Approaches To Systematic And Evolutionary Studies Of Perplexing Groups: An Example Using Fenestrate Bryozoa

By: **Steven J. Hageman**

Abstract

Recognition of discrete taxa is an enduring problem in the biological sciences, especially for taxonomists who work with groups that display a great degree of homeomorphy at low taxonomic levels. Selection of the type and number of characters used to make taxonomic distinctions is important because it reflects taxonomic concepts for a group as a whole. Often the validity of characters used to develop classifications is not documented and resulting classifications are therefore suspect. However, classifications can be tested for their objectivity with numerical analysis and characters can be evaluated for their relative value for making taxonomic splits by a variety of statistical techniques. In addition, evaluation of the distribution of character states can lead to insights into evolutionary histories of any group. This study provides such an analysis. Fenestrate cryptostome Bryozoa are abundant and diverse in many upper Paleozoic rocks, and are therefore potentially highly useful for a variety of paleontologic studies. However, study of fenestrates is hampered by necessary complex preparation techniques and problems encountered with homeomorphy. In addition, inconsistent applications of inadequate methodologies have contributed to an unsatisfactory taxonomy. Results from cluster and discriminant analyses demonstrate that fenestrate species can be objectively recognized. Species distinctions are most clear when all available characters are used, although some characters are more diagnostic than others.

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APPROACHES TO SYSTEMATIC AND EVOLUTIONARY STUDIES OF PERPLEXING GROUPS: AN EXAMPLE USING FENESTRATE BRYOZOA

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ABSTRACT—Recognition of discrete taxa is an enduring problem in the biological sciences, especially for taxonomists who work with groups that display a great degree of homeomorphy at low taxonomic levels. Selection of the type and number of characters used to make taxonomic distinctions is important because it reflects taxonomic concepts for a group as a whole. Often the validity of characters used to develop classifications is not documented and resulting classifications are therefore suspect. However, classifications can be tested for their objectivity with numerical analysis and characters can be evaluated for their relative value for making taxonomic splits by a variety of statistical techniques. In addition, evaluation of the distribution of character states can lead to insights into evolutionary histories of any group. This study provides such an analysis.

Fenestrate cryptostome Bryozoa are abundant and diverse in many upper Paleozoic rocks, and are therefore potentially highly useful for a variety of paleontologic studies. However, study of fenestrates is hampered by necessary complex preparation techniques and problems encountered with homeomorphy. In addition, inconsistent applications of inadequate methodologies have contributed to an unsatisfactory taxonomy. Results from cluster and discriminant analyses demonstrate that fenestrate species can be objectively recognized. Species distinctions are most clear when all available characters are used, although some characters are more diagnostic than others.

Results from cluster and discriminant analyses suggest that fenestrate genera represent major evolutionary shifts associated with the development of key character(s) that allowed entry into new adaptive zones. Key characters allow for an oligothetic classification of genera, which is not merely an artifact created to simplify taxonomic analysis. Diversification of species within adaptive zones resulted in a natural hierarchy of genus-level and species-level characters. Iterative evolution at the species level within separate adaptive zones resulted in a great deal of homeomorphy.

Morphometric analysis provides insights into several aspects of the paleobiology of this traditionally problematic group. Similar comprehensive studies may prove equally productive for other groups.

INTRODUCTION

THE GOAL of the work reported here was to refine taxonomic procedures for the suborder Fenestellina (Cryptostomata, Bryozoa, sensu Blake (1975), hereafter referred to as "fenestrate(s)"). Fenestrate abundance and diversity in many middle and upper Paleozoic rocks means that they are potentially highly useful for students of evolution, paleoecology, and biostratigraphy; however, they are a perplexing group in the sense that they have long resisted viable classification.

Numerical methods were employed to address a series of questions about fenestrates. 1) Can discrete taxa be objectively recognized? If so, are they real (i.e., monophyletic) or artificial (i.e., morphological conveniences)? 2) Which types of characters are most useful for making taxonomic distinctions? 3) How many characters are required to make taxonomic distinctions? 4) Can the same types of characters be used to make taxonomic distinctions at different taxonomic levels? 5) What are the character distributions among taxa and how can they be interpreted?

Numerical approaches proved productive, implying that other taxa could benefit from similar applications. The accessibility of relatively powerful statistical programs for new microcomputers means that numerical methods can now become a standard part of routine taxonomic procedures.

The purposes of this paper are fourfold: 1) to review the historical development of fenestrate species concepts in order to illustrate difficulties encountered in exploiting their rich and potentially valuable fossil record; 2) to discuss concepts behind numerical methods employed in this study, including the information that the methods provide, and how that information may be interpreted; 3) to demonstrate how these methods were applied in a study of a Mississippian fenestrate fauna; and 4) to discuss interpretations and their consequences for future studies of fenestrate Bryozoa.

FENESTRATE SPECIES CONCEPTS

Fenestrates have long been mistreated taxonomically. With over 2,000 species assigned to *Fenestella* (Morozova, 1974), they are the epitome of a group plagued by homeomorphy and inconsistent application of inadequate taxonomic concepts.

Over the past 150 years, fenestrate species concepts have been ambiguous because different authors have emphasized different sets of taxonomic characters, often with unclear justification for their character selection. Many authors have avoided dealing with ill-defined species concepts in a variety ways: 1) genera were used as the working taxonomic unit, and species names were avoided (e.g., *Fenestella* sp. is frequently found in the literature); 2) the names of superficially similar species were often applied without adequate comparison; or 3) new, equally ambiguous, species were named, thereby perpetuating the taxonomic trauma.

Early workers employed general descriptions of exterior features (e.g., Lonsdale, 1839; M'Coy, 1844; Hall, 1857; Prout, 1859). Building upon the work of Nicholson and Lydekker (1889), who apparently were the first to study fenestrates in thin section, Ulrich (1890) emphasized the value of interior features. Ulrich (1890) employed quantitative ranges of values for exterior features, such as number of branches in 10 mm, number of fenestrules in 10 mm, number of nodes in 5 mm, and number of apertures in 5 mm. These characters, used by Nekhoroshev (1928) and subsequent Soviet workers, make up the so-called "meshwork formula" of Condra and Elias (1944), or the "micrometric formula" of Miller (1961), which are really shorthand notations rather than true formulae.

Regrettably, later western workers did not follow Ulrich's methods of interior analysis, but instead emphasized meshwork formulae, which are of low discriminatory power. The greatest weakness of meshwork formulae is that zooecial characters are neglected. For example, Snyder (1991, Pl. 1:1–12 and Pl. 9:3–11) illustrated two specimens with similar exteriors, but very different zooecial shapes, sizes, and orientations. The interiors of the two specimens clearly demonstrate affinities with separate genera (Snyder, 1984, 1991). Miller (1961) demonstrated the inadequacy of the meshwork formula to characterize the external appearance of fenestrates. Two taxa with very similar mesh-

work formulae but distinctly different exteriors are illustrated in Figure 1. Nevertheless, many fenestrate species have been based on small differences in their formulae (e.g., Cumings, 1906; McNair, 1942; Elias and Condra, 1957; Koenig, 1958; Burckle, 1960; Malone and Perry, 1965; Simonsen and Cuffey, 1980; Yang et al., 1988). Problems encountered with poor species concepts are compounded by the fact that many species have been described from single zoarial fragments, without regard for intraspecific variation.

Beginning with Nekhoroshev (1928), Soviet workers have emphasized interior characters, successfully applying their work in a long series of biostratigraphic studies of strata in the U.S.S.R. and surrounding countries. Morozova (e.g., 1962, 1974) developed a consistent descriptive format that included mesh type, branch width, fenestrule shape, dissepiment width, zooecial shape in median (tangential) section, apertural features, carina (keel), nodes, and heterozooecia. Whereas the consistency of Morozova's treatment was an improvement over that of previous works, adherence to ranges, reliance solely on median tangential sections, ambiguity of relative dimensional terms, and minimal exterior analysis were limiting factors.

Malone and Perry (1965) recognized the limitations of ranges to describe the variability of meshwork characters, but Tavener-Smith (1966) was the first to apply parametric statistical analysis to fenestrate taxonomy. He provided ranges, means, standard deviations, and coefficients of variance for each taxon. He expanded the list of characters, making distinctions between colonial and zooecial characters; under zooecial features, he included inter-apertural distance, branch width, apertural diameter, and zooecial-chamber shape and size. Colonial features included fenestrule length, number of apertures per fenestrule, internodal distance, and dissepiment width. Although Tavener-Smith (1966) established statistical credibility for fenestrate taxonomic analysis, his reliance primarily on exterior features, due to the silicified nature of his fauna, limits applicability of his work.

