EVALUATION OF THE UTILITY OF TWO-DIMENSIONAL FOURIER SHAPE ANALYSIS FOR THE STUDY OF OSTRACODE CARAPACES

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ABSTRACT

EVALUATION OF THE UTILITY OF TWO-DIMENSIONAL FOURIER SHAPE ANALYSIS FOR THE STUDY OF OSTRACODE CARAPACES

BY

JEAN KAY YOUNKER

Shapes of organisms and of their constituent structures are manifestations of innate genetic limits, modified by environmental conditions. Because fossil organisms are generally represented by a residuum of hard parts, studies of the variation of those structures have been used to construct genetic and environmental models.

A group of organisms whose morphologic variation is considered to be an important information carrier are the ostracodes. Reflection of this variation through two-dimensional shape has been qualitatively studied but quantitative determination of the exact nature of shape variation and correct interpretation of the information carried by shape has been difficult.

Shape description by means of a Fourier Shape Program developed by Ehrlich and Weinberg (1970), permits evaluation of the relative contribution of shape components for taxonomic and environmental studies.

This shape analysis was performed on lateral outlines of ostracode carapaces of a number of specimens from the families Trachyleberididae, Hemicytheridae, and Bairdiidae. Discriminant analysis using the shape information indicated that taxonomic information carried by ornamental structures, hingement, and muscle scars is also reflected in two-dimensional shape variation. Because the taxonomic characteristics are considered to be important manifestations of genetic differences, the related shape components must represent similar responses.

With this established, it was then possible to describe the inter-specific shape variation caused by sexual dimorphism and the nature of shape changes during growth of the ostracode. These results indicate that shape variation, measured and expressed as a continuous variable, should be a good index of the effects of evolutionary or environmental changes.

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INTRODUCTION

The shapes of entire organisms and of their constituent structures are a manifestation of innate genetic limits modified by environmental conditions. Under uniform growth conditions, shape variations of many varieties of organisms would reflect primarily genetic variability. Variation in environmental history from individual to individual would impress additional shape variability on the population. Because fossil organisms are generally represented by a residuum of hard parts, studies of the variations of those structures have been used to construct genetic and environmental models. Whereas appearance and disappearance of discrete structures can be readily observed, the nature of a continuous change, such as the shapes of those structures, is less easily monitored.

A group of organisms whose shape variation is considered an important carrier of information are the Ostracoda. Morphologic variation in ostracodes serves as a medium for expression of sexual dimorphism and as an important source of information used in classification.

Shape ratios which characterize variation in length-height dimensions are a common method for semi-quantitative description of ostracode shapes. Inappreciable change in this ratio with increasing carapace size has been used to demonstrate the nearly allometric nature of ostracode growth. Three dimensional shape ratios have been devised using three shape parameters and triangular graphs (Shaver, 1960).

In the absence of a priori information to the contrary, there is no way to assess the relative amount of useful information contained in shape ratios. Evaluation of complete shape information necessitates a method which accounts for all aspects of shape and shape variation.

The object of this study is to demonstrate the application of a new method of shape analysis, previously applied successfully in non-organic forms. Developed by Ehrlich and Weinberg (1970), this method yields a mathematical description of two-dimensional shape as precise as desired. The potential of this method in taxonomic, growth, and evolutionary studies are evaluated herein.

NATURE OF SHAPE VARIATION IN OSTRACODES

Both hard and soft-part morphologies provide sources of taxonomic information in living ostracodes but only the carapace is available for study of fossil taxa. As a result, such features as ornamentation on the carapace surface, muscle scar patterns, hingement, and shape of the carapace provide diagnostic criteria in fossil ostracodes.

The ontogeny of the individual ostracode is recorded in distinct growth stages or molts. Graphs showing length-height ratios have previously been used to express the relatively constant shape-size relationship during growth, and to define groups of specimens representing specific molt stages. Kesling (1951), in a detailed study of the morphology of growth stages in the fresh water cyprid Cypridopsis vidua (Muller, 1785), concluded that in his specimens, the early molts appeared more rounded while the seventh and eighth molts were more elongate. Kesling also concluded that adults appeared to be more rounded than the eighth molt, probably furnishing space for the sex organs which reach full development in the adult stage. Results of shape analysis of the outlines of specimens used in Kesling's study will be presented later in this paper.

DESCRIPTION OF SPECIMENS USED IN SHAPE STUDIES

Two-dimensional lateral outlines of the following genera and families were used to test the utility of the shape description in paleontological studies. Uniform orientation of specimens is essential, especially in the study of specimens of similar shape. A very slight change in orientation may significantly alter the shape description. Comparison of specimens oriented by a single individual would partially eliminate this problem, but the possibility for an additional source of shape variability must be considered.

Family TRACHYLEBERIDIDAE
Sylvester-Bradley, 1948

Subfamily ECHINOCYTHEREIDINAE
Hazel, 1967

Genus RABILIMIS
Hazel, 1967

Species of the genus Rabilimis were used in an initial evaluation of the usefulness of the new method of shape description in ostracode study. Species differentiation in Rabilimis is based on subtle differences in shape of lateral outline in addition to variation in position of normal pore canals, surface fossae, and ridges. Rabilimis is important in recognition of frigid or subfrigid climatic conditions in Pleistocene deposits and appears to be a biostratigraphically useful taxa in the Plio-Pleistocene of Alaska. One species, R. paramirabilis (Swain, 1963) is an extinct taxon known from Alaska and Russia (Swain, 1963; Lev, 1964). The other two, R. mirabilis (Brady, 1874) and R. septentrionalis (Brady, 1866) occur in Pleistocene and Recent deposits in the Artic and northern parts of the North Atlantic.

Genus ECHINOCYTHEREIS
Puri, 1953

The genus Echinocythereis is closely related to Rabilimis, most likely the progenitor of Rabilimis (Hazel, 1967). Table 1 is a complete list of all specimens of Echinocythereidinae from which tracings of illustrations were taken for use in this part of the study. If the original illustration was a right lateral view of a carapace, the illustration was reversed and treated with left valves and left lateral views of carapaces. This is permissible in this group because left valves are larger; therefore right lateral outlines of carapaces actually represent the left valves.

Table 1. Specimens of Rabilimis and Echinocythereis used in this study.

Genus Rabilimis

1. Rabilimis mirabilis (Brady, 1868)
    - a. Female carapace. Holocene, East Greenland. Unpublished photograph.
    - b. Female left valve. Pleistocene of Scotland. From Brady, Crosskey, and Robertson (1874, pl. 7, fig. 22)
    - c. Female carapace. Recent, eastern North Atlantic. From Elofson (1943, fig. 2)
    - d. Male carapace. Recent, eastern North Atlantic. From Elofson (1943, fig. 6)
    - e. Female left valve. Recent, Laptev Sea. From Akatova (1946, fig. 6a.)
    - f. Male left valve. Recent, Laptev Sea. From Akatova (1946, fig. 6b)
    - g. Juvenile? left valve. Recent (very likely Pleistocene), The Minch. From Brady (1868, pl. 29, fig. 7)

2. Rabilimis paramirabilis (Swain, 1963
    - a. Male left valve. Pliocene, Beringian stage, Submarine beach at Nome, Alaska. Unpublished photograph.
    - b. Female carapace. Upper Pliocene, Beringian stage, Submarine beach at Nome, Alaska. Unpublished photograph.
    - c. Female left valve. Upper Pliocene. Beringian stage, Gubik fm., Artic Coastal Plain, Alaska. Simpson Core Test Well # 1, 72-73 ft., Unpublished photograph of holotype.
    - d. Female left valve. Upper Pliocene. Beringian stage, Bering Sea, Bureau of Mines Drill Hole 12, 98-100 ft. Unpublished photograph.
    - e. Female left valve. Pliocene, Alaska. Unpublished drawing by K. G. Mckenzie.
    - f. Female left valve. Pliocene, Alaska. From Swain (1963, text-fig. 12b)
    - g. Male left valve. Pliocene, Alaska. From Swain, (1963, pl. 99, fig. 10c)

Table 1. (cont'd)

3. Rabilimis septentrionalis (Brady, 1866)
    - a. Female left valve. Upper Pleistocene, Kotzebuan Stage, Baldwin Peninsula, Alaska. Unpublished photograph.
    - b. Male left valve. Upper Pleistocene, Kotzebuan Stage, Baldwin Peninsula, Alaska. Unpublished photograph.
    - c. Male? left valve. Upper Pleistocene, ? Kotzebuan Stage, Gubik Fm., Artic Coastal Plain, Alaska. Teshekpuk shothole, Line 1-48. Unpublished photograph of holotype of Pseudocythereis simpsonensis Swain, 1963.
    - d. Male left valve. Upper Pleistocene, Kotzebuan Stage, Baldwin Peninsula, Alaska. Unpublished photograph.
    - e. Female left valve. Unpublished drawing by K. G. Mckenzie.
    - f. Female? left valve. Recent Hunde Islands, Western Greenland. From Brady and Norman (1889, pl. 16, fig. 13)
    - g. Female left valve. Pleistocene, Alaska. From Swain (1963, text-fig. 12a)
    - h. Female? left valve. Recent, Hunde Islands, Western Greenland. From Brady (1866, pl. 60, fig. 4c)
    - i. Male left valve. Pleistocene, Alaska. From Swain (1963, pl. 99, fig. 10b)

Genus Echinocythereis

1. E. planibasalis (Ulrich and Bassler, 1904. Female left valve. Recent, Gulf of Maine. From Hazel (1967, pl. 6, fig. 5)
2. E. margaritifera (Brady, 1870). Female left valve. Recent, Atlantic shelf east of New Jersey. From Hazel (1967, pl. 6, fig. 6)
3. E. margaritifera (Brady, 1870). Male left valve. From Hazel (1967, pl. 6, fig. 7)
4. E. echinata (Sars, 1865). ? left valve. From Hazel (1967, pl. 6, fig. 11)

Family HEMICYTHERIDAE
Puri, 1953

Six genera of the family Hemicytheridae from three subfamilies were chosen for shape analysis. Original classification was based on a combination of both hard and soft part features. In general, family level discrimination is based on structure of appendages; muscle scars and shape were subfamily characteristics; hingement, type of duplicature, shape details, muscle scars, and primary ornamentation represent generic criteria (Hazel, 1967). Table 2 lists the specimens used in this generic level study.

Table 2. Specimens of Hemicytheridae used in this study.

Note: All specimens are taken from Hazel (1967).

Subfamily Hemicytherinae

1. Genus *Hemicythere* Sars, 1865
    - a. *H. villosa* (Sars, 1865)
      Plate 2, # 4
    - b. *H. borealis* (Brady, 1868)
      Plate 2, # 5
    - c. *H. borealis* (Brady, 1868)
      Plate 2, # 11
    - d. *H. borealis* (Brady, 1868)
      Plate 2, # 10

2. Genus *Elofsonella* Pokorny, 1955 (= *Paracythereis* Elofson, 1941)
    - a. *E. concinna* (Jones, 1857)
      Plate 4, # 10
    - b. *E.concinna* (Jones, 1857)
      Plate 4, # 11
    - c. *E. concinna* (Jones, 1857)
      Plate 4, # 13

3. Genus *Baffinicythere* Hazel, 1967
    - a. *B. emarginata* (Sars, 1865)
      Plate 2, # 8
    - b. *B. costata* (Brady, 1866)
      Plate 2, # 13
    - c. *B. costata* (Brady, 1866)
      Plate 2, # 14

4. Genus *Finmarchinella* Swain, 1963
    - a. *F. finmarchica* (Sars, 1865)
      Plate 1, # 4
    - b. *F. finmarchica* (Sars, 1865)
      Plate 1, # 6
    - c. *F. angulata* (Sars, 1865)
      Plate 1, # 9
    - d. *F. angulata* (Sars, 1865)
      Plate 1, # 10

Table 2. (cont'd)

Subfamily Coquimbinae

1. Genus Muellerina Bassiouni, 1965
    - a. *M. abyssicola* (Sars, 1865)
      Plate 3, # 1
    - b. *M. lienenklausi* (Ulrich and Bassler, 1904)
      Plate 3, # 5
    - c. *M. abyssicola* (Sars, 1865)
      Plate 3, # 8
    - d. *M. canadensis* (Brady, 1870)
      Plate 3, # 13
    - e. *M. canadensis* (Brady, 1870)
      Plate 3, # 19
    - f. *M. lienenklausi* (Ulrich and Bassler)
      Plate 3, # 4
    - g. *M. canadensis* (Brady, 1870)
      Plate 3, # 12
    - h. *M. canadensis* (Brady, 1870)
      Plate 3, # 20

Subfamily Campylocytherinae

1. Genus Bensonocythere Hazel, 1967
    - a. *B. americana* Hazel, 1967
      Plate 5, # 1
    - b. *B. whitei* (Swain, 1951)
      Plate 5, # 2
    - c. *B. whitei* (Swain, 1951)
      Plate 5, # 9

Family, BAIRDIIDAE
Sars, 1887

A second generic study was carried out using genera of the family Bairdiidae (Sohn, 1960). Bairdia McCoy, 1844 is a smooth genus to which over two-hundred Paleozoic species have been assigned. Sohn's goal was to demonstrate that several distinct generic categories could be distinguished within the genus Bairdia. This would partially solve the obvious problems encountered when dealing with an unornamented genus supposedly containing two-hundred species. Sohn used a punched-card technique calling for sixty-seven features per individual. Experimentation with various combinations of characters determined which variables most readily divided the specimens into natural groups.

