subspecies of *P. gossypinus*. Genetically, the Cumberland Island mice are unique, they are well differentiated from other populations, and they represent a genetic resource that deserves conservation and further study. It is likely that other biota on the islands will be found to be genetically differentiated. Rowland (1989) conducted a genetic study of the White-tail deer (*Odocoileus virginianus*) on Cumberland Island and found them to be significantly different from deer on the mainland, and the deer on Black Beard Island just

north of Sapelo are the most genetically divergent of any white-tail deer population studied (Hillestad, 1984). Thus, if our goal is to conserve the maximum amount of biological diversity, then conservation of the island habitats is particularly important because they contain the most genetically divergent populations, even if they do not provide habitat for any known unique subspecies.

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**Appendix 1.** Individual-specific collection site information.

Animals included for genetic analysis are listed by Jim Boone's collection number, location, date collected, and number collected.

<u>ID Numbers</u>	<u>location</u>	<u>date</u>	<u>n</u>	<u>total</u>
001 to 032	Camden Co., GA. 1.5 mi S Ent. to Crooked River SP	1Mar88	32	
407 to 413	Camden Co., GA. 1.5 mi S Ent. to Crooked River SP	6Aug88	7	39
033 to 077	Jekyll Island, Glynn Co., GA	11Mar88	45	45
078 to 108	St. Simons Island, Glynn Co., GA	13Mar88	31	31
109 to 137	SE of Altamaha Campground, Everett, Glynn Co., GA	16Mar88	29	29
158 to 175	Sapelo Island (south), McIntosh Co., GA	26Jun88	18	
236 to 246	Sapelo Island (south), McIntosh Co., GA	16Jul88	11	29
247 to 301	Cumberland Island, Camden Co., GA	22Jul88	55	55
	south: 249-262, 291-301; north: 247-248, 263-290			
302 to 305	Northern Nassau Co., FL.	27Jul88	4	
	302-4. N bank St. Marys R. at FL Rt. 2 (= GA 94)			
	305. Fla 121 3 mi S Hwy 301			
414 to 431	414-418: Hwy 121A 0.6 mi N Hwy 1087	Aug88	18	22
	419-422: Hwy 121A 11.8 mi N Hwy 108			
	423-425: Hwy 121A 2.3 mi N Hwy 108			
	426: Hwy 108 3.5 mi E Hwy 115A			
	427: Hwy 108 0.2 mi W 115A			
	428: Hwy 108 2.0 mi E Hwy 121A			
	429: Hwy 121A 9.1 mi N hwy 108			
	430-431: 1.5 mi W Agri. Inspect. Stn. off Hwy 17			
338 to 359	Gulf Hammock, Levy Co., FL	29Jul88	22	22
	338-345. jct Hwy 19 & 336			
	346-348. Gulf Hammock Quarry			
	349-359 3 mi N jct Hwys 121 & 19			
360 to 371	Dunnellon, FL	29Jul88	12	12
	360-361. Sumter Co. Rt 44 E Withlacoochee R.			
	362-366. Sumter Co. Rt 44 1 mi E Withlacoochee R			
	367-368. Marion C .25 mi W jct Hwy 475 and 484			
	369-371. Citrus Co. Rt 39 3.8 mi E Hwy 41			
432 to 447	Okefenokee Swamp, Fargo area, Clinch Co., GA	8Aug88	16	
	432: Hwy 177 3.0 mi N Hwy 441			
	433-434: Hwy 177 6.9 mi N Hwy 441			
	435-439: Hwy 177 at Sweet Water Creek			
	440-441: Hwy 94 2.9 mi E Hwy 441			
	442: Hwy 177 0.5 mi N Hwy 441			
	443-447: Hwy 441 at Suwannee River			
650 to 655	Okefenokee Swamp, Fargo area, Clinch Co., GA	22Jun89	6	22
502 to 524	Tuscaloosa, Tuscaloosa Co., AL	26Aug88	23	23
	502-507: Moody Swamp			
	508-524: Hwy 82 at Sipsey River			
602 to 606	Merritt Island NWR, Brevard Co., FL	30Jul88	5	
607 to 610	Merritt Island NWR, Brevard Co., FL	1Sep88	4	
716 to 723	Merritt Island NWR, Brevard Co., FL	23Jul89	8	
724 to 733	Merritt Island NWR, Brevard Co., FL	20Aug89	10	27
611 to 621	Choccolocco Game Mgmt. Area, Calhoun Co., AL	15Jan89	11	11
645 to 649	Amelia Island, Nassau Co., FL	23Jun89	5	
656 to 662	Amelia Island, Nassau Co., FL	24Jun89	7	12
	<b>TOTAL</b>			<b>379</b>



**Appendix 2.** Specimens examined for electrophoretic analysis.

All specimens were deposited at the University of Georgia Museum of Natural History.

*Peromyscus gossypinus anastasae*.—(n = 55) GEORGIA: Camden Co., Cumberland Island (55).

*Peromyscus gossypinus gossypinus*.—(n = 229) GEORGIA: Camden Co., 1.5 miles south of entrance to Crooked River State Park (39); Glynn Co., Jekyll Island, (45); St. Simons Island (31); Altamaha Campground north of Everett (29); McIntosh Co., Sapelo Island (29); Clinch Co., Okefenokee Swamp: Highway 177, 3.0 miles N Highway 441 (1); Highway 177, 6.9 miles N Highway 441 (2); Highway 177, at Sweet Water Creek (5); Highway 94, 2.9 miles E Highway 441 (2); Highway 177, 0.5 miles N Highway 441 (1); Highway 441 at Suwannee River (5); Fargo area (6). FLORIDA: Northern Nassau Co., N. bank, St. Marys River at Route 2 (= GA 94) (3); Route 121, 3 miles S Highway 301 (1); Highway 121A, 0.6 miles N Highway 1087 (5); Highway 121A, 11.8 miles N Highway 108 (4); Highway 121A, 2.3 miles N Highway 108 (3); Highway 108, 3.5 miles E Highway 115A (1); Highway 108, 0.2 miles W 115A (1); Highway 108, 2.0 miles E Highway 121A (1); Highway 121A, 9.1 miles N Highway 108 (1); 1.5 miles W Highway 17 Agricultural Inspection Station (2); Amelia Island (12).

*Peromyscus gossypinus megacephalus*.—(n = 34) ALABAMA: Calhoun Co., Choccolocco Game Management Area (11); Tuscaloosa Co., Moody Swamp (6); Highway 82 at Sipsey River (17).

*Peromyscus gossypinus palmarius*.—(n = 73) FLORIDA: Levy Co., junction Highways 19 and 336 (8); Gulf Hammock Quarry (3); 3 miles N junction Highways 121 and 19 (11); Sumter Co., Route 44, E bank Withlacoochee River (2); Route 44, 1 mile E Withlacoochee River (5); Marion Co., 0.25 miles W junction Highway 475 and 484 (2); Citrus Co., Route 39, 3.8 miles E Highway 41 (3); Brevard Co., Merritt Island National Wildlife Refuge (27).

### Appendix 3. Specimens examined for morphological analysis.

Acronyms for museums are defined in the Acknowledgements.

*Peromyscus gossypinus anastasae*.—(n = 97) GEORGIA: Camden Co., Cumberland Island (6 AMNH, 4 CM, 7 DMNH, 68 UGA); FLORIDA: St Johns Co., Anastasia Island (8 FMNH, 3 USNM, 1 MCZ).

*Peromyscus gossypinus megacephalus*.—(n = 135) ALABAMA: DeKalb Co., Mentone (3 USNM, 1 LSUMZ); Ft. Payne (2 USNM); Buck's Pocket (2 USNM); Jackson Co., Scottsboro (1 USNM); Woodville (24 USNM); Sand Mountain near Carpenter (1 USNM); Bessemer (1 UAL); Marshall Co., Guntersville (2 USNM); Guntersville, Sand Mountain (2 USNM); Calhoun Co., Choccolocco Wildlife Management Area (4 UGA); Tuscaloosa Co., 7 miles E Tuscaloosa (2 UAL); 8 acre rock (1 UAL); Big Sandy Creek (3 UAL); Big Sandy Springs (5 UAL); Bryce Branch Ravine (10 UAL); Bryce Lake (1 UAL, Bryce Lake area (1 UAL); Canebrake (1 UAL); Lock 13 (1 UAL); Lock 14 (1 UAL); Lock 14, Warrior River (4 UAL); Moody Swamp (36 UAL); Riverside (1 UAL); Sandy Springs (1 UAL); Tidewater, 4 miles N Lock 14 (1 USNM); Tuscaloosa (7 UAL); University Arboretum (1 UAL); Warrior River (6 UAL); no specific location (9 UAL).

*Peromyscus gossypinus gossypinus*.—(n = 346) FLORIDA: Nassau Co., Amelia Island (24 AMNH, 5 UGA); 1.5 miles W Highway 17 Agricultural Inspection Station (2 UGA); 0.25 miles S Mulberry Landing on FL 121 (1 UGA); Highway 121A, 11.8 miles N Highway 108 (1 UGA); Highway 108, 0.2 miles W Highway 115A (1 UGA); Highway 108, 2 miles E Highway 121A (1 UGA); Highway 108, 3.5 miles E Highway 115A (1 UGA); Highway 121A, 0.6 miles N Highway 108 (4 UGA); Highway 121A, 11.8 miles N Highway 108 (2 UGA); Highway 121A, 2.3 miles N Highway 108 (2 UGA); Highway 121A, 9.1 miles N Highway 108 (1 UGA); N side bridge over St. Marys River (3 UGA). GEORGIA: Camden Co., 1.5 miles S Crooked River State Park (9 UGA); no specific location (15 UGA); no specific location (9 MCZ); St. Marys (1 USNM); St. Marys (7 UGA); Charlton Co., 1 mile S Camp Cornelia on Ga 23 (2 UGA); Camp Cornelia (4 UGA, 1 USNM); Camp Cornelia Dump (2 UGA); Chessers Island (1 ANSP); Cowhouse Island, 7 miles S Lydia Road (2 UGA); Floyd Island (8 AMNH, 2 USNM, 4 ANSP, 1 UGA); Okefenokee (6 KU); The Pocket (5 UGA); Clinch Co., Dinner Pond Lake (2 USNM); Fargo (8 UGA); Highway 177, 0.5 miles N Highway 441 (3 UGA); Highway 177 6.9 miles N 441 (2 UGA); Highway 177 at Sweetwater Creek (1 UGA); Highway 94 2.9 miles E Highway 441 (1 UGA); Okefenokee (1 ANSP, 1 JMM, 11 UGA); Cypress Creek (2 UGA); Suwannee River at Highway 441 (2 UGA); Glynn Co., Everett, Altamaha Camp (2 UGA); Sterling (3 MCZ); no specific location (18 UGA); Jekyll Island (43 UGA);

McIntosh Co., 15 miles N Darien (8 CM); 2 miles E Eulonia (2 CM); Barrington (3 MCZ); Sapelo Island (34 UGA); St. Simons Island (18 UGA); Ware Co., 11 miles SE Waycross (1 UI); Blackgum swamp (20 UGA); Blackgum swamp, site 32 (12 UGA); Cane Creek Bridge (2 UGA); drift fence site (1 UGA); Minne's Island (2 UGA); Okefenokee (2 ANSP, 1 UGA); Site C, W side Okefenokee (2 UGA); Soldier Camp (9 UGA); Surveyors Creek (1 UGA); Waycross (1 UGA).