In a comprehensive study of the fenestrate fauna of the Warsaw Formation (Osagean–Meramecian) of the Mississippi River Valley, Snyder (1984, 1991) significantly improved the taxonomic treatment of fenestrates. Snyder recommended a research strategy that included consistent evaluation of an expanded list of interior and exterior morphometric characters on populations of at least 10 specimens. He defined terms more precisely by providing ranges of variation that were used in formatted taxonomic descriptions. Snyder emphasized the importance of the three-dimensional zooecial shape; he demonstrated this by illustrating two specimens with similar appearances in tangential sections, but significantly different reverse wall budding angles (Snyder, 1991, text fig. 3). Snyder (1984, 1991) was the first to comprehensively collect data for virtually every morphometric character available (total of 47 characters; see Appendix A), and from a large number of specimens (approximately 680) from a diverse fenestrate fauna (37 species and 11 genera; see Appendix B).

Problems encountered with species concepts, including the large number of nominal species assigned to the form genus *Fenestella,* raise the question of whether or not recognizable fenestrate bryozoan species-level morphs can be identified. Snyder's (1984) large morphometric data set, for the first time, provides an opportunity for the quantitative evaluation of fenestrate species concepts and the relative value of characters.

MATERIALS AND METHODS

As exemplified here, procedures for working with a taxonomically difficult group can be divided into two major parts. The first, which is a refinement of traditional taxonomic procedures, is further subdivided into three parts as follows: 1) qualitative sorting of specimens into groups of similar morphs; 2) exhaustive character evaluation that includes recognition and data collection for all available characters (morphometric, discrete and qualitative) in a consistent format; and 3) resorting of specimens based on information gained from Step 2.

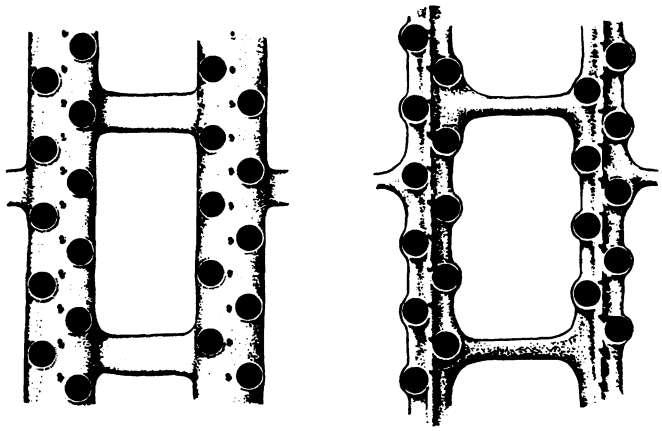

FIGURE 1—Idealized reconstruction of two fenestrate taxa that have very similar values for their meshwork formulae, but have distinctly different exteriors (from Miller, 1961, fig. 1, p. 223), approx. ×30.

This sequence maximizes the worker's familiarity with phenotypes, while minimizing the perplexity that results from complex character states. The procedure is discussed in detail in Snyder (1991), where it is applied to a fenestrate fauna.

The second part of this approach involves a series of numerical analyses designed to: 1) determine whether the proposed classification is objective; 2) determine which characters are most important for making taxonomic distinctions; and 3) investigate character distributions for phylogenetic and other biologic information. Adjustments are then made to original groups based on insights gained from numerical analyses and a formal taxonomy is proposed.

Overview of numerical methods.—Although it is not the purpose of this paper to introduce the mathematics behind the numerical methods employed here, a brief introduction to the concepts is provided for those unfamiliar with the techniques. Explanations of numerical methods provided here are much simplified. A variety of statistical approaches exists for each of these analyses, and many factors must be taken into consideration when employing these methods. The purpose of this discussion is merely to show that the concepts behind the methods are relatively straightforward and often intuitively obvious. The utility of these methods has been demonstrated in many paleontologic studies. Recent examples include approaches to the recognition of fossil scleractinian coral species (Foster, 1984, 1985), recognition of discrete morphs in a cheilostome bryozoan lineage (Cheetham, 1986), and a study of planktonic foraminiferal chronospecies (Wei, 1988).

The emphasis in the approach taken here goes beyond objective recognition of discrete morphologic groups. The goal is to determine the role that individual characters and character complexes play in distinguishing among groups. This is accomplished in an exploratory manner by varying characters and specimens included in a series of numerical analyses. The more familiar a researcher is with the nature and distribution of available characters within and among groups, the better prepared he or she is to make formal taxonomic distinctions based on criteria that include biologic and phylogenetic considerations. This approach is particularly well suited for paleontologic studies, where the vast majority of taxa are recognized solely on the phenotype of hard parts.

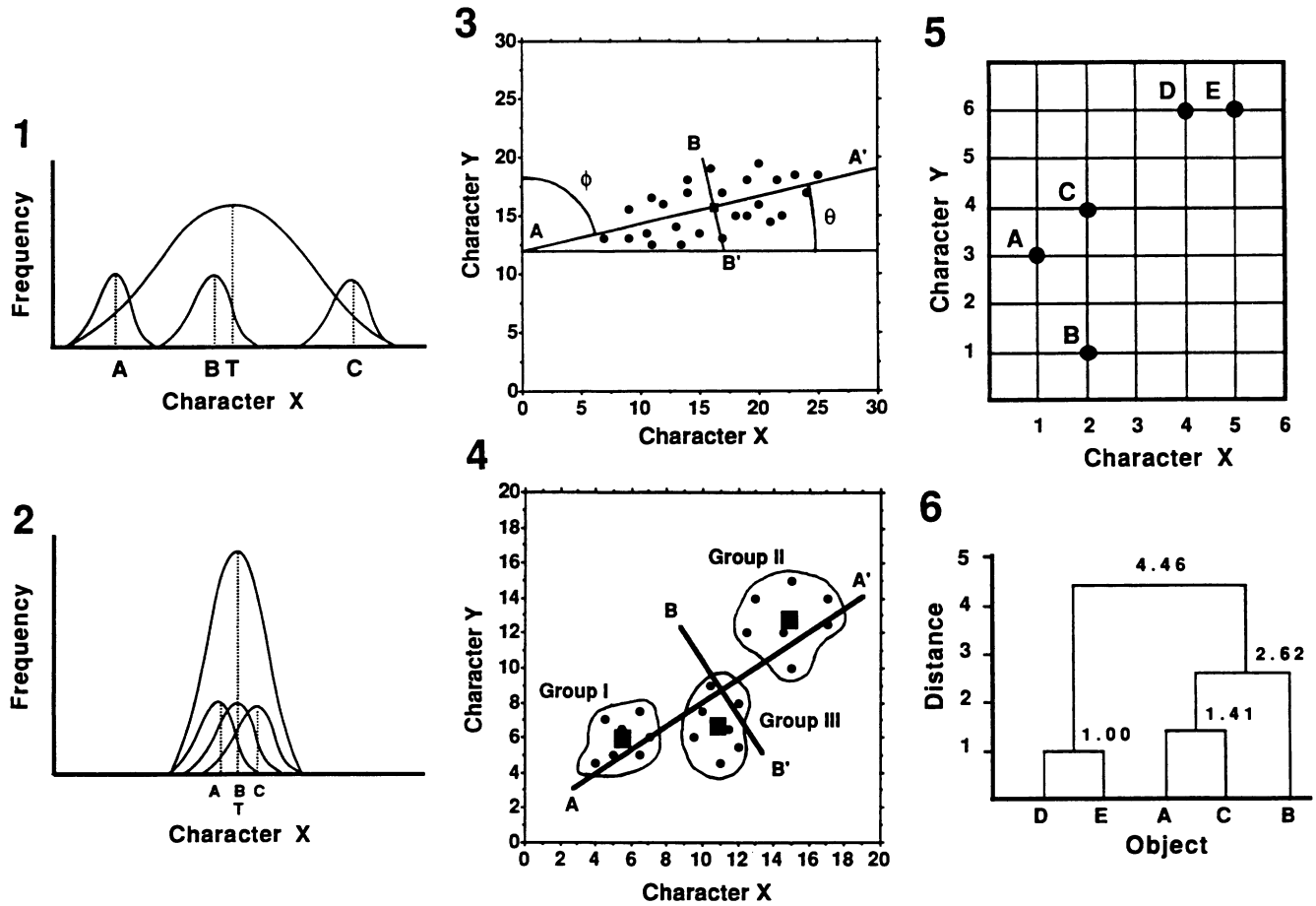

FIGURE 2—*1, 2,* three populations with mean values of A, B, and C, that have an overall mean of T. ANOVA test with constraints of those in *1* would have a large F-ratio, suggesting that multiple populations are present. ANOVA test with constraints of *2* would have a small F-ratio, suggesting that the three populations actually represent random samples from a single population. *3,* scatter diagram of data collected on 25 specimens for two characters; A–A′ is the first principal component (direction of maximum variability in the data cloud), which corresponds to the linear regression line based on variables X and Y; B–B′ is the second principal component (direction of maximum variability orthogonal to first principal component). The cosine of angles Θ and Φ are the coefficients corresponding to variables X and Y respectively in the first principal component. *4,* line segments A–A′ and B–B′ represent the first and second principal components of a canonical analysis; they are based on the mean values (designated by squares) of Groups I, II, and III. *5,* five specimens are plotted in the two-dimensional morphospace of characters X and Y. *6,* a phenogram showing the relative distances between the samples and groups, based on distances shown in Table 1.

