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Investigation of the Classification of the Rodent Genus *Eumys* from the Middle Oligocene of the Big Badlands of South Dakota Using Multivariate Statistical Analysis

SUE VILHAUER ROSSER
UNIVERSITY OF WISCONSIN, MADISON

ABSTRACT

The dental morphology of 292 specimens of the cricetid rodent genus *Eumys* from the Lower Nodular Zone of the Big Badlands of South Dakota was studied. The study was undertaken to determine the number of species present in the genus *Eumys* during Middle Oligocene time in the area from which the specimens were collected. The *Eumys* specimens were divided qualitatively into three groups: an *E. elegans*-like group, an *E. obliquidens*-like group, and a group with both *E. elegans*-like and *E. obliquidens*-like characters. The same quantitative measurements were then taken on all three of these groups.

Three methods of statistical analysis were used to quantitatively analyze measurements taken on the *Eumys* teeth: multiple discriminant, principal component, and agglomerative analysis.

The results of the study clearly indicated that only one group was present in the *Eumys* specimens. The one group is considered to belong to the one valid species *Eumys elegans*.

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INTRODUCTION

The cricetid rodent genus *Eumys* has been somewhat of a puzzle to paleontologists for several decades. Variations in the dental morphology of *Eumys* have led students of the genus to claim as many as 13 separate species within it. Recently some paleontologists have begun to doubt the validity of some of the species of *Eumys*. This doubt is primarily due to the extensive collections of the genus available for comparative study and to knowledge about individual variation within a species population. Indeed, one student (Alker, 1967) has claimed that nine species should be considered simply as individual variants of one valid species, *Eumys elegans*. In an attempt to resolve this controversy, the dental morphology of the *Eumys* specimens from the collection at Field Museum of Natural History was studied to determine whether this genus is monospecific or polyspecific. This is a fairly large collection of over 400 specimens collected from one level, the Lower Nodular Zone, in the Big Badlands of South Dakota. A study of the collection might be expected to yield information as to the individual variation present in a limited geographical range and limited time geologically.

Three different methods of quantitative statistical analysis were carried out on the measurements taken on the *Eumys* teeth: Multiple discriminant, principal component, and agglomerative analysis. The results of these three methods were then synthesized to determine the number of valid species of *Eumys* present in the collection studied.

Materials.—The 292 *Eumys* specimens used in the study consisted of fossilized jaws and teeth from the collection of the Department of Geology of Field Museum of Natural History. All the specimens were collected by Dr. John Clark and his co-workers in the years 1962, 1968, and 1969 from the Lower Nodular Zone of the Brule Formation of the Big Badlands in Pennington County, South Dakota. The geology and paleoecology of this formation from which the specimens were taken have been described by Dr. Clark (Clark et al., 1967). The specimens come from seven separate collections. (The

raw data concerning number of specimens in each collection, year of collection, and exact site location along with the measurements of the specimens have been listed previously (Rosser, 1973).)

Of the 292 *Eumys* specimens, 56 are maxillae and 236 are mandibles. This is approximately a 1:4 ratio of maxillae to mandibles, a situation often found in collections of fossil rodent teeth (Wilson, pers. comm.). Although the sample contains two complete palates, no complete mandibles are included. There are also no upper and lower jaws in occlusion.

The 292 specimens include edentulous mandible fragments and specimens with one, two, or all three molars present. Only jaws with all three molars present were employed for purposes of statistical analysis. However, measurements were taken on the specimens containing one and two molars. These measurements are presented with the data from complete specimens (Rosser, 1973). The incisors were not measured.

One problem which always exists when one deals with fragmented fossil material is the correlation of number of individuals with specimen fragments. Compatible specimen fragments, particularly from a small animal such as *Eumys*, cannot be assumed to belong to the same individual even if found close to each other, since small fragments are easily transported by natural forces. Thus, each jaw fragment found was marked as a separate specimen. One cannot assume, therefore, that each of the 292 specimens studied represents an individual *Eumys*. Indeed it is quite possible that a left mandible containing only molars 1 and 2 may have, in fact, belonged to the same individual as a right mandible containing all three molars. This inability to correlate number of specimen fragments with number of individuals may present a serious problem when trying to do a population study of the entire fauna in which one seeks to obtain ratios between various genera. However, since the purpose of this study is to determine the number of species of *Eumys* present in the collection on the basis of characters of dental morphology, the problem of correlation of specimen fragments with number of individuals is not relevant here, although the lumping of right and left mandibular rami may result in a lowered variance as a result of some specimens making a double contribution.

A second problem, which is of relevance in this study, was caused by tooth wear. Only 45 of the 52 mandibles containing three molars and 11 of the 13 maxillae containing three molars were usable for

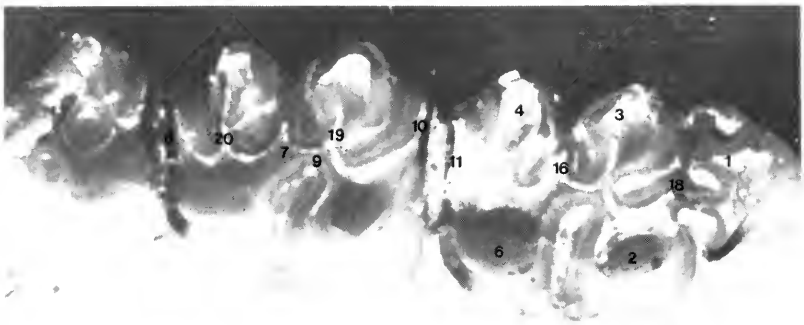


FIG. 1. Upper teeth of *Eumys*.

Key to Figures 1 and 2.

Cusp or other feature:	Lower teeth	Upper teeth
1	Anteroconid	Anterocone
2	Protoconid	Protocone
3		Paracone
4	Metaconid	Metacone
5	Entoconid	
6	Hypoconid	Hypocone
7	Mesoconid	Mesocone
8	Posteroconid	Posterocone
9	Mure	Mure
10	Anterior cingulum	Anterior cingulum
11	Posterior cingulum	Posterior cingulum
12	Metalophulid I	
13	Metalophulid II	
14	Hypolophulid I	
15	Hypolophulid II	
16	Mesolophid	Mesoloph
17	Posterior arm of protoconid	
18	Protolophid	Protoloph
19		Paraloph
20		Transverse metaloph

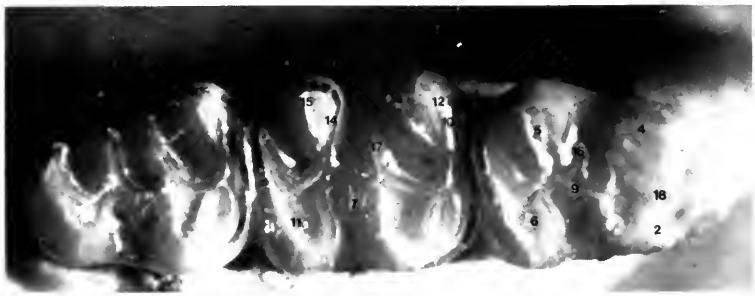


FIG. 2. Lower teeth of *Eumys*.

the final statistical analysis; the other nine specimens were too badly worn to allow complete measurements to be taken on them.

