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A MORPHOMETRIC ANALYSIS OF THE BAT
SPECIES IN THE GENUS *CAROLLIA*
(MAMMALIA:PHYLLOSTOMIDAE)

presented by

Laura John McLellan Moritz

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A MORPHOMETRIC ANALYSIS OF THE BAT SPECIES IN THE GENUS *CAROLLIA* (MAMMALIA:PHYLLOSTOMIDAE)

By

Laura John McLellan Moritz

A THESIS

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ABSTRACT

A MORPHOMETRIC ANALYSIS OF THE BAT SPECIES IN THE GENUS *CAROLLIA* (MAMMALIA:PHYLLOSTOMIDAE)

by

Laura John McLellan Moritz

The species of bats in the genus *Carollia* present a complex pattern of morphological variation. This variability complicates species identification. I examined sexual and geographic variation in cranial and mandibular measurements of 475 *Carollia* specimens selected to represent the distributional range of each species. The presently accepted species include: *brevicauda*, *castanea*, *perspicillata*, and *subrufa*.

The species were easily separated by canonical variates analysis, with *C. castanea* the most distinctive species. Sexual dimorphism is present in all species and males are consistently larger than females. Significant differences between populations are present in all species. *C. subrufa* and *C. brevicauda* have morphologically distinct populations in the northern and southern portions of their range, while different populations of *C. castanea* show no clear geographic pattern. *C. perspicillata* populations form a continuum with nonoverlapping individuals from the northernmost and southernmost portion of the range.

To my mother and father

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Bats of the genus *Carollia* (family Phyllostomidae) are among the most common mammals in tropical America. They range from northern Mexico to Paraguay living in most habitats, except those at higher elevations and in very arid regions. Despite their abundance, the taxonomy of *Carollia* has been confused largely because of difficulty in accurately delimiting species. The past difficulties in determining species limits is reflected in the nomenclatural history of the genus.

Linnaeus (1758) first described a *Carollia* under the name *Vespertilio perspicillatus*. In part because of the ambiguity of his description, considerable nomenclatural confusion existed for members of this genus until 1907, when Hahn (1907) produced the first revision of the genus. He recognized three species of *Carollia* under the generic name *Hemiderma*: *H. perspicillata* with subspecies *perspicillatum* and *aztecum*, *H. subrufum* Hahn and *H. castaneum* H. Allan. Unfortunately, at that time only 374 specimens were available for Hahn to study and these poorly represented the distributional range of the genus. In 1924, Miller resurrected the generic name *Carollia* (previously thought to be a junior synonym of the fossil pelcypod *Carolia*). The species *subrufum* and *castaneum* were considered conspecific by Felten (1956) who, following Elliot (1904) presented a key based on measurements to separate the two species (*perspicillata* and *castanea*) that he recognized. Subsequently, there was a fair amount of confusion over the number of species of *Carollia*. It proved particularly difficult to find distinguising characters that consistently separated species over their entire range. Hall and Kelson (1956; species *perspicillata* and *castanea* recognized) noted that individuals of each species were larger in the northern part of their geographic range than those from the southern portion. They were unable to make a key that could distinguish the species they recognized from one another at all locations.

Pine (1972) presented a revision of the genus where he recognized four species, adding *C. brevicauda* to the list of widely accepted species. He used classical methods in his revision of the genus, examining a large number of specimens from throughout the range of each species, in search of distinguishing characters. He was able to find a combination of characters to distinguish four species. These characters include cranial features, tooth morphology, body size and pigment distribution in hair shafts. Pine provided a key to the species that is useful when both skins and cleaned skulls are available and when the specimens are from the same geographic region. Although Pine's classical approach has proven useful at the species level, intraspecific variation between populations has not been clearly described. Pine noted that intraspecific variation existed, but was unable to quantify this variation using a classical approach. Two intraspecific size trends noted by Pine are: (1) individuals from the northern populations were larger than those from the south in all species except C. castanea and (2) male C. perspicillata tended to be larger than females. He further noted that sympatric species populations were easier to distinguish from one another than were allopatric populations of the same species. Pine treated C. perspicillata as polytypic and suggested that C. subrufa may also have more than one form (but was uncertain of how many and what their taxonomic status should be).

I re-examined the genus Carollia extending Pine's analysis to describe character variation within the four species. Morphometric techniques were used on cranial and mandibular measurements to evaluate individual, intrapopulational and intraspecific variation. I examined the following points:

1. How distinctive, in a quantitative sense, are the four nominate species recognized by Pine?
2. How is the variation due to individuals, sex and location apportioned?
3. How do the individual species vary between sexes and between populations?

4. Is the variation within each species concordant across the species?
5. What are the phenetic relationships of the populations within and between species?

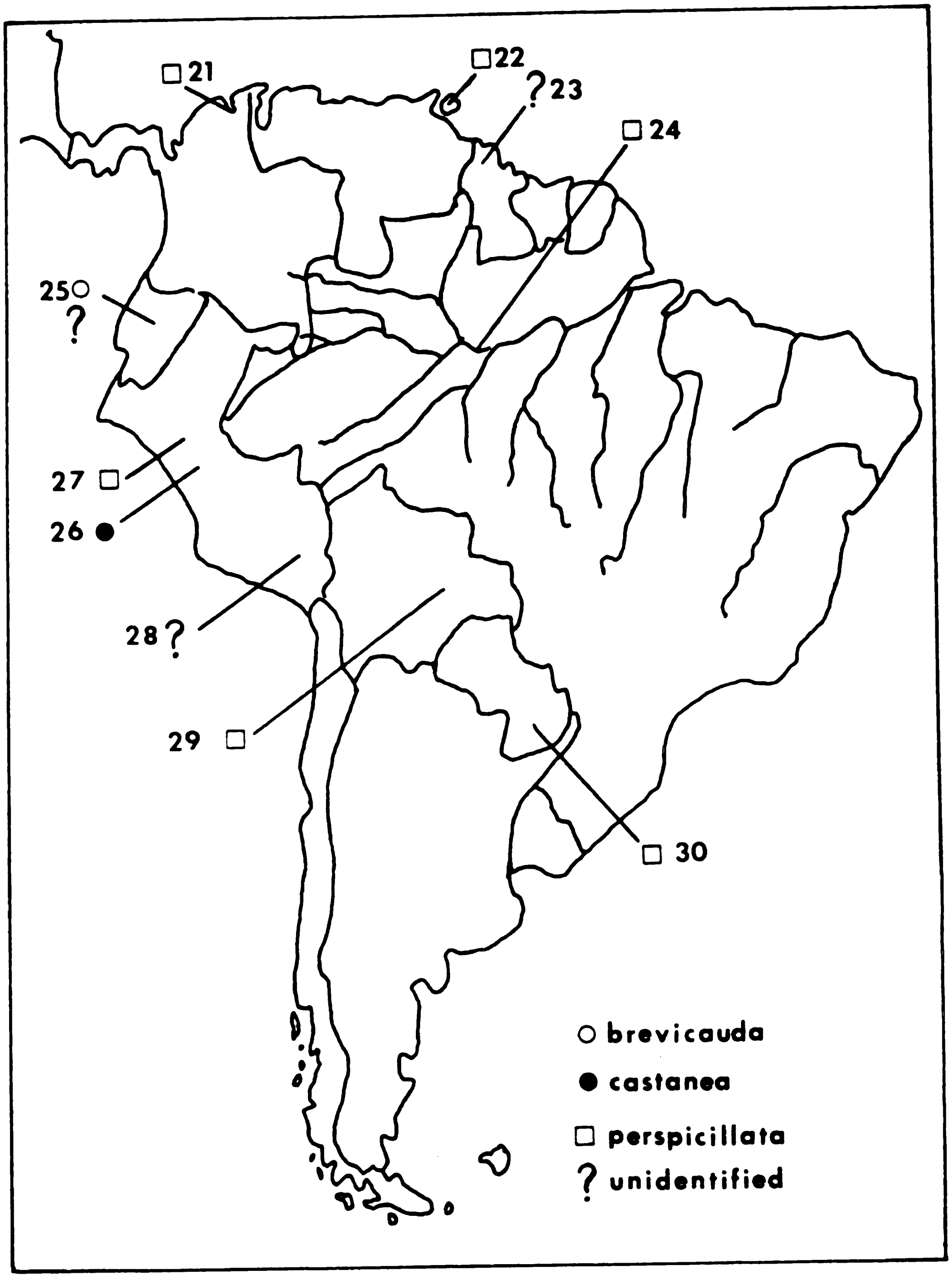
This analysis will aid in identifying the patterns of geographic variation as well as sexual and individual variation within <u>Carollia</u> species. Once the patterns are described, hypotheses concerning factors responsible for these patterns of variability can be addressed.

METHODS AND MATERIALS

I examined a total of 475 male and female *Carollia* skulls from locations selected to represent the distributional range of the genus (Appendix A). All of the specimens were examined previously by Pine (1972) in his study of the genus. I used only specimens judged adult by Pine (1972), based on fusion of the epiphyses of the metacarples and phalanges. Only populations from Pine's study with more than two individuals were included in the analysis. The average number of individuals examined per population was 13. Specimens of *C. castanea* (n=64) were examined from four localities extending from Honduras to Peru. *C. subrufa* (n=73) were examined from eight localities along the Pacific versant of Central America, from Mexico to Nicaragua. Nine populations of *C. brevicauda* (n=123) are represented, ranging from Mexico to Ecuador. *C. perspicillata* (n=215) is the best represented species with specimens examined from 15 localities ranging from Mexico to Paraguay (Figures 1 and 2). Pine left four specimens unclassified to species. These individuals were from separate localities in Nicaragua, British Guiana, Ecuador and Peru. They were included in certain of the analyses

Figure 1. Mexican and Central American localities from which populations were sampled. Numbers correspond to localities listed in Appendix A. Vertical lists of symbols indicate sympatric populations of several species.

Figure 2. South American localities from which population samples were examined. Numbers correspond to localities listed in Appendix A. Vertical lists of symbols indicate sympatric populations.


21
22
23
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25
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27
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29
30
○ brevicauda
● castanea
□ perspicillata
? unidentified

Figure 2.

to more accurately determine their phenetic relationships with <u>Carollia</u> species.

A total of 22 cranial and mandibular characters were measured (Figure 3). Linear measurements were taken to the nearest 0.1 mm using dial calipers and one angular measurement was taken using a goniometer mounted on a dissecting microscope. In order to measure the slope of the forehead, the skull was set on its side in a clay block on top of a piece of graph paper. The upper edge of the maxillary tooth row was aligned with a line on the graph paper and used as a base line. The crosshair of the goniometer was aligned perpendicular to the tooth row and passing through the inflection point between the cranium and the rostrum. The angular measure was taken between this perpendicular crosshair and the forehead. Linear characters include: basilar length (BAL), palatar length (PL), postglenoid width (PGW), breadth of braincase (BB), depth of braincase (DB), least interorbital breadth (LIB), rostral breadth (RB), length of maxillary spur (MSL), length of maxillary tooth row (MTR), width between first molars (MW), width between second pre-molars (PMW), width between canines (CW), dorsal rostral length (DRL), ventral rostral length (VRL), palatal width (PW), foramen magnum width (FMW), mandibular length (ML), mandibular depth (MD), coronoid-angular distance (CAD), height of coronoid (CH), and post-dentary ramus length (PDRL).

Figure 3. Views of Carollia skull and mandibular ramus showing measurements used in study: 1. basilar length (BAL); 2. palatar length (PL); 3. postglenoid width (PGW); 4. breadth of brain case (BB); 5. depth of brain case (DB); 6. least interorbital breadth (LIB); 7. rostral breadth (RB); 8. maxillary spur length (MSL); 9. maxillary tooth row (MTR); 10. width between first molars (MW); 11. width between second premolars (PMW); 12. width between canines (CW); 13. dorsal rostral length (DRL); 14. ventral rostral length (VRL); 15. palatar width (PW); 16. foramen magnum width (FMW); 17. mandibular length (ML); 18. mandibular depth (MD); 19. coronoid angular distance (CAD); 20. coronoid height (CH); 21. postdentary ramus length (PDRL); 22. slope of forehead (SF).

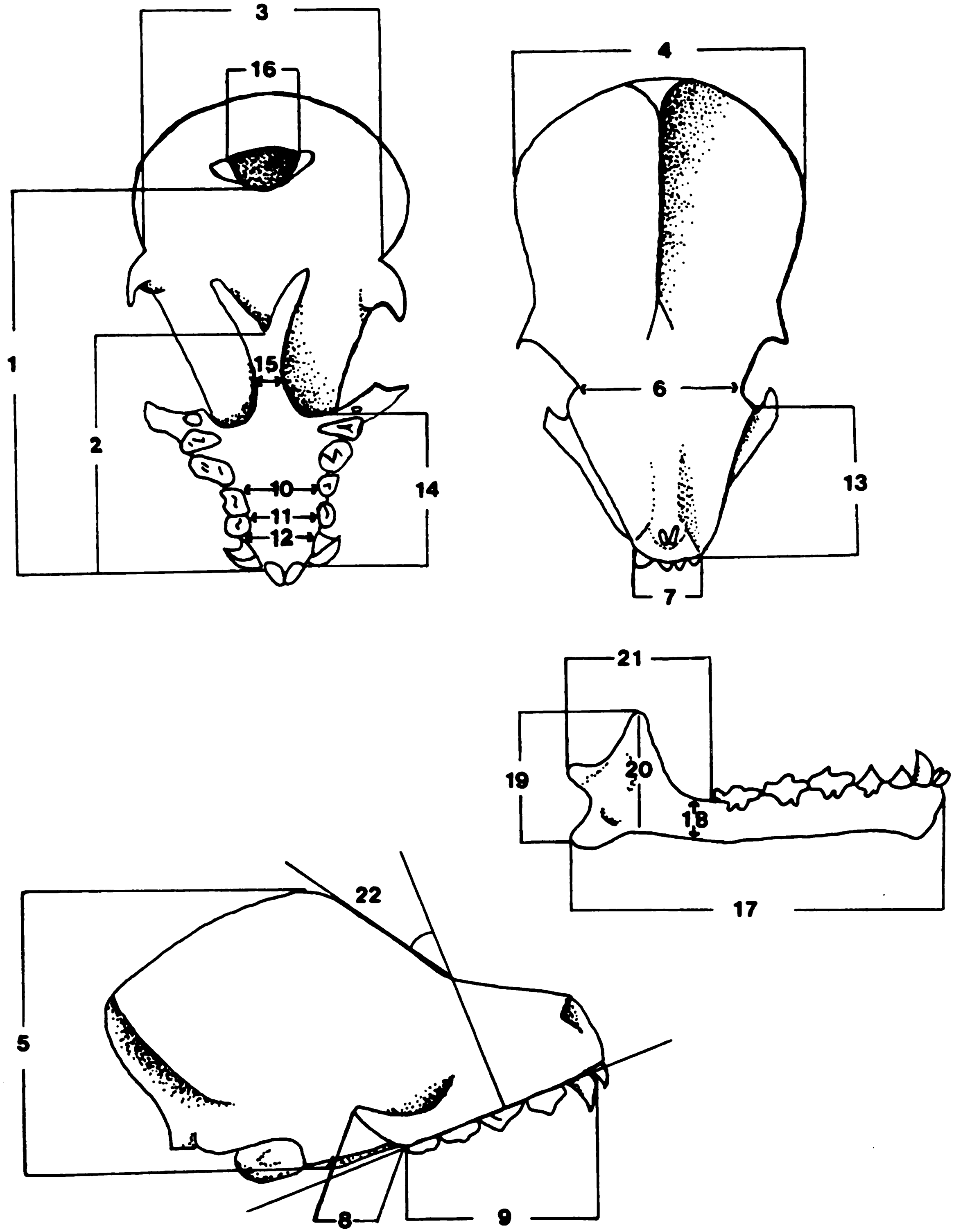


Figure 3.

Statistical analysis of the data was performed at Michigan State University using the Statistical Package for the Social Sciences (SPSS; Nei et al., 1975) and Clustan (Cluster Analysis Package; Wishart, 1978). The mean squares for differences due to species and due to populations and sexes within species are calculated in two separate nested one-way analyses of variance using SPSS MANOVA; from these the magnitude of the respective variance components are estimated. The variance components themselves are not comparable over characters or taxa because of varying sample sizes and unequal variances, but the magnitude relative to the total variance within each character can be compared. The relative magnitude of these variance components was used to determine the importance of sources of variation (Straney, 1978; Leamy, 1982).

Characters that vary across localities were examined for latitudinal trends by correlating population character means with geographic coordinates for each species. Significant differences between character means of the populations within each species was determined using a one-way analysis of variance and Scheffe's multiple range test ($P=.05$). A univariate F test was used for testing for differences between characters for the sexes within each species.

Discriminant analysis was used to assess the distinctiveness of species, populations within species and the sexes within species. Classical discriminant analysis produces a linear function of the characters for each group producing scores that can be used to assign unknown specimens to _a priori_ groups. Closely related to discriminant function analysis is canonical variates analysis, both of which were obtained from the same program, SPSS DISCRIMINANT. Canonical variates analysis maximally separates _a priori_ groups by maximizing the between group variance relative to the within group variance of the characters used in the analysis. This is accomplished by giving characters which vary according to group (species, population or sex) high weightings and those that vary independently low weightings. This procedure corrects for correlated characters and adjusts for differing covariance between groups compared. The first canonical variates axis always explains the greatest amount of the character variance between groups. The second axis explains the next greatest amount of variance of an axis orthogonal to the first axis and so on for each additional axis. On each axis, the individual characters are given a value (standardized canonical variates coefficient) which corresponds to their importance in separating groups; the larger the absolute value, the more important the character.