*Peromyscus gossypinus palmarius*.—(n = 105) FLORIDA: Brevard Co., Cape Canaveral (1 AMNH); Merritt Island National Wildlife Refuge (6 UGA); E. Peninsula opposite Micco (1 AMNH, 3 FMNH); Route 1, 4 miles E EauGalli (6 CH); Micco (4 FMNH); Citrus Co., Homsassa Springs (11 AMNH); Route 39, 3.8 miles E Highway 41 (1 UGA); Crystal River (5 FMNH); Levy Co., 1 mile S Watson bridge (1 FSM); 2 miles N Gulf Hammock (2 AMNH); 2 miles S Gulf Hammock Quarry (2 UGA); 3 miles N junction Highways 121 and 19 (4 UGA); 6 miles S Gulf Hammock (2 UGA); 7.8 miles SW Archer (1 FSM); Gulf Hammock (2 FSM); Highway 19 at 336 (5 UGA); Hudson Place (1 FSM, 11 FSM); Wekini Creek (3 FSM); Otter Creek (4 FSM); Marion Co., 0.25 miles W junction Highway 475 and 484 (1 UGA); 1 mile S 8 miles E Silver Springs (1 CM); Juniper Springs (3 FMNH); St John's Co., Highway 16, 0.5 miles E St. Johns River (2 UGA); 0.7 miles S junction 13 and 16 at 6-mile Creek (3 UGA); 10.7 miles N Vilano Beach access road (3 FSM); 2 miles N St. Augustine (1 FSM); 2 miles W junction 206 and A1A (1 FSM); 3 miles W St. Augustine (2 UGA); 0.5 miles E St. Johns River on FL16 (6 UGA); Highway 208, 5 miles E junction Highway 13 (1 UGA); Highway 25, 0.5 miles E St. Johns River (1 UGA); Sumter Co., Route 44, 1 mile E Withlacoochee River (1 UGA); Route 44, E Withlacoochee River (2 UGA); Route 44, 1 mile E Withlacoochee River (1 UGA).

#### Appendix 4. Morphological measurements and definitions

The following 27 characters were measured on all specimens as defined. Measurements were taken on left (l), middle (m), and right (r) right side of the body.

##### External Measurements

1. Total body length: total length minus tail length (m)
2. Tail length (m): length of tail vertebra. (m)
3. Hind foot length: posterior edge of heel to distal tip of longest claw. (r)

##### Cranial Measurements

4. Skull length: anterior-most point of nasals to posterior-most point of skull. (m)
5. Basonasal length: anterior-most inferior border of foramen magnum to anterior-most point of nasals. (m)
6. Basilar length: posterior margin of incisive alveolus to anterior-most point of inferior border of foramen magnum. (m)
7. Rostral length: anterior-most point of nasals to anterior edge of zygomatic arch. (m)
8. Greatest rostral breadth: breadth across rostrum anterior to infraorbital foramen. (m)
9. Nasal length: along midline from anterior-most tip to posterior edge of suture. (m)
10. Interorbital constriction: least infraorbital distance. (m)
11. Zygomatic breadth: greatest width across zygomas. (m)
12. Greatest cranial breadth: across braincase posterior to zygomatic arches. (m)
13. Bony palate length (palatilar): posterior margin of incisive alveolus to posterior margin of palate. (m)
14. Palatal (incisive) foramen length. (m)
15. Posterior palatal length: posterior edge of palate to anterior edge of foramen magnum. (l)
16. Maxillary tooth row length: crown surface. (r)
17. Total tooth row length: crown surface of incisor to third upper molar. (r)
18. Maxillary diastema: posterior margin of incisive alveolus to anterior edge of first upper molar alveolus. (l)
19. Palatal width: between alveoli of first upper molar. (m)
20. Pterygoid breadth: least breadth between medial borders. (m)
21. Bullar length: long axis of bullae. (l)
22. Bullar width: narrow axis of bullae. (l)
23. Bullar depth (depth skull): highest surface of braincase to lowest surface of bullae. (m)
24. Mandibular tooth row length: crown surface of molars. (r)
25. Caranoid depth: tip of caranoid process to tip of angular process. (l)
26. Condylar depth: top of mandibular condyle to ventral border of angular process. (m)
27. Mandibular diastema. (m)

##### Schmidly's Age Group Classification

Age 1: third upper molar not completely erupted (does not reach the height of the first and second upper molars), juvenile pelage.

Age 2: third upper molar at full height of tooth row, little or no wear on cheek teeth, juvenile pelage.

Age 3: first and third upper molars partially worn, skin in juvenile pelage or molting into adult pelage.

Age 4: all major cusps worn smooth, cusp pattern identifiable, skin in adult pelage.

Age 5: heavy wear on all upper molars, cusps obliterated by wear, skin in adult pelage.

Age 6: extreme wear on all upper molars, all cusps obliterated, skin in adult pelage.

### Appendix 5. SAS program for sheared principle components analysis.

This SAS program performs a sheared principle components analysis using the method of Burnaby (1966). Program adapted from Bookstein et al. (1985) and was tested on data from Rohlf and Bookstein (1987).

```

OPTIONS LINESIZE=79;
  * Put Header Info Above If Necessary.....;
  * Data And Input Statements .....;
DATA SKULLS;          * ----[[[[[ Change As Necessary ]]]];
INPUT V1-V5;         * ----[[[[[ Change As Necessary ]]]];
CARDS;
  * Start Data Here.....;

;  * End Data Here .....;

PROC MATRIX;
  FETCH X DATA=SKULLS;  * Put SAS-dataset Into "X";
  NIND = NROW(X);       * Get # Individuals In Dataset;
  NGRP = X(NIND,1);     * Get # Groups In Dataset;
  NVAR = NCOL(X)-1;     * Get # Morph Variables In Dataset;

  D = DESIGN(X,(1));
  X = LOG10(X,(2:NVAR+1)); * Log10 Transform Data;
  C = X(.);            * Calculate Grand Centroid;

  * PC Analysis, Procedure & Notation Of Green (1978).....;
  ONES = J(NIND,1,1);  * Column Vector Of Ones;
  XD = X-ONES*C;      * XD Is Mean Corrected Data;
  S = XD'* XD;        * SSCP Of Mean Corrected Data;
  Q = S#/(NIND-1);    * Q = Total Covariance Matrix;
  EIGEN A E Q;        * Eigen Analysis Of Q;
  RETAIN = 4;         * -----[[[[[ Change As Necessary ]]]]-----;
  E = E(,1:RETAIN);   * Only Keep As Many Pc'S As Desired;
  PC = X * E;         * Calculate Principle Components;

  *Within-Grps Cov Mat, Procedure & Notation Of Green (1978).....;
  XG=(INV(D' * D))* D' * X; * Group Centroids;
  P=X-D*XG;          * Within-Gr Deviations From Centroid;
  W=P' * P;          * Within Groups SSCP Matrix;
  QP=W/#(NIND-NGRP); * Within Groups Covariance Matrix;

  * Apply Burnaby's Method.....;
  EIGEN AP EP QP;
  L = I(NVAR) - EP(,1)* INV(EP(,1)' * EP(,1))* EP(,1)';
  HPP = L* E;        * Burnaby Adjusted Vectors;
  XP = X* L;         * Adjusted Data;

  * Output Desired Matrices.....;
  PRINT HPP;
  PRINT XP;

```



Locus	Population													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Carbonic Anhydrase 2 (fluorescent, mobilities are approximate)														
(N)	27	12	55	45	31	29	12	22	22	37	29	23	11	
130	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	
100	1.00	1.00	0.89	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00	
Esterase 1 (Naphyl-AS-Acetate)														
(N)	27	12	54	45	31	29	12	22	21	22	39	28	23	11
173	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
160	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
147	0.02	0.00	0.26	0.00	0.05	0.00	0.04	0.09	0.07	0.07	0.09	0.14	0.02	0.00
131	0.00	0.00	0.00	0.01	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00
125	0.17	0.88	0.13	0.36	0.29	0.02	0.33	0.30	0.41	0.27	0.41	0.32	0.61	0.36
121	0.06	0.00	0.00	0.00	0.03	0.00	0.04	0.05	0.05	0.05	0.05	0.04	0.04	0.05
111	0.35	0.08	0.04	0.26	0.00	0.38	0.21	0.07	0.10	0.09	0.13	0.16	0.07	0.18
107	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.02	0.03	0.00	0.00	0.00
100	0.22	0.00	0.49	0.13	0.29	0.60	0.29	0.32	0.14	0.27	0.15	0.11	0.00	0.00
88	0.06	0.00	0.00	0.09	0.00	0.00	0.04	0.00	0.07	0.02	0.00	0.02	0.00	0.00
84	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00
73	0.07	0.04	0.00	0.14	0.18	0.00	0.04	0.09	0.17	0.21	0.14	0.20	0.26	0.41
Esterase 7 ( $\alpha$ -Naphyl Propionate)														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	22	11
128	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00
121	0.00	0.00	0.00	0.08	0.32	0.00	0.00	0.02	0.00	0.00	0.10	0.19	0.02	0.00
100	0.82	0.42	0.93	0.50	0.68	1.00	0.50	0.64	0.82	0.48	0.64	0.55	0.41	0.36
68	0.19	0.58	0.07	0.42	0.00	0.00	0.50	0.30	0.18	0.50	0.09	0.26	0.55	0.64
34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.02	0.12	0.00	0.02	0.00
Esterase $\beta$ NP ( $\beta$ -Naphyl Acetate)														
(N)	9	12	54	43	17	29	12	22	22	22	39	27	23	11
144	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
122	0.06	0.04	0.00	0.01	0.00	0.00	0.04	0.00	0.00	0.02	0.22	0.00	0.00	0.00
100	0.89	0.46	0.92	0.43	0.29	1.00	0.46	0.77	0.82	0.55	0.58	0.56	0.39	0.36
72	0.06	0.50	0.08	0.54	0.71	0.00	0.50	0.21	0.18	0.41	0.17	0.44	0.59	0.64
59	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.02	0.00	0.02	0.03	0.00	0.02	0.00
Esterase M ( $\alpha$ -Naphyl Propionate)														
(N)	8	12	37	44	31	23	7	17	20	21	38	26	22	11
111	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.02	0.00
103	0.00	0.00	0.00	0.00	0.08	0.00	0.07	0.00	0.00	0.02	0.00	0.02	0.18	0.00
100	0.31	0.92	0.00	0.71	0.50	0.67	0.57	0.44	0.75	0.55	0.29	0.69	0.11	0.18
91	0.19	0.04	1.00	0.19	0.00	0.33	0.21	0.27	0.25	0.41	0.63	0.00	0.46	0.82
86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.02	0.00
84	0.50	0.04	0.00	0.10	0.42	0.00	0.07	0.29	0.00	0.00	0.08	0.29	0.21	0.00
Fumarate Hydratase 2														
(N)	27	12	54	45	31	29	12	22	22	22	39	29	23	11
121	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00
100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96	1.00	1.00	0.95	0.97	1.00	1.00
72	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.05	0.00	0.00	0.00
General Plasma Protein 1														
(N)	27	12	55	44	31	29	12	22	22	22	37	29	23	11
100	0.46	0.00	0.96	0.99	0.98	0.97	0.92	0.11	1.00	0.73	0.99	1.00	0.17	0.00
98	0.32	0.63	0.03	0.01	0.02	0.03	0.08	0.89	0.00	0.27	0.01	0.00	0.52	0.64
96	0.22	0.38	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.36
94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00
Glucose Phosphate Isomerase														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	23	11
123	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00

