SYSTEMATICS AND BIOGEOGRAPHIC ANALYSES OF FOUR SPECIES OF *STURNIRA* (CHIROPTERA: PHYLLOSTOMIDAE), WITH EMPHASIS ON PERUVIAN FORMS

by

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ABSTRACT

Analyses of morphological and genetic differentiation are presented for four New World leaf-nosed bats of the genus *Sturnira*, *S. erythromos*, *S. bogotensis*, *S. oporaphilum* and *S. ludovici* in order to clarify their taxonomic status. Analysis of nongeographic variation showed significant sexual dimorphism for *S. oporaphilum* and *S. ludovici*, but not for *S. erythromos* or *S. bogotensis*. We conducted an UPGMA cluster analyses for the four species to understand patterns of distribution through most of their range in South America.

Morphological and genetic variation is later examined in relation to major geographic features of Peru, such as the Río Marañón and the Huancabamba Depression. Morphological data were regressed on elevation and latitude; and Nei's and Roger's genetic distances were correlated with linear and indirect geographic distance using Mantel tests. Regression results showed no correlations of elevation (R^2=0.080) and latitude (R^2=0.067) with morphological data for *Sturnira erythromos*. For *S. bogotensis*, *S. oporaphilum* and *S. ludovici*, R^2 values for elevation were also not significant. Mantel test results showed that geographic distances among populations of *Sturnira erythromos* explained a significant percentage of genetic differentiation. Nei's genetic distance was significantly correlated ($P<0.005$) with both linear (0.4643) and indirect geographic distances (0.5411). These suggest that the isolation-by-distance model (Wright, 1943) is appropriate for interpreting the genetic variation of *S. erythromos* samples. Geographic features such as the Río Marañón and Huancabamba Depression apparently do not influence levels of genetic differentiation in this species, as they do for some reptiles, frogs, birds and rodents.

RESUMEN

Se presenta un análisis de diferenciación morfológica y genética para cuatro murciélagos del género *Sturnira*, *S. erythromos*, *S. bogotensis*, *S. oporaphilum* y *S. ludovici*, con el fin de aclarar sus estados taxonómicos. El analisis de variación no-geográfica mostró dimorfismo sexual significativo para *S. oporaphilum* y *S. ludovici*, pero no para *S. erythromos* o *S. bogotensis*. Continuamos luego con un análisis de agrupación UPGMA para las cuatro especies, para entender los patrones de distribución a través de la mayor parte de su distribución en Sudamérica.

Después se examinó la variación morfológica en relación a importantes factores geográficos del Perú, tales como el Río Marañón y la Depresión de Huancabamba. Se regresionó los datos morfológicos

con elevación y latitud; las distancias genéticas de Nei y de Roger fueron correlacionadas con las distancias geográficas lineales e indirectas usando la prueba de Mantel. Los resultados de la regresión no mostraron correlación alguna de la elevación (R^2=0.080) o latitud (R^2=0.067) con los datos morfológicos para *Sturnira erythromos*. Para *S. bogotensis*, *S. oporaphilum* y *S. ludovici*, los R^2 para elevación tampoco fueron significativas. La prueba de Mantel muestra que las distancias geográficas entre las poblaciones de *Sturnira erythromos* explican un porcentaje significativo de la diferenciación genética. La distancia genética de Nei fue correlacionada significativamente (P<0.005) con las distancias lineales (0.4643) y las geográficas indirectas (0.5411). Esto sugiere que el modelo de aislamiento por distancia (Wright, 1943) es apropiado para interpretar la variación genética de las muestras de *S. erythromos*. Factores geográficos tales como el Río Marañón y la Depresión de Huancabamba aparentemente no influencian sobre los niveles de diferenciación genética en esta especie, como si lo hacen para algunos reptiles, anfibios, aves y roedores.

INTRODUCTION

The resolution of systematic studies on Neotropical bats has increased substantially in recent years due to the availability of modern techniques, with electrophoretic methods of studying allozymes one of the most widely used. For New World bats of the genus *Sturnira*, interest has mainly focused on the phylogenetic relationships within the Phyllostomidae, whether *Sturnira* belongs to the subfamily Stenodermatinae or instead represents a subfamily in its own right (for a review see Pacheco & Patterson, 1991). Phylogenetic relationships within the genus have recently been analyzed using morphological and genetic characters (Pacheco & Patterson, 1991). However, the taxonomic status of some *Sturnira* species is still poorly understood.

Sturnira bogotensis was initially reported as a subspecies of *Sturnira lilium*, based on the large size of specimens from La Uribe, Colombia (Shamel, 1927). De la Torre (1961), in his revision of the genus *Sturnira*, recognized *bogotensis* as a large subspecies of *erythromos*, but considered *bogotensis* as a northern race of *erythromos*. Handley (1976) reported *erythromos* and *bogotensis* from Venezuela, granting species rank to *S. bogotensis* without comment on its morphological differentiation. However, he later cited sympatry of both taxa as the basis for this action (Handley, pers. comm.). Linares (1986) also recognized *S. bogotensis* as a species, distinguishing it from *S. erythromos* by the absence of bilobate upper incisors; however, he acknowledged the subtle nature of the distinction and the difficulty of a correct identification. Because of its large size, *S. bogotensis* has been commonly misidentified and allied to either *S. oporaphilum* or *S. ludovici*. De la Torre (1961) showed that *bogotensis* was incorrectly considered a synonym of *S. ludovici* by Hershkovitz (1949), but the misplacement continued. Jones & Carter (1976) suggested that *oporaphilum* and *bogotensis* were related to *ludovici*, but that they might be valid species or subspecies. Koopman, in recent studies on the genus *Sturnira* reported divergent conclusions, calling the eastern Peruvian samples *S. ludovici* (Koopman, 1978), *S. bogotensis* (Koopman, 1982), and lastly *S. oporaphilum* (*in* Anderson *et al.*, 1982). He still maintains this view in which *oporaphilum* is distributed in Peru and Bolivia and *ludovici* replaces it to the north (Koopman, pers. comm.), a similar result reported by de la Torre (1961). This view clarifies much of the confusion, but implies that neither *S. bogotensis* Shamel, 1927 nor *S. ludovici* Anthony, 1924 are present in Peru. Finally, Pacheco & Patterson (1991) found *S. erythromos* and *S. bogotensis* to be closely related as a pair, sister group. Here, we recognize *S. erythromos*, *S. bogotensis*, *S. oporaphilum*, and *S. ludovici* as distinct taxa, following Handley (1976) and Pacheco & Patterson (1991). The intent of this article is to clarify their taxonomic status through most of their distributional range, emphasizing data from Peruvian populations.

Detailed studies of morphological variation of species of *Sturnira* throughout their distribution ranges have not been conducted, except for *Sturnira magna* (Tamsitt & Valdivieso, 1986). The preceding taxonomic controversies stem from this imprecise and outdated taxonomic history. We analyze morphological variation within populations of *Sturnira erythromos*, *S. bogotensis*, *S. oporaphilum*, and *S. ludovici* at various localities spread over South America, with emphasis on the Peruvian region, to investigate and further refine species limits. Analysis of allozyme variation based on starch gel electrophoresis was also conducted, but restricted to Peruvian populations because of the availability of tissue samples.

Subsequently, we look for patterns of distribution based on within-species variation that might be related to geographic features. Zoogeographic studies of Peru have often emphasized the role of geographic features such as the Río Marañón or the Huancabamba Deflection (Duellman, 1979; Vuilleumier, 1969, 1984; Cracraft, 1985; Parker *et al.*, 1985). The distributions of species and subspecies relative to those geographic features have been used to argue that

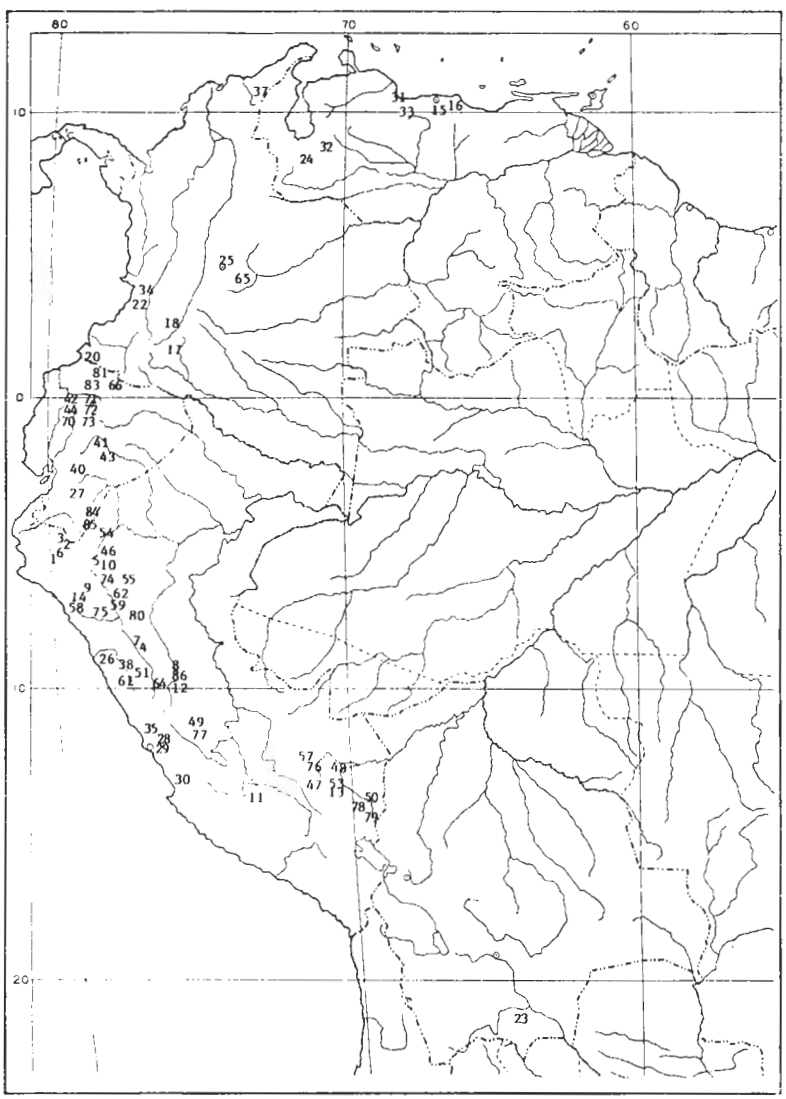

Fig. 1. Representation of locality samples for the *Sturnira* species included in these analyses. Numbers refer to the localities described in Appendix.

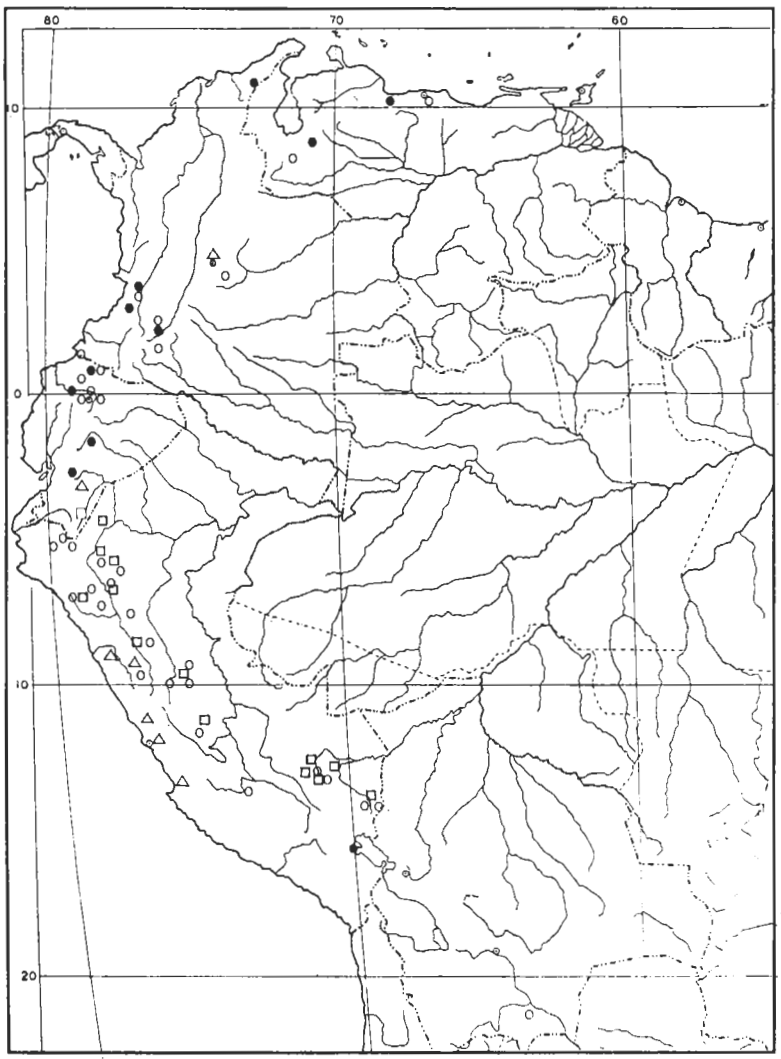

Fig. 2. Representation of taxa included in these analyses. *Sturnira bogotensis* (△); *S. erythromos* (○); *S. ludovici* (●); *S. oporaphilum* (□).

vicariance events are involved in processes of allopatric speciation. However, few works have analyzed whether morphological and genetic variation within species are correlated with those geographic features. Most species of *Sturnira* are thought to have widespread distributions in the Neotropics, suggesting that geographic features that function as barriers for other taxa might have little or no influence on their distribution. We outline here a hypothetical explanation for genetic differentiation among *Sturnira erythromos* populations in relation to those geographic features.

MATERIALS AND METHODS

MULTIVARIATE ANALYSIS

Analyses of nongeographic and geographic variation were performed independently on sets of five external, 20 cranial and mandibular, and six dental characters. External variables (HBL,

Head and body length; HFL, Hind foot length; EARL, Ear length; WEIGHT, Weight) were taken from field tags. Forearm Length (FORL) was measured from olecranon process to the shallow notch proximal to thumb including carpals. The other characters were measured to the closest 0.01 mm. In all, 413 specimens of *S. erythromos*, *S. bogotensis*, *S. ludovici*, and *S. oporaphilum* were examined. The localities are fully described the first time and are referenced by an arbitrary code. A complete list of specimens, localities (and their codes) appears in the Appendix and are plotted in maps (Fig. 1 and 2).

CRANIAL, MANDIBULAR AND DENTAL MEASUREMENTS.

The set of measurements taken, their abbreviations, and how they were obtained are described below and illustrated in Figure 3.

1. Greatest Skull Length (GSL): Greatest length not including incisors.
2. Condylobasal Length (CBL): Occipital condyle to anterior border of incisive alveolus.
3. Palatal Length (PALTL): Posterior palatal notch to anterior border of incisive alveolus.
4. Maxillary Toothrow Length (MXTRL): Anterior alveolar border of canine to posterior alveolar border of M3.
5. Molariform Toothrow Length (MLTRL): Posterior border of last molar alveolus to anterior border of first premolar alveolus.
6. Zygomatic Width (ZYGW): Greatest breadth across zygomatic arches.
7. Mastoid Width (MSTW): Least breadth across the base of the zygomatic arches.
8. Braincase Width (BRW): Greatest breadth of braincase, not including mastoid or paroccipital processes.
9. Maxillary Breadth (MXBR): Greatest width across maxilla from the lingual sides of M2.
10. Lacrimal Width (LACW): Greatest breadth across lacrimal protuberances.
11. Postorbital Width (POW): Least breadth of postorbital constriction.
12. Width at First Molar (M1M1): Least width of palate across M1s.
13. Palatal Width at Second Molar (M2M2): Least width across palate between second upper molars.
14. Palatal Width at Canines (C1C1): Least width across palate between bases of upper canines.
15. Braincase Height (BRH): Greatest height from basioccipital bone to top of braincase (not including sagittal crest).
16. Dentary Length (DENL): Midpoint of mandibular condyle to anterior-most point of dentary.
17. Mandibular Toothrow Length (MANDL): Posterior-most border of m3 alveolus to anterior border of canine alveolus.
18. Width at Mandibular Condyles (MANDCW): Greatest width between outer margins of mandibular condyles.
19. Coronoid Height (CORH): Perpendicular height from ventral mandibular border to tip of coronoid process.
20. Dentary Thickness (DENT): Vertical height of dentary at anterior edge of second molar.
21. Molar 1 Length (M1L): Greatest antero-posterior length of crown.
22. Molar 2 Length (M2L): Greatest antero-posterior length of crown.
23. Molar 1 Width (M1W): Greatest width of crown.
24. Molar 2 Width (M2W): Greatest width of crown.
25. First Lower Molar Length (m1L): Greatest antero-posterior length of crown.
26. First Lower Molar Width (m1W): Greatest width of crown.

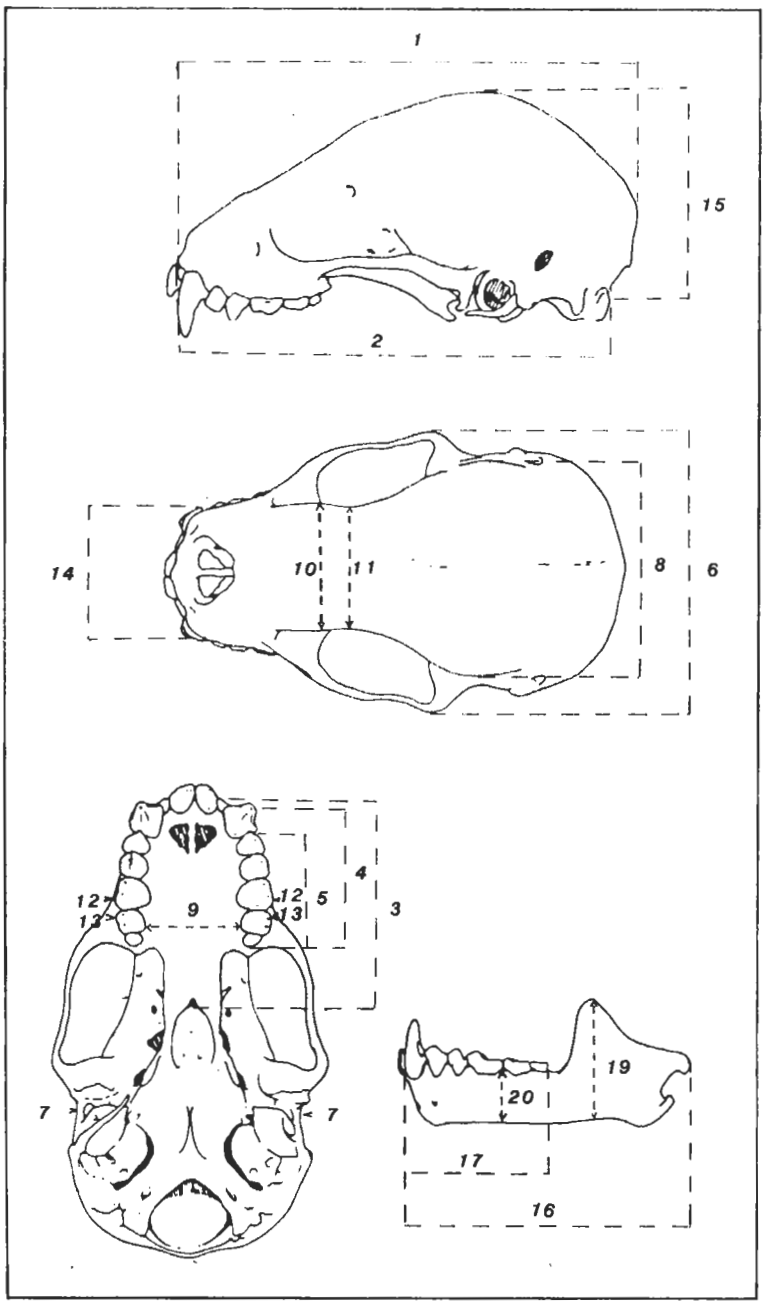

Fig. 3. Cranial and mandibular measurements used in the morphometric analysis.

AGE CRITERIA. Age classes were determined based upon the degree of fusion of the basisphenoid-basioccipital suture, the finger joints and by the degree of tooth wear. Five age classes were defined:

Class I (juvenile) specimens lacked fusion in several cranial sutures other than the basisphenoid-basioccipital one, possessed areas of incomplete ossification especially in the rostrum, had

conspicuously translucent and cartilaginous epiphyses of the finger bones, and presented pelage color consistently darker and more homogeneous than the other classes.

Class II (sub-adult) specimens were identified by the nearly closed basisphenoid-basioccipital suture and the complete closure of other cranial sutures. Moreover, the sutures of the finger bones were usually completely ossified, but dark pelage coloration persisted in some specimens.

Class III (adult) specimens showed complete ossification of cranial sutures and regions and adult pelage, but tooth wear was not apparent.

Class IV (adult) was similar to class III in all respects except for the more conspicuous degree of tooth wear, especially of the upper premolars and molars.

Class V (adult) showed a higher degree of tooth wear in all the upper and lower teeth, including the incisors, but the molar shape still resembled the other two adult classes.

Reproductive activity (i.e., scrotal males, pregnant or lactating females) was detected only in classes III to V. Specimens presumably older than age class V, because of highly eroded or lost teeth, were not included in any analysis, although some of them were still reproductively active.

