ASSESSMENT OF MORPHOMETRIC VARIATION IN NATURAL POPULATIONS: THE INADEQUACY OF THE UNIVARIATE APPROACH

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Abstract.—Systematists often attempt to avoid the problem of correlated characters by establishing an arbitrary number of variables that must be significant before groups are considered distinct. The appropriateness of this approach has not been evaluated empirically in the biological literature. We analyzed morphometric data for 27 species of bats from the Brazilian Northeast. Twenty-two mensural characters (12 cranial, 10 external) were analyzed for interlocality and secondary sexual variation in each species using ANOVA and MANOVA. The univariate and multivariate analyses showed little correspondence; no predictable relationship between the number of characters exhibiting significance for a particular treatment effect in the univariate analyses and the significance level for that treatment in the multivariate analysis was discernible. Small sample sizes or disparate sample sizes do not contribute to this phenomenon. Results ranged from: 11 of 12 characters significant using ANOVA and nonsignificance in the MANOVA; to no character significant using the ANOVA with significance in the multivariate analysis. Because MANOVA utilizes rather than ignores correlations among characters, it is the correct statistical test for evaluating overall group differences. We show that even conservative interpretations of the univariate results can lead to erroneous systematic conclusions. [Morphometric variation; MANOVA; multivariate statistics; ANOVA; univariate statistics; natural populations; Chiroptera; bats; Brazil.]

By comparing variation within and among different populations, one can determine how and to what extent differences among individuals are molded into the differences that separate races and species (Mayr, 1942; Simpson, 1944; Yablokov, 1974). Thus, systematics is concerned with ascertaining real differences (or the lack thereof) between groups of organisms for a variety of reasons. Differences among populations (whether geographically separated or not) commonly are considered indicative of taxonomic distinctness. Both age-group variation and secondary sexual dimorphism are of potential interest in their own right (see, for example, Ralls, 1977; Myers, 1978; Williams and Findley, 1979; Schnell et al., 1985; Webster and Jones, 1985) and should be considered in other analyses because their presence may confound the detection of intertaxon variation. Additionally, current evolutionary theory suggests a relation between sexual dimorphism and polygamous mating systems, differential maturation rates, unequal sex ratios, and differential resource

utilization (Sealander, 1957; Daly and Wilson, 1978). Also, a number of hypotheses—such as sexual selection (Darwin, 1859; Trivers, 1972; Wilson, 1975), resource utilization (Selander, 1966, 1972), and the Big Mother Hypothesis (Ralls, 1976)—that are not necessarily mutually exclusive have been elaborated to account for dimorphism in natural demes. The veracity or generality of such theories cannot be evaluated until the dimorphic condition of particular species is properly ascertained. Describing a set of conditions that distinguish dimorphic from monomorphic populations is counterproductive if one has not correctly identified statistically significant sexual dimorphism.

A primary tool for systematic analysis of animal populations involves assessment of morphometric variation among and within groups. Frequently, studies of geographic or sexual variation include univariate analyses of a suite of characters; an implicit assumption of this procedure is that the characters are uncorrelated. Of the statistical methods commonly used to as-

certain significant differences among populations (or sexes), Analysis of Variance (ANOVA) frequently is the method of choice. ANOVA does not assume a priori intergroup differences, and does have known probability levels for resultant statistics. Univariate ANOVAs have been used in the recent literature to test for intergroup differences in, for example, insects (Carson et al., 1982), birds (Adkisson, 1977; Grant, 1982), and mammals (Genoways, 1973; Nelson and Shump, 1978; Krohne, 1980; Williams and Genoways, 1980, 1981; Rogers and Schmidly, 1982; Owen and Webster, 1983; Kennedy and Lindsay, 1984).

It is well understood, however, that a series of univariate ANOVAs actually tests a series of null hypotheses concerning equalities of means for each variable independently. In contrast, the systematist's objective should be to test the hypothesis that the population multivariate centroids are equal (Pimentel, 1979). Although it has long been recognized that the multivariate case is usually appropriate in systematic applications of linear statistical models, only a relatively small number of workers have consistently avoided the misuse of univariate models in such situations. Jolicoeur (1959), for instance, pointed out that "When comparing evolutionary groups of organisms . . . such joint comparisons call for multivariate analysis . . . ." More recently, Baron and Jolicoeur (1980), Jolicoeur (1984), Jolicoeur et al. (1984), and Cheverud et al. (1985), among others, have reiterated and expanded the (primarily theoretical) justifications for use of the multivariate case in various statistical methods within the field of biometrics. Stated generally, correlations among characters for each species reduce the reliability of univariate statistics as indicators of overall differences among groups.

To empirically evaluate the severity of this problem and its effect on systematic conclusions concerning these taxa, we employed multivariate analysis of variance (MANOVA) because it utilizes rather than ignores correlations among variables to determine significance levels. The degree to which univariate results are coincident with multivariate results will assess the utility of the univariate approach.

MATERIALS AND METHODS

Bats were collected during a 22-month period (September 1976 to May 1978) from two sampling localities: Caatingas (Municipality of Exu, Pernambuco) and edaphic Cerrado (Municipality of Crato, Ceará) habitats of northeastern Brazil. At each locale, specimens were taken within a circular area with a 10-km radius. The edaphic Cerrado sites were located on the Chapada do Araripe in the Foresta Nacional Araripe-Apodí, approximately 40 km northeast of the Caatingas locale. Half of the collection is housed in the Carnegie Museum of Natural History (USA) and half is deposited in the Museu de Zoologia da Universidade de São Paulo (Brazil).

The Caatingas is a large heterogeneous semiarid area that occupies approximately 650,000 km² (Frota Pessoa et al., 1971; Reis, 1976); xeric adapted plants of the Bromeliaceae, Euphorbiaceae, and Cactaceae are common constituents of Caatingas habitats. In areas unaffected by post-Cretaceous erosion, a sandstone substrate still covers the crystalline basement and produces large mesalike plateaus and chapadas (James, 1942; Ab'Saber, 1970). The elemental and hydrological properties of these chapadas produce edaphic Cerrado habitats throughout northeastern Brazil. Physiognomically, the edaphic Cerrado is an open woodland-savannah. Trees and shrubs rarely exceed heights of 15 m, and characteristically have gnarled trunks and twisted branches. The characteristic floras of both Caatingas and edaphic Cerrado habitats have been described in detail elsewhere (Mares et al., 1981; Streilein, 1982; Willig, 1983). The biogeography and paleoecology of the region were summarized by Mares et al. (1985).

More than 5,000 bats representing 38 species, 29 genera, and 8 families were obtained during this study. A complete list of species and a summary of their ecology, reproductive biology, and morphometric variation are presented by Willig (1983,

1985a, b, c). Twenty-one species (18 genera, 5 families) were captured in sufficiently large numbers (Table 1) from one or both habitats to permit the analyses described herein. Ten external and 12 cranial characters (Appendix) were measured for each species. Morphometric variation within each species was evaluated using ANOVAs in all cases (Sokal and Rohlf, 1981). When possible, two-way ANOVAs (sex versus area) were employed for each mensural character; one-way ANOVAs were performed if a species was obtained only from a single area (SAS Institute, Inc., 1982). Levene's test (Brown and Forsythe, 1974) was used to evaluate the equality of cell variances for each univariate test because it is less sensitive to departure from normality than other techniques.

MANOVAs (Procedure GLM; SAS Institute, Inc., 1982) were calculated separately for cranial, external, and combined variable suites. Pillai and Jayachandran (1967) compared powers of Roy's Maximum Root, Wilks' Lambda, the Lawley-Hotelling Trace, and Pillai's Trace statistics, and found them similar ($\alpha = 0.05$), particularly when departures from the null hypothesis were small (Morrison, 1976:223–224). We found F and P to be identical (to two and four decimal places, respectively) for Lawley-Hotelling Trace, Pillai's Trace, and Wilks' Lambda statistics for all bat populations tested. MANOVA probability values listed below may be taken as derived from any of these three statistics.

RESULTS AND DISCUSSION

The unresolved dilemma in univariate morphometric analyses is represented in the question: how many morphometric characters must exhibit significant ANOVA treatment effects before overall significance for a particular effect is declared? If characters are uncorrelated, then the overall error rate (OER) is given by the relation:

$$\text{OER} = 1 - \left[\prod_{i=1}^{c} (1 - \alpha_i) \right], \quad (1)$$

TABLE 1. Sample sizes[a] (maximum n) for each species by locale and sex used in statistical analyses.

Species	Caatingas		Edaphic Cerrado	
	♂♂	♀♀	♂♂	♀♀
Peropteryx macrotis	15	7	—	—
Noctilio leporinus	20	20	—	—
Micronycteris megalotis	7	4	—	—
Tonatia silvicola	13	36	—	—
Phyllostomus discolor	10	16	20	20
P. hastatus	—	—	20	20
Trachops cirrhosus	16	19	—	—
Glossophaga soricina	20	20	20	20
Lonchophylla mordax	37	35	—	—
Anoura geoffroyi	11	14	20	20
Carollia perspicillata	20	20	20	20
Sturnira lilium	3	4	3	19
Vampyrops lineatus	20	20	20	20
Artibeus concolor	—	—	6	6
A. jamaicensis	20	20	20	20
A. lituratus	20	20	20	20
Desmodus rotundus	20	20	20	20
Myotis nigricans	20	20	16	20
Eptesicus furinalis	—	—	7	15
Neoplatymops mattogrossensis	22	26	—	—
Molossus molossus	20	20	20	20

[a] In some univariate calculations, a few individuals were eliminated from consideration in a particular ANOVA because of broken structures. In corresponding multivariate calculations, a single missing value for any character eliminates that individual from the MANOVA. This situation, which reduces n for statistical purposes, was rare.

where α_i represents the level of significance for character i in the ANOVA for a particular species, and c equals the total number of variables in the character suite. However, some morphometric characters are most likely correlated and, in such situations, OER cannot be calculated by this method. Systematists have attempted to overcome this problem by examining a large suite of characters and requiring some number of characters to be significant before an overall treatment effect is recognized (for example, see Genoways, 1973; Owen and Webster, 1983; Willig, 1983; Wayne et al., 1986). These univariate criteria were assumed to represent a conservative mechanism of ascertaining significance. Such a strategy has two shortcomings. If few characters are correlated, the conservative nature of the criterion decreases the chances of detecting true overall group differences. If many characters are correlated, no criterion value

TABLE 2. Results of ANOVAs and MANOVAs for cranial and external characters combined (total of 22 characters). Numbers indicate number of characters significant ($P \leq 0.05$) in the ANOVAs; asterisks indicate level of significance in MANOVA.[a] Species listed in taxonomic order (Anderson and Jones, 1984). No value in the "Area" or "Interaction" columns indicates a one-way analysis only.

Species	Sex	Area	Inter-action
Noctilio leporinus	19***	—	—
Tonatia silvicola	5	—	—
Phyllostomus discolor	13	4*	10***
P. hastatus	19***	—	—
Trachops cirrhosus	1	—	—
Glossophaga soricina	6	0	0
Lonchophylla mordax	6*	—	—
Anoura geoffroyi	8***	6***	1
Carollia perspicillata	6***	7**	0
Sturnira lilium	8	1	1
Vampyrops lineatus	8**	7***	2
Artibeus jamaicensis	5	13***	5
A. lituratus	2	2**	2
Desmodus rotundus	13*	3***	1
Myotis nigricans	0	1*	0
Neoplatymops matto-grossensis	14***	—	—
Molossus molossus	16***	7**	5

a *, $0.05 \geq P > 0.01$ in the MANOVA, using Wilks' criterion for calculation of exact F; **, $0.01 \geq P > 0.001$ in the MANOVA, using Wilks' criterion for calculation of exact F; ***, $0.001 \geq P$ in the MANOVA, using Wilks' criterion for calculation of exact F.

for the required number of significant ANOVA treatment effects leads to conclusions with known levels of significance.

Statistical conclusions for univariate and multivariate analyses are compared in Tables 2 and 3. The results of the two types of analysis are not in concordance. Indeed, no discernible relationship exists between the number of variables that yield significant effects in the ANOVAs for a particular species and the significance of the effect in the MANOVA. For example, in the Glossophaga soricina external data set, none of the 10 characters yielded significant area effects in the ANOVAs, yet the MANOVA is significant for area ($P \leq 0.05$). The cranial data set for Phyllostomus discolor yielded 11 of 12 characters significant for secondary sexual variation, but the corresponding MANOVA treatment (sex) was not significant. Moreover, in the same data set for P. discolor, only eight characters had significant area-by-sex in-

teractions in the ANOVAs, whereas the MANOVA yielded a significant area-by-sex interaction at the 0.001 level. In data sets that yielded significant treatment effects in the MANOVAs for the combined character suites (22 characters), the number of significant corresponding ANOVA treatments ranged from 1 to 19. In data sets that yielded nonsignificant MANOVAs for the same combined character suite, the number of corresponding significant ANOVA treatment effects ranged from 0 to 13 (Table 2). Comparable ranges were obtained for the external character suite (10 characters): zero to eight significant ANOVA treatment effects with corresponding significant MANOVA treatment effects, and zero to five significant ANOVA treatment effects with corresponding nonsignificant MANOVA treatment effects (Table 3). The cranial character suite (12 characters) gave similar results: 1 to 12 significant ANOVA treatment effects with corresponding significant MANOVA treatment effects; and 0 to 11 significant ANOVA treatment effects with corresponding nonsignificant MANOVA treatment effects (Table 3).

MANOVA is considered to be a robust statistical test of the equality of group centroids (Pimentel and Frey, 1968). Nonetheless, a variety of conditions could lead to results similar to those reported herein. Small sample sizes lead to conservative ANOVAs and may produce unreliable MANOVAs such that univariate and multivariate results are not in accord. This is generally not the case in our analyses. In situations with small cell sample sizes ($n < 10$) either the correlation matrix was singular and no comparisons were possible, or no discrepancies between univariate and multivariate results were obtained, except for the single case of P. macrotis, where only 4 of 12 cranial characters were significant in the ANOVAs and the MANOVA was highly significant (Table 3).

Disparate sample sizes for treatment cells could also lead to problems. In our data, species with disparate sample sizes (including those with small sample sizes in

TABLE 3. Results of ANOVAs and MANOVAs for cranial and external characters separately. Explanation of content as in Table 2, except that no value in the "Sex" column indicates singularity of the MANOVA error matrix, with no comparison possible.

Species	Cranial[a]			External[b]		
	Sex	Area	Inter-action	Sex	Area	Inter-action
Peropteryx macrotis	4**	—	—	5	—	—
Noctilio leporinus	12***	—	—	7***	—	—
Micronycteris megalotis	—	—	—	1	—	—
Tonatia silvicola	4**	—	—	1	—	—
Phyllostomus discolor	11	3	8***	2	1*	2**
P. hastatus	12***	—	—	7***	—	—
Trachops cirrhosus	1	—	—	0	—	—
Glossophaga soricina	2***	0	0	4*	0*	0
Lonchophylla mordax	3*	—	—	3*	—	—
Anoura geoffroyi	4***	4*	0	4*	2***	1
Carollia perspicillata	5***	5	0	1	2**	0
Sturnira lilium	7*	0	0	1	1	1
Vampyrops lineatus	0	3***	2	8***	4**	0
Artibeus concolor	—	—	—	2	—	—
A. jamaicensis	5*	8***	5*	0	5***	0
A. lituratus	0	2**	1	2	0	1
Desmodus rotundus	5	2***	1	8***	1	0
Myotis nigricans	0	1*	0	0	0	0
Eptesicus furinalis	2	—	—	—	—	—
Neoplatymops mattogrossensis	11***	—	—	3*	—	—
Molossus molossus	12***	4**	4*	4***	4**	1

[a] Total of 12 cranial characters.
[b] Total of 10 external characters.

at least one treatment cell) are *P. macrotis*, *M. megalotis*, *T. silvicola*, *S. lilium*, *A. concolor*, and *E. furinalis*. Of these, only *P. macrotis* and *T. silvicola* yield results in which univariate and multivariate interpretations somewhat differ. *Peropteryx macrotis* was discussed in connection with small samples, and *T. silvicola* was significant for sex in the univariate suite for only 4 of 12 cranial characters, whereas the analogous MANOVA was highly significant (Table 3). In cases where major differences are seen between ANOVA and MANOVA (*P. discolor*, cranial-sex, external-area, external-interaction; *G. soricina*, cranial-sex, external-area; *A. geoffroyi*, external-area, combined-area; *C. perspicillata*, external-area; *V. lineatus*, cranial-area; *A. lituratus*, cranial-area, combined-area; *D. rotundus*, cranial-area, combined-area; *M. nigricans*, cranial-area, combined-area; *N. mattogrossensis*, external-sex; *M. molossus*, cranial-interaction, combined-area [Tables 2 and 3]), sample sizes are adequate and not disparate. The most likely factor contributing to

our results is the degree of correlation among variables. This situation is well known to yield erroneous conclusions when viewed from a univariate perspective (Kramer, 1972).

We cannot find any consistent evaluation of univariate results that corresponds with the multivariate results and, therefore, consider the univariate results to be of little or no value in assessing overall differences among groups in this data set. Moreover, our data indicate that no consistent application of a criterion value parallels the conclusions derived from the analogous MANOVA (Fig. 1). We, like many others (e.g., Rao, 1952; Cooley and Lohnes, 1962; Seal, 1964; Kramer, 1972), consider the multivariate results to represent the best statistical evaluation of overall significance. Accordingly, we were interested in elucidating the relation between possible univariate criterion values and their correspondence with the statistical conclusions of the MANOVAs. In this context, success is defined as corre-
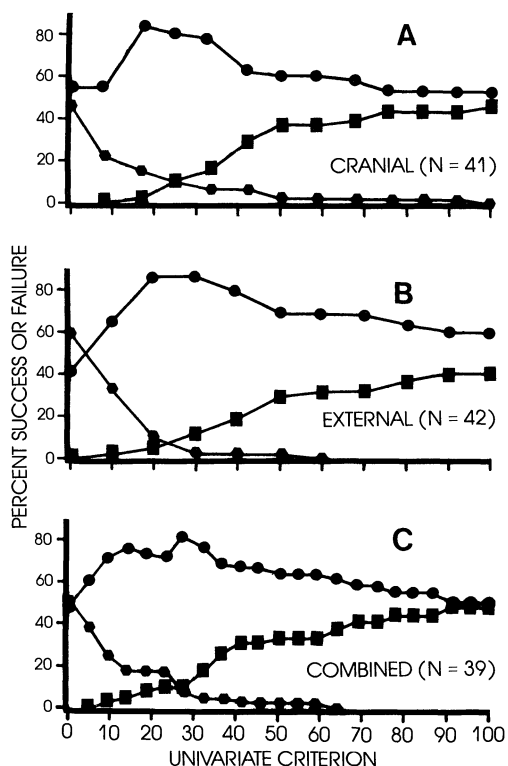
FIG. 1. Concordance between univariate and multivariate evaluations of morphometric data. Percent success (circles) and error (hexagons, Type I; squares, Type II) based upon a comparison of ANOVA criterion values (expressed as percentage of total number of characters in each data set) with statistical conclusion of corresponding MANOVA. Each case is one effect (sex, area, or sex versus area) assessed for one species (N = number of cases evaluated for a particular set).

spondence between the statistical interpretation of the univariate criterion value and the MANOVA result. We examined this relation for the cranial, external, and combined data sets separately. For both univariate and multivariate analyses, we considered results to be significant if $P \le$ 0.05. For example, if the criterion value was chosen such that overall significance was declared only if 5 or more univariate ANOVAs out of 10 (50%) were significant, and only 4 characters were significant in reality, then this result would agree with a nonsignificant MANOVA (success) and conflict with a significant MANOVA (error). However, if the criterion value had

been established at 30%, then the univariate results in the previous example would be considered in accord (success) with a significant multivariate result.

No criterion value (Fig. 1) enabled the univariate approach to achieve better than an 86% success rate compared with the MANOVA results. Surprisingly, the best success rate was obtained when the univariate criterion value was set between 17 and 30% of the characters. Criterion values less than this yielded higher Type I errors, whereas criterion values greater than 30% yielded gradually increasing Type II errors. Type I error gradually declined as the criterion value increased to 64%; thereafter, the application of the univariate criterion never led to statements of statistical difference that were not in accord with a statistical interpretation of the corresponding MANOVA. Because of these relations between error rate and the univariate criterion, the success rate actually declines gradually beyond the 30% level. Type I error is trivial at criterion values of 50% or greater, indicating that if these morphometric data are representative, then investigators who believe they are employing progressively more "conservative" standards at higher criterion values are misguided.

Microgeographic variation and sexual dimorphism in bats from northeast Brazil.—Sixteen species of bats were considered to exhibit statistically significant sexual dimorphism based upon a univariate criterion value of 16.6% (5 of 30 characters) in the combined data set (Willig, 1983). Herein, three species (*Peropteryx macrotis, Artibeus concolor,* and *Lasiurus borealis*) were not included in the multivariate analysis of the combined data set because the error matrix for each was singular. Of the remaining 13 species, 8 were successfully identified as dimorphic (*Lonchophylla mordax, Vampyrops lineatus, Desmodus rotundus, Noctilio leporinus, Phyllostomus hastatus, Anoura geoffroyi, Neoplatymops mattogrossensis,* and *Molossus molossus*), and 5 erroneously were considered dimorphic (*Glossophaga soricina, Tonatia silvicola, Phyllostomus discolor, Sturnira lilium,* and *Artibeus jamaicen-*

sis). Erroneously, one species (*Carollia perspicillata*) was not identified as dimorphic.

Of the 11 species with nonsingular error matrices and which were obtained from both locales, five were evaluated successfully by the univariate criterion as exhibiting microgeographic variation (*Carollia perspicillata, Vampyrops lineatus, Artibeus jamaicensis, Molossus molossus,* and *Anoura geoffroyi*), and two were successfully identified by the univariate criterion as not exhibiting significant microgeographic variation (*Glossophaga soricina* and *Sturnira lilium*); four exhibited significant microgeographic variation that was undetected by the univariate criterion (*Phyllostomus discolor, Artibeus lituratus, Desmodus rotundus,* and *Myotis nigricans*).

CONCLUSION

Regardless of the manner in which the morphometric data set is partitioned (i.e., cranial characters, external characters, or combined characters), a univariate statistical approach to systematic questions leads to unreliable and frequently erroneous conclusions concerning overall differences among groups. An apparent dilemma may arise if a MANOVA is nonsignificant but some characters exhibit significance in the analogous ANOVAs. Such results indicate that the observed number of significant univariate characters would be expected to occur at least 5% of the time when examining a character suite (with a similar correlation matrix) from randomly obtained replicate samples of a single population. If the original question or hypothesis of interest only refers to a single character, then the multivariate approach is not germane and the data on additional characters are superfluous. Systematic hypotheses are clearly multivariate in nature when considering morphometric data.

The actual structure of the character correlation matrix in the bat species studied herein clearly prohibits assuming that any particular univariate criterion value will lead to successful interpretation of phenotypic variation. If other animal taxa exhibit systematic characters that are cor-

related in a fashion similar to those considered herein, then univariate analyses of morphometric variation are likely to produce erroneous conclusions, or at best produce results lacking in the statistical rigor that univariate ANOVAs purport to achieve. Based upon our analyses, Multivariate Analysis of Variance is the preferred statistical methodology from both a theoretical and a practical point of view. Clearly the well-intended desire to avoid "complicated" statistical procedures when possible if simpler methodologies are efficacious is a less than benign myth that needs to be avoided in systematic research.

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APPENDIX

Characters Analyzed

Descriptions are given for the 10 external and 12 cranial characters measured on bat specimens used in morphometric analyses.

External characters.—*Total length,* greatest distance from anteriormost portion of snout to distal point of tail; *Hind foot length,* distance from heel of foot to tip of longest toe including claw; *Ear length,* distance from basal notch of ear to furthermost point on edge of pinna; *Tragus length,* distance from base of tragus to its distal edge; *Forearm length,* distance from outside of wrist to outside of elbow when wing folded; *Length of digit one,* length from wrist to distalmost point of first digit, including claw; *Length of digit three,* length from wrist to distal point on phalanx of third digit when wing maximally extended; *Length of digit four,* length from wrist to distal point on phalanx of digit four when wing maximally extended; *Length of digit five,* length from wrist to distal point on phalanx of digit five when wing maximally extended; *Tibia length,* length from outermost point of ankle to outermost point of knee.

Cranial characters.—*Greatest length of skull,* distance from most anterior part of rostrum (excluding teeth) to posteriormost point of skull; *Condylobasal length,* distance from anteriormost edge of premaxillae to posteriormost projection of occipital condyles; *Postorbital constriction,* least distance across top of skull posterior to postorbital process; *Mastoid breadth,* greatest width of skull, including mastoid; *Breadth of braincase,* greatest width across braincase posterior to zygomatic arches; *Rostral breadth,* width of rostrum at suture between premaxilla and maxilla; *Breadth across upper molars,* maximum width from outer alveolus of one molar to outer alveolus of opposite molar; *Breadth across upper canines,* width from outer alveolus of one canine to outer alveolus of other canine; *Length of maxillary tooth row,* length from anterior edge of alveolus of first tooth present in maxillae to posterior edge of alveolus of last molar; *Length of upper molariform toothrow,* maximum length from anterior edge of alveolus of last molar; *Greatest length of mandible,* length from anteriormost point on ramus (excluding teeth) to posteriormost point on coronoid process; *Length of mandibular toothrow,* length from anterior edge of alveolus of canine to posterior edge of alveolus of last molar in mandible.