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Gordon K. Weddle  
*Fort Hays State University*

Jerry R. Choate  
*Fort Hays State University*

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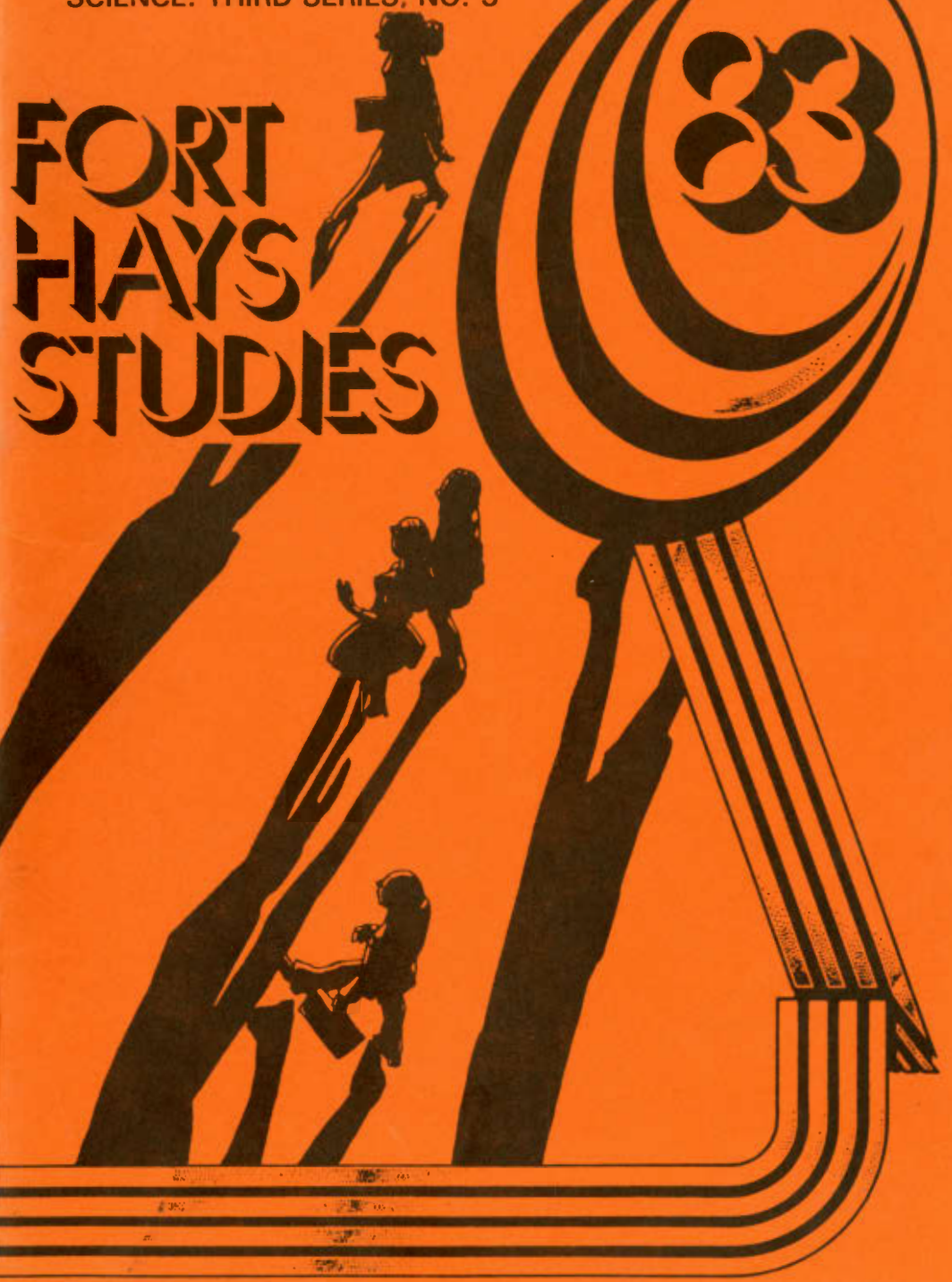
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# FORT HAYS STUDIES





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By  
Gordon K. Weddle and Jerry R. Choate



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**FORT HAYS STATE UNIVERSITY**  
**Museum Of The High Plains**

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# DENTAL EVOLUTION OF THE MEADOW VOLE IN MAINLAND, PENINSULAR, AND INSULAR ENVIRONMENTS IN SOUTHERN NEW ENGLAND

Gordon K. Weddle and Jerry R. Choate

Because of the slow rate at which morphological evolution usually occurs, the characters of a taxon that are evolving most rapidly often are best suited for evolutionary study. Accordingly, it has been documented (Hibbard, 1959) that the molar dentition of microtine rodents has undergone especially rapid evolutionary change since the middle Pliocene, comparable to that of the dentition and appendicular skeleton of the Equidae during the Tertiary (see also Phillips and Oxberry, 1972). As a result of a dietary shift that occurred in the late Pliocene (from an omnivorous cricetine diet to a more specialized herbivorous diet consisting largely of siliceous grasses), the molar dentition of microtine rodents has evolved toward progressive hypsodonty and occlusal complexity (Guthrie, 1965; Repenning, 1968). Some of the principal causes and effects of this abrupt evolutionary change were discussed by Guthrie (1971).

Guthrie (1965) analyzed the effects of sustained directional selection on intrapopulation variability, and concluded that the intensity of directional selection is positively correlated with the variability of evolving characters (see, however, comments by Van Valen, 1969). More recently, Kluge and Kerfoot (1973) demonstrated a positive correlation between variability and divergence in several vertebrate taxa, and this relationship was largely substantiated by Sokal (1976). However, Kellog and Hays (1975) found no consistent relationship between variability and rate of evolution in five fossil radiolarians.

If selection pressure is directly correlated with variability of evolving characters (which seems unlikely), then it might be possible to estimate the relative intensity of directional selection operating on different populations by comparing the variability of rapidly evolving characters in those populations (Guthrie, 1971; see contradictory comments by Riska, 1979). The occurrence in southern New England of several insular populations of *Microtus pennsylvanicus* (Ord), and the closely related *M. breweri* (Baird), which have undergone evolutionary divergence during the Recent epoch, affords an opportunity to examine microtine dental evolution. Accordingly, the objectives of this study were: 1) to compare the extent of variability (both quantitative and qualitative) in the dentitions of populations of *Microtus* inhabiting mainland, peninsular, and insular environments; 2) to identify some of the selective forces that affect mainland and maritime populations of *Microtus*; 3) to examine Guthrie's hypothesis regarding the relationship between intensity of selection and variation.

## METHODS AND MATERIALS

Seven populations inhabiting mainland, peninsular, and continental island areas of southern New England (Fig. 1) were selected for study. The taxa sampled were: *Microtus pennsylvanicus pennsylvanicus* (Ord) from an inland region (Tolland County) of Connecticut (abbreviated herein as TC), Barnstable (BA), Massachusetts (on the Cape Cod Peninsula), and Nonomasset Island

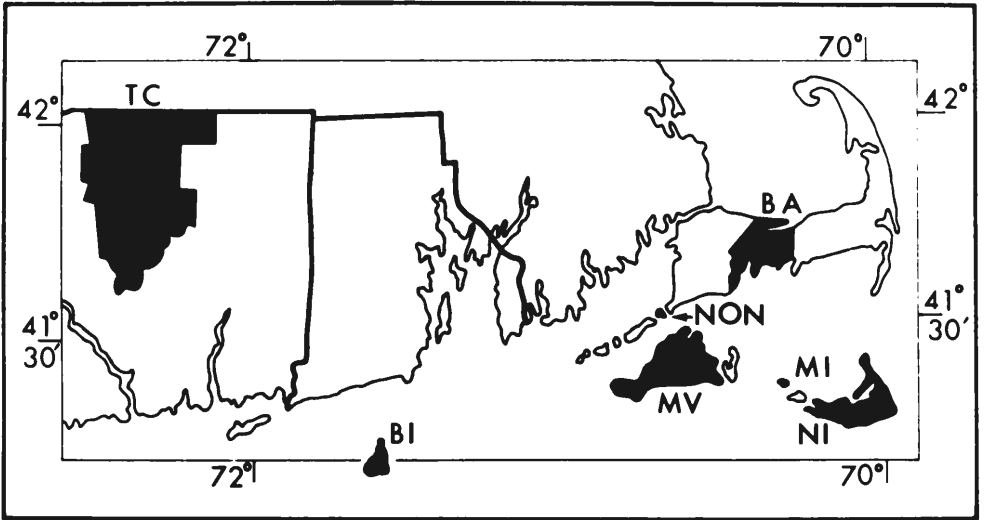


Fig. 1. Map of southern New England, showing sample areas darkened. Abbreviations for sample areas are given in Table 2 and in the text.