ANALYSES OF NONGEOGRAPHIC VARIATION

Analyses of nongeographic variation in each of four *Sturnira* taxa were based on the largest single sample available. For *S. erythromos*, nongeographic variation was assessed in a sample of 30 specimens collected at Canchaque, Piura, (v) at 1737 m elevation from 5-10 December, 1984. Both sexes and all age classes except class II were represented. Unfortunately, none of the other samples included all the age classes or was large enough to be analyzed for nongeographic variation. For *S. bogotensis* samples from Bosque de Zárate and San Bartolomé, Lima were combined into a single locality (28 specimens). These samples were assumed to represent a single population as the two localities are only 3 km apart in the same river system (Río Seco, Lima); this sample was represented by age classes II to V. The largest locality sample analyzed for *S. ludovici* was from Los Venados, Caracas, Venezuela (14 specimens); and for *S. oporaphilum* the largest sample was from Cerro de Pantiacolla, Madre de Dios, Peru (22 specimens).

All analyses were performed using subroutines of Version 6 of the Statistical Analysis System (SAS; SAS Institute, Inc., 1987). Standard statistics (mean, range, standard error, coefficient of variation, skewness, and kurtosis) were calculated for each variable within each age class (MEANS and UNIVARIATE procedures). Normality of distributions, assumptions of ANOVA and MANOVA procedures, was tested for each variable with the NORMAL option (UNIVARIATE procedure), utilizing the results of the Shapiro-Wilk's test and the skewness and kurtosis coefficients. ANOVAs were calculated to test the null hypothesis of no significant differences in each character between sexes or among age classes nested within sex. MANOVA multiple test statistics (i.e., Wilks' Lambda, Pillai's Trace and Hotelling-Lawley trace) were scored ($P < 0.05$) for each set of variables for an overall sex and age effect. Because this method uses correlations among the variables, in contrast to the analogous univariate statistics, it is considered the most appropriate for evaluating overall group differences (Willig *et al.*, 1986). Subsequently, Duncan's multiple range test was used to determine differences between sexes and age classes. Because no overall sex differences were found for *Sturnira erythromos* and *bogotensis*, sexes were grouped for subsequent analyses. Only the juveniles were found to differ significantly from other age classes and were excluded from all subsequent analyses.

The other two species, *S. oporaphilum* and *S. ludovici*, were found to be significantly sexually dimorphic.

To increase sample sizes for study of geographic variation, specimens from the individual localities were combined to form grouped localities. Geographic proximity and statistical homogeneity were used as guides in combining samples. Nearby localities that were not separated by major geographic features such as rivers, mountains, or elevational differences were tentatively grouped. Duncan's multiple range ($P < 0.05$) performed for each character across the original localities provided assurance that the grouped localities enclosed homogeneous groups of the original localities.

Because of the extensive variation of continuous and discrete characters between *Sturnira erythromos* and *S. bogotensis* and between *S. ludovici* and *S. oporaphilum* throughout their geographic ranges, we pursued the geographic analyses on pairs of closely related taxa, *erythromos-bogotensis* and *ludovici-oporaphilum*, based upon results of phylogenetic relationships (Pacheco & Patterson, 1991). Homogeneity among grouped localities across all characters was also examined using a one-way MANOVA (SAS: GLM, MANOVA). Duncan's tests were conducted as well for each character, to determine whether grouped localities were internally homogeneous.

Principal component analyses (PCA) were performed, based on matrices of correlations among characters (SAS: PRINCOMP). The analyses examined patterns of variation among the grouped localities for each pair of taxa. Mean scores of the first three components for grouped localities were used, to project a three-dimensional pattern of variation.

Mean values of each variable for each grouped locality (MEANS procedure) were determined for the *erythromos-bogotensis* and *ludovici-oporaphilum* pairs. Standardized average distance coefficients among localities (defined as the Euclidean distance among samples in a character space of n dimensions) were prepared and used by the UPGMA (unweighted pair-group method using arithmetic averages) clustering method to compose phenetic dendrograms (Sneath & Sokal, 1973). The UPGMA algorithm computes the average similarity of a candidate object to an existing cluster, weighting each object in that cluster equally, regardless of the cluster's structural subdivision (Sneath & Sokal, 1973). To maximize sample size and retain most localities, only cranial and dental characters were used for each pair of taxa. Because *Sturnira ludovici* and *S. oporaphilum* samples were found to be sexually dimorphic, the characters for males and females were treated as independent characters. Thus, cluster analyses were based on a data matrix with doubled number of characters (Schnell *et al.*, 1978; Owen, 1987).

GENETIC ANALYSIS

Electrophoretic analysis of frozen tissues was done by running aqueous extracts of tissues prepared by standard procedures on horizontal starch gels. The procedures and recipes for buffers and stains followed Selander *et al.* (1971) and Harris & Hopkinson (1976). Additional information for procedures applied to *Sturnira* samples is reported in Pacheco & Patterson (1991).

To examine genetic variation among populations of each species, we calculated the index of average polymorphism $P(\%)$ and the observed values of heterozygosity H for each population containing more than two individuals. A locus was considered polymorphic when allele frequencies were not greater than 0.95.

Phenetic analysis of electrophoretic data was pursued by conversion of the allele frequency data (Pacheco & Patterson 1991, Table 3) to genetic distances. Genetic distances Nei's D and Rogers' D (Wright, 1978) were subjected to the Fitch-Margoliash tree-generating algorithm

(Fitch & Margoliash, 1967) using the PHYLIP program (Felsenstein, 1985). The Jackknifing Strict Consensus approach was pursued as well to identify strong and weak portions of the tree (Lanyon, 1985). These analytical procedures are described in detail in Pacheco & Patterson (1991).

In addition, a hierarchical analysis of genetic variation among populations was conducted for *erythromos-bogotensis*, using F_{st} values, corrected for sampling bias (Wright, 1978). Geographic features such as the Andes and the Río Marañón were used to delimit regions. The limited number of locality samples and specimens permitted only the following hierarchical levels of comparison: localities within regions, and regions within species. The allele frequency values for regions were calculated from individuals instead of populations. F_{st} values were calculated using the maximum number of polymorphic loci available for each comparison.

BIOGEOGRAPHIC ANALYSES

Biogeographic analyses were conducted using the morphometric data matrices for *Sturnira erythromos*, *S. bogotensis*, *S. oporaphilum* and *S. ludovici* and genetic distances for *S. erythromos*. Elevational data were obtained from tag labels and were converted to the metric equivalent where necessary. Latitude values were estimated from maps or from appropriate gazetteers (Stephens & Traylor, 1983). Specimens with imprecise localities were not used in the analyses. Although it would have been meaningful to examine climatic and vegetational variables (e.g., temperature, precipitation, forest type), these could not be reliably inferred for many of the sample localities.

We conducted regression analyses to determine whether size variation among specimens is associated with elevation and latitude (SAS: PROC REG). For this purpose, cranial and mandibular variables were used in principal component analyses (SAS: PRINCOMP) and the first component (PC I) was selected as a general indicator of size. Loading of all variables on PC I were positive indicating that this interpretation is well justified. The scores on PC I were then regressed on elevation and latitude in separate analyses. The four taxa were analyzed independently.

The correlation between genetic differentiation in *Sturnira erythromos* samples and geographic distances was tested using a Mantel's test (Mantel, 1967). Linear and indirect geographic distances were estimated from maps. Linear geographic distance was defined as the shortest linear distance between two localities. Indirect distance means the approximate shortest distance between two localities at elevations below 3000 m. This elevation corresponds to the elevation of passes in the Huancabamba Deflection. Indirect distance rather than linear distance is taken to indicate that bats cannot disperse across the higher cordilleras of the Andes but instead use low-elevation corridors. The test indicates whether the levels of genetic differentiation are correlated with geographic distances at non-random levels.

RESULTS

NONGEOGRAPHIC VARIATION

Analysis of nongeographic variation is intended to identify significant sources of heterogeneity within a given sample. Variation between sexes and among age classes are the most common sources of population heterogeneity in mammals. Consequently, these must be

understood before assessing geographic variation. Main effects due to sex and age were determined for each of the four *Sturnira* taxa.

Tests of normality conducted on non-transformed data for the samples from Canchaque and Lima showed a leptokurtic distribution for HBL and WEIGHT characters for both populations, and a skewed distribution for WEIGHT in the Canchaque sample; all the remaining characters were normally distributed. As none of the external characters were included in the geographic analyses, locality samples were assumed to fulfill the assumption of normality made by the statistical analyses. Therefore, logarithmic transformations common to morphometric analyses were not conducted.

For *Sturnira erythromos*, the Canchaque sample ($n = 30$; age classes I, III-V) was analyzed for main effects due to sex and age. The sample sizes for each character set and ANOVA results are shown in Appendix D of Pacheco (1989). MANOVA results between sexes indicated no overall differences between males and females ($P < 0.05$). Marginally significant differences were found only for C1C1 and MANDCW. MANOVA results among age classes with sexes pooled showed an overall significant age effect in the cranial set of characters ($n = 29$; $P < 0.1$ for Wilk's Lambda; and $P < 0.05$ for Pillai's Trace). PALTL, ZYGW, BRW, MXBR, LACW, MANDCW, M2M2 and DENT differed significantly with age. Duncan's test identified age class I as differing from the remaining age classes. The external and dental character sets did not differ significantly among age classes, as might be expected from the rapid growth of juveniles (Kunz, 1987).

The analyses of *Sturnira bogotensis* (Lima sample) was based on 28 individuals (age classes II-V), but the sample size varied for each character set because of missing values. MANOVA results for the external and dental character sets showed that overall differences due to sex and age were nonsignificant, although males averaged larger than females in most characters. No multivariate test was possible for the cranial character set due to small sample size and the number of cranial characters; however, Duncan's multiple range test differentiated male and female classes on seven of the 20 external characters (PALTL, MXTRL, ZYGW, LACW, C1C1, DENL, DENT)($P < 0.05$). This indication of sexual dimorphism has to be considered cautiously because it might be due to the unequal number of individuals per sex. In any case, the degree of sexual dimorphism seems small compared to other highly dimorphic bat species (McLellan, 1984; Power & Tamsitt, 1973; Tamsitt & Valdivieso, 1986) and it is considered negligible hereafter. With regard to age, Duncan's multiple range tests showed age differences only for MXTRL and M2L, with all the remaining characters being homogeneous among age classes. These results, like those for *S. erythromos*, indicate the absence of significant variation among age classes II to V, permitting them to be treated collectively in the geographic analyses.

Sturnira oporaphilum and *S. ludovici* samples were examined for sex differences with age classes II to V (pooled) using one-way MANOVA. Because of small sample sizes, the results should be considered indicative rather than conclusive. For *S. oporaphilum* from Pantiacolla, Madre de Dios, Peru ($n = 22$) none of the overall multivariate tests for the three character sets were significant ($P < 0.05$). However, ANOVA results showed 12 of the cranial characters to have moderate ($P < 0.05$) to highly significant ($P < 0.001$) sex differences (GSL, CBL, ZYGW, MSTW, BRW, LACW, C1C1, MANDL, MANDCW, CORH, M2M2, and DENT). In the dental character set, M2L was marginally significant ($P < 0.1$). It seems that *S. oporaphilum* tends to be a sexually dimorphic species and so was considered hereafter

For *Sturnira ludovici* ($n = 14$) from Los Venados, Caracas, Venezuela, results showed significant sex differences for 11 of the 20 cranial characters (GSL, ZYGW, MSTW, LACW, POW, M1M1, C1C1, DENL, MANDL, MANDCW and M2M2). The sample size was too

small to obtain overall multivariate results, so a one-way MANOVA for two pooled Venezuelan localities (Caracas, Los Venados and, Altamira, La Vega) was used. This sample ($n = 27$) showed significant sex differences over the entire cranial character set ($P < 0.01$). We concluded that *S. ludovici* and *S. oporaphilum* showed significant sexual dimorphism. As a consequence, for geographic analyses their characters were treated independently for each sex, resulting in twice the number of characters for these analyses (Schnell *et al.*, 1978; Owen, 1987).