Locus	Population													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<b>Glucose-6-Phosphate Dehydrogenase</b>														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	23	11
100	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
88	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Glutamate Dehydrogenase</b>														
(N)	26	12	54	45	30	29	12	22	22	22	39	29	23	11
107	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
100	0.98	1.00	0.96	0.98	0.98	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
92	0.02	0.00	0.04	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Glyceraldehyde Phosphate Dehydrogenase</b>														
(N)	27	12	55	45	31	28	12	22	22	22	39	29	23	11
105	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00
100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	1.00	1.00
<b><math>\alpha</math>-Glycerophosphate Dehydrogenase</b>														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	23	11
110	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
103	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
100	1.00	0.96	1.00	0.99	1.00	0.95	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00
88	0.00	0.00	0.00	0.01	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Isocitrate Dehydrogenase 1</b>														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	23	11
127	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.02	0.00	0.00	0.00	0.00
100	0.96	1.00	1.00	0.77	1.00	1.00	0.92	1.00	0.98	0.96	0.94	1.00	1.00	1.00
71	0.04	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.02	0.02	0.06	0.00	0.00	0.00
45	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Lactate Dehydrogenase 1</b>														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	23	11
102	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.12	0.00	0.00	0.00
100	1.00	0.96	1.00	0.96	0.87	0.97	1.00	1.00	0.96	0.91	0.87	0.98	1.00	1.00
98	0.00	0.00	0.00	0.04	0.03	0.03	0.00	0.00	0.02	0.07	0.01	0.02	0.00	0.00
91	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Malic Enzyme (mobilities are approximate due to short total distance moved)</b>														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	23	11
133	0	0.00	0.00	0.02	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00
100	0.94	1.00	1.00	0.98	0.97	1.00	1.00	1.00	0.98	1.00	1.00	0.97	0.91	1.00
50	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.09	0.00
<b>Peptidase 1 (Leucyl-alanine)</b>														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	23	11
102	0.06	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.09	0.01	0.00	0.00	0.00
100	0.87	0.42	0.77	0.16	0.05	1.00	0.83	1.00	0.61	0.68	0.17	0.57	0.44	0.59
98	0.04	0.17	0.23	0.83	0.92	0.00	0.17	0.00	0.36	0.23	0.76	0.43	0.57	0.23
94	0.04	0.00	0.00	0.01	0.03	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.18
<b>Peptidase 2 (Leucyl-alanine)</b>														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	23	11
113	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.05
105	0.00	0.29	0.01	0.01	0.24	0.19	0.00	0.00	0.07	0.09	0.00	0.05	0.02	0.00
100	0.93	0.71	0.99	0.99	0.76	0.81	1.00	0.98	0.91	0.91	1.00	0.95	0.98	0.96
95	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00
<b>Peptidase 3 (Leucyl-glycyl-glycine)</b>														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	23	11
111	0.02	0.00	0.00	0.23	0.00	0.17	0.00	0.07	0.02	0.02	0.19	0.03	0.00	0.00
100	0.94	1.00	1.00	0.77	1.00	0.83	1.00	0.93	0.96	0.93	0.80	0.95	1.00	1.00
87	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.02	0.00	0.00
84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00



Locus	Population													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<b>Peptidase 4 (Leucyl-alanine)</b>														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	23	11
102	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.03	0.00	0.00	0.00
100	1.00	1.00	1.00	1.00	0.71	1.00	1.00	1.00	1.00	0.96	0.97	0.97	1.00	1.00
93	0.00	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00
85	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Phosphoglucomutase 1</b>														
(N)	27	12	54	44	28	29	12	22	22	22	39	29	23	11
105	0.02	0.00	0.08	0.00	0.00	0.00	0.08	0.21	0.00	0.00	0.01	0.02	0.07	0.00
100	0.67	0.96	0.89	0.49	0.95	0.28	0.67	0.68	0.73	0.66	0.68	0.60	0.76	1.00
95	0.32	0.04	0.03	0.51	0.05	0.72	0.25	0.11	0.27	0.34	0.31	0.38	0.17	0.00
<b>Phosphoglucomutase 3</b>														
(N)	27	12	54	45	31	29	12	22	22	22	39	29	23	11
100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	0.97	1.00	1.00
68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.03	0.00	0.00
<b>6-Phosphogluconate Dehydrogenase</b>														
(N)	27	12	55	45	31	29	12	22	22	22	39	29	23	11
125	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
100	0.96	1.00	1.00	0.94	0.95	1.00	1.00	0.89	0.93	0.96	0.97	1.00	1.00	1.00
75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.05	0.00	0.00	0.00	0.00
65	0.00	0.00	0.00	0.06	0.05	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
<b>Post Albumin Protein</b>														
(N)	27	12	54	45	31	29	12	22	22	22	37	29	23	11
100	0.83	0.88	0.94	0.94	1.00	0.88	1.00	1.00	0.89	0.96	0.97	1.00	0.85	0.96
97	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
93	0.11	0.00	0.06	0.06	0.00	0.10	0.00	0.00	0.11	0.05	0.03	0.00	0.09	0.05
91	0.06	0.13	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00
<b>Purine Nucleoside Phosphorylase (mobilities are approximate due to short distance moved)</b>														
(N)	27	12	54	45	31	29	12	22	22	22	39	29	23	11
333	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
226	0.19	0.04	0.43	0.19	0.19	0.07	0.21	0.23	0.21	0.09	0.05	0.19	0.07	0.00
100	0.72	0.50	0.57	0.80	0.81	0.93	0.79	0.75	0.77	0.91	0.91	0.74	0.94	1.00
-100	0.06	0.46	0.00	0.01	0.00	0.00	0.00	0.02	0.02	0.00	0.04	0.03	0.00	0.00
-400	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00
<b>Sorbitol Dehydrogenase</b>														
(N)	27	12	54	45	31	29	12	22	22	22	39	29	23	11
100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00
93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00
<b>Superoxide Dismutase 2</b>														
(N)	27	12	54	45	31	29	12	22	22	22	39	29	23	11
100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	0.98	1.00	1.00	1.00	1.00	1.00
88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.00	0.00
<b>Transferrin</b>														
(N)	27	12	54	45	31	29	12	22	22	22	37	29	23	11
128	0.11	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00
114	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00
100	0.89	1.00	0.99	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.93	1.00	1.00

### Appendix 7. Matrices of Rogers' and Nei's genetic distances.

Matrices of Rogers' (1972) and Nei's (1972) genetic distance and similarities, and Nei's (1978) unbiased genetic identity and unbiased genetic distance.

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Rogers' (1972) genetic similarity below diagonal, and genetic distance above diagonal.

Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Merritt	—	.104	.081	.095	.109	.077	.069	.061	.059	.070	.085	.070	.097	.105
2 Amelia	.896	—	.134	.108	.111	.131	.086	.103	.094	.088	.120	.093	.088	.087
3 Cumberland	.919	.866	—	.106	.111	.082	.078	.083	.070	.086	.083	.088	.112	.106
4 Jekyll Island	.905	.892	.894	—	.075	.089	.056	.101	.062	.061	.055	.052	.091	.110
5 St. Simons	.891	.889	.889	.925	—	.119	.079	.110	.082	.083	.076	.070	.111	.124
6 Sapelo	.923	.869	.918	.911	.881	—	.078	.097	.069	.079	.089	.085	.125	.127
7 Dunnellon	.931	.914	.922	.944	.921	.922	—	.067	.050	.037	.065	.044	.081	.087
8 Gulf Ham.	.939	.897	.917	.899	.890	.903	.933	—	.072	.068	.088	.077	.097	.100
9 Nassau	.941	.906	.930	.938	.918	.931	.950	.928	—	.051	.060	.042	.091	.103
10 Okefenokee	.930	.912	.914	.939	.917	.921	.963	.932	.949	—	.058	.049	.077	.083
11 St. Marys	.915	.880	.917	.945	.924	.911	.935	.912	.940	.942	—	.061	.092	.107
12 Everett	.930	.907	.912	.948	.930	.915	.956	.923	.958	.951	.939	—	.087	.100
13 Tuscaloosa	.903	.912	.888	.909	.889	.875	.919	.903	.909	.923	.908	.913	—	.046
14 Choccolocco	.895	.913	.894	.890	.876	.873	.913	.900	.897	.917	.893	.900	.954	—

Nei's (1972) genetic identity below diagonal, and genetic distance above diagonal.