(NON), Massachusetts (in the Elizabeth Islands Archipelago); *M. p. rufidorsum* (Baird) from the island of Martha's Vineyard (MV), Massachusetts; *M. pennsylvanicus* (subspecies undetermined) from Nantucket Island (NI), Massachusetts; *M. p. provectus* (Bangs) from Block Island (BI), Rhode Island; *M. breweri* (Baird) from Muskeget Island (MI), Massachusetts (Hall and Kelson, 1959:725).

The upper and lower molar toothrows of 152 museum specimens of these taxa and of 18 upper and 23 lower molar toothrows removed from owl pellets found on Martha's Vineyard were photographed through a binocular dissecting microscope at constant magnification. Negatives were enlarged equally and printed (Guthrie, 1965) to enable comparison of variability in the seven populations. All specimens are housed in the University of Connecticut Museum; photographs are on file in the Museum of the High Plains.

Forty-two measurements (20 on the uppers and 22 on the lowers) were taken with dial calipers accurate to  $\pm 0.05$  mm from photographs of each specimen (Fig. 2; Guthrie, 1965). Measurements were taken from the outermost edge of the enamel, and those which were not well defined were omitted.

Occlusal dimensions are not sexually dimorphic in *Microtus* (Guthrie, 1965; Oppenheimer, 1965; Martin, 1973); therefore, sexes were pooled for analysis. However, variation with age in dimensions of teeth has been demonstrated (Oppenheimer, 1965; Lidicker and MacLean, 1969; Martin, 1973). Accordingly, obvious juveniles were excluded; however, it was not possible to age specimens from owl pellets. Therefore, a statistical technique (Gould, 1974) was employed to determine which of the 42 characters were covariates of age. A set of characters (1L, 2L, 5L, and 6L) that was known to vary with age was selected prior to analysis. Pooled data from all samples then were subjected to r-mode factor analysis (varimax rotation). Resulting factors were examined to determine if Guthrie's (1965) "evolving characters" were covariates of the selected age variables. All subsequent analyses treated the teeth as prismatic structures that exhibit no significant age variation.

Coefficients of variation were used to compare mensural variability of characters. Standard statistics, including coefficients of variation, were computed for each character in each population sampled. Because the data were derived from populations suspected of undergoing directed change, normality of distributions could not be assumed and parametric tests involving multivariate analogs of the coefficient of variation could not be applied (Sokal and Braumann, 1980). Therefore, Wilcoxon's two-sample signed ranks test (Sokal and Rohlf, 1969:400; Ashton and Rowell, 1975) was applied to coefficients of variation (for selected character sets) to determine significant differences in variability between pairs of samples.

Photographs of the dentition of the three syntypes of *M. breweri*, together with photographs from each population sampled, were examined to determine qualitative variation in occlusal patterns within and among samples. Eleven pattern characteristics were recorded for each specimen. Frequency distributions were computed for these characters within populations, and an R X C contingency table (G-test) was calculated for each character, employing populations as rows and coded character states as columns. Variables exhibiting significant differences among samples were subjected to arcsin transformation



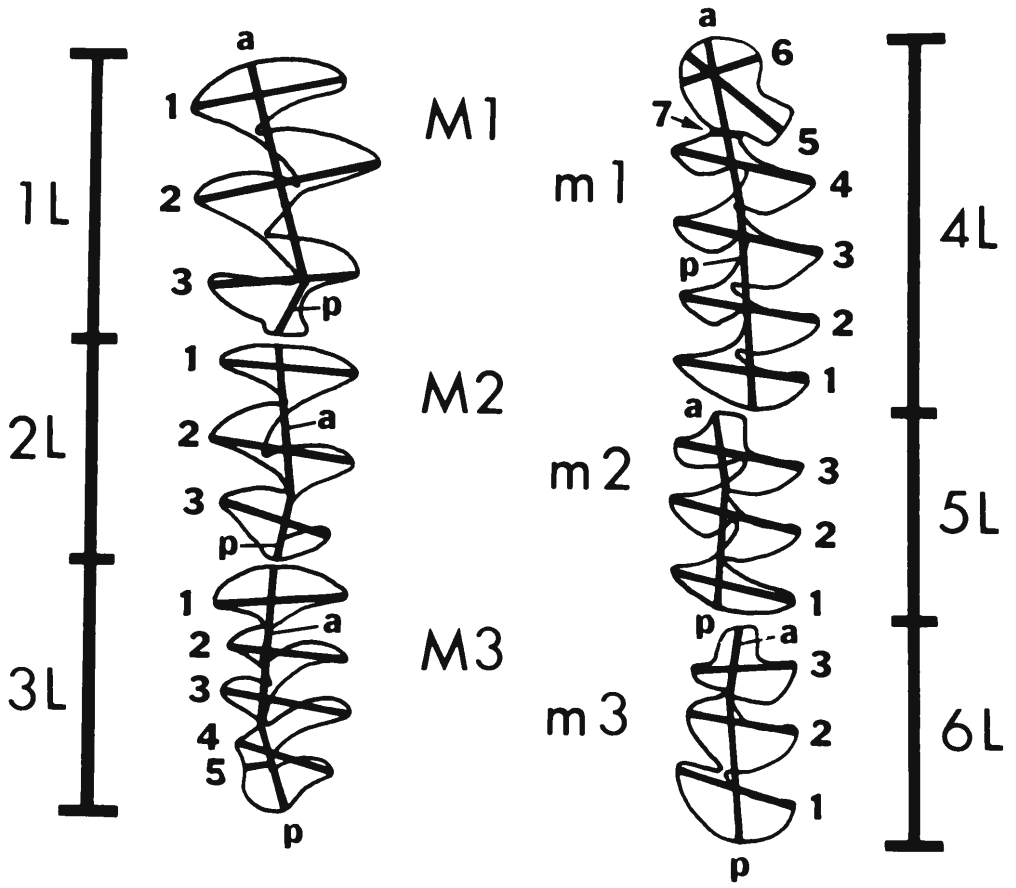


Fig. 2. Measurements recorded from photographs of upper and lower molar tooththrows (modified from Guthrie, 1965).

tests of the differences between percentages for character states in pairs of samples (Sokal and Rohlf, 1969:608).

Frequency data for occlusal patterns were subjected to a multivariate analysis of distance (Grewal, 1962; Berry and Rose, 1975). Results were arranged as a matrix of calculated "measures of divergence" between samples. Average measures of divergence for each population were regarded as "measures of uniqueness." This technique has been used as an estimate of genetic divergence between populations (see Berry and Rose, 1975, for a summary of the literature). All statistical analyses were completed at the Indiana State University Computer Center, primarily with programs contained in SPSS 6000 (Nie *et al.*, 1975).