ANALYSIS OF GEOGRAPHIC VARIATION

Geographic differentiation among grouped localities of each taxon was tested by multivariate analyses guided by results of nongeographic variation. The multivariate test statistics showed significant geographic differences ($P < 0.05$) for each character set and for each of the four taxa. Almost all the characters exhibited significant ($P < 0.05$) variation among localities. Duncan's multiple range tests ($P < 0.01$) were conducted for the two pairs of taxa and for each character, permitting the inspection of variation in means among the grouped localities (see Appendix F in Pacheco, 1989). No distinctive regional groups were found in either pair of taxa to aid in recognizing these taxa or in delimiting their ranges. This result supports the treatment of the four taxa in pairs.

Cluster analysis was used to summarize the morphometric data by constructing a pattern of similarity (or differences) among the grouped localities. For the pair *erythromos-bogotensis*, two main clusters were defined (Fig. 4). The upper cluster included the samples previously identified as *bogotensis* from the type locality in Colombia, Bogota, La Uribe (a); an Ecuadorian specimen from Azuay (b); and the Peruvian samples from the Lima western slope and the Huaylas localities (c, d, e, f, g, h). Similarity supports the placement of these three disjunct localities in the same taxon *bogotensis*. Surprisingly, the Ancash, Río Mosna (d) and Ancash, Huaylas (c)

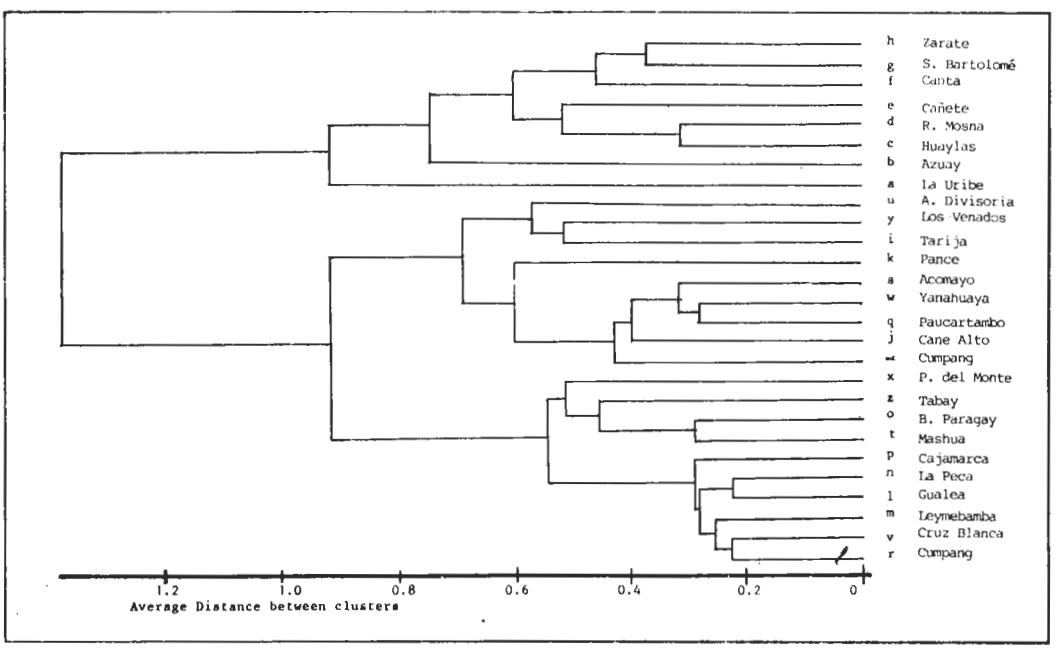

Fig. 4. UPGMA dendrogram for *Sturnira erythromos* and *S. bogotensis* based on 27 grouped localities from South America. Codes for grouped localities are the same as in Appendix.

samples cluster tightly in spite of the Cordillera Blanca (over 4000 m high) which separates these localities. The Ecuadorian sample included in this group suggests that *bogotensis* may indeed have a continuous distribution along the Andes, particularly at higher altitudes. The two samples from Lima, San Bartolomé and Bosque de Zárate (g, h), from the Río Seco valley, cluster tightly suggesting that both samples comprise a single effective population and that differences due to elevation (1500 versus 3000 m) on the western slope are minor or non-existent. The lower cluster includes samples that were initially assigned to *erythromos* or *bogotensis* from Venezuela, Tabay; however the internal subdivisions are difficult to interpret. At a distance of 0.65, three subgroups are formed, each comprising widely distant samples from Venezuela or Colombia to Bolivia or Peru. This similarity suggests no major morphological differentiation among populations along the eastern slope of the Andes, from Venezuela to Bolivia. The *bogotensis* sample from the Colombian type locality separates from the western Peruvian samples at an average distance of 0.75. It should be noted that this difference is based on only one Colombian specimen. Direct observations of the variables reveals that this specimen differs from the Peruvian samples in having larger values of ZYGW, MSTW, BRW, MXBR. However, another Colombian specimen from the type locality (unfortunately with several missing values, and not included in the cluster analysis) was more similar, in the mentioned characters, to the western Peruvian samples than to the paratype. Thus, it seems likely that these differences represent individual variation. We assign then the western Peruvian specimens to *bogotensis* based on the above analyses with the limited number of Colombian specimens.

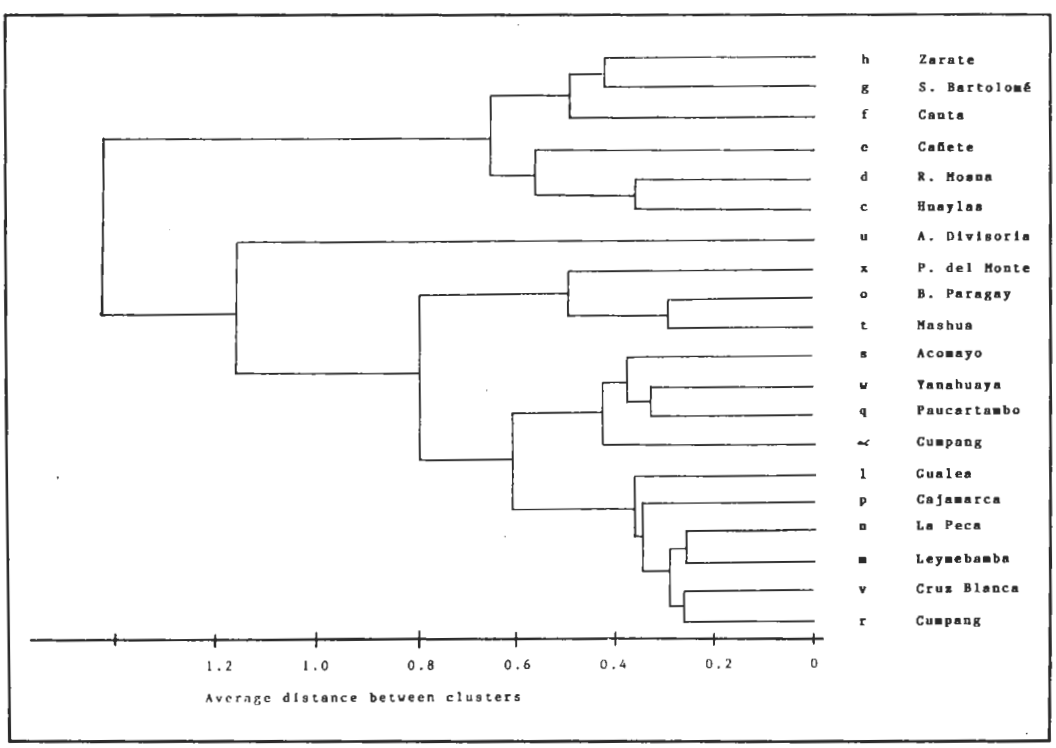

Fig. 5. UPGMA dendrogram for *Sturnira erythromos* and *S. bogotensis* restricted to 19 grouped localities from Peru and one from Ecuador. Codes are the same as in Appendix.

A second cluster analysis was based mostly on Peruvian samples and one from Ecuador (Fig. 5). This analysis was intended to compare western versus eastern populations in the Peruvian region without the effect of northern populations of *Sturnira erythromos* and *S. bogotensis*. This dendrogram also showed two main clusters; the upper referred to *S. bogotensis* and the lower to *S. erythromos*. At a distance of 0.55, the lower cluster contains four subunits. The identification of locality (u) as distinct at this level is probably due to small sample ($n = 2$, both females). The three other subdivisions involved almost the same localities as the first dendrogram. The first cluster (x, o, t) enclosed samples that were not neighbors. The second cluster (s, w, q, α), except for locality α, represented samples from central and southern Peru (Huánuco, Puno and Cuzco). Finally, the third cluster (l, p, n, m, v, r) is made up of samples from northern Peru and one from Ecuador. The two samples from Amazonas, Peru (n, m) were most similar, while the sample from Peru, Piura (v) was most similar to sample (r) from La Libertad. It appears from these comparisons that UPGMA primarily clustered neighboring localities, but regional subdivision is not clearly defined.

Because the *ludovici-oporaphilum* samples exhibited significant differences due to sex, cluster analysis was performed using the mean character of each sex as a separate variable. Unfortunately, grouped localities not having both sexes, or with missing values, could not be analyzed. However, separate dendrograms by sex, and with sexes pooled were conducted mostly for comparisons. At a distance of 1.1, UPGMA identified two main clusters (Fig. 6). The first (I, H, C) was composed of samples identified as *S. ludovici* and the second cluster (E, N, K, G, F, S, O, M, B) by samples of both *S. ludovici* and *S. oporaphilum*. The Venezuelan samples (H and I) were widely separated from the Colombian sample (C), from samples of *S. ludovici* from Ecuador (paratype included) and from representatives of *S. oporaphilum* that are placed in the second cluster. It is proposed that these Venezuelan samples represent a different morph. On the other hand, Peruvian samples (N and K) of *S. oporaphilum* from Cajamarca, Zaña and Amazonas, Río Cenepa were clustered with the Ecuadorian sample from Zamora-Chinchipe (G). This resemblance seems to indicate that this Ecuadorian sample is better referred to *oporaphilum* and that samples were not affected by geographic barriers such as the Río Marañón or the Huancabamba Depression. Moreover, it indicates that the northern Peruvian samples more closely resemble the eastern Ecuadorian samples than the western Ecuadorian specimens.