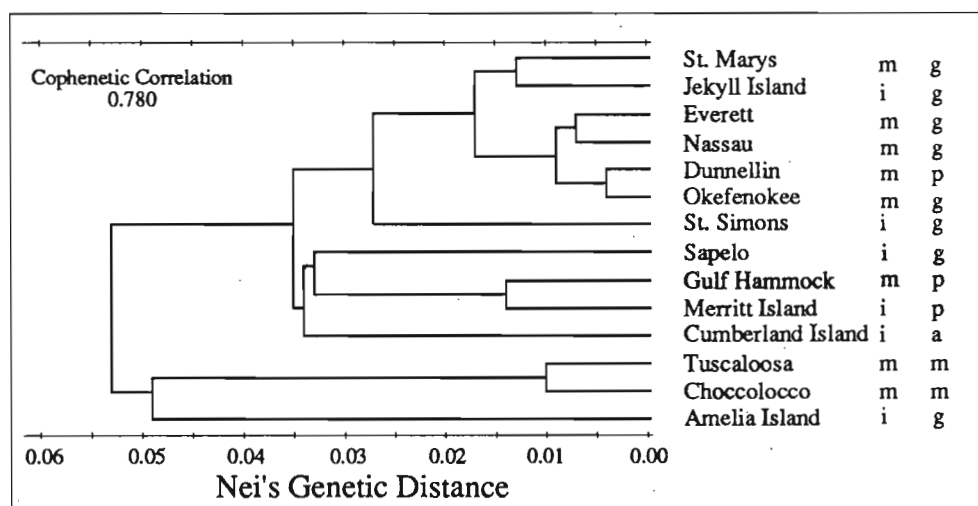
Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Merritt	—	.043	.029	.039	.051	.024	.019	.014	.018	.018	.032	.020	.047	.055
2 Amelia	.958	—	.082	.052	.061	.082	.040	.037	.043	.034	.060	.042	.046	.052
3 Cumberland	.971	.921	—	.051	.057	.034	.030	.039	.025	.029	.028	.038	.057	.059
4 Jekyll	.961	.949	.950	—	.023	.043	.018	.054	.017	.017	.013	.010	.043	.063
5 St. Simons	.950	.941	.944	.977	—	.069	.032	.063	.030	.032	.024	.020	.058	.080
6 Sapelo	.977	.922	.966	.958	.934	—	.027	.042	.021	.026	.039	.029	.073	.080
7 Dunnellon	.981	.961	.970	.982	.969	.973	—	.026	.010	.004	.022	.007	.039	.047
8 Gulf Ham.	.986	.964	.962	.948	.939	.958	.975	—	.031	.020	.047	.034	.042	.044
9 Nassau	.983	.958	.976	.983	.970	.979	.990	.969	—	.010	.015	.007	.048	.061
10 Okefenokee	.982	.966	.972	.983	.969	.974	.996	.980	.990	—	.017	.010	.032	.038
11 St. Marys	.968	.942	.973	.987	.976	.962	.978	.954	.985	.983	—	.017	.042	.057
12 Everett	.980	.959	.963	.990	.980	.971	.993	.966	.993	.990	.983	—	.043	.060
13 Tuscaloosa	.954	.955	.945	.958	.944	.930	.962	.959	.954	.968	.959	.958	—	.010
14 Choccolocco	.946	.950	.942	.939	.923	.923	.954	.957	.941	.963	.944	.942	.990	—

Nei's (1978) Unbiased Genetic Identity below diagonal, and Unbiased Genetic Distance  
above diagonal.

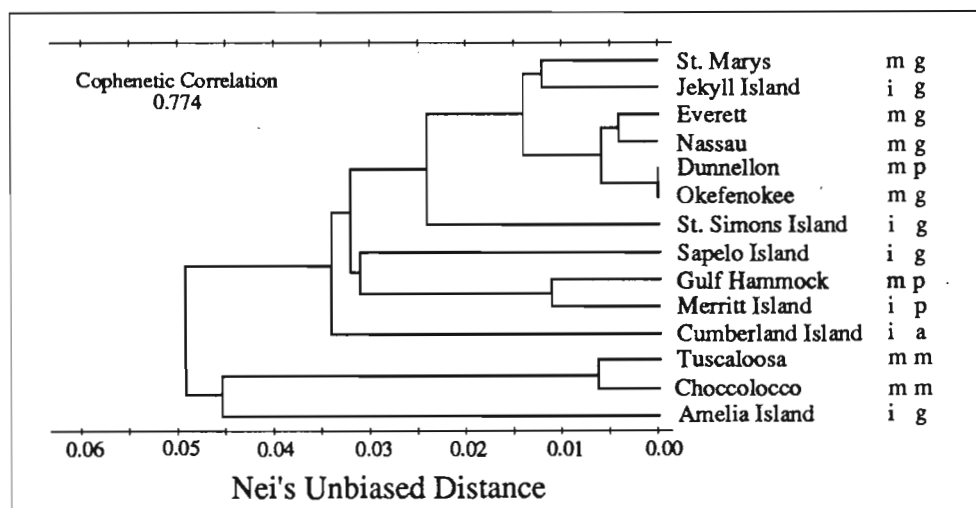
Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Merritt	—	.039	.027	.037	.048	.021	.015	.011	.014	.014	.030	.017	.043	.051
2 Amelia	.962	—	.079	.049	.057	.079	.034	.033	.039	.030	.057	.038	.042	.047
3 Cumberland	.973	.924	—	.050	.056	.033	.027	.037	.023	.027	.026	.036	.055	.057
4 Jekyll	.964	.952	.951	—	.021	.041	.015	.051	.015	.014	.012	.008	.041	.060
5 St. Simons	.953	.944	.946	.979	—	.067	.028	.060	.028	.029	.022	.018	.056	.077
6 Sapelo	.979	.924	.967	.959	.935	—	.023	.040	.019	.024	.037	.027	.070	.077
7 Dunnellon	.985	.966	.973	.985	.972	.977	—	.021	.006	.000	.019	.003	.034	.042
8 Gulf Ham.	.989	.968	.964	.950	.941	.961	.979	—	.028	.017	.044	.031	.039	.040
9 Nassau	.986	.962	.977	.985	.973	.981	.994	.972	—	.007	.013	.004	.045	.057
10 Okefenokee	.986	.970	.974	.986	.971	.976	1.000	.983	.993	—	.014	.007	.029	.034
11 St. Marys	.971	.945	.974	.988	.978	.963	.982	.957	.987	.986	—	.015	.040	.054
12 Everett	.983	.962	.964	.992	.982	.973	.997	.969	.996	.993	.985	—	.040	.057
13 Tuscaloosa	.958	.959	.946	.960	.946	.932	.966	.962	.956	.971	.961	.960	—	.006
14 Choccolocco	.950	.954	.945	.942	.926	.925	.959	.960	.945	.966	.947	.945	.994	—

### Appendix 8. Genetic dendrograms.

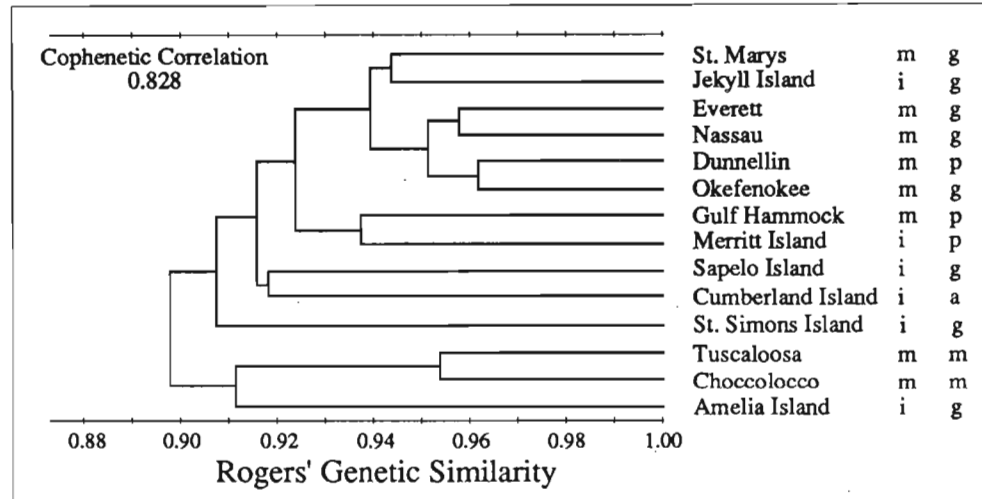
Dendrograms based on UPGMA clustering of matrices formed from Nei's Distance, Nei's Unbiased Distance, and Rogers' Similarity. Symbols to the right of population names indicate whether the population is insular (i) or mainland (m), and to which subspecies the population belongs: *anastasiae* (a), *gossypinus* (g), *palmarius* (p), or *megacephalus* (m).



Dengrogram based on Nei's (1972) genetic distance.



Dengrogram based on Nei's (1972) unbiased genetic distance.



Dendrogram based on Rogers' (1972) genetic similarity. This dendrogram differs from that in Fig. 2 in that this shows the original ordering of populations presented by BIOSYS. For comparative purposes, recall that  $D = 1 - S$ , where  $D$  is Rogers distance and  $S$  is Rogers' similarity.

**Appendix 9.** Comparisons of means for total, foot, and skull lengths.

Twenty populations arrayed in order of increasing mean total length. Vertical lines beside the table indicate sets of means that are not significantly different from each other as determined by Fisher's least significant difference test using alpha of 0.05. Symbols are as follows: 1 = subspecies: *Peromyscus gossypinus anastasiae* (a), *P. g. gossypinus* (g), *P. g. palmarius* (p), and *P. g. megacephalus* (m); and 2 = island (i) or mainland (m).

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Population	19	23740.44	1249.50	8.55	0.0001
Residual	572	83588.54	146.13		

Dependent: total length (mm)

	1	2	Count	Mean	Fisher's LSD
Sapelo Island	g	i	32	155.1	
Anastasia Island	a	i	11	159.5	
Jekyll Island	g	i	43	159.5	
St.Simons Island	g	i	15	159.5	
Cumberland Island	a	i	67	161.0	
Everett	g	m	21	161.5	
Amelia Island	g	i	29	163.0	
Ware	g	m	50	163.3	
St. Johns	p	i	19	164.9	
Gulf Hammock	p	i	38	165.7	
Tuscaloosa	m	m	52	167.0	
Merritt Island	p	i	6	167.5	
Nassau	g	m	19	168.7	
Okefenokee	g	m	27	169.1	
St. Marys	g	m	36	169.3	
McIntosh	g	m	13	170.0	
Dunnellon	p	m	26	171.4	
Charlton	g	m	34	178.1	
Brevard	p	m	10	178.3	
Choccolocco	m	m	37	178.8	

Twenty populations arrayed in order of increasing mean hind foot length. Vertical lines beside the table indicate sets of means that are not significantly different from each other as determined by Fisher's least significant difference test using alpha of 0.05. Symbols are as follows: 1 = subspecies: *Peromyscus gossypinus anastasiae* (a), *P. g. gossypinus* (g), *P. g. palmarius* (p), and *P. g. megacephalus* (m); and 2 = island (i) or mainland (m).