## RESULTS

Analysis of age covariation among measured characters is summarized in Table 1. Eight factors accounted for 76.3 percent of the total variance of the pooled sample. Factors one and two probably represented age covariation. Characters 3L and 3a loaded strongly on factor two; however, none of the measurements of posterior length of the upper molars (1p, 2p, or 3p) loaded strongly on this axis. Factor two apparently represented the stable anterior length of the upper molars and, consequently, the anterior length of M3 rather than the rapidly evolving posterior length. In fact, the posterior length of M3 (character 3p) loaded only with characters 3L, 6L, and 6p on factor five. This relationship was expected because these measures are from occluding teeth. Character 4L loaded strongly with character 5L on factor three but, as with characters 3L and 3a, this axis represented the stable lengths of these teeth rather than the evolving lengths. Others of Guthrie's evolving characters (posterior measures of the upper molars and anterior measures of the lower molars) were distributed among the remaining factors, but in no instance did they covary with a predetermined age measure.

Because this method is somewhat subjective, the results might be interpreted differently. For example, certain interrelationships among length measures and between length measures and other characters might reflect differences in size among populations rather than differences in age. The results do not demonstrate that all samples were of uniform age structure but, simply, that certain characters vary independently of age.

**Mensural Variation.**—The posterior ends of the upper molars and the anterior ends of the lower molars were the most variable parts of the teeth in all samples. These findings are consistent with those of Guthrie (1965) and Martin (1973). Coefficients of variation for 42 measurements in each of the seven samples are listed in Table 2. Examination of the data reveals that populations exhibiting the highest coefficients of variation for Guthrie's evolving characters did not necessarily exhibit highest coefficients of variation for stable characters. For example, samples from Tolland County and Barnstable possessed the highest coefficients of variation for evolving characters but were among the least variable in stable characters. Conversely, other samples (especially those from Nantucket and Muskeget islands) tended to be more variable with regard to stable dental characters and less variable with regard to

TABLE 1.—Factor loadings for varimax solution.

Character	Communality	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8
1L	0.864	0.062	0.589	0.346	0.597	0.034	0.162	0.051	0.093
1a	0.722	-0.118	0.614	0.434	0.301	0.009	0.129	-0.015	0.187
1p	0.681	0.187	0.113	0.018	0.742	-0.056	0.198	0.161	-0.117
1l	0.710	0.540	0.269	-0.033	0.414	0.027	0.341	-0.207	-0.115
12	0.586	0.406	0.433	0.273	0.381	0.097	0.057	0.035	0.030
13	0.817	0.380	0.551	0.313	0.494	0.107	0.045	0.019	0.110
2L	0.881	0.255	0.600	0.294	0.540	0.192	0.182	0.069	0.044
2a	0.753	0.206	0.723	0.252	0.161	0.190	0.193	0.090	0.132
2p	0.702	0.256	0.160	0.184	0.739	0.113	0.064	0.041	-0.113
2l	0.754	0.433	0.604	0.172	0.393	-0.002	0.084	0.065	-0.071
22	0.813	0.399	0.740	0.206	0.134	0.140	-0.039	0.157	0.027
23	0.664	0.305	0.283	0.047	0.555	0.398	0.059	-0.127	0.046
3L	0.917	0.104	0.659	0.182	0.015	0.657	0.063	0.061	-0.002
3a	0.758	0.147	0.755	0.159	0.046	0.307	0.066	0.179	0.084
3p	0.652	0.161	0.249	0.077	0.015	0.723	0.054	-0.094	-0.151
3l	0.781	0.471	0.604	0.088	0.277	0.178	0.277	0.044	-0.013
32	0.717	0.425	0.679	0.082	-0.097	0.221	0.023	0.097	0.015
33	0.800	0.550	0.589	0.027	0.231	0.277	0.127	0.026	0.053
34	0.471	0.287	0.196	-0.142	0.223	0.398	0.268	-0.019	-0.222
35	0.598	0.050	-0.096	-0.122	0.318	-0.037	-0.090	0.662	0.149
4L	0.924	0.329	0.313	0.678	0.008	0.041	0.497	0.072	-0.061
4a	0.851	0.308	0.161	0.238	0.035	0.041	0.818	0.013	-0.034
4p	0.881	0.299	0.342	0.815	0.017	0.014	0.021	0.086	-0.038
4l	0.678	0.679	0.061	0.216	0.356	0.176	0.080	0.056	-0.004
42	0.830	0.650	0.366	0.408	0.177	0.090	0.116	0.171	0.160
43	0.850	0.685	0.300	0.346	0.174	0.123	0.174	0.191	0.243
44	0.859	0.472	0.192	0.321	0.255	0.008	0.285	0.034	0.590
45	0.847	0.258	-0.047	0.056	0.420	0.257	0.721	-0.027	0.115
46	0.680	-0.120	0.171	-0.220	0.260	0.379	0.465	0.236	0.324
47	0.428	0.068	0.163	-0.101	-0.294	-0.131	0.101	0.520	-0.040
5L	0.908	0.394	0.323	0.721	0.299	0.127	0.090	0.118	-0.016
5a	0.714	0.436	0.350	0.202	0.215	-0.052	0.155	0.522	-0.116
5p	0.839	0.190	0.146	0.777	0.206	0.225	-0.020	-0.266	0.117
5l	0.710	0.636	0.223	0.231	0.346	0.141	0.198	0.151	0.027
52	0.840	0.676	0.315	0.375	0.096	0.171	0.050	0.251	0.199
53	0.796	0.635	0.278	0.382	0.141	0.266	0.183	0.163	0.136
6L	0.878	0.398	0.222	0.370	0.147	0.588	0.199	0.323	0.150
6a	0.682	0.230	0.237	0.220	0.027	0.260	0.007	0.673	-0.061
6p	0.775	0.389	0.154	0.355	0.142	0.586	0.239	0.015	0.234
6l	0.816	0.603	0.279	-0.004	0.131	0.330	0.450	0.113	0.181
62	0.854	0.657	0.334	0.223	0.005	0.284	0.320	0.160	0.227
63	0.773	0.191	0.106	-0.011	-0.243	-0.068	-0.011	-0.013	0.813

TABLE 2.—*Coefficients of variation for dental measurements of samples from six populations of Microtus pennsylvanicus and M. breweri. Measurements are identified in Fig. 2. Abbreviations and sample sizes are as follows: TC = Tolland County (Mainland) (31); BA = Barnstable (Cape Cod) (15); NON = Nonomasset Island (27); MV = Martha's Vineyard (13 museum specimens; 23 lower and 18 upper molar tooththrows from owl pellets); NI = Nantucket (26); MI = Muskeget Island (18); BI = Block Island (20).*