Mahalanobis distance was used to place the four unknown specimens (left by Pine, 1972) to species. Mahalanobis distance is the Euclidean distance squared in the space defined by the canonical variates. Each specimen is assigned to the species sample with the closest group centroid (mean character vector).

The relationship between populations was summarized using cluster analysis (unweighted pair group method). This analysis produces a dendrogram which graphically represents similarity between populations in a branching diagram. The squared Euclidean distance between population centroids was used to calculate the similarity matrix. Populations of all species are entered together.

RESULTS

Variation Between Species

Table 1 presents the relative proportion of variation between and within species for each of the 22 characters examined. Characters with large variance components attributed to species differences are potentially useful characters from discriminating between species. Differences between species accounts for only 57.5% of the average character variance leaving on average 42.5% of the variance attributable to within species differences. The best characters for distinguishing between species appear to be basilar length, maxillary tooth row length, ventral rostral length, coronoid-angular distance, mandibular length, and coronoid height. Each of these characters differ significantly between species, determined by a one-way analysis of variance and Sheffe's multiple range test. For each character, the mean measurement is greatest for *C. perspicillata* followed in decreasing order by *C. brevicauda*, *C. subrufa* and *C. castanea* (Table 2).

There are six characters that vary more within species than between species. They are least interorbital width, maxillary spur length, distance between the first molars, foramen magnum width, mandibular depth and slope

TABLE 1

Percent of Total Variation Attributable to Species Differences. Total Variation is the Character Variance Over All Species.

Variable	% Variation		Total Variance
	Between Species	Within Species	
Basilar length	78.4	21.6	150.18
Palatar length	58.8	41.2	42.57
Post-glenoid width	63.2	36.8	21.03
Breadth of brain case	56.7	43.4	12.42
Depth of brain case	60.9	39.1	20.45
Least interorbital breadth	18.6	81.4	3.85
Rostral breadth	55.5	44.5	7.50
Maxillary spur length	36.5	63.5	7.45
Maxillary tooth row	82.8	17.2	36.73
Width between first molars	43.4	56.6	6.94
Width between second premolars	71.1	28.3	17.98
Width between canines	60.9	39.1	7.08
Dorsal rostral length	64.8	35.2	25.84
Ventral rostral length	79.4	20.6	27.11
Palatal width	57.1	42.9	3.50
Foramen magnum width	15.8	84.2	3.65
Mandibular length	78.3	21.7	95.64
Mandibular depth	40.2	59.8	6.01

Table 1 continued

Variable	Between Species	Within Species	Total Variance
Coronoid angular distance	79.1	20.9	42.29
Coronoid height	78.3	21.7	38.88
Post-dentary ramus length	72.3	27.7	31.08
Slope of forehead	11.4	88.6	11.47
Mean	57.48	42.55	

TABLE 2

Mean Character Values (mm ± 2 $S\bar{x}$) for those Characters
Useful in Species Discrimination

	C. perspicillata	*C. brevicauda*	*C. subrufa*	*C. castanea*
BAL	181.1 ± .86	176.5 ± .95	167.3 ± .99	155.2 ± .97
MTR	75.3 ± .42	69.5 ± .43	67.3 ± .39	62.8 ± .40
VRL	63.0 ± .38	58.8 ± .42	56.7 ± .36	51.3 ± .39
ACD	57.0 ± .51	53.9 ± .45	50.8 ± .47	43.0 ± .45
ML	144.1 ± .76	138.5 ± .80	133.9 ± .62	123.3 ± .75
CH	51.5 ± .50	48.0 ± .43	44.5 ± .36	38.3 ± .55

of forehead. These characters vary in accordance with other factors.

The four species of *Carollia* described by Pine (1972) were easily separated in canonical variates analysis (Figure 4) using all 22 characters. Over all species, 98.67% of the specimens were correctly assigned to species using three canonical axes. *C. castanea* is the most distinctive species examined, with 100% of the specimens correctly classified. *C. subrufa* individuals group tightly with 100% of the specimens correctly classified. *C. subrufa* falls closer (using Mahalonobis distance) to *C. brevicauda* and *C. perspicillata* than to *C. castanea*. *Carollia brevicauda* and *C. perspicillata* overlap slightly with 3.4% of the *C. brevicauda* classified as *C. perspicillata* and 1% of the *C. perspicillata* classified as *C. brevicauda*.

Species are maximally separated along the first canonical variates axis with *C. subrufa* and *C. brevicauda* falling between *C. castanea* and *C. perspicillata*. Characters with high loadings on this axis are maxillary tooth row (-.56) width between first molars (.42) and palatar length (.49). The second canonical axis separates *C. brevicauda* from the rest of the species. Characters important here are basilar length (1.14), maxillary tooth row (1.77) and post-dentary ramus length (.49). The third axis separates *C. subrufa*, *C. castanea* and *C. brevicauda*. Important in this separation are maxillary tooth row (-1.12) and maxillary spur length (-.66). Maxillary tooth row is

Figure 4. Canonical variates analysis of *Carollia* species. Each species is represented by a tracing of the perimeter of the cluster formed by individual specimens included in the analysis. Group centroid for each species is represented by a solid dot. The x and y axes are the first and second canonical axes respectively; the third axis value is printed below the group centroid. Units of these axes represent the canonical variates scores. Areas of overlap represent specimens which fall into species groups other than the *a priori* assigned group.

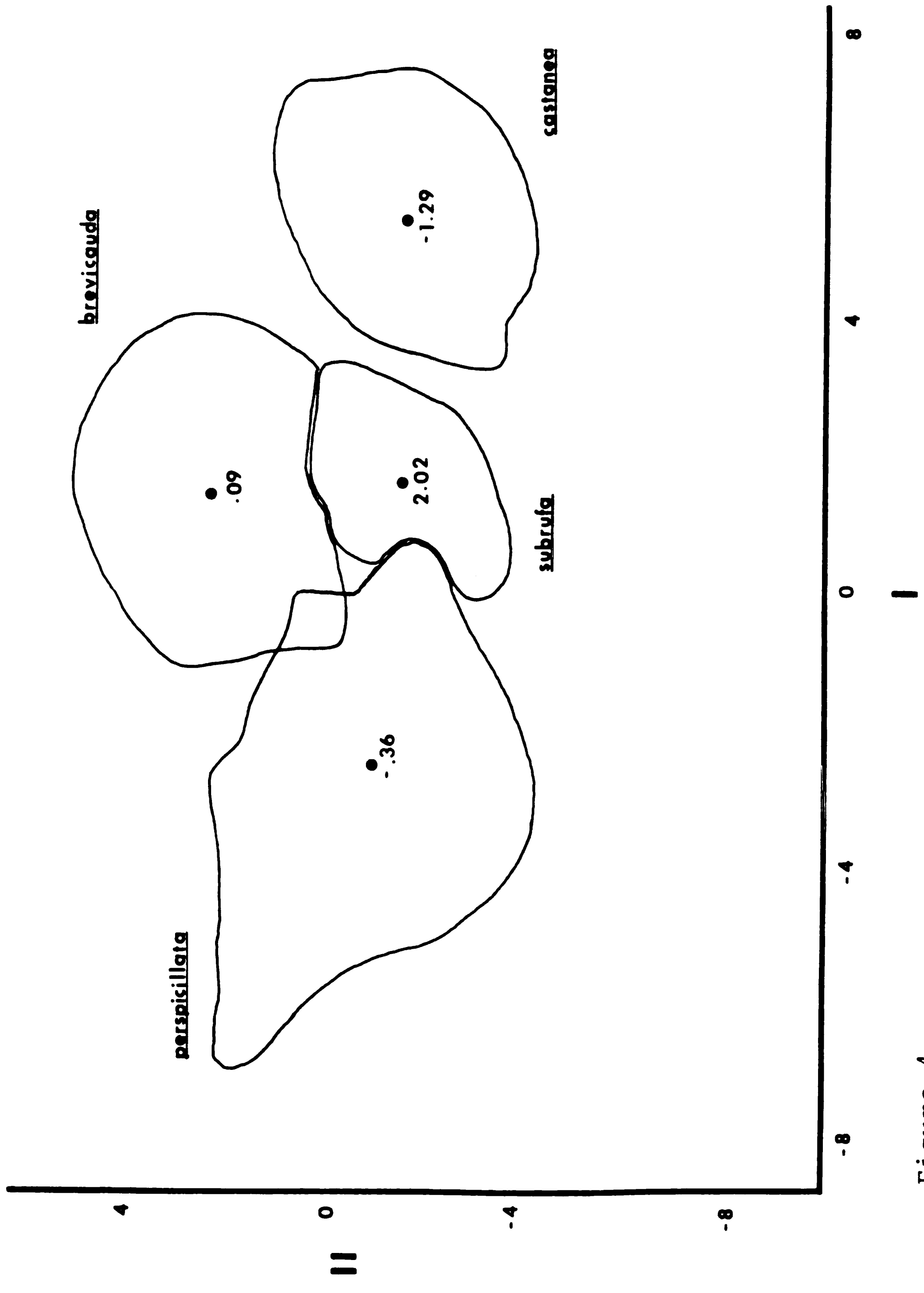

perspicillata
brevicauda
subrufa
castanea
-.36
.09
2.02
-1.29
I
-8
-4
0
4
8
II
4
0
-4
-8

Figure 4.

consistently important in species separation. The nature of some of these variables (palatar length, maxillary tooth row length and basilar length) suggests skull length is a major factor in species separation using canonical variates analysis.

Size appears to be an important factor in discriminating between _Carollia_ species. The first canonical axis accounts for 71.59% of the total variation between species. Low values correspond with the largest individuals in the study (specimens of _C_. _perspicillata_), while the high values are associated with the smallest specimens (_C_. _castanea_). Specimens of _C_. _subrufa_ and _C_. _brevicauda_ are not separated on the first axis, but are on the second. The second axis separates _C_. _brevicauda_ and _C_. _subrufa_ from one another and the third axis fully separates _C_. _subrufa_ _C_. _brevicauda_, and _C_. _perspicillata_.

The specimens left unidentified by Pine (1972) were classified to species using discriminant analysis. Unknowns were placed to the species with the nearest group centroid (least Mahalonobis distance). The specimens from Yalaguina, Nicaragua and Napo Pastaza, Ecuador were placed with _C_. _brevicauda_. The specimen from Kartobo, British Guiana was placed with _C_. _subrufa_ and the specimen from San Juan, Peru was placed with _C_. _perspicillata_. All four of these specimens fell close to the region where _C_. _subrufa_, _C_. _brevicauda_ and _C_. _perspicillata_ individuals come into close proximity in canonical variates space.

Patterns of Variation Within Species

The relative importance of the sources of variation within species was examined in a two level nested analysis of variance estimating variance components due to (1) differences between localities, (2) differences between sexes within localities and (3) residual variation. Expressed as a percentage of the total variation within each species and averaged over 22 characters, most of the variation is residual (58.6-77.9%) and between localities (16.0-29.3%) in all four species (Table 3). The contribution due to sex is the smallest source of variation examined (4.1-6.9%) in agreement with the results of Leamy (1983) using laboratory mice and Straney (1978) using ocelots, skunks and wild mice to measure variance components.

The pattern of character variation within each species varies between species (Appendix B). All *Carollia* have a large locality component in basilar and ventral rostral lengths (>30%). Both *C. castanea* and *C. perspicillata* have locality effects in all 22 characters. Rostral breadth is sexually dimorphic in all four species. The distribution of variance components due to sex are similar in *C. subrufa* and *C. brevicauda*. Both have characters with large sex components independent of locality effects. Three of these characters are common to both species including depth of braincase, rostral breadth, and mandibular depth.

TABLE 3

Percent Contribution to Total Variance of Locality,
Sex and Residual for Each Species of *Carollia*
(Values are Averaged Over 22 Characters).

Species	Locality	Sex	Residual	Total
C. castanea	29.25	4.07	66.68	116.64
C. subrufa	16.02	6.10	77.88	88.36
C. brevicauda	20.18	6.86	72.96	163.53
C. perspicillata	34.60	6.83	58.57	271.23
Mean	25.01	5.97	69.02	

Sexual Dimorphism

Sexual dimorphism is a relatively minor source of variation in all *Carollia* species, ranging from 4.07% of the total variation within species for *C. castanea* to 6.8% for *C. perspicillata*. Pine (1972) saw no average difference between the sexes except possibly in *C. perspicillata* where males were larger than females in average measurements. This is considered in more detail in order to describe which characters differ between sexes. All species are considered because variance component analysis indicates that there are some sex effects in each species and these have not been previously described.

Variance component analysis across characters for each species reveals differences in the distribution of dimorphism between the 22 characters. *C. castanea* shows very little sexual dimorphism. Only 8 characters have a portion of their total variation due to sex; palatar length (sex component=17.19%), coronoid angular (23.19%) and mandibular depth (18.26%) are most dimorphic. In contrast, *C. perspicillata* has a larger amount of character variance attributable to sex distributed throughout 16 characters; rostral breadth (36.65%), depth of brain case (19.4%) and mandibular depth (18.48%) show the greatest sex effects. *C. brevicauda* has 17 characters with sex variance components; rostral breadth (24.31%), coronoid angular distance (20.89%) and mandibular depth (21.26%) have a relatively large sex component. *C. subrufa* has only 13 characters with sex effects, but several with large sex components including: depth of brain case (35.65%), rostral breadth (21.88%), mandibular depth (29.93%) and slope of forehead (21.68%). All four species show dimorphism in mandibular depth and all but *C. castanea* have a relatively large effect on rostral width attributable to sexual dimorphism.

Discriminant analysis between males and females, within species, over localities reveals a greater distinction between the sexes than noticed by Pine (1972). The highest percent of males and females correctly assigned to sex were specimens of *C. subrufa* with 94.37% correctly classified. *C. brevicauda* had 88.14% and *C. castanea* had 80.33% correctly classified to species. Lowest is *C. perspicillata* with 79.4% classified correctly. Although *C. perspicillata* has a relatively large proportion of variability attributed to sex differences, discrimination is difficult due to the distribution of this variation among many characters that also vary with locality. *C. subrufa* has a much more restricted range with few characters with sex effects, but four have large sex components. This may in part explain the better discrimination between the sexes than seen in the other species.

The standard coefficents for the canonical variates separating male and female *C. castanea* indicates that variation between sexes relates largely to basilar and mandibular length, which are larger in males.

Coefficients for *C. subrufa* identify depth of brain case as the primary variate for separating sexes. Males have a significantly deeper brain case than females. *C. brevicauda* has several characters with high loadings including: rostral breadth, dorsal and ventral rostral lengths. Only rostral breadth differs significantly between sexes. Males have wider rostrum than females. Rostral breadth is also the most important character in distinguising between male and female *C. perspicillata*.

The identification of characters which differ between *Carollia* sexes differs depending on the approach. The variance component analysis is indicating which characters vary in accordance to sex, given as a proportion of the total variance. Characters with a small variance that only vary according to sex will have a large sex component even though the difference between males and females may not be great. The canonical variates analysis identifies characters which can be used in discrimination. These characters have a greater magnitude of difference between sexes, even though the proportion of variation due to sex may not appear as large.

Locality Trends

The four populations of *C. castanea* examined show a complex pattern of character variation using variance component analysis. All characters but one (coronoid angular distance) have some portion of their variability associated with location (Table 4). An average of 29.25% of all

TABLE 4

Percent of the Total Variation Attributable to Locality, Sex and Residual from 4 Populations of *C. castanea*. Total Variation is the Character Variance Over Individuals, Sex and Locality.

Character	Locality	Sex	Within	Total
Basilar length	49.43	8.76	41.81	19.30
Palatar length	19.35	17.19	19.35	11.80
Postglenoid width	45.75	0.09	54.26	4.28
Breadth of brain case	18.18	0.0	81.82	3.23
Depth of brain case	6.79	0.0	93.39	3.48
Least interorbital breadth	19.06	0.0	80.95	2.60
Rostral breadth	18.79	9.68	71.34	2.24
Maxillary spur length	2.72	0.0	97.22	4.71
Maxillary tooth row	26.81	0.0	73.24	2.99
Width between first molars	23.76	0.0	76.75	2.28
Width between second premolars	38.33	0.0	61.64	4.80
Width between canines	43.22	0.0	56.77	2.02
Dorsal rostral length	19.43	0.0	80.53	6.23
Ventral rostral length	64.21	0.0	35.79	6.76
Palatal width	9.76	0.0	90.24	1.17
Foramen magnum width	17.57	1.41	80.98	3.05
Mandibular length	41.11	0.0	58.89	11.02
Mandibular depth	27.20	18.26	54.55	1.98
Coronoid angular distance	0.0	23.19	76.80	3.38

Table 4 continued

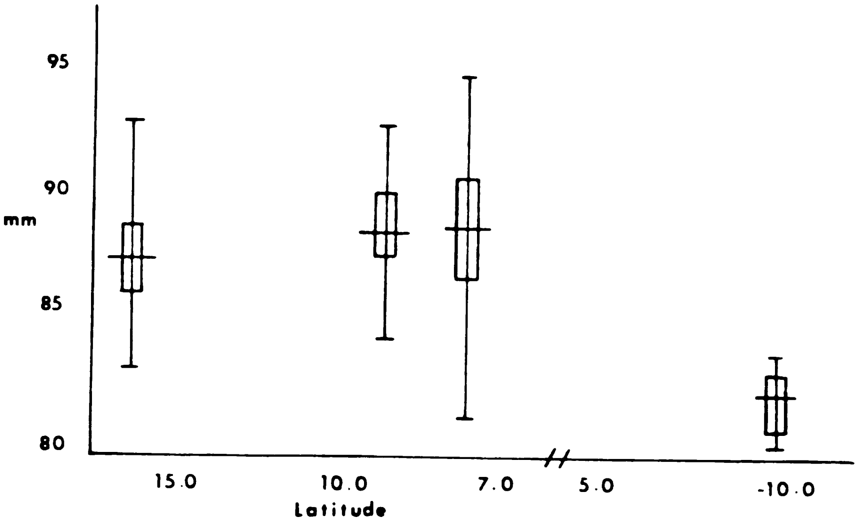
Character	Locality	Sex	Within	Total
Coronoid height	35.78	0.0	62.43	5.75
Post-dentary ramus length	21.14	4.25	74.68	3.95
Slope of forehead	3.75	5.93	90.37	9.60

variability within the 22 characters is attributed to differences in collecting locality. The characters with the largest locality effect (over 40% of the total) are postglenoid width, width between canines, ventral rostral length, basilar and mandible lengths.

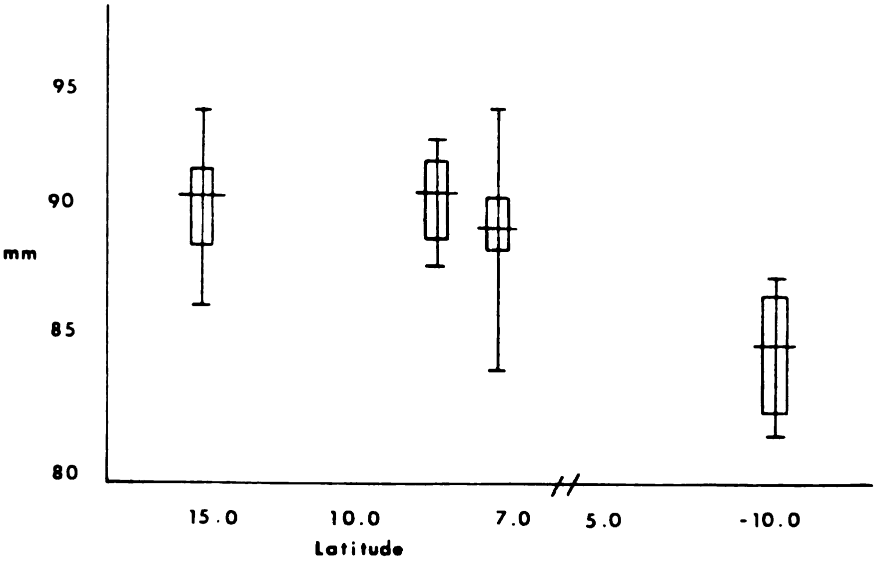
Character trends were found to correspond with latitude. The southernmost population from Peru has the smallest character values in all but two characters (dorsal rostral length and foramen magnum width). Scheffe's multiple range test identifies 5 characters which show significant differences between the Peruvian population and the other more northern populations. These characters are basilar length, palatar length, coronoid height, postdentary ramus length, and slope of forehead. The formen magnum width is largest in the Peruvian population sample composed of the smallest individuals. Figure 5 illustrates the pattern of geographic variation in basilar and palatar length, and is representative of variation in the other 15 characters showing significant differences across populations with the exception of the formen magnum width.

The distinctiveness of populations was examined using canonical variates analysis. The degree of differentiation is high between _C. castanea_ populations (Figure 6). Classification results placed specimens into their respective populations with 98.4% accuracy, the highest of any of the species populations of _Carollia_. The first canonical axis separates the populations from Costa Rica and Peru from the

Figure 5. Dice-Leras diagrams representing character trends for basilar and palatar length across latitudes (corresponding to collecting localities) for _C_. _castanea_. Vertical lines show observed ranges; rectangles mark standard deviation; horizontal lines represent the mean for the population sample. Latitude is given along the x axis in degrees, a positive value is given for north latitude and a negative for south latitude. The y axis indicates scale for character values.



Basilar Length



Palatar Length

Figure 5.

Figure 6. Canonical variates analysis of four populations of *C. castanea*. Populations examined: 1. Rio Coco, Honduras; 2. Palamar, Costa Rica; 3. Tucarcuna Village Camp, Panama; 4. Huanuco, Peru. All three canonical axes are represented, one and two on the x and y axis respectively. The third axis is diagramed in the insert. Group centroids are represented by solid dots.

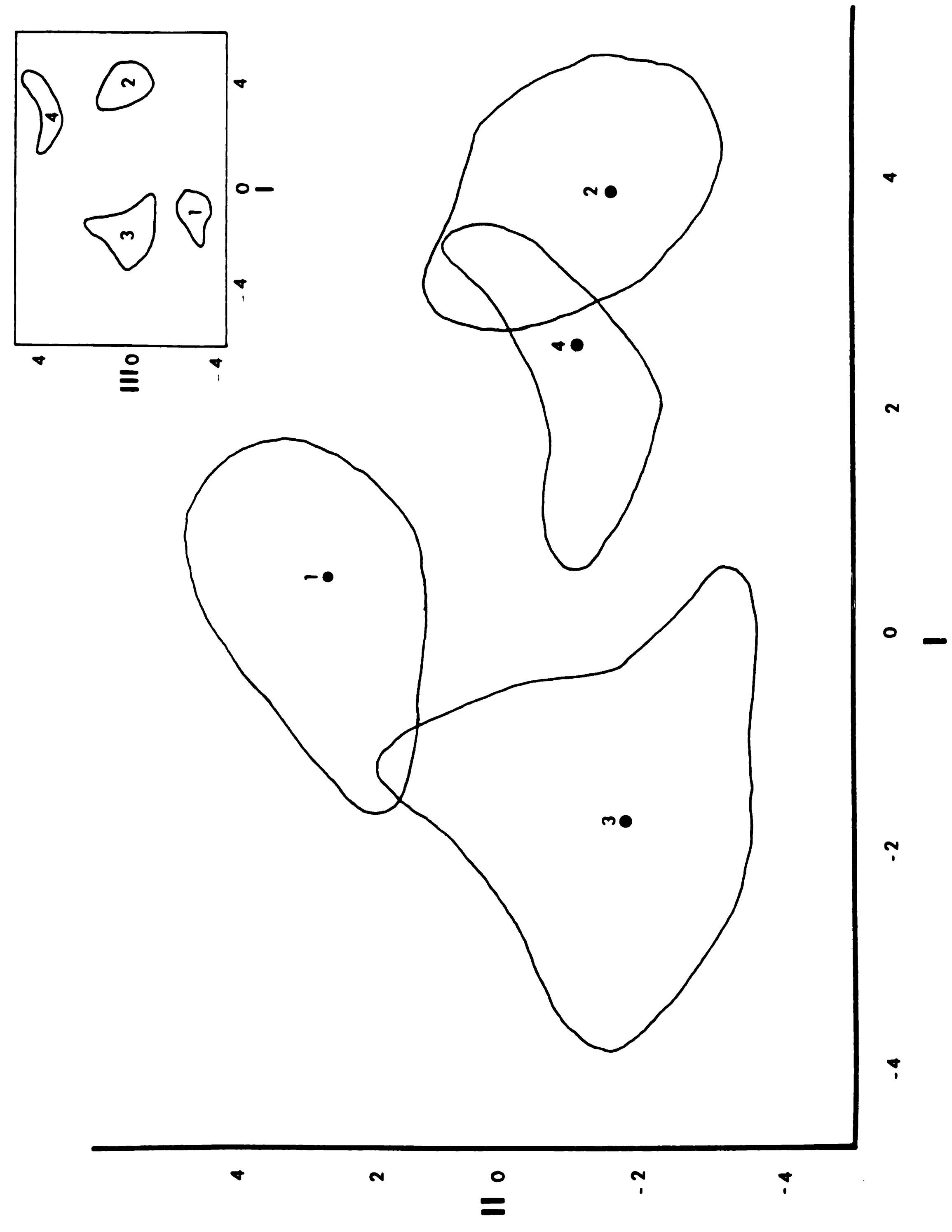


Figure 6.

population from Panama. The population samples from Costa Rica and Peru appear more similar to one another than they are to the population from Panama, which is curious. Standardized canonical coefficients for the first canonical axis indicates that variation in the width between the second premolars and breadth of brain case are most important in this separation. On the second canonical axis the population from Honduras is separated from the other populations due to differences in the rostral breadth and width between canines. The third axis separates populations from Peru and Costa Rica; post-glenoid width and coronoid height are important in this separation.

The eight populations of C. subrufa examined had 16.02% of their total variation due to locality differences. Variance component analysis indicates that all but four characters vary with locality (Table 5). Characters which vary most with location include basilar length, palatar length, ventral rostral length and foramen magnum width (all greater than 32% of total variation). Multiple range test results show only four characters which differ significantly between populations. The characters are: basilar length, palatar length, width between first molars and foramen magnum width. The two southernmost populations have significantly smaller values for these characters.

The two southernmost populations from Sabana Grande, Honduras and San Antonio, Nicaragua have the smallest character means. Geographic trends in basilar and mandibular

TABLE 5

Percent of the Total Variation Attributable to Locality, Sex and Residual from 8 Populations of *C. subrufa*. Total Variation is the Character Variance Over Individuals, Sex and Locality.

Character	Locality	Sex	Within	Total
Basilar length	47.69	0.0	52.31	18.17
Palatar length	42.38	0.0	57.62	9.19
Post-glenoid width	28.65	1.31	70.02	3.17
Breadth of brain case	16.63	9.63	73.75	2.91
Depth of brain case	0.0	35.65	64.43	4.90
Least interorbital breadth	8.69	2.37	88.93	2.27
Rostral breadth	0.0	21.88	79.11	1.74
Maxillary spur length	7.43	0.84	91.18	3.10
Maxillary tooth row	24.50	0.0	75.61	2.71
Width between first molars	14.73	0.0	85.37	1.35
Width between second premolars	1.62	0.0	98.58	2.10
Width between canines	14.85	1.51	83.49	1.66
Dorsal rostral length	19.23	0.29	80.48	4.85
Ventral rostral length	32.71	7.25	60.03	2.29
Palatal width	13.63	0.0	86.47	0.82
Foramen magnum width	33.19	0.0	65.54	2.04
Mandibular length	21.54	0.0	78.45	7.24
Mandibular depth	0.0	20.93	79.34	1.90
Coronoid angular distance	1.61	3.41	94.96	3.66

Table 5 continued

Character	Locality	Sex	Within	Total
Coronoid height	1.76	5.95	92.33	2.15
Post-dentary ramus length	22.42	0.0	77.59	3.03
Slope of forehead	0.0	21.68	78.32	7.12

length are illustrated (Figure 7). These characters were chosen to represent skull and mandibular length across localities. The difference in size between northern and southern populations was also noticed by Pine (1972). These results show a stepped cline in character values.

Population samples of _C_. _subrufa_ form two distinct subgroups using canonical variates analysis (Figure 8). This separation occurs along the first canonical axis with 40.19% of the variance explained. The six populations from Valle, Honduras and north into Mexico form one large overlapping group, while individuals from Sabana Grande, Honduras and San Antonio, Nicaragua are clearly distinct. In this separation, basilar length and slope of forehead are most important. The second canonical axis further separates populations accounting for 20.52% of the total variance. On this axis populations from San Antonio, Nicaragua and Sabana Grande, Honduras are separated from each other and the populations from El Salvador, Guatemala and Nicaragua are separated from the northernmost populations from Mexico. Characters with high loadings on this axis are breadth of brain case, width between canines and width between second premolars. The third axis separates the population from Valle, Honduras from the other populations with maxillary tooth row contributing most to group distinction.

Classification results between populations placed 100% of the individuals from El Salvador, Nicaragua and

Figure 7. Dice-Leras diagrams representing character trends in basilar and mandibular length across latitude (corresponding to collecting localities) for C. subrufa. Vertical lines show observed ranges; rectangles mark standard deviation; horizontal lines represent the mean for the population sample. Latitude is given along the x axis in degrees, a positive value is given for north latitude and a negative for south latitude. The y axis indicates scale for character values.

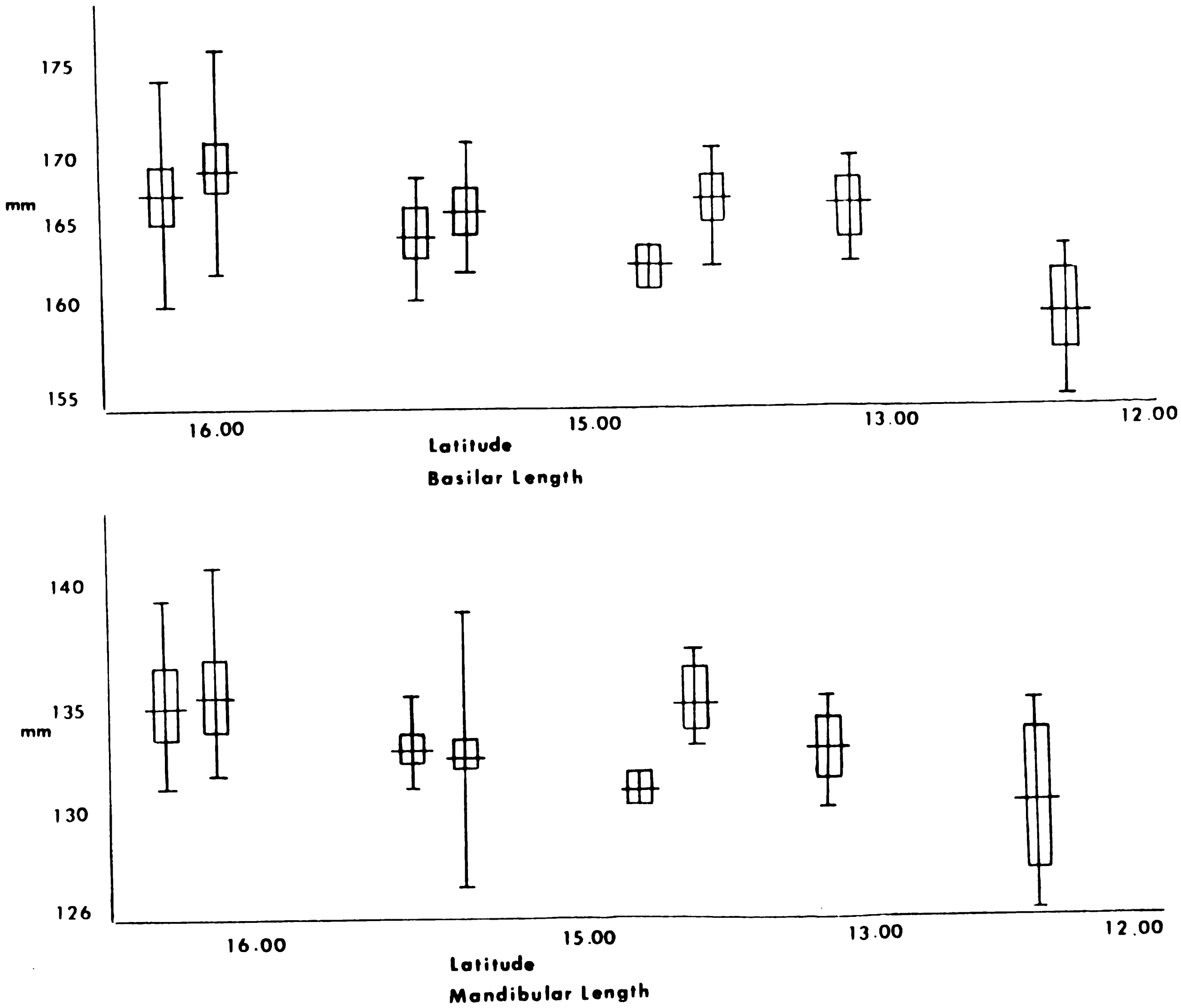

175
170
mm
165
160
155
16.00
15.00
13.00
12.00
Latitude
Basilar Length
140
135
mm
130
126
16.00
15.00
13.00
12.00
Latitude
Mandibular Length

Figure 7.

Figure 8. Canonical variates analysis of eight populations of *C. subrufa* sampled. Populations included are: 1. Tapanetepec, Mexico; 2. Arriaga, Mexico; 3. Tapachula, Mexico; 4. Chiquimula, Guatemala; 5. La Libertad, El Salvador; 6. Valle, Honduras; 7. Sabana Grande, Honduras; 8. San Antonio, Nicaragua. The first and second canonical axes are represented by the x and y axes respectively. The third axis is in the insert. Units on these axes represent canonical variates scores. Group centroids are indicated by solid dots.

Honduras into their respective population locality. These populations are well differentiated from one another. The populations from Mexico and southern Guatemala are not as distinctive; only 79% of the individuals were placed into their correct population locality.

The nine populations of C. brevicauda sampled had an average of 20.18% of the total variation due to locality differences. Variance component analysis of each of the 22 characters reveals that 16 characters have a locality effect (Table 6). Eight characters have a large (>26%) contribution to the total variance. These include the basilar length, palatar length, maxillary tooth row length, width between first premolars, dorsal rostral length, ventral rostral length, coronoid height and post-dentary ramus length. Multiple range test results show that 11 of the characters differ significantly between localities. Characters that are indicative of skull length (basilar, palatar, maxillary tooth row lengths, etc.) all show significantly smaller measurements from individuals taken from Ecuador than those taken from more northern populations. The population from Panama has character values which are significantly larger than those in the sample from Ecuador and the more northern populations.

Geographic trends in character values are illustrated for basilar, palatar, rostral and maxillary tooth row lengths (Figures 9 and 10). These characters were chosen to represent the general patterns seen in the 22 measurements

TABLE 6

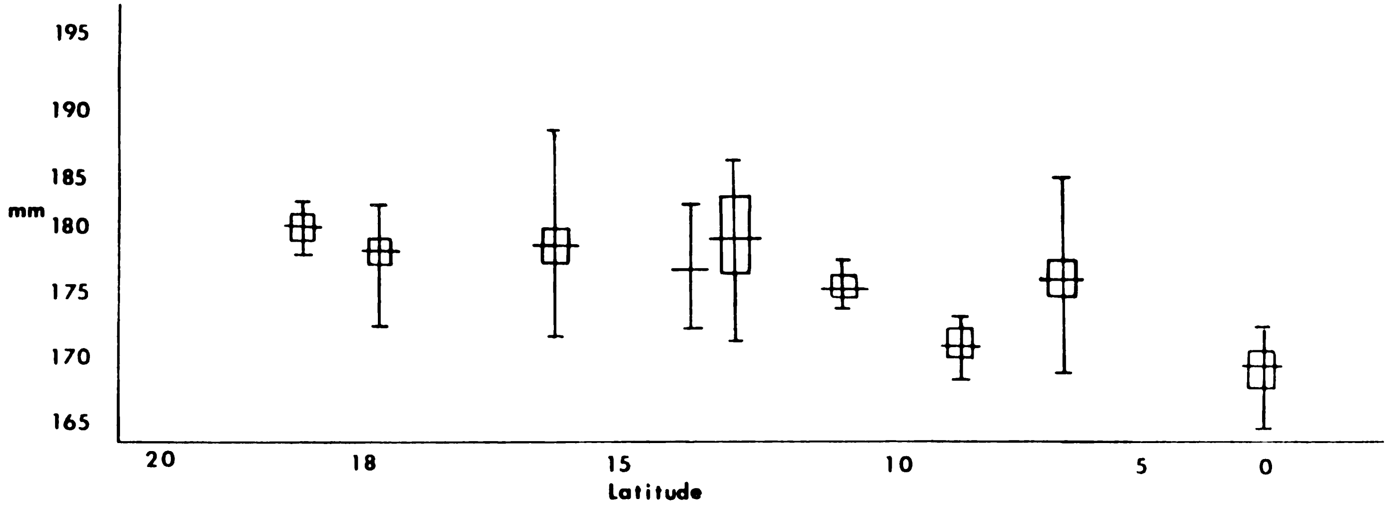
Percent of the Total Variation Attributable to Locality, Sex and Residual from 9 Populations of *C. brevicauda*. Total Variation is the Character Variance Over Individuals, Sex and Locality.

Character	Locality	Sex	Within	Total
Basilar length	44.51	2.90	52.79	30.67
Palatar length	42.72	0.0	57.28	18.45
Postglenoid width	11.76	8.29	79.96	6.50
Breadth of brain case	0.0	10.58	89.56	4.66
Depth of brain case	0.0	17.81	82.36	6.44
Least interorbital breadth	23.28	4.39	72.20	2.87
Rostral breadth	0.0	24.31	75.77	2.25
Maxillary spur length	0.0	12.30	87.70	3.68
Maxillary tooth row	38.11	0.0	61.88	5.95
Width between first molars	20.34	1.43	78.23	3.29
Width between second premolars	40.82	0.74	58.39	4.04
Width between canines	15.73	2.56	81.70	2.07
Dorsal rostral length	46.69	0.30	52.99	10.09
Ventral rostral length	37.09	1.27	61.73	5.50
Palatal width	17.18	0.0	82.20	1.56
Foramen magnum width	7.09	4.38	87.72	2.11
Mandibular length	23.54	7.78	68.68	19.03
Mandibular depth	0.53	21.26	78.24	2.10
Coronoid angular distance	0.0	20.89	79.11	5.70

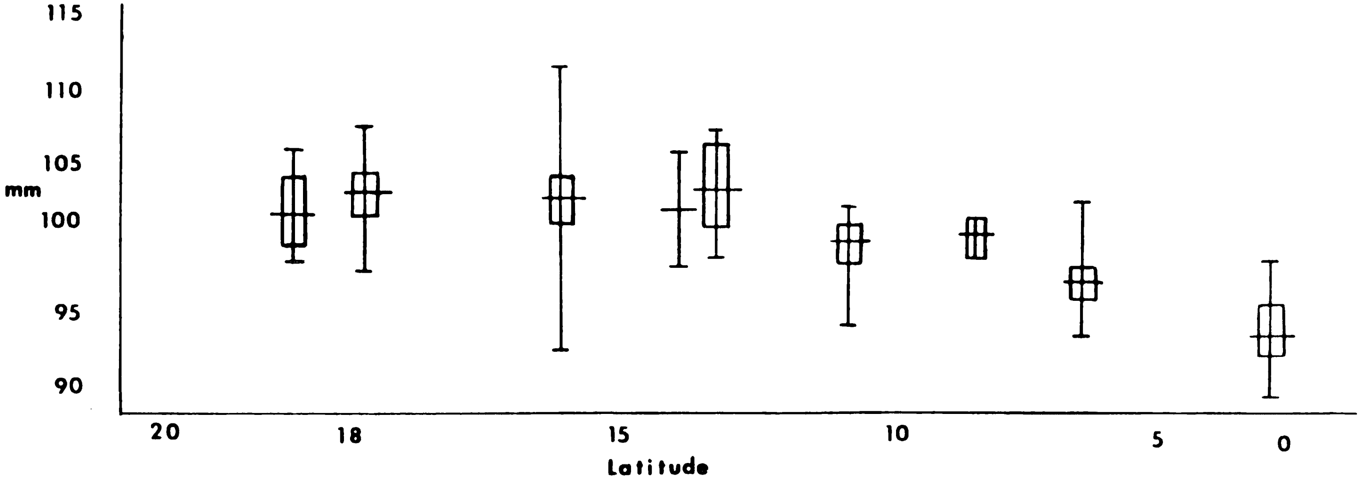
Table 6 continued

Character	Locality	Sex	Within	Total
Coronoid height	44.79	9.66	45.53	8.99
Post-dentary ramus length	26.64	0.0	73.35	7.31
Slope of forehead	2.09	0.0	97.91	10.30

Figure 9. Dice-Leras diagrams representing character trends in basilar and palatar length across latitudes (corresponding to collecting localities) for *C. brevicauda*. Vertical lines show observed ranges; rectangles mark standard deviation; horizontal lines represent the mean for the population sample. Latitude is given along the x axis in degrees, a positive value is given for north latitude and a negative for south latitude. The y axis indicates scale for character values.



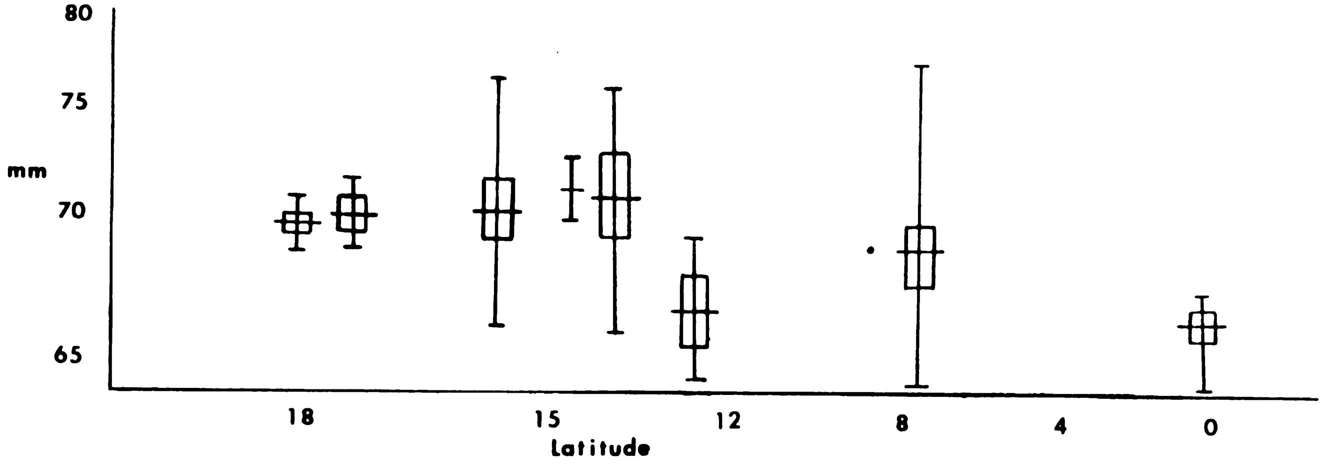
Basilar Length



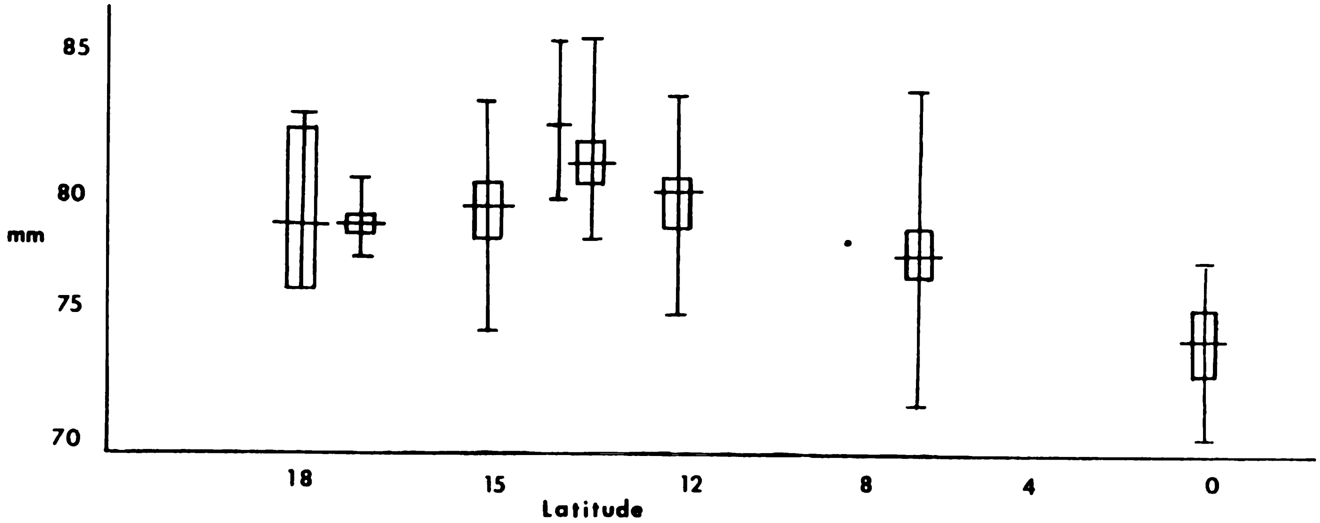
Palatar Length

Figure 9.

Figure 10. Dice-Leras diagrams representing character trends in maxillary tooth row and dorsal rostral length across latitude (corresponding to collecting localities) for C. *brevicauda*. Vertical lines show observed ranges; rectangles mark standard deviation; horizontal lines represent the mean for the population sample. Dots represent population sample with equal character values. Latitude is given along the x axis in degrees, a positive value is given for north latitude and a negative for south latitude. The y axis indicates scale for character values.



Maxillary Tooth Row



Dorsal Rostral Length

Figure 10.

examined. There appears to be a clinal trend in palatar and dorsal rostral lengths, but a bimodal trend in the basilar and maxillary tooth row lengths from the same populations. Palatar and dorsal rostral lengths are decreasing in length from north to south, while basilar and maxillary tooth row lengths are small in Nicaragua and increasing in length in Panama becoming small again in Ecuador. The population from Panama has shorter palatar and dorsal rostral lengths and larger basilar and maxillary tooth row lengths, thus becoming more like *C. perspicillata*. Pine (1972) noted in his treatment of the species that *C. brevicauda* had a relatively long rear extension of the palate. This population from Tacarcuna Village Camp, Panama appeared odd to Pine (1972). It has pelage characteristics resembling *C. subrufa*; short, sparse, coarse, indistinct, basal banding. He suggested the possibility of hybridization between *C. subrufa* and *C. brevicauda*. The greater length of the skull and shorter palate seen in the *C. brevicauda* sampled in this study suggests possible hybridication with *C. perspicillata*.

Multiple range testing of characters identifies characters from the Tacarcuna Village Camp, Panama population which are significantly larger than those of the northern populations; these are width between the second molars, palatal width and maxillary length. These character differences indicate that there are shape differences not only size differences between this population from Panama and the other _C_. _brevicauda_ populations examined. The palatal width, not only its length, is greater.

Distinctiveness of the nine populations was examined using canonical variates analysis (Figure 11). A northern and southern grouping is formed along the first canonical axis, accounting for 47.87% of the total variation between populations. The northern populations include individuals from Mexico south to Costa Rica. The southern two populations are from Panama and Ecuador. Characters with high loadings include width between the second premolars and basilar length. Populations from Panama and Ecuador are separated from one another by the second canonical axis, which accounts for 20.95% of the total variance. Characters with high loadings are width between second premolars and width between canines. The third canonical axis further separates the northern populations of Teapa, Mexico; Talanga, Honduras and Cariblanco, Panama from the other populations sampled. This axis explains 14.81% of the total variation. Characters with high loadings include basilar length and width between canines.

Classification results place 79.66% of the individuals in their correct population locality. Individuals from Ecuador are placed correctly 100% of the time, but only three individuals are examined. Those from Panama are next most distinctive with 92.7% correctly placed. The populations from Guatemala and Honduras are not as distinctive. Individuals from Guatemala are difficult to place and only

Figure 11. Canonical variates analysis of nine populations of *C. brevicauda* sampled. Populations include: 1. Rio Quezalapam, Mexico; 2. Teapa, Mexico; 3. Puerto Barrios, Guatemala; 4. Danli, Honduras; 5. Talanara, Honduras; 6. Yalaguina, Nicaragua; 7. Alajuela Cariblanco, Costa Rica; 8. Tacarcuna Village Camp, Panama; 9. Puyo, Ecuador. The x and y axes represent the first and second discriminant axes. The third axis is in the insert. Units on these axes represent canonical variates scores. Group centroids are represented by solid dots.

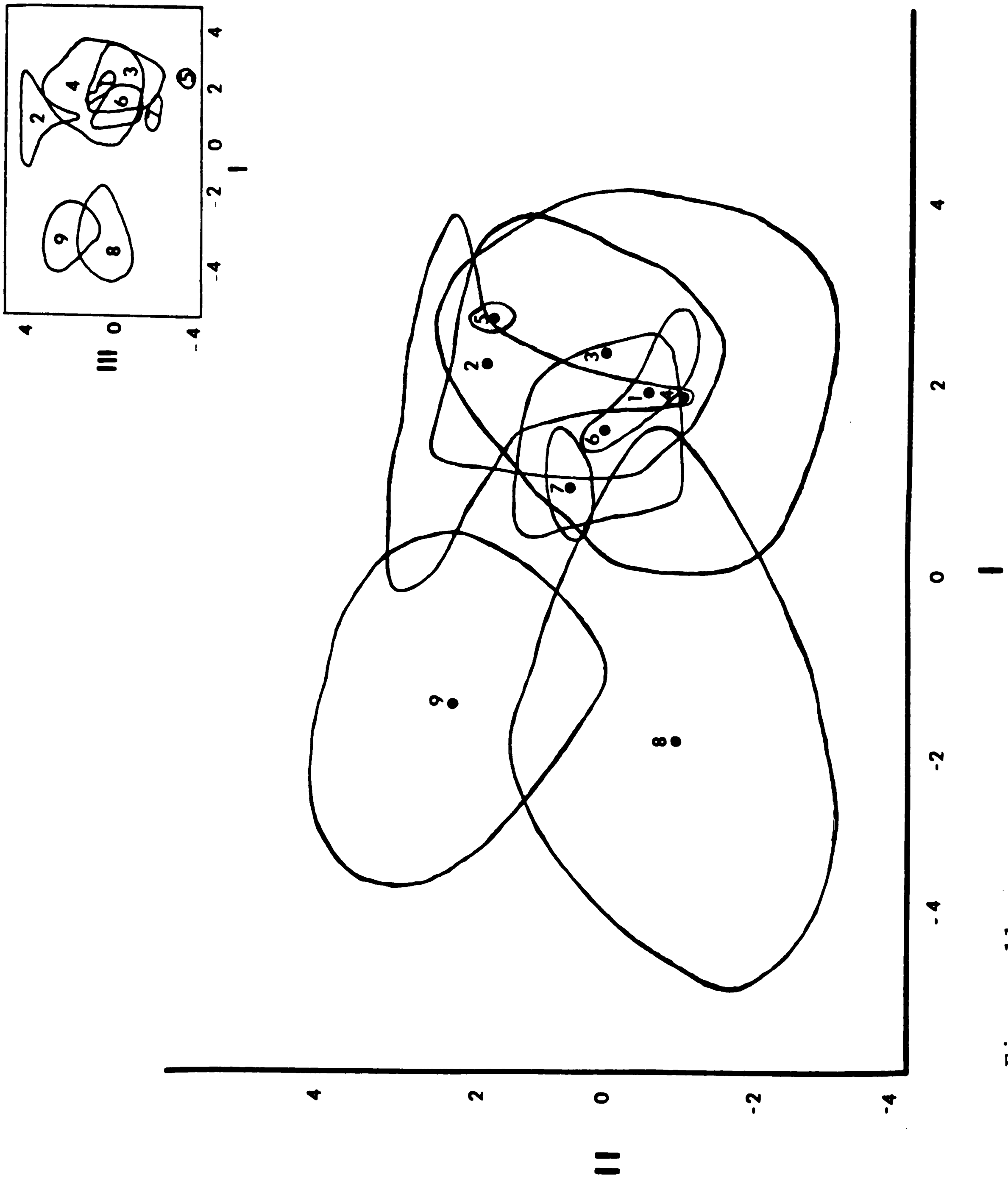


Figure 11.

58% fall into the actual population sample. The other 42% could just as easily be placed with the sample from Teapa, Mexico or Danli, Honduras. Those from Honduras are placed correctly 53% of the time. The other 47% are assigned to populations from the more northern localities.

The fifteen populations of *C. perspicillata* sampled had 34.6% of their total variation attributable to locality differences. Variance component analysis discloses locality effects in all 22 characters examined (Table 7). Four of the characters have more than 50% of their variation due to locality effects; these include basilar length, post-glenoid width, maxillary tooth row, and post-dentary ramus length. Multiple range testing identifies 16 characters that differ significantly between localities. Characters which do not differ significantly between localities include least interorbital width, maxillary spur length, width between second premolars, palatar width, foramen magnum width and slope of forehead.

Geographic trends in skull length for *C. perspicillata* is illustrated by correlating basilar and mandibular length with latitude (Figure 12). The character trends are bimodal with large measurements from individuals from Mexico and Honduras as well as those from Bolivia, ruling out a smooth cline in character values corresponding with latitude. The populations from Paraguay and Brazil do, however, have character values significantly smaller than most of the more northern populations examined.

TABLE 7

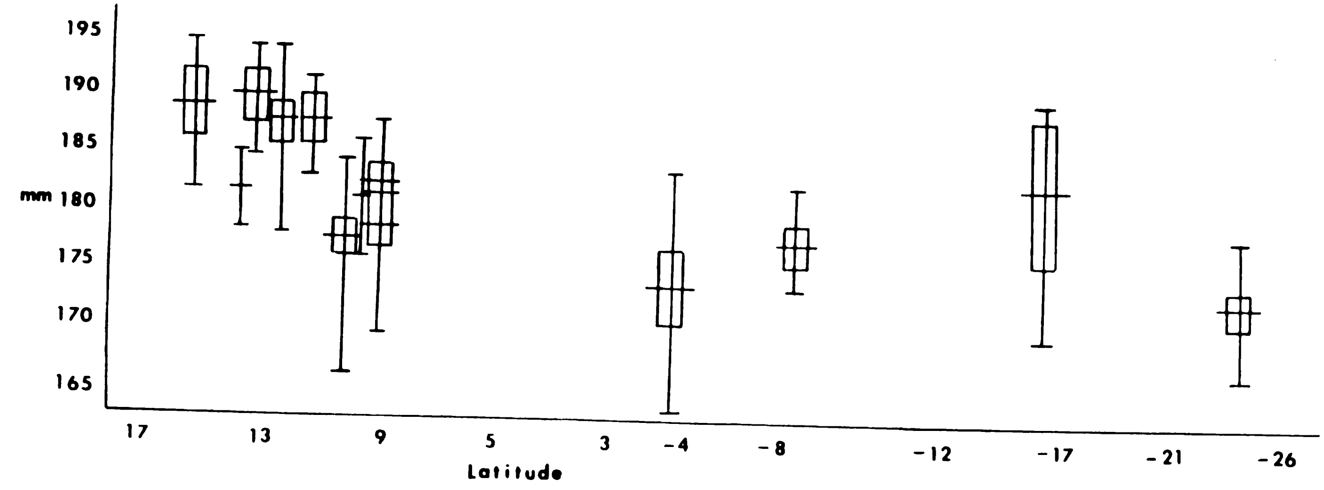
Percent of the Total Variation Attributable to Locality, Sex and Residual from 15 Populations of C. perspicillata. The Variation is the Character Variance Over Individuals, Sex and Locality.

Character	Locality	Sex	Within	Total
Basilar length	66.79	0.99	32.22	50.75
Palatar length	46.41	0.0	53.59	24.63
Postglenoid width	55.77	0.0	44.23	11.99
Breadth of brain case	20.35	9.22	70.42	7.75
Depth of brain case	13.92	19.40	66.68	12.00
Least interorbital breadth	11.76	4.38	83.86	3.97
Rostral breadth	3.56	36.65	64.45	5.79
Maxillary spur length	23.87	7.17	75.19	6.27
Maxillary tooth row	53.66	4.29	42.05	10.04
Width between first molars	36.43	0.0	63.60	5.96
Width between second premolars	22.07	5.24	72.69	7.69
Width between canines	34.88	12.12	52.99	4.47
Dorsal rostral length	46.62	2.70	50.67	12.32
Ventral rostral length	46.12	1.31	52.52	8.24
Palatal width	22.86	0.0	77.14	1.94
Foramen magnum width	21.64	4.44	73.87	4.16
Mandibular length	48.44	7.39	44.15	32.79
Mandibular depth	38.43	18.48	43.04	6.32
Coronoid angular distance	39.79	7.58	52.63	14.95

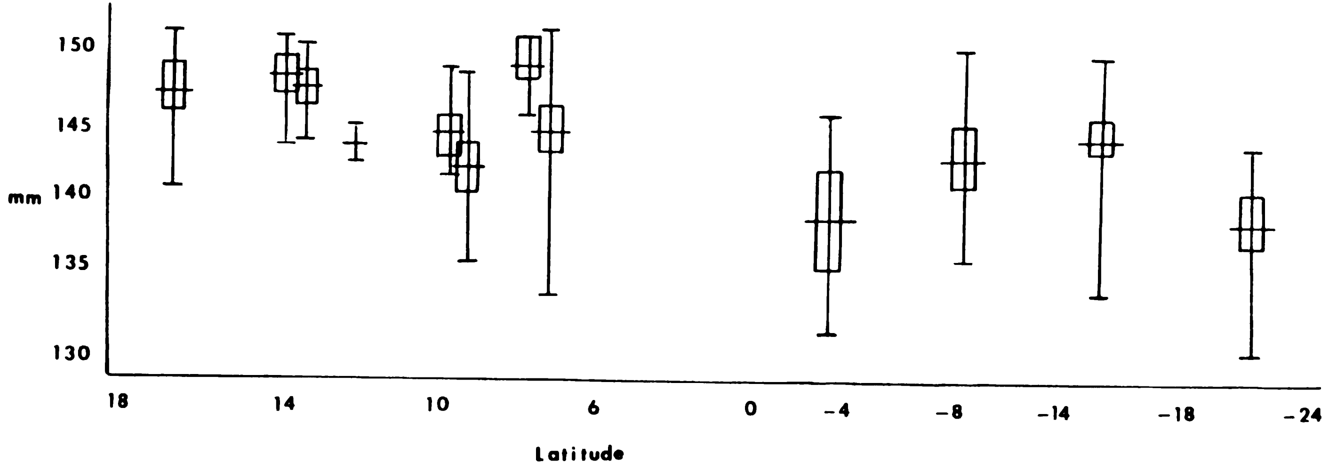
Table 7 continued

Character	Locality	Sex	Within	Total
Coronoid height	49.95	7.12	43.01	14.40
Post-dentary ramus length	50.33	1.83	47.83	13.87
Slope of forehead	18.23	0.0	81.72	11.12

Figure 12. Dice-Leras diagrams representing character trends in mandibular and basilar lengths across latitude (corresponding to collecting localities) for C. *perspicillata*. Vertical lines show observed ranges; rectangles mark standard deviation; horizontal lines represent the mean for the population sample. Latitude is given along the x axis in degrees, a positive value is given for north latitude and a negative for the south latitude. The y axis indicates scale for character values.



Basilar Length



Mandibular Length

Figure 12.

A complex pattern of relationships is produced when canonical variates analysis is performed on all fifteen populations. There is much overlap in the groups formed making interpretation difficult. Subsets of this one analysis are examined so that the relationships between individual populations can be examined. First, populations with more than twelve individuals are examined separately (Figure 13). Populations from Mexico and Honduras are fully separated from the South American populations which extend south and east of Colombia on the first canonical axis. This first axis accounts for 49.09% of the total variance, with only basilar length loading highly. The most divergent population examined, from Tacaruna Village Camp, Panama, is separated from the other populations on the second canonical axis. Characters with high loadings on the second axis are basilar length, mandibular depth and coronoid-angular distance. The population from Costa Rica and Panama are completely separated on this axis, which accounts for 11.9% of the total character variance. Along the third axis, populations from Costa Rica, Colombia and Peru are separated from each other. Characters with high loadings include maxillary tooth row length and coronoid angular distance; 10.04% of the character variance is accounted for on this axis. Two more axes, the fourth and fifth, remain significant in this analysis and further separate the population from Trinidad from the other populations sampled. Mandibular and palatar

Figure 13. Canonical variates analysis of eight populations of *C. perspicillata* sampled. All fifteen populations were included in the analysis; only those with greater than 12 individuals are illustrated in this figure. Populations included are: 1. Teapa, Mexico; 2. Rio Coco, Honduras; 6. Palmar, Costa Rica; 9. Madden Dam Road, Panama; 10. Valledupas, Columbia; 12. Rosharinho, Brazil; 13. Pucallpa, Peru; 15. Sapucay, Paraguay. The first and second canonical axes are represented by the x and y axes respectively. The third axis separation is presented in the insert. Units along the axes represent the canonical variates scores. The group centroids for each population are represented by solid dots.

length have high loadings on the fourth and fifth axes respectively.

Mexican and Central American populations of *C. perspicillata* are illustrated separately from South American populations; drawn from the canonical variates analysis which includes all populations (Figure 14). The Mexican and Central American population samples are separated very little on the first two canonical axes. The third axis, however, separates all of the populations. The populations most differentiated here are those from two localities in Costa Rica, Palmar and Cariblanco and one from 18 m WSW of Chepo, Panama. The South American populations (Figure 15) group tightly on the first three canonical axes. On the fourth and fifth, Trinidad is differentiated from the mainland populations. There is very little differentiation between South American *C. perspicillata* populations.

Phenetic Relationships Between Populations

Cluster analysis was performed on all species populations to examine how populations from throughout the range of each species group phenetically. Population means of canonical variates for each of the 22 characters were used to calculate the squared Euclidean distance between populations. The average linkage method of Clustan's hierarchic fusion procedure was used for this analysis (Clustan, 1975). The average linkage method uses the average of all

Figure 14. Canonical variates analysis of C. *perspicillata* populations sampled, illustrating only Mexican and Central American populations. These include nine populations: 1. Teapa, Mexico; 2. Rio Coco, Honduras; 3. Sabana Grande, Honduras; 4. La Gatiada, Nicaragua; 5. Yalaguina, Nicaragua; 6. Palmar, Costa Rica; 7. Alajuela Cariblanco, Costa Rica; 8. R. de Panama; 9. Madden Dam Road, Panama. First and second canonical axes are represented by the x and y axes respectively. The third axis is presented in the insert. Units along axes represent canonical variates scores. Group centroids are indicated by solid dots.

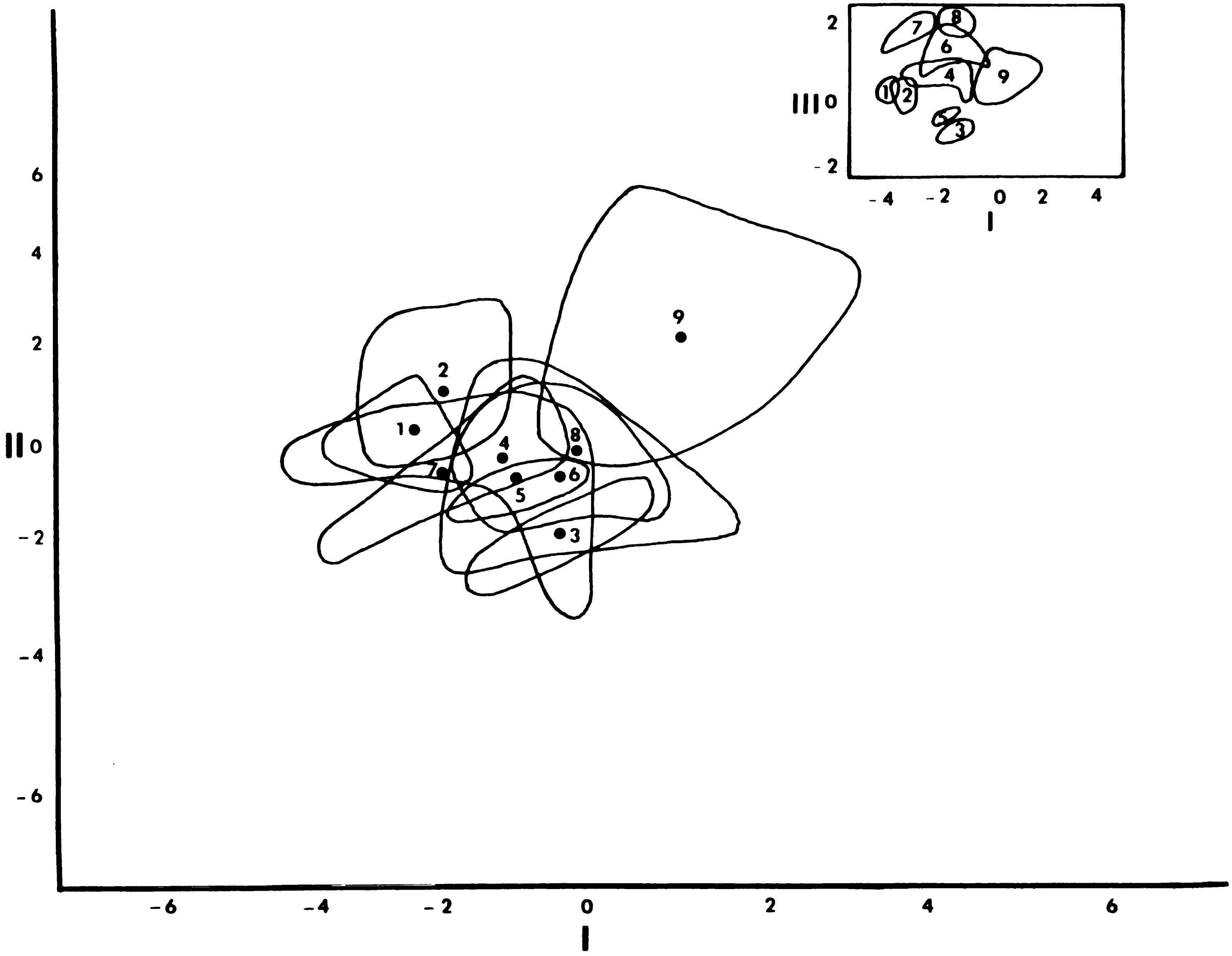


Figure 14.

Figure 15. Canonical variates analysis of *C. perspicillata* populations sampled, illustrating only those from South America. Populations include: 10. Valledupar, Colombia; 11. San Rafael, Trinidad; 12. Rosarinho, Brazil; 13. Pucallpa, Peru; 14. Buena Vista, Bolivia; 15. Sapucay, Paraguay. The first and second canonical axes are represented by the x and y axes, respectively. The third axis is indicated in the insert. Units along the axes represent the canonical scores. Group centroids are represented by solid dots.

similarity coefficients for pairs of populations, one from each cluster (Clustan, 1975). This procedure will find clusters of populations that are more similar within groups than between groups. This method for computing similarity coefficients attempts to take account of group structure. The clusters of populations produced are organized into a heirarchy based on similarity, which is represented in a dendrogram.

The resulting dendrogram (Figure 16) provides a summary of the phenetic relationships between the species populations sampled. The four populations of *C. castanea* cluster alone, in agreement with earlier taxonomic observations. The *C. castanea* population from Costa Rica is more morphologically differentiated from the other *C. castanea* populations sampled than are the other species from each other. The populations of *C. subrufa* sampled are divided into a northern group of six populations ranging from Mexico to Valle, Honduras and a southern group of two populations from Sabana Grande, Honduras and San Antonio, Nicaragua. Between these two groups lie two populations of *C. brevicauda* from Teapa, Mexico and Talanga Honduras. The populations of *C. brevicauda* and *C. perspicillata* are ambiguous. As Pine had noticed, southern *C. perspicillata* overlap northern *C. brevicauda*. Southern *C. perspicillata* appears as a subgroup within *C. brevicauda*. The northern populations of *C. perspicillata* ranging from Mexico to Panama form a distinct group,

Figure 16. Dendrogram of all 36 species populations resulting from cluster analysis. Species abbreviations used are: c-*castanea*, s-*subrufa*, b-*brevicauda*, p-*perspicillata*. Distance indicated across top of diagram.

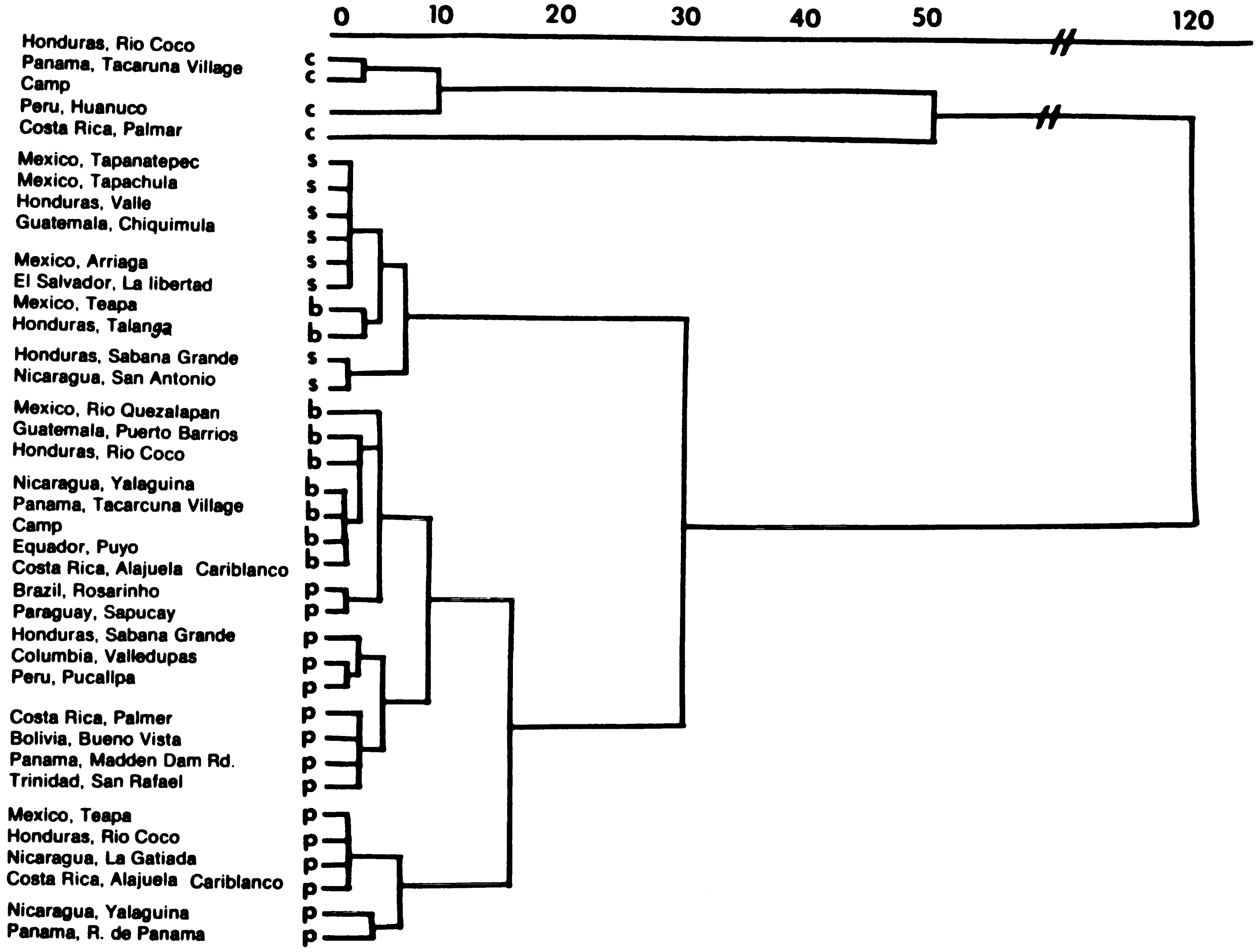

0
10
20
30
40
50
120
Honduras, Rio Coco c
Panama, Tacaruna Village Camp c
Peru, Huanuco c
Costa Rica, Palmar c
Mexico, Tapanatepec s
Mexico, Tapachula s
Honduras, Valle s
Guatemala, Chiquimula s
Mexico, Arriaga s
El Salvador, La libertad s
Mexico, Teapa b
Honduras, Talanga b
Honduras, Sabana Grande s
Nicaragua, San Antonio s
Mexico, Rio Quezalapan b
Guatemala, Puerto Barrios b
Honduras, Rio Coco b
Nicaragua, Yalaguina b
Panama, Tacarcuna Village Camp b
Equador, Puyo b
Costa Rica, Alajuela Cariblanco b
Brazil, Rosarinho p
Paraguay, Sapucay p
Honduras, Sabana Grande p
Columbia, Valledupas p
Peru, Pucallpa p
Costa Rica, Palmer p
Bolivia, Bueno Vista p
Panama, Madden Dam Rd. p
Trinidad, San Rafael p
Mexico, Teapa p
Honduras, Rio Coco p
Nicaragua, La Gatiada p
Costa Rica, Alajuela Cariblanco p
Nicaragua, Yalaguina p
Panama, R. de Panama p

Figure 16.

except for three populations within this range (Sabana Grande, Honduras; Palmar, Costa Rica; Canal Zone, Panama), which group with the South American populations sampled.

There is morphological differentiation between Central America and South American populations of *C. perspicillata* that in part corresponds to the subspecific designation suggested by Pine (1972). Specimens from north and west of the Amazon Basin have been assigned to the subspecies *C. p. azteca* and those from the Amazon Basin and Parana drainage have been called *C. p. perspicillata* and *C. p. tricolor* respectively. Cluster analysis separates the Mexican and Central American populations from South American populations in correspondence with the distinction of *C. p. azteca* from the South American *C. perspicillata*. There is no distinction made between South American populations corresponding to the subspecies *C. p. perspicillata* and *C. p. tricolor*. The distinction between Central American and South American populations is not free from overlap. Several Central American populations sampled cluster with the samples from South America.

DISCUSSION

In past taxonomic treatments of Carollia there has been little difficulty in distinguishing *C. castanea* while *C. subrufa*, *C. brevicauda* and *C, perspicillata* were not clearly defined until Pine recognized *C. brevicauda* in 1972 (Pine, 1972). The distinctiveness of the four species of *Carollia* defined by Pine (1972), is more clearly observed using canonical variates analysis than classical means. Canonical variates analysis results agree with past taxonomic observations in identifying *C. castanea* as the most distinctive species and the species *C. subrufa*, *C. brevicauda* and *C. perspicillata* are less clearly defined. *C. brevicauda* appears intermediate to *C. subrufa* and *C. perspicillata* in character values and shares phenetic similarity with both species. The intermediate nature of *C. brevicauda*, in part, explains the past difficulty in defininging species limits. The species are still difficult to distinguish when relying on classical means. Morphological overlap between populations of *C. subrufa* and *C. brevicauda* and also between *C. brevicauda* and *C. perspicillata* populalations may be the reason for this continuing difficulty in species distinction.

The specimens left unidentified by Pine (1972) were easily assigned to existing species using discriminant function analysis. Unknowns were placed with the species having the closest group centroid and thus the greatest similarity in cranial measures examined. This does not mean that these specimens are actually members of the species group that they are placed with, but that this is the most likely group membership. The specimen from Kartabo, British Guiana was placed with *C. subrufa* in my analysis. Pine notes external features such as pelage which resembles that of *C. brevicauda* and that size is small as that in *C. castanea*. The teeth, however, do resemble those of *C. subrufa*. It is easy to see here that when all factors are considered, identification to species is complicated, since not all features agree. The specimen from Napo Pastaza, Ecuador was placed with *C. brevicauda* using skull characters. Pine also wanted to place this specimen with *C. brevicauda*, but its small size excluded it from the rest of the series of *C. brevicauda* taken from the same locality. The specimen from San Juan, Peru was placed with *C. perspicillata*. Pine noted that this specimen had a skull reminiscent of both *C. perspicillata* and *C. brevicauda*, the size is a good deal larger than any *Carollia* species from that far south, the central lower incisors are small for *C. perspicillata* and the body hair is quite long and tricolored as found in *C. brevicauda*. The above mentioned specimens were considered as possible undescribed species by Pine (1972). The last unidentified specimen was an old female individual with worn teeth and pelage, that Pine was sure belonged in the genus Carollia but he could not place it to species. He thought it was either C. subrufa or C. brevicauda. Discriminant analysis placed it with C. brevicauda.

The most important source of variation in the cranial morphology with Carollia species is the individual variance component which averaged over species accounts for 69% of the total variation. The potential causes for this variability include measurement error, response to changing environment, sampling more than one biological population, random change and unexamined environmental effects. A portion of this residual variation can be explained by measurement error which is on the average only 5% of the total variation. Other factors must also be contributing to this large amount of individual variation.

The variables exhibiting high residual variance components (LIW, MSL, MW, FMW, MD, SF) were not examined in Pine's (1972) treatment of the genus. This coincides with the approach in character evaluation that is taken by a taxonomist. These characters are of no use in distinguishing between species because they are more variable within species than between. A taxonomist is always looking for characters that can be used consistently to distinguish between species, while ruling out those creating confusion. These areas overlooked represent the most plastic regions of the skull.

Foraging patterns unique to individuals of the same species may be contributing to this high individual variation. Heithaus and Fleming (1978) studied the foraging pattern of C. perspicillata in Costa Rica during the wet season and found that individuals used the same feeding areas consistently with very little overlap between individuals. Feeding on fruits which differ in thickness of skin and consistency could cause a change in the magnitude of forces acting on the skull and mandible produced by the muscles involved in mastication: the masseter and temporalis. The bones in the mammalian skull undergo a constant remodeling by absorption and deposition of bone tissue, that may be functionally influenced (Straney, 1983; personal communication). If the individuals within a population have consistent differences in the food eaten, the areas where the muscles involved in mastication originate and insert would be the most variable. Comparison of the areas of origination and insertion to regions of the skull and mandible with high residual variance components shows a fair correspondence (Table 8).

Maxillary spur length has a high residual variance component across Carollia species. The maxillary spur is the anterior portion of the incomplete zygomatic arch of Carollia species where the masseter originates. The posterior mandibular regions including the

TABLE 8

Characters with High Residual Variance Components
(Expressed as a % of the Total Variance)

C. castanea		*C. subrufa*		*C. brevicauda*		*C. perspicillata*	
MSL	97.2	PMW	98.6	SF	98.0	LIB	83.9
SF	96.4	CAD	95.0	BB	89.6	SF	81.7
DB	93.4	CH	92.3	MSL	87.7	MSL	75.2
PW	90.2	MSL	91.3				

coronoid angular distance and coronoid height have a large residual component in C. subrufa. These regions are insertion sites for the masseter and the temporalis. It is possible that the effects of resource partitioning, between individuals of the same species population, may be contributing to this high individual variance in character values.

There are, however, other explanations for the high variability in a few of these characters. The maxillary spur is a cranial feature which is prone to damage because of its shape (long and narrow) and position (extending laterally) on the skull. The slope of forehead was one of the more involved measurements to take and thus may have a larger error due to measurement technique. There are aspects of the population structure not yet considered as potential cause for this large residual component of variation seen within populations.

A biological population can be defined as a group of interbreeding individuals that breed more among themselves than with other such populations. In bat species, a biological population may consist of only the individuals occupying one roost site. When specimens are collected with a mist net, there is no assurance that only the individuals from one such population are taken. It is possible that individuals from several biological populations are represented in each population sample. Individuals from different biological populations are likely to differ due to genetic divergence. This genetic divergence may be reflected in morphological variation within populations. This is one more level at which *Carollia* may be organized and at which variation is occurring. The data in this analysis is purely morphological, so genetic differentiation cannot be compared to morphological differences between populations.

Factors, such as random genetic variability and unexplained environmental effects, must also be considered as potential sources of variation. Genetic variability is present between *Carollia* species (Straney, 1980) but genetic variation between populations has not been examined in detail. The specimens examined were taken over a span of 100 years; in this time environmental change has most likely occurred. Changing environmental factors provide an external influence which may affect morphology.

Secondary sexual dimorphism contributes a small proportion to the total variation within each species, but is present to varying degrees within all *Carollia* species. Males are larger than females in all species. This is commonly seen in other mammal species. The adaptive significance most often assigned in Darwinian sexual selection, whereby males must compete for mates and large body size is selected because it is advantageous (Darwin, 1859). This is one possible explanation, but little is known about the breeding behavior of *Carollia* except that Porter (1975) noticed harem behavior in a laboratory colony of *C*.

perspicillata. Other phyllostomid bats in which males are larger than females are *Uroderma bilobatum* (Baker *et al*., 1972), *Phyllostomus discolor* (Power and Tamsitt, 1973; Bradbury, 1977) and in *Anoura cultrata* (Nagorsen and Tamsitt, 1981). In some vespertilionid bats, the opposite trend is seen, particularly in wing dimension (Myers, 1979). This trend has been associated with a need to compensate for extra loading of pregnancy and the transport of young, coined the "Big Mother" hypothesis by Rall (1976). Female *Carollia* also must deal with the extra loading of pregnancy and carrying young. Examination of Pine's (1972) data indicates that females have forearm lengths equal to those of the males, who are larger in weight. Females appear to have longer wing dimensions relative to body size, which may compensate for the extra loading of pregnancy.

Sexual dimorphism differs in degree and in the characters that vary between *Carollia* species. *Carollia subrufa* and *C. brevicauda* are the most dimorphic. They share a number of characters that vary most between sexes, with no locality affects. These include depth of brain case, rostral breadth and mandibular depth, which are larger in males. From these measurements, it appears that males in these two species have a deeper brain case and a wider muzzle than do females. The other two *Carollia* species are less sexually dimorphic in terms of the ability to discriminate between males and females. Rostral breadth is the most important character exhibiting sexual dimorphism in _C. perspicillata_, with only a small sex effect in a large number of characters. Many of the characters with a small sex effect also have locality effects which may reduce the effectiveness of discrimination between male and female _C. perspicillata_. Least dimorphic is _C. castanea_. Very few characters are involved and only palatar length and coronoid-angular distance have a large variance component due to sex. Pine (1972) had noticed an average difference between male and female cranial measurements only for _C. perspicillata_. He had not noticed differences between the sexes for the other _Carollia_ species. The reason for these differences between species is impossible to interpret from these data. Perhaps a study of the differences in social structure and behavior of _Carollia_ species might aid in understanding these differences.

Geographic differentiation of cranial morphology is great in all four species of _Carollia_. Past taxonomic problems can in part be attributed to an attempt to combine specimens from throughout the range of each species without taking geographic variation into account. This variability between collecting localities was first described in general terms by Pine (1972) who notices regular differences among populations of _C. subrufa_, _C. brevicauda_ and _C. perspicillata_. Morphometric examination of cranial features reveals a latitudinal trend in skull length in all *Carollia* species. Individuals from the northern portion of the range of each species are consistently larger than those from the southern portion. Similar patterns have been found in other phyllostomid bats. Nagorson and Tamsitt (1981), for example, revealed a south to north increase in size for *Anoura cultrata*. Johnston and Selander (1972) found a large size factor associated with climate in North American house sparrows. Rees (1976) found that a size factor in measurements on white-tailed deer correlated positively with latitude. The biological significance of these size trends seen in a variety of animal species is not clear. The usual assumption is this increase in size along a latitudinal gradient must have some adaptive significance.

Bergman's rule has been used to explain an increase in body size from south to north, with animals in cooler (more northern) environments tending to have larger body size to provide a smaller relative surface area. The adaptive advantage gained is an increase in heat retention efficiency. One problem with this explanation in the case of *Carollia* is that size would be expected to increase as a function of distance from the equator, but individuals from south of the equator in Bolivia (25 S latitude) are smaller than those from closer to the equator. Another problem is that the northern and southernmost populations are still in a warm climate; Bergman's rule is usually associated with populations of the same species which are found in both a cold and warm climate. It seems likely that other principles are operating.

Another hypothesis used to explain an increase in size in more northern populations, advanced by Grant (1965) and Heaney (1978), is based on the assumption that interspecific competition is greater in species-rich areas, like the tropics, and so selection favors smaller sized individuals that can occupy more specialized feeding niches. By the same reasoning, areas with fewer species should have less competition for resources and so selection may favor larger size so that a wider range of resources can be utilized. The smallest Carollia do come from tropical South America and the largest are from Mexico, but detailed ecological data are lacking for each of the populations sampled. There are, however, fewer phyllostomid, glossophagine and total bat species in Central America than South America (Nagorsen and Tamsitt, 1981). With fewer species of bats in Central America, a greater variety of food may be available to Carollia species and so there may be a selected advantage for larger size. The general trend in bat species diversity does display differences across the range of Carollia species that are concordant with the size change within these species. McNab (1971) suggested that latitudinal change in body size may be the result of the distribution of food species, or of competitors for the same food resources. An interaction between these factors is likely.

The populations of *C. castanea* are very distinct from one another. Pine had noticed differences in the average measurements between *C. castanea* populations. The differences between the four populations sampled were greater than those between any of the other species populations; the population from Costa Rica is particularly distinctive. A reduction in gene flow through geographic distance may account for this large divergence. *C. castanea* is known to be habitat specific preferring tropical evergreen forests and to have a relatively small home range (Handley, 1966; La Val, 1970). These factors may be enough to hinder gene flow allowing small populations to differentiate more than other species. A closer look at *C. castanea* populations would be interesting to see if this apparent divergence is genuine, not just a function of the small number of populations used in this study.

Geographic differentiation is well developed in *C. subrufa*. *C. subrufa* has the smallest range of all four *Carollia* species. It is distributed from Mexico to Honduras occurring only on the Pacific coast side of the Sierra Madre. *C. subrufa* is the only species of *Carollia* throughout most of its range. It occurs sympatrically with *C. perspicillata* in Chiapas and Nicaragua, and with *C. brevicauda* on the gulf coast side of Honduras. *C. subrufa* is primarily an inhabitant of tropical deciduous forests. Distinct populations from Honduras and Nicaragua cluster separately from the more northern populations. The southern populations are smaller in skull and mandibular lengths than the northern populations. One possible explanation for this divergence is character displacement, due to contact with other *Carollia* species in this southern portion of the range. This has been described in birds and mammals by Grant (1972, 1975). Selection acts against similarity between sympatric populations of two systematically related species (as compared to their allopatric populations) so that they do not compete for food or mates. Pine (1972) makes note of collecting *C. brevicauda* in the same net as *C. subrufa* in Honduras, 2 miles west of San Pedro Sula. At this location he noted an exaggerated difference between the two species and suggests the possibility of character displacement. The *C. subrufa* sampled from Sabana Grande, Honduras and San Antonio, Nicaragua, the regions where sympatry is likely, are very distinct from the more northern populations where *C. subrufa* occurs allopatrically from *C. brevicauda*. In order to be sure that character displacement is occurring, a large sample of *C. subrufa* and *C. brevicauda* caught in the same net is needed for comparison. Such specimens could be compared to known allopatric populations of the same species. Pine treats *C. subrufa* as monotypic, but notes that individuals from the northern part are larger than those of the southernmost part, and specimens taken west of the Isthmus of Tehauntepec have hairier forearms than do those from the other side of the Isthmus. He suggested that with examination of more specimens, the existence of subspecies may become apparent. Both canonical variates analysis and cluster analysis identify a distinct southern population of *C. subrufa* that may represent a recognizable subspecies.

Carollia brevicauda is widely distributed and complementary to *C. subrufa* along the wet Gulf-Caribbean coast of Central America, north of Honduras. It has been collected sympatrically with *C. castanea*, *C. subrufa* and *C. perspicillata*. There may be character displacment occurring between *C. brevicauda* and *C. perspicillata*. Pine (1972) has mentioned that specimens of these species taken from the same collecting locality are more easily distinguished from those from allopatric populations. The populations of *C. brevicauda* from Teapa, Mexico and Talanga, Honduras cluster with *C. subrufa*. This divergence may represent character displacement between *C. brevicauda* and *C. perspicillata*. Sympatric populations of *C. brevicauda* and *C. perspicillata* were not examined from Teapa, Mexico or Talanga. Sympatric populations from Rio Coco, Honduras, Yalaguina, Nicaragua and Alajuela Cariblanco, Costa Rica were examined and do show a large morphological distance in the cluster analysis results. Character displacement may be occurring between *C. brevicauda* and *C. perspicillata*; another potential source of intraspecific variation that must be considered at the population level.

Discriminant analysis of *C. brevicauda* populations separates the southern populations from Panama and Ecuador from the more northern populations. The divergent population sample from Panama corresponds to an unusual population noticed by Pine (1972), that he first regarded as a hybrid swarm of *C. subrufa* and *C. brevicauda*. Externally, they lack the hairiness of the forearm normally seen in *C. brevicauda*. The skull dimensions differ in palatar and dorsal rostral lengths, decreasing in length while the maxillary tooth row and basilar lengths increase. These differences in dimension are evident when correlating character means with latitude. The decrease in palatar length and increase in maxillary tooth row length are changes toward a more *C. perspicillata*-like skull, which suggests possible hybridization with *C. perspicillata*, not *C. subrufa* as suggested by Pine (1972).

Carollia perspicillata is the most widespread and common of the four species. It is found in both tropical evergreen and deciduous forests. Bloedel (1955) noted that individuals may be found solitary or clustered in colonies of as many as 1,000 individuals. Greenhall (1959) wrote that it "is probably the most abundant fruit eating bat in the American tropics." Darwin (1859) observed that the wide ranging and common species tend to be the most variable. When the percent contributions to the total variance due to locality is compared between *Carollia* species, variation increases with an increase in the size of the species range. The highest value of 34.6% is found in *C. perspicillata*, the most wide ranging species. The lowest value of 16.0% is that of *C. subrufa*, with the most restricted range. Darwin's prediction is right in this case. This is not very surprising, as the wide ranging and common species must adapt to many local environments and develop genetic isolation because of distance.

Geographic differentiation is greater in *C. perspicillata* than any of the other *Carollia* species. The northern populations from Mexico and Honduras do not overlap the southernmost populations from Peru, Bolivia and Paraguay, but the populations which fall in between form a continuum. There is no clear division between populations north and west of the Amazon Basin that would correspond to the subspecific designation *C. p. azteca*, given by Pine (1972). Nor is there a clear division between the subspecies *C. p. perspicillata* and *C. p. tricolor* from the Amazon Basin and Parana drainage respectively, when considering cranial morphology alone. Pine distinguished *C. p. azteca* from *C. p. perspicillata* on the basis of its larger size, and distinguished *C. p. tricolor* from *C. p. perspicillata* on the basis of its small size, soft tricolor pelage and hairy forearms and toes. The characters used by Pine (1972) were all external features, mine were cranial measurements. This indicates that the pattern of variation in cranial morphology varies independently from the external features used by Pine (1972) to distinguish between *C. perspicillata* populations from different geographic regions.

Two of the southernmost *C. perspicillata* populations (Rosarinho, Brazil; Sapucay, Paraguay) cluster with northern populations of *C. brevicauda*. This agrees with Pine's (1972) observations that the southern *C. perspicillata* are morphologically similar to northern *C. brevicauda*. Southern *C. perspicillata* are small (relative to northern populations) and Northern *C. brevicauda* are large (relative to southern populations), so a size factor may in part be responsible for this similarity. External features are also shared, including hairy forearms and toes, characteristic of *C. brevicauda*.

The affinity between the species of *Carollia* can be reexamined in light of these morphometric findings. Pine (1972) has suggested that Central America may be the center of origin for the species of *Carollia*, since they all co-occur there and *C. subrufa* occurs nowhere else. The continental divide may have played a major role in forming a barrier to gene flow leading to the differentiation of *C. subrufa* and *C. brevicauda* from a common ancestor (Pine, 1972). Using classical techniques, Pine (1972) postulated that the relationship between species went: *C. perspicillata* - *C. brevicauda* - *C. subrufa* - *C. castanea* -- representing a sequence from least modified to most highly modified from a common ancestor. My morphometric results provide a distance (Mahalanobis distance) between each pair of species. Mahalanobis distance between *C. castanea* and the other species is greater than the distance between any of the other species, indicating that *C. castanea* is the most phenetically divergent, as Pine (1972) has also noted. The phenetically closest species are *C. subrufa* and *C. brevicauda*, and these are about equidistant from *C. perspicillata* in canonical variates analysis. Cluster analysis provides slightly different results; *C. brevicauda* and *C. perspicillata* cluster together equidistant from *C. subrufa*. Canonical variates analysis results are probably a better representation of phenetic affinity between species because separation occurs in multidimensional space rather than the two dimensions of cluster analysis. Both techniques indicate that *C. brevicauda*, *C. perspicillata*, and *C. subrufa* have morphologically similar cranial features.

Another source of data that can be considered is chromosomal morphology. There is an X-autosomal translocation in all species populations, except for some of the *C. castanea* from Peru (Patton and Gardner, 1971). Heterochromatin patterns (in C bands) of *C. brevicauda* and *C. perspicillata* are very similar, but the chromosomes of *C. castanea* lacked much of the heterochromatin common to the other two species (Stock, 1975; *C. subrufa* was not examined by Stock). The lack of a chrosomal translocation in some of the Peruvian *C. castanea* indicates that either this population has lost this trait or all of the others gained this translocation at some point during the evolution of *Carollia*. Heterochromatin patterns further indicate the uniqueness of Peruvian *C. castanea* and the similarity of *C. brevicauda* and *C. perspicillata*. This chromosomal affinity agrees with the morphological similarities and differences between these three species.

Isoelectric focusing results group *C. castanea* and *C. perspicillata* and also *C. brevicauda* and *C. perspicillata* (Straney, 1980). The distinctiveness of *C. castanea* is evident in the morphological and chromosomal data, but the electrophoretic data show possible convergence between *C. castanea* and *C. perspicillata*.

The most morphologically and chromosomally differentiated species is *C. castanea*. The relationships among *C. subrufa*, *C. brevicauda* and *C. perspicillata* is more problematic due to conflicting information. An association between *C. brevicauda* and *C. perspicillata* is found most often; morphological, heterochromatin (C banding) and isoelectric focusing results agree. The position of *C. subrufa* is not clear. Morphologically it is closest to *C. brevicauda*. The geographic distribution of *C. subrufa* and *C. brevicauda* indicates that they may have split from a common ancestor in Central America and spread north on separate sides of the Sierra Madres, where they speciated allopatrically. The possible convergence between *C. castanea* and *C. perspicillata*, identified by isoelectric focusing data, is not evident in the morphological or chromosomal data.

The relationships that can be constructed are numerous. *C. castanea* is the most morphologically and chromosomally derived species. The affinity between *C. castanea* and any of the other *Carollia* is unclear, morphologically it is closest to *C. subrufa* while biochemically it is closest to *C. perspicillata*. The species *C. subrufa* and *C. brevicauda* are phenetically very similar and have a geographic distribution which suggests a split from a common ancestor. *C. perspicillata* and *C. brevicauda* show a close affinity at all levels considered. There is not one diagram that can be used to represent species affinity that fully agrees with all sources of information available. The most generalized diagram that can be used to represent the relationship between *Carollia* species in agreement with all data considered is indicated in Figure 17. The direction of change is difficult to determine, as is the point of the original divergence of *Carollia* species. This diagram indicates that the affinity between *C. perspicillata*, *C. subrufa* and *C. brevicauda* is unclear and *C. castanea* has diverged first from an ancestor common to the other three species.

Figure 17. Diagram of species affinities.

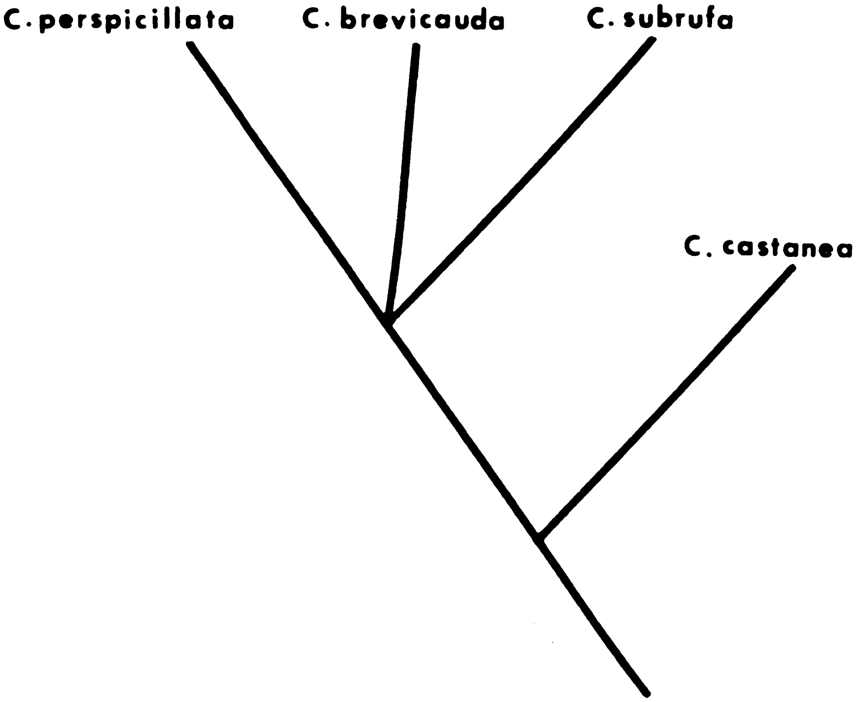


Figure 17.

CONCLUSIONS

Bat species in the genus *Carollia*, defined by Pine's (1972) classification, are easily distinguished using canonical variates analysis. They form four distinct morphological species: *C. castanea*, *C. subrufa*, *C. brevicauda* and *C. perspicillata*. The most distinct species is *C. castanea*, which displays no morphological overlap with any of the other *Carollia* species. The species *C. subrufa* and *C. brevicauda* overlap slightly, while *C. brevicauda* and *C. perspicillata* overlap to a greater degree. These findings are in agreement with past taxonomic observations. *C. brevicauda* was the last species recognized, probably because of its morphological similarity with both *C. subrufa* and *C. perspicillata*. The four specimens which Pine (1972) was unable to identify to species using classical methods were easily placed to species using discriminant analysis. This ease is due in part to using only cranial and mandibular features. Pine's (1972) placement based on cranial and dental features alone agreed with my findings. The external features did not agree with these and so Pine (1972) did not place these specimens to species. Discriminant analysis provides an answer in terms of the most probable group membership.

There are apparent sympatric effects between *C. subrufa* and *C. brevicauda*. *C. subrufa* inhabits the Pacific coast, while *C. brevicauda* is primarily a Gulf-Caribbean versant, separated from one another by the Sierra Madre in the northern portion of their range. There is a narrow region of contact on the Gulf-Caribbean side of Honduras. The *C. subrufa* populations sampled from Sabana Grande, Honduras and San Antonio, Nicaragua are well differentiated from the six northern populations. This differentiation may be the result of character displacement due to sympatry with *C. brevicauda* in these locations. Pine (1972) noted the possibility when *C. brevicauda* and *C. subrufa* caught in the same net in Cortes, Honduras showed exaggerated differences. Further comparison of sympatric populations of *C. subrufa* and *C. brevicauda* to allopatric populations would be useful in testing for sympatric effects.

Sympatric populations of *C. brevicauda* and *C. perspicillata* are examined from Honduras, Nicargua and Costa Rica and also show apparent character displacement. These sympatric populations are phenetically distant compared to allopatric populations of the same species. These sympatric effects provide a source of intraspecific variation which should be more closely examined.

Intraspecific variation is great in all *Carollia* species. The individual component of variance is the largest source of variation for all four species of *Carollia*. This indicates that the characters used (all considered together) vary more between individuals than between sexes or between localities. This is not true for each character separately. This indicates that much of the variability seen in *Carollia* species is caused by factors other than the location or sex of the species. Other factors include measurement error, response to changing environment, sampling more than one biological population, random change or consistent individual differences in feeding strategy.

Geographic variation is the second largest source of intraspecific variation in all *Carollia* species. *C. perspicillata* has the largest proportion of the total character variation attributable to location, followed by *C. castanea*, *C. brevicauda* and then *C. subrufa*. The most important variable used to discriminate between populations is basilar length (all four species). This may correspond to the general north-south trend in skull length noted across species of *Carollia*. Pine (1972) had noticed a size trend in all *Carollia* species except *C. castanea*. He noted larger individuals in the north and populations of smaller individuals in the southern portion of their range. In both *C. subrufa* and *C. brevicauda* population samples, it is possible to distinguish between a northern and southern group of populations. *C. castanea* population samples are distinctive, but show no geographic pattern. Populations of *C. perspicillata* form a continuum in canonical variates space. The distinction between northern and southern populations is not without overlap. The subspecific distinction between these populations may only represent two ends of a cline. Without examination of a large number of specimens representing the range of a species, it is difficult to see whether the variation is continuous or discrete. This is a limitation in all studies of geographic variation. The number and location of population samples included in a study is often limited to what is available in museum collections.

Sexual dimorphism is evident in all four species of *Carollia*. Pine (1972) had noted that male *C. perspicillata* were larger than females, but had not noticed dimorphism in the other species. In all species, males are larger than females. Most dimorphic is *C. subrufa* followed by *C. brevicauda*, *C. castanea* and then *C. perspicillata*. Rostral breadth is wider in males of the species *C. perspicillata*, *C. brevicauda* and *C. subrufa*. *C. castanea* males have a greater palatar length than females. The variation attributable to sex is a relatively minor source of variation in all *Carollia* species. Although the sex component is small, future analysis involving populations differences may benefit by treating sexes separately, providing sample sizes are larger than those available in this study.

The results of this study confirms much of the past observations concerning morphological variation within and between *Carollia* species. Patterns of variation are more apparent and can better be compared when morphometric techniques are applied to problematic groups. The morphometric techniques used allowed quantification of the relative amounts of variation due to species, locality, sex and individual differences which could not be achieved by classical means. From this information, hypotheses concerning the underlying causes for these observed differences can be advanced and when possible, tested.

APPENDIX A

SPECIMENS EXAMINED

The collecting localities are grouped below according to species. Specific localities from which specimens were examined are grouped by country. Museum acronyms are: AMNH - American Museum of Natural History; CM - Carnegie Museum, Pittsburgh; FMNH - Field Museum of Natural History; KU - University of Kansas Museum of Natural History; LACM - Los Angeles County Museum; TCWC - Texas Cooperative Wildlife Collection; USNM - United States National Museum.

C. brevicauda

MEXICO -- Veracruz: Rio Quezalapam (1), 2 mi. E Lago Catemaco, 5♂♂, 7♀♀ (TCWC 11131-11137, 11140, 11142-11145); Chiapas, 21 km WSW Teapa (Tabasco) in Chiapas (5), 200 ft, 3♂♂, 4♀♀ (TCWC 16502, 16504-16509). GUATEMALA: Izabal (6), 25 km WSS Puerto Barrios, 300 ft, 15♂♂, 10♀♀ (TCWC 17295-17319). HONDURAS: Francisco Morazan (9), 10 mi NE Talanga, 3400 ft, 1♂, 1♀ (TCWC 10844-10845); Rio Coco (10), 78 mi ENE Danli, 900 ft, 1 sex?, 3♂♂, 8♀♀ (TCWC 9893, 9898, 9901, 9907, 9913-9918, 10654-10655). NICARAGUA: Dept. Madriz Yalaguina (14), 10 km E Somoto, 2200 ft, 5♂♂, 1♀ (TCWC 8873, 8888-8889, 8900-8902). COSTA RICA: Alajuela Cariblanco (16), 18 mi NE Naranjo, 3000 ft, 1♂, 2♀♀ (TCWC 9867, 9872, 9876). PANAMA: Tacarcuna Village Camp (20), 3200 ft, 18♂♂, 24♀♀ (USNM 309474-309479, 309481-309497, 309499-309509, 309516-309526). ECUADOR: Napo Pastaza (25), 8 mi WNW Puyo, 3800 ft, 9♂♂, 7♀♀ (TCWC 12047-12051, 12054, 12056-12057, 12059-12062, 12064-12067).

C. castanea

HONDURAS: Rio Coco (10), 78 mi ENE Danli, 900 ft, 8♂♂, 3♀♀ (TCWC 9935-9945). COSTA RICA: Puntarenas Prov. (17), 4 mi NE Palmar, 300 ft, 2♂♂, 6♀♀ (TCWC 9919-9926). PANAMA: Darien, Tacarcuna Village Camp (20), 1850 ft, 28♂♂, 13♀♀ (USNM 309406-309411, 309413-309420, 309423, 309425-309431, 309433-309438, 309441, 309443-309449, 309453-309456). PERU: Huanuco (26), 19 mi S Tingo Maria, 2800 ft, 3♂♂, 2♀♀ (TCWC 11915-11919).

C. perspicillata

MEXICO -- Chiapas: 21 km WSW Teapa (Tabasco) (5), 200 ft, 5♂♂, 6♀♀ (TCWC 16435-16439, 16441-16446). HONDURAS: Francisco Morazan, 2 mi SE Sabana Grande (11), 1♂, 1♀ (TCWC 10856-10857); Rio Coco (10), 78 mi ENE Danli, 900 ft, 4♂♂, 14♀♀ (TCWC 9889, 9891-9892, 9894-9897, 9899-9900, 9902-9906, 9908-9911). NICARAGUA: Dept. Madriz Yalaguina (13), 10 mi E Somoto, 2200 ft, 1♂, 1♀ (TCWC 8874-8875); Dept. Chontales, 1 km NW La Gatiada (14), 1300 ft, 4♂♂, 6♀♀ (TCWC 8860-8865, 8867-8870). COSTA RICA: Alajuela Cariblanco (16), 18 mi NE Naranjo, 2900-3000 ft, 4♂♂, 3♀♀ (TCWC 9864, 9866, 9868-9871, 9873); Prov. de Puntarenas (17), 4 mi NE Palmar, 300 ft, 6♂♂, 12♀♀ (TCWC 9845-9848, 9850, 9852-9863). PANAMA: Bat Caves, Madden Dam Rd. (19), 10♂♂, 5♀♀ (LACM 20075, 20079-20093); R de Panama (18), 18 km WSW Chepo, 200 ft, 7♂♂, 6♀♀ (TCWC 11920-11921,11923, 11926-11929, 11937-11940, 11942-11943). COLUMBIA: Magdalena Sierra Negra (21), Villanueva Valledupar, 7♂♂, 4♀♀, 1 sex? (USNM 281106-281115, 281121-281122). TRINIDAD: San Rafael (22), 2♂♂, 2♀♀ (FMNH 61926-61929). BRAZIL: Rio Madeira Rosarinho (24), 26♂♂, 26♀♀ (AMNH 92056-92061, 92063-92070, 92072-92078, 92080-92100, 92182-92187, 92220, 92627, 92629, 92632, 92634). PERU: Loreto (27), 11 mi SE Pucallpa, 300 ft, 500 ft, 5♂♂, 15♀♀ (TCWC 11982-11983, 11985-12002). BOLIVIA: Dept. Santa Cruz, Prov. de Sara, Beunavista (29), 400 m, 450 m, 500 m, 10♂♂, 4♀♀ (LACM 8942; FMNH 22442, 22444-22447; CM 2163, 2200; AMNH 61755-61760). PARAGUAY: Sapucay (30), 1♂, 13♀♀ (FMNH 18208-18209); USNM 114005--the holotype of *C. p. tricolor*, 115003-115012).

C. subrufa

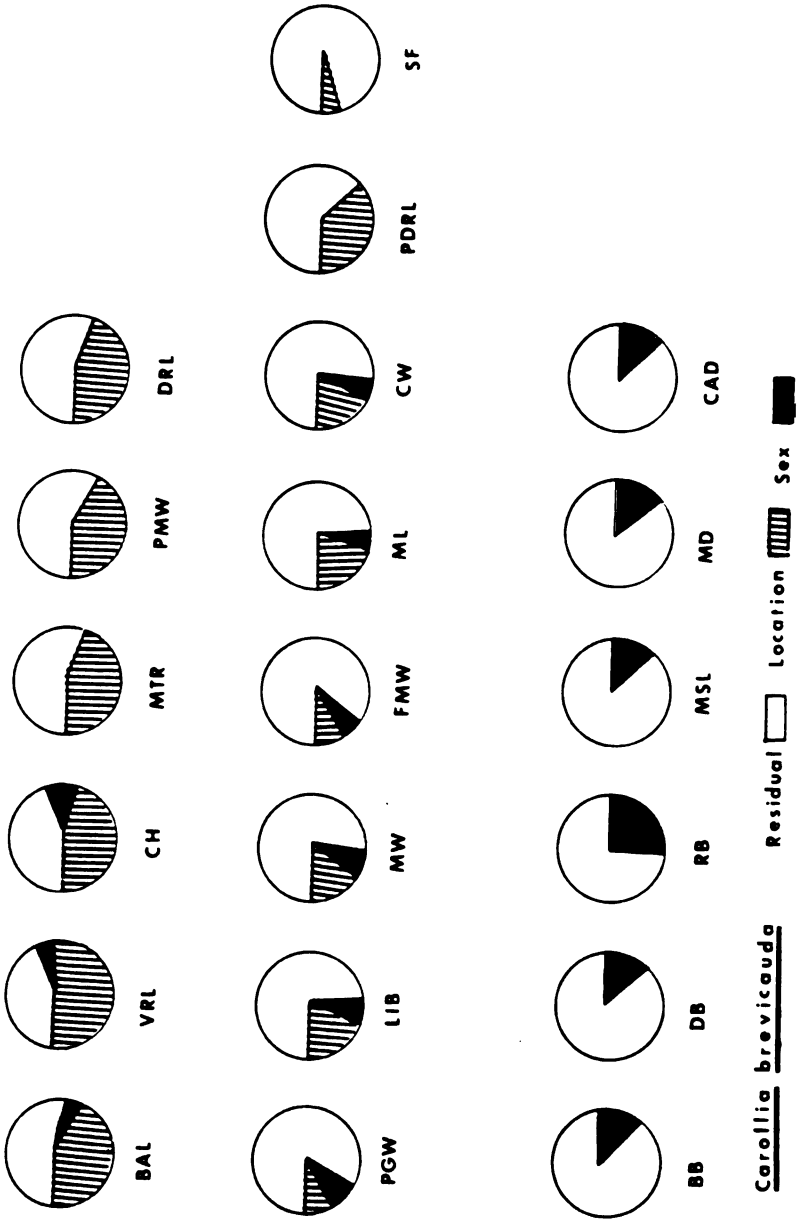
MEXICO -- Oaxaca: 4 mi E Tapanatepec (2), 800 ft, 4♂♂, 8♀♀ (TCWC 16449-16450, 16452-16455, 16458-16560). Chiapas: 5 5 mi N Arriaga (3), 800 ft, 7♂♂, 10♀♀ (TCWC 16478-16494); 4 km NW Tapachula (4), 450 ft, 7♂♂, 12♀♀ (TCWC 14276-14284, 14499-14508). GUATEMALA: Chiquimula (1), 20 km SSE Chiquimula, 550 m, 3♂♂, 7♀♀ (TCWC 17269-17278). HONDURAS: Valle (10), 10 km E San Lorenzo, 25 ft, 4♂♂, 2♀♀ (TCWC 18353-18359); Francisco Morazan, 3 mi S Sabana Grande (11), 1500 ft, 1♂, 1♀ (TCWC 10846, 10859). EL SALVADOR: La Libertad (8), 20 mi W La Libertad, 3♂♂, 1♀ (TCWC 8903-8905, 9807). NICARAGUA: Chinandega (15), San Antonio, 15 mi, 2♂♂, 4♀♀ (KU 97660-97665).

Specimens Not Assigned to Species

NICARAGUA: 1 km SE Yalaguina 2600+ ft,♀ (TCWC 7414). BRITISH GUINA (Guyana): Kartabo, ♀ (AMNH 64168). ECUADOR: Napo Pastaza, 8 mi WNW Puyo, 3800 ft, ♀ (TCWC 12068). PERU: Puno, Sandia Prov. San Juan, Tambopata Valley, 5000 ft, ♂ (FMNH 78394).

APPENDIX B

Pie diagrams of each character with percent contribution to total variance for residual, sex and locality for each *Carollia* species.


Carollia brevicauda
Residual □
Location ▥
Sex ■
BB
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PMW
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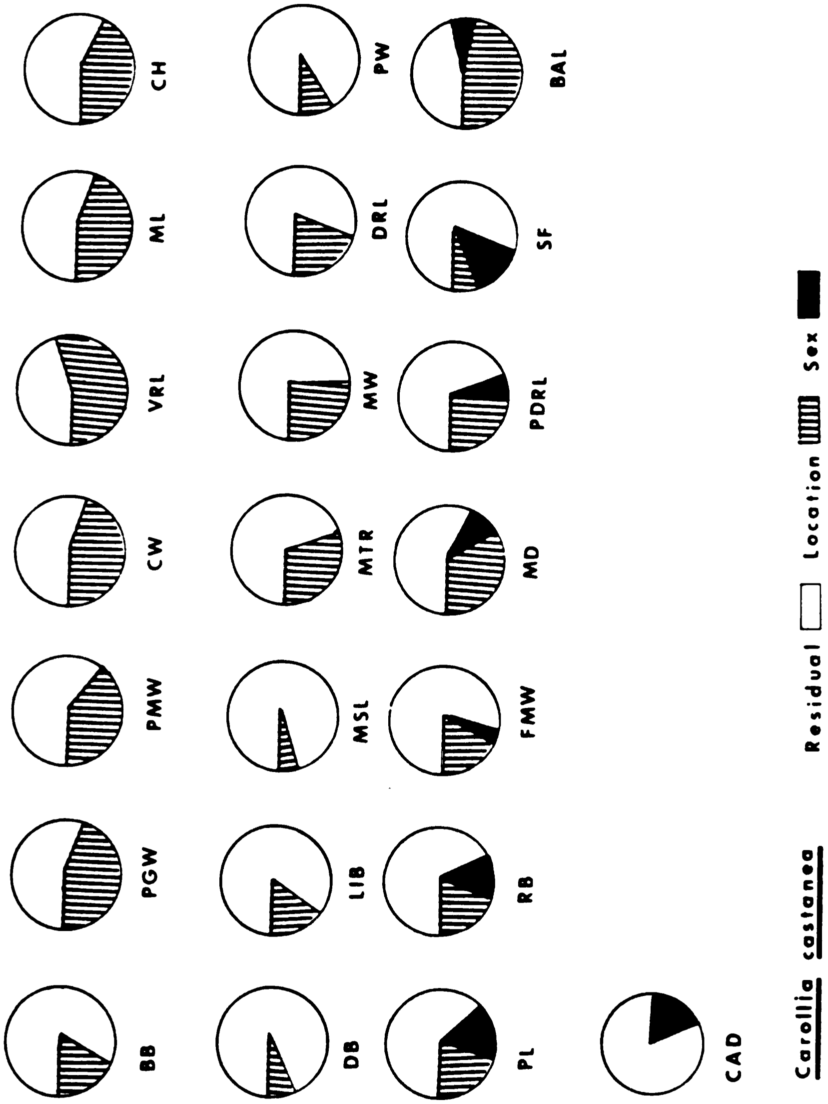
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MD
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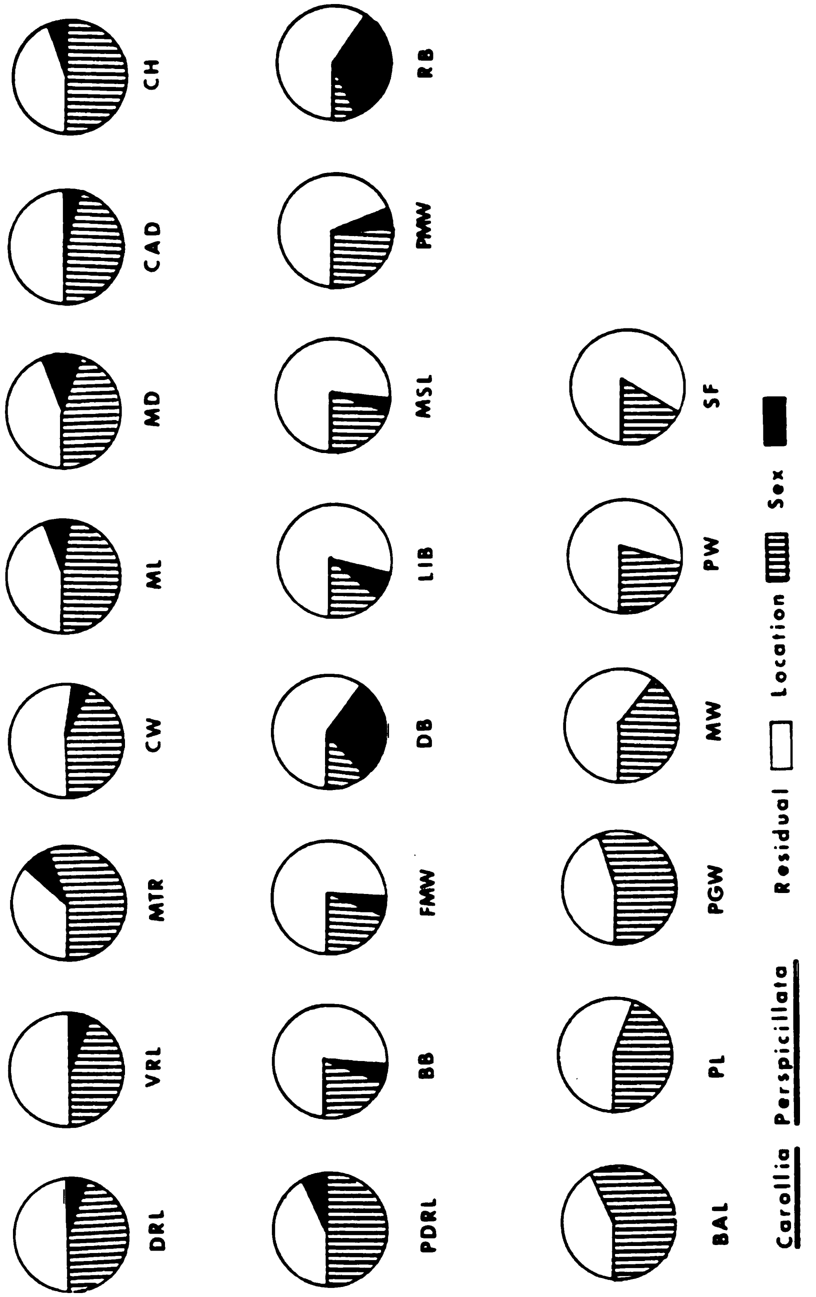
SF
BAL
CAD
Carollia castanea
Residual ☐ Location ▤ Sex ■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PDRL
BB
FMW
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PMW
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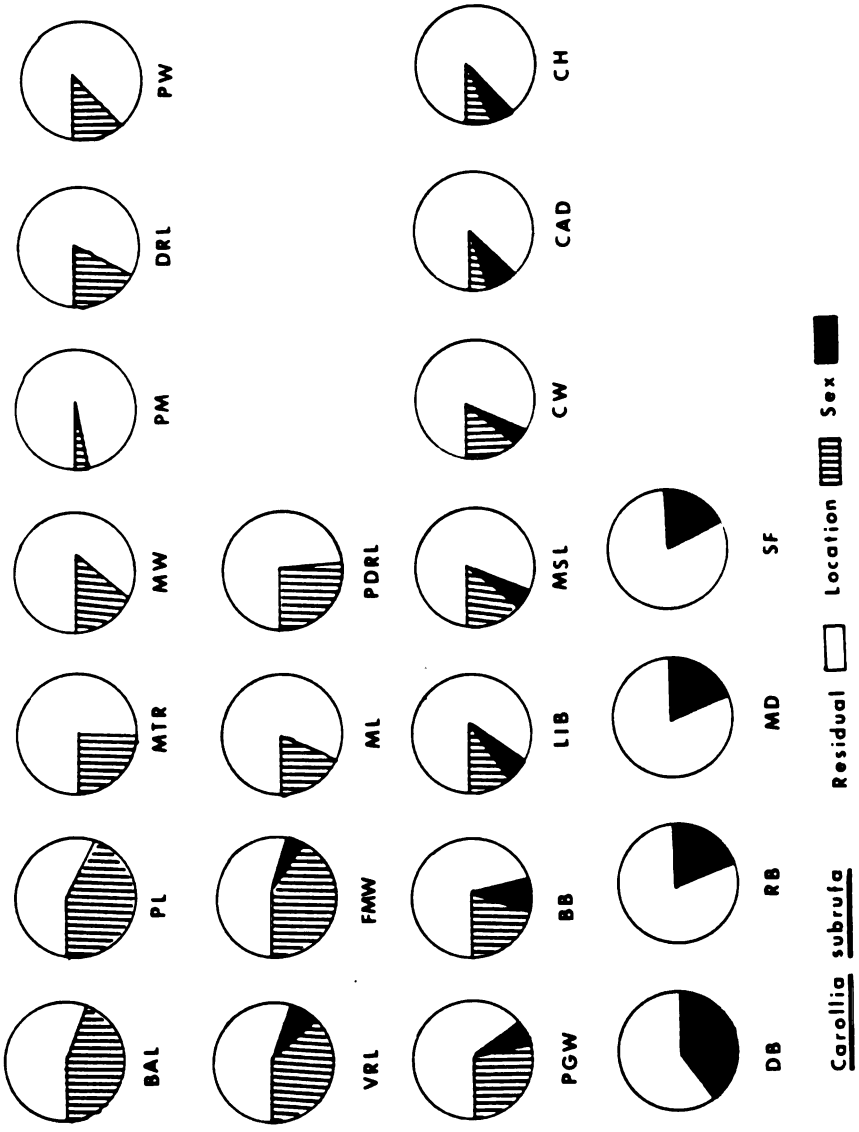
BAL
PL
PGW
MW
PW
SF
Carollia Perspicillata
Residual □ Location ▤ Sex ■


BAL
PL
MTR
MW
PM
DRL
PW
VRL
FMW
ML
PDRL
PGW
BB
LIB
MSL
CW
CAD
CH
DB
RB
MD
SF
Carollia subrufa
Residual □
Location ▥
Sex ■

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