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Population	19	133.34	7.02	4.98	0.0001
Residual	569	802.51	1.41		

Dependent: foot length (mm)

	1	2	Count	Mean	Fisher's LSD
Sapelo Island	g	i	32	20.9	
Merritt Island	p	i	6	21.2	
Anastasia Island	a	i	11	21.3	
Tuscaloosa	m	i	52	21.3	
Cumberland Island	a	i	67	21.5	
Amelia Island	g	m	29	21.7	
Jekyll Island	g	i	43	21.7	
Ware	g	m	50	21.7	
St. Johns	p	i	19	21.8	
St. Marys	g	i	37	22.0	
Dunnellon	p	m	26	22.0	
Nassau	g	i	19	22.1	
Everett	g	m	23	22.1	
St. Simons	g	m	15	22.1	
Brevard	p	m	10	22.1	
Okefenokee	g	m	28	22.3	
Gulf Hammock	p	m	38	22.4	
Charlton	g	m	34	22.4	
Choccolocco	m	m	37	22.5	
McIntosh	g	m	13	23.4	

Twenty populations arrayed in order of increasing mean skull length. Vertical lines beside the table indicate sets of means that are not significantly different from each other as determined by Fisher's least significant difference test using alpha of 0.05. Symbols are as follows: 1 = subspecies: *Peromyscus gossypinus anastasiae* (a), *P. g. gossypinus* (g), *P. g. palmarius* (p), and *P. g. megacephalus* (m); and 2 = island (i) or mainland (m).

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Population	19	99.02	5.21	6.69	0.0001
Residual	652	507.83	0.78		

Dependent: greatest length of skull (mm)

	1	2	Count	Mean	Fisher's LSD
Anastasia Island	a	i	6	26.3	
Sapelo Island	g	i	30	26.7	
Everett	g	m	23	27.3	
St. Simons	g	i	17	27.5	
Brevard	p	m	14	27.5	
Merritt Island	p	i	7	27.6	
Amelia Island	g	i	28	27.6	
Dunnellon	p	m	26	27.6	
Gulf Hammock	p	m	38	27.7	
Ware	g	m	54	27.7	
Clinch	g	m	33	27.8	
Nassau	g	m	19	27.8	
St. Johns	p	m	20	27.8	
Cumberland Island	a	i	84	27.9	
St. Marys	g	m	41	28.0	
McIntosh	g	m	13	28.0	
Tascaloosa	m	m	92	28.0	
Jekyll Island	g	i	40	28.1	
Charlton	g	m	38	28.1	
Choccolocco	m	m	41	28.5	



**Appendix 10.** Summary statistics for 27 morphological characters.

Summary statistics for 27 morphological characters in 20 populations of *Peromyscus gossypinus* sorted by mean. Entries in the table are population (pop), sample size per character (n), range (minimum to maximum), mean, and standard error (se). All measurements are in mm. Population designations are as follows: Merr = Merritt Island, Anas = Anastasia Island, Amel = Amelia Island, Cumb = Cumberland Island, Jeky = Jekyll Island, StSi = St. Simons Island, Sape = Sapelo Island, Brev = Brevard, StJo = St. Johns, Dunn = Dunnellon, GuHa = Gulf Hammock, Nass = Nassau, Okef = Okefenokee, Ware = Ware, Char = Charlton, StMa = St. Marys, Ever = Everett, McIn = McIntosh, Tusc = Tuscaloosa, and Choc = Choccolocco. In addition, i = island, and m = mainland.

Total Length						Tail Length					
	pop	n	range	mean	se		pop	n	range	mean	se
i	Sape	32	136-189	155.1	1.611	i	Sape	32	51.0-85.0	63.0	1.069
i	Anas	10	142-167	158.3	2.629	i	Jeky	43	44.0-78.0	64.0	1.024
i	Jeky	43	140-191	159.5	2.008	i	Cumb	67	52.0-76.0	64.6	0.751
i	StSi	15	143-178	159.5	2.522	i	Anas	10	54.0-71.0	65.3	1.562
i	Cumb	67	131-187	161.0	1.271	i	StSi	15	58.0-78.0	66.8	1.771
m	Ever	21	150-196	161.5	2.481	i	Amel	29	55.0-84.0	66.9	1.185
i	Amel	29	146-185	163.0	2.068	m	Ever	22	58.0-87.0	66.9	1.405
m	Ware	50	144-198	163.3	1.887	m	Nass	19	61.0-78.0	67.7	1.094
m	StJo	19	150-185	164.9	2.122	m	StJo	19	51.0-78.0	68.0	1.447
m	GuHa	38	140-193	165.7	2.151	m	GuHa	38	55.0-85.0	68.4	1.157
m	Tusc	52	142-190	167.0	1.937	m	Dunn	26	55.0-78.0	69.1	1.218
i	Merr	6	159-172	167.5	1.979	m	Ware	50	57.0-83.0	69.2	0.946
m	Nass	19	154-182	168.7	1.661	m	StMa	36	54.0-84.0	69.2	1.306
m	Okef	27	140-205	169.1	2.838	m	McIn	13	63.0-84.0	71.1	1.693
m	StMa	36	147-217	169.3	2.522	i	Merr	6	65.0-76.0	71.2	1.778
m	McIn	13	160-183	170.0	2.115	m	Okef	27	60.0-88.0	71.2	1.381
m	Dunn	26	145-192	171.4	2.244	m	Tusc	52	53.5-86.0	71.9	1.080
m	Char	34	150-206	178.1	2.090	m	Char	34	63.0-88.0	74.7	1.198
m	Brev	10	157-195	178.3	4.232	m	Choc	37	57.0-92.0	76.7	1.268
m	Choc	37	150-205	178.8	1.947	m	Brev	10	71.0-94.0	78.5	2.404

## Body Length

pop	n	range	mean	se
i Sape	32	78-104	92.2	1.066
i StSi	15	75-108	92.7	2.144
m Ware	50	76-116	94.2	1.326
i Anas	11	88-101	94.2	1.419
m Ever	21	87-109	94.6	1.186
m Tusc	52	78-111	95.2	1.177
i Jeky	43	82-113	95.5	1.280
i Amel	29	80-110	96.1	1.298
i Merr	6	92-105	96.3	1.874
i Cumb	67	67-114	96.4	0.861
m StJo	19	88-108	96.9	1.126
m GuHa	38	82-115	97.3	1.222
m Okef	27	78-117	97.9	1.941
m McIn	13	95-108	98.9	1.106
m StMa	43	83-133	99.6	1.451
m Brev	10	85-110	99.9	2.536
m Nass	19	93-107	101.0	0.795
m Choc	37	88-113	102.0	0.984
m Dunn	26	89-118	102.3	1.518
m Char	34	87-120	103.4	1.252

## Skull Length

pop	n	range	mean	se
i Anas	6	25.3-27.2	26.3	0.259
i Sape	30	24.4-27.9	26.7	0.146
m Ever	24	25.7-29.1	27.2	0.203
i StSi	17	26.0-28.9	27.5	0.231
m Brev	14	25.7-29.7	27.5	0.298
i Merr	7	26.4-29.1	27.6	0.315
i Amel	28	26.6-30.2	27.6	0.160
m Dunn	26	26.7-29.8	27.6	0.162
m GuHa	38	26.4-29.6	27.7	0.134
m Ware	54	26.2-29.7	27.7	0.105
m StJo	20	26.7-29.2	27.8	0.167
m Nass	19	26.7-28.7	27.8	0.148
m Okef	33	26.0-29.6	27.8	0.142
i Cumb	84	26.3-29.9	27.9	0.091
m StMa	41	26.4-30.2	28.0	0.139
m McIn	13	25.4-29.8	28.0	0.301
m Tusc	92	25.5-29.9	28.0	0.100
i Jeky	40	26.6-30.2	28.1	0.150
m Char	38	26.1-30.7	28.1	0.152
m Choc	41	26.7-30.0	28.5	0.143

## Hind Foot Length

pop	n	range	mean	se
i Sape	32	15.0-23.0	20.9	0.327
i Merr	6	20.0-22.0	21.2	0.307
i Anas	10	19.5-22.5	21.3	0.335
m Tusc	52	15.0-24.0	21.3	0.298
i Cumb	67	20.0-24.0	21.5	0.107
i Amel	29	20.0-24.0	21.7	0.137
i Jeky	43	19.0-24.0	21.7	0.144
m Ware	50	19.0-23.0	21.7	0.150
m StJo	19	20.0-24.0	21.8	0.271
m Dunn	26	20.0-24.0	22.0	0.172
m StMa	37	20.0-23.0	22.0	0.125
i StSi	15	21.0-24.0	22.1	0.236
m Nass	19	21.0-23.0	22.1	0.162
m Ever	23	21.0-24.0	22.1	0.170
m Brev	10	20.5-24.0	22.2	0.279
m Okef	28	20.0-26.0	22.3	0.225
m GuHa	38	19.0-24.0	22.4	0.162
m Char	34	20.0-24.0	22.4	0.198
m Choc	37	20.0-24.0	22.5	0.187
m McIn	13	21.0-25.0	23.4	0.331

## Basinasal Length

pop	n	range	mean	se
i Anas	6	22.7-24.5	23.6	0.237
i Sape	30	22.1-25.0	23.9	0.133
m Brev	14	22.8-27.0	24.7	0.324
i Merr	7	23.6-25.9	24.8	0.303
i StSi	16	23.0-26.5	24.8	0.288
i Amel	28	23.7-27.5	24.9	0.181
m GuHa	38	23.6-27.0	24.9	0.149
m Dunn	26	23.7-27.2	25.0	0.178
m Okef	33	23.0-26.8	25.0	0.149
m Ware	54	23.2-27.1	25.0	0.118
i Cumb	83	23.0-27.6	25.1	0.105
m Nass	19	23.5-26.1	25.1	0.169
m StJo	20	24.0-26.5	25.2	0.159
m Ever	24	22.7-32.4	25.2	0.380
m McIn	13	22.4-26.7	25.2	0.281
m Tusc	92	22.4-27.3	25.2	0.110
m StMa	41	23.7-27.7	25.3	0.166
i Jeky	39	23.5-27.8	25.4	0.182
m Char	38	23.2-27.9	25.5	0.146
m Choc	42	23.7-27.4	25.6	0.152

## Basilar Length

pop	n	range	mean	se	
i	Anas	9	18.4-20.2	19.5	0.174
i	Sape	34	18.5-21.7	20.2	0.136
m	Brev	14	19.0-22.1	20.5	0.254
i	Amel	29	19.6-22.5	20.6	0.133
i	Merr	7	19.7-21.4	20.7	0.215
i	StSi	17	19.4-22.2	20.7	0.233
m	Ever	24	19.5-22.4	20.7	0.152
m	Dunn	26	19.5-22.5	20.8	0.141
m	GuHa	38	19.8-22.6	20.8	0.114
i	Cumb	84	18.9-22.9	20.9	0.082
m	Nass	19	19.6-21.9	20.9	0.147
m	Ware	54	19.6-22.5	20.9	0.094
m	McIn	13	18.9-22.0	20.9	0.217
m	Okef	34	19.5-22.6	21.0	0.131
m	Tusc	92	18.9-22.6	21.0	0.090
m	StJo	20	20.0-22.2	21.1	0.127
m	StMa	41	19.8-23.2	21.1	0.137
i	Jeky	42	19.4-22.7	21.2	0.132
m	Choc	43	19.4-22.7	21.2	0.129
m	Char	38	19.5-23.5	21.3	0.121

## Rostral Breadth

pop	n	range	mean	se	
i	Anas	12	2.8-3.2	3.0	0.031
i	Merr	7	2.9-3.3	3.1	0.048
i	Jeky	43	2.9-3.4	3.1	0.024
i	Sape	34	2.7-3.6	3.1	0.035
m	Brev	14	2.9-3.2	3.1	0.031
m	StJo	20	2.9-3.4	3.1	0.031
m	Dunn	26	2.7-3.4	3.1	0.032
i	Amel	29	3.0-3.5	3.2	0.024
i	Cumb	85	2.8-3.6	3.2	0.017
m	GuHa	38	2.7-3.5	3.2	0.028
m	Nass	19	3.0-3.4	3.2	0.026
m	Okef	34	3.0-3.5	3.2	0.023
m	Ware	54	2.8-3.5	3.2	0.024
m	Char	38	2.7-3.6	3.2	0.035
m	StMa	41	2.9-3.5	3.2	0.030
m	Ever	24	2.9-3.5	3.2	0.034
m	McIn	13	2.8-3.7	3.2	0.064
m	Tusc	92	2.9-3.7	3.2	0.016
i	StSi	18	2.9-3.7	3.3	0.045
m	Choc	43	2.9-3.7	3.3	0.031

## Rostral Length

pop	n	range	mean	se	
i	Sape	30	7.4-8.7	8.2	0.062
i	Merr	7	7.9-9.1	8.5	0.194
i	Anas	9	7.8-9.0	8.5	0.126
m	Brev	14	7.6-10.0	8.6	0.169
i	StSi	17	7.8-9.3	8.7	0.115
m	Dunn	26	8.1-9.6	8.7	0.082
m	Nass	19	7.8-9.4	8.7	0.086
m	Ever	24	7.9-9.4	8.7	0.089
i	Amel	28	8.3-9.8	8.8	0.079
m	StJo	20	8.1-9.7	8.8	0.095
m	Ware	54	7.8-9.7	8.8	0.063
m	GuHa	38	8.3-10.0	8.9	0.065
m	Okef	33	7.9-10.0	8.9	0.088
m	Tusc	92	7.8-10.1	8.9	0.056
i	Cumb	84	8.0-10.6	9.0	0.057
i	Jeky	40	8.1-10.2	9.0	0.079
m	StMa	41	8.2-10.1	9.0	0.077
m	Char	38	8.0-10.2	9.1	0.085
m	McIn	13	8.4-10.4	9.1	0.137
m	Choc	42	8.2-10.4	9.3	0.080

## Nasal Length

pop	n	range	mean	se	
i	Anas	9	9.6-11.4	10.3	0.183
i	Sape	30	9.3-11.6	10.6	0.101
m	Brev	14	9.7-12.0	10.7	0.163
i	Amel	28	10.1-12.2	10.8	0.112
i	StSi	17	9.7-11.6	10.8	0.133
m	Dunn	26	9.9-12.1	10.8	0.115
m	Nass	19	10.0-11.5	10.8	0.112
m	Ever	24	9.7-12.6	10.8	0.137
m	GuHa	38	10.1-12.5	10.9	0.085
m	McIn	13	10.0-11.9	10.9	0.156
m	Tusc	92	9.5-11.9	10.9	0.066
m	StJo	20	10.3-11.6	11.0	0.082
m	Okef	33	9.9-12.2	11.0	0.100
m	Ware	54	9.7-12.0	11.0	0.076
m	Char	38	10.2-11.9	11.0	0.087
m	StMa	41	9.8-12.1	11.0	0.097
i	Cumb	85	10.0-12.9	11.1	0.059
i	Merr	7	10.3-11.9	11.2	0.207
m	Choc	42	10.2-13.0	11.3	0.094
i	Jeky	40	10.2-21.1	11.6	0.263

## Interorbital Constriction

pop	n	range	mean	se
i Sape	34	3.6-4.9	4.2	0.040
i Anas	12	4.1-4.6	4.3	0.047
i StSi	18	3.9-4.7	4.3	0.041
m Brev	14	4.2-4.6	4.3	0.037
m GuHa	38	4.0-4.7	4.3	0.028
m Ware	54	4.0-4.7	4.3	0.021
m Char	38	4.0-4.6	4.3	0.027
m Ever	24	4.0-4.8	4.3	0.031
m McIn	13	4.1-4.5	4.3	0.040
i Merr	7	4.1-4.8	4.4	0.084
i Amel	29	4.1-4.6	4.4	0.024
i Jeky	43	4.1-4.8	4.4	0.024
m StJo	19	4.1-4.7	4.4	0.043
m Dunn	26	4.1-5.0	4.4	0.034
m Nass	19	4.0-5.0	4.4	0.056
m Okef	34	4.1-4.8	4.4	0.025
m StMa	41	4.1-4.7	4.4	0.026
m Tusc	92	4.0-4.8	4.4	0.017
m Choc	43	4.0-4.7	4.4	0.020
i Cumb	85	4.1-4.9	4.5	0.015

## Cranial Breadth

pop	n	range	mean	se
i Anas	7	10.9-11.6	11.3	0.113
m Brev	13	10.8-12.1	11.5	0.097
i Amel	29	11.2-12.4	11.6	0.048
i Sape	33	10.5-12.0	11.6	0.053
m Ever	24	11.1-12.3	11.6	0.055
m Tusc	92	11.0-12.5	11.6	0.033
i Merr	7	11.2-12.1	11.7	0.125
i Jeky	43	11.1-12.4	11.7	0.042
m Choc	43	11.2-12.3	11.7	0.040
m StJo	20	11.1-12.4	11.8	0.068
m Dunn	26	11.2-12.7	11.8	0.069
m GuHa	38	11.3-12.8	11.8	0.056
m Nass	19	11.2-12.2	11.8	0.059
m Ware	53	11.0-12.6	11.8	0.045
i StSi	18	11.4-12.4	11.9	0.065
m Okef	33	11.3-12.7	11.9	0.069
m StMa	41	11.4-12.8	11.9	0.047
i Cumb	80	11.3-12.8	12.0	0.036
m Char	38	11.1-12.7	12.0	0.059
m McIn	13	11.3-12.7	12.1	0.123

## Zygomatic Breadth

pop	n	range	mean	se
i Anas	10	12.7-13.5	13.2	0.081
i Sape	30	12.4-14.1	13.6	0.067
m Brev	13	13.2-14.6	13.6	0.112
i Amel	29	13.0-14.8	13.7	0.085
m StJo	19	13.0-14.5	13.8	0.086
m Dunn	25	13.0-14.7	13.9	0.097
m GuHa	38	12.8-15.1	13.9	0.081
m Ever	23	13.2-15.4	13.9	0.099
m McIn	13	13.0-14.6	13.9	0.146
i Merr	7	13.5-14.4	14.0	0.149
m Ware	53	12.7-15.4	14.0	0.072
m Tusc	92	12.9-15.0	14.0	0.049
i Cumb	77	13.2-15.3	14.1	0.049
i Jeky	41	12.8-15.1	14.1	0.075
m Nass	19	13.4-14.6	14.1	0.078
m Okef	34	12.8-15.3	14.1	0.086
m StMa	38	13.1-15.3	14.1	0.091
m Choc	38	13.2-15.2	14.2	0.077
i StSi	17	13.4-15.3	14.3	0.119
m Char	35	13.1-15.7	14.3	0.097

## Bony Palate Length

pop	n	range	mean	se
i Anas	12	9.4-10.6	10.2	0.096
i Sape	34	9.5-11.4	10.3	0.071
m Brev	14	9.4-11.5	10.4	0.145
i Amel	29	9.8-11.5	10.5	0.066
i Merr	7	10.1-10.9	10.6	0.117
m Dunn	26	10.0-11.8	10.6	0.077
m Ever	23	10.1-11.9	10.6	0.081
m GuHa	37	9.9-11.4	10.7	0.062
i Jeky	43	10.2-11.8	10.8	0.061
i StSi	17	10.1-11.7	10.8	0.121
m Nass	19	9.8-11.5	10.8	0.099
m StMa	41	10.0-11.8	10.8	0.078
m McIn	13	10.0-11.4	10.8	0.107
i Cumb	85	10.0-11.8	10.9	0.045
m StJo	20	10.4-11.7	10.9	0.078
m Okef	34	10-11.6	10.9	0.066
m Ware	54	10.2-11.9	10.9	0.051
m Tusc	92	9.7-11.7	10.9	0.045
m Char	38	10.0-12.2	11.0	0.066
m Choc	43	10.2-12.0	11.1	0.065

## Anterior Palatal Foramen Length

	pop	n	range	mean	se
i	Anas	12	4.6-5.3	5.0	0.055
i	Amel	29	4.9-5.7	5.3	0.041
i	Cumb	85	4.8-5.8	5.3	0.028
i	Sape	34	4.7-5.9	5.3	0.049
i	Merr	7	4.7-6.1	5.4	0.177
i	StSi	18	5.0-6.2	5.4	0.082
m	Brev	14	4.7-6.2	5.4	0.097
m	Dunn	26	5.0-5.8	5.4	0.046
m	GuHa	37	5.0-6.5	5.4	0.048
m	Ever	24	4.8-5.9	5.4	0.049
m	StJo	20	5.0-5.8	5.5	0.045
m	Nass	19	5.2-6.1	5.5	0.055
m	Ware	54	4.9-6.4	5.5	0.039
m	StMa	41	4.7-6.3	5.5	0.051
m	Okef	34	5.0-6.3	5.6	0.057
m	McIn	13	5.1-6.1	5.6	0.066
i	Jeky	43	5.0-6.7	5.7	0.051
m	Char	38	4.9-6.4	5.7	0.050
m	Tusc	92	5.1-6.5	5.8	0.031
m	Choc	43	5.0-6.6	5.8	0.048

## Maxillary Tooth Row Length

	pop	n	range	mean	se
i	Anas	7	3.7-3.8	3.7	0.018
i	Sape	34	3.2-3.9	3.7	0.025
i	Merr	7	3.6-4.0	3.8	0.053
i	Amel	29	3.6-4.1	3.8	0.025
m	Brev	14	3.6-4.1	3.8	0.047
m	Tusc	92	3.2-4.2	3.8	0.016
i	Cumb	83	3.5-4.1	3.9	0.013
i	Jeky	42	3.5-4.2	3.9	0.022
i	StSi	18	3.7-4.1	3.9	0.028
m	Dunn	24	3.7-4.0	3.9	0.021
m	GuHa	38	3.5-4.2	3.9	0.024
m	Nass	19	3.7-4.2	3.9	0.032
m	Ware	54	3.4-4.3	3.9	0.028
m	Char	37	3.6-4.3	3.9	0.025
m	StMa	41	3.6-4.2	3.9	0.021
m	Ever	24	3.6-4.2	3.9	0.026
m	McIn	13	3.7-4.1	3.9	0.042
m	Choc	42	3.4-4.2	3.9	0.027
m	StJo	20	3.8-4.2	4.0	0.029
m	Okef	34	3.7-4.1	4.0	0.019

## Posterior Palatal Length

	pop	n	range	mean	se
i	Anas	9	9.0-9.7	9.4	0.080
i	Sape	34	9.1-10.8	9.8	0.077
i	Cumb	84	8.7-11.1	10.0	0.052
i	StSi	16	9.2-11.1	10.0	0.140
m	Ever	23	9.2-10.8	10.0	0.085
i	Merr	7	9.5-10.5	10.1	0.122
i	Amel	29	9.5-11.1	10.1	0.080
m	Dunn	26	9.4-10.9	10.1	0.081
m	GuHa	37	9.0-11.5	10.1	0.084
m	Okef	34	9.1-11.0	10.1	0.084
m	Ware	54	9.2-11.0	10.1	0.063
m	McIn	13	9.0-10.6	10.1	0.118
m	Tusc	92	8.7-11.3	10.1	0.055
m	Brev	14	9.4-11.3	10.2	0.148
m	Nass	19	9.4-11.0	10.2	0.102
m	Choc	43	9.1-11.4	10.2	0.086
i	Jeky	42	9.2-11.3	10.3	0.081
m	StJo	20	9.6-11.7	10.3	0.104
m	StMa	41	9.5-11.6	10.3	0.078
m	Char	38	9.2-11.3	10.4	0.075

## Total Tooth Row Length

	pop	n	range	mean	se
i	Anas	7	11.7-12.6	12.1	0.125
i	Sape	34	10.9-13.0	12.1	0.073
m	Brev	14	11.5-13.3	12.3	0.146
i	Merr	7	12.1-13.1	12.4	0.127
i	Amel	29	11.8-13.6	12.4	0.075
m	Ever	24	11.9-13.1	12.4	0.065
m	Dunn	24	11.8-13.7	12.5	0.089
m	McIn	13	11.8-13.1	12.5	0.096
i	Cumb	84	11.9-13.8	12.6	0.043
i	StSi	18	11.8-13.5	12.6	0.121
m	StJo	20	12.1-13.6	12.6	0.078
m	GuHa	38	11.7-13.5	12.6	0.063
m	Nass	19	11.9-13.0	12.6	0.076
m	Ware	54	11.4-13.5	12.6	0.053
i	Jeky	43	11.8-13.6	12.7	0.067
m	Okef	34	11.8-13.7	12.7	0.073
m	StMa	41	11.9-13.8	12.7	0.068
m	Tusc	92	11.2-13.5	12.7	0.048
m	Char	37	12.1-13.9	12.8	0.068
m	Choc	42	12.2-13.7	12.9	0.058

## Maxillary Diastema

pop	n	range	mean	se	
i	Anas	10	6.4-7.0	6.7	0.075
i	Sape	34	6.5-7.9	7.0	0.052
m	Brev	14	6.1-7.6	7.0	0.122
i	Merr	7	6.8-7.5	7.1	0.108
i	Amel	29	6.4-7.9	7.1	0.062
m	Dunn	26	6.7-8.0	7.1	0.070
m	Ever	24	6.7-7.8	7.1	0.056
i	StSi	18	6.5-8.0	7.2	0.106
m	GuHa	38	6.5-7.9	7.2	0.055
m	Nass	19	6.7-7.7	7.2	0.068
m	StMa	41	6.4-8.2	7.2	0.065
i	Cumb	84	6.5-8.2	7.3	0.036
i	Jeky	42	6.5-8.0	7.3	0.058
m	StJo	20	6.8-8.3	7.3	0.073
m	Okef	34	6.6-8.0	7.3	0.055
m	Ware	54	6.6-8.1	7.3	0.048
m	McIn	13	6.6-7.8	7.3	0.102
m	Char	38	6.8-8.3	7.4	0.053
m	Tusc	92	6.4-8.1	7.4	0.041
m	Choc	42	6.8-8.2	7.5	0.057

## Pterygoid Breadth

pop	n	range	mean	se	
m	Char	37	1.1-1.7	1.4	0.025
m	McIn	13	1.0-1.6	1.4	0.043
i	Cumb	78	1.2-1.8	1.5	0.017
i	Sape	30	0.8-1.8	1.5	0.037
m	Brev	14	1.4-1.7	1.5	0.021
m	GuHa	36	1.0-1.8	1.5	0.031
m	Okef	34	1.1-2.0	1.5	0.025
m	Ware	53	1.2-2.0	1.5	0.021
m	Ever	22	1.3-1.9	1.5	0.028
m	Tusc	92	1.2-1.9	1.5	0.014
m	Choc	42	1.3-1.9	1.5	0.021
i	Merr	6	1.4-1.9	1.6	0.071
i	Anas	9	1.5-1.7	1.6	0.026
i	Amel	29	1.3-1.8	1.6	0.022
i	Jeky	42	1.2-1.9	1.6	0.025
i	StSi	16	1.3-1.8	1.6	0.031
m	StJo	19	1.0-1.8	1.6	0.036
m	Dunn	25	1.3-1.9	1.6	0.023
m	StMa	40	1.2-1.9	1.6	0.022
m	Nass	18	1.4-1.9	1.7	0.035

## Palatal Width

pop	n	range	mean	se	
i	Amel	28	2.6-3.2	2.9	0.033
m	Dunn	25	2.6-3.2	2.9	0.031
m	Okef	34	2.7-3.3	2.9	0.025
m	Ware	54	2.7-3.1	2.9	0.016
i	Anas	9	2.9-3.1	3.0	0.026
i	StSi	17	2.7-3.4	3.0	0.043
i	Sape	33	2.3-3.3	3.0	0.033
m	Brev	14	2.5-3.7	3.0	0.088
m	GuHa	38	2.6-3.5	3.0	0.032
m	Char	38	2.8-3.3	3.0	0.025
m	StMa	41	2.7-3.4	3.0	0.025
m	Ever	24	2.7-3.4	3.0	0.033
m	McIn	13	2.7-3.4	3.0	0.051
m	Tusc	92	2.5-3.4	3.0	0.017
i	Merr	7	3.0-3.2	3.1	0.036
i	Cumb	81	2.8-3.5	3.1	0.017
i	Jeky	41	2.7-3.6	3.1	0.035
m	StJo	19	2.8-3.3	3.1	0.035
m	Nass	18	2.8-3.4	3.1	0.037
m	Choc	42	2.8-3.7	3.1	0.030

## Bullar Length

pop	n	range	mean	se	
i	Anas	8	4.2-4.7	4.5	0.062
i	Jeky	41	4.0-5.1	4.6	0.040
i	Sape	34	4.1-5.2	4.6	0.038
i	Merr	7	4.5-5.0	4.7	0.061
i	Amel	29	4.2-5.1	4.7	0.045
i	Cumb	81	4.1-5.2	4.7	0.026
m	StJo	20	4.3-5.0	4.7	0.044
m	Dunn	26	4.2-5.0	4.7	0.044
m	GuHa	36	4.2-5.3	4.7	0.042
m	Okef	34	4.4-5.0	4.7	0.030
m	Ware	54	4.3-5.0	4.7	0.026
m	Char	37	4.2-5.4	4.7	0.042
m	StMa	41	4.2-5.5	4.7	0.037
m	Ever	24	4.3-5.0	4.7	0.035
m	McIn	13	4.4-5.2	4.7	0.075
i	StSi	17	4.4-5.0	4.8	0.041
m	Brev	14	4.4-5.1	4.8	0.056
m	Nass	19	4.3-5.2	4.8	0.052
m	Tusc	92	4.2-5.2	4.8	0.022
m	Choc	42	4.4-5.5	4.8	0.035

## Bullar Width

pop	n	range	mean	se	
i	Jeky	42	3.8-4.7	4.3	0.030
i	Anas	8	4.2-4.7	4.4	0.083
i	Amel	29	4.1-4.9	4.4	0.034
i	Cumb	82	3.9-4.8	4.4	0.026
i	Sape	34	4.1-4.8	4.4	0.029
m	Brev	14	3.8-4.8	4.4	0.068
m	StJo	20	3.9-4.8	4.4	0.046
m	Dunn	26	4.0-4.8	4.4	0.040
m	Ware	54	3.8-4.8	4.4	0.029
m	McIn	13	4.0-4.8	4.4	0.069
m	Tusc	92	3.9-5.0	4.4	0.022
m	Choc	42	4.0-4.8	4.4	0.030
i	Merr	7	4.2-4.9	4.5	0.087
m	GuHa	36	4.0-4.9	4.5	0.038
m	Okef	34	4.0-5.0	4.5	0.038
m	Char	37	4.0-5.0	4.5	0.037
m	StMa	41	4.2-4.9	4.5	0.029
m	Ever	24	4.1-4.8	4.5	0.038
i	StSi	18	4.0-4.8	4.6	0.050
m	Nass	19	4.3-5.0	4.6	0.037

## Mandibular Tooth Row Length

pop	n	range	mean	se	
i	Anas	8	3.7-4.0	3.8	0.032
i	Merr	7	3.7-4.1	3.9	0.061
i	Amel	29	3.6-4.1	3.9	0.023
i	Sape	33	3.2-4.2	3.9	0.036
m	Brev	14	3.7-4.2	3.9	0.041
m	Dunn	26	3.6-4.2	3.9	0.027
m	GuHa	38	3.7-4.2	3.9	0.022
m	Tusc	92	3.3-4.3	3.9	0.017
i	Cumb	79	3.5-4.3	4.0	0.018
i	Jeky	41	3.7-4.3	4.0	0.019
i	StSi	18	3.8-4.2	4.0	0.029
m	StJo	20	3.6-4.3	4.0	0.036
m	Nass	19	3.8-4.2	4.0	0.033
m	Okef	34	3.8-4.3	4.0	0.020
m	Ware	53	3.4-4.4	4.0	0.027
m	Char	36	3.7-4.3	4.0	0.025
m	StMa	40	3.7-4.3	4.0	0.021
m	Ever	24	3.7-4.3	4.0	0.030
m	McIn	13	3.7-4.3	4.0	0.049
m	Choc	43	3.7-4.4	4.0	0.026

## Bullar Depth

pop	n	range	mean	se	
i	Anas	7	8.8-9.6	9.2	0.108
i	Sape	33	8.3-9.8	9.3	0.047
i	Amel	29	9.0-9.9	9.4	0.044
i	Cumb	81	8.6-10.1	9.4	0.032
m	Brev	13	9.0-9.8	9.4	0.068
m	StJo	20	9.0-10.0	9.5	0.063
m	Dunn	26	9.0-10.1	9.5	0.066
m	GuHa	36	9.0-10.0	9.5	0.044
i	Merr	7	9.2-10.1	9.6	0.123
i	StSi	18	9.1-9.9	9.6	0.053
m	StMa	41	8.7-10.2	9.6	0.046
m	Tusc	92	9.0-10.4	9.6	0.032
m	Choc	41	8.8-10.1	9.6	0.048
m	Nass	19	9.2-10.1	9.7	0.059
m	Okef	34	9.9-10.4	9.7	0.055
m	Ware	54	8.8-10.5	9.7	0.046
m	Ever	24	9.1-10.1	9.7	0.052
m	McIn	13	9.3-10.3	9.7	0.082
i	Jeky	42	9.1-10.4	9.8	0.050
m	Char	38	9.2-10.2	9.8	0.047

## Caranoid Depth

pop	n	range	mean	se	
i	Sape	31	4.9-6.2	5.6	0.049
i	Anas	10	5.5-6.1	5.8	0.064
m	Ever	22	5.2-6.2	5.9	0.050
m	StJo	18	5.7-6.4	6.0	0.049
i	Cumb	73	5.3-7.3	6.1	0.040
m	Nass	19	5.6-6.5	6.1	0.058
m	Tusc	92	5.3-6.8	6.1	0.035
i	Amel	27	5.6-6.6	6.2	0.059
i	Jeky	38	5.6-6.8	6.2	0.047
i	StSi	16	5.5-6.5	6.2	0.081
m	Dunn	23	5.5-6.8	6.2	0.070
m	GuHa	34	5.5-6.8	6.2	0.054
m	Okef	34	5.4-7.1	6.2	0.069
m	Ware	53	5.5-7.3	6.2	0.045
m	Choc	38	5.5-6.9	6.2	0.053
i	Merr	6	6.1-6.6	6.3	0.070
m	Brev	12	5.7-7.3	6.3	0.125
m	Char	35	5.8-7.7	6.3	0.062
m	StMa	38	5.8-6.9	6.3	0.050
m	McIn	11	5.9-6.8	6.3	0.085

## Condyle Depth

pop	n	range	mean	se	
i	Anas	7	4.9-5.9	5.4	0.136
i	Sape	30	5.0-6.1	5.5	0.054
m	Ever	21	5.2-6.4	5.6	0.058
i	Amel	22	5.1-6.2	5.7	0.062
m	GuHa	28	5.0-6.5	5.7	0.070
m	McIn	11	5.2-6.5	5.7	0.114
i	Cumb	67	4.8-6.6	5.8	0.050
i	Jeky	39	5.0-6.7	5.8	0.068
m	Dunn	16	5.4-6.6	5.8	0.087
m	Okef	32	5.1-6.9	5.8	0.070
m	Ware	52	5.0-6.6	5.8	0.050
m	Tusc	92	4.9-6.6	5.8	0.033
i	Merr	3	5.5-6.2	5.9	0.219
m	StJo	15	5.3-6.4	5.9	0.098
m	Nass	17	5.3-6.3	5.9	0.071
m	Char	31	5.3-7.0	5.9	0.076
m	StMa	38	5.0-6.6	5.9	0.064
m	Choc	30	5.2-6.7	5.9	0.068
i	StSi	13	5.0-6.5	6.0	0.120
m	Brev	13	5.6-7.0	6.0	0.106

## Mandibular Diastema

pop	n	range	mean	se	
i	Anas	11	2.7-3.4	3.0	0.067
m	Brev	14	2.7-3.5	3.0	0.070
m	StMa	41	2.4-3.8	3.0	0.038
i	Merr	7	2.8-3.4	3.1	0.077
i	Amel	29	2.5-3.6	3.1	0.042
i	Cumb	82	2.7-3.6	3.1	0.022
i	Jeky	41	2.5-3.6	3.1	0.041
i	Sape	33	2.7-3.5	3.1	0.039
m	StJo	19	2.7-3.4	3.1	0.045
m	Dunn	26	2.5-3.5	3.1	0.051
m	Nass	19	2.6-3.5	3.1	0.052
m	Okef	34	2.7-3.8	3.1	0.039
m	Ever	24	2.8-3.7	3.1	0.044
m	McIn	13	2.9-3.4	3.1	0.047
i	StSi	18	2.8-4.1	3.2	0.069
m	GuHa	37	2.8-3.7	3.2	0.035
m	Ware	52	2.8-3.8	3.2	0.029
m	Tusc	92	2.7-3.7	3.2	0.021
m	Choc	42	2.8-3.7	3.2	0.032
m	Char	38	2.8-4.2	3.3	0.049



Appendix 11. Lower triangle of symmetric correlation matrix of raw data for 27 morphological characters from 20 populations of *Peromyscus gossypinus* with a total sample size of 683 mice. Correlation coefficients greater than 0.078 are significant at  $p > 0.05$ .

1	Body length	1
2	Tail length	.45 1
3	Hind foot length	.25 .27 1
4	Length of the skull	.54 .49 .27 1
5	Basonasal length	.52 .46 .26 .88 1
6	Basilar length	.54 .46 .27 .89 .87 1
7	Rostral length	.46 .42 .28 .81 .74 .71 1
8	Rostral breadth	.08 .11 .08 .09 .10 .06 .03 1
9	Nasal length	.29 .25 .15 .59 .56 .54 .58 -.01 1
10	Interorbital constriction	.22 .10 .08 .32 .30 .29 .21 .26 .13 1
11	Zygomatic breadth	.41 .38 .19 .66 .62 .68 .53 .13 .39 .34 1
12	Cranial breadth	.37 .23 .23 .52 .47 .51 .42 .15 .32 .36 .57 1
13	Bony palate length	.47 .41 .25 .80 .76 .84 .69 .10 .51 .28 .62 .46 1
14	Palatal foramen length	.32 .40 .17 .61 .58 .62 .51 .05 .35 .10 .42 .21 .59 1
15	Posterior palatal length	.50 .41 .23 .74 .79 .86 .57 .03 .45 .21 .57 .44 .57 .49 1
16	Maxillary tooth row length	.09 .01 .17 .14 .12 .12 .13 .18 .01 .21 .12 .15 .16 .06 .08 1
17	Total tooth row length	.48 .45 .22 .83 .77 .82 .71 .12 .50 .31 .62 .48 .82 .61 .63 .26 1
18	Maxillary diastema	.46 .44 .19 .80 .75 .84 .68 .04 .51 .24 .59 .42 .83 .65 .63 -.06 .83 1
19	Palatal width	.29 .19 .15 .45 .42 .46 .34 .02 .28 .29 .48 .38 .42 .25 .38 .02 .40 .45 1
20	Pterygoid breadth	-.08 -.09 .04 -.04 -.03 -.06 -.06 .05 -.03 .05 .00 -.02 -.06 -.05 -.04 .09 -.04 .10 1
21	Bullar length	.28 .28 .18 .42 .40 .40 .33 .12 .22 .18 .31 .23 .29 .27 .41 .07 .31 .32 .17 -.02 1
22	Bullar width	.14 .09 .14 .20 .21 .23 .17 .16 .08 .13 .26 .26 .20 .09 .21 .09 .17 .17 .15 .06 .37 1
23	Bullar depth	.15 .13 .10 .32 .28 .27 .21 .14 .16 .34 .33 .34 .27 .24 .20 .14 .28 .22 .14 .04 .14 .16 1
24	Mandibular tooth row length	.08 .04 .19 .13 .12 .14 .10 .17 .03 .17 .18 .18 .18 .08 .08 .69 .22 .00 .04 .10 .08 .08 .15 1
25	Caranoid depth	.46 .38 .18 .59 .57 .61 .51 .11 .34 .23 .53 .40 .53 .38 .55 .13 .58 .50 .26 -.08 .28 .17 .18 .15 1
26	Condyle depth	.33 .32 .08 .48 .46 .50 .38 .09 .29 .18 .46 .36 .44 .35 .42 .09 .51 .44 .20 -.02 .19 .14 .22 .12 .54 1
27	Mandibular diastema	.22 .27 .11 .44 .43 .46 .40 .06 .32 .07 .31 .26 .46 .39 .35 -.04 .45 .54 .20 -.08 .21 .14 .21 -.04 .28 .29 1
1		1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27