Wear greatly influences dental patterns in cricetids, as in most other rodents. With wear the cusp heights and relative relation of cusps may be altered, thus changing the details of the original pattern. Reconstruction of the original pattern is almost impossible when greatly advanced wear is present.

Wear may or may not influence tooth dimensions. It obviously influences height, which has been used (Fahlbusch, 1967) for diagnosis of European cricetids. Although the brachydont cricetid tooth is always somewhat smaller when greatly worn, moderate wear does not appreciably change the length and width dimensions of the tooth. All 45 mandibular and all 11 maxillary specimens used for statistical analysis were in stage D as designated by Alker (1968):

> D. Full maturity: M_3^3 lophs and lophids with occlusal surfaces less than 50% enamel-covered; M_1^1 and M_2^2 worn but dental pattern still showing original arrangement; and cusps not basined.

METHODS

Measurements.—Figures 1 and 2 of *Eumys* specimens show the terminology used in this study for upper (fig. 1) and lower (fig. 2) teeth. The terminology employed here is essentially that suggested by Wood and Wilson (1936) with minor modifications (see key to Figures 1 and 2).

Tables 1 and 2 list the points of measurement taken on the lower (1) and upper (2) *Eumys* teeth. Since the purpose of this study is to determine the number of species of the genus *Eumys* present in the collection of Field Museum, measurements were chosen that might best elucidate the possible differences between the Eumyine

TABLE 1

1. Anterior-posterior tooth row length
2. Anterior-posterior length of M_1
3. Width of M_1 at anteroconid
4. Width of M_1 at protoconid
5. Width of M_1 at hypoconid
6. Length of posterior arm of protoconid on M_1
7. Length of mesolophid on M_1
8. Anterior-posterior length of M_2
9. Width of M_2 at protoconid
10. Width of M_2 at hypoconid
11. Length of posterior arm of protoconid on M_2
12. Distance between lingual end of posterior arm of protoconid and entoconid on M_2
13. Length of mesolophid on M_2
14. Anterior-posterior length of M_3
15. Width of M_3 at protoconid
16. Width of M_3 at hypoconid
17. Length of posterior arm of protoconid on M_3
18. Distance between lingual end of posterior arm of protoconid and entoconid on M_3

TABLE 2

1. Anterior-posterior tooth row length
2. Anterior-posterior length of M^1
3. Width of M^1 at anterocone
4. Width of M^1 at protocone
5. Width of M^1 at hypocone
6. Length of mesoloph of M^1
7. Anterior-posterior length of M^2
8. Width of M^2 at protocone
9. Width of M^2 at hypocone
10. Length of mesoloph on M^2
11. Anterior-posterior length of M^3
12. Width of M^3 at protocone
13. Width of M^3 at hypocone

species. After studying all of the specimens carefully under a stereo dissecting microscope and comparing them with descriptions and diagrams of the various *Eumys* species described, it became clear that the lower molars of some individuals in the collection appeared to look like *E. elegans* Leidy. Some appeared to look like *E. obliquidens*, and some appeared to have characters of both of these species. None of the individuals in the collections seemed to resemble the description or diagrams of any of the other 10 *Eumys* species that have been described. A possible exception might have been *E. parvidens*, which can only be separated from *E. elegans* on the basis

of size, since *E. parvidens* is about 15 per cent smaller than *E. elegans* and has a primitive *E. elegans* pattern (Wood, 1937).

Preliminary studies, in which anterior-posterior tooth row length and width of M_2 were compared for all specimens, indicated that the specimens fit a normal distribution curve with respect to these two characters. The coefficients of variation of the measurements were approximately 5 per cent and the tests for goodness of fit gave a Chi-square that was not significant. Therefore it was concluded that no *E. parvidens* specimens were present in the sample.

A logical step thus seemed to be to choose the measurements of the molars of *Eumys* that would not only yield the usual information about tooth width and length, but that would also best take into account known differences between *E. elegans* and *E. obliquidens* as described by Leidy (1856), Cope (1884), Wood (1937), and Galbreath (1953). Although each measurement was taken on every specimen, the measurements were chosen with particular consideration for the following four characters which Galbreath (1953) used to distinguish *E. obliquidens* from *E. elegans*.

1. Mesolophid of M_1 should be as long or longer than the posterior arm of the protoconid in *E. obliquidens*. In *E. elegans* the mesolophid of M_1 should be shorter than the posterior arm of the protoconid.

2. Posterior arms of the protoconid on M_2 and/or M_3 extend postero-mesiad to unite with the entoconids on either or both teeth in *E. obliquidens*. In *E. elegans*, the posterior arm of the protoconid on M_2 and/or M_3 should turn forward and be reduced on either or both teeth.

3. In *E. obliquidens* the protoconid on M_1 is united to the anteroconid and and the metaconid remains free. In *E. elegans*, the protoconid on M_1 is united to the anteroconid and the arm from the metaconid is united to the protoconid crest.

4. In *E. obliquidens* the anterior lingual cingulum on M_1 is not reduced. In *E. elegans*, the anterior lingual cingulum on M_1 is reduced.

It should be noticed that the characters distinguishing *E. elegans* from *E. obliquidens* are in general relevant only to the lower teeth since the upper teeth have no equivalent of the posterior protoconid arm.

The measurements on all the *Eumys* specimens were taken using an optical micrometer on a binocular dissecting microscope. The specimens were placed on a piece of plasticene on the stage of the microscope. Each specimen was placed as nearly as possible in the center of the field of vision through the microscope.

Each specimen was placed so that the anterior end of M_1 and the posterior end of M_3 were in focus when the measurements for anterior-posterior tooth row length were taken. The two rows of maxillary molars are further apart than the two rows of molars in the mandible. Thus the tooth row of the maxilla slants inward and downward and runs diagonally so that the left M^1 and the right M^1 of the upper jaw are closer together than are the left and right M^3. In the lower jaw, the tooth row slants outward and upward, also running diagonally to match the corresponding maxillary row. Thus, it was impossible to have the entire tooth row in focus at one time. All length measurements of individual teeth and entire tooth rows were measured on a line parallel to the line of the tooth row from posterior to anterior, regardless of whether it was left, right, upper, or lower jaw. All width measurements were taken on a line perpendicular to the tooth row line from the lateral to medial side of the tooth. All measurements were taken to the nearest tenth of an optical micrometer unit.

The magnification under which the measurements were taken was such that the anterior-to-posterior-tooth-row length of *Eumys* was magnified 10 times, with 12.8 optical micrometer units equalling 1 mm. Measurements on individual *Eumys* teeth were magnified 20 times with 30.3 optical micrometer units equalling 1 mm.

Each specimen was completely measured once. Several months later all specimens were again measured without looking at the original measurements. If the two measurements of a particular character disagreed by more than 0.01 mm., the character was again measured until two measurements that were the same were obtained.