Other problems exist in the classification of Bairdia. Sex differentiation is extremely difficult and as a result, shape variations due to sexual dimorphism are probably hidden in different specific or generic names.

Four genera from Sohn's resultant classification were chosen for shape examination. Bairdia McCoy, 1844; Cryptobairdia Sohn, 1960; Bairdiacypris Bradfield, 1935; and Orthobairdia Sohn, 1960. Choice of the particular genera was solely based on availability of sufficient numbers of photographs from Sohn's plates showing similar views. Exact listing and source of each specimen studied can be found in Table 3.

Table 3. Specimens of Bairdiidae used in this study.

Note: All specimens are taken from Sohn (1960).

Bairdia

1. *B. beedei* Ulrich and Bassler, 1906
   Plate 1, # 5
2. *B. hispida*? Harlton, 1928
   Plate 1, # 6
3. *B. beedei* Ulrich and Bassler, 1906
   Plate 1, # 8
4. *B. grahamensis* Harlton, 1928
   Plate 1, # 9
5. *B. grahamensis* Harlton, 1928
   Plate 1, # 16
6. *B. pecosensis* Delo, 1930
   Plate 1, # 22
7. *B. rhomboidalis* Hamilton, 1942
   Plate 1, # 27
8. *B. hassi* Sohn, 1960
   Plate 1, # 29
9. *B. whitesidei* Bradfield, 1935
   Plate 1, # 30
10. *B. whitesidei* Bradfield, 1935
    Plate 1, # 31
11. *B. girtyi* Sohn, 1960
    Plate 1, # 33

Orthobairdia

1. *O. oklahomaensis* (Harlton, 1927)
   Plate 3, # 13
2. *O. oklahomaensis* (Harlton, 1927)
   Plate 3, # 15
3. *O. oklahomaensis* (Harlton, 1927)
   Plate 3, # 17
4. *O. oklahomaensis* (Harlton, 1927)
   Plate 3, # 19
5. *O. oklahomaensis* (Harlton, 1927)
   Plate 3, # 21

Table 3. (cont'd)

6. *O. cestriensis* (Ulrich, 1891)
   Plate 3, # 24
7. *O. cestriensis* (Ulrich, 1891)
   Plate 3, # 27

Bairdiacypris

1. *B. bedfordensis* (Geis, 1923)
   Plate 2, # 9
2. *B. curvis* (Cooper, 1941)
   Plate 2, # 11
3. *B. deloi* Bradfield, 1935
   Plate 3, # 4
4. *B. transversus* (Roth, 1929)
   Plate 6, # 28
5. *B. transversus* (Roth, 1929)
   Plate 6, # 20

Cryptobairdia

1. *C. forakerensis* (Kellett, 1934)
   Plate 2, # 2
2. *C. recta* (Harlton, 1929)
   Plate 2, # 7
3. *C. coryelli* (Roth & Skinner, 1931)
   Plate 2, # 16
4. *C. hoffmanae* (Kellett, 1943)
   Plate 2, # 28

DESCRIPTION OF METHOD OF SHAPE ANALYSIS

Two-dimensional maximum projection area is enlarged to approximately two inches long and superimposed on an X-Y grid. Coordinates of points on the periphery are recorded by an automatic digitizer which punches the values directly on data cards. Fourier shape approximation produces a mathematical description of the shape defined by this set of coordinates.

Center of gravity of the shape is calculated and the rectangular coordinates are converted to polar coordinates about this origin. A Fourier series is then used to estimate the shape by an expansion of periphery radius as a function of angle about the center of gravity. Precision of shape description is dependent upon spacing of initial peripheral points in addition to the number of harmonic orders considered. Harmonic orders in polar coordinates are analogous to harmonic orders in rectangular coordinates except the waves are closed forms. The zeroth harmonic is a centered circle with an area equal to the total area. The radius of the zeroth harmonic is set equal to unity in this analysis in order to allow shape comparisons independent of size. The first harmonic is an off-set circle, second a figure eight, third a three-leaf clover, and fourth a four-leaf clover. Qualitatively speaking, each harmonic represents a figure with "n bumps" where "n" is the number of the harmonic order. The sum of an adequate number of harmonics will completely reproduce the given shape.

The mathematical expression obtained gives the amplitude of the contribution from each harmonic order and a phase angle orienting the figure in relation to the coordinate system. It is expressed as follows:

$$R(\theta) = R_o + \sum_{n=1} R_n(\cos n\theta - \phi_n)$$

where $R(\theta)$ is the radius as a function of polar angle, R_o the average radius, n the harmonic order, R_n the harmonic amplitude, and ϕ_n the phase angle.

The harmonic amplitudes (R_n) for each harmonic order are the important variables. Shape changes are reflected by changes in the relative amplitude contribution of the harmonics.

Each shape can be characterized by a unique harmonic spectrum. Comparison with spectra of other shapes may allow location of specific harmonics responsible for major similarities and differences. Of taxonomic interest, the shape most representative of a given taxon can be selected by locating the specimen with harmonic amplitude values nearest the median values for the group. Shapes yielding extreme values can also be observed, potentially of value in identification of transitional specimens.

As an example of the application of individual harmonic spectra, Figure 1 shows a specimen of *R. mirabilis* and its characteristic amplitude spectrum. For comparison, a specimen of *R. septentrionalis* is also shown. In dissimilar shapes, variation in amplitude spectra corresponds to large scale variations in two-dimensional shape. Amplitude differences in similar shapes report only minor variations, as demonstrated by the higher second harmonic for the specimen of *R. septentrionalis*, indicating it is slightly more elongate than the specimen of *R. mirabilis*. A general decrease in amplitude values over the entire spectrum describes a change toward a more circular shape.

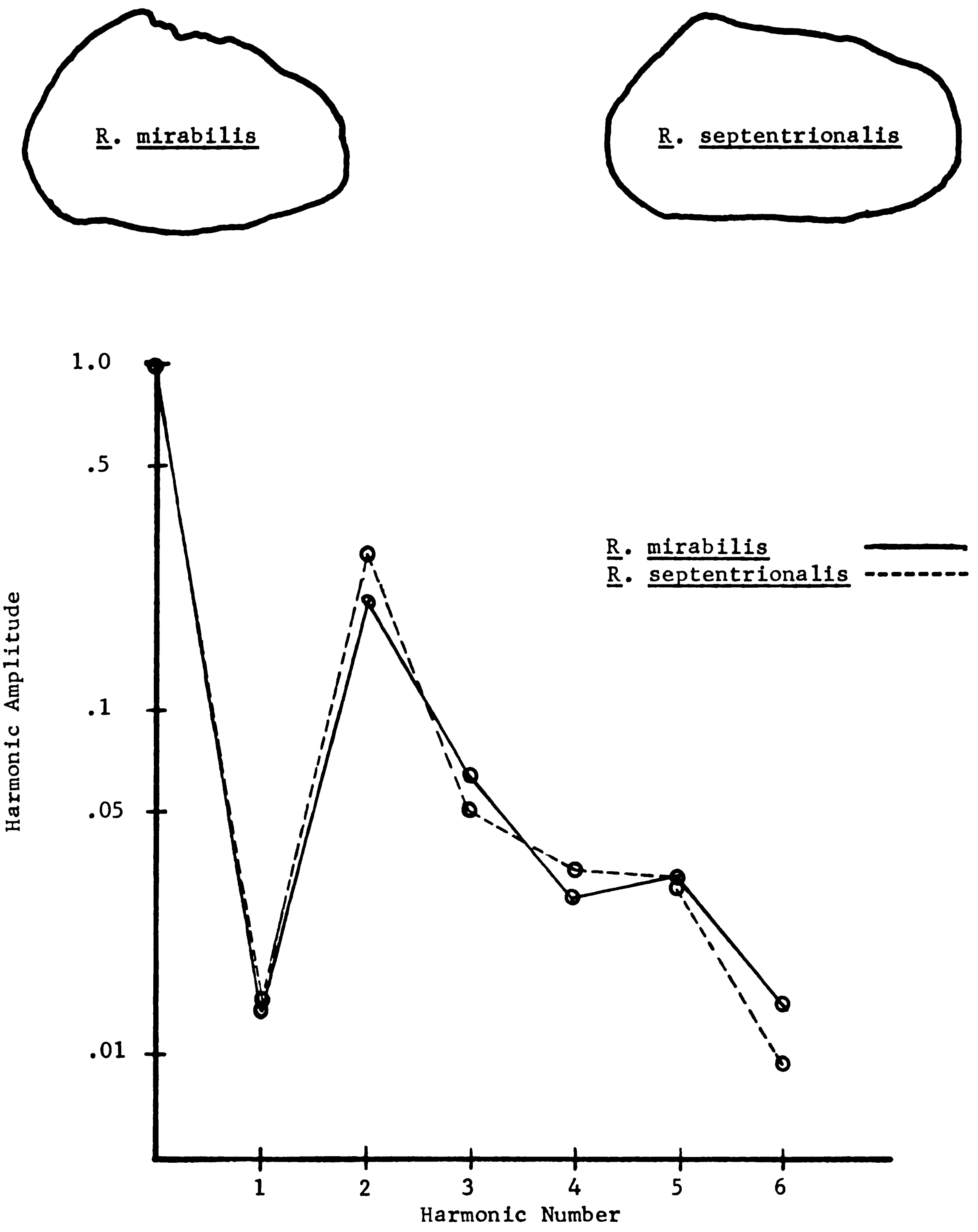


Figure 1. Comparison of amplitude spectra of Rabilimis mirabilis and Rabilimis septentrionalis

CONSTRUCTION AND USE OF CHI-SQUARE CONTINGENCY TABLES

Although the entire harmonic spectrum is required to completely describe a given shape, it is possible the shape information is not uniformly distributed over the harmonic orders. Certain harmonics may carry identical information thus creating redundancy in information content, whereas other harmonics may reflect unique shape characteristics. As a preliminary analysis, harmonic amplitude values, one harmonic at a time were tested for information content by use of a chi-square contingency table.

This test is designed to reveal a degree of association statistically greater than is likely to occur by chance. Data is arranged in rows and columns, in this case taxonomic categories are placed in row positions and four amplitude intervals make up the column divisions. Contingency tables were set up for both specific and generic taxa. The null hypothesis is that no association exists between the harmonic amplitude values and the taxonomic categories.

Expected values based on marginal totals are calculated and deviations of observed values from expected values are used to calculate a chi-square value for the contingency table. The calculated value is compared with a theoretical value which must be exceeded in order for the association between harmonic amplitude intervals and taxa to be declared significant. A level of significance chosen prior to setting up the table indicates the statistical reliability of the results. If the selected level is .05, a significant chi-square result indicates the interaction observed between harmonic amplitude intervals and taxonomic classes will occur only once in twenty times if they are not in some way associated.

DISCRIMINANT ANALYSIS TECHNIQUES

Multivariate discriminant analysis was used to test the potential usefulness of the shape description in taxonomic studies. This is a statistical method for assigning unknown samples to previously defined groups on the basis of a number of variables considered simultaneously. The discriminant analysis used is a maximum likelihood classification which assumes normal distributions for the special case of equal training class covariance matrices. This condition is obtained by pooling the individual matrices (Nilsson, 1965).

Discriminant analysis can also be used to test the internal consistency of the original categories, thus offering an external means for reinforcing or discrediting a classification scheme. Amplitude values for the first six harmonic orders were used as the independent variables in this study.

A population defined by the variables may be pictured as a cluster of sample points in six-dimensional space. Dimensions of the cluster are defined by the amount of variance in each parameter. Representative samples from different populations should occupy distinct regions in six-dimensional space. Some variables may overlap causing the clusters to merge in certain directions but in other directions the clusters should be distinct if they actually represent different populations.

The "location" of a cluster is described by the six-dimensional coordinates of its multivariate mean. Discriminant analysis is based on computation of the six-dimensional surfaces most efficient in separating the clusters. It operates in such a way as to minimize the distance between the multivariate mean of an unknown and the multivariate mean of the nearest cluster.

In this study, specimens representing previously defined taxonomic categories are used to establish clusters, each with a distinct multivariate mean. Once the clusters have been established, the original specimens are then classified by the discriminant analysis. It distributes these specimens throughout the established clusters on the basis of the six shape variables. If the multivariate mean of a specimen belonging to a given taxon falls closer to the multivariate mean of a different taxon, the discriminant analysis assigns this individual to the second group.

Correct classification of individuals into the original classes is expected only if the information carried by shape duplicates the information carried by the taxonomic characteristics used to define the categories. If the discriminant analysis distributes the specimens randomly through the classes, several interpretations are possible. Two-dimensional shape may not carry the same information as those features used in taxonomic discrimination, or shape alone may not be an important information carrier. On the other hand, if shape information was used in defining the original categories, any specimen reclassified by the discriminant analysis must be carefully examined.

USE OF SHAPE CHARACTERISTICS FOR SEX DISCRIMINATION IN FOSSIL OSTRACODES

Most species of Ostracoda are sexually dimorphic with respect to shell characteristics. In the major Mesozoic and Cenozoic group, the Podocopida, this is usually manifested in relative differences in the elongation of the carapace, with males tending to be more elongate than females. Consequently, sexual dimorphism can be expected to contribute to the range of shape variation within a species.

The range of amplitude values for the second harmonic and corresponding sex of individual specimens of the three species of *Rabilimis* are shown in Figure 2. Males are characterized by higher relative amplitude values within each species. Because of the nature of the second harmonic, a figure eight, higher relative amplitude values represent more elongate shapes.

Specimens whose sex was questionable (Hazel, personal communication) are noted by question marks in Figure 2. The intermediate nature of the amplitude values for these individuals verifies their shapes are less elongate than typical male members of the species, yet more elongate than the typical female shape. *R. paramirabilis* displays the most distinct segregation of males and females, with the second harmonic values clearly separated into two groups. *R. mirabilis* shows

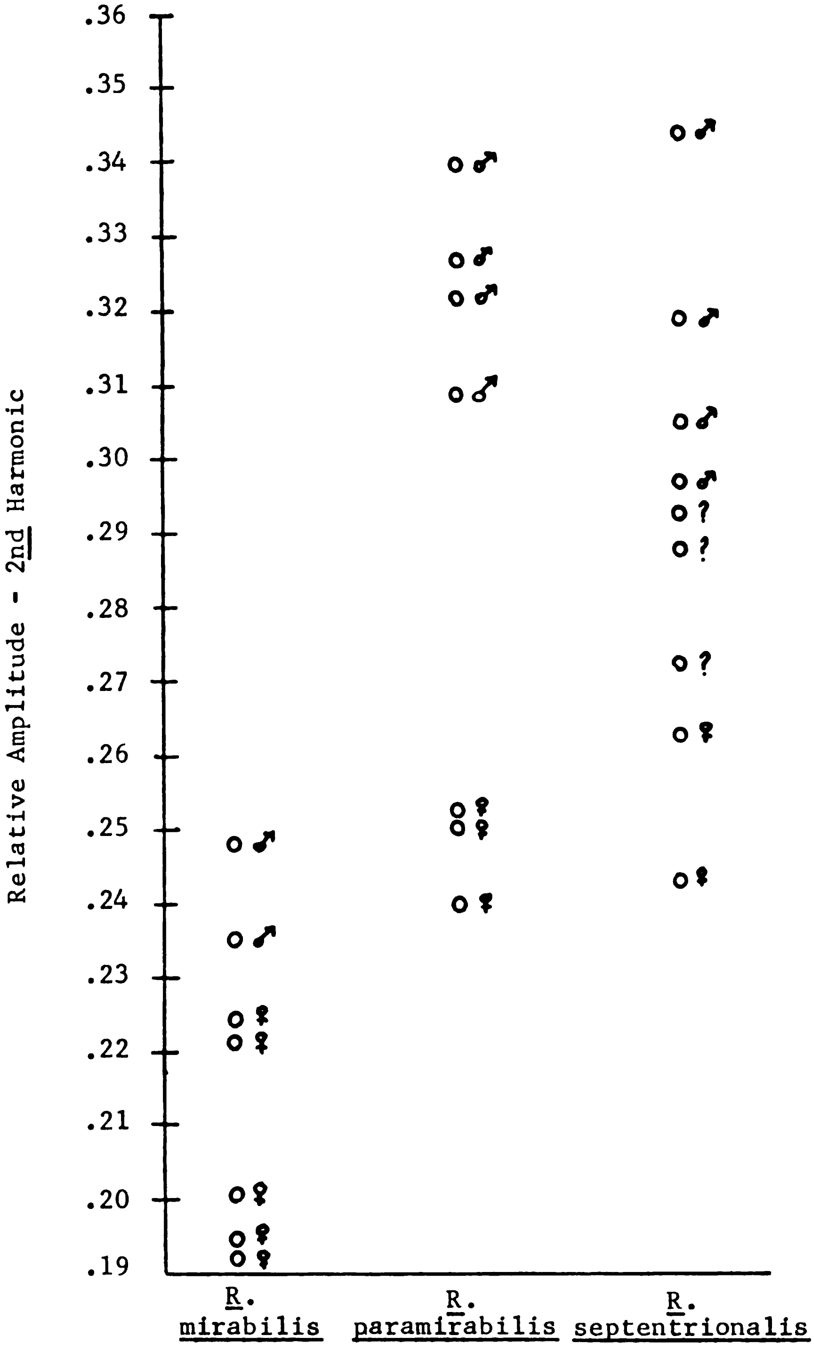


Figure 2. Relationship between sex and amplitude of second harmonic

a less definite separation, with two females exhibiting harmonic amplitude values lying closer to the male end of the spectrum. *R. septentrionalis* exhibits a continuum of shape variation with one extreme representing "maleness" and the other extreme representing "femaleness". No other harmonics were found to carry information useful in sexual discrimination.

The continuum observed in the specimens representing *R. septentrionalis* suggests that lateral outline is not a good discriminator of sex in this species. This suggests that other orientations such as dorsal or ventral views may carry information useful in sex discrimination in certain taxa.

SHAPE ANALYSIS OF MOLT STAGES

As was previously discussed, ostracodes offer an excellent potential for the study of shape alteration with growth. Observed shape changes are generally attributed to addition of appendages in early stages and attainment of sexual maturity in later stages.

Figure 3 shows the change in contribution of each harmonic amplitude over the nine molt stages studied by Kesling (1951). Shapes used for the growth study are shown in Figure 4, and represent average outlines of over five-hundred specimens of <u>Cypridopsis</u> <u>vidua</u> (O. F. Muller, 1785).

Continuous increase in the second harmonic through stage eight verifies Kesling's observation that elongation is the major shape change during growth. Increase in the second harmonic relative to the other harmonic orders indicates an increasing "oblateness". The eighth molt reaches maximum elongation and the ninth molt is a slightly more rounded adult shape, shown by the decrease in amplitude of the second harmonic. The strong, monotonous increase in the second harmonic indicates the fundamental shape change is expressed through this harmonic. Other harmonics show less distinct trends, with the fifth harmonic describing a shape component not

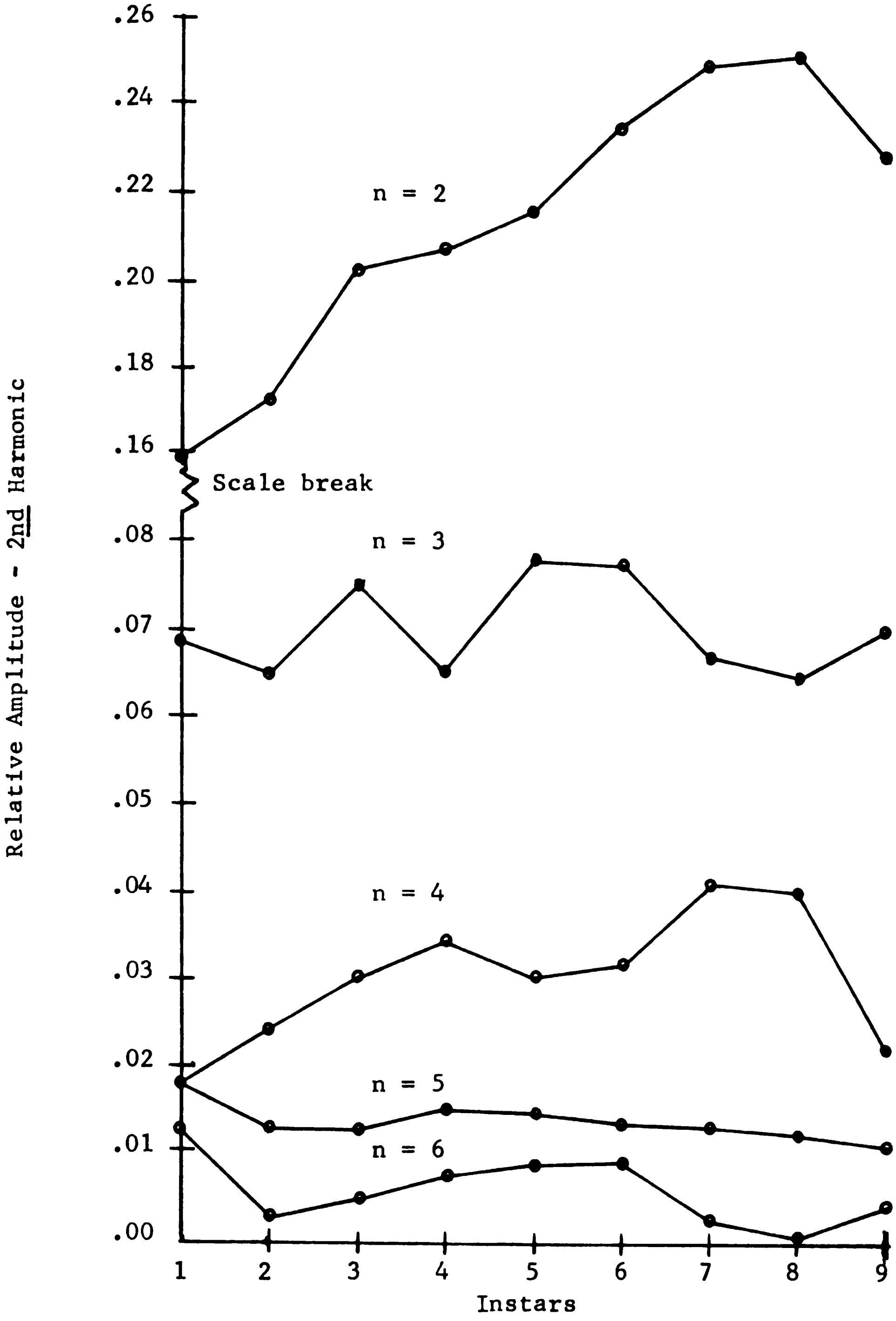


Figure 3. Shape change with growth of *Cypridopsis vidua*; shapes from Kesling (1951)

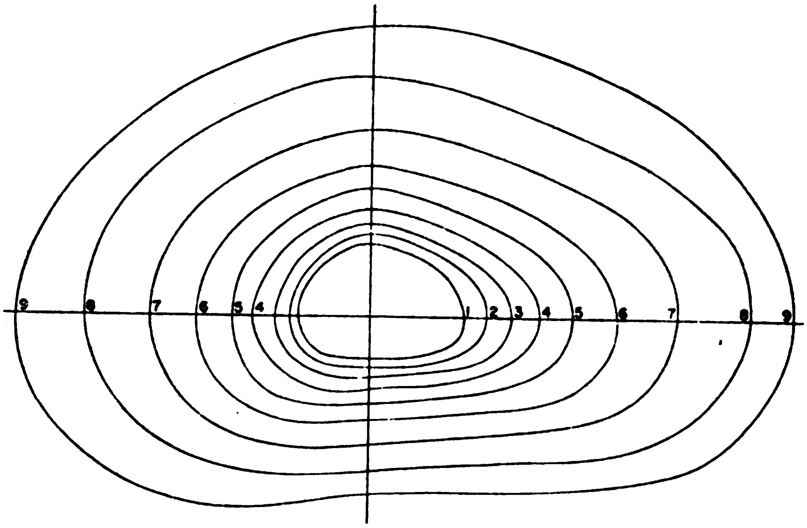


Figure 4. Average outlines of molt stages of over 500 specimens of Cypridopsis vidua (after Kesling, 1951)

changing from instar to instar.

Because outlines used in this study represent only a single species, comparison with shape changes during growth in other closely related and non-related taxa should be made. The nature of variation in shape during growth may represent a unique taxonomic characteristic, or may prove to be similar in other ostracodes.

INFROMATION CONTENT OF HARMONIC ORDERS

SPECIFIC LEVEL CHI-SQUARE

RABILIMIS

Computation of chi-square contingency tables for the species of Rabilimis indicated that only the second and third harmonics were making statistically significant contributions to intra-specific variation. These results were obtained by means of a four by three contingency table with columns designated by amplitude intervals and individual species occupying the row positions. Special chi-square tables (Craddock and Flood, 1970), designed for small contingency tables and small sample sizes were used. Confidence level of .05 was set prior to construction of the tables.

For sample size twenty-three, the critical chi-square value to be exceeded is 12.15. Results of the chi-square calculations are given in Table 4, page 33. Chi-square values for harmonic orders two and three are both large enough to be statistically significant at the .05 level. As shown in the table, no other harmonics yielded significant chi-square values.

GENERIC LEVEL CHI-SQUARE

BAIRDIIDAE

A contingency table was prepared for the four genera of Bairdiidae. A four by four table with twenty-seven specimens was constructed. Results are shown in Table 5 on page 33. At the .05 confidence level, the critical chi-square value is 16.92, and as indicated in the table, two harmonic orders gave significant results. The fifth harmonic is significant with a calculated chi-square value of 20.75 and the sixth with chi-square of 21.08.

HEMICYTHERIDAE

The same procedure was carried out on twenty-six specimens from Hemicytheridae. Six generic categories were used and in this case, only the fifth harmonic yielded a significant chi-square result of 31.84, with the critical value for this table at 24.99. Results can be found in Table 6, page 33.

Table 4 Chi-Square results for the species of *Rabilimis*.

Harmonic Number	Calculated Chi-Square Results
2	20.15*
3	16.47*
4	7.46
5	4.36
6	9.92

* Values exceed critical chi-square value (.05) of 12.15.

Table 5 Chi-Square results for the genera of Bairdiidae.

Harmonic Number	Calculated Chi-Square Results
2	16.45
3	14.29
4	13.09
5	20.75*
6	21.08*

* Values exceed critical chi-square value (.05) of 16.92.

Table 6 Chi-Square results for the genera of Hemicytheridae.

Harmonic Number	Calculated Chi-Square Results
2	21.55
3	18.86
4	12.95
5	31.84*
6	18.93

* Value exceeds critical chi-square value (.05) of 24.99.

INTERPRETATION OF CHI-SQUARE RESULTS

Significant chi-square results indicate association between row categories (taxa) and columns (harmonic amplitude intervals) is greater than would be expected by chance. Because the significant chi-square values occur at different harmonic orders for the taxa considered, it appears shape information is not uniformly distributed over all the harmonics nor is it carried by the same harmonics at different taxonomic levels.

Significant chi-square values for the fifth and sixth harmonic orders in Bairdiidae and the fifth in Hemicytheridae indicate that subtle shape differences are significant in describing generic shape variation in these taxa. The intraspecific variation in lateral outline in *Rabilimis* is reflected most strongly by the second and third harmonic orders, suggesting it is the relative "elongate-triangular" character of a specimen that allows species discrimination within this genus.

The nature of the characteristic shape of a taxon and the variation which this basic shape exhibits, determines which harmonic or harmonics contribute the most to taxonomic discrimination. Since shape variation is thought to be influenced by both genetic and environmental factors, the specific harmonics responsible for reporting major shape variations are probably unique to the given taxon.

USE OF THE SHAPE VARIABLES IN TAXONOMY

Results of chi-square contingency tables indicated variations in harmonic amplitude spectra may be useful in the study of shape variation within and between taxonomic categories. To further investigate this possibility, harmonic amplitude values for the first six harmonic orders were used as independent variables in multivariate discriminant analysis.

SPECIFIC LEVEL - RABILIMIS

The species of Rabilimis were used to assess the taxonomic significance of the shape description at the intra-specific level. Discriminant analysis results are given in Table 7.

Table 7. - Discriminant function classification matrix for species of Rabilimis

Original classes	Number of samples	Number of samples assigned to each class		
		1	2	3
1. R. mirabilis	7	7	0	0
2. R. paramirabilis	7	0	5	2
3. R. septentrionalis	9	0	1	8

Using only the shape information carried by the first six harmonic orders, the discriminant analysis assigned all specimens of R. mirabilis to the correct category. Seventy-one percent of the specimens representing *R. paramirabilis* were correctly assigned to this species by discriminant analysis. Two specimens of *R. paramirabilis* were classified as *R. septentrionalis*, indicating an overlap in the two species clusters and a similarity in shapes. Specimens representing *R. septentrionalis* were correctly ~~correctly~~ classified, except for one specimen. This individual was assigned to *R. paramirabilis*, again reflecting an overlap of *R. septentrionalis* and *R. paramirabilis*.

Figures 5a and 5b show the mean harmonic amplitude spectra for specimens of *R. paramirabilis* and *R. septentrionalis*. In 5a, the two specimens of *R. paramirabilis* assigned to *R. septentrionalis* are shown by dashed lines. In 5b, the spectrum of the specimen of *R. septentrionalis* reassigned to *R. paramirabilis* is shown by a dashed line.

Qualitative comparison of the actual outlines of the reassigned specimens with members of the original class and the new class illustrates the reasons for the discriminant analysis results. In Figure 6, each specimen is compared with a representative of both the original species and the species to which the specimen was assigned. Hazel (personal communication, 1971) indicated the shapes of certain specimens may, in fact, be more similar to one species whereas type of surface ornamentation and arrangement of pore canals indicate a closer affinity with members of another species.

Figure 5. a. Relationship between amplitude spectra of specimens of *R. paramirabilis* assigned to *R. septentrionalis* and the mean amplitude spectra of the two species

b. Relationship between amplitude spectrum of specimen of *R. septentrionalis* assigned to *R. paramirabilis* and the mean amplitude spectra of the two species.

Figure 5a.

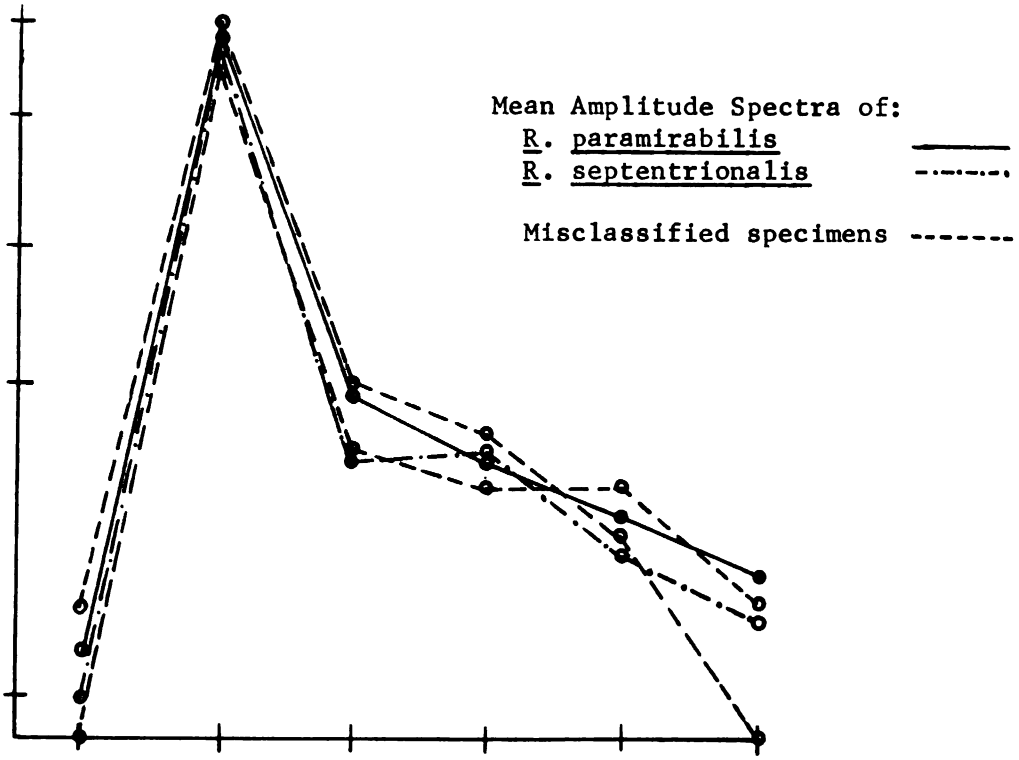
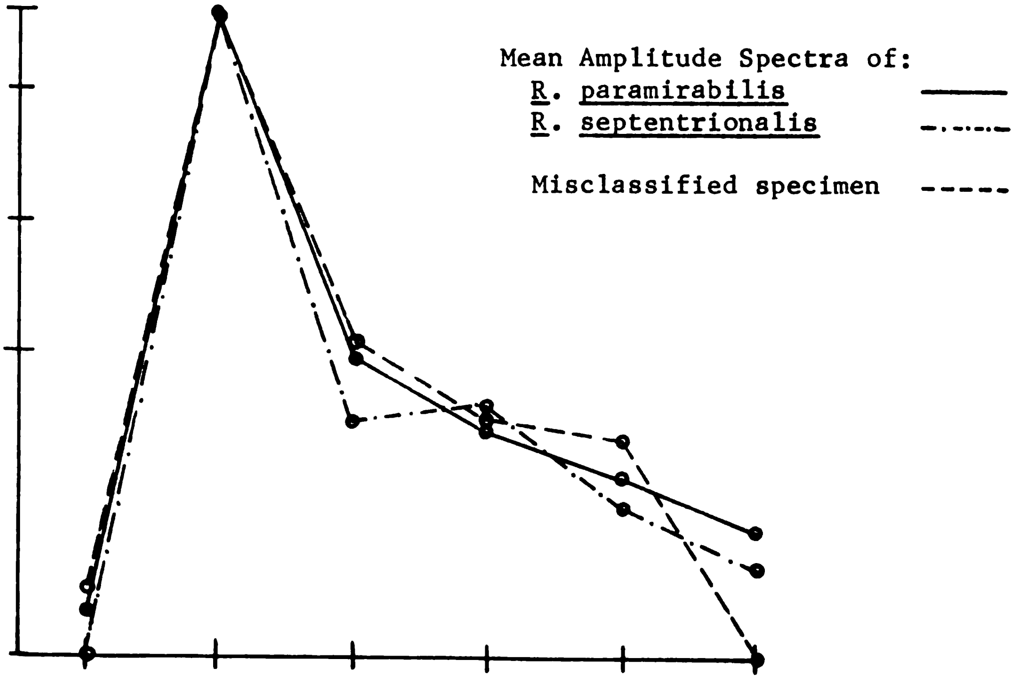


Figure 5b.