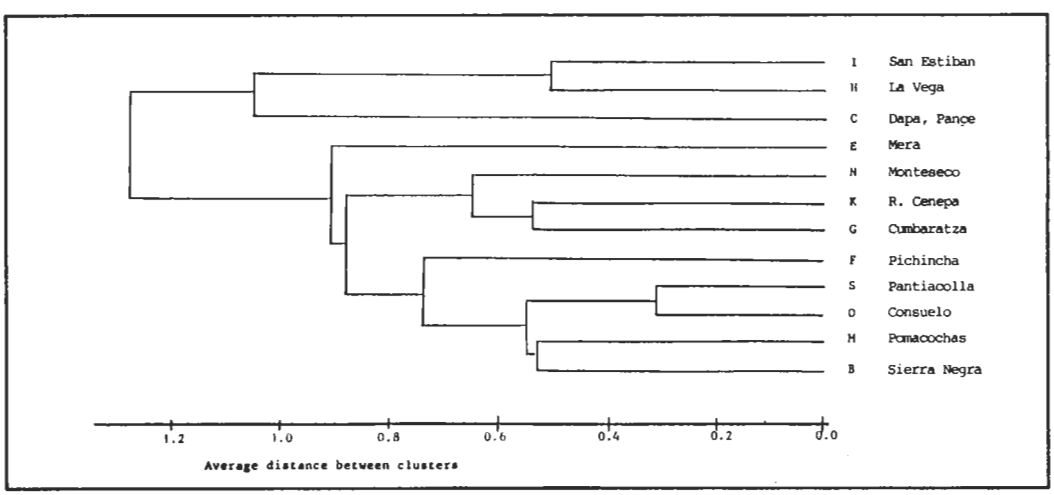

Fig. 6. UPGMA dendrogram for *Sturnira ludovici* and *S. oporaphilum* derived from morphological data. Codes are the same as in the Appendix.

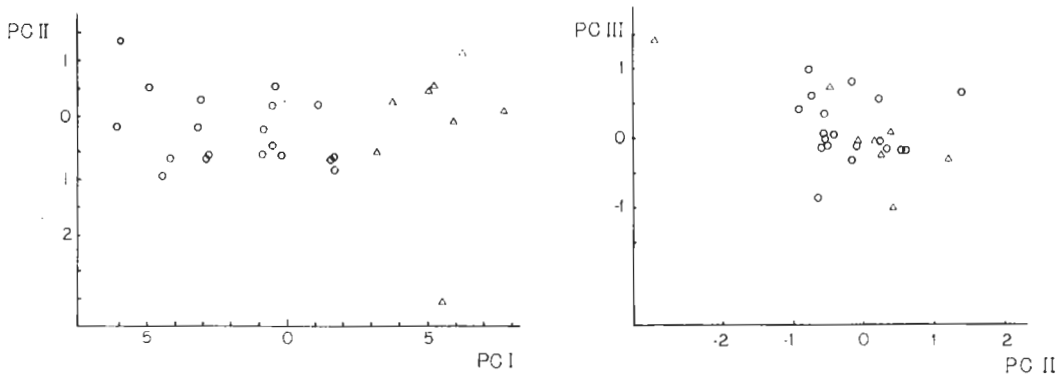

Fig. 7. Plots of Principal component analysis for *Sturnira erythromos* (∘) and *S. bogotensis* (△).

The cluster (S and O) represent nearby samples from southeastern Peruvian (Cuzco, Madre de Dios and Puno). The analysis joined two distant localities: *Sturnira ludovici* from Colombia, Magdalena, Sierra Negra, Valledupar (B) and *S. oporaphilum* from Peru, Amazonas, La Peca (M). This resemblance is likely due to convergence in size, since the Valledupar specimens are smaller than other Colombian samples of *S. ludovici*. In addition, sample (M) was closer to the couple (S and O) in dendrograms based on each sex and with the sexes pooled. Surprisingly, other Ecuadorian samples (F, E) do not cluster together and they join with other clusters at larger average distance. Finally, this dendrogram was quite similar to another obtained for males, except that (M) joined first to (E) instead of (B).

Principal component analysis was conducted for the two pairs of taxa. In the *erythromos-bogotensis* analysis, four components had eigenvalues larger than 1.0. The first three components are plotted in Figure 7. In plots of PC II and PC III versus PC I, *bogotensis* specimens differed mostly in being larger than *erythromos* (i.e., higher loadings on PC I, similar loadings on PC II and PC III). Plot of PC II versus PC III, usually considered to be "shape" components, did not differentiate the two taxa. On the other hand, plots for the *ludovici-oporaphilum* pair suggest that *S. ludovici* is the morph with larger size and that "shape" is an important factor for differentiating these two taxa (Fig. 8).

ANALYSIS OF GENETIC VARIATION

INTRA AND INTERSPECIFIC VARIABILITY. Allelic frequencies for the species here studied have been presented elsewhere (Table 3 in Pacheco & Patterson, 1991). Ten of the 19 loci analyzed were polymorphic among the *Sturnira erythromos* and *S. bogotensis* samples. The average number of polymorphic loci *P*(%) for samples containing more than two individuals was 17.6%, and the average observed heterozygosity (*H*) was 0.0304 for *S. erythromos*; and *P*(%) of 5.3% and *H* of 0.0215 for *S. bogotensis*. *H* was calculated locus by locus, and then averaged over all loci. These values were relatively lower than *P*(%) and *H* given for mammals (Lewontin, 1974), but are comparable to values given for other Phyllostomidae (Koop & Baker, 1983). Values of polymorphism and heterozygosity for *S. oporaphilum* and other *Sturnira* species are reported in Pacheco & Patterson (1991).

Nei's *D* and Rogers' *D* for the *erythromos* and *bogotensis* populations are presented in Table 1. Nei's *D* among these samples ranged from 0.0422 to 0.0833; the largest pairwise comparisons were always interspecific (i.e., between *S. bogotensis* and *S. erythromos*.

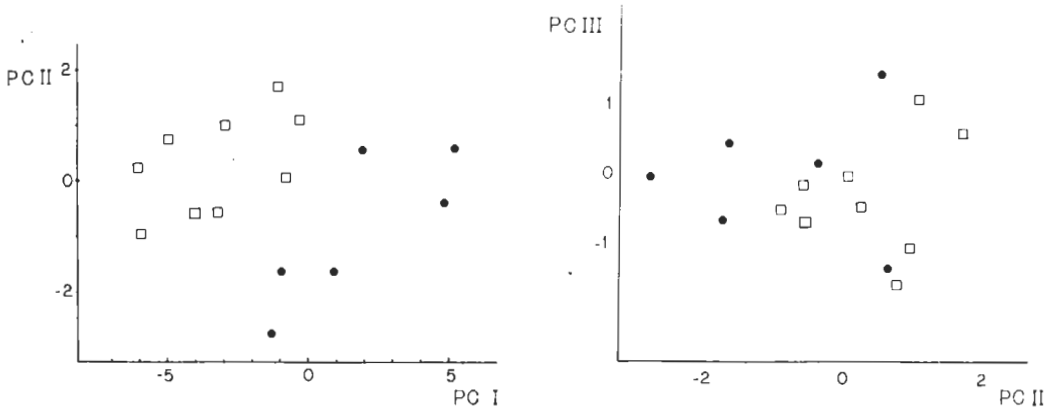

Fig. 8. Plots of Principal component analysis for ***Sturnira ludovici*** (●) and ***S. oporaphilum*** (□).

PHENETIC ANALYSIS. The Fitch-Margoliash dendrogram for the *erythromos* and *bogotensis* populations using Nei's *D* after jackknifing procedures is presented in Figure 9. Two populations from the eastern slope of the Andes (er-5, er-3) were consistently joined in all the replicates. This pair of localities, from Leymebamba in Amazonas and from Paucartambo in Cuzco, seem to represent a single broad genetic unit. Another cluster consistently supported by pseudoreplicate runs contained samples (er-0), (er-6), and (er-8). The sample from Piura, Lucuma-Zapalache (er-6) joined the sample from Ancash, Río Mosna (er-0) in all pseudoreplicates, although the two are separated by the Huancabamba Depression. This pair was followed by the sample from Huánuco, Unchog (er-8) which is on the eastern side of the Andes, separated from sample (er-0) by the Cordillera Oriental and the Río Marañón. It is interesting that geographic features thought to constitute distributional barriers do not disrupt this resemblance. The dendrogram also indicates that the Piura, Lucuma-Zapalache population (er-6) clustered closer to the eastern relatives than to the Lima sample (bo-1), although both were considered to be from the Western slope. The sample (er-1) from Balsas in Amazonas, was closer to the group (er-0, er-6, er-8) in five of the six replicates. The Fitch-Margoliash dendrogram produced using Roger's *D* distance resulted in identical topology.

Table 1. Matrices of modified Rogers' *D* (upper right) and Nei's *D* (Lower left) for *erithromos* and *bogotensis*

bo-1[a]	- -	0.0071	0.005	0.0064	0.0053	0.0060	0.0071
er-0	0.0833	- -	0,0033	0.0043	0.0048	0.0019	0.0036
er-1	0.0735	0.0573	- -	0.0026	0.0031	0.0021	0.0036
er-3	0.0791	0.0642	0.0508	- -	0.018	0.0023	0.0040
er-5	0.0719	0.0681	0.0556	0.0422	- -	0.0027	0.0042
er-6	0.0761	0.0425	0.0460	0.0468	0.0514	- -	0.0022
er-8	0.0830	0.0590	0.0603	0.0619	0.0630	0.0460	- -

[a] See Appendix 1 for the population that correspond to these codes

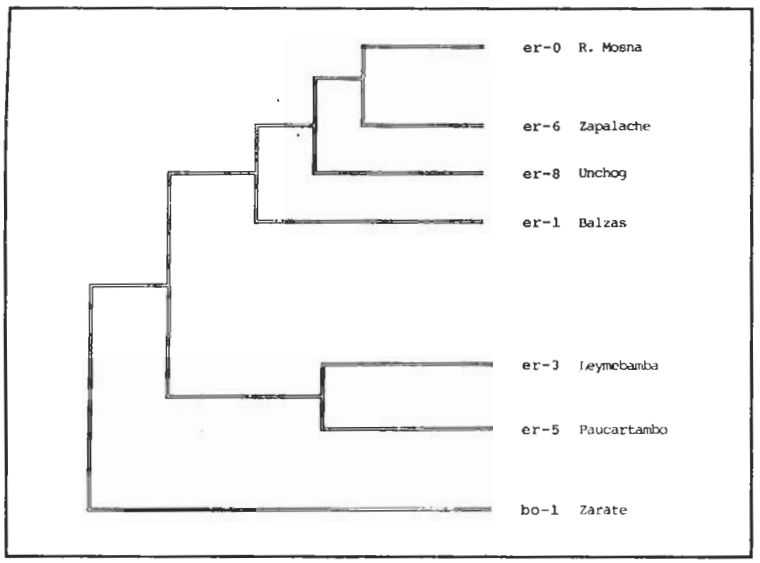

Fig. 9. Jackknifed strict consensus Fitch-Margoliash tree showing electrophoretic similarity for Peruvian samples of *Sturnira erythromos* and *S. bogotensis*. Branch lengths do not correspond to genetic distances. Codes refer to samples listed in the Appendix.