In the past, multivariate numerical methods required use of main-frame computers that required a certain degree of programming skills. Today most of these tools are available in user-friendly statistical packages for personal computers that will accept data transferred from spread sheets, or even tables from word processing files. The accessibility of these programs means that numerical methods can become a standard part of routine taxonomic procedures. Data that are regularly collected for the characterization of taxa in formal systematic descriptions now can be more fully utilized in interpretations. Suggested references include Sokal and Rohlf (1981) for univariate methods, Neff and Marcus (1980) for introduction to multivariate concepts, and Johnson and Wichern (1988) for discussion of multivariate methods.

ANOVA.—One Way Analysis of Variance, or ANOVA, treats one character at a time and tests whether multiple populations are independent or whether they represent random samples taken from a single population. For example, in Figure 2.1, there are three populations, which have mean values A, B, and C for a morphometric character X and variances of V_a, V_b, and V_c, respectively. If the observations were treated as though they came from a single population, they would have a mean of T and a variance V_t.

An ANOVA test calculates the ratio of the variance among groups to the variance within groups $[V_t/(V_a + V_b + V_c)]$. This is called the F-ratio, and the larger it is, the more likely it is that the groups represent different populations. Figure 2.2 illustrates an ANOVA test that has a small F-ratio, which implies that there is little difference among the three populations. Tables that provide critical values for F-ratios are available for various levels of confidence limits. Because critical F-values depend on the number of groups and observations involved, relative differences between multiple groups are more important than significance between any two specific groups. Failure to recognize "significant difference" between any two isolated groups can be as much a reflection of the diligence of the worker in data collection as lack of difference between the groups (Foster and Kaesler, 1988).

Figure 2.1 and 2.2 illustrates extreme cases. ANOVA tests only report whether or not multiple populations are present; they do not distinguish how many populations are present. An ANOVA test with three groups could have a significant F-ratio

if two of the groups were identical, but the third was independent. Therefore, post-hoc pair-wise comparisons of means are necessary in order to determine which populations are most similar. Note that this is not the same as performing multiple *t*-tests (two group condition of ANOVA), as multiple *t*-tests propagate errors to such a degree that final conclusions are dubious.

Results from ANOVA tests can provide information about the relative differences between populations, and the separation of the groups in question. They also provide information about the relative importance of the characters themselves. Characters with large F-ratios generally have greater discriminatory power, whereas those with low F-ratios are of little value for distinguishing between morphologic groups (see Figure 2.1 and 2.2).

Canonical analysis.—In order to understand the nature of canonical analysis, one must understand the relationship between principal components and the variance of a population. In multivariate situations an axis exists for each of n characters, and every specimen corresponds to a point in a n-dimensional data cloud. A bivariate example is illustrated in Figure 2.3, which is a scatter plot of hypothetical observations of two morphometric variables X and Y on 25 objects. Note that in Figure 2.3, the dimension of greatest variability (A–A′) within the data ellipse is actually oblique to the X, Y coordinate system. The line that defines the orientation of the maximum variation within the data cloud is known as the first principal component. The second principal component (B–B′) is the line representing the next greatest amount of variation in the data cloud that is perpendicular to the mid-point of the first principal component. For any multivariate data set the number of principal components is equal to the number of variables (as long as each variable is partially independent). One can consider the principal components to be a rotation of the original coordinate system to the orientation that accounts for the most variation within the data cloud.

Any given data point may be transformed by a simple function from its X, Y coordinate system to its value on a principal component axis. Each coefficient in the function is equal to the cosine of the angle between the principal component and the corresponding coefficient's original axis. In Figure 2.3, the first principal component may be found as:

$$\Theta = 13.5°$$
$$\Phi = 76.5°$$
$$PC_1 = (\cos 13.5)X + (\cos 76.5)Y$$
$$PC_1 = 0.97X + 0.23Y$$

Therefore, to find the value of an observation expressed in the scale of the first principal component, its X and Y values are entered into equation 2.

Each principal component contains additional information. The square of each coefficient is the proportion of variation that each of the corresponding original characters provides to the principal component. Therefore, in the example of Figure 2.3, $(\cos 13.5)^2 = 0.95 = 95\%$ of the variance of the first principal component is attributable to the variable X and $(\cos 76.5)^2 = 0.05 = 5\%$ of the variance is attributable to the variable Y. This allows one to quickly determine which characters account for the most variation. In the case of the bivariate plot of Figure 2.3, this information could have been gleaned from visual inspection, but when many variables are involved this relationship is quite valuable. Scatter plots that use principal components as their axes provide more information about the distribution of the data than do plots that employ only raw data because each principal component contains information about many different variables.

Canonical analysis is a special type of principal component analysis in which the observations correspond to group means (i.e., groups that were derived, for example, by sorting according to morphologic similarity; see Figure 2.4). Therefore, the principal components of the canonical analysis correspond to the directions of the most variability *among* groups, and the coefficients of each component are proportional to the relative amount of the variation attributable to the corresponding character. This method highlights characters that are most useful for making distinctions between groups.

TABLE *1*—Euclidean distances between objects in Figure 2.5.

Objects	$(X^2 + Y^2)^{1/2}$ Distance
A–B	$(1^2 + 2^2)^{1/2} = 2.24$
A–C	$(1^2 + 1^2)^{1/2} = 1.41$
A–D	$(3^2 + 3^2)^{1/2} = 4.24$
A–E	$(4^2 + 3^2)^{1/2} = 5.00$
B–C	$(0^2 + 3^2)^{1/2} = 3.00$
B–D	$(2^2 + 5^2)^{1/2} = 5.39$
B–E	$(3^2 + 5^2)^{1/2} = 5.83$
C–D	$(2^2 + 2^2)^{1/2} = 2.83$
C–E	$(3^2 + 2^2)^{1/2} = 3.46$
D–E	$(1^2 + 0^2)^{1/2} = 1.00$

Cluster analysis.—Cluster analysis is a general term for a variety of numerical methods used to classify objects into groups. In its simplest form, cluster analysis can be performed using Euclidean distances between objects in a space defined by their morphologic characters. For example, in Figure 2.5 data are plotted for two morphological characters, X and Y, collected from five specimens. The first step is to calculate the distance of each object from every other object using the Pythagorean Theorem ($X^2 + Y^2 = Z^2$), as shown in Table 1. Distances between the objects can be represented in a graph, where lines link objects at corresponding distances, as in Figure 2.6. The two closest objects (D and E) link at a distance of 1.00 unit. The next closest (A and C) link at a distance of 1.41 units. The next shortest distance is from object B to A, but that distance has to be modified to account for the fact that A has already linked with C. One way to make the modification is to average the distance of B–A and B–C, which equals 2.62. The next shortest distance is D–C, but to account for previous linkages, this is modified by taking the average of D–A, D–B, D–C, E–A, E–B, and E–C, which equals 4.46 units.

The graph in Figure 2.6, known as a phenogram, provides information about the overall similarity of specimens, and may be converted into a hierarchical classification. When numerical taxonomic methods were originally being developed, it was thought that these techniques could be used to generate objective groupings that could be adopted directly as taxonomic classifications. However, there are many different methods of performing cluster analysis, which involve varying the metric used to calculate the distances (i.e., other than Euclidean) and methods for dealing with conversion of a distance matrix to the phenogram. One reason that cluster analysis has failed to replace traditional methods of taxonomic analysis is that different methods produce different results, and no single method can be considered the correct one. However, cluster analysis is a very valuable tool with which to test the objectivity of a proposed classification.

An exploratory investigative method that employs various combinations of characters in a series of cluster analyses (using insights gained from ANOVA and canonical analyses) can provide information about character distributions. Additional information can be obtained by omitting different groups of specimens in a series of cluster analyses to see how their absence affects the grouping structure of other specimens.

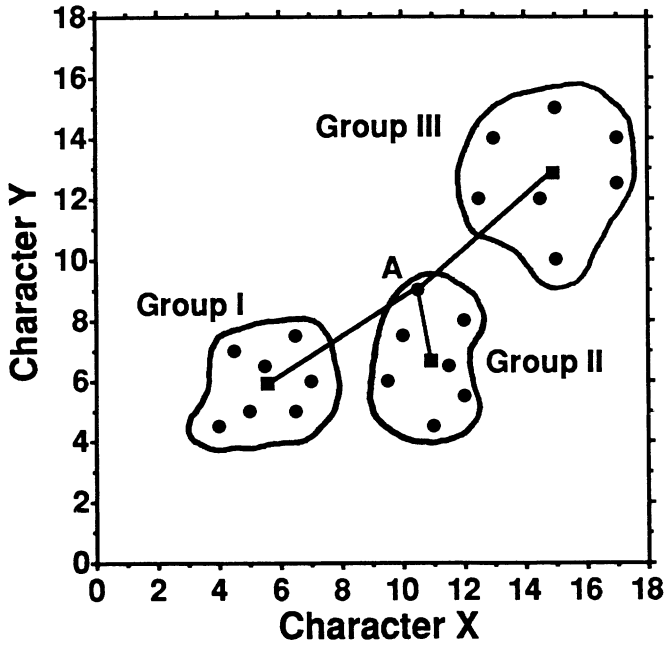

FIGURE 3—Scatter diagram of specimens assigned to three a prori groups. A type of discriminant analysis is performed by calculating the distance between an observation and the mean of each of group, allocating the specimen to the group that has the shortest respective distance and comparing the original group assignments to those based on distances from group means.