Statistical Analysis.—Three basic methods of statistical analysis were used to analyze the data obtained from measuring *Eumys* specimens. The three techniques are multiple discriminant, principal component, and agglomerative analysis. These methods were chosen primarily because they all are methods of multivariate analysis. All three methods allow one to assess the relationships of multiple measurements within multiple populations. The primary

restriction on these populations is that they must be assumed to be multivariate normal. If each population under consideration may be described by a series of q dimensions, then each individual within a population may be represented by a point in q-dimensional hyperspace, where each axis is equivalent to one univariate dimension. Individuals within the populations that are similar to each other with respect to many measurements will tend to group together around particular co-ordinates in the q-dimensional hyperspace and will have a characteristic dispersion around those co-ordinates. Thus a characteristic dispersion around those individuals clustering together around the same co-ordinates may be thought of as belonging to the same group, or in this case, species.

Although all three methods of analysis are multivariate, agglomerative analysis differs from the other two methods. Agglomerative analysis starts with individuals as separate entities and unites them according to their affinities. Multiple discriminant and principal component analysis both are divisive techniques which separate individuals and groups according to their differences. Several other basic differences exist among the three techniques, both in mathematical theory and practical application. For a theoretical and complete discussion of discriminant and agglomerative analysis see Sokal and Sneath (1963). For a discussion of principal components analysis and its association with the approach of numerical taxonomy see Gittins (1968).

DATA

Selection of Eumys *groups.*—After measurement and careful study of the *Eumys* specimens, they were divided into groups for statistical analysis. The divisions were based upon species as defined by the descriptions of the type specimens (Cope, 1884; Wood, 1937). Three groupings were made from the lower jaw specimens: Group 1 included 21 individuals fitting the description of *Eumys elegans* (Cope, 1884). Group 2 included nine individuals fitting the description of *Eumys obliquidens* (Wood, 1937). Group 3 included 15 individuals which could not be placed with certainty into either group 1 or group 2.

The individuals in group 3 seemed to possess some characters of the *E. elegans* type and some characters of the *E. obliquidens* type. A group 3 individual might have a combination of characters such as the following: Posterior arm of protoconid of M_2 extends postero-

mesiad to unite with entoconid (*E. obliquidens* character). Mesolophid on M_1 is shorter than posterior arm of protoconid (*E. elegans* character). Protoconid of M_1 is united to anteroconid and arm from metaconid is united to protoconid crest (*E. elegans* character). The anterior cingulum is not reduced (*E. obliquidens* character). It would be impossible to classify the above individual as either *E. elegans* or *E. obliquidens*.

The 11 complete *Eumys* maxillae all seemed to fit the criteria for *E. elegans*. Thus, they were randomly divided into two groups so that the statistical tests could be run. However, it should be noted that all the criteria that have been used to separate *E. elegans* and *E. obliquidens* are characters of the mandibular teeth alone. For example, the upper teeth do not even have a posterior protoconid arm. Furthermore, in the literature there are no examples of upper jaws belonging to *E. obliquidens*. Even though upper jaws are only one-third to one-fourth as common as lower jaws, it seems strange that no maxillae have been described. One may question whether the type specimens of *E. elegans* and *E. obliquidens* could be distinguished from each other on the basis of upper teeth. Only a specimen of *E. obliquidens* with upper and lower jaws in occlusion could answer this question with certainty.

Data Analysis.—The multiple discriminant computer program used for analysis in this study was a tape called Muldis written by Robert Avery of the University of Wisconsin Department of Economics. A few points about this program should be mentioned. Some of these are unique to the Muldis program; others are common in multiple discriminant analysis.

As with other multiple discriminant programs, the variance-covariance matrices of the groups are assumed to be equal in Muldis. Although this assumption may not always be true, Rao (1970) suggests that this is robust and probably will not affect the results even if the assumption is occasionally violated.

Like other multiple discriminant programs, Muldis requires that any individual considered must include all of the measurements being used. Thus, specimens for which a complete series of measurements are not available cannot be used.

A feature unique to Muldis is a stepwise procedure which permits evaluation of the importance to the overall discrimination of each variable when combined with other variables. This differs from the univariate ranking of the variable which may be obtained also. The

univarate ranking indicates how well each variable would discriminate if used alone.

Another feature unique to Muldis is the classification section. During the first part of Muldis, individuals with complete measurements are put into the program as predetermined groups. The centroids (co-ordinates of points in space), dispersion (variance), and various group statistics are calculated as a function of the discriminant analysis. The second part of Muldis has a classification section. Individuals are entered without being placed in groups. Muldis groups them on the basis of the criteria set up for each group in the multiple discriminant section of the program. *A priori* probabilities of particular group membership may be assigned. In this study the *a priori* probabilities of all groups were assumed to be equal. Thus, individual 28, which may have been entered with group 2 in the multiple discriminant part of the program, may be classified as belonging to group 3 by the classification section of Muldis because it has more features in common with the other members of group 3 than with those of group 2. Individuals not entered in the multiple discriminant section of Muldis may be entered in the classification section of the program and be assigned to one of the groups. The program then graphs the individuals entered as groups in the multiple discriminant section of Muldis in reduced space; it also graphs the individuals after classification in reduced space. Thus, the two graphs before and after classification can be compared.

Data sets on which multiple discriminant analysis was run.—

A. Forty-five complete *Eumys* mandibles with 18 variables each. They were entered as 30 individuals in two groups of nine and 21 individuals each in the multiple discriminant section. They were entered as 45 individuals in the classification section.

B. Eleven complete *Eumys* maxillae with 13 variables each. They were entered as 11 individuals in two groups of five and six individuals each in the multiple discriminant section. The classification section could not be run because the sample size was too small.

Data sets on which principal component analysis was run.—

The data for principal component analysis was run on a computer program written by T. F. Allen, S. M. Bartell, and W. Post of the University of Wisconsin Botany Department. The particular program used carried out an Orloci transformation of the data, which removes any influence on the analysis of differences in the numbers of attributes in different individuals. Since all the individuals com-

pared had the same number of attributes, the transformation should have made no difference.

The principal component program was run on the following data:

A. Forty-five complete *Eumys* mandibles with 17 variables each. (Measurement 1 of anterior-posterior tooth row length was deleted because it was known to be very highly correlated with anterior-posterior length of M_1, M_2, and M_3.)

B. Eleven complete *Eumys* maxillae with 12 variables each. (Measurement 1 was again deleted due to known correlation with other measurements.)

Data sets on which agglomerative analysis was run.—

The data for agglomerative analysis was run on a computer program written by S. M. Bartell of the University of Wisconsin Botany Department. It is essentially a modification of the Orloci agglomerative analysis. The program may be run in two forms, with or without an Orloci relativization of the data. The *Eumys* data was run using both forms of the program. Without the Orloci transformation absolute distances between the individuals are considered when calculating the D or D^2. Absolute distances reflect the differences among individuals in the absolute number of attributes measured. The Orloci transformation corrects for differences in number of attributes measured.

The agglomerative programs were run both with and without Orloci relativization on the following data:

A. Forty-five complete *Eumys* mandibles with 17 variables. (Measurement 1 was deleted because of known high correlation with other variables.)

B. Eleven complete *Eumys* maxillae with 12 variables. (Measurement 1 was deleted because of known high correlation with other variables.)