F_{st} analyses were conducted to investigate genetic structure among the populations of *Sturnira erythromos* and *S. bogotensis*. An overall analysis resulted in a value of $F_{st} = 0.10$ (S.E. =0.0246) suggesting moderate genetic differentiation. However, continuous gene flow seems likely among the eastern slope populations (see above). In spite of its proximity to the Ancash, Huaylas sample (assigned to *S. bogotensis*), the Río Mosna sample (er-0), clustered with the eastern population group of *S. erythromos*. This result is also reflected in the low genetic differentiation ($F_{st} = 0.0042$, SE = 0.0042) between the eastern samples (er-1, er-3, er-5, er-8) and the Río Mosna samples. This suggests that the Río Mosna sample is best assigned to *S. erythromos*. An F_{st} analysis comparing the Piura, Lucuma sample (er-6) and pooled specimens from the eastern slope (er-1, er-3, er-5, er-8) also showed a low degree of differentiation (F_{st} = 0.0013, *SE* = 0.0013). The *S. bogotensis* sample from Lima (bo-1) differed significantly from eastern slope ($F_{st} = 0.0632$, *SE* = 0.0215), from the Piura, Lucuma ($F_{st} = 0.0562$, *SE* = 0.0509), and from the Ancash, Río Mosna ($F_{st} = 0.0435$, *SE* = 0.0319) samples. These values corroborate the genetic distance analyses which showed that samples from the eastern slope (er-1, er-3, er-5, er-8), from the northwestern side of the Andes (er-6) and from the headwaters of the Río Marañón (er-0) are not genetically different. These values indicate that certain degree of genetic differentiation exists to separate the Lima sample allied to *S. bogotensis* and the eastern samples allied to *S. erythromos*, supporting the results obtained by morphological data. Although no fixed allelic differences were found between them, this might be a result of the limited number of polymorphic loci found.

The Zaña Valley, in Cajamarca, Peru is a critical locality because it is placed between the Huancabamba and Lima regions of the western slope. However, only a single specimen from the region is available, and was not included in the genetic analysis. Morphologically, this specimen resembles and clusters closer to the eastern slope populations than to the Lima population (Fig. 8); therefore, it is here aligned to *S. erythromos*. Moreover, genetically it has alleles more frequent in *S. erythromos* than to *S. bogotensis* (see Table 3 in Pacheco & Patterson, 1991).

The F_{st} value of 0.1158 (SE = 0.0263) for all *Sturnira oporaphilum* populations suggests moderate genetic differentiation. However, pairwise comparison of samples from Northern

Peru to Bolivia, Santa Cruz, San Rafael de Amboro, showed very low genetic differentiation (F_{st} ranged from 0.0208 to 0.0366). This suggests that, at least south of the Río Marañón, *S. oporaphilum* populations are not genetically differentiated and likely represent one genetic unit.

BIOGEOGRAPHIC RESULTS

Regression analyses showed that neither elevation nor latitude was correlated with size variation. For *Sturnira erythromos*, R^2 was 0.080 for elevation and 0.067 for latitude, and neither value was significant. For other species elevation regressed on size was also not significant, *S. bogotensis* (R^2 = -0.032), *S. ludovici* (R^2 = 0.066), *S. oporaphilum* (R^2 = 0.044).

Mantel tests involving the *Sturnira erythromos* populations showed that geographic distance explained a significant percentage of the genetic differentiation. Linear geographic distance was correlated with Nei's *D* at 0.4643 and with Rogers' *D* at 0.440. In both cases, the observed values were significantly different from values expected by chance alone ($P < 0.005$). Obviously, the different underlying assumptions of the genetic distance measures do not influence results.

Mantel tests were also conducted for indirect geographic distance using *Sturnira erythromos*. The results showed higher observed correlations than with linear distances. The observed correlations were 0.5411 and 0.5768 with the Nei's *D* and Rogers' *D* respectively. In both cases, the observed results were significantly different from the values expected at random: 0.00398 and -0.019 respectively. Considering that geographic distances are indeed very simple variables, with no historical or ecological implications for the species, it is significant that geographic distances explained a large percentage of the genetic distance values.

DISCUSSION

With regard to the status of *Sturnira erythromos*, de la Torre mentioned, "The few specimens available suggest the existence in the Andes of a large race in the north (Colombia, Venezuela), and of a smaller race in the south (Peru)" (de la Torre, 1961:128). Implicitly, he recognized *S. e. bogotensis* for the northern morph and *S. e. erythromos* for the southern one. Subsequently, additional specimens of the large morph were collected in Venezuela (Handley, 1976) and accorded recognition as a species, based on sympatric distributions with *S. erythromos*. Thus, *S. bogotensis* has been used in the literature (Corbet & Hill, 1986; Honacki *et al.*, 1982; Linares, 1986). The discovery of *Sturnira bogotensis* populations in the central western slopes of Peru resulted in a southern extension of its range by more than 1500 km. Our results suggest that de la Torre's distinction of northern versus southern morphs can best be explained by a pattern of distribution of western (*bogotensis*) versus eastern (*erythromos*) over a comparable range of latitudes.

The high degree of genetic similarity among the *Sturnira erythromos* samples was demonstrated in Table 1. This similarity is especially striking with respect to the sample from Ancash, Río Mosna (d) which is identified as *S. erythromos* despite its proximity to the Ancash population of *S. bogotensis* (c) on the western side of the Cordillera Blanca. A certain degree of genetic differentiation is found between *S. erythromos* and *S. bogotensis* based on larger genetic distances between them than when comparing any two conspecific samples. Our cluster and *Fst* analyses also show evidence that *S. bogotensis* and *S. erythromos* in Peru are genetically distinct. As mentioned earlier, the Lima sample was allocated to *S. bogotensis* based on greater morphological similarity with specimens from Colombia, La Uribe (the type locality) than with the smaller specimens from the eastern side of Peru (Fig. 7). However, this

level of morphological variation is not paralleled by marked genetical differentiation, at least relative to the other species of *Sturnira* (see Table 6 in Pacheco & Patterson, 1991). Where morphological differences are sufficient to recognize distinct taxa, one expects also to find evidence of genetic differentiation expressed by allozyme variation. Although speciation events may not be related to genetic differentiation (Patton & Yang, 1977; Patton, 1980), but rather be a function of time and degree of separation of populations (Avise & Ayala, 1976; Soulé, 1976), still allozyme differentiation often accompanies speciation.

These results can be interpreted in at least two ways. First, as a case of a recent speciation event that has not yet produced significant genetic differentiation; in this event *S. erythromos* and *S. bogotensis* constitute two different species. This would be similar to a case reported for two species of minnows (*Hesperoleucus*) with Nei's $D = 0.055$ (Avise and Ayala, 1976) or with sibling bird species (Avise & Zink, 1988). Second, the morphological and genetic differences may be indications of the presence of two well-differentiated subspecies, *S. e. erythromos* and *S. e. bogotensis*, as proposed by de la Torre (1961); in which event, both taxa would not have extensive reproductive isolation. The answer could be decisive support for the first hypothesis given the sympatry reported by Handley (1976). However, Venezuelan *bogotensis* from Tabay (z), although larger than nearby *erythromos*, are not as large as or similar to typical *bogotensis* as can be seen in results of our cluster analysis (Fig. 4). On the other hand, the western Peruvian samples closely fit the description of *bogotensis*, and this similarity is reinforced by direct comparisons (Fig. 4). Unfortunately, frozen tissues and therefore genetic data for Venezuelan and Colombian *Sturnira* were not available at this time. Only additional genetic data from Venezuelan and Colombian *bogotensis* will help to resolve their taxonomic status. We consider then that the existing morphological and genetic variation reported here for *S. erythromos* and *S. bogotensis* from Peru is better interpreted as supporting the recognition of two species.

The taxonomic status of *Sturnira oporaphilum* and *S. ludovici* appears more complex. Unfortunately, tissue samples and genetic data were limited to Peru and Bolivia. The morphological and genetic data suggest that only one species exists in Peru and Bolivia, and is assigned to *oporaphilum* using the oldest available name (Tschudi, 1844). As mentioned above, the Ecuadorian (including types) and Colombian *ludovici* did not differ much from the Peruvian *oporaphilum*, at least as compared to the samples from Venezuela (H, I; Fig. 6). In general, the northern samples are larger than the southern ones (Fig. 8), and it may be tentatively suggested that at least Colombian and Ecuadorian *ludovici* are indeed large *oporaphilum*, but further taxonomic comments on these species must await a more integral revision that includes the taxa *hondurensis* Goodwin, 1940 and *occidentalis* Jones and Phillips, 1974.

Morphologically, a number of bat species of Phyllostomidae are found to be homogeneous in the Neotropics. Reported works are: *Carollia perspicillata* from the Amazonian region (McLellan, 1984), *Phyllostomus discolor* from samples of the eastern side of the Andes (Power and Tamsitt, 1973), and *Sturnira magna* in most of its distributional range (Tamsitt and Valdivieso, 1986). Although few species have been analyzed for morphological variation, other species appear to be as phenetically homogeneous as *S. erythromos*. Tamsitt and Valdivieso (1986) examined correlations of morphometric variation in *S. magna* with climatological variables. They failed to find significant correlation with temperature, precipitation, evapotranspiration, elevation or latitude. Similarly, our results of regression analyses suggest that morphological variation (size) is not correlated with either elevation or latitude across a major part of the distributional ranges of four species of *Sturnira*. Thus, neither elevation nor latitude explains much of the existing morphological variation.

Additionally, we have attempted to explain the biogeographic distribution of *Sturnira erythromos*, because of its larger sample size. We have shown above that populations of *Sturnira erythromos* in South America are phenetically homogeneous. Two geographic barriers in the Peruvian region (i.e., the arid lower Río Marañón and the Huancabamba Depression) apparently do not promote morphological differentiation between populations on either side. In analyses of genetic differentiation, we found very little genetic variation among six populations in the Peruvian region, suggesting that gene flow among those samples is important in impeding morphological and genetic differentiation.

Platnick & Nelson (1978) showed that dispersal patterns can be explained in many ways which make testing the role of specific variables difficult. *Sturnira erythromos*, and likely other bat species, have many ways to overcome what might otherwise appear to be barriers. Mountains could be bypassed directly by flying over the tops or indirectly along the slopes. Both alternatives were evaluated with the Mantel tests. Results show that both are possible, although the correlations with the indirect distances were slightly higher. Dispersal along the slopes of the Andes seems also the most feasible as it requires fewer changes (e.g., in habitats, diet, temperature and precipitation) than when crossing the mountains. In addition, stenodermatine bats have not been found at elevations higher than 3800 m (Koopman, 1978) and most of the Andean Cordillera is well above 4000 m.

Major river systems such as the Río Marañón can likely be crossed directly or by dispersing along the slopes of the valleys. Finally, low mountain passes such as the Huancabamba Depression could be crossed by using the small patches of suitable forest at both sides of the pass, or when habitat conditions are temporarily less xeric, as for example during cycles of the El Niño Southern Oscillation.

Few data are available on the dispersal potential of neotropical bats (Humphrey & Bonaccorso, 1979). In a detailed study of *Carollia perspicillata*, Fleming (1988) gives 2.6 y of average life expectancy, and mentioned a high percentage of philopatry in adult specimens (over 80%). Dispersal takes place mostly at juvenile stages. One specimen of *Artibeus jamaicensis* was recaptured in Barro Colorado Island, Panama seven years after its initial capture (Wilson & Tyson, 1970), suggesting a pattern similar to that of *Carollia perspicillata*. Assuming that *Sturnira erythromos* shares this pattern, the isolation-by-distance model implicated in analyses of genetic variation agrees with this philopatry pattern. Species with higher dispersal abilities (high dispersion rate or distance) would have larger neighborhood size, which is the area where mating is expected to be at random.

The role of dispersal as a major zoogeographic factor has also been emphasized by Koopman (1978, 1982). He analyzed the distribution of bat species with special reference to the Andes and did not find many cases which implicated the Andes as an important biogeographic barrier to east-west dispersal. He concluded that bat distribution offers little support for a vicariance hypothesis. Our results confirm that gene flow and morphological homogeneity in *S. erythromos* are not greatly impeded by two geographic features such as the Río Marañón and the Huancabamba Depression.

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LITERATURE CITED

ANDERSON, S., K. K. KOOPMAN & G. K. CREIGHTON. 1982. Bats of Bolivia: an annotated checklist. *American Museum Novitates* 2750: 1-24.

AVISE, J. C. & F. J. AYALA. 1976. Genetic differentiation in speciose versus depauperate phylads: evidence from the California minnows. *Evolution* 30: 46-52.

AVISE, J. C. & R. M. ZINK. 1988. Molecular genetic divergence between avian sibling species: king and clapper rails, long-billed and short-billed dowitchers, boat-tailed and great-tailed grackles, and tufted and black-crested titmice. *Auk* 105: 516-528

CORBET, G. B. & J. E. HILL. 1986. *A World List of Mammalian Species, Second Edition.* Facts On File Publications, New York.

CRACRAFT, J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. *Ornithological Monographs* 36: 49-84

DE LA TORRE, L. 1961. *The Evolution, Variation and Systematics of the Neotropical Bats of the Genus* Sturnira. Ph.D. dissertation, University of Illinois, Urbana.

DUELLMAN, W. E. 1979. The herpetofauna of the Andes: patterns of distribution, origin, differentiation, and present communities, pp. 371-459. *In*: Duellman, W. E. (Ed.), The South American Herpetofauna: its Origin, Evolution, and Dispersal. *Monographs, Museum of Natural History, University Kansas* 7.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39(4): 783-791

FITCH, W. M. & E. MARGOLIASH. 1967. Construction of phylogenetic trees. *Science* 155: 279-284

FLEMING, T. H. 1988. *The Short-tailed Fruit Bat: a Study in Plant-animal Interactions.* The University of Chicago Press, Chicago.

HANDLEY, C. O., JR. 1976. Mammals of the Smithsonian Venezuelan Project. *Brigham Young University Science Bulletin, Biological Series* 20(5): 1-91.

HARRIS, H. & D. A. HOPKINSON. 1978. *Handbook of Electrophoresis in Human Genetics.* North-Holland Publishing Co.

HERSHKOVITZ, P. 1949. Mammals of northern Colombia, Preliminary report no. 5: Bats (Chiroptera). *Proceedings of the United States National Museum* 99: 429-454.

HONACKI, J. H., K. E. KINMAN & J. W. KOEPPL (Eds.). 1982. *Mammal Species of the World.* Allen Press and Association of Systematics Collections, Lawrence.

HUMPHREY, S. R. & F. J. BONACCORSO. 1979. Population and community ecology. *In*: Baker, R.J., J.K. Jones, Jr. & D.C. Carter (Eds.), Biology of Bats of the New World Family Phyllostomatidae. Part III, *Special Publications, Museum, Texas Tech University* 16: 409-441.

JONES, J. K. & D. C. CARTER. 1976. Annotated checklist, with keys to subfamilies and genera. *In*: Baker, R.J., J.K. Jones, Jr., & D.C. Carter (Eds.), Biology of Bats of the New World family Phyllostomatidae. Part I. *Special Publications, Museum, Texas Tech University* 10: 7-38.

KOOP, B. F. & R. J. BAKER. 1983. Electrophoretic studies of relationships of six species of *Artibeus* (Chiroptera: Phyllostomidae). *Occasional Papers, Museum, Texas Tech University* 83: 1-12.

KOOPMAN. K. F. 1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. *American Museum Novitates* 2651: 1-33.

KOOPMAN, K. F. 1982. Biogeography of the bats of South America. *In*: Mares M. A. & H. H. Genoways (Eds.), Mammalian Biology in South America. *Special Publication Series, Pymatuning Laboratory of Ecology* 6: 273-302.

KUNZ, T. H. 1987. *Post-natal growth and energetics of suckling bats*, pp. 395-420. *In*: Fenton, M. B., P. Racey, & J. M. V. Rayner (Eds.), *Recent Advances in the Study of Bats.* Cambridge University Press, Cambridge.

LANYON, S. M. 1985. Detecting internal inconsistencies in distance data. *Systematic Zoology* 34(4): 397-403

LEWONTIN, R. C. 1974. *The Genetic Basis of Evolutionary Change.* Columbia University Press, New York.

LINARES, O. J. 1986. *Murciélagos de Venezuela.* Cuadernos Lagoven, Caracas.

MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27: 209-220.

McLELLAN, L. J. 1984. Morphometric analysis of *Carollia* (Chiroptera, Phyllostomidae). *American Museum Novitates* 2791: 1-35.

OWEN, R. D. 1987. Phylogenetic analyses of the bat subfamily Stenodermatinae (Mammalia: Chiroptera). *Special Publications Museum, Texas Tech University* 26: 1-65.

PACHECO, V. 1989. *Systematics and Biogeography of some Sturnira (Chiroptera: Phyllostomidae) with emphasis on Andean Forms.* Master of Science Thesis, University of Illinois, Chicago.

PACHECO, V. & B. D. PATTERSON. 1991. Phylogenetic Relationships of the New World Bat Genus *Sturnira* (Chiroptera: Phyllostomidae). *Bulletin of the American Museum of Natural History* 206: 101-121.

PARKER, T. A., III, T. S. SCHULENBERG, G. R. GRAVES & M. J. BRAUN. 1985. The avifauna of the Huancabamba Region, Northern Peru. *Ornithological Monographs* 36: 169-197.

PATTON, J. L. 1980. *Chromosomal and genic divergence, population structure, and speciation potential in* Thomomys bottae *pocket gophers*, pp. 255-295. *In*: Reig, O.A. (Ed.) *Ecology and Genetics of Animal Speciation*. Universidad Simón Bolivar, Caracas.

PATTON, J. L. & S. Y. YANG. 1977. Genetic variation in *Thomomys bottae* pocket gophers: macrogeographic patterns. *Evolution* 31: 697-720.

PLATNICK, N. I. & G. NELSON. 1978. A method of analysis for historical biogeography. *Systematic Zoology* 27: 1-16.

POWER, D. M. & J. R. TAMSITT. 1973. Variation in *Phyllostomus discolor* (Chiroptera: Phyllostomatidae). *Canadian Journal of Zoology* 51: 461-468.

SAS INSTITUTE. 1987. *SAS/STAT Guide for personal computers, Version* 6 *Edition*. Cary, North Caroline.

SCHNELL, G. D., T. L. BEST & M. L. KENNEDY. 1978. Interspecific morphologic variation in kangaroo rats (*Dipodomys*): degree of concordance with genic variation. *Systematic Zoology* 27: 34-48.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON & J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). *University of Texas Publications* 7103: 49-90.

SHAMEL, H. H. 1927. A new bat from Colombia. *Proceedings of the Biological Society of Washington* 40: 129-130.

SNEATH, P. H. A. & R. R. SOKAL. 1973. *Numerical taxonomy*. W. H. Freeman, San Francisco.

SOULE, M. 1976. *Allozyme variation: Its determinants in space and time*, pp. 60-77. *In*: Ayala, F. J. (Ed.), *Molecular evolution*, Sinauer and Associates, Sunderland.

STEPHENS, L. & M. A. TRAYLOR, JR. 1983. *Ornithological Gazetteer of Peru*. Museum of Comparative Zoology, Harvard University, Cambridge.

TAMSITT, J. R. & D. VALDIVIESO. 1986. Variacion morfometrica en el murciélago *Sturnira magna* (Chiroptera: Phyllostomidae). *Caldasia* 15: 743-760.

TSCHUDI, J. J. Von. 1844. *Therologie. In*: Tschudi, J. J., *Untersuchungen über die Fauna Perus* 1: 1-262, pls. 1-18.

VUILLEUMIER, F. 1969. Pleistocene speciation in birds living in the high Andes. *Nature* 223: 1179-1180.

VUILLEUMIER, F. 1984. Zoogeography of Andean Birds: Two major barriers; and speciation and taxonomy of the *Diglossa carbonaria* superspecies. *National Geographic Society Research Reports* 16: 713-731.

WILLIG, M. R., R. O. OWEN & R. L. COLBERT. 1986. Assessment of morphometric variation in natural populations: The inadequacy of the univariate approach. *Systematic Zoology* 35(2): 195-203.

WILSON, D. E. & E. L. TYSON. 1970. Longevity records for *Artibeus jamaicensis* and *Myotis nigricans*. *Journal of Mammalogy* 51: 203.

WRIGHT, S. 1943. Isolation by distance. *Genetics* 28: 114-138.

WRIGHT, S. 1978. *Evolution and the genetics of populations, Volume* 4: *Variability within and among natural populations*. University of Chicago Press, Chicago.

APPENDIX

Number before the localities were plotted in Figure 1. Parenthesis ending each record show the enclosing grouped locality for the multivariate analysis, and square brackets indicate specific samples used in the electrophoretic analysis. Museum acronyms are as follow: AMNH, American Museum of Natural History; EPN, Escuela Politécnica Nacional; FMNH, Field Museum of Natural History; LSUMZ, Museum of Zoology, Louisiana State University; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos; MVZ, Museum of Vertebrate Zoology, University of California; USNM, National Museum of Natural History (United States); PZE, Peruvian Zoological Expedition (FMNH uncatalogued).