Character	TC	BA	NON	MV	NI	MI	BI	Character	TC	BA	NON	MV	NI	MI	BI
1L	4.6	5.9	5.4	6.1	5.8	6.0	5.3	4a	7.8	7.0	6.2	7.4	8.5	9.8	6.5
1a	4.4	6.2	6.6	5.5	6.2	9.8	9.3	4p	5.6	5.1	6.6	7.3	6.4	5.5	8.3
1p	10.4	16.9	10.7	11.2	10.4	9.5	8.3	41	4.7	7.3	10.4	6.8	7.3	6.3	6.7
11	5.5	7.4	7.0	5.7	6.8	7.5	5.9	42	4.8	5.5	5.4	6.4	8.4	6.6	7.1
12	5.5	4.7	5.9	5.0	6.3	5.3	10.0	43	4.7	3.6	5.4	5.4	6.8	7.4	5.8
13	5.9	6.8	4.6	5.4	6.8	6.5	6.2	44	5.7	5.0	6.2	5.9	8.1	7.7	5.6
2L	5.1	7.4	5.0	5.6	7.7	7.4	5.8	45	7.8	8.3	5.5	9.5	10.0	10.7	8.0
2a	4.6	7.4	6.5	5.8	7.7	9.4	6.6	46	18.0	13.7	8.2	14.4	12.0	14.9	14.9
2p	8.7	14.1	11.4	9.8	9.7	8.9	8.1	47	27.3	19.8	14.7	13.3	19.4	20.2	23.0
21	6.3	9.9	7.3	6.8	6.8	7.0	6.7	5L	5.2	7.6	6.1	5.5	6.7	5.5	5.7
22	5.5	4.3	5.6	5.2	6.9	7.2	5.6	5a	7.9	9.9	12.4	7.6	9.8	8.0	6.1
23	8.6	6.8	7.6	8.7	7.0	7.9	6.6	5p	5.4	7.4	10.9	6.2	6.5	4.5	6.9
3L	8.3	9.7	6.2	7.2	9.6	9.4	6.3	51	6.7	8.4	6.4	7.5	6.6	4.7	7.1
3a	8.2	8.2	10.3	7.3	11.4	10.4	9.2	52	5.9	3.3	6.4	8.2	7.4	6.4	6.6
3p	14.4	14.0	10.6	10.6	12.5	10.2	8.5	53	6.5	8.8	6.6	7.5	8.3	7.4	7.0
31	7.6	10.5	7.5	6.5	9.1	8.4	6.3	6L	8.3	7.6	10.6	9.1	9.6	11.3	7.0
32	7.3	5.4	8.1	6.9	13.8	9.0	10.1	6a	12.6	17.6	17.3	12.0	13.1	12.4	9.0
33	8.0	5.4	8.7	7.4	8.5	7.2	7.5	6p	9.4	6.7	12.0	10.0	10.4	11.8	7.8
34	11.5	7.6	11.0	7.6	9.5	8.6	7.9	61	8.2	4.4	6.9	8.2	10.5	11.4	7.9
35	19.6	20.1	11.5	16.5	13.6	11.9	12.2	62	8.0	5.0	7.5	9.6	12.4	9.7	8.2
4L	5.1	4.4	4.5	5.1	6.8	7.0	6.4	63	9.5	8.8	10.7	9.9	12.5	7.2	9.2

rapidly evolving characters. Accordingly, comparisons of differences in inter-population variation were based on this dichotomy.

Results of Wilcoxon's signed ranks tests of differences in variability between pairs of populations are given in Table 3. For the purpose of these tests, characters 1p, 13, 2p, 23, 3p, 34, 35, 4a, 45, 46, 47, 5a, 53, 6a, and 63 (posteriors of uppers and anteriors of lowers) were considered as evolving. The remaining 27 characters (anteriors of uppers and posteriors of lowers) were considered as stable. Although the samples from Nantucket and Muskeget islands were more variable overall ( $P \ll 0.01$  and  $P = 0.056$ , respectively) than the sample from Tolland County, the differences in variability were not the result of increased variation of evolving characters. In fact, only one sample differed significantly from the sample from Tolland County with regard to variability of evolving characters (the sample from Block Island was less variable than the sample from Tolland County,  $P \ll 0.01$ ). The greater overall variation in samples from Nantucket and Muskeget islands resulted from greater variation in stable dental characters. All samples (excepting the one from Barnstable) were significantly more variable with regard to stable characters than was the sample from the mainland (see Table 3 for significance levels).

Comparisons of intrapopulation variation among island populations revealed that the samples from Nonomesset and Muskeget islands did not differ ( $P \gg 0.10$ ) in variability of either stable or evolving characters from the sample from Nantucket Island. However, samples from Martha's Vineyard and Block Island were less variable than the sample from Nantucket with regard to both evolving ( $P \ll 0.05$  and  $P \ll 0.01$ , respectively) and stable ( $P \ll 0.01$  and  $P \ll 0.05$ , respectively) characters. A final Wilcoxon test comparing variability in samples from Martha's Vineyard and Block Island revealed that the sample from Martha's Vineyard was the more variable ( $P \ll 0.05$ ) with regard to evolving characters and did not differ from the sample from Block Island with regard to stable characters.

**Variation in Occlusal Patterns.**—Because the second and third lower molars did not vary appreciably in any of the samples, the following results pertain largely to M1, M2, M3, and m1. Line drawings that depict the range of variation in occlusal patterns of these teeth in each sample are shown in Figures 3-6. These drawings represent (from left to right) a gradation from simplest to most complex forms within each sample. Most of the variation in occlusal patterns can be described in terms of 1) the number of closed triangles or 2) the number of salient and re-entrant angles (peripheral enamel complexity). In many individuals closure of triangles was not correlated strongly with peripheral enamel complexity (see particularly Fig. 3, BI, b and d; Fig. 3, MI, a-h; and Fig. 4, MI, a and b). Accordingly, structural dental traits were selected to enable quantification of these categories of variation.

Table 4 lists frequencies of occurrence within each sample of eleven structural dental traits. Because these traits were selected as measures of occlusal complexity, higher percentages indicate relative advancement beyond a presumed primitive condition. Nine of eleven characters demonstrated significant differences among samples in frequency of occurrence. Frequencies for characters 6 and 8 each differed only in one population; therefore, R X C tables were not computed for those characters. Tests of equality of percentages

**TABLE 3.—Results of Wilcoxon's signed ranks tests to determine variability differences for selected character sets among populations. All comparisons are made with Tolland County. Significant probabilities are starred. (+) indicates that a population is more variable than the population from Tolland County for a given character set. (-) indicates lower variability.**

<i>Characters compared</i>	<i>BA</i>	<i>NON</i>	<i>MV</i>	<i>BI</i>	<i>NI</i>	<i>MI</i>
All variables	▶0.10	▶0.10	▶0.10	▶0.10	◀0.01*(+)	0.056*(+)
All variables on M3 and m1	▶0.10	▶0.10	▶0.10	▶0.10	▶0.10	▶0.10
All variables on M1, M2, m2, and m3	▶0.10	◀0.01*(+)	◀0.01*(+)	▶0.10	◀0.01*(+)	◀0.05*(+)
Posteriors of uppers and anteriors of lowers	▶0.10	▶0.10	▶0.10	◀0.01*(-)	▶0.10	▶0.10
Anteriors of uppers and posteriors of lowers	▶0.10	◀0.01*(+)	◀0.05*(+)	◀0.01*(+)	◀0.01*(+)	◀0.01*(+)

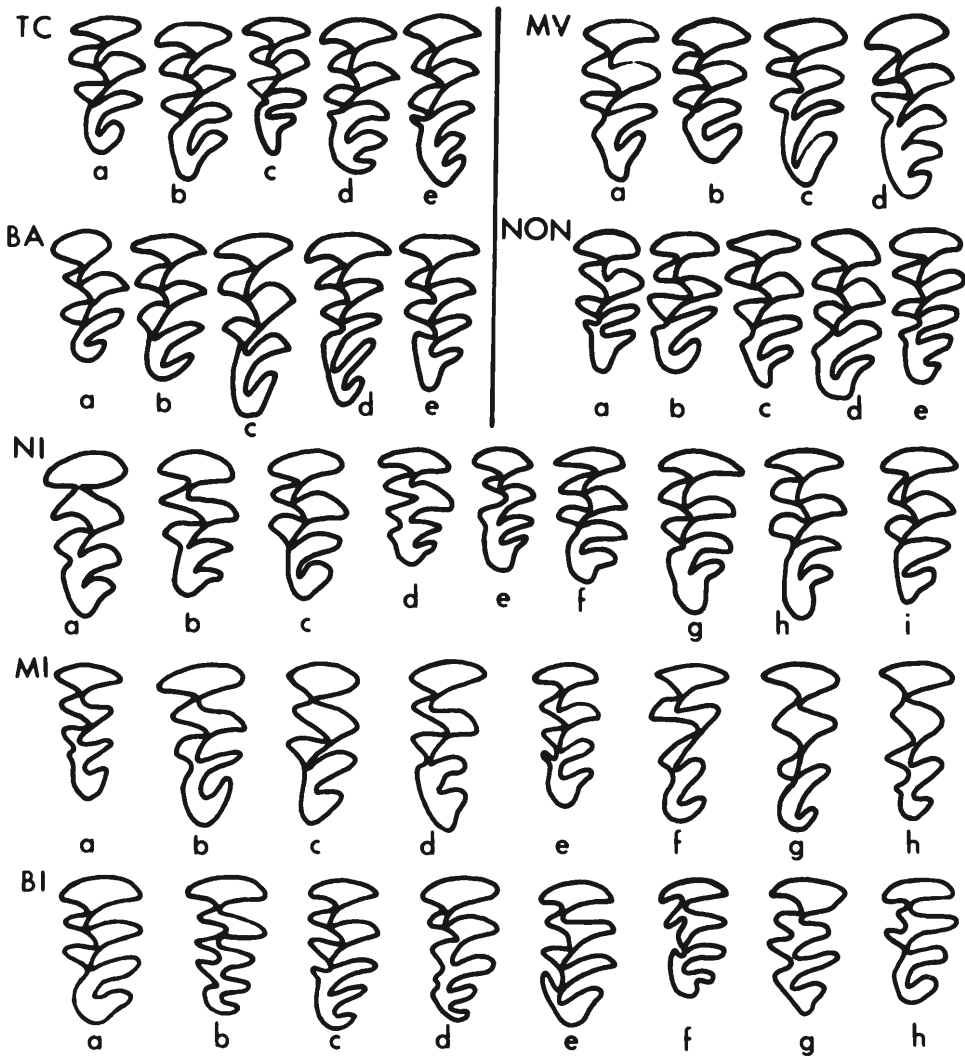


Fig. 3. Line drawings that depict the range of morphological variation of third upper molars in each of seven samples. Abbreviations are listed in the text.

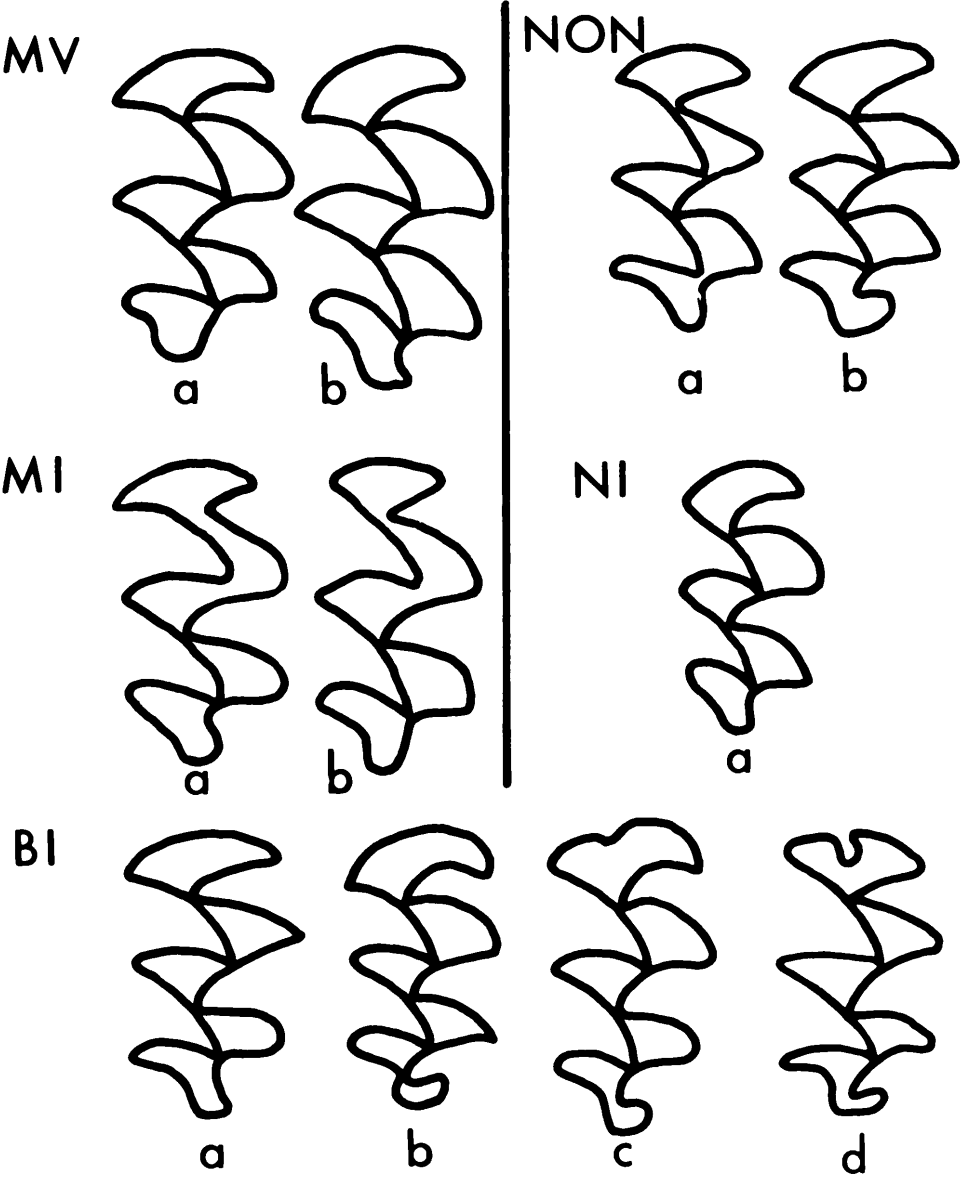


Fig. 4. Line drawings that depict the range of morphological variation of first upper molars in each of five samples. Abbreviations are listed in the text.



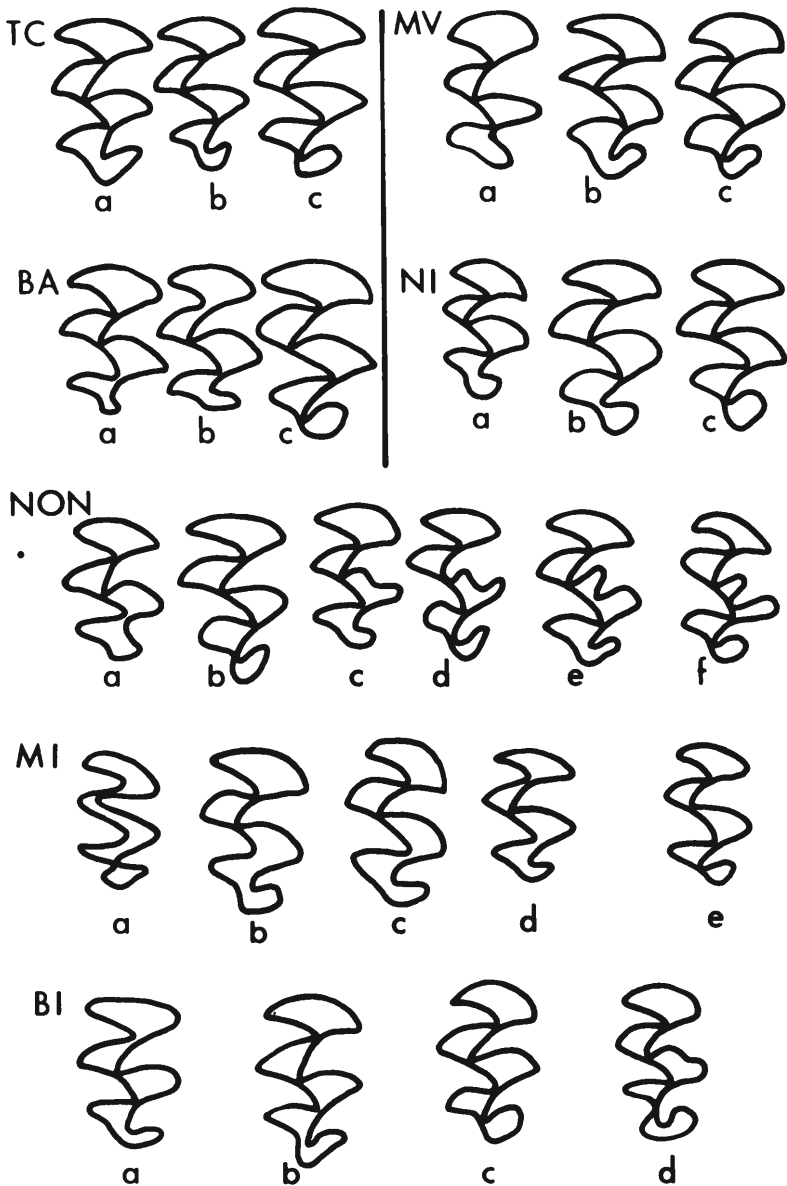


Fig. 5. Line drawings that depict the range of morphological variation of second upper molars in each of seven samples. Abbreviations are listed in the text.

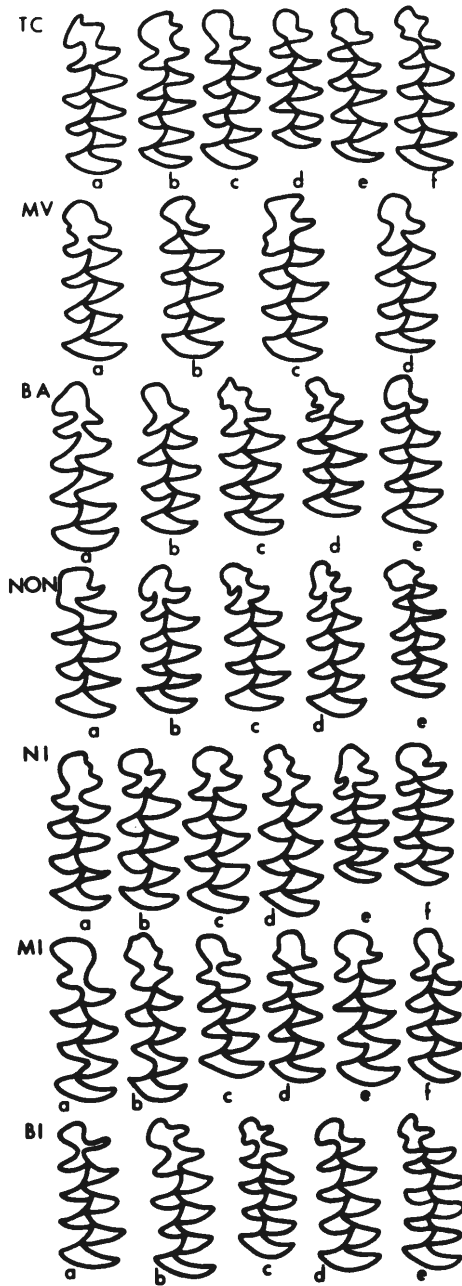


Fig. 6. Line drawings that depict the range of morphological variation of first lower molars in each of seven samples. Abbreviations are listed in the text.

were performed to determine whether frequencies for characters in other samples differed from those for characters in the sample from Tolland County. Significance levels are listed below the frequencies in Table 4; summary data for significant differences are given at the bottom of Table 4.

Dentitions of individuals from Barnstable and Martha's Vineyard were similar to those of individuals from Tolland County. The range of variation in the third upper molar in the mainland sample is shown in Fig. 3, TC. Only 8 percent of the individuals from Cape Cod demonstrated the complex form of the third upper molar (Table 4, character 2; Fig. 3, BA, d), whereas 39 percent of the individuals from the mainland possessed a well developed posterior loop (Fig. 3, TC, d and e). The sample from Barnstable exhibited slightly (but not significantly) reduced dental complexity in five of the remaining characters. Conversely, the sample from Martha's Vineyard contained significantly more individuals with complex third upper molars than did the sample from the mainland (Table 4, characters 3 and 4; see Fig. 3, MV, a). The range of variation found in samples from both Barnstable and Martha's Vineyard was within the continuum of variation demonstrated by the sample from the mainland.

The anterior edge of the second alternating triangle on M2 was distinctive in 7 percent of the individuals from Nonomasset Island (Table 4, character 6; Fig. 5, NON, c-f). This character state was not present in any other sample but has been reported to occur in *Microtus chrotorrhinus* (Martin, 1973) and *M. oeconomus* (Jorga, 1974). Third upper molars and first lower molars of individuals from Nonomasset Island were simpler than those of individuals from Tolland County (Table 4, character 2; Fig. 3, NON, a-d; character 9, Fig. 6, NON, a-d). On the other hand, the first upper molars of specimens from Nonomasset were somewhat more complex than those of specimens from the mainland (Table 4, character 7; Fig. 4, NON, b). Overall, however, dentitions from the population on Nonomasset Island were simpler than those from the mainland population.

The sample from Block Island exhibited more variation in occlusal pattern than any other sample and tended toward increased occlusal complexity. Peripheral enamel complexity and closure of triangles were not strongly correlated in the sample from Block Island. In some instances, teeth that were complex with regard to peripheral enamel pattern possessed only one closed triangle (see Fig. 3, BI, b and d). This relationship was particularly evident in third upper molars, which had significantly fewer closed triangles ( $P \ll 0.01$ ) but significantly more labial salients ( $P \ll 0.05$ ) than in the mainland sample. Other teeth from this sample tended toward increased complexity with regard to both peripheral pattern and closure of triangles (Fig. 4, BI, c and d; Fig. 5, BI, c and d; and Fig. 6, BI, e). In fact, the sample from Block Island contained more individuals with complex first lower molars (Table 4, character 10) and more individuals with highly developed posterior loops on the first upper molars (Table 4, character 7) than did any other sample.

Dentitions from Nantucket Island were simple more frequently than complex (Table 4, characters 2, 9, 10, and 11) although a few complex forms were found (Fig. 4, NI, c; Fig. 6, NI, e and f). The population from Nantucket had the least complex dentitions of any of the populations sampled excepting that on Muskeget.

The most striking characteristics of the dentition in the sample from

TABLE 4.—Frequency expressed as percent occurrence of eleven structural dental characters in six populations of *Microtus pennsylvanicus* and *M. breweri*. Results of  $R \times C$  contingency test are tabulated in the last three columns. Probability levels of significant differences between the frequency of a character in a given population and the frequency of the same character in the population in Tolland County are listed below in individual frequencies; ns signifies no difference. Total number and net number of significant differences between a population and the mainland population are listed in the last two rows. An asterisk signifies sample size might be inadequate to state that significant differences exist at the level indicated.

Character	TC	BA	NON	MV	BI	NI	MI	G	X <sup>2</sup>	df	p
1) Three closed triangles on M3	84.7	85.8 ns	89.4 ns	93.0 ns	36.8 ◀0.01	79.4 ns	33.3 ◀0.01	65.978	18.548	6	◀0.005
2) Five lingual salients on M3	39.4	7.7* ◀0.05	11.1* ◀0.02	25.0 ns	25.0 ns	0.0 ◀0.001	0.0 ◀0.001	25.264	18.548	6	◀0.005
3) Four labial salients on M3	46.4	64.3 ns	50.0 ns	73.3* ◀0.05	75.0* ◀0.05	43.4 ns	26.7 ns	15.496	14.449	6	◀0.025
4) M3 extended posteriorly	57.7	38.5 ns	55.6 ns	70.9 ◀0.02	31.6 ns	27.3 ns	7.6 ◀0.001	36.470	28.300	12	◀0.005
5) Separate posterior loop on M2	57.7	35.7 ns	40.8 ns	64.4 ns	58.0 ns	74.0 ns	16.7* ◀0.001	24.790	18.548	6	◀0.005
6) Second lingual salient bisected on M2	0.0	0.0 ns	7.1* ◀0.05	0.0 ns	0.0 ns	0.0 ns	0.0 ns	—	—	—	—
7) Posterior loop extended lingually on M1	21.4	42.9 ns	55.6* ◀0.02	18.5 ns	100.0 ◀0.001	20.7 ns	5.6 ns	61.932	18.548	6	◀0.005
8) Three or more closed triangles on M1	100.0	100.0 ns	100.0 ns	100.0 ns	100.0 ns	100.0 ns	66.7 ◀0.001	—	—	—	—
9) More than five closed triangles on m1	18.5	13.3 ns	0.0 ◀0.01	11.8 ns	10.5 ns	0.0 ◀0.01	0.0* ◀0.01	61.732	45.558	24	◀0.005
10) More than five lingual salients on m1	24.2	6.7 ns	24.0 ns	14.8 ns	58.9* ◀0.05	4.3* ◀0.05	0.0 ◀0.01	27.500	18.548	6	◀0.005
11) More than four labial salients on m1	14.3	6.7 ns	4.0 ns	2.9 ns	5.6 ns	0.0 ◀0.01	15.8 ns	24.790	18.548	6	◀0.005
Total number of significant frequency differences		1	4	2	4	4	7				
Net number of significant differences (negative values indicate reduced complexity)		-1	0	+2	+2	-4	-7				

TABLE 5.—*Matrix of measures of divergence (see Berry and Rose, 1975) for six populations of Microtus pennsylvanicus and M. breweri. Calculations are based on frequency of occurrence of eleven structural dental traits listed in Table 4. The final column lists uniqueness values that are, simply, arithmetic averages of the divergence measures. Higher values of uniqueness indicate that a population is more distinct.*

						Uniqueness	
						TC	12.4
						BA	9.9
						NON	12.2
						MV	13.5
						BI	18.4
						NI	12.6
MI	13.7	21.1	19.6	17.1	12.9	17.1	16.9
		19.5	11.6	11.4	8.3	11.3	
		20.6	15.4	14.5	19.1		
		12.3	9.0	7.7			
		5.6	10.2				
		8.8					

Muskeget Island were a prevalence (67 percent) of individuals with open triangles on M3 (Fig. 3, MI, b and d-h) and an absence of complex forms. Additionally, the dentition in the sample from Muskeget consistently exhibited lower frequencies of advanced characteristics than did the other sample (Table 4). Examination of photographs of the dentitions of the three syntypes of *M. breweri*, however, revealed that the sample studied from Muskeget was comprised of individuals with somewhat simpler dentitions than those of the syntypes. Two of the syntypes had two closed triangles on M3, whereas in the sample studied all individuals had either one or none. Also, the syntypes had more triangles on both m1 and M1 than did specimens in the sample studied.

Table 5 lists results of multivariate distance statistics calculated with frequency data from Table 4. The greater the measure of divergence between two samples, the greater the "distance" between those populations. From the matrix in Table 5, it is evident that the populations inhabiting Block and Muskeget islands were the most unique dentally of the seven populations sampled. The population in Tolland County and those on Barnstable, Nonomesset Island, and Martha's Vineyard were closely related to one another and less closely related to the other insular populations. The population on Muskeget Island was closely related to those on Barnstable and Nantucket Island, whereas the population on Block Island was not closely related to any other population.

## DISCUSSION

The paleontological record for microtine rodents in North America is extensive (Zakrzewski, 1967; Guilday, 1971; Guthrie, 1971; Guilday and Hamilton, 1973; Hibbard *et al.*, 1978; Martin, 1979; and others). The consensus of these authors was that evolution in the Microtinae has graded progressively toward more complex dentitions. However, Guthrie (1971) asserted that there have been numerous evolutionary "flats" and reversals during the microtine radiation. In this regard, we contend that the dentition in continental populations of *M. pennsylvanicus* has changed little since the Wisconsin glaciation. This contention is supported by Martin's (1973) data, which revealed no marked differences in dentitions of three contemporary species of *Microtus* (including *M. pennsylvanicus*) and late Pleistocene representatives of the same taxa. The only evidence found in the literature for post-glacial grade evolution of *M. pennsylvanicus* is that of Guilday (1971), who proposed that post-glacial climatic moderation has resulted in a slight increase in overall size of meadow voles in Pennsylvania.

Work by Hibbard (1956), and more recently by McMullen (1978), demonstrated that dentitions of fossil meadow voles of late Illinoian age were at least as complex as those of Recent populations. In fact, McMullen (1978) found a frequency of occurrence (34 percent) of more than five closed triangles on m1 in late Illinoian voles that was higher than those exhibited by any of our Recent samples (see Table 4). It is apparent that the continuum of variation exhibited by the sample from Tolland County has been in existence at least since the Wisconsin. Accordingly, it is reasonable to designate the population inhabiting Tolland County as most nearly like the ancestral form and to use it as a reference with regard to Recent dental evolution in the remaining samples.

The geology of southern New England is known sufficiently (Schafer and Hartshorn, 1965; Emory, 1967; Flint, 1971) to permit the assumption that divergence of the populations studied has occurred since the end of the Wisconsin glacial period. The coastal islands of southern New England are remnants of a Wisconsin terminal moraine (Weatherbee *et al.*, 1972). Wetzel (1955), in his analysis of geographic variation of *Synaptomys cooperi*, suggested that the exposed continental shelf served as a periglacial refugium during the Wisconsin. According to Wetzel's hypothesis (as refined by Starrett, 1958, and Youngman, 1967), populations of mammals that now occupy the coastal islands of southern New England at one time were part of a large, panmictic population which inhabited periglacial and more southerly regions of the continental shelf. As the glaciers receded and sea level rose, islands were formed and populations of *Microtus* became isolated. Continued post-glacial rise of sea level has substantially decreased the size of the islands under study, as documented for Muskeget Island (Weatherbee *et al.*, 1972).

Starrett (1958) used hydrographic data to propose a sequence for formation of the islands under consideration in this study, excepting Block Island. Martha's Vineyard, Nantucket, and Muskeget probably separated, as a unit, from the mainland approximately 10,000 years ago. Martha's Vineyard separated from Nantucket and Muskeget 4,000-5,000 years ago, whereas Nonomasset and Muskeget islands became isolated 2,000-3,000 years ago. Block Island possibly separated from Long Island (Ralph M. Wetzel, pers. comm.), the mainland, or both 2,000-6,000 years ago.

Currently, gene flow is likely only between populations inhabiting Tolland County and Barnstable; the canal separating the mainland from the Cape Cod Peninsula probably is not a totally effective dispersal barrier (see Fig. 1). On the other hand, strong and misdirected currents act to restrict opportunities for colonization of any of the islands (see Tamarin, 1978, for a reference to Muskeget) and, accordingly, it is not likely that colonizers reach the islands unless introduced accidentally by man (as suggested by Wheeler, 1956, for Block Island).

At least part of the similarity in dental morphology and mensural variation exhibited by adjacent populations may be attributed to recency of land connections. For example, the population on Nonomasset Island seems closely related to populations in Barnstable and Tolland County (Tables 4 and 5). However, other factors, particularly vegetation and ecological interaction, probably are more important determinants of dental variation.

Appreciable adjustments in the ecology of insular populations can occur as those populations adapt (under reduced competition) to utilize unexploited niches. Tamarin (1977a; 1977b; 1978) has extensively studied the beach vole on Muskeget Island. Compared to its mainland counterpart, the beach vole exhibits larger size, lowered reproductive output, increased longevity, and an absence of cyclic fluctuations in density. These observations led Tamarin to propose that this island's species was K-selected. It is not known whether taxa inhabiting the other islands of this study are K-selected, but this is conceivable because all are known (unpublished data; Starrett, 1958) to be slightly larger than those on the mainland. If K-selection is the driving force of evolution in the island populations, then it is probable that two major selective responses are active: 1) a response to ecological release caused by an absence of competitors; 2) an adaptive change toward optimal utilization of available habitats.

Guthrie (1971) demonstrated, for several microtine taxa, that interspecific or intergeneric competition (or its absence) can elicit changes in complexity of enamel patterns. According to Guthrie's model, a species with complex teeth should develop less complex teeth when isolated on islands, primarily as a result of ecological release from competition. That insular populations may occupy broader ecological niches than their mainland counterparts has been documented by a number of researchers (see Rothstein, 1973, for a summary of the literature). However, niche breadth of an insular taxon also may depend on the ecological diversity of the island (see summary of literature by Rothstein, 1973) and the absolute size of the population. Therefore, taxa occupying large, ecologically diverse islands might be expected to exhibit greater dental variation than those inhabiting small, ecologically depauperate islands; indeed, taxa occupying small islands; might exhibit reduced variation because of genetic bottlenecks.

*Microtus pennsylvanicus* occurs sympatrically with another microtine, *Clethrionomys gapperi*, on the mainland and at least part (including Barnstable) of the Cape Cod Peninsula, but the latter is not present on any of the islands studied. According to Guthrie's (1971) model, insular populations of voles should exhibit simpler dentitions than populations inhabiting the mainland and the Cape Cod Peninsula. Indeed, the occlusal patterns exhibited by the sample from Muskeget Island are exceptionally simple and those from Nantucket are not nearly so complex as those in the population on the mainland. However, the population on Nonomasset Island exhibits dentitions that are only slightly (if at all) simpler than those found on the mainland, and

populations on Martha's Vineyard and Block Island have dentitions that are slightly more complex than those in the mainland population. Similarity of patterns exhibited by populations in Tolland County and Barnstable and on Nonomasset might simply reflect recency of sympatry, and a number of other factors can be employed to explain increased complexity of patterns from Martha's Vineyard and Block Island.

Because native forests were cleared on both Martha's Vineyard and Block Island, it is possible that development of a new grazing niche influenced a change from a relatively simple dentition to the more complex forms found today. It also is possible that intergeneric competition by sheep and cattle on those islands (Wheeler, 1956; Ogden, 1958; Kieth, 1969) selected for divergence toward more complex dentitions. Competition may be amplified by restrictions on dispersal, particularly on islands. Consequently, if competition indeed is a selective agent, then introductions of competitors might intensify selection and, conceivably, even reverse its orientation. Finally, multiple introductions (via agricultural products) from the mainland might have contributed to the diversity of morphological forms found in those populations (Wheeler, 1956). It is probable that increased occlusal complexity in populations inhabiting Martha's Vineyard and Block Island are the result of an interplay of all of these factors.

A fundamental precept of Guthrie's (1971) and Van Valen's (1965) hypotheses regarding expanded niches in insular taxa is that, in the absence of competitors, a species broadens its feeding niche in order to utilize the available habitats optimally. Riewe's (1973) investigation of foods consumed by *M. pennsylvanicus* on the islands of coastal Newfoundland supports this proposal; voles inhabiting those islands utilized 73 species of plants. However, Rothstein and Tamarin (1977) demonstrated that *M. breweri* consumes only 2 of the 131 species of plants recorded on Muskeget Island (Weatherbee *et al.*, 1972) and this taxon has the least complex dentitions of all the taxa studied. This specialization of food habits apparently is in contrast with Guthrie's proposal. However, the beach vole, although it is non-cyclic (Tamarin, 1977b), might have experienced several density bottlenecks (Kohn and Tamarin, 1978); it reportedly was driven nearly to extinction as a result of predation by feral cats in 1891, and was reestablished by a propagule of 26 individuals from the now extinct South Point Island (Miller, 1896; Tamarin and Kunz, 1974). Our evidence suggests the existence of one or more density bottlenecks sometime after the syntypes of *M. breweri* were collected. In this regard, Kohn and Tamarin (1978) found a higher than normal incidence of monomorphic gene loci in *M. breweri*. Whether bottlenecks decreased the diversity of foods consumed on Muskeget is not known conclusively but seems possible. Data on feeding habits were not available for the other insular populations studied.

None of the results of this paper firmly support or refute Guthrie's (1965) hypothesis that intensity of directional selection is directly related to variability of evolving characters. No differences between the variability of evolving characters in the population in Tolland County and in those represented by other samples (excepting that from Block Island) were found. The high variability of stable characters exhibited by populations on Nantucket, Muskeget, Nonomasset, and, to a lesser extent, Martha's Vineyard and Block Island suggest that selection in insular populations has favored the very parts of the teeth that Guthrie (1971) has shown to have high heritabilities. This is possible, but would require substantially more intense selection than



would similar changes in parts of the dentition which express lower heritability. Studies of heritability in insular populations of *Microtus* would be necessary to determine whether differences in variability are the result of natural selection or merely an ecophenotypic response to different insular habitats.

Because Guthrie (1965) examined only continental populations of *Microtus*, he hypothesized that the evolutionary trend in *M. pennsylvanicus* was toward greater complexity of occlusal pattern. However, if dentitions of voles inhabiting the islands sampled in this study are undergoing selective change, the results of this paper indicate that evolution of *M. pennsylvanicus* in insular populations apparently favors decreased rather than increased complexity and suggest that competition is the major determinant of dental complexity (Guthrie, 1971). In this regard, it is likely that most nominal taxa of fossil microtines were members of large, continental populations and would have experienced competition because populations occupying isolated, peripheral areas less likely would have been preserved. If complexity of dentition in microtines depends appreciably on the extent of competition, the fossil record thereby might be biased toward increased complexity. If grade evolution has occurred in the Microtinae, then the fossil record might underrepresent taxa with simple dentitions; conversely, if punctuated equilibria (Gould and Eldredge, 1977) is the principal mode of evolutionary change, then the evolutionary history of the Microtinae probably consisted of a number of isolated speciation events wherein breadth of the occupiable niche was more important than increased specialization for herbivory. New species of microtines, formed in isolation, would have been immediately tested by competition when they became sympatric with their parental populations. The proposal (Guthrie, 1971) that the microtine radiation progressed in only one direction (divergence from cricetine rodents) would imply that newly sympatric congeners would have been successful only if they could occupy an unexploited part of the grazing niche, and that evolution in the Microtinae was, at least in part, a response to increasingly specialized competitors.

## SUMMARY

Morphological and mensural variation in the molar dentitions of populations of *Microtus* inhabiting mainland, peninsular, and insular environments of southern New England were analyzed in order to assess Recent evolutionary trends in those populations. Occlusal patterns of voles from mainland Connecticut do not differ appreciably from those of representatives of late Illinoian age. However, all but the most ecologically diverse of the islands studied are inhabited by voles which exhibit reduced dental complexity. Dentitions of mainland voles have remained relatively constant because of the stabilizing effects of competitive interaction. Dentitions of insular taxa exhibit responses to the absence of competitors and to selection which favors broad ecological niches.

No conclusive evidence was found that either supports or refutes the relationship between intensity of selection and variability proposed by Guthrie (1965). Interpopulational differences were shown only for normally stable parts of the dentition and not for that portion of the dentition which normally is considered to be evolving rapidly. Heritability studies of dentitions of insular microtines would be of value in determining whether variability is influenced by intensity of selection in insular habitats. Finally, the implications of this investigation for studies of microtine evolutionary history are outlined.

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**Address of authors:** Museum of the High Plains, Fort Hays State University, 600 Park Street, Hays, KS 67601-4099.

**Present address of Weddle:** Department of Biology, Campbellsville College, Campbellsville, KY 42718.













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- Dr. James Murphy*
- Dr. Nancy Vogel*
- Dr. D. Dean Willard,*  
*Chairman*