It was necessary to test to see whether or not the two groups into which the agglomerative program had placed the *Eumys* individuals in each case were valid groups statistically. Thus, a t-test had to be run. For the t-test to be performed, it was necessary to know the within-group variance of each of the groups. W. Post of the University of Wisconsin Botany Department wrote a variance program which takes the individuals clustered by a particular pass of the agglomerative program and calculates the within-group variance. The variance program was run on the following data:

1. Two agglomerative groups of 45 complete *Eumys* mandibles with 17 variables each with Orloci relativization.

2. Two agglomerative groups of 45 complete *Eumys* mandibles with 17 variables each without Orloci relativization.

3. Two agglomerative groups of 11 complete *Eumys* maxillae with 12 variables each with Orloci relativization.

4. Two agglomerative groups of 11 complete *Eumys* maxillae with 12 variables each without Orloci relativization.

RESULTS

Results of Multiple Discriminant Analysis:

A. *Multiple discriminant analysis and classification of 45 complete* Eumys *mandibles with 18 variables each.*—Figure 3 shows the results of the multiple discriminant analysis of group 1 (A), consisting of 21 individuals qualitatively identified as being *E. elegans*, and group 2 (B), consisting of nine individuals qualitatively identified as *E. obliquidens*. The centroid of group 1 is at .0393 and that of group 2 at .150; there is no overlap between the two groups. Since the first eigenvalue (axis) accounts for 100 per cent of the discrimination, the results were graphed in linear space.

Using the information from multiple discriminant analysis, it is possible to find the amount each variable contributes to separation of the groups. It is thus possible to rank the variables according to the importance of their contribution to the discrimination of groups. The technique for ranking is analogous to analysis of variance in that the within-group variance from the major diagonal of the pooled within-groups deviation sums-of-squares and cross products matrix is divided by the between-groups variance from the major diagonal of the pooled between-groups deviation sums-of-squares and cross products matrix for each variable. Using this method, the following ranking of variables was obtained; the first one listed is the most important and the last one listed is the least important:

*Variable 18—Distance from posterior arm of protoconid to entoconid on M_3

*Variable 12—Distance from posterior arm of protoconid to entoconid on M_2

Variable 13— Length of mesolophid on M_2

*Variable 11—Length of posterior protoconid arm on M_2

Variable 10—Width of M_2 at hypoconid

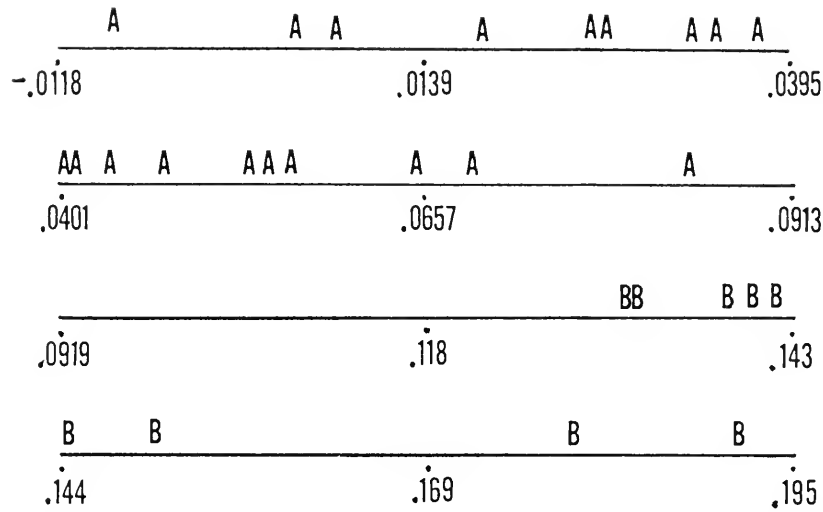


FIG. 3. Graph of observations in eigenvector space. A indicates one or more objects in group 1; B indicates one or more objects in group 2; Z indicates an overlap between two groups.

*Variable 6—Length of posterior protoconid arm on M_1

*Variable 17—Distance from posterior arm of protoconid to entoconid on M_3

Variable 3—Width of M_1 at anterocone

*Variable 7—Length of mesolophid on M_1

Variable 14—Anterior-posterior length of M_3

Variable 5—Width of M_1 at hypoconid

Variable 9—Width of M_2 at metaconid

Variable 4—Width of M_1 at metaconid

Variable 1—Anterior-posterior tooth row length

Variable 15—Width of M_3 at metaconid

Variable 2—Anterior-posterior length of M_1

Variable 17—Width of M_3 at hypoconid

Variable 8—Anterior-posterior length of M_2.

The nine most important variables include all those measurements (*) which are considered to be the criteria by which Wood (1937) and Galbreath (1953) separated *E. elegans* and *E. obliquidens*. These criteria were also used in this study for the qualitative separation of the two groups.

Classification of the 45 complete *Eumys* mandibles was then carried out. The individuals were placed in either group 1 (A) or 2 (B) by the computer on the basis of the criteria set up for separating the two groups in the multiple discriminant section of the program. In addition to the 30 individuals that had been used as the basis for forming the two groups in the multiple discriminant section of the program, 15 individuals of unknown group membership were classified. These 15 individuals could not be placed with certainty into either group on the basis of the descriptions. They seemed to have characteristics of both *E. elegans* and *E. obliquidens*. The computer was programmed to put these individuals in either group 1 (A) or 2 (B). Thus, an individual from the unknown group was placed in the one of the two groups with which the individual had the most similar characters.

The results of the computer classification are shown in Figure 4. The 30 individuals used for the discriminant part of the program were classified into exactly the same groups as predicted by the group criteria. There were no misclassifications.

Of the 15 individuals of unknown group membership (represented by circled letters in Figure 4) 60 per cent were placed in group 1 (A)

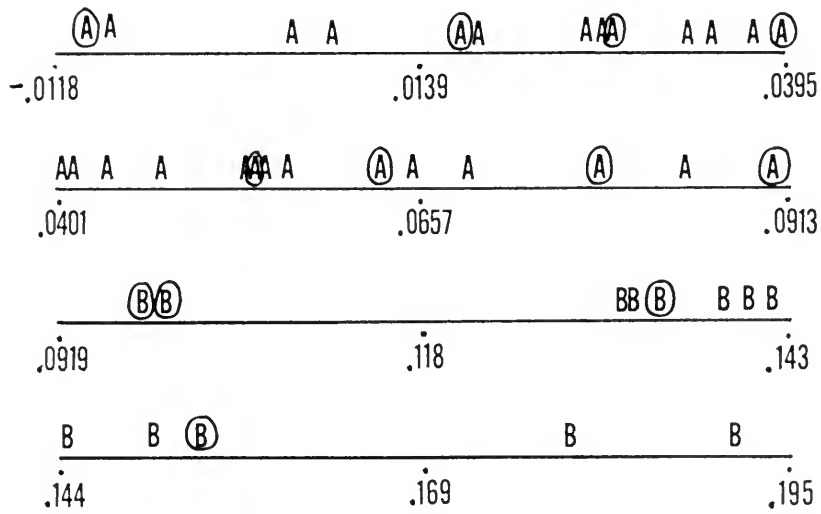
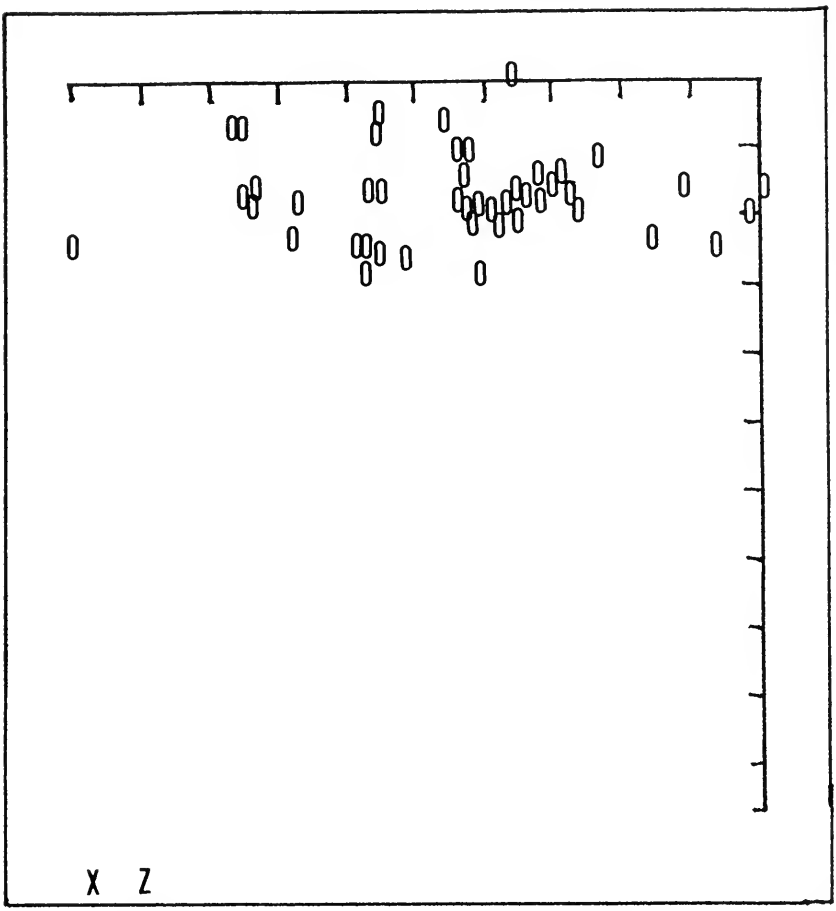


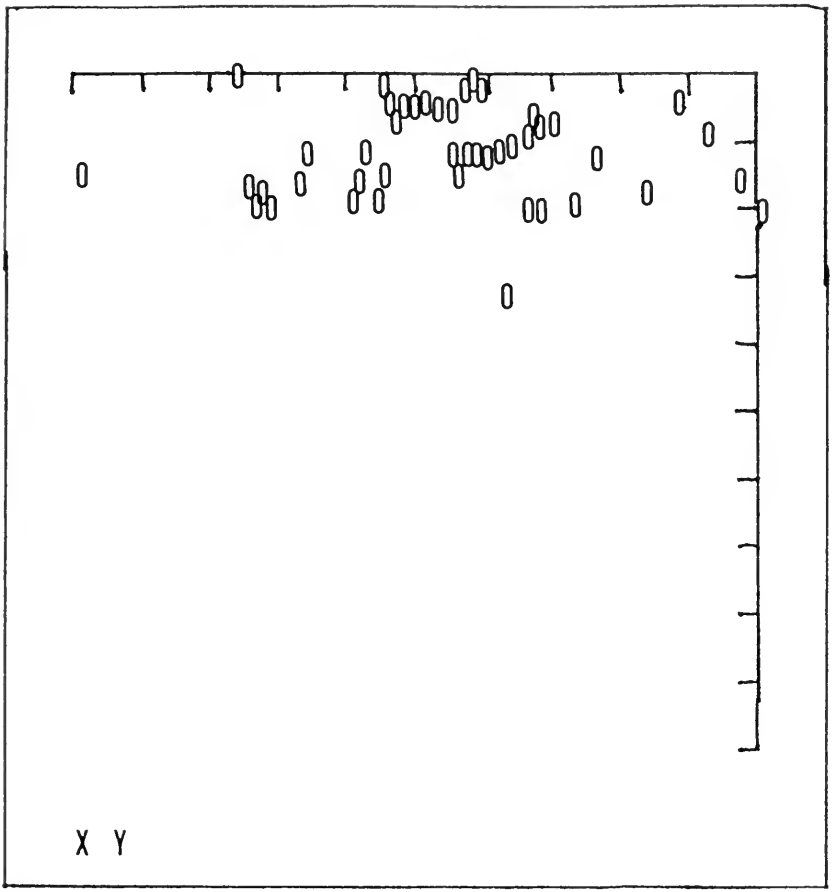
FIG. 4. Graph of observations in eigenvector space. A indicates one or more objects in group 1; B indicates one or more objects in group 2; Z indicates an overlap between two groups.



PRINCIPAL COMPONENTS DIAGRAM 1. Individual number that each zero represents is known, but was omitted for clarity of diagram.

and 40 per cent were placed in group 2 (B). Two individuals were off the graph to the right. Three individuals fell exactly between groups 1 (A) and 2 (B).

These results from the 45 *Eumys* mandibles do not support the idea that there is a clear separation between the *E. elegans* and *E. obliquidens*, which should be the case if they are two good species. This is especially clear since the characters used by the computer include those used to define the two species. Although many individuals seem to fit one extreme or the other, several individuals have characters of both groups. One continuous group, rather than two discrete groups, seems to be formed by the 45 individuals.

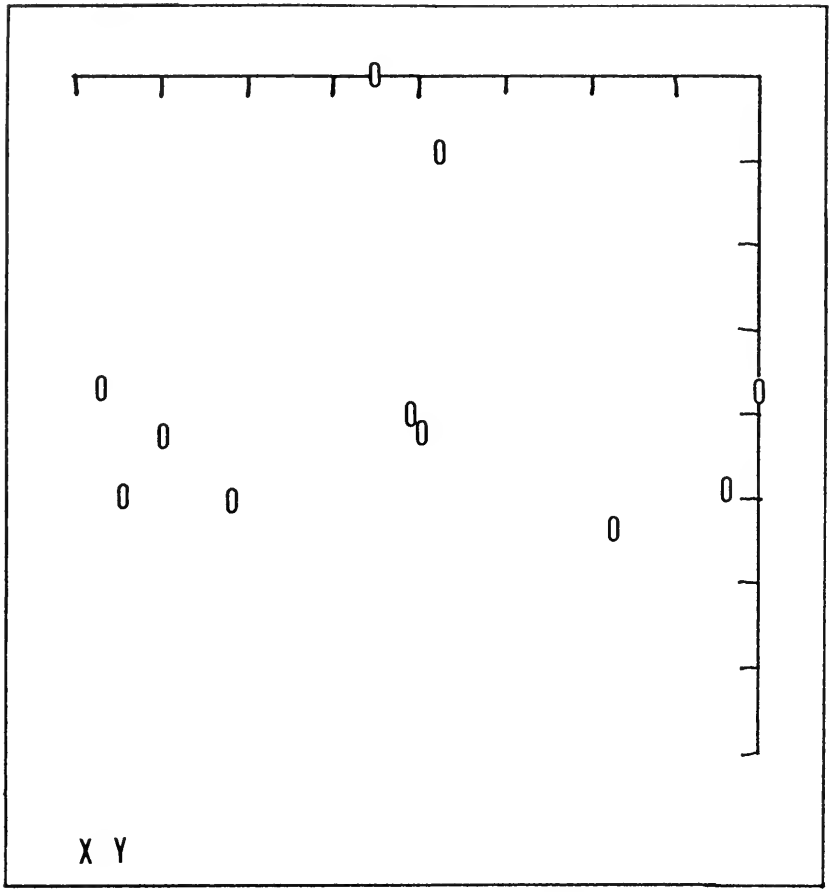


PRINCIPAL COMPONENTS DIAGRAM 2. Individual number that each zero represents is known, but was omitted for clarity of diagram.

B. *Multiple discriminant analysis of 11 complete* Eumys *maxillae with 13 variables each.*—Although the program began to run and did calculate some statistics, it was terminated because the sample size was too small compared to the number of variables. Thus, no significant information was obtained from the program.

PRINCIPAL COMPONENTS ANALYSIS:

A. *Principal components analysis was run on the 45 complete* Eumys *mandibles with 17 variables each.*—Measurement 1 of anterior-posterior tooth row length was deleted because it was

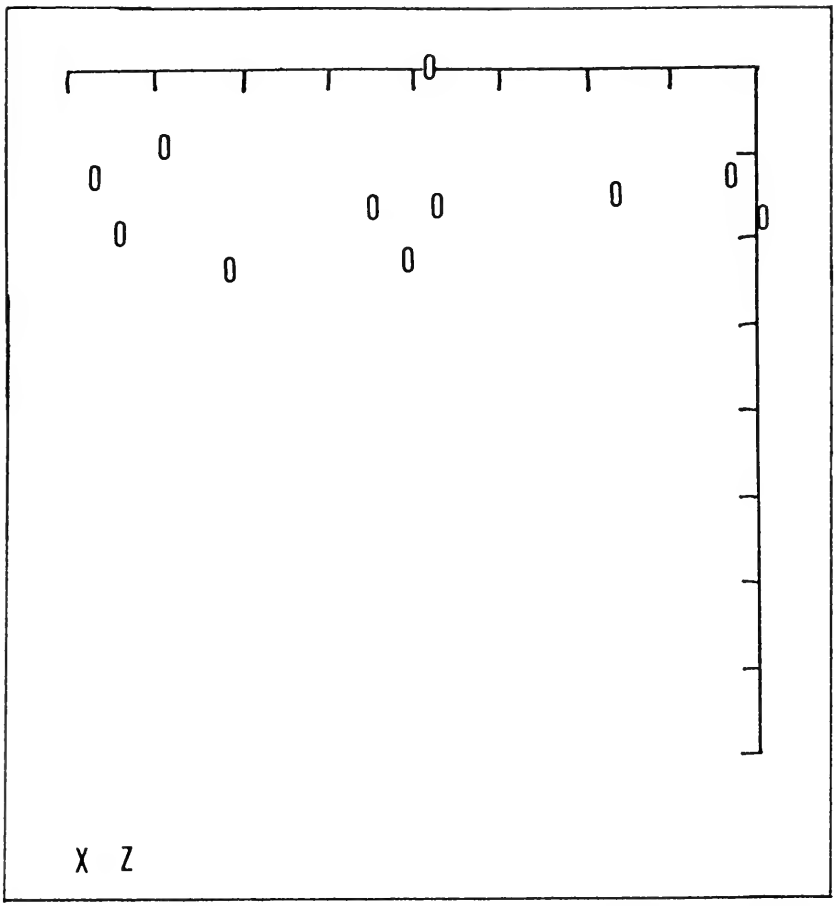


PRINCIPAL COMPONENTS DIAGRAM 3. Individual number that each zero represents is known, but was omitted for clarity of diagram.

known to be very highly correlated with anterior-posterior length of M_1, M_2, and M_3.

Principal components diagrams 1 and 2 show the results of the analysis. The X axis accounts for 74.4 per cent of the variance. The Y axis accounts for 4.8 per cent of the variance, and the Z axis accounts for 3.9 per cent of the variance. Diagram 1 shows the individuals graphed on the X and Z axes; diagram 2 shows the same individuals graphed on the X and Y axes.

The three-dimensional diagrams show that the mandibles are essentially one continuous group with an almost normal distribu-



PRINCIPAL COMPONENTS DIAGRAM 4. Individual number that each zero represents is known, but was omitted for clarity of diagram.

tion. The small break in the center is not considered to be significant.

The individuals were numbered so that numbers 1-21 fit the *E. elegans* description; numbers 22-30 fit the *E. obliquidens* description; numbers 31-45 had characters of both *E. elegans* and *E. obliquidens*. The slight separation in the middle of the three-dimensional diagram does not separate the individuals corresponding to the *E. elegans* type and *E. obliquidens* type. Numbers 2, 26, 13, 21, 29, etc. are on the same side of the break. Thus, the principal components analysis yields one group for all the *Eumys* mandibles.

B. *Principal components analysis was run on the 11 complete* Eumys *maxillae with 12 variables each.*—(Measurement 1 of anterior-posterior tooth row length was deleted because it was highly correlated with anterior-posterior length of M^1, M^2, and M^3.) Principal components diagrams 3 and 4 show the results of the analysis. The X axis accounted for 43.0 per cent of the variance. The Y and Z axes accounted respectively for 27.0 per cent and 10.5 per cent of the variance. Diagram 3 shows the individuals graphed on the X and Y axes; diagram 4 shows the individuals graphed on the X and Z axes.

Although the three-dimensional graphs seem to show the individuals separated into three groups, the sample size is so small that this grouping is more likely to be due to lack of data rather than a representation of actual groups.

AGGLOMERATIVE ANALYSIS:

A. *Agglomerative analysis was run on the 45 complete* Eumys *mandibles with 17 variables each.*—(Measurement 1 was again eliminated.) The analysis was run both with and without the Orloci transformation. Theoretically, there should be no difference in results between the two methods, since all 45 individuals had all 17 attributes. The Orloci transformation corrects for differences in numbers of attributes in different individuals.

Figure 5 is a dendrogram showing the results of analysis with the Orloci transformation; the dendrogram in Figure 6 shows the results of analysis without the Orloci transformation. In Figure 5

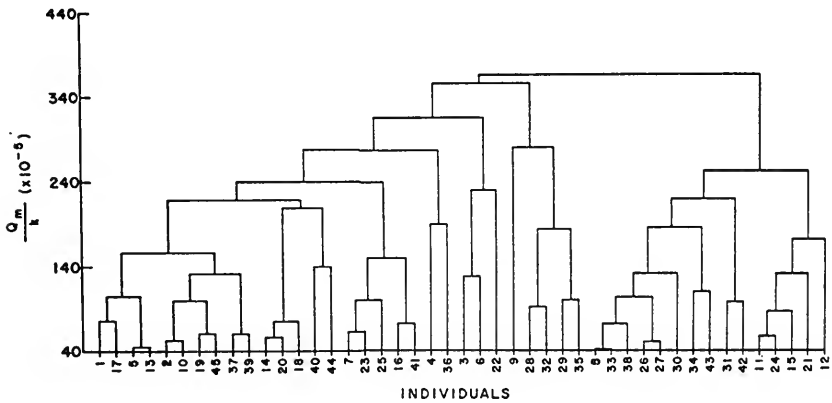


FIG. 5. Dendrogram showing the results of analysis with the Orloci transformation on the 45 complete *Eumys* mandibles with 17 variables each.

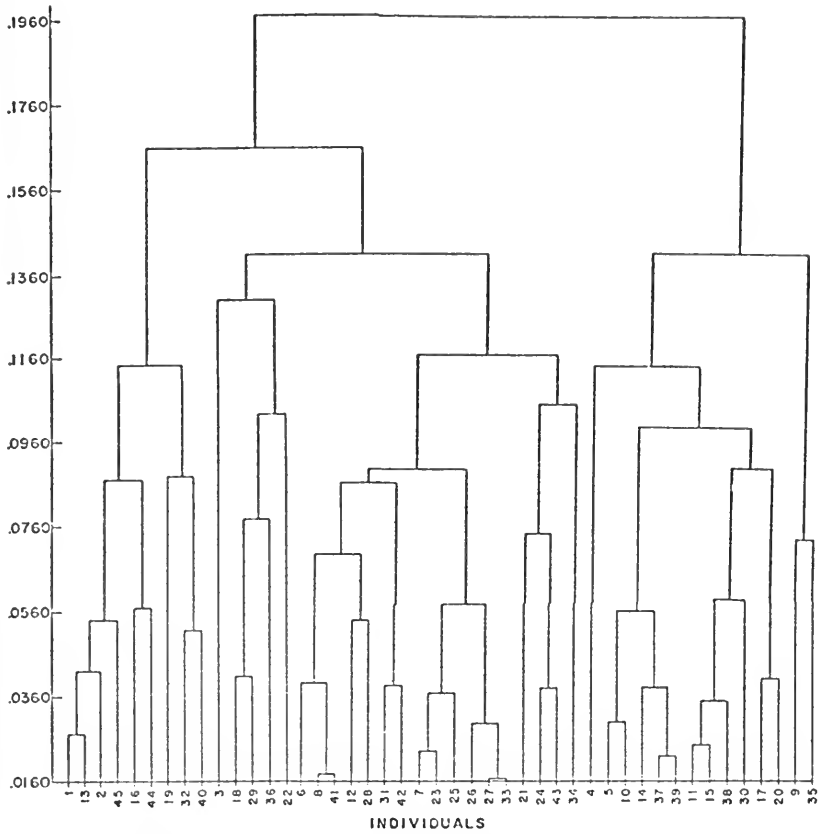


FIG. 6. Dendrogram showing the results of analysis without the Orloci transformation on the 45 complete *Eumys* mandibles with 17 variables each.

the final two groups are of sizes 30 and 15; in Figure 6 the final two groups are of sizes 31 and 14. Although group 1 in both dendrograms has 20 individuals in common and group 2 in both dendrograms has four individuals in common, the other 10 or 11 individuals in both groups differ in the two dendrograms.

When one examines the data, a possible reason for the differences in the two dendrograms becomes apparent. The absolute size of every measurement for the individuals that are in group 1 in both dendrograms is larger than the absolute size of every measurement for the individuals that are in group 2 in both dendrograms. The individuals that fall into different groups in the two dendrograms have some measurements that are large in absolute size and some that are small in absolute size. Thus, these individuals fall into one

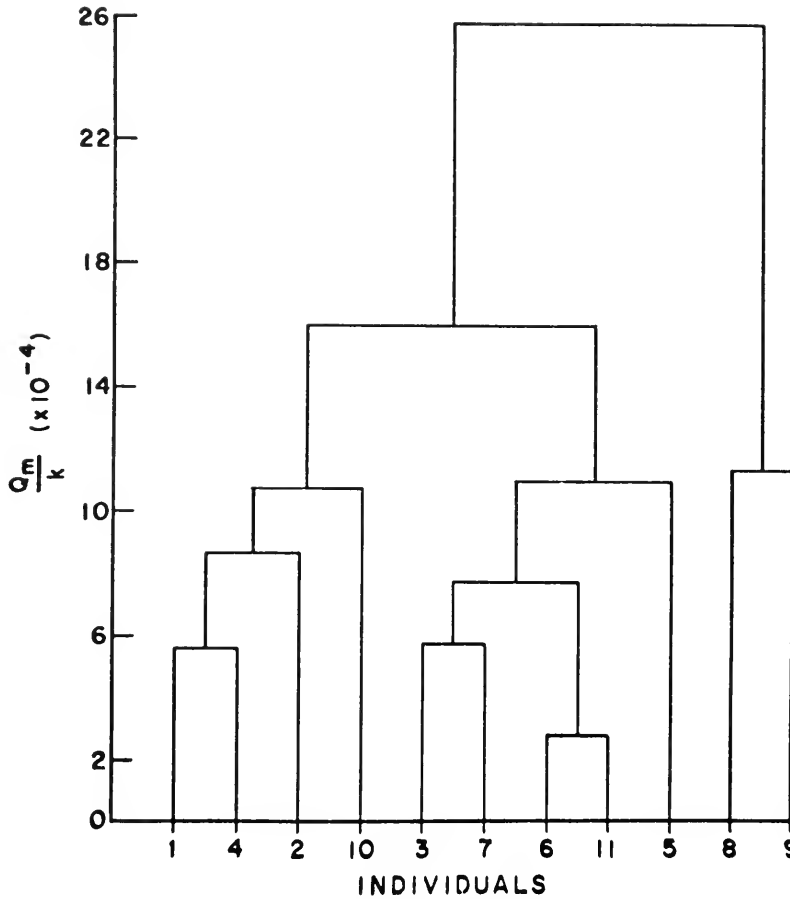


FIG. 7. Dendrogram showing the results of analysis with the Orloci transformation on the 11 complete *Eumys* maxillae with 12 variables each.

group with the Orloci transformation and another group without the Orloci transformation.

The appearance of the dendrograms, with the so-called "chaining effect," indicates that the individuals are probably all members of a single group, rather than two or three groups. The t-tests for difference of means run on the two-group-level of both dendrograms confirm this.

The t value for the difference between means for dendrogram 1 (fig. 5) with the Orloci transformation was 0.0099 with 43 df. This value certainly indicates that there is no significant difference between the means of the two groups.

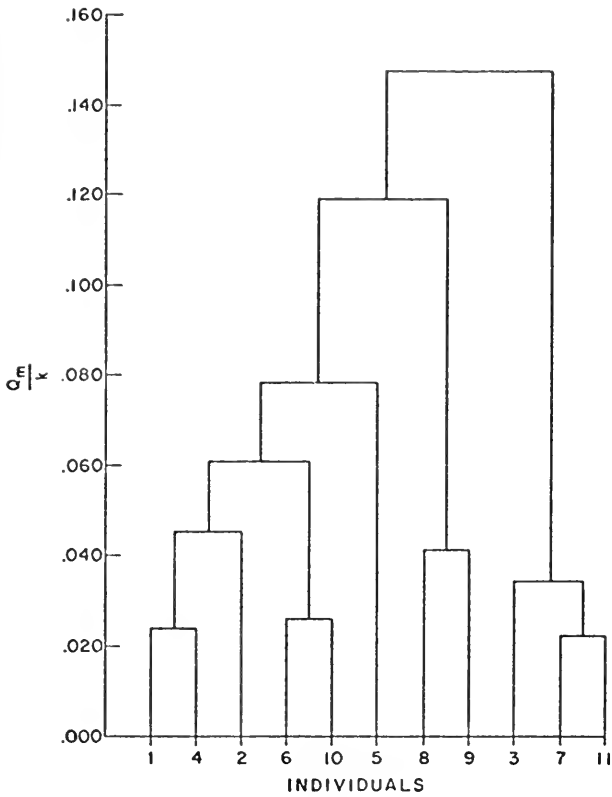


FIG. 8. Dendrogram showing the results of analysis with the Orloci transformation on the 11 complete *Eumys* maxillae with 12 variables each.

B. *Agglomerative analysis was run on the 11 complete* Eumys *maxillae with 12 variables each.*—(Measurement 1 was eliminated.) The analysis was run both with and without the Orloci transformation.

Dendrogram 3 (fig. 7) shows the results of analysis with the Orloci transformation. Dendrogram 4 (fig. 8) shows the results of analysis without the Orloci transformation. In dendrogram 3, the final two groups are of sizes 9 and 2; in dendrogram 4, the final two groups are of sizes 8 and 3. Although the larger groups in both dendrograms have six individuals in common, the other two or three individuals differ in the two dendrograms. Differences in absolute size of measurements are probably responsible again for the apparent discrepancy caused by the Orloci transformation.

The t-test for the difference between means for dendrogram 3 with the Orloci transformation was 0.017 for 9 df. This indicates that there is no significant difference between the means of the two groups. The t-test for the difference between means of dendrogram 4 without the Orloci transformation was 0.272 for 9 df. This value indicates that there is no significant difference between the means of the two groups.

DISCUSSION

The results of all analyses when considered separately and together indicate that the teeth of the 45 complete *Eumys* mandibles all fall into one group, rather than two or three separate groups. Using qualitative-type descriptions that purport to describe two different species, the specimens could be partially divided on the basis of simple observation. This division yielded three categories: an *E. elegans*-like group, an *E. obliquidens*-like group, and an intermediate group between the first two which contained individuals with some *E. elegans*-like characters and some *E. obliquidens*-like characters. The individuals of the intermediate group, which obliterated the gap between the other two, could not be placed with certainty into either of the first two groups.

Multiple discriminant analysis separated the *E. elegans*-like group from the *E. obliquidens*-like group. However, when the intermediate group was added, the program classified some of the individuals belonging to it as being within both groups and some individuals as falling between the two groups. Thus a continuum was formed among all of the groups.

It has been suggested that multiple discriminant analysis should show the best separation between groups if any separation is present. If one assumes that correlated variables might be controlled by the same genetic factors, then the fact that multiple discriminant analysis weights correlated variables less heavily might lead to less emphasis being placed on characters controlled by the same gene.

Principal components analysis yielded no separation into groups of the *Eumys* individuals. The *E. elegans*-like individuals were mixed with those of the *E. obliquidens*-like and intermediate types along the axes.

Agglomerative analysis differs from the above two types of analysis in that it groups individuals according to their affinities, rather than separating them according to their differences. Thus, agglomerative analysis has a different method of forming groups of

individuals. Nevertheless, there was no significant difference between the means of the two groups formed by agglomerative analysis. Furthermore, both groups formed had *E. elegans*-like, *E. obliquidens*-like, and intermediate - type individuals.

Thus, the results of all methods of analysis used treated the 45 complete mandibles as belonging to a single group.

The group of 11 complete *Eumys* maxillae was really too small in sample size for significant statistical analysis. However, the quantitative tests that were run indicated that the maxillae also formed only one group. By qualitative observation it was also impossible to find more than one group. Furthermore, in the literature no upper teeth of *E. obliquidens* have ever been mentioned or described. Although it is usually the case that the upper teeth are more conservative evolutionarily, it seems unlikely that the upper teeth of the *E. elegans*-like and *E. obliquidens*-like forms would not show some difference, if the two forms are really separate species. Since all the upper teeth look like the *E. elegans* form, a specimen in which upper and lower teeth of the *E. obliquidens* form are in occulsion would be necessary to finally prove this point.

Although the results showing that the *Eumys* specimens all are members of one group are fairly conclusive, the taxonomic interpretation of these results is not so clear-cut. The literature indicates that it is often not possible to separate living cricetid rodents solely on the basis of dental morphology (Hooper, 1968; Lindsay, 1972; Rosser, 1973), although the work of Schmidly (1973) on *Peromyscus boylei* offers some hope.

Many characters other than dental morphology are used to separate extant species. Characters such as pelt color, hind-foot length, tail length, and features of the male reproductive tract are used for separation. Furthermore, many geographic clines, sympatric species, and sibling species are found among modern cricetid rodents.

Sibling species can never be distinguished as fossils. None of the characters such as pelt color are ever fossilized either. Most of the other characters such as hind-foot length are not usually preserved. The paleontologist primarily has tooth material with which to work. Since it seems that dental morphology is not a reliable indicator of species separation in cricetid rodents, the paleontologist is left in a very ambiguous position with respect to defining taxa at the species level.

Solely on the basis of dental morphology, it seems a bit extreme to go as far as Alker (1967) did and suggest that nine of the 13 species of *Eumys* are invalid and that those nine should all be placed in *E. elegans*. On the other hand, most of the *Eumys* species were named using a typological approach without taking into account individual variation within populations. Without consideration of individual variation within a population, undoubtedly too many species were named. Wood (1937), who originally named many of the *Eumys* species, has recently suggested (Wood, 1969) that there are too many species, and that many are, in fact, variants of *E. elegans*.

CONCLUSIONS

In evaluating the results in this study, it may be said that the individuals all fall into one group. However, when one considers the taxonomic question of whether or not this means that the *E. elegans*-like forms and the *E. obliquidens*-like forms represent individual variation within the one *E. elegans* species, one must recommend with reservation.

The quantitative statistical results and the qualitative fact that there are intermediate types that have both characters indicate one species. The literature indicates that species cannot always be distinguished from each other on the basis of dental morphology. Thus, the *E. elegans*-like form and *E. obliquidens*-like form and their intermediates might represent separate sympatric species or sibling species.

However, the kind of behavioral evidence necessary for determination of sibling species is never fossilized. Nor will the characters such as pelt color that are used to separate extant species ever be fossilized. But, the taxa made with the fossil material must be based on the sort of evidence that is preserved and must be distinguishable objectively so that specimens can be assigned to the correct taxa with reasonable certainty.

The evidence from this study indicates that there was only one group of *Eumys* present in the Lower Nodular Zone of Sage Creek in the Big Badlands of South Dakota in Middle Oligocene time. Thus, this study suggests that all individuals in this group should be considered to be variants of the one species *E. elegans* and that there was no such species as *E. obliquidens* in that area during Middle Oligocene time.

The decision to eliminate the species *E. obliquidens* and consider all the individuals to be members of *E. elegans* is made solely on the

basis of the fossil evidence of dental morphology. Dental morphology may not be the best indicator of species differences in cricetid rodents. However, when evidence from dental morphology is the primary evidence available, as is the case with *Eumys*, then one must make decisions on that basis. Thus, all the individuals in this study are considered to be members of the one species, *Eumys elegans*.

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