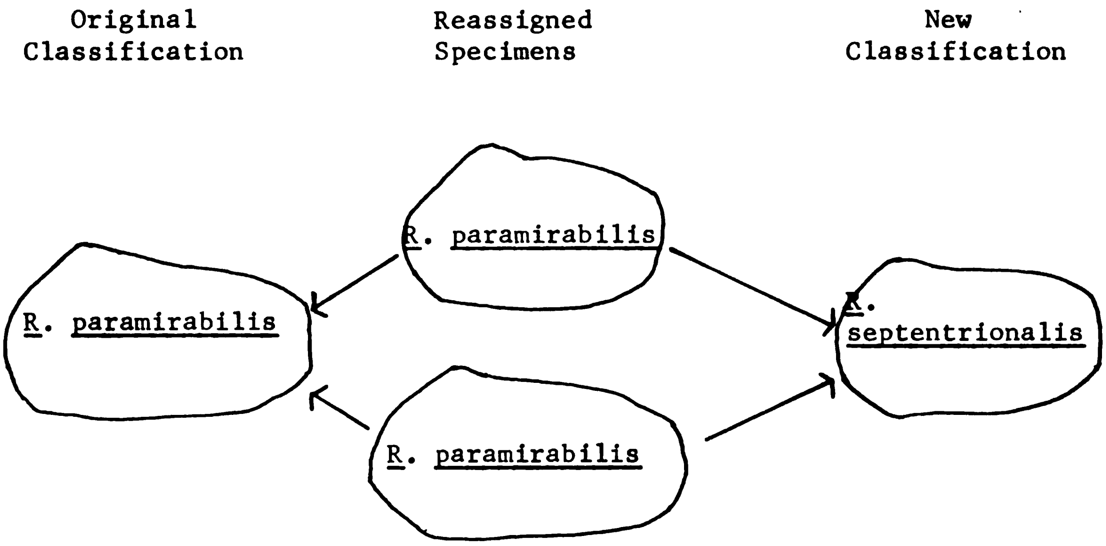


Figure 6a.

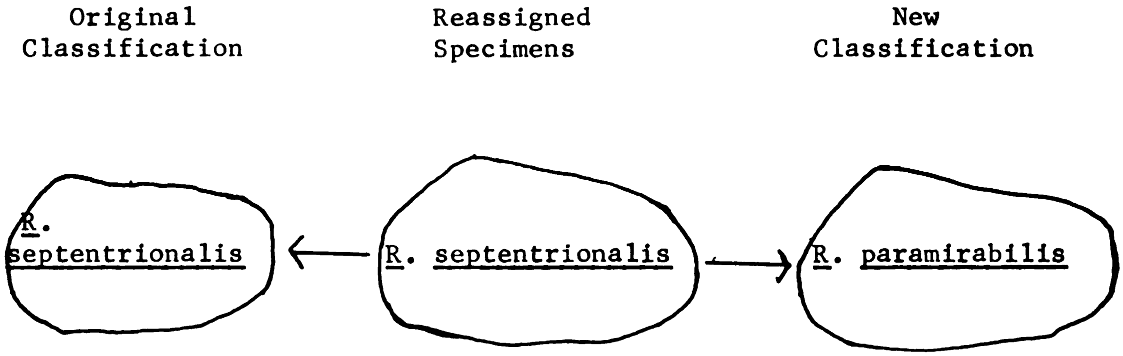


Figure 6b.

Figure 6. Comparison between mean shapes of *R. paramirabilis* and *R. septentrionalis* and the outlines of specimens misclassified by discriminant analysis: a. Specimens of *R. paramirabilis* classified as *R. septentrionalis* b. Specimen or *R. septentrionalis* classified as *R. paramirabilis*

It was also suggested by Hazel that the extinct *R. paramirabilis* is the progenitor of both *R. septentrionalis* and *R. mirabilis*, and that *R. septentrionalis* has diverged less morphologically than has *R. mirabilis*. Discriminant results indicate several individuals of *R. paramirabilis* and *R. septentrionalis* may have two-dimensional outlines exhibiting transitional shape properties. Because all specimens of *R. mirabilis* were correctly classified, less information about the nature of this species was available. However, chi-square results indicate harmonics two and three are significant in species discrimination. By inspection of the amplitudes of harmonic two plotted opposite harmonic three, more information on the character of the individual species can be obtained. This graph, shown in Figure 7, confirms the overlap of *R. paramirabilis* and *R. septentrionalis*, further supporting the inferred close relationship of the two species.

Specimens of *Echinocythereis*, a genus thought to be a closely related ancestor of *Rabilimis*, were added as a fourth category for a second discriminant analysis. Table 8 shows the classification matrix obtained.

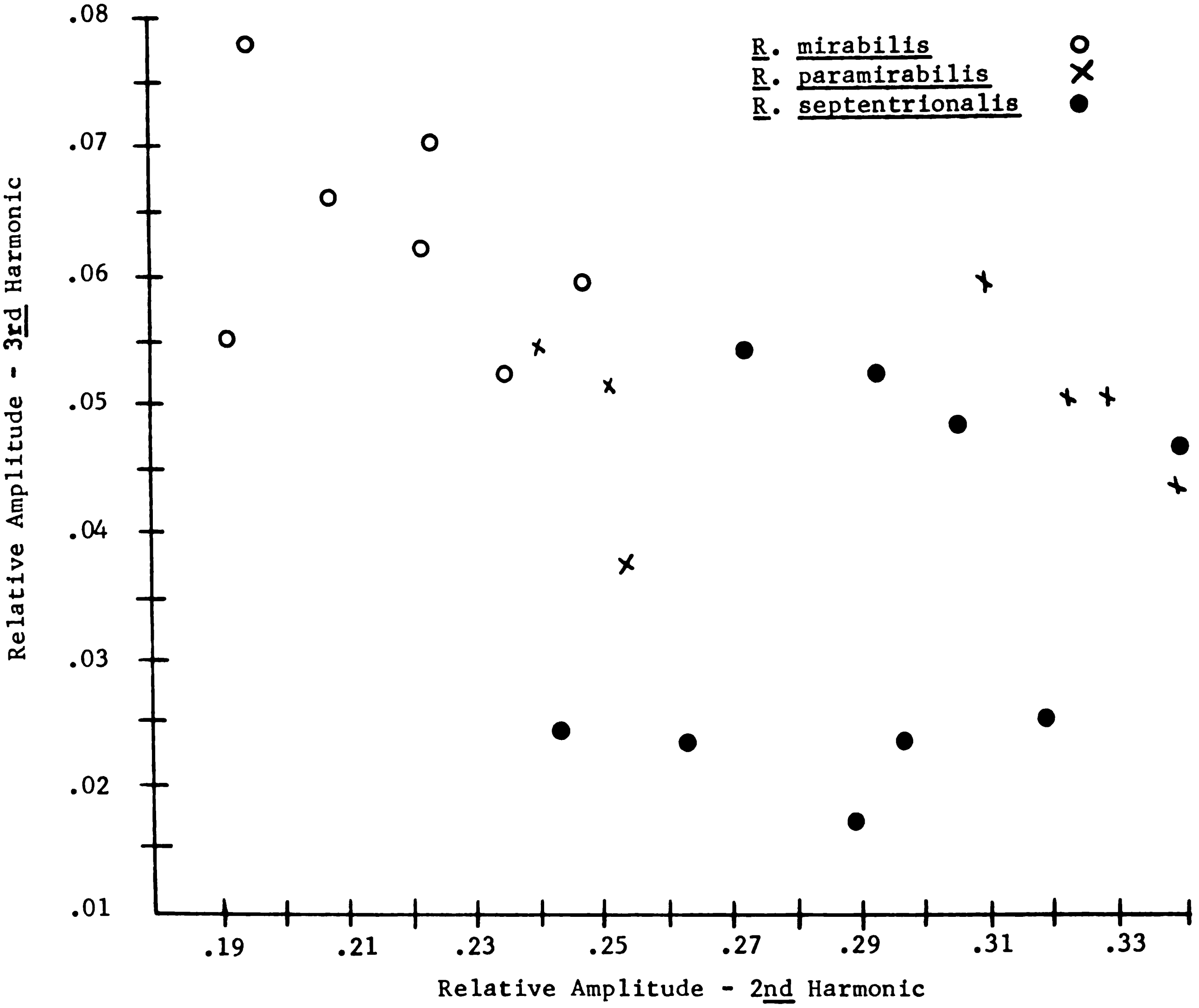


Figure 7. Shape relationships between specimens of R. mirabilis, R. paramirabilis, and R. septentrionalis

Table 8. - Discriminant analysis classification matrix for species of Rabilimis + Echinocythereis

Original classes	Number of samples	Number of samples assigned to each class			
		1	2	3	4
1. R. mirabilis	7	7	0	0	0
2. R. paramirabilis	7	0	5	1	1
3. R. septentrionalis	9	0	0	7	2
4. Echinocythereis	4	0	0	0	4

All specimens of Echinocythereis were correctly classified indicating the genus represents a group distinct from Rabilimis. However, one specimen of R. paramirabilis which was previously assigned to R. septentrionalis and two specimens of R. septentrionalis were assigned to Echinocythereis. Figure 8 compares the shapes of reclassified specimens with representatives of both their original class and the class to which the specimen was assigned by the discriminant analysis.

Results of the first discriminant analysis*which excluded Echinocythereis, indicate that R. mirabilis is the specific taxa representing the most distinct cluster on the basis of shape properties. Transfer of specimens between R. paramirabilis and R. septentrionalis suggests that portions of the clusters defining these taxa overlap, further indicating the taxa may be similar in two-dimensional shapes.

The second set of results ** which include Echino-

* Complete discriminant analysis data is given in Appendix A.
** Complete discriminant analysis data is given in Appendix B.

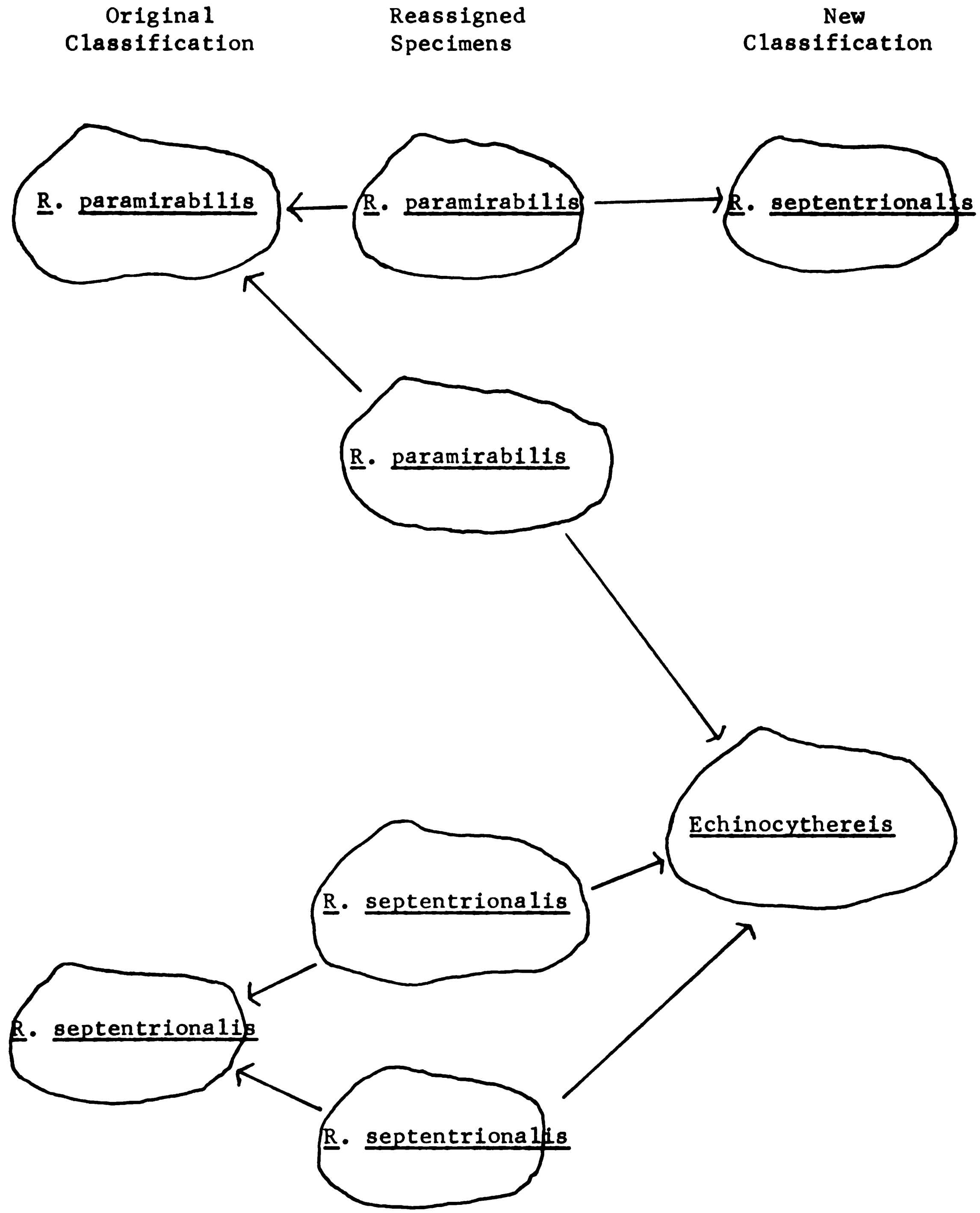


Figure 8. Comparison between mean shapes of R. paramirabilis, R. septentrionalis, and Echinocythereis, and the outlines of specimens misclassified by discriminant analysis.

cythereis provides additional information, indicating both *R*. *paramirabilis* and *R*. *septentrionalis* are more similar morphologically to the ancestral stock than is *R*. *mirabilis*, which remained a completely distinct category in both analyses.

GENERIC LEVEL - BAIRDIIDAE

Discriminant analysis was carried out on right valves of Bairdia McCoy, 1844, Orthobairdia Sohn, 1960, Bairdiacypris Bradfield, 1935, and Cryptobairdia Sohn, 1960. The classification matrix obtained is given in Table 9.

Table 9. - Discriminant analysis classification matrix for genera of Bairdiidae

Original Classes	Number of samples	Number of samples assigned to each class			
		1	2	3	4
1. Bairdia	11	7	2	0	2
2. Orthobairdia	7	0	7	0	0
3. Bairdiacypris	5	0	0	4	1
4. Cryptobairdia	4	1	1	0	2

Seven out of eleven specimens of the genus Bairdia were correctly classified. Two of the specimens were assigned to Orthobairdia. These were a cotype and a holotype of B. beedei Ulrich and Bassler, 1906, which apparently are more similar in shape to the specimens of Orthobairdia. The other two reassigned specimens were a paratype of B. hispida (Harlton, 1928) and a specimen of B. whitesidei (Bradfield, 1935). These specimens were assigned to Cryptobairdia.

Specimens belonging to Orthobairdia were correctly classified in all cases. This included five specimens of O. oklahomaensis, (Harlton, 1927) and two specimens of O. cestriensis (Ulrich, 1891).

Specimens of *Bairdiacypris* were correctly classified in four of five cases, with a paratype of *B. transversus* (Roth, 1929) reclassified as *Cryptobairdia*. *B. bedfordensis* Geis, 1923, *B. curvis*, 1941, *B. deloi* Bradfield, 1935, and a holotype of *B. transversus* Roth, 1929 were properly assigned to *Bairdiacypris*.

The last category, *Cryptobairdia*, was not as well defined by shape with only two out of four specimens correctly classified. *C. forakerensis* Kellet, 1934, and *C. recta* (Harlton, 1929) remained in the *Cryptobairdia* category, but *C. coryelli* (Roth and Skinner, 1931), and *C. hoffmanae* (Kellet, 1943) were assigned to *Orthobairdia* and *Bairdia* respectively.

GENERIC LEVEL RESULTS - HEMICYTHERIDAE

Genera of the family Hemicytheridae were also used to test the power of discrimination of the shape information at the generic level. Four genera of subfamily Hemicytherinae, one genus of subfamily Coquimbinae, and a genus from subfamily Campylocytherinae were studied. Harmonic amplitude values were obtained for a total of twenty-six specimens and twenty-five were correctly classified by discriminant analysis, again using only the shape information carried by the first six harmonic orders. Table 10 gives the classification matrix for this analysis.

Table 10. - Discriminant analysis classification matrix for genera of Hemicytheridae

Original classes	Number of samples	Number of samples assigned to each class					
		1	2	3	4	5	6
1. Hemicythere	4	4	0	0	0	0	0
2. Elofsonella	3	1	2	0	0	0	0
3. Baffincythere	3	0	0	3	0	0	0
4. Finmarchinella	4	0	0	0	4	0	0
5. Muellerina	8	0	0	0	0	8	0
6. Bensonocythere	4	0	0	0	0	0	4

All specimens of Hemicythere were correctly classified. These include *H. villosa* Sars, 1865, and three specimens of *H. borealis* Brady, 1868. *Elofsonella* was represented by three specimens of *E. concinna* Jones, 1857. Two were properly assigned and the third was classified with *Hemicythere*. *Baffincythere* was represented by two specimens of *B. emarginata* Sars, 1865, and one of *B. costata* Brady, 1866. All three were correctly classified as *Baffincythere* by the discriminant analysis. Specimens defining the genus *Finmarchinella* were two specimens of *F. finmarchica* (Sars, 1865), and two specimens of *F. angulata* Sars, 1865. *Finmarchinella* represented a distinct category with all specimens correctly classified by the discriminant analysis. *Muellerina* was represented by two specimens of *M. abyssicola* Sars, 1865, two specimens of *M. lienenklausi* Ulrich and Bassler, 1904, and four specimens of *M. canadensis* Brady, 1870. All of these specimens were correctly classified as *Muellerina* on the basis of two-dimensional shape.

The genus from the subfamily Campylocytherinae was *Bensoncythere* Hazel, 1967. This genus was represented by one specimen of *B. americana* Hazel, 1967, and two specimens of *B. whitei* Swain, 1951. Again, 100% discrimination indicates the specimens used to define *Bensonocythere* represent a distinct shape class separate from the other five generic classes in this analysis.

Results of the generic level discriminant analyses* demonstrate that two-dimensional shape carries important taxonomic information at this level as well as the specific level. If shape information alone allows accurate classification, the original categories must have been established primarily on the basis of shape, or the taxonomic characteristics used to construct the original classification are expressed through the medium of two-dimensional shape variation.

* Complete discriminant analysis data for Bairdiidae is given in Appendix C.

Complete discriminant analysis data for Hemicytheridae is given in Appendix D.

SUMMARY AND CONCLUSIONS

This investigation indicates two-dimensional shape of the ostracode carapace contains information in addition to that obtained by simple shape ratios. In most cases, the mathematical shape description is shown to be of equivalent taxonomic value to the qualitative features more commonly used in taxonomic discrimination. Since other taxonomic characteristics such as ornamentation, muscle scars, and hingement are considered to be important manifestations of genetic differences, the related shape components must represent similar responses.

Demonstration of this clear-cut relationship provides confidence that shape information can be used in at least two additional ways. Because shape variation measured in the manner described is a continuous variable, it can be used as a direct measure of taxonomic similarity or distance. For the same reason, shape variables can also be used in the study of inter-specific and intra-specific variation resulting from sex differences, environmental effects, or phylogenetic distance.

In addition to the study of fossil taxa, the shape response of recent taxa to environmental gradients can be monitored. Estuaries or bays offer environments where specimens living under depth or salinity gradients are available. Using the Fourier shape technique, the possibility of a shape continuum in these specimens can be studied, and if one is confirmed, the exact nature of the shape change can be diagnosed.

The shape variables produced by this analysis also provide an external means for testing the reasonableness of certain evolutionary models. Many phylogenetic sequences involve morphologic changes which should be reflected through two-dimensional shape. Verification of the existence of a shape continuum over a sequence of morphologic forms representing a proposed phylogenetic series would corroborate the accuracy of the predicted pattern of evolution.

The results discussed above suggest a number of possibilities for further use of this technique. Although the general utility of this method of shape analysis has not been verified, an inspection of ostracode literature indicates that taxonomic descriptions place great emphasis on the shape of lateral and dorsal outlines. This, along with the results already obtained, suggests the Fourier technique should be of general utility over a wide range of ostracode groups. Because similar criteria are used in other groups, notably pelecypods, brachiopods, and echinoderms, this method may be of general importance in paleontological research.

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APPENDICES

APPENDIX A

DISCRIMINANT ANALYSIS RESULTS FOR SPECIES OF *RABILIMIS*

DISCRIMINANT ANALYSIS RESULTS
FOR SPECIES OF RABILIMIS

```
 V    T   S1   S2   S3   S4   S5   S6   S7   S8   S9  S10   C
 6    3    7    7    9   -0   -0   -0   -0   -0   -0   -0   0        (6F7.5/)
TRAINING CLASS    1
.01436 .22169 .06181 .02863 .03195 .01266

.01670 .22431 .07019 .03250 .03362 .01123

.01394 .20790 .06623 .02936 .03338 .01412

.01502 .24775 .05923 .03275 .04162 .01476

.01056 .19179 .05465 .03437 .01298 .01028

.01288 .23470 .05169 .02882 .02559 .01781

.01544 .19807 .07803 .03424 .01794 .01707
```

Training Class 1:
R. mirabilis

Rows are individual specimens. Columns are the relative harmonic amplitude values for harmonic orders 1-6.

```
TRAINING CLASS    2
.00860 .25316 .03681 .03054 .03080 .01718

.01493 .32253 .05006 .03464 .03148 .02640

.01297 .34035 .04335 .03702 .02995 .02110

.01118 .23997 .05376 .03024 .01896 .02579

.01145 .25098 .05070 .02902 .02267 .01987

.01584 .32717 .05010 .03977 .02416 .00618

.01632 .30922 .05951 .03472 .02315 .01791
```

Training Class 2:
R. paramirabilis

```
TRAINING CLASS    3
.00461 .24330 .02452 .02559 .02191 .01611

.00648 .31889 .02462 .04351 .01985 .02088

.00358 .28850 .01688 .02991 .01738 .02250

.00628..29686 .02293 .03590 .01434 .01847

.01311 .30526 .04817 .04036 .02646 .01493

.01464..29327 .05173 .03407 .03128 .00951

.00575 .26328 .02342 .03389 .01361 .01445

.01275 .27236 .05367 .03006 .01486 .00839

.01541 .34423 .04632 .05542 .03699 .01636
```

Training Class 3:
R. septentrionalis

```
MEANS FOR EACH TRAINING CLASS
 .01416      .01290      .00918
 .21760      .29190      .29179
 .06312      .04918      .03469
 .03152      .03371      .03652
 .02815      .02588      .02185
 .01399      .01920      .01573
```

Columns are the three species of Rabilimis .

Rows are the mean harmonic amplitude for harmonic orders 1-6.

```
COVARIANCE MATRIX
.00001    .00006    .00003    .00001    .00001   -.00001
.00006    .00102    .00004    .00014    .00014   -.00000
.00003    .00004    .00013    .00002    .00002   -.00002
.00001    .00014    .00002    .00004    .00002   -.00000
.00001    .00014    .00002    .00002    .00006   -.00000
-.00001  -.00000   -.00002   -.00000   -.00000    .00002

INVERSE OF COVARIANCE
3945720. -159758. -925031.  -37101. -199047.  390564.
-159758.    8922.   38486.   -6245.    4539.  -15447.
-925031.   38486.  227043.    2094.   43144.  -83882.
 -37101.   -6245.    2094.   55257.    6085.   -5675.
-199047.    4539.   43144.    6085.   33244.  -21311.
 390564.  -15447.  -83882.   -5675.  -21311.   84875.

INVERSE CHECK    DETERMINATE  .57162E-27  TOTAL SAMPLES  23
1.00000   .00000   -.00000  -.00000   -.00000    .00000
 .00000  1.00000    .00000   .00000    .00000   -.00000
 .00000  -.00000   1.00000   .00000    .00000   -.00000
 .00000   .00000    .00000  1.00000    .00000   -.00000
 .00000   .00000    .00000   .00000   1.00000   -.00000
 .00000  -.00000   -.00000  -.00000   -.00000   1.00000

CLASS  ACTUAL    EXPONENT FOR TRAINING SET R. mirabilis
  1      1   .923E+00  .135E+02  .207E+02
  1      1   .895E+00  .175E+02  .253E+02
  1      1   .349E+01  .191E+02  .245E+02
  1      1   .355E+01  .148E+02  .216E+02
  1      1   .724E+01  .233E+02  .206E+02
  1      1   .890E+01  .154E+02  .266E+02
  1      1   .680E+01  .233E+02  .327E+02

CLASS  ACTUAL    EXPONENT FOR TRAINING SET R. paramirabilis
  2      3   .929E+01  .744E+01  .611E+01
  2      2   .257E+02  .403E+01  .152E+02
  2      2   .325E+02  .496E+01  .752E+01
  2      2   .103E+02  .635E+01  .169E+02
  2      2   .733E+01  .192E+01  .867E+01
  2      3   .266E+02  .975E+01  .710E+01
  2      2   .206E+02  .272E+01  .123E+02

CLASS  ACTUAL    EXPONENT FOR TRAINING SET R. septentrionalis
  3      3   .194E+02  .108E+02  .471E+01
  3      3   .426E+02  .183E+02  .671E+01
  3      3   .369E+02  .113E+02  .491E+01
  3      3   .308E+02  .923E+01  .263E+01
  3      3   .169E+02  .395E+01  .168E+01
  3      2   .129E+02  .483E+01  .532E+01
  3      3   .224E+02  .122E+02  .434E+01
  3      3   .251E+02  .102E+02  .804E+01
  3      3   .245E+02  .174E+02  .127E+02

 CLASSIFICATION MATRIX
CLASS SAMPLES        1     2     3
  1       7          7     0     0
  2       7          0     5     2
  3       9          0     1     8
```

Explained in text, pg. 35.

```
MEAN EQUALITY  DEGS OF FREE.   12 CHI SQUARE      98.
```

APPENDIX B

DISCRIMINANT ANALYSIS RESULTS FOR SPECIES OF *RABILIMIS* AND *ECHINOCYTHEREIS*

DISCRIMINANT ANALYSIS RESULTS FOR SPECIES OF <u>RABILIMIS</u> AND <u>ECHINOCYTHEREIS</u>

~~Refer to Appendix A,~~ pg. 52, for explanation of output.

```
  V     T    S1    S2    S3    S4    S5    S6    S7    S8    S9   S10     C
  6     4     7     7     9     4    -0    -0    -0    -0    -0    -0     0          (6F7,5/)
TRAINING CLASS    1
```

Training Class 1: R. mirabilis

```
,01436 ,22169 ,06181 ,02863 ,03195 ,01266

,01670 ,22431 ,07019 ,03250 ,03362 ,01123

,01394 ,20790 ,06623 ,02936 ,03338 ,01412

,01502 ,24775 ,05923 ,03275 ,04162 ,01476

,01056 ,19179 ,05468 ,03437 ,01298 ,01028

,01288 ,23470 ,05169 ,02882 ,02559 ,01781

,01564 ,19507 ,07803 ,03424 ,01794 ,01707

TRAINING CLASS    2
```

Training Class 2: <u>R. paramirabilis</u>

```
,00860 ,25316 ,03681 ,03054 ,03080 ,01718

,01403 ,32253 ,05006 ,03464 ,03148 ,02640

,01287 ,34035 ,04335 ,03702 ,02995 ,02110

,01118 ,23997 ,05376 ,03024 ,01896 ,02579

,01145 ,25090 ,05070 ,02902 ,02267 ,01997

,01584 ,32717 ,05010 ,03977 ,02416 ,00618

,01632 ,30922 ,05951 ,03472 ,02315 ,01791

TRAINING CLASS    3
```

Training Class 3: <u>R. septentrionalis</u>

```
,00461 ,24338 ,02452 ,02559 ,02191 ,01611

,00648 ,31889 ,02462 ,04351 ,01985 ,02088

,00358 ,28859 ,01688 ,02991 ,01738 ,02250

,00628 ,29686 ,02293 ,03590 ,01434 ,01847

,01311 ,30526 ,04812 ,04036 ,02546 ,01493
,01464 ,29327 ,05173 ,03407 ,03128 ,00951

,00575 ,26328 ,02342 ,03389 ,01361 ,01445

,01275 ,27236 ,05367 ,03006 ,01486 ,00839

,01541 ,34423 ,04632 ,05542 ,03599 ,01636

TRAINING CLASS    4
```

Training Class 4: <u>Echinocythereis</u>

```
,01121 ,27942 ,04714 ,03612 ,02774 ,01218

,01092 ,26851 ,04326 ,01925 ,02444 ,01638

,01201 ,29340 ,04558 ,02943 ,02878 ,01626

,01394 ,28796 ,05281 ,03610 ,03312 ,01085
```

Refer to Appendix A, pg. 53' for explanation of output.

```
MEANS FOR EACH TRAINING CLASS
 .01416     ,01290     ,00918     ,01202
 .21760     ,29190     ,29179     ,28232
 .06312     ,04918     ,03469     ,04720
 .03152     ,03371     ,03652     ,03022
 .02815     ,02588     ,02185     ,02852
 .01399     ,01920     ,01573     ,01392

COVARIANCE MATRIX
 ,00001   ,00005   ,00003   ,00001   ,00001  -,00001
 ,00005   ,00091   ,00003   ,00013   ,00012  -,00000
 ,00003   ,00003   ,00011   ,00002   ,00002  -,00002
 ,00001   ,00013   ,00002   ,00004   ,00002  -,00000
 ,00001   ,00012   ,00002   ,00002   ,00006  -,00000
-,00001  -,00000  -,00002  -,00000  -,00000   ,00002

INVERSE OF COVARIANCE
3658453, -162642, -870758,   71211, -170935,  335595,
-162642,    9681,   39616,   -9573,    4000,  -15283,
-870758,   39616,  218710,  -22562,   36903,  -71586,
  71211,   -9573,  -22562,   46060,   -1489,    9227,
-170935,    4000,   36903,   -1489,   33914,  -16498,
 335595,  -15283,  -71586,    9227,  -16498,   82120,

INVERSE CHECK   DETERMINATE  ,46439E-27  TOTAL SAMPLES  27
 1,00000  -,00000  -,00000  -,00000  -,00000   ,00000
  ,00000  1,00000   ,00000   ,00000   ,00000  -,00000
 -,00000  -,00000  1,00000   ,00000  -,00000   ,00000
 -,00000   ,00000   ,00000  1,00000   ,00000   ,00000
  ,00000   ,00000   ,00000   ,00000  1,00000  0,00000
 -,00000  -,00000  -,00000  -,00000  -,00000  1,00000
```

R. mirabilis

```
CLASS  ACTUAL   EXPONENT FOR TRAINING SET
  1      1   ,955E+00  ,150E+02  ,229E+02  ,159E+02
  1      1   ,999E+00  ,190E+02  ,283E+02  ,210E+02
  1      1   ,356E+01  ,198E+02  ,278E+02  ,179E+02
  1      1   ,405E+01  ,162E+02  ,242E+02  ,169E+02
  1      1   ,745E+01  ,240E+02  ,233E+02  ,271E+02
  1      1   ,710E+01  ,162E+02  ,257E+02  ,259E+02
  1      1   ,757E+01  ,253E+02  ,373E+02  ,333E+02
```

R. paramirabilis

```
CLASS  ACTUAL   EXPONENT FOR TRAINING SET
  2      4   ,105E+02  ,781E+01  ,692E+01  ,597E+01
  2      2   ,272E+02  ,416E+01  ,146E+02  ,120E+02
  2      2   ,364E+02  ,552E+01  ,501E+01  ,705E+01
  2      2   ,107E+02  ,722E+01  ,178E+02  ,172E+02
  2      2   ,762E+01  ,217E+01  ,371E+01  ,633E+01
  2      3   ,304E+02  ,109E+02  ,782E+01  ,104E+02
  2      2   ,217E+02  ,277E+01  ,115E+02  ,957E+01
```

R. septentrionalis

```
CLASS  ACTUAL   EXPONENT FOR TRAINING SET
  3      3   ,219E+02  ,118E+02  ,532E+01  ,648E+01
  3      3   ,457E+02  ,163E+02  ,632E+01  ,163E+02
  3      3   ,412E+02  ,125E+02  ,523E+01  ,111E+02
  3      3   ,347E+02  ,103E+02  ,272E+01  ,130E+02
  3      3   ,188E+02  ,290E+01  ,184E+01  ,363E+01
  3      4   ,147E+02  ,518E+01  ,577E+01  ,241E+01
  3      3   ,255E+02  ,136E+02  ,478E+01  ,154E+02
  3      4   ,284E+02  ,110E+02  ,917E+01  ,616E+01
  3      3   ,260E+02  ,156E+02  ,132E+02  ,228E+02
```

APPENDIX C

DISCRIMINANT ANALYSIS RESULTS FOR GENERA OF BAIRDIIDAE

DISCRIMINANT ANALYSIS RESULTS FOR GENERA OF BAIRDIIDAE

```
 V    T   S1   S2   S3   S4   S5   S6   S7   S8   S9  S10   C
 6    4   11    7    5    4   .0   .0   .0   .0   .0   .0   0                (6F8,5/)
TRAINING CLASS   1
 ,01213   ,19471   ,05158   ,04803   ,01377   ,02652
 ,01072   ,23956   ,03878   ,05508   ,02140   ,01602
 ,00822   ,20631   ,03809   ,06825   ,01319   ,02108
 ,01179   ,25073   ,04727   ,06224   ,02151   ,02694
 ,01544   ,21934   ,06808   ,06504   ,03057   ,04075
 ,03008   ,28209   ,10148   ,08183   ,04318   ,03623
 ,01198   ,21305   ,05176   ,06097   ,03181   ,02751
 ,01305   ,18851   ,06682   ,03953   ,02527   ,02751
 ,02992   ,30584   ,08036   ,05431   ,04164   ,03313
 ,02625   ,28914   ,07444   ,04468   ,03154   ,02281
 ,03200   ,42536   ,05818   ,12647   ,04377   ,05498
```

Training Class 1:
Bairdia

```
TRAINING CLASS   2
 ,01440   ,22223   ,05911   ,05789   ,01150   ,02120
 ,01469   ,21201   ,05822   ,05699   ,01705   ,02027
 ,01278   ,22398   ,04976   ,05791   ,01897   ,02320
 ,01451   ,26733   ,04900   ,06992   ,01388   ,02825
 ,01722   ,23861   ,05977   ,07279   ,01946   ,03373
 ,00787   ,25870   ,02315   ,03208   ,01375   ,02148
 ,01181   ,25893   ,03575   ,06410   ,01370   ,02937
```

Training Class 2:
Orthobairdia

```
TRAINING CLASS   3
 ,01642   ,35442   ,03434   ,06555   ,02999   ,01545
 ,05184   ,44178   ,07788   ,09167   ,06077   ,01103
 ,03752   ,40006   ,06573   ,08208   ,05189   ,01424
 ,01468   ,19326   ,07217   ,01942   ,01657   ,01280
 ,02256   ,22034   ,09635   ,04094   ,02947   ,00629
```

Training Class 3:
Bairdiacypris

```
TRAINING CLASS   4
 ,01212   ,28583   ,03863   ,05734   ,01348   ,00658
 ,00982   ,23070   ,04028   ,04296   ,01021   ,01087
 ,00919   ,14732   ,05302   ,03726   ,00743   ,01890
 ,02888   ,33616   ,07257   ,07870   ,04138   ,02834
```

Training Class 4:
Cryptobairdia

```
  MEANS FOR EACH TRAINING CLASS
   ,01833      ,01333      ,02860      ,01500
   ,25588      ,24026      ,32197      ,25000
   ,06153      ,04782      ,06929      ,05112
   ,06422      ,05881      ,05993      ,05406
   ,02888      ,01547      ,03774      ,01812
   ,03032      ,02536      ,01196      ,01617
```

Refer to pg. 53 for
explanation of output.

```
 COVARIANCE MATRIX
 ,00009   ,00054   ,00010   ,00014   ,00011   ,00004
 ,00054   ,00513   ,00003   ,00129   ,00068   ,00029
 ,00010   ,00003   ,00033   ,00004   ,00010   ,00004
 ,00014   ,00129   ,00004   ,00349   ,00019   ,00012
 ,00011   ,00068   ,00010   ,00019   ,00014   ,00005
 ,00004   ,00029   ,00004   ,00012   ,00005   ,00007

 INVERSE OF COVARIANCE
166561,  -12231,  -39700,   -3537,  -40536,   22382,
-12231,    2174,    4724,   -1192,   -2584,   -1428,
-39700,    4724,   16888,    1137,   -3739,   -7876,
 -3537,   -1192,    1137,    7763,     -81,   -6781,
-40536,   -2584,   -3739,     -81,   54201,   -5772,
 22382,   -1428,   -7876,   -6781,   -5772,   28459,

 INVERSE CHECK   DETERMINATE   ,14758E-28  TOTAL SAMPLES  27
1.00000  -,00000  -,00000  -,00000  -,00000  -,00000
-,00000  1,00000   ,00000  -,00000  -,00000  -,00000
0.00000   ,00000  1,00000   ,00000   ,00000  -,00000
 ,00000   ,00000  0,00000  1,00000   ,00000  -,00000
 ,00000   ,00000   ,00000   ,00000  1,00000   ,00000
-.00000  0,00000  -,00000  -,00000  -,00000  1,00000

CLASS  ACTUAL   EXPONENT FOR TRAINING SET                    Bairdia
   1     2   ,467E+01   ,183E+01   ,203E+02   ,679E+01
   1     4   ,436E+01   ,674E+01   ,832E+01   ,403E+01
   1     2   ,667E+01   ,461E+01   ,189E+02   ,627E+01
   1     1   ,124E+01   ,311E+01   ,122E+02   ,399E+01
   1     1   ,401E+01   ,124E+02   ,278E+02   ,183E+02
   1     1   ,673E+01   ,147E+02   ,149E+02   ,137E+02
   1     1   ,742E+01   ,185E+02   ,231E+02   ,192E+02
   1     1   ,224E+01   ,912E+01   ,160E+02   ,107E+02
   1     1   ,569E+01   ,117E+02   ,129E+02   ,126E+02
   1     4   ,759E+01   ,819E+01   ,680E+01   ,614E+01
   1     1   ,132E+02   ,143E+02   ,352E+02   ,224E+02

 CLASS  ACTUAL   EXPONENT FOR TRAINING SET                   Orthobairdia
   2     2   ,919E+01   ,233E+01   ,151E+02   ,312E+01
   2     2   ,408E+01   ,167E+01   ,111E+02   ,190E+01
   2     2   ,163E+01   ,149E+01   ,118E+02   ,267E+01
   2     2   ,835E+01   ,170E+01   ,186E+02   ,464E+01
   2     2   ,494E+01   ,200E+01   ,222E+02   ,765E+01
   2     2   ,107E+02   ,847E+01   ,197E+02   ,107E+02
   2     2   ,626E+01   ,110E+01   ,214E+02   ,624E+01

 CLASS  ACTUAL   EXPONENT FOR TRAINING SET                   Bairdiacypris
   3     3   ,147E+02   ,171E+02   ,760E+01   ,965E+01
   3     3   ,326E+02   ,342E+02   ,120E+02   ,243E+02
   3     3   ,169E+02   ,220E+02   ,254E+01   ,125E+02
   3     4   ,102E+02   ,940E+01   ,740E+01   ,537E+01
   3     3   ,225E+02   ,264E+02   ,727E+01   ,145E+02

 CLASS  ACTUAL   EXPONENT FOR TRAINING SET                   Cryptobairdia
   4     4   ,194E+02   ,132E+02   ,876E+01   ,540E+01
   4     4   ,952E+01   ,401E+01   ,800E+01   ,824E+00
   4     2   ,834E+01   ,371E+01   ,207E+02   ,714E+01
   4     1   ,333E+01   ,810E+01   ,485E+01   ,530E+01

   CLASSIFICATION MATRIX
 CLASS SAMPLES        1     2     3     4
   1      11          7     2     0     2          Explained in text, pg. 44.
   2       7          0     7     0     0
   3       5          0     0     4     1
   4       4          1     1     0     2

MEAN EQUALITY   DEGS OF FREE,    18 CHI SQUARE      70,
```

Echinocythereis

```
CLASS  ACTUAL   EXPONENT FOR TRAINING SET
  4      4    ,234E+02   ,106E+02   ,625E+01   ,357E+01
  4      4    ,232E+02   ,688E+01   ,126E+02   ,547E+01
  4      4    ,215E+02   ,307E+01   ,541E+01   ,616E+00
  4      4    ,155E+02   ,674E+01   ,612E+01   ,168E+01

   CLASSIFICATION MATRIX
 CLASS SAMPLES          1      2      3      4
    1        7          7      0      0      0
    2        7          0      5      1      1
    3        9          0      0      7      2
    4        4          0      0      0      4

MEAN EQUALITY  DEGS OF FREE,   1M CHI SQUARE    120,
```

Explained in text, pg. 41.

APPENDIX D

DISCRIMINANT ANALYSIS RESULTS FOR GENERA OF HEMICYTHERIDAE

DISCRIMINANT ANALYSIS RESULTS
FOR GENERA OF HEMICYTHERIDAE

```
  V     T   S1    S2    S3    S4    S5    S6    S7    S8    S9  S10     C
  6     6    4     3     3     4     8     4    -0    -0    -0   -0     0                 (6F7.5/)
TRAINING CLASS    1                                                       Hemicythere
.00596 .26811 .03030 .01250 .02060 .00920

.01442 .29375 .05615 .04161 .02028 .00599

.01356 .28107 .04826 .03463 .02425 .00124

.01118 .32314 .04353 .04481 .02165 .01170

TRAINING CLASS    2                                                       Elofsonella
.02743 .32727 .06250 .03977 .02898 .01743

.01784 .29965 .05354 .02459 .01875 .00891

.01613 .28334 .05863 .03086 .02474 .00391

TRAINING CLASS    3                                                       Baffincythere
.01981 .29620 .06079 .04254 .02414 .01598

.02852 .31900 .04497 .05092 .03812 .00164

.02397 .41968 .04235 .06609 .04918 .00389

TRAINING CLASS    4                                                       Finmarchinella
.03489 .42767 .07390 .09639 .03681 .00416

.02400 .32571 .06410 .03470 .03907 .01054

.02179 .30335 .07032 .02015 .03633 .00435

.01487 .31356 .04677 .02480 .03279 .01667

TRAINING CLASS    5                                                       Muellerina
.02284 .39329 .05987 .05524 .03876 .00691

.02207 .39209 .06697 .05602 .03787 .00545

.01838 .35819 .05962 .02773 .04778 .00762

.01403 .36350 .04465 .04835 .03022 .00901
.01148 .39608 .03288 .05496 .02722 .01254

.01839 .34550 .06807 .02904 .03146 .00732

.02279 .40061 .06419 .07187 .02980 .00725

.02088 .36719 .05371 .03342 .03282 .01825

TRAINING CLASS    6                                                       Bensonocythere
.01176 .34386 .02961 .03941 .01359 .00513

.01025 .37383 .02964 .06332 .02002 .00433

.00301 .33093 .00950 .03821 .01561 .01498

.01684 .33926 .05742 .02498 .02158 .01553
```

Refer to pg. 53 for explanation of output.

```
MEANS FOR EACH TRAINING CLASS
 .01128    .02047    .02410    .02389    .01882    .01046
 .29153    .30342    .34496    .34257    .37704    .34697
 .04456    .05822    .05604    .06377    .05624    .03154
 .03339    .03174    .05318    .04401    .04708    .04148
 .02169    .02416    .03715    .03625    .03449    .01770
 .00703    .01005    .00717    .00893    .00929    .00999

COVARIANCE MATRIX
 .00003   .00010   .00005   .00005   .00001  -.00001
 .00010   .00124  -.00001   .00058   .00008  -.00004
 .00005  -.00001   .00017   .00002   .00002  -.00002
 .00005   .00058   .00002   .00036   .00001  -.00004
 .00001   .00008   .00002   .00001   .00004  -.00001
-.00001  -.00004  -.00002  -.00004  -.00001   .00003

INVERSE OF COVARIANCE
 240249.  -10414.  -74464.  -15616.  -33738.  -23680.
 -10414.    6339.    5221.   -9126.  -11531.   -5315.
 -74464.    5221.   30273.    1507.    4306.    8220.
 -15616.   -9126.    1507.   20447.   24238.   15865.
 -33738.  -11531.    4306.   24238.   63436.   27156.
 -23680.   -5315.    8220.   15865.   27156.   51251.

INVERSE CHECK   DETERMINATE  .36275E-25  TOTAL SAMPLES  26
1.00000  -.00000  -.00000  -.00000  -.00000  -.00000
-.00000  1.00000   .00000   .00000  -.00000  -.00000
 .00000  -.00000  1.00000  -.00000   .00000  -.00000
 .00000   .00000   .00000  1.00000   .00000  0.00000
 .00000   .00000   .00000  -.00000  1.00000  -.00000
0.00000   .00000  -.00000   .00000  0.00000  1.00000

CLASS  ACTUAL   EXPONENT FOR TRAINING SET                  Hemicythere
  1     1   .303E+01  .824E+01  .179E+02  .161E+02  .221E+02  .110E+02
  1     1   .134E+01  .788E+01  .143E+02  .109E+02  .177E+02  .169E+02
  1     1   .256E+01  .807E+01  .111E+02  .128E+02  .267E+02  .219E+02
  1     1   .334E+01  .115E+02  .169E+02  .108E+02  .973E+01  .113E+02

CLASS  ACTUAL   EXPONENT FOR TRAINING SET                  Elofsonella
  2     2   .215E+02  .659E+01  .569E+01  .930E+01  .297E+02  .319E+02
  2     2   .109E+02  .376E+01  .218E+02  .161E+02  .210E+02  .822E+01
  2     1   .168E+01  .475E+01  .102E+02  .795E+01  .185E+02  .185E+02

CLASS  ACTUAL   EXPONENT FOR TRAINING SET                  Baffincythere
  3     3   .102E+02  .941E+01  .804E+01  .848E+01  .267E+02  .333E+02
  3     3   .236E+02  .159E+02  .557E+01  .142E+02  .456E+02  .521E+02
  3     3   .275E+02  .247E+02  .107E+02  .110E+02  .171E+02  .331E+02

CLASS  ACTUAL   EXPONENT FOR TRAINING SET                  Finmarchinella
  4     4   .240E+02  .163E+02  .967E+01  .841E+01  .186E+02  .325E+02
  4     4   .139E+02  .862E+01  .238E+01  .122E+01  .165E+02  .321E+02
  4     4   .105E+02  .722E+01  .102E+02  .394E+01  .113E+02  .230E+02
  4     4   .934E+01  .977E+01  .777E+01  .393E+01  .110E+02  .218E+02

CLASS  ACTUAL   EXPONENT FOR TRAINING SET                  Muellerina
  5     5   .180E+02  .170E+02  .167E+02  .714E+01  .107E+01  .171E+02
  5     5   .227E+02  .257E+02  .272E+02  .138E+02  .161E+01  .219E+02
  5     5   .274E+02  .310E+02  .242E+02  .135E+02  .741E+01  .353E+02
  5     5   .956E+01  .155E+02  .188E+02  .996E+01  .187E+01  .950E+01
  5     5   .212E+02  .268E+02  .347E+02  .228E+02  .516E+01  .791E+01
  5     5   .221E+02  .234E+02  .352E+02  .186E+02  .378E+01  .145E+02
  5     5   .176E+02  .197E+02  .243E+02  .129E+02  .296E+01  .151E+02
  5     5   .229E+02  .140E+02  .219E+02  .109E+02  .581E+0   .150E+02

CLASS  ACTUAL   EXPONENT FOR TRAINING SET                  Bensonocythere
  6     6   .263E+02  .231E+02  .480E+02  .405E+02  .320E+02  .569E+01
  6     6   .115E+02  .199E+02  .306E+02  .239E+02  .132E+02  .339E+01
  6     6   .123E+02  .189E+02  .305E+02  .273E+02  .229E+02  .531E+01
  6     6   .236E+02  .191E+02  .397E+02  .233E+02  .936E+01  .874E+01
```

```
   CLASSIFICATION MATRIX
  CLASS SAMPLES           1     2     3     4     5     6
    1          4          4     0     0     0     0     0
    2          3          1     2     0     0     0     0
    3          3          0     0     3     0     0     0
    4          4          0     0     0     4     0     0
    5          8          0     0     0     0     8     0
    6          4          0     0     0     0     0     4

 MEAN EQUALITY  DEGS OF FREE.    30 CHI SQUARE     151.
```

Explained in text, pg. 46.