Sturnira bogotensis

25. COLOMBIA: Bogotá, La Uribe, USNM 251986-251987 (a).
27. ECUADOR: Azuay, Yanasacha, AMNH 244948 (b).
26. PERU: Ancash, Huaylas, PH 50-51 (FMNH uncatalogued), MUSM 4002-4003, 4047-4049(c).
38. PERU: Ancash, Yungay, Quebrada Llanganuco, MUSM 4004 (c).
28. PERU: Lima, Bosque de Zárate, FMNH 128935, 128793-128794 [bo-1]; MUSM 4013-4020 (h).
35. PERU: Lima, Canta, Obrajillo, MUSM 4010-4011 (f).
30. PERU: Lima, Cañete, Aiza, MUSM 4038-4039 (e).
29. PERU: Lima, San Bartolomé, FMNH 128789-128792 [bo-1], MUSM 4022-4034 (g).

Sturnira erythromos

23. BOLIVIA: Tarija, Tarija, FMNH 105953; Entre Ríos, 25 km NW, FMNH 105990 (i).
17. COLOMBIA: Huila, El Parque las Cuevas, FMNH 58721-58725 (j).
18. COLOMBIA: Huila/Cauca, Río la Plata, 1 mi N Moscopas, USNM 483453 (j).
65. COLOMBIA: Meta, Cane Alto, NW Restrepo, FMNH 121259 (j).
20. COLOMBIA: Nariño, La Victoria, FMNH 113462 (l).
22. COLOMBIA: Valle, S Pance, 20 km SW Cali, USNM 483451-483452 (k).
66. ECUADOR: Hda. la Calera, El Angel, EPN 7821 (l).
67. ECUADOR: El Carchi, Gruta de la Paz, EPN 78853 (l).
68. ECUADOR: Ec. Esmeraldas, Cordillera de Toisán, EPN 851215 (l).
42. ECUADOR: Gualea, Gualea, EPN 2484 (l).
70. ECUADOR: Pichincha, Chiriboga, EPN 79917 (l).
71. ECUADOR: Pichincha, Perucho, EPN 81350 (l).
72. ECUADOR: Pichincha, Volcán Pichincha, EPN 6658-6659 (l).
73. ECUADOR: Uyunabicho, EPN 7479 (l).
59. PERU: Amazonas, 19 km by road E Balsas, FMNH 128796-128799 [er-1],(m).
55. PERU: Amazonas, Corosha, Río Chiriaco, MVZ 139977-139978 (n).
62. PERU: Amazonas, ca. 20 km (by road) W Leymebamba, FMNH 128800-128808 [er-3](m).
5. PERU: Amazonas, ca. 20 km trail E La Peca, LSUMZ 21379-21380, 21382-21383, 21387-21390, 21392-21396, 21844 (n).
10. PERU: Amazonas, ca. 6 road km, SW Lake Pomacochas, LSUMZ 18986- 18988, 18991-18995; MVZ 135573-135574 (n).
74. PERU: Amazonas, Utcubamba, between Churuja and Pedro Ruiz, FMNH 128809 (n).
61. PERU: Ancash, Río Mosna, FMNH 128781-128788 [er-0](d).

51. PERU: Ancash, San Marcos, Huari MUSM 4005-4006, 4008-4009 (d).
11. PERU: Apurímac, Bosque Paragay, FMNH 42-44; MUSM 4035-4037 (o).
75. PERU: Cajamarca, Cajamarca, MVZ 137909-137911 (p).
9. PERU: Cajamarca, 7 km N, 3 km E Chota, LSUMZ 22106 (p).
14. PERU: Cajamarca, 11.5 km N, 2 km W Lajas, LSUMZ 22108-22114 (p).
58. PERU: Cajamarca, Río Zaña, 2 km N Monteseco, FMNH 128811 (p).
13. PERU: Cuzco, Marcapata, FMNH 75182-75185 (q).
53. PERU: Cuzco, 32 km NE Paucartambo (km 112), MVZ 171436- 171437, 171440-171442 [er-5]; MVZ 166598-166599, 171438-171439 (q).
76. PERU: Cuzco, Pillahuata, FMNH 123888 (q).
12. PERU: Huánuco, Bosque Taprag, ca. Acomayo, FMNH 110921 (s).
64. PERU: Huánuco, Unchog, pass between Churubamba and Hacienda Paty, NNW Acomayo, LSUMZ 28167-28168, 28173, 28179-28180, 28182, 28185-28188 [er-8](s).
77. PERU: Junín, Tarma, FMNH 51520 (s).
4. PERU: La Libertad, Cumpang above Utcubamba, on trail to Ongón, LSUMZ 24701, 24706, 24675-24676, 24680-24682, 24685, 24687-24689, 24691, 24697, 24699 (r).
7. PERU: La Libertad, Mashua, E of Tayabamba on trail to Ongón, LSUMZ 24658, 2466024661, 24667-24671, 24673-24674 (t).
4. PERU: La Libertad, Cumpang above Utcubamba, on trail to Ongón, LSUMZ 24695-24696 (a).
8. PERU: Ucayali, 3rd. km NE Abra Divisoria on Tingo María-Pucallpa highway, LSUMZ 22105, 22115 (u).
1. PERU: Piura, 15 km road E Canchaque, LSUMZ 18952-18956, 18958-18959, 18960-18965, 18967-18971, 18973-18979, 18981, 18983-18985, 19704 (v).
6. PERU: Piura, Cruz Blanca, 33 km road SW Huancabamba, LSUMZ 26930-26933 [er-6], 27107 (v).
2. PERU: Piura, Cerro Chinguela, 5 km N Zapalache, LSUMZ 26925-26927 [er-6](v).
3. PERU: Piura, Machete on Zapalache-Carmen trail, LSUMZ 26928-26929 [er-6](v).
78. PERU: Puno, 3 mi NNE Limbani, Agualani, MVZ 139521 (w).
79. PERU: Puno, 14 km W Yanahuaya, MVZ 172586-172590 (w).
80. PERU: San Martín, Puerta del Monte, 30 km NE Los Alisos, LSUMZ 27280-27281 (x).
16. VENEZUELA: Caracas, 9.4 km N of, Hotel Humboldt, USNM 370265-370269 (y).
15. VENEZUELA: Caracas, 5 mi N of, Los Venados, USNM 370226-370227, 370229-370234, 370236-370237, 370240-370242, 370245-370246, 370248-370249, 370251, 370253 (y).
24. VENEZUELA: Mérida, 5.5 km E, 2 km S of Tabay, middle refugio, USNM 386564; Mérida, 4 km E of Tabay, La Mucuy, USNM 373798 (z).

Sturnira ludovici

18. COLOMBIA: Huila/Cauca, 1 mi S Moscopas, Río La Plata, USNM 483510 (A).
37. COLOMBIA: Magdalena, Sierra Negra, Villanueva, Valledupar, USNM 281259-281261, 281264 (B).
34. COLOMBIA: Valle, Dapa, 15 km NW Cali, USNM 483511 (C).
22. COLOMBIA: Valle, 2 km S de Pance, ca. 20 km SW Cali, USNM 483512-483516 (C).
81. ECUADOR: Carchi, Maldonado, EPN 7975 (F).
40. ECUADOR: San José, 12 mi SW Huicra, FMNH 48785 (D).
40. ECUADOR: San Juan, 15 mi W. Huicra, FMNH 48786 (D).
39. ECUADOR: Esmeraldas, ca. Río Cauce, FMNH 44296-44297 (not located) (F).
42. ECUADOR: Gualea, W side Pichincha AMNH 67329 (F).

43. ECUADOR: Pastaza, Mera, USNM 548146 (E).
41. ECUADOR: Pastaza, 1.5 km E Mirador, USNM 513456-513457 (E).
83. ECUADOR: Imbabura, Paramba, USNM 113370 (F).
44. ECUADOR: Pichincha, Tela Mines, FMNH 48949-48950, 48784 (not located) (F).
45. ECUADOR: Pichincha, Zaracalles, USNM 513448-513449 (F).
32. VENEZUELA: Altamira, 2 km SW of, La Vega del Río Santo Domingo, USNM 440134-440148 (H).
31. VENEZUELA: San Esteban, SMF 12440 (I).
33. VENEZUELA: Caracas, 5 km N of Los Venados, USNM 370374, 370387, 370389 (I).

Sturnira oporaphilum

82. ECUADOR: Loja E, Santa Bárbara, EPN 2485 (not located) (G).
84. ECUADOR: Zamora-Chinchipe, 3 km NE Cumbaratza, USNM 513452-513455 (G).
85. ECUADOR: Zamora-Chinchipe, 4 km NE Sabanilla, USNM 513451 (G).
59. PERU: Amazonas, 3 km E Balsas, FMNH 128919 (J).
54. PERU: Amazonas, Río Cenepa, headwater of Río Kafka, MVZ 154846-154847, 154849-154851, 154853-154854, 154859 (K).
46. PERU: Amazonas, 43 road km NE Chiriaco, LSUMZ 21511 (L).
5. PERU: Amazonas, 12 km E la Peca, LSUMZ 21400-21407, 21409 (M).
5. PERU: Amazonas, 20 km E la Peca, LSUMZ 21416 (M).
10. PERU: Amazonas, 6 road km SW Lake Pomacochas, LSUMZ 19032, 22458; MVZ 135560-135565 (M).
74. PERU: Amazonas, Río Utcubamba, 15 km N of Pedro Ruiz, FMNH 128920-128923 (M).
58. PERU: Cajamarca, 2 km N of Monteseco, Río Zaña, FMNH 128926-128934, 128795 (N).
47. PERU: Cuzco, Consuelo, FMNH 123903-123904, 123906-123907, 123910 (O).
13. PERU: Cuzco, Marcapata, FMNH 75186-75189 (O).
53. PERU: Cuzco, 72 km NE Paucartambo (by road km 152), MVZ 166600, 166602-166604 (O).
49. PERU: Junín, Huacapistana, FMNH 54939 (P).
4. PERU: La Libertad, Utcubamba, on trail to Ongón, LSUMZ 24704-24705 (Q).
86. PERU: Ucayali, Tingo María-Pucallpa highway, LSUMZ 22103 (R).
48 PERU: Madre de Dios, Hacienda Amazonia, FMNH 125844, 125847-125848 (S).
57. PERU: Madre de Dios, Pantiacolla, FMNH 122132 (S).
57. PERU: Madre de Dios, Pantiacolla, PZE 580-581, 586-587, 601, 610, 616-618, 656, 666, 668, 681, 692, 703, 722, 732, 735, (S).
50. PERU: Puno, 5 km by road, NE San José on Río Huari, LSUMZ 22461 (S).

Pacheco, V., and B. D. Patterson. 1992. Systematics and biogeographic analysis of four species of Sturnira (Chiroptera: Phyllostomidae), with emphasis on Peruvian forms, Pp. 57-81 in Biogeografía, ecología y conservación del bosque montano en el Perú (K. R. Young and N. Valencia, eds.). Universidad Nacional Mayor de San Marcos, Lima.