Discriminant analysis.—Discriminant analysis is a general term that describes numerical methods that test the ability of a set of variables to discriminate between a priori groups, and the ability of the variables to allocate a number of unclassified objects to those groups. Discriminant analysis is similar to cluster analysis in that it is based on distances between objects in multidimensional space defined by the variables, but in discriminant analysis the groupings have been previously defined, whereas cluster analysis generates groupings.

In the example illustrated in Figure 3, data are plotted for two characters, X and Y, collected from a number of specimens that have been preassigned to three groups (I, II, III), based on some criteria such as scores on principal component axes, cluster analysis, or general qualitative sorting procedure. The mean values for each group are plotted as squares in Figure 3. In its most simple mode, a discriminant analysis can be performed by finding the distance between each data point and the mean of each group using the Pythagorean Theorem. For example, in Figure 3, data point A is 5.80 units from the mean of Group I, 2.33 units from the mean of Group II, and 5.81 units from the mean of Group III. Therefore, the discriminant analysis would allocate point A to Group II. These calculations would be performed for each data point and a tally kept for the number of points assigned to their a priori group versus the number of points assigned to a different group. These figures can be used to calculate an allocation efficiency rate. Note that this allocation efficiency rate will be inflated when the same set of data are used to calculate the original group means and to assess the allocation efficiency.

An exploratory method of employing various combinations of characters in a series of discriminant analyses can provide information about how robust the original groups are and the ability of various character sets to discriminate between those groups.

Data collection and analysis.—Statistical analyses described here were performed on the data set of Snyder (1984). The precision and accuracy of Snyder's data exceed those of typical earlier papers, because he used calipers placed on photographs of both exteriors and acetate peels of interiors, whereas earlier workers used eye-piece micrometers on microscopes; Snyder's data can be reproduced by an independent worker.

The morphometric data were explored with a variety of univariate and multivariate statistical methods to determine the relative value of characters for taxonomic distinctions, including: 1) which are the most useful; 2) which, if any, could be disregarded; and 3) the type and minimum number of characters needed to recognize taxa with different degrees of confidence. Methods employed included one-way ANOVA and Fisher's PLSD (post-hoc comparison of means), stepwise discriminant analysis, canonical discriminant analysis, and discriminant function analysis. Tests were completed using the following SAS (version 5.18) procedures: ANOVA, STEPDISC, CANDISC, and DISCRIM, respectively.

The data set was evaluated with hierarchical cluster analyses using a FORTRAN 77 taxonomic program (Cluster, written by R. B. Selander with subroutines from D. L. Swofford) on a CYBER 175 computer. Cluster analyses were performed using weighted pair-group method WPGMA, and similarity matrices were produced using both average taxonomic distances and mean character differences. The taxonomy was also evaluated with discriminant analyses using the DISCRIM procedure from SAS(5.18) software on an IBM 3081 computer.

Non-normality and heteroscedasticity.—A series of Kolmogorov-Smirnov tests demonstrated that observations for characters from the Warsaw data are generally not normally distributed within species groups. Visual inspection of frequency histograms of observations within species also revealed non-normality of the data. F_{max}-tests (Sokal and Rohlf, 1981, p. 403) demonstrated that most characters had equal variances among groups. Unequal variances (heteroscedasticity) for a given character between groups were usually due to one or more of the groups having a character expressed at a much larger or smaller scale, thereby changing the mean as well as the magnitude of variance. Because the parametric statistical tests employed in this study assume that the data are normally distributed, and that groups have equal variance, effects of non-normality and heteroscedasticity were tested in two ways using data from three genera: *Apertostella* Snyder, *Cubifenestella* Snyder, and *Rectifenestella* Morozova, which are all traditional *Fenestella* forms.

Species group means were compared using Fisher's Protected Least Significant Difference (PLSD) test with both original data and normal order equivalents. Normal order equivalents, or "rankits," are rankings of the original data converted to normal deviates (see Sokal and Rohlf, 1981, p. 122). Rankits are a transformation of the data to an equivalent normal distribution with a mean of zero and variance of one; rankits can be substituted for original observations used in any parametric test. Results obtained using both original data and normal order equivalents can be compared to test effects of non-normality and heteroscedasticity (Ghent, 1974). Conclusions differed in only six (2.5%) of the 237 post hoc group mean comparisons based on results obtained with original data versus results obtained using rankits. In four comparisons (1.7%), group means were found to be significantly different ($P \leq 0.01$) with rankits, but not with original data; two group mean comparisons (0.8%) were significant with real data, but not with rankits.

In a second test, a total of 297 group means were compared using Fisher's Protected Least Significant Difference (PLSD) test with original data and Dunn's test (Zar, 1984, p. 200) with ranked data. Dunn's test is a nonparametric equivalent of Fish-

er's PLSD with unequal group sizes. Conclusions from twenty-three (7.7%) of the group mean comparisons were different between the two methods. Twenty-two group means were found to be significant with real data ($P \leq 0.01$), but not with Dunn's rank test. However, this pattern of conservativism of Dunn's test is consistent with results of other studies.

Results from rankit comparisons demonstrate that conclusions based on original data are only slightly more conservative (less likely to reject the null hypothesis) than if the data were normally distributed with equal variances between groups. Conclusions based on Dunn's nonparametric test were more conservative than those based on original data. Although the absolute values of significance for individual comparisons are affected by non-normality and heteroscedasticity, the differences are demonstrably small, and do not affect the overall patterns recognized with parametric analyses.

EVALUATION OF SPECIES CONCEPTS

Snyder's (1984, 1991) assignments of fenestellid specimens to species were evaluated using hierarchical cluster analysis of ranked morphometric data for characters listed in Appendix A, which are illustrated in Figures 4 and 5; 99.2 percent of the specimens using average taxonomic distance and 96.8 percent using mean characters differences (125 specimens, 25 species) clustered into their correct species groups sensu Snyder (1984, 1991). When all Warsaw fenestrate species were evaluated using discriminant analysis, discriminant functions based on all morphometric characters assigned 672 (99.4 percent) of the 676 specimens to their a priori species. These results leave little doubt that Snyder (1984, 1991) recognized viable taxonomic, morphologic entities.

Jackson and Cheetham (1990) have documented a very strong correlation between morphospecies and maternal inheritance in seven species of living cheilostome Bryozoa. In addition, preliminary electrophoretic data have not yielded any morphologically cryptic species (Jackson and Cheetham, 1990). The fact that real biological cheilostome species can apparently be recognized from skeletal characters suggests that Snyder (1984, 1991) also recognized real species.

The fact that viable species-level OTU's can be objectively recognized for fenestrate Bryozoa is significant, especially considering the history of their taxonomy. Once it became clear that fenestrate morphospecies are recognizable (and that careful workers, such as Ulrich, 1890, recognized many such species in the past), the fundamental problem of fenestrate taxonomy became one of how to characterize species in such a way that others could recognize and use them. Focus was turned toward developing a minimal list of diagnostic characters suitable for making taxonomic distinctions.

Morphometric characters were evaluated with a variety of numerical techniques. Results from one-way ANOVA, performed with Snyder's (1991) species as the class variable, demonstrated that all 47 morphometric characters are significant at well beyond the .0001 confidence limit. However, not all characters are necessarily significant within a single genus. Step-wise discriminant analysis was performed, but because every morphometric character improved discriminatory value of a given function as it was added, characters were accepted into functions in the the order in which they were input, and none was rejected. Because stepwise discriminant analysis was ineffective in determining the relative value of characters for species discrimination, a variety of indirect methods was employed. These methods, taken individually, are insufficient to make unequivocal conclusions, but as a whole they illuminate the role of various sets of characters in fenestrate systematics.

A series of one-way ANOVA tests using all morphometric characters, with Snyder's (1984, 1991) species as the class variable, were applied to specimens within generic groups. That is, each character was tested for significance in its ability to discriminate between species of the same genus. The validity of generic groupings will be discussed later. Characters were ranked separately based on three criteria: 1) the total number of times there was a significant difference in the character between two species ($P < 0.01$ confidence level); 2) the number of times a character could be used to distinguish one species from all other species within the same genus; and 3) the number of times the character was able to distinguish among all species within a single genus. Scores (ranks) were summed across these three criteria for each character, and a final ranking of the relative value of characters was developed. The 12 most useful morphometric characters for distinguishing among species within genera, based on ANOVA, are listed in Table 2.

Morphometric characters were also evaluated for their relative value with canonical discriminant analysis. Analyses were performed on 676 Warsaw fenestrate specimens with Snyder's (1984, 1991) species as the class variable. There is no method to evaluate the relative value of characters directly from canonical discriminant analysis because it produces a series of uncorrelated linear functions. However, in canonical discriminant analysis, characters that account for the most variance among species relative to within species receive the most weighting in a canonical variate (the absolute value of their coefficients is large; Neff and Marcus, 1980). Therefore, characters were evaluated in an indirect method. Coefficients were ranked from one to ten within each canonical variate, based on their absolute value (all lesser coefficients within each variate were assigned a rank of ten). The sum of the ranks across the first eight canonical variates, which accounted for 95.3 percent of the total variance, was ranked. Characters selected from canonical variates, shown in Table 3, are very similar to those deemed most useful by ANOVA.

Results from ANOVA and canonical variates indicate that characters that reflect the zooecial and apertural size and shape account for most of the variation among species relative to within species. When the following 10 characters (deemed most useful by ANOVA and canonical analysis) were employed in discriminant analysis, discriminant functions correctly assigned 84.7 percent of 676 specimens to their a priori species: CL–chamber length, CD–chamber depth, MAW–chamber width, CL × CD–chamber length × depth, MAW/CL–chamber width/length, VOL–chamber length × width × depth, RA–reverse wall budding angle, AL–aperture length, AW–aperture width, and AA–aperture length × width. These characters should be the most useful for making taxonomic distinctions. However, because many of these characters are strongly correlated with each other, they can only discriminate between similar groups of taxa. Other characters, not included in the list, prove useful because they can be used to distinguish among a larger number of taxa, in spite of their smaller F-ratio (ratio of variance among groups relative to within groups). For example, Figure 6 illustrates four hypothetical populations plotted against three variables. Length and width each have larger F-ratios than height, so results from ANOVA and canonical analysis imply that length and width are more diagnostic than height. However, because length and width are correlated, they divide the data into two identical groups, whereas height is diagnostic for all four groups, even though it has less overall variation.

In order to determine which sets of characters have the greatest potential for distinguishing among the most different taxa, two canonical discriminant analyses were performed, one using only the ten previously identified characters, and the other using all remaining characters. Characters were ranked based on the

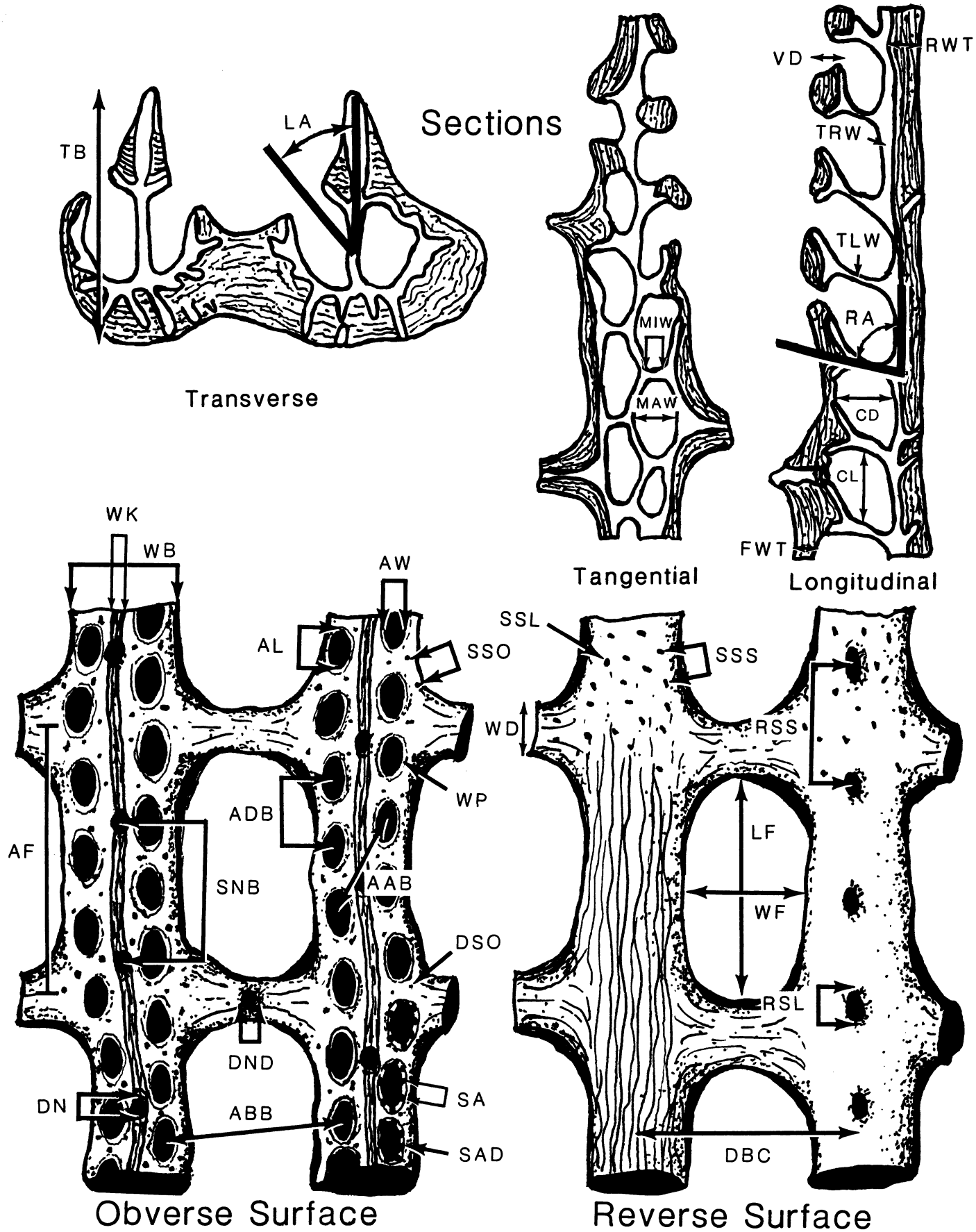

FIGURE 4—Generalized fenestrate bryozoan, approximately ×80, illustrating the orientation of morphometric characters 1–24 and 32–43 listed in Appendix A. See Snyder (1991) for character discussion.

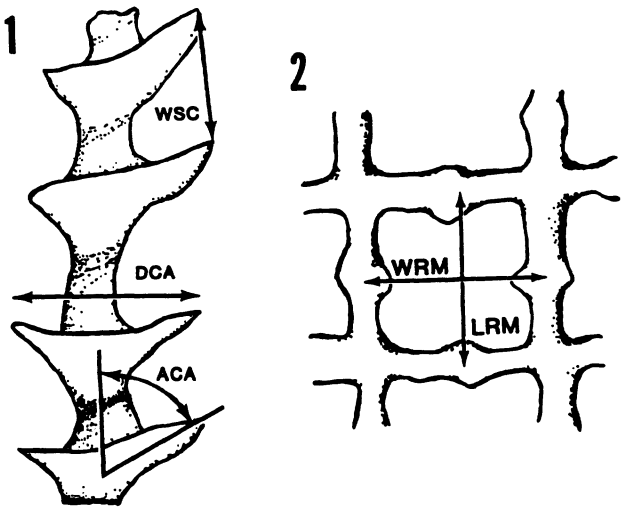

FIGURE 5—*1*, central spire of an *Archimedes*, illustrating the orientation of morphometric characters 27–29 listed in Appendix A. *2*, reticulate meshwork superstructure of a *Hemitrypa*, illustrating the orientation of morphometric characters 25–26 listed in Appendix A.

TABLE 2—Relative value of characters based on one-way ANOVA of species within genera of Warsaw fenestrates; ranking methods: 1) total number of times there was a significant difference in a character between two species ($P \leq 0.01$); 2) number of times a character distinguished one species from all other species within the same genus; 3) number of times a character was able to distinguish among all species within a single genus. Final Rank is rank of sum of the three methods; see Appendix A for character abbreviations.

Final rank	Method 1	Method 2	Method 3	Sum
1. CLCD	1	1	1.5	3.5
2. CL	2	3	1.5	6.5
3. SNB	3	2	3	8
4. VOL	4	5	4	13
5. RA	5	8	6.5	19.5
6.5 CD	6.5	8	6.5	21
6.5 AL	11.5	5.5	4	21
8. AA	8.5	5.5	9	23
9. WP	14.5	8	9	31.5
10. TRW	11.5	12	12	35.5
11. LF	6.5	18.5	12	37
12. MAW/CL	11.5	18.5	15	45

number of times the absolute value of the corresponding loading coefficient in standardized canonical variates was the greatest, or second greatest, in the first five canonical variates. Tables 4 and 5 show that the following six characters are the most useful: SNB–spacing of nodes on the obverse surface, LF–length of fenestrule, AAB–spacing of apertures along branch, AA–aperture length × width, CL–chamber length, and CL × CD–chamber length × depth. Although characters CL × CD, VOL, and MAW/CL are ranked higher than CD, MAW and RA in canonical analysis, the latter have more discriminatory power as a group, because they are less correlated with each other (see character set number two, Table 6).

Table 6 lists the percentage of Warsaw specimens correctly assigned to their a priori species by discriminant analyses that used different sets of characters. Also included are sets based on character lists used by different authors, but applied to the Warsaw data. The respective post-hoc error rate for species assignments indicates that selected morphometric characters would suffice for the *identification* of only varying proportions of the specimens, employing the *classification* that was developed using all 47 characters. Respective percentages do not represent the number of nominal taxa that would be recognized in a classification developed using only these characters. Only morphometric characters were included in these analyses; Snyder (1984, 1991), as well as the other authors listed in Table 6, also included additional discrete and qualitative characters in their taxonomic analyses. Results from discriminant analyses shown in Table 6 can be summarized as follows. 1) Specimens are most effectively assigned to their a priori species when all available characters are used. 2) Some characters are more useful than others in making species distinctions. 3) A combination of zooecial and zoarial characters is more effective in distinguishing among a greater number of different taxa than zooecial characters taken alone, even though zooecial characters have greater F-ratios. In Table 6, set number nine is more effective than set ten. 4) The total number of characters used in analyses is almost as important as the type of character used. For example, the 13 characters deemed least useful by this study were more effective in distinguishing among a greater number of taxa than the smaller number of characters used by several previous authors; in Table 6, set number 11 is more effective than sets 12–15.

Because the Warsaw data set was very large and complex, an independent test of discriminant procedures was performed. Six OTU's were exchanged between all related species, and discriminant analysis was applied to the new mixed groups in order to determine if discriminant functions could be generated that could recognize other ad hoc groupings of the data. This resulted in only 65.2 percent of the specimens assigned to their ad hoc, a priori group, which was approximately the degree to which the specimens were rearranged. This further supports the robustness of Snyder's (1984, 1991) species groupings.

In summary, all available characters are important and should be used in the description and classification of fenestrate species because different sets of characters are diagnostic for different taxa, even though a minimal number of characters can be used to identify individual species. Even if a given character may not serve to differentiate between related species in a single fauna, the character may prove important for comparison to other faunas and thus should be included in the species description. This becomes clear in light of the surprisingly broad value of all characters employed in this study. In future taxonomic treatments, an expanded remarks section, indicating which characters are useful for ready identification of taxa within a fauna, would make fenestrates accessible to nonspecialists.

GENERIC CONCEPTS

Traditional generic concepts for fenestrate bryozoans have been based on: 1) unique colony growth forms (*Archimedes* Owen, *Lyropora* Hall, *Helicopora* Claypole); 2) number of zooecia across branches (*Polypora* M'Coy, *Fenestralia* Prout); or 3) zoarial superstructures (*Hemitrypa* Phillips, *Isotrypa* Hall). Whereas these generic distinctions have proven practical for ready identification, it has never been clearly documented whether fragments of zoarial fronds separated from their skeletal superstructures can be assigned to the appropriate genus. In addition, traditional generic concepts (e.g., Bassler, 1953) left an enormous number of species within *Fenestella*, based on the presence of two rows of zooecia separated by a median keel, and a general fan-shaped or conical zoarial form.

Elias and Condra (1957) divided *Fenestella* into three groups, based on the length of fenestrules, apertures per fenestrule, and node distribution, and 13 subgroups, based on a variety of cri-

TABLE 3—Relative value of morphometric characters based on coefficients of canonical variates. Rank of coefficients within each variate is subscript, unlabeled coefficients given a rank of 10; see Appendix A for character abbreviations.

Final rank	CAN1	CAN2	CAN3	CAN4	CAN5	CAN6	CAN7	CAN8
1. AA	45.5_2	7.9_8	74.2_1	24.5_1	15.9_4	27.1_3	-12.4_7	-55.8_1
2. CL	55.9_1	-37.0_4	31.9_6	-11.7_5	-51.5_1	-49.6_2	60.4_1	2.7
3. CLCD	11.2_6	14.5_6	-24.0_8	-14.3_4	31.8_2	-13.6_7	-38.5_4	20.3_4
4. VOL	−2.9	-45.9_1	54.4_2	6.9	1.5	57.0_1	23.3_5	-18.0_5
5. MAW	3.5	39.9_2	-35.1_3	−1.5	15.4_5	-25.2_4	-38.5_3	8.5_8
6. MAWCL	-6.3_8	-37.3_3	32.1_5	2.4	-20.7_3	11.7_9	43.7_2	-9.5_8
7. AW	-19.9_3	−3.9	-33.0_4	-11.1_7	-7.1_9	-13.5_8	6.2	24.5_2
8. CD	−1.7	29.4_5	−5.1	17.6_2	-15.1_6	-16.5_5	17.3_6	−4.9
9. RA	-16.2_5	-11.5_7	18.4_9	14.8_3	14.8_3	-15.7_6	-14.7_8	−11.9
10. AL	-17.7_4	−1.8	-30.9_7	-10.4_9	-8.4_8	−10.9	6.3_9	22.6_3
11. SNB	8.1_7	−6.4	−0.5	11.3_6	5.5	1.8	1.7	7.4_9
12. LF	3.4_9	-7.3_9	−11.1	10.2_8	−3.6	5.2	−0.6	−4.4
AAB	1.5	0.5	−1.8	−1.7	9.3_7	2.3	4.1	−19.2
ABB	−0.3	−0.4	−3.4	5.1	−1.6	3.2	−2.5	−2.3
ADB	3.8	1.0	−2.3	0.7	0.9	2.6	3.7	−2.3
AF	1.3	−6.2	−7.1	3.2	−1.7	0.8	4.1	1.6
DBC	−1.2	−0.2	−1.6	1.3	−1.3	0.5	−2.2	−0.3
DN	2.2	−1.6	−0.3	3.6	4.2	1.3	2.0	0.8
FWT	−0.3	0.3	0.6	−0.2	−0.6	1.9	0.1	0.2
LA	−2.4	−4.0	0.5	0.2	6.4	1.4	3.2	0.2
RWT	−0.9	2.2	1.3	−1.1	−2.6	2.8	1.9	3.8
TB	0.5	6.5	5.3	−3.7	−1.5	9.0	3.5	12.5_6
TLW	−1.2	0.0	0.5	−1.1	−1.6	0.7	−2.6	0.0
TRW	−0.6	1.3	−0.3	−1.1	−2.3	−0.1	−1.4	0.4
VD	0.9	3.9	1.5	−0.8	−4.8	4.2	−1.1	−4.7
WB	3.1	−1.2	−0.5	0.5	−6.8	3.6	−5.5	−2.6
WD	0.9	−0.7	2.2	0.9	−1.4	2.7	−3.9	1.8
WF	2.3	−2.1	−2.4	1.8	−1.0	−0.6	−3.1	−0.3
WP	0.8	−0.6	0.3	−0.6	−1.0	2.0	−2.0	2.2

teria. Their distinctions have not proved useful because of their rather arbitrary choice of characters, which were not applied consistently even by these authors. Termier and Termier (1971) divided *Fenestella* into six new genera. Diagnoses and type species designations were lacking for several of their new genera, rendering them invalid according to the International Code of Zoological Nomenclature (Morozova, 1974). In addition, many distinctions were based solely on exterior features.

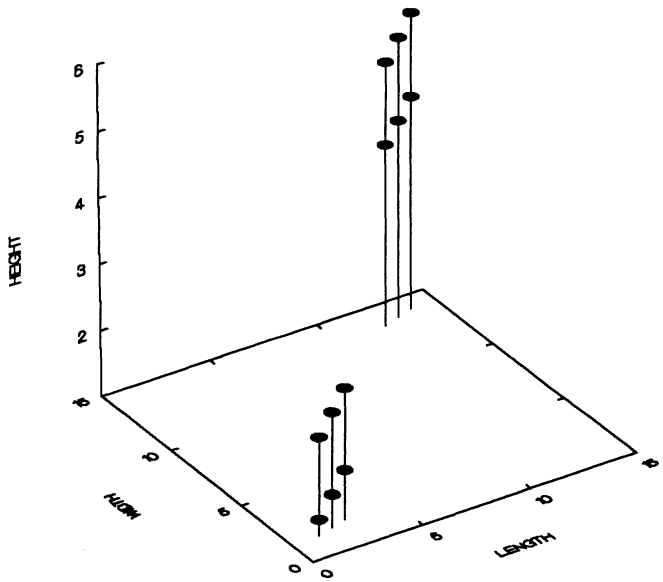

FIGURE 6—Dots represent 12 hypothetical taxa that belong to four species. Characters length and width have greater variability among groups relative to within groups than does the height variable. Length and width separate two groups (A,B and C,D), whereas the height variable differentiates all four groups.

Morozova (1974) described 10 new genera and retained four previously separated from *Fenestella*. Her classification scheme and methodology (discussed previously) has been applied by many later authors (e.g., Gorjunova, 1975; Morozova, 1981; Snyder, 1984; McKinney and Kriz, 1986); however, it suffers from the weakness of a strictly two-dimensional approach.

In his redescription of *Utropora* Pocta, McKinney (1980) recognized the three-dimensional shape of the living chambers and orientation of apertures relative to branch surfaces as diagnostic characters for the genus. He also documented the distribution of the primary granular skeleton relative to the secondary lamellar skeleton. Snyder (1984, 1991) demonstrated the limitations of the two-dimensional approach with specimens from two genera that cannot be differentiated based solely on midtangential sections (see Snyder, 1991, text fig. 3). He emphasized zooecial features by placing illustrations of three-dimensional zooecial reconstructions directly in generic diagnoses. Snyder divided Warsaw fenestrates among 11 genera, three of which were new.

TABLE 4—Relative value of exterior morphometric characters based on coefficients of the first five canonical variates, rank of coefficients within each variate is subscript; see Appendix A for abbreviations.

Character	CAN1	CAN2	CAN3	CAN4	CAN5
1. SNB	13.4_2	0.1	4.6	14.6_1	-13.2_1
2. LF	15.0_1	-9.5_2	−2.7	−4.3	3.9
3. TB	−1.9	15.8_1	−3.0	7.6	11.6_2
4. AAB	2.3	6.9	12.5_2	-8.6_2	−4.4
5. WB	5.3	4.4	-12.6_1	−6.3	−2.0
DBC	1.0	−1.4	−1.0	0.0	2.6
WD	1.5	2.8	−6.6	1.0	−9.2
WF	3.1	−2.6	−0.5	0.1	1.8
AF	6.3	−7.2	3.3	3.6	4.9
ADB	6.0	5.5	1.1	−8.3	1.5
ABB	5.1	−2.9	−1.8	−2.1	1.9

TABLE 5—Relative value of interior morphometric characters based on coefficients of the first five canonical variates, rank of coefficients within each variate is subscript; see Appendix A for abbreviations.

Character	CAN1	CAN2	CAN3	CAN4	CAN5
1. CL	61.9_1	42.3	−10.6	24.2	-94.1_1
2. CLCD	15.4	5.1	46.4_1	-89.2_2	57.8_2
3. AA	45.3_2	12.2	−9.7	97.9_1	37.6
4. VOL	−8.5	53.4_1	-37.0_2	59.3	−0.9
5. MAWCL	−8.9	50.8_2	−3.3	16.2	−44.2
AW	−19.8	−5.5	4.8	−43.2	−17.5
AL	−17.5	−6.8	3.6	−38.5	−16.9
CD	2.2	−32.6	19.9	21.0	−30.6
MAW	7.2	−49.6	11.2	−21.7	30.7
RA	−14.9	22.2	16.0	8.8	7.2

EVALUATION OF WARSAW GENERA

Snyder's (1984, 1991) classification of fenestrate genera from the Warsaw Formation was evaluated with cluster analysis and discriminant analysis. The 47 characters used in cluster analyses were from Snyder's (1984) format for generic diagnoses (Appendix C). One composite OTU per species was developed, based on idealized character states from Snyder's species descriptions.

In resulting cluster phenograms, generic distinctions were clear among species of the Polyporidae. Species of the family Fenestellidae tended to fall into larger groups of existing genera, but these groups were not consistent enough to be used as the basis of new generic concepts. When actual specimens were used (five per species, with ranked morphometric data), as opposed to idealized concepts, generic groupings were even more ambiguous. Analyses performed using different clustering methods resulted in a large number of varied phenograms, but groupings can be summarized as follows:

1) *Rectifenestella* and *Minilya* species tended to cluster together, but in some treatments were split into two distinct groups.
2) *Laxifenestella* and *Exfenestella* species formed a cluster, in some treatments distinct from each other and in others not.
3) The two groups mentioned above usually clustered into a larger group, with individual species often being mixed.
4) *Archimedes* species almost always clustered into a distinct group. This strongly supports *Archimedes* as a discrete morph (i.e., valid genus) and suggests that zoarial fragments separated from their central axes can be correctly identified as belonging to the genus.
5) *Hemitrypa, Cubifenestella,* and *Apertostella* species usually clustered into a large group. *Hemitrypa* species often clustered together, but it was common for *Cubifenestella* or *Apertostella* species also to be included in *Hemitrypa* clusters.
6) There were several OTU's in each phenogram that did not align with the patterns listed above. However, anomalous taxa were not consistent among clustering methods, either in the individuals involved, or the groups into which they clustered.

Details of the resultant phenograms are not as important as the fact that, based on results from hierarchical cluster analyses, generic distinctions for the Warsaw fenestellids are not nearly as clear as species distinctions using the same techniques.

Only one ad hoc character set could be found that would cause all 37 species to cluster into existing genera sensu Snyder (1984, 1991). The set consists of: secondary zooecial superstructures, mode of zooecial emplacement, hemisepta, reverse wall budding angles, and orientation of apertures relative to branch surfaces. When any other character(s) were included in the analysis, generic distinctions became clouded, and worsened as more characters were added.

In contrast, discriminant analysis performed on 508 specimens of Fenestellidae using all morphometric characters and none of the ad hoc characters, assigned 93.7 percent of the specimens to their a priori genus. When members of Polyporidae were included in the analysis, 90.7 percent of the 676 specimens were assigned to their a priori genus. This demonstrates that fenestrate genera can be objectively recognized with morphometric data, if certain characters are weighted in discriminant functions. Although discriminant analysis is an effective tool with which to test the validity of an existing classification, it can not be used to erect one.

REEVALUATION OF GENERIC CONCEPTS

Results from cluster analysis and discriminant analysis raise questions regarding generic concepts for fenestrates. Snyder (1984, 1991) thought that all available characters should be used, and he cautioned that deletion of viable characters solely because they do not allow ready taxonomic breaks based on variation between taxa invites establishment of a monothetic

TABLE 6—Results from discriminant analysis of species. Abbreviations correspond to characters listed in Appendix A; asterisks denote characters that authors measured from tangential thin sections rather than exterior (apertures) or longitudinal sections (chamber length) as per Snyder (1984). Respective post-hoc error rate for species assignments indicates that selected morphometric characters would suffice for identification of varying proportions of the specimens, employing the classification developed using all 47 characters. Respective percentages do not represent the number of nominal taxa that would be recognized in a classification developed using these characters only.

Author	Number of characters	Characters used in function	% correct to a priori species
1. Snyder (1984)	47	Morphometric possessed by all taxa	99.4%
2. ———	10	LF, AAB, AA, SNB, WB, CL, CD, TB, MAW, CLCD	95.9%
3. ———	8	LF, AAB, AA, SNB, CL, VOL, TB, CLCD	91.7%
4. ———	8	LF, AAB, AA, SNB, CL, VOL, TB, MAW	91.7%
5. ———	8	LF, AAB, AA, SNB, CL, VOL, WB, CLCD	91.6%
6. ———	8	LF, AAB, AA, SNB, CL, VOL, WB, MAW	91.4%
7. ———	8	LF, AAB, AA, SNB, CL, VOL, WD, RA	91.3%
8. Bancroft (1986a)	9	LF, AAB, AL, SNB, DBC, WD, WB, *CL, MAW	89.5%
9. ———	6	LF, AAB, AA, SNB, CL, VOL	88.2%
10. ———	10	AL, AW, AA, CL, CD, MAW, RA, MAWCL, CLCD, VOL	84.3%
11. ———	13	DBC, ADB, ABB, WF, WP, AF, WD, FWT, RWT, TLW, TRW, LA, VD	79.2%
12. Tavener and Smith (1971)	8	DBC, LF, AAB, AF, WB, WD, SNB, AW	74.3%
13. Stratton & Horowitz (1977)	7	DBC, LF, AAB, ADB, WB, WD, AW	67.3%
14. McKinney and Kriz (1986)	6	DBC, LF, AAB, WB, *AW, MAW	60.0%
15. Elias & Condra (1957)	4	DBC, LF, AAB, SNB	53.1%

TABLE 7—List of characters, with plausible biologic interpretations, that under appropriate circumstances could represent key innovations that allowed entry into and recognition of adaptive zones. Also included are references where recent authors used characters to make generic distinctions.

1. Food:
   - A. *Size, shape and orientation of polypides:* Zooecial dimensions and shape, including hemisepta which controlled the orientation of polypides within the zooecia (Morozova, 1974; McKinney, 1980; Snyder, 1984).
   - B. *Size and feeding orientation of mouths:* Size and orientation of apertures (Snyder, 1984); reticulate meshwork superstructures (Bancroft, 1986a).
   - C. *Length and number of tentacles:* Interapertural distances (McKinney and Kriz, 1986), and nature of apertural stylets (guides for tentacles) (Snyder, 1984).
2. Space:
   - A. *Budding characteristics:* Monoserial vs. biserial vs. polyserial emplacement of zooecia; orientation of budding loci (Morozova, 1974).
   - B. *Colony growth forms:* Significant and consistent zoarial forms such as central axis of *Archimedes* or basal structure of *Lyropora.*
   - C. *Nonfeeding zooids:* Heterozooecia that regulate spacing of autozooecia (Morozova, 1974; Bancroft, 1986b).
   - D. *Brood chambers:* Ovicells (Morozova, 1974; Bancroft, 1986d).
   - E. *Gonozooids:* Possibly some heterozooecia.
3. Protection:
   - A. *Extrazooecial skeletal modifications:* Superstructures over obverse surface such as reticulate meshwork of *Hemitrypa* (Bancroft, 1986a), *Isotrypa* and others (McKinney and Kriz, 1986).
   - B. *Intrazooecial skeletal modifications:* Hemisepta, which partition living chamber from the vestibules (Morozova, 1974; Snyder, 1984; McKinney and Kriz, 1986).
   - C. *Defensive polymorphs:* Possibly secondary nanozooecia (Bancroft, 1986c), cyclozooecia and other heterozooecia (Bancroft, 1986b).

classification with a high probability of polyphyletic groupings. Boardman et al. (1983, p. 12–18) emphasized the importance of a polythetic classification at all taxonomic levels of Bryozoa. They cautioned against use of a restricted group of characters, because in the past such characters have been chosen rather arbitrarily and have resulted in unstable classifications.

Nevertheless, results from cluster analysis and discriminant analysis demonstrate that some characters are much more important for making generic distinctions than others. There is a natural hierarchy of characters within fenestrate Bryozoa. In order to explain character distributions observed here, it is hypothesized that what have come to be recognized as fenestrate genera represent major evolutionary shifts, associated with the development of new character(s) that allowed entry into new adaptive zones.

Occupants of an adaptive zone possess some innovative character or characters that allow them to utilize resources (food and space) or protect themselves from predation and parasitism in a way that is significantly different from the way other related organisms perform the same function (Van Valen, 1971). A key innovation may or may not provide an adaptive advantage for a descendant over its ancestor, but it must provide a significantly different method of obtaining food or space or providing protection. In Van Valen's usage of the term (1971, p. 421), "Adaptive zones are part of the environment that exist independently of a taxon to exploit them." Therefore, key innovations allow entry into adaptive zones; they do not define them.

Recent workers have recognized fenestrate genera based on relatively few characters. Many of these characters can be considered key innovations associated with the occupation of adaptive zones. Table 7 provides a list of these characters with associated soft parts (in italics) and preservable hard parts, classified according to basic biologic functions. Also included are citations of generic diagnoses that emphasized these characters.

The central spire of extrazooecial skeleton of *Archimedes* was a key innovation that allowed its members to grow up into the water column; this life mode was significantly different from those of other fenestrates. The superior reticulate meshwork of *Hemitrypa* provided protection from predators. It is argued here that these innovations allowed entry into (and our recognition of) well-defined adaptive zones. It is further suggested that generic-level characters used by Morozova (1974), McKinney (1980), and Snyder (1984, 1991), such as the placement of hemisepta and shape of the zooecial chamber, represent equally valid, albeit more subtle, key innovations because they controlled the shape and orientation of the feeding polypides. These characters may have allowed for feeding specialization, as suggested by work of Winston (1977, 1978, 1981), and provided variable degrees of protection. Several studies have demonstrated that there is moderate correlation between dimensions of soft parts, such as number and length of tentacles, diameter of lophophore, and size of mouth, and preservable hard parts, such as size and spacing of apertures (Winston, 1981; McKinney and Boardman, 1985; McKinney and Jackson, 1989, p. 123–128).

Characters listed in Table 7 perhaps did not all have equal adaptive significance, and they probably do not represent the complete adjustment to the adaptive zone as it existed in nature. It is possible that the biologic significance of some characters is incorrectly interpreted. Nevertheless, each of these characters is consistent within a group of taxa, and potentially would have allowed for a unified life mode for all species within the group that differed from life modes of other groups.

There are two plausible ways in which the diversity of species within an adaptive zone may increase. In the first case, an adaptive zone is occupied by one taxon that develops a key innovation either gradually or by a punctuational event, and then diversity increases by speciation within the zone. This results in a monophyletic clade occupying an adaptive zone. In the second case, unrelated forms independently develop a functionally equivalent key innovation as a consequence of convergent evolution.

If the second process is the more typical, then what have come to be recognized as fenestrate genera are actually polyphyletic grades of evolution. If evolutionary processes are such that speciation events allow for repeated development of characters that have in the past been considered generic-level characters, then the prospects for recognition of monophyletic genera among fenestrates become bleak. Generic concepts are reduced to convenient groupings that have no relationship to natural phylogenetic events. If, however, the development of key innovations is an infrequent event followed by speciation within adaptive zones, then characters associated with those events allow for an oligothetic classification of monophyletic genera that is not merely an artifact created to simplify taxonomic analysis.

A critical question is now raised: Do traditional generic concepts for fenestrates represent monophyletic clades occupying adaptive zones, or are they really polyphyletic grades of evolution established for taxonomic convenience? This question can be addressed by looking at the distribution of characters within and among fenestrate genera, and then proposing the most parsimonious sequence of events that would explain the observed distributions, given our knowledge of evolutionary principles.

The following model of character distributions explains how, in cluster analysis, species could become better defined as more characters were added to analyses at the specimen level, but when species were the OTU's, generic distinctions became clouded with the addition of characters. It also accounts for the fact that discriminant analysis performed on Warsaw fenestrates

TABLE 8—Model for fenestrate character distribution. I. Genus-level: characters that are key innovations that allow occupation of an adaptive zone. II. Species-level: other characters that in themselves do not allow entry into an adaptive zone, but may be correlated with key characters or may vary independently; IIA, characters that vary within generic groups, which may be used to define species; IIB, characters that are consistent within generic groups, but are not necessarily unique to the group; IIB1, primitive characters (i.e., remnant ancestral); IIB2, shared derived characters; IIB3, independently derived characters that are convergent (homoplasous).

		Type I			Type IIB1		Type IIB2		Type IIA			
		A	B	C	f	g	m	n	s	t	y	z
Genus 1	species 1	1	0	0	1	1	2	2	0	2	1	0
	species 2	1	0	0	1	1	2	2	1	2	2	1
	species 3	1	0	0	1	1	2	2	1	0	2	2
		Type I			Type IIA				Type IIB1		Type IIB2	
		A	B	C	f	g	m	n	s	t	y	z
Genus 2	species 4	0	1	0	0	0	2	1	1	1	2	2
	species 5	0	1	0	1	0	1	1	1	1	2	2
	species 6	0	1	0	1	1	2	0	1	1	2	2
		Type I			Type IIB1		Type IIB3		Type IIA			
		A	B	C	f	g	m	n	s	t	y	z
"Genus 3"	species 7	0	0	1	1	1	1	2	1	2	0	1
	species 8	0	0	1	1	1	1	2	0	1	0	1
	species 9	0	0	1	1	1	1	2	1	2	1	1
	species 10	0	0	1	2	2	1	2	1	1	2	0
	species 11	0	0	1	2	2	1	2	0	1	2	2
	species 12	0	0	1	2	2	1	2	2	0	1	0

did assign 93.7 percent of fenestellid specimens to their a priori genus based only on morphometric characters, and *none* of the ad hoc characters (key innovations) that were required to "push" OTU's into existing generic groups in cluster analysis. Results from discriminant analysis demonstrate that generic distinctions for fenestrates are polythetic and that phenetic generic-level morphs exist.

As noted earlier, there is a hierarchy of fenestrate characters; there are genus-level characters (key innovations associated with entry into adaptive zones) and species-level characters, which may be correlated with key characters or vary independently. It is important to note that character-level partitioning is not necessarily absolute within a genus; variation of a genus-level character within an adaptive zone could aid in species recognition. There are two types of species-level characters, ones that vary within generic group sand ones that are consistent within generic groups. There are three ways in which a character could be constant for all species within an adaptive zone: 1) the character could be primitive (remnant ancestral); 2) it could be shared derived; or 3) it could be homoplasous (a result of convergence). The following example is given to illustrate character distributions and inferred phylogenetic events. It is important that primitive and derived states are assigned, but in practice have not yet been differentiated. A classification of the historical development of character states can be summarized as follows. The purpose of this classification is only to provide a nomenclature with which to communicate the complex yet subtle concepts in the following discussion.

I. Genus-level characters that are key innovations that allow occupation of an adaptive zone.
II. Species-level: other characters that in themselves do not allow entry into an adaptive zone, but may be correlated with key characters or may vary independently.
   A. Characters that vary within generic groups, which may be used to define species.
   B. Characters that are consistent within generic groups, but are not necessarily unique to the group.
      1. Remnant ancestral characters (plesiomorphies).
      2. Shared derived characters (synapomorphies).
      3. Independently derived characters that are convergent (homoplasies).

Type IIