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ON THE PHYLETIC WEIGHT OF MENSURAL  
CRANIAL CHARACTERS IN CHIPMUNKS  
AND THEIR ALLIES (RODENTIA: SCIURIDAE)

BRUCE D. PATTERSON

July 29, 1983

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### ON THE PHYLETIC WEIGHT OF MENSURAL CRANIAL CHARACTERS IN CHIPMUNKS AND THEIR ALLIES (RODENTIA: SCIURIDAE)

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## ABSTRACT

This study outlines a method for investigating the phyletic information or "weight" in mensural cranial characters in the Scuridae. Five isolated populations of least chipmunks (*Eutamias minimus*) form the frame of reference for this analysis. The study examines the hypothesis that divergence in a set of mainly cranial characters used in taxonomy ("taxonomic" characters) differs from that evident in a set of "mandibular" characters. Mandibular characters in many other animals are known to be genetically and ontogenetically responsive to ecological conditions. Therefore, if taxonomic characters are to provide unique information on the phyletic relationships of chipmunks, patterns in their variability should contrast with mandibular patterns.

Taxonomic and mandibular characters differ in mean values among the five populations to comparable extents. Although mandibular characters tend to be more variable, they tend also to be more highly correlated with one another than are taxonomic characters. Correlations of characters within the taxonomic and mandibular sets are apparently no greater than between-set correlations; both are low. The relative interdependence of taxonomic and mandibular characters is emphasized by a canonical correlation analysis which suggests that individuals tend to occupy the same relative positions in each of the two morphological spaces. Results of the canonical correlation analysis must be considered tentative in view of the facts that (1) relatively little of the variation in original characters is represented in the canonical variates, and (2) no comparable study exists for contrast.

Nevertheless, this study helps to explain some confusing patterns of cranial morphology in chipmunks and, by extension, their allies. Cranial morphology in these animals is apparently tied to environmental conditions, to an extent at least comparable with mandibular morphology. In this respect, chipmunks resemble tree squirrels more closely than ground squirrels. Because of this responsiveness, phenetic studies of cranial morphology in chipmunks may lead to better classifications of ecological conditions than of phyletic relationships (cf. Patterson, 1981).

## INTRODUCTION

Characters of the skin and skull have served for many years as the foundation of mammalian classification. Higher taxa are commonly distinguished by one or more qualitatively different characters, whose variation is thereby amenable to "phylogenetic" analysis (e.g., Marshall, 1977). In contrast, mammalian species and subspecies commonly lack such distinctive attributes, and the study of their interrelationships is thus typically limited to "phenetic" approaches (e.g.,

Genoways, 1973). With the advent of computers and the development of multivariate statistical packages, mammalian systematists have increasingly employed mensural cranial characters in taxonomic decision-making.

The use of mensural cranial characters in mammalian classification is clouded by our ignorance of components of cranial variability (cf. Leamy, 1977; Straney & Patton, 1980). While distinct patterns of cranial morphology may reflect degrees of phyletic relatedness, it is equally possible that they may result from the distinctive responses of a given underlying genome to different environmental conditions. Problems raised by environmental determination of cranial morphology are exacerbated by the fact that phyletic lineages and environments are both based in geography. Thus, simple geographic patterns of cranial morphology can, themselves, neither support nor refute the importance of environmental determination. Are complex, laboratory analyses of morphological genetics (e.g., Atchley et al., 1981) the only reasonable avenue of inquiry?

Another means of approaching this question is afforded by the intercorrelations of characters. Specifically, if one can establish *a priori* a character set that is genetically or ontogenetically responsive to ecological conditions, then one can assess the concordance of these characters with those in question. Close correspondence of characters in the two sets would argue for the importance of ecological determination. Conversely, independent responses would permit cranial characters to have "phyletic weight" (*sensu* Mayr, 1969) and hence taxonomic utility.

Available data indicate that characters of the mandible are often environmentally plastic. Functional morphologists generally recognize that the "size and shape [of the mandible] is maintained in being as a response to the primary morphogenetic demands of functionally related tissues" (Moss & Meehan, 1970, p. 11). Characters of the mandible can thereby reflect the developmental importance of environmental conditions, such as nutrition and diet (McCance, 1962; Moore, 1965; Tonge & McCance, 1965). Characters of the mandible may also reflect divergent selection pressures resulting from different resource-use patterns (the "Darwin principle"; e.g., Johnston, 1969; Behle, 1973; Barnett, 1977). In either case, such characters should be accorded "particularly low taxonomic value" (Mayr, 1969, p. 125). If the assumption is valid that mandibular morphology closely corresponds to environmental conditions, then it is possible to assess the taxonomic worth of traditionally employed characters of the general conformation of the cranium.

This paper compares patterns of variability in taxonomic and mandibular characters among isolated, montane populations of chipmunks, genus *Eutamias* (Rodentia: Sciuridae). A recent study of geographic variation in the Colorado chipmunks (*Eutamias quadri vittatus* group) suggested that cranial and mandibular characters being used in chipmunk taxonomy may be responsive to environmental conditions associated with the habitats that different montane populations occupy (Patterson, 1981). Another study suggested that the cranial morphology of Douglas squirrels (*Tamiasciurus douglasii*) reflects the conifer species they feed upon (Lindsay, 1982). If such conclusions are warranted, then patterns of morphology in taxonomic and mandibular character sets should largely coincide, both being principally determined by ambient environmental conditions. If, in contrast, taxonomic (chiefly cranial) characters more closely reflect phyletic affinities, discordance in the two character sets should be evident, because mandibles can be

expected to reflect ecological conditions. The test of this hypothesis examined cranial and mandibular characters in a group of chipmunks, all currently classified as *Eutamias minimus operarius*, which occupy a spectrum of environmental conditions.

#### METHODS AND MATERIALS

Five montane populations of least chipmunks were selected for study, representing a considerable latitudinal extent (fig. 1). Populations are as follows: (1) Sierra Blanca, New Mexico (lat. 33°23'N, long. 105°48'W), (2) northeast of Santa Fe, New Mexico (lat. 35°47'N, long. 105°49'W), (3) northeast of Canjilon, New Mexico (lat. 36°28'N, long. 106°26'W), (4) west, northwest of Tres Piedras, New Mexico (lat. 36°43'N, long. 106°14'W), and (5) LaSal Mountains, Utah (lat. 38°23'N, long. 109°11'W). Precise locality information for specimens comprising these populations is given in the Appendix. On Sierra Blanca in southern New

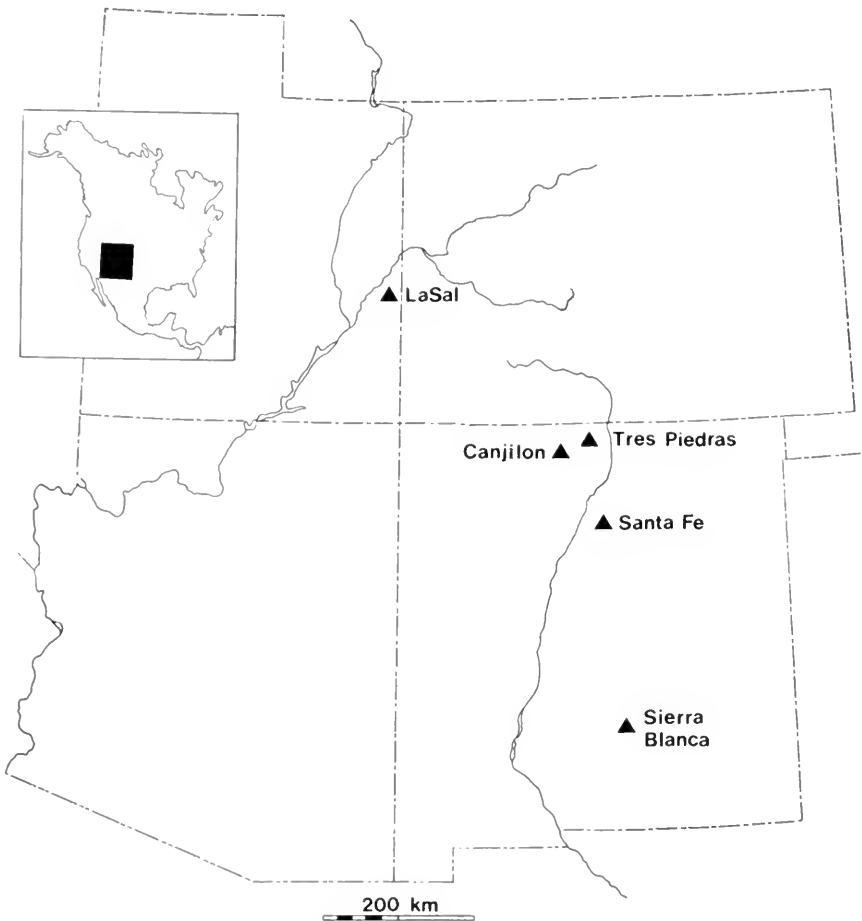


FIG. 1. Geographic locations of the five sampled populations.

Mexico, least chipmunks are confined to habitats within the glacial cirque on that peak, which are characterized by extensive boulder fields (Conley, 1970). In northern New Mexico, *E. minimus* occurs in mesic coniferous forests, sage brushlands, and alpine meadows (Bailey, 1931). In contrast, I collected the sample from the LaSal Mountains in 1980 from an open, xeric pine forest along the southeastern foothills of the mountains proper. The five studied populations therefore occur in a variety of ecological conditions.

Information on head-and-body length and weight was taken from the collector's tag; other data were gathered by me from skulls and jaws using dial calipers and were recorded to the nearest 0.1 mm. Cranial and mandibular characters used in the present analysis are defined by numbers in the various aspects (denoted by letters) of Figure 2. The characters may be classified into three groups, the first two being combined as "taxonomic" characters, consisting of cranial and mandibular characters used in making taxonomic inferences in various systematic studies of chipmunks, and the third consisting of exclusively "mandibular" characters selected in this study for their probable functional significance. The first group is comprised of characters I employed in systematic studies of the *Eutamias quadri-vittatus* species complex (Patterson, 1980, 1981; see also Johnson, 1943; Conley, 1970). These include: GLS, greatest length of skull—1, 2 (A); ZB, zygomatic breadth—3, 4 (A); CB, cranial breadth—5, 6, (A); ML, mandibular length—33, 34 (E; see Levenson et al., in review, for another study drawing taxonomic conclusions from mandibular morphology in chipmunks); NL, nasal length—1, 9 (A); MTR, length of maxillary molar toothrow—16, 21 (C); IOB, least interorbital breadth—11, 12 (A); NW, nasal width—13, 14 (A); DOL, diagonal length of orbit—22, 23 (C); PL, premaxillary length—1, 10 (A, B); CD, cranial depth—17, 18 (B). The second group consists of other characters of general cranial conformation, some of which have been used in taxonomic investigations by Howell (1929) and Hoffmeister & Ellis (1979). These are: PTL, palatillar length—15, 24 (C); MD, length of maxillary diastema—15, 16 (B, C); LAB, length of auditory bulla—25, 26 (C); OIL, distance between orbit and incisive foramen—22, 27 (C); PW, palatal width at third premolar—28, 29 (C); BOS, basioccipital length—30, 31 (C); IL, length of incisive foramen—27, 32 (C); TZ, length of zygomatic arch at posterior union with skull—19, 20 (B); and FW, frontal width—7, 8 (A).

Patterns of variation in these "taxonomic" (mainly cranial) characters were compared with those shown by mandibular characters. Mandibular characters examined (in addition to ML, above) are: MC, distance between mental foramen and articular condyle—33, 35 (D); MAD, distance between anterior alveolus of M3 and articular condyle—33, 36 (E); CVH, distance between tips of coronoid and ventral angular processes—37, 38 (D); CDH, distance between tips of coronoid and dorsal angular processes—37, 39 (D); AG, greatest width of angular processes—38, 40 (E); AL, least width of angular processes—41, 42 (D); AF, distance between mandibular foramen and articular condyle—33, 43 (E); WMM, width of mandibular molars (M2 and M3)—36, 44 (E).

Descriptive statistics and univariate analyses of variance were obtained for adult specimens (i.e., permanent P<sup>4</sup> showing wear) via BMDP7D (Dixon, 1977). The equality of group means was assessed via analysis of variance, assuming equality of group variances. Inspection of Welch and Brown-Forsythe test statistics (Dixon, 1977), which do not assume equal variances, provided highly similar results.

Relative variability of characters was determined by the coefficient of variation, calculated on a desk calculator as the standard deviation divided by the mean



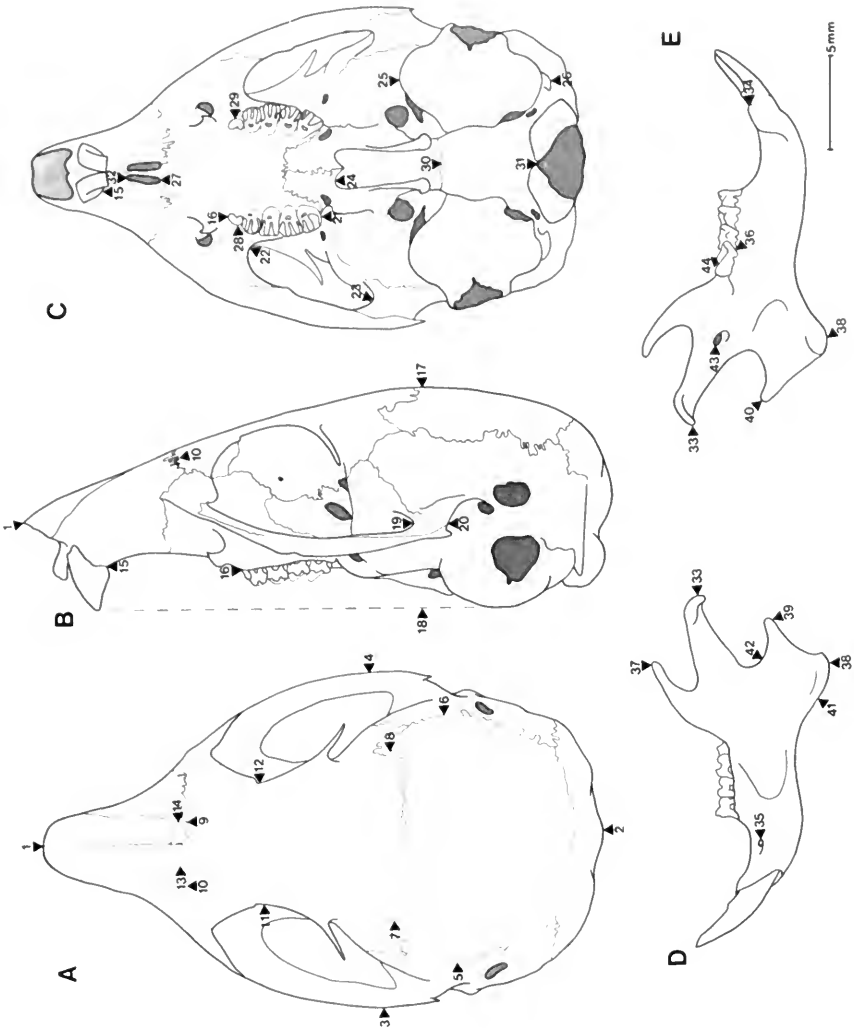


FIG. 2. Skull of *Eutamias minimus* (NMSU 11896) from the LaSal Mountains, Utah. Numbers define measurements used in this analysis (see Methods and Materials). A, Dorsal aspect of cranium; B, left lateral aspect of cranium; C, ventral aspect of cranium; D, labial aspect of left mandible; E, lingual aspect of left mandible.

(BMDP7D) times 100. Coefficients of variation were then pooled across characters and localities within character sets to determine differences in the relative variability of characters of taxonomic and mandibular sets. The equality of relative variability in these sets was determined by the Mann-Whitney  $U$  test (Siegel, 1956), a distribution-free nonparametric test. This test was considered one-tailed because characters responsive to environmental influences might be expected *a priori* to be more variable than those marked by great phyletic weight.

Bivariate correlations between characters were examined using Pearson product-moment correlation coefficients (BMDP6M; Dixon, 1977). Examinations of within- and between-set correlations were made by simple proportions and by histograms.

Correspondence between the sets of taxonomic and mandibular characters was assessed via canonical correlation analysis (BMDP6M; Dixon, 1977). Canonical correlation provides a convenient summary of multiple bivariate correlations between previously defined sets of normally distributed variables. The procedure relies on eigenvector-eigenvalue solutions to a series of linear functions; it is canonical in the sense that the number of variates, and hence their non-zero correlations, is reduced to a minimum number equal to the number of variables in the smaller original set. Excellent discussions of this methodology may be found in Cooley & Lohnes (1971) and Pimentel (1979).

Geometrically, canonical correlation analysis indicates the extent to which individuals occupy the same relative positions in terms of the separate sets of measurements (Cooley & Lohnes, 1971). It is similar to principal components analysis in that original variable axes are rotated to a new set of axes that is mutually orthogonal and does not warp the original euclidean spaces. It differs from principal components analysis in that axes are selected so that between-set pairs have the maximum possible correlation; principal components are selected to maximize extracted variation (Pimentel, 1979).

Bartlett's chi-square test (Dixon, 1977; Pimentel, 1979) was used to determine the significance of remaining eigenvalues and hence the number of canonical variables necessary to express the dependency between the two sets of characters. In order to assess the influence of body size variation on the canonical variates, I regressed canonical variates on head-and-body length and the cube root of weight, both statistically independent variables, using regression routines programmed in a TI-59 desk calculator. The cube root of weight, rather than weight *per se*, was used to satisfy statistical assumptions of normality. The transformation may be visualized as one reducing a three-dimensional property, weight, into a one-dimensional one compatible with linear measurements or transformations of them. The significance of these regressions was judged via tables given in Rohlf & Sokal (1969).

## RESULTS

### UNIVARIATE ANALYSES

Means and coefficients of variation of the "taxonomic" and "mandibular" characters are given for five populations in Table 1. Significant mean differences exist among these populations in 19 of 28 (68%) characters. Within the taxonomic character set, 13 of 20 characters (65%) differ significantly among the five populations ( $P < .05$ ), and five characters (25%) differ at highly significant levels

TABLE 1. Means, coefficients of variation (in parentheses), and sample size (N) of 28 cranial and mandibular characters of least chipmunks. Statistics are given for each of five populations from the southern Rocky Mountains and for a composite population based on these. *F* values represent univariate tests of the equality of five population means, assuming equal variances; *F* values have 4 and 81 degrees of freedom.

Characters	Sierra Blanca (N=13)	Santa Fe (N=13)	Canjilon (N=14)	Tres Piedras (N=28)	LaSal (N=18)	Overall (N=86)	<i>F</i>
GLS	32.08 (1.6)	32.63 (1.6)	32.14 (1.8)	32.20 (1.7)	31.79 (1.7)	32.15 (1.8)	4.59**
ZB	17.95 (2.3)	18.15 (2.7)	17.90 (2.6)	17.81 (1.9)	17.52 (2.1)	17.84 (2.5)	5.12***
CB	13.88 (1.7)	14.22 (2.7)	14.33 (3.0)	14.28 (2.3)	14.17 (2.8)	14.19 (2.7)	3.52*
ML	18.15 (1.4)	18.42 (2.3)	18.04 (1.9)	18.28 (1.8)	18.01 (1.6)	18.18 (1.9)	4.09**
NL	8.75 (4.9)	8.74 (5.2)	8.44 (3.5)	8.40 (4.6)	8.62 (6.3)	8.56 (5.2)	2.58*
MTR	5.15 (2.6)	5.20 (2.7)	5.19 (2.1)	5.18 (3.0)	5.13 (3.2)	5.17 (2.8)	0.56
IOB	6.83 (3.4)	6.86 (5.3)	6.74 (4.1)	6.83 (4.0)	6.94 (3.8)	6.84 (4.1)	1.08
NW	2.73 (9.0)	2.60 (12.8)	2.64 (8.6)	2.72 (6.7)	2.85 (7.4)	2.72 (8.9)	2.73*
DOL	8.22 (2.8)	8.45 (2.9)	8.23 (3.2)	8.30 (2.3)	8.25 (2.2)	8.29 (2.7)	2.51*
PL	9.78 (3.3)	9.76 (3.0)	9.36 (3.4)	9.50 (3.1)	9.81 (3.2)	9.62 (3.6)	6.63***
CD	13.24 (1.6)	13.51 (2.4)	13.45 (2.7)	13.29 (2.1)	13.31 (2.3)	13.35 (2.3)	2.16
PTL	13.58 (2.7)	13.76 (2.4)	13.61 (1.6)	13.65 (1.8)	13.29 (2.0)	13.58 (2.3)	6.56***
MD	8.25 (3.3)	8.35 (3.3)	8.20 (2.6)	8.30 (2.8)	7.93 (2.6)	8.21 (3.4)	2.15
LAB	7.97 (2.6)	8.05 (2.8)	8.01 (2.7)	7.86 (2.7)	7.91 (3.0)	7.94 (2.8)	8.16***
OIL	6.96 (2.7)	6.94 (2.7)	6.91 (2.6)	6.87 (2.7)	6.63 (2.5)	6.85 (3.1)	8.86***
PW	6.07 (5.0)	5.96 (3.1)	6.01 (3.2)	5.96 (3.1)	5.87 (3.4)	5.96 (3.6)	1.91
BOS	5.28 (3.5)	5.26 (3.2)	5.34 (3.5)	5.19 (2.8)	5.18 (3.4)	5.24 (3.3)	2.49*
IL	2.21 (7.3)	2.25 (5.0)	2.21 (5.8)	2.27 (7.5)	2.34 (7.6)	2.26 (7.1)	2.10
TZ	2.42 (4.4)	2.39 (5.1)	2.34 (6.8)	2.36 (4.8)	2.29 (6.2)	2.36 (5.6)	2.21
FW	8.97 (3.9)	9.24 (5.0)	8.88 (5.4)	9.14 (4.7)	9.30 (3.0)	9.12 (4.6)	2.88*
MC	14.93 (1.6)	15.10 (2.5)	14.82 (2.5)	14.80 (2.2)	14.61 (1.9)	14.83 (2.4)	4.78**
MAD	10.01 (2.2)	10.13 (3.1)	9.91 (3.7)	10.04 (2.4)	9.94 (2.3)	10.01 (2.8)	1.48
CVH	9.95 (2.8)	10.27 (3.5)	10.24 (3.3)	10.17 (3.1)	9.78 (3.4)	10.08 (3.6)	6.87***
CDH	7.15 (3.0)	7.48 (4.3)	7.37 (5.1)	7.33 (3.6)	6.86 (4.4)	7.23 (5.0)	11.35***
AGW	5.18 (6.2)	5.41 (3.9)	5.29 (5.3)	5.32 (6.4)	5.07 (5.1)	5.26 (5.9)	3.35**
ALW	3.75 (2.9)	3.59 (4.5)	3.78 (4.2)	3.73 (6.7)	3.66 (4.5)	3.70 (5.4)	2.02
ALF	5.07 (4.5)	5.22 (4.4)	5.04 (5.2)	5.17 (3.7)	4.96 (4.2)	5.10 (4.6)	3.76**
WMM	1.41 (4.5)	1.40 (5.1)	1.49 (3.6)	1.45 (4.4)	1.47 (4.6)	1.45 (4.8)	4.94**

\**P* < .05. \*\**P* < .01. \*\*\**P* < .001.

( $P < .001$ ). For mandibular characters, six of eight (75%) differ significantly ( $P < .05$ ), two of these (25%) highly so ( $P < .001$ ). The pattern of mean differences for the two character sets appears grossly comparable.

However, there are apparent differences in the variability of taxonomic and mandibular characters. The most frequently occurring coefficient of variation in the taxonomic data set is 2.7 (10 occurrences); that for mandibular characters is 4.5 (four occurrences). One-half the coefficients of variation for taxonomic characters are less than or equal to 3.0; the median for mandibular characters is 3.7. The tendency of mandibular characters to exhibit greater variation relative to mean values can be demonstrated via the Mann-Whitney test of 100 taxonomic vs. 40 mandibular coefficients of variation ( $U = 1487.5$ ;  $t = 2.36$ ;  $P < .01$ , one-tailed test). It should be noted, however, that the greater relative variability of mandibular characters does not obviate mean differences in mandibular characters among these populations (Table 1).

The univariate analyses show that: (1) significant differences in mean values exist among sampled populations in the character sets analyzed; (2) significant differences among populations are not confined to one character set or the other, but are typical of both, to roughly comparable extents; and (3) the mandibular characters analyzed tend to show greater variability relative to mean values than do the taxonomic ones. However, the univariate analyses do not address themselves to the intercorrelations of characters: taxonomic and mandibular characters may be either fully integrated, so that changes in one set demand changes in the other, or largely independent but parallel, producing the same univariate effects. Bivariate and multivariate analyses are necessary to distinguish between these possibilities.

#### BIVARIATE ANALYSES

If "taxonomic" and "mandibular" characters comprise two distinctly different morphological domains which have undergone comparable degrees of change during the divergence of these populations, closer correlations can be expected between characters of the same set than between characters of different sets. Conversely, if taxonomic and mandibular characters are fully integrated, either genetically or ontogenetically, so that changes in one set imply corresponding changes in the other, then such differences in the degree of intercorrelation should not exist.

It is possible to distinguish three sets of correlation coefficients from the set of 378 unique bivariate correlations of the 28 characters analyzed: correlations within the taxonomic character set, correlations within the mandibular character set, and correlations between taxonomic and mandibular characters. Coefficients for these three sets of correlations are presented in Tables 2, 3, and 4, respectively. Coefficients of correlation in all three sets are low. The number of correlations with negative coefficients is at first surprising, given that all correlations are of mensural characters confounding size variation. However, only one negative correlation differs significantly from zero (TZ and NW, table 2), and this correlation holds at the 5% level but not at the 1% level. Generally, those characters showing the greatest number of negative or nonsignificant correlations with others (e.g., NW, IL, and WMM) are similar in having small mean values (table 1). The lack of correlation between these and others may be attributed in part to the relative

TABLE 2. Product-moment correlation matrix for "taxonomic" characters (within-set correlations). Correlation coefficients are based on 86 cases and have 84 degrees of freedom.  $P$  ( $r = 0.212$ ) = .05;  $P$  ( $r = 0.277$ ) = .01.

	ZB	CB	ML	NL	MTR	IOB	NW	DOL	PL	CD	PTL	MD	LAB	OIL	PW	BOS	IL	TZ	FW
GLS	0.66	0.27	0.68	0.40	0.44	0.26	-0.12	0.56	0.40	0.23	0.76	0.60	0.39	0.55	0.12	0.40	0.07	0.28	0.23
ZB		0.21	0.65	0.33	0.33	0.26	-0.17	0.44	0.26	0.23	0.59	0.57	0.38	0.53	0.25	0.44	-0.00	0.38	0.06
CD			0.27	0.02	0.22	0.15	-0.11	0.35	-0.03	0.55	0.06	-0.15	0.13	-0.03	0.12	0.03	0.12	-0.07	0.17
ML				0.28	0.33	0.37	0.00	0.57	0.27	0.23	0.59	0.46	0.28	0.43	0.04	0.31	0.01	-0.27	0.13
NL					0.21	0.20	-0.01	0.10	0.56	-0.08	0.29	0.25	0.19	0.37	0.02	0.32	-0.01	0.19	0.16
MTR						0.18	0.01	0.31	0.12	0.22	0.40	0.13	0.17	0.21	0.13	0.08	0.25	0.10	0.27
IOB							0.19	0.14	0.30	0.14	0.21	0.18	0.16	0.11	0.09	0.21	0.08	0.08	0.26
NW								0.05	0.11	-0.20	0.02	-0.13	0.05	-0.10	-0.07	-0.12	0.07	-0.25	0.07
DOL									0.28	0.33	0.47	0.22	0.31	0.01	0.08	0.12	0.03	-0.11	0.20
PL										-0.04	0.19	0.03	0.21	0.17	-0.11	0.12	0.07	0.07	0.33
CD											0.01	-0.19	0.29	-0.04	0.15	-0.00	0.10	-0.03	0.13
PTL												0.78	0.27	0.62	0.11	0.38	0.05	0.16	0.11
MD													0.17	0.60	0.17	0.39	-0.06	0.30	-0.02
LAB														0.29	0.18	0.24	0.08	-0.00	0.04
OIL															0.13	0.38	0.18	0.31	-0.02
PW																0.17	0.06	0.14	-0.06
BOS																	-0.18	0.23	-0.15
IL																		-0.17	0.40
TZ																			-0.04
FW																			

TABLE 3. Product-moment correlation matrix for "mandibular" characters (within-set correlations). Correlation coefficients are based on 86 cases and have 84 degrees of freedom.  $P(r = 0.212) \cong .05$ ;  $P(r = 0.277) \cong .01$ .

	MAD	CVH	CDH	AGW	ALW	ALF	WMM
MC	0.77	0.54	0.47	0.50	0.31	0.49	0.05
MAD		0.52	0.41	0.44	0.28	0.64	0.01
CVH			0.71	0.73	0.40	0.44	0.06
CDH				0.34	0.16	0.45	-0.06
AGW					0.55	0.38	0.18
ALW						0.13	0.29
ALF							-0.01

TABLE 4. Product-moment correlation matrix for "taxonomic" (rows) and "mandibular" (columns) characters (between-set correlations). Correlation coefficients are based on 86 cases and have 84 degrees of freedom.  $P(r = 0.212) \cong .05$ ;  $P(r = 0.277) \cong .01$ .

	MC	MAD	CVH	CDH	AGW	ALW	ALF	WMM
GLS	0.64	0.63	0.56	0.46	0.51	0.20	0.42	-0.00
ZB	0.63	0.62	0.72	0.60	0.62	0.31	0.46	0.07
CB	0.18	0.22	0.22	0.12	0.15	0.22	0.25	0.14
ML	0.75	0.73	0.57	0.50	0.48	0.18	0.55	-0.01
NL	0.27	0.28	0.12	0.07	0.04	-0.08	0.02	-0.15
MTR	0.38	0.32	0.29	0.27	0.36	0.25	0.17	0.35
IOB	0.29	0.28	0.23	0.05	0.14	0.22	0.06	0.22
NW	-0.09	-0.05	-0.13	-0.17	-0.12	0.03	-0.16	0.02
DOL	0.47	0.52	0.40	0.36	0.29	0.06	0.36	-0.02
PL	0.24	0.27	0.13	-0.04	0.14	-0.00	0.08	-0.04
CD	0.22	0.18	0.25	0.22	0.10	0.13	0.29	0.12
PTL	0.59	0.51	0.54	0.50	0.51	0.25	0.33	-0.10
MD	0.43	0.40	0.48	0.46	0.45	0.12	0.30	-0.15
LAB	0.34	0.31	0.29	0.26	0.13	0.04	0.09	-0.02
OIL	0.48	0.39	0.42	0.35	0.45	0.23	0.22	-0.12
PW	0.14	0.01	0.11	0.15	-0.03	0.18	0.06	0.10
BOS	0.48	0.36	0.37	0.29	0.19	0.17	0.10	0.03
IL	-0.05	-0.01	-0.03	-0.04	0.03	0.22	-0.04	0.28
TZ	0.31	0.32	0.24	0.18	0.30	0.08	0.29	-0.03
FW	0.02	0.12	0.08	-0.04	0.14	0.06	0.04	0.15

imprecision with which these characters were measured with dial calipers; each 0.1-mm increment corresponds to 6.9% of the mean value of WMM vs. only 0.3% of GLS (table 1).

The extent of correlations of characters within taxonomic and mandibular sets differs substantially. Seventy-nine of 190 (36.3%) intercorrelations of taxonomic characters (table 2) differ significantly from zero ( $P < .05$ ), whereas 20 of 28 (71.4%) correlations of mandibular characters (table 3) are significant. The greater proportion of significant correlations among characters of the mandibular set can likely be attributed to the relative structural and functional simplicity of the mandible in comparison with that of the cranium.

The extent of correlation between taxonomic and mandibular data sets (table 4) appears intermediate to correlations within these sets. Eighty-four of 160 between-set correlations (52.5%) are significant ( $P < .05$ ) vs. 99 of 218 (45.4%) total within-set correlations. The relation of correlations within and between character sets is made evident in the histogram of all 378 correlation coefficients (fig. 3). The median correlation coefficient for within-set correlations is 0.19 ( $P > .05$ ), whereas

■ within sets

□ between sets

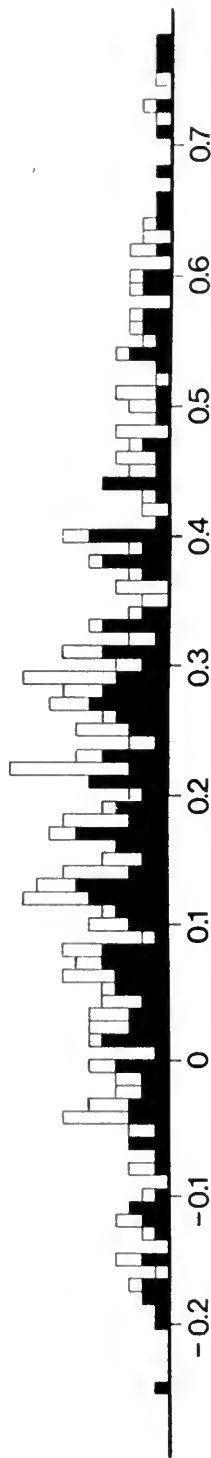


FIG. 3. Histogram of correlation coefficients among the 28 mensural characters in chipmunks, comparing 218 within-set correlations (black) to 160 between-set correlations (white). Correlation coefficients greater than 0.212 differ significantly from zero ( $P < .05$ ). See text for discussion.

that for between-set correlations is 0.31 ( $P < .01$ ). There is no evidence from the comparison of correlation coefficients to indicate that taxonomic and mandibular characters are less closely related to one another than characters of either set are to each other.

#### MULTIVARIATE ANALYSES

The complexity of relationships shown by the bivariate analysis can be readily summarized by canonical correlation analysis. Table 5 contains the results of the canonical correlation analysis. Of the eight pairs of canonical variates calculated from the original matrix, only the first is judged significant ( $P < .001$ ) by Bartlett's test for the remaining eigenvalues (Dixon, 1977). The correlation of scores on the first canonical variate is high ( $R_c = 0.91310$ ), indicating that 83.4% of the variance on the first canonical variates is shared. A close correspondence exists between the relative positions that individuals occupy on the first canonical variates.

Results of the canonical correlation analysis are presented graphically in Figure 4. Only the first canonical variates are shown, as only these are statistically significant. As indicated by the strong correlation between canonical variates, individuals tend to occupy the same relative positions in the two morphological spaces. The possession of a given mandibular morphology strongly implies a corresponding cranial morphology.

Because canonical variates represent linear transformations of original variables, the importance of any canonical correlation is critically dependent upon the success of the initial transformation. Table 6 contains canonical variate loadings (correlations between original variables and canonical variates), variance extracted, and redundancy for the first two canonical variates. Most variables show positive correlations with elements of the first canonical vectors and negative correlations with elements of the second.

"Taxonomic" and "mandibular" character sets are expressed with unequal precision by their respective canonical variates. The proportion of variance extracted by each canonical variate is analogous to the variance accounted for by each principal component (Pimentel, 1979). The first canonical variate extracts 43.2% of the variance exhibited by mandibular characters, whereas the corresponding canonical variate for taxonomic characters accounts for only 23.6%. This difference in the extent to which canonical variates account for variance in the two character

TABLE 5. Results of canonical analysis, showing Bartlett's test for the remaining eigenvalues. Bartlett's test indicates the number of canonical variables necessary to express the dependency between the two sets of characters; in the present analysis, only one is necessary. See text for discussion.

Eigenvalue	Canonical correlation	No. of eigenvalues	$\chi^2$	d.f.	Probability
		0	271.79	160	0.00000
0.83376	0.91310	1	145.29	133	0.21995
0.46498	0.68190	2	101.20	108	0.66556
0.42337	0.65067	3	62.38	85	0.96896
0.27130	0.52086	4	40.07	64	0.99172
0.18206	0.42669	5	25.90	45	0.99000
0.15116	0.38880	6	14.35	28	0.98454
0.13347	0.36533	7	4.25	13	0.98827
0.05846	0.24179				



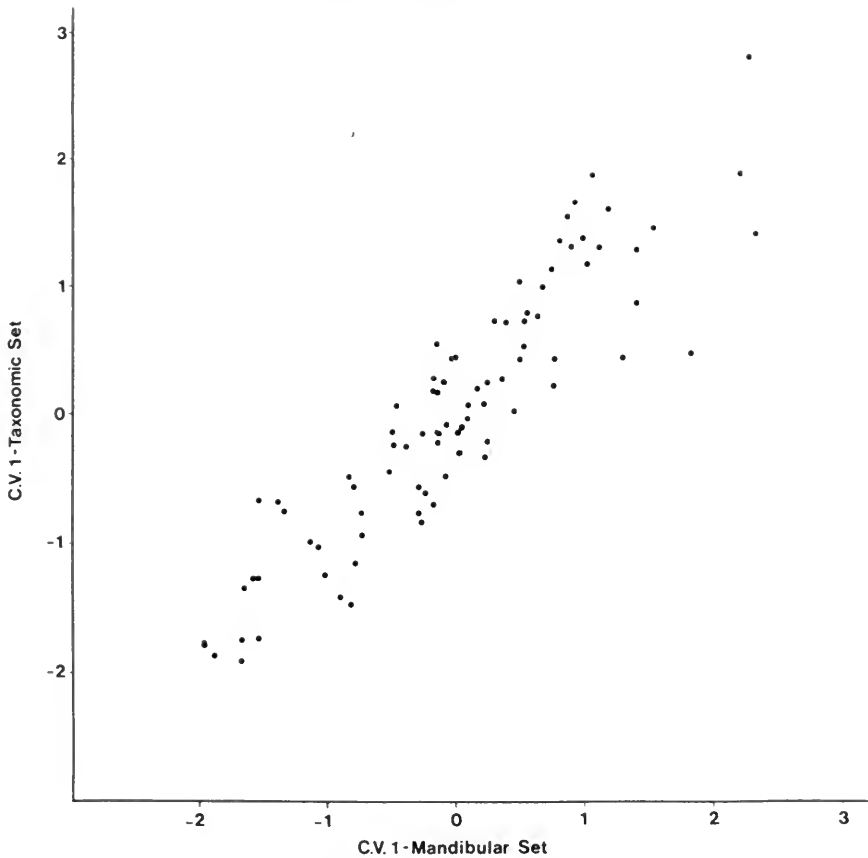


FIG. 4. Plot of canonical variate loadings of 86 chipmunks on the first canonical variates for "taxonomic" and "mandibular" characters. Of the variation along these axes, 83.3% is shared, indicating a close relationship between the relative positions individuals occupy in the two morphological spaces. Only one pair of canonical variates is necessary to express the dependency between "taxonomic" and "mandibular" data sets.

sets can be attributed to the differential intercorrelations of taxonomic and mandibular characters (tables 2 and 3), as well as to differences in dimensionality. The space defined by measurements of mandibular characters has eight dimensions, whereas that defined by taxonomic characters has 20 dimensions. The greater dimensionality of taxonomic characters is also reflected in cumulative variance extracted: together, the eight canonical variates completely account for variance among mandibular characters, but account for only 56% of the variance exhibited by taxonomic characters. Such differences are inevitable in comparisons of spaces differing initially in intercorrelation and dimensionality.

Redundancy provides a measure of the actual overlap of sets in canonical space. Redundancy is calculated as the proportion of total variance extracted by a canonical variate times the canonical correlation between the variate and the corresponding canonical variate of the other set. Measures of redundancy, therefore, vary in parallel with extracted variance: for the first pair of canonical variates, redundancy

TABLE 6. Canonical variate loadings (correlations between original variables and canonical variates), variance extracted, and redundancy for the first two canonical variates. Only the first canonical correlation is significant ( $P < .001$ ).

"Taxonomic" character	Canonical variates		"Mandibular" character	Canonical variates	
	1	2		1	2
GLS	0.794	-0.079	MC	0.845	-0.394
ZB	0.858	-0.075	MAD	0.822	-0.185
CB	0.193	-0.264	CVH	0.786	-0.088
ML	0.864	-0.167	CDH	0.692	0.032
NL	0.254	-0.143	AGW	0.725	0.199
MTR	0.448	-0.191	ALW	0.269	-0.366
IOB	0.229	-0.544	ALF	0.611	0.123
NW	-0.164	-0.164	WMM	0.015	-0.394
DOL	0.584	-0.090	Variance		
PL	0.233	-0.130	extracted	0.4322	0.0678
CD	0.212	-0.295	Redundancy	0.3604	0.0315
PTL	0.736	-0.003			
MD	0.633	0.237			
LAB	0.369	-0.260			
OIL	0.582	0.029			
PW	0.038	-0.422			
BOS	0.437	-0.501			
IL	-0.069	-0.204			
TZ	0.399	0.097			
FW	0.090	0.022			
Variance					
extracted	0.2358	0.0603			
Redundancy	0.1966	0.0281			

is 36% for mandibular characters and 20% for taxonomic characters. Because only the first canonical correlation is significant, no justification exists for interpreting subsequent canonical variates. Loadings, extracted variance, and redundancy for the second canonical variates are included in Table 6 for illustrative purposes only.

Is the correspondence between the taxonomic and mandibular canonical variates based simply on body size variation, or does it represent a more complex interdependency? The relationship between loadings on the first canonical variates and body size was assessed by means of regression analysis. Two independent variables related to body size were considered: head-and-body length and the cube root of weight. The results of these regressions are presented in Table 7. Both measures of body size are positively and significantly correlated with both canonical scores. A stronger relationship is evident between the cube root of weight and canonical variate scores than between the latter and head-and-body length. This is noteworthy in that (1) weight is known to fluctuate daily and seasonally, and (2) the specimens examined herein were collected by several rather than dozens of collectors. Both conditions would suggest that head-and-body length would be a better criterion of size than weight; instead, the reverse seems true.

In spite of the significant correlation between canonical variate loadings and body size, size explains no more than one-fourth of the variation in canonical variate scores. The remaining variation is typically considered under the general rubric of "shape." The implication of the finding that canonical variates are not comprised of simply size-related variation seems clear: the canonical variates sum-

TABLE 7. Simple linear regression analyses of loadings on the first canonical variates (CV1) vs. body size. Two independent measures of size have been used: HBL—head-and-body length, in millimeters, and CUBEWT—cube root of weight, in grams. Each entry includes a least-squares equation, a correlation coefficient ( $r$ ), a coefficient of determination ( $R^2$ ), and a statement of the likelihood that the regression slope is not different from zero.

**"Taxonomic" set**

$$\begin{aligned} \text{CV1} &= -5.6056 + 0.0496 \text{ HBL} \\ r &= 0.2954 \quad R^2 = 0.0873 \quad P < .01 \\ \text{CV1} &= -15.0598 + 4.2660 \text{ CUBEWT} \\ r &= 0.5380 \quad R^2 = 0.2894 \quad P < .001 \end{aligned}$$

**"Mandibular" set**

$$\begin{aligned} \text{CV1} &= -4.7336 + 0.0419 \text{ HBL} \\ r &= 0.2494 \quad R^2 = 0.0622 \quad P < .05 \\ \text{CV1} &= -14.2736 + 4.0433 \text{ CUBEWT} \\ r &= 0.5099 \quad R^2 = 0.2600 \quad P < .001 \end{aligned}$$

marize a complex morphological hyperspace with no unitary explanation. The relatively small coefficients of determination in these regressions imply that cranial and mandibular morphology may vary in an integrated manner, irrespective of changes in body size.

## DISCUSSION

The present analysis has uncovered some interesting results which bear on the taxonomic value of mensural, cranial characters in chipmunks. The analysis of mean values (table 1) demonstrates that significant differences exist among the studied populations in both "taxonomic" and "mandibular" characters. Comparable proportions of characters of each set show significant differences. A check on the ecological and evolutionary significance of such differences is provided by the geographical proximity of least chipmunk populations from Canjilon and Tres Piedras (see fig. 1). Reference to Table 1 indicates that these two populations agree closely in both cranial and mandibular morphology, implying that significant differences in characters among the remaining populations probably have a strong geographical component.

Analyses of the relative variability of these characters suggests that mandibular characters tend to be relatively more variable than taxonomic ones. Unfortunately, the strength of this conclusion is limited by the analytical resolution afforded by coefficients of variation; no more rigorous parametric test appears as appropriate. The greater variability of mandibular characters may be attributed to either the variety of developmental factors known to affect mandibular morphology or the lesser number of constraints operating on the generally simpler structure of the mandible. It could be argued that these data support the operation of diversifying selection on a character set related to resource-use (e.g., Van Valen, 1965), but this would appear unlikely for reasons given in Patterson (1981).

The correlations of characters within character sets were surprisingly low, especially those for taxonomic characters. While low correlations of small characters may be attributed to experimental error in measurement, loose correlations of larger characters defy a simple explanation. Perhaps the behavioral plasticity of chipmunks lessens their reliance on any single constellation of cranial characters (cf. Patterson, 1981).

Certainly, the morphological differences between even different *species complexes* of chipmunks do not prevent them from functioning in an ecologically similar manner. Where members of the *minimus* complex of chipmunks are absent from mountain ranges in the American Southwest, members of the *quadrivittatus* group occupy habitats characteristic of *E. minimus* populations where these are found (Findley, 1969; Patterson, 1981). Similarly, *E. dorsalis* (a member of the *townsendii* group) expands the range of habitats it occupies to include those of both *E. minimus* and chipmunks of the *quadrivittatus* complex where these are absent from a montane biota (Findley, 1969). Loose correlations of cranial morphology may facilitate such niche shifts by presenting a wider spectrum of cranial configurations to natural selection. It seems more probable, however, that such loose correlations exist in the absence of selection for the close integration of characters, and that behavioral plasticity inhibits selection among particular suites of characters.

The correlation of characters within taxonomic and mandibular sets apparently differs. The mandibular character set would appear to be more highly integrated, based on the proportion of significant intercorrelations (tables 2 and 3). This difference in degree of intercorrelation of characters is difficult to test, however. Tests of the equality of correlation coefficients between sets suffer from the interdependence of correlations: if characters A and B and characters B and C are positively correlated, then a positive relation between A and C is implied. In addition, the two sets under consideration differ in dimensionality, obviating the possibility of a principal components approach to determining the proportion of shared variation among characters. The elementary course followed here of presenting the proportions of significant correlations within sets seems sufficient to establish the difference (but not the significance thereof) in degree of character correlations within sets.

A difference in the degree of intercorrelation of characters comprising the two sets may not be surprising. The morphology of bones is currently recognized as constituting a response to the demands of functionally related tissues (or periosteal matrices), especially muscles (e.g., Moss & Meehan, 1970). The periosteal set affecting mandibular growth and maintenance is likely to be far simpler than that affecting the cranium because of the radical difference in the complexity of these two structures. By this interpretation, one could expect that the greater number of constraints on cranial morphology would lead to reduced variability of cranial characters, but a greater degree of independence among them, because each subset of characters would be responding to its own periosteal matrix. Each of these patterns of morphology has been suggested by the preceding analyses. Although tentative, this explanation accounts for two seemingly contradictory morphological patterns, namely, the greater variability, yet greater intercorrelation, of mandibular characters.

The canonical correlation analysis indicated that the dependency between the two character sets could be described by a single pair of canonical variables (table 5). The strength of this correlation is such that more than 80% of the variance expressed by the first canonical variates is shared. These data demonstrate that individuals tend to occupy the same relative positions in the two character sets and that changes in one character set imply corresponding changes in the other.

However, these conclusions can be no stronger than the canonical correlation analysis itself. The transformation of original data to canonical axes was accomplished with only moderate success: 24% of the variation in taxonomic characters

and 43% of the variation in mandibular characters is represented in the first canonical variates. Loose correlations among characters is the probable cause of such low proportions of extracted variance. Thus, the actual overlap between characters in canonical space ("redundancy," table 6) is too low to warrant sweeping generalizations regarding the functional or developmental interdependency of taxonomic and mandibular characters.

It is noteworthy, however, that such loose correlations between characters have also plagued other studies of chipmunk craniometrics. In principal components analyses, axes are derived which extract a maximum amount of variation in the original data matrix. In a principal components analysis of *Eutamias quadrivittatus* chipmunks involving three external and 12 cranial characters, Hoffmeister & Ellis (1979) found only 48% of the variation among characters was extracted by the first principal component; the second component expressed only 20%. These results are compatible with those of the present analysis.

#### MANDIBULAR MORPHOLOGY

The present analysis is critically dependent on the assumption that mandibular characters are responsive to ecological conditions. Two different avenues for the ecological responsiveness of the mandible are possible: mandibular morphology may be subject to selection for a specific adaptive function, or mandibular morphology may reflect developmental history or patterns of individual use within a specific set of ecological conditions.

Clear-cut demonstrations of *ad hoc* adaptations of the mandible among populations of mammalian species are few, but such specializations are often assumed to underlie the radiation of trophic morphologies between species. Much study has been directed toward the bills of birds and their relations to food resources (e.g., Kear, 1962; Grant, 1967; Willson, 1971). Bill morphology has been found to parallel, and may in fact determine, the range of food resources used by populations. Characters associated with particular adaptations are unreliable bases for taxonomy (under the "Darwin principle"), and those "associated with shifts in the food niche are particularly susceptible to a rapid attainment of conspicuous differences or, conversely, of convergent similarities" (Mayr, 1969, p. 223). Mayr illustrated this point by comparing the piscivorous bills of fish-eating mergansers (*Mergus*) with more typical ducklike bills of related goldeneyes (*Bucephala*). Evolutionary adaptation to particular "stations in life" may obscure underlying phyletic relationships by convergence or spurious divergence of characters involved in that adaptation.

Ontogenetic modifications of mandibular morphology in response to prevailing ecological conditions are also known. A variety of studies has elucidated components of mandibular variability in laboratory rats and mice. For example, experimental studies indicate that the final dimensions of bones, including the mandible, may depend on levels of nutrition during growth (McCance, 1962; Park, 1968; Park & Nowosielski-Slepowron, 1971; McAnulty, 1977). The type of nutrition may also influence mandibular development. Moore (1965) fed laboratory rats an abnormally soft diet, thereby lessening the utility of masticatory muscles. Effects of this regimen included a 12% reduction in the mass of the cranium and mandible, a 1% to 2% decrease in the dimensions of the cranial and facial skeleton, and a 4% decrease in the length of the angular process of the mandible (Moore, 1965).

Subsequent studies of the effects of surgical removal of masticatory muscles corroborate these findings, suggesting a direct role of muscle development and use in mandibular growth and maintenance. Moss & Meehan (1970, p. 12) showed that "temporalis muscle removal in the juvenile rat is followed rapidly by a marked change in the form of the coronoid process," the related microskelatal unit of the temporalis. Moore (1973), studying the effects of bilateral masseterectomy in rats, found a 25% reduction in the dimensions of the angular process; lesser effects (all involving reductions) were also discerned in the length (11%) and width (17%) of the condyloid process, in the height of the condyloid (10%), and in the length of the base (5%). Again, Mayr (1969) has argued that characters marked by high variability are not useful in taxonomic decision-making.

Thus, both genetic and ontogenetic mechanisms exist for the correspondence of mandibular morphology with ecological conditions. Holbrook (1982) has recently documented a case in which free-living *Peromyscus maniculatus* in different, nearby habitats exhibit different mandibular morphologies. Dietary differences between habitats may account for the mandibular differences observed in these deer-mice, but genetic studies of morphological traits are necessary to fully distinguish between genetic and ontogenetic effects (e.g., Leamy, 1974, 1977; Atchley et al., 1981).

Mammalogists have long recognized the problems inherent in a taxonomy based on mandibular characters; this is reflected in the common choice of cranial over mandibular characters. However, the present study indicates that cranial and mandibular morphologies in these chipmunks are not as insulated from one another as the traditional taxonomic use of cranial characters would suggest. Changes in one character set apparently imply changes in the other. I believe the parallel responses of cranial and mandibular characters warrant a reassessment of those cranial characters used to classify chipmunks and their allies.

#### CRANIAL MORPHOLOGY IN CHIPMUNKS AND RELATED FORMS

Complex patterns of variation in cranial and external morphology have long puzzled students of chipmunk taxonomy. Allen (1877, p. 797), in the *North American Rodentia*, stated: "While the five varieties of *T. asiaticus* [that were then recognized and] above characterized so thoroughly intergrade that they are not to be trenchantly defined, the extreme phases of differentiation are often quite widely diverse, and would require recognition as distinct species were they not found to be so inseparably connected." Several years later, in the description of a new species, Merriam (1886, p. 28) observed: "That this genus is peculiarly susceptible to environmental influences is amply attested by the number and perplexing characteristics of the incipient species already known from the United States." Allen (1889, p. 178) believed that, with additional collecting, "Many well-marked and easily definable forms will be found confined to very limited regions, and to peculiar environmental conditions." These early assessments of morphological variation in chipmunks are best summarized by Allen (1890, p. 53) in his generic revision:

From the extreme susceptibility of this plastic group to the influences of environment, it is one of the most instructive and fascinating groups among North American mammals. No one can doubt its comparatively recent differentiation from a common stock, and its dispersion from some common centre. Whether the type originated at some point in North America, or in the northern part of Eurasia, it is perhaps idle to

speculate, but that it has increased, multiplied, spread, and become differentiated to a wonderful degree in North America is beyond question; as it is found from the Arctic regions to the high mountain ranges of Central Mexico, and has developed some twenty to thirty very palpable local phases. Some of them easily take rank as species, others as subspecies. Probably a more striking illustration of evolution by environment cannot be cited.

Nearly 40 years later, Howell (1929) undertook a generic revision of chipmunks, involving more than 13,000 specimens and 60 taxa in *Eutamias* alone. He emphasized external and pelage characters, as well as geographic distribution, to the exclusion of cranial characters. Howell's reduced reliance on cranial characters is reflected in his generic key (Howell, 1929, pp. 30-33); in no case does a cranial character other than size (greatest length of skull) define a bifurcation in the key. Howell's classification is still generally accepted (e.g., Hall, 1981), albeit with minor alterations of taxonomic status and descriptions of new forms (e.g., White, 1953; Callahan & Davis, 1977).

A more recent evaluation of cranial (and other) characters in chipmunks was offered by White (1953, p. 565):

The differences in anatomy and color between many species of chipmunks are subtle, and refined techniques are required to discover them. When "measuring" chipmunks taxonomically, it is necessary to use a "chipmunk scale" and not, for example, a "pocket-gopher scale." In explanation, some species of pocket gophers closely allied to each other, and even some subspecies of the same species, differ markedly in color and in size and shape of parts of the skeleton; comparable differences are not so pronounced among many species of chipmunks.

Other characters, especially those of the baculum, have since been shown to be superior to cranial characters in making inferences about reproductive limits in chipmunks (e.g., White, 1953; Sutton & Nadler, 1974; Callahan, 1980).

Nor are such confusing patterns of cranial morphology confined only to chipmunks; they appear to be characteristic of many members of the Sciuridae. In fact, the baculum was first named as such in a taxonomic work on *Sciurus*, in which Thomas (1915, p. 383) stated:

There has always appeared to be something wrong with the inclusion of the Oriental squirrels in the same genus as *Sciurus vulgaris*, although when classifying the group some years ago I was unable to find any material differences in their skulls and teeth.

Now, however, I have found a character by which such squirrels as are still put in *Sciurus* may be sorted into several groups, each sharply defined from the others.

This is the structure of the *os penis*, which shows very striking differences between the various groups of species, and may evidently be of great service in classifying the members of this difficult family.

Shortly after, Pocock (1923, p. 211) surveyed the baculum in many sciurids, altering previous classifications based on skulls and teeth: ". . . the conclusion very forcibly suggested by the literature of the subject is the untrustworthiness of such characters." An excellent example of this is provided by *Sciurus* and *Tamiasciurus*, forms considered congeneric on the basis of cranial and dental characters until the highly significant differences in the male reproductive tracts of these forms were recognized (Mossman et al., 1932).

Bryant (1945), in his review of all Nearctic squirrels, acknowledged three major subdivisions of the family: flying squirrels, tree squirrels, and chipmunks and ground squirrels; however, "The significant phylogenetic differences apparent in the skulls of sciurids are principally associated with the masticatory mechanism and with the differential development of the parts of the brain" (p. 288). These characters would therefore appear to document the major branches of the adaptive

radiation of the Sciuridae, but would appear impotent, under the "Darwin principle" (Mayr, 1969), for assessing the phyletic relations of taxa within these adaptive zones.

Moore (1959, p. 159) judged the value of cranial characters to sciurid taxonomy as follows:

For the tree squirrels in particular, no one has been able to report any satisfactory skull characters that distinguish, even at the generic level, the tree squirrels of the Palearctic and Nearctic regions (*Sciurus*) from *Callosciurus* and others of the Indo-Malayan region, or *Heliosciurus* and others of the Ethiopian region, or *Guerlinguetus* and others from the Neotropical region.

Moore's "assiduous" search for skull characters supporting these taxonomic distinctions did reveal some meristic and qualitative ones (e.g., the number of transverse septa in the auditory bulla, the inclination and shape of foramina, suture ankylosis), but, in sum, "the various genera that may be ecologically classified as tree squirrels possess few distinguishing skull characters" (p. 192). Specific differences in skull characters are known for semiterrestrial and ground squirrels, however (e.g., Moore & Tate, 1965).

Others studies of ground squirrels also suggest that they may show patterns of cranial morphology contrasting with those exhibited by chipmunks and tree squirrels. In his study of North American ground squirrels, Howell (1938) listed a number of cranial and dental characters by which the various genera and subgenera could be recognized. The relative stability of ground squirrel classification in comparison with those of chipmunks and tree squirrels is also suggestive of the greater phyletic information embodied in the cranial characters of ground squirrels. It appears likely, therefore, that results of this study are more pertinent for character divergence among tree squirrels than among ground squirrels.

The present study thus provides quantitative support for conclusions reached earlier by Allen, Merriam, and others: mensural cranial characters of chipmunks appear responsive to environmental conditions, and hence are unreliable grounds for phyletic inference. Purely phenetic studies of cranial morphology in these animals could describe patterns of variability more closely related to ecological conditions than to phyletic history (cf. Patterson, 1981), especially in areas of great topographic and ecological heterogeneity. In such cases, taxonomic distinctions based on cranial morphology might reflect nothing more than contrasting environmental conditions in different parts of a taxon's geographical range.

Problems raised by this source of cranial variability can be illustrated by the systematics of Southwestern chipmunks. For nearly half a century (cf. Bailey, 1931), chipmunks from the Organ Mountains, New Mexico, were assigned to *Eutamias cinereicollis cinereus*. As such, they were thought to be a transition series joining widely separated populations on the Sacramento Mountains to the east with populations inhabiting the Mogollon Rim to the west under *E. cinereicollis*. Fleharty (1960) subsequently noted the distinctive baculum of the eastern members of this group, elevating these populations to specific status as *E. canipes*. Patterson (1980) then found that both karyotypic and bacular evidence indicated that the Organ Mountains population in fact represents a southern derivative of *E. quadrivittatus*. Rather than representing a transition series between *E. canipes* and *E. cinereicollis* (cf. Findley et al., 1975), the Organ Mountains population of *E. quadrivittatus* documents a more complex biogeographic history detailed elsewhere (Patterson, 1982). Previous considerations of *E. canipes*, *E. cinereicollis*, and *E. quadrivittatus australis* as conspecific populations reflect the convergent responses



of populations inhabiting a region whose climatic regimen is dominated by the northern Chihuahuan Desert (Patterson, 1980).

An additional example of the taxonomic effects of this evolutionary potential is afforded by red squirrels. The Baja California red squirrel, *Tamiasciurus mearnsi*, was accorded specific status because cranial characters showed it to be as distinct from *T. douglasii* and *T. hudsonicus* as these two are from one another (Lindsay, 1981). For the last two species, the "test of sympatry" is present in the Pacific Northwest and affords a "phenetic yardstick" by which to assess allopatric cases (e.g., Mayr, 1969). However, the cranial distinctiveness of Baja red squirrels may not signify specific divergence, but instead reflect the divergent environmental conditions pertaining there. Lindsay's (1982) more recent work on northern red squirrels indicates that patterns of cranial morphology can be traced to the different types of conifers in which various populations live. Is the Baja population of *Tamiasciurus* distinctive because of its phyletic history or the forests it occupies? At present, no concrete answer seems possible.

The present study of chipmunk morphology would be strengthened by an explicit demonstration that mandibular characters in chipmunks are closely specified by ecological conditions. I have not attempted such an analysis because the environmental determination of mandibular morphology is expected on both genetic and ontogenetic grounds. In addition, other studies demonstrate a relationship between mandibular morphology and environmental conditions, both in other rodents and in more distantly related taxa. Thus, assuming a relationship between mandibular morphology and environmental conditions in chipmunks seems warranted, if not substantiated.

It is unfortunate that the most pertinent kind of data for conclusions of this nature seems unavailable. Because chipmunks and tree squirrels do not acclimate readily to laboratory conditions, controlled genetic studies of morphological variability cannot be conducted (cf. Atchley et al., 1981). Barring such direct approaches, this alternative, employing correlations among characters, appeared most fruitful.

In spite of these limitations, it is recommended that strictly phenetic studies of cranial morphology not be incorporated into the taxonomy of chipmunks and tree squirrels. Many other characters exist in these taxa, and they may serve in studies of phyletic relationships (e.g., karyotypes, pelage, and postcranial morphology, especially of the reproductive tract, baculum, and feet). On the other hand, the noteworthy plasticity of cranial characters in these groups may provide much insight into patterns of ecological and evolutionary divergence and help to explain the notable success of the family Sciuridae.

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## APPENDIX

### SPECIMENS EXAMINED

All specimens in the following list are currently classified as *Eutamias minimus operarius* and are deposited in the Vertebrate Museum, New Mexico State University.

NEW MEXICO: *Lincoln Co.*: N. Ridge, Sierra Blanca Pk., 11,500 ft (3). *Otero Co.*: East face, Sierra Blanca Pk., 11,500 ft (8); ¼ mi N top, Sierra Blanca Pk., 11,500 ft (2). *Rio Arriba Co.*: 1.9 mi N, 1.7 mi E Canjilon, 8,200 ft, T26NR5Esec9 (2); 5.0 mi E, 4.7 mi N Canjilon, 9,800 ft, T27NR6Esec30 (12); 15.0 mi W, 3.1 mi N Tres Piedras, 9,750 ft, T29NR7Esec30 (3); 15.3 mi W, 3.1 mi N Tres Piedras, 9,800 ft, T29NR7Esec31 (10); 15.4 mi W, 3.0 mi N Tres Piedras, 9,750 ft, T29NR7Esec31 (1); 15.4 mi W, 3.0 mi N Tres Piedras, 9,800 ft, T29NR7Esec31 (1); 15.5 mi W, 5.8 mi N Tres Piedras, 9,800 ft, T29NR7Esec19 (3); 24.1 mi W, 3.8 mi N Tres Piedras, 9,800 ft (10). *Santa Fe Co.*: Little Tesuque Creek, 8,200 ft (1); Santa Fe Ski Basin, Little Tesuque, 8,200 ft (1); Santa Fe Ski Basin (3); Santa Fe Ski Basin, 10,000 ft, T18NR11Esec7 (2); Santa Fe Ski Basin, 10,500 ft (1); Santa Fe Ski Basin, upper (1); Upper Santa Fe Ski Basin, 10,500 ft, T18NR11E (4).

UTAH: *San Juan Co.*: 6.8 mi S, 1.3 mi E Mount Peale, LaSal Mts., 7,650 ft, T28SR25Esec30 (14); 8.2 mi S, 0.3 mi E Mount Peale, LaSal Mts., 7,650 ft, T28SR24Esec36 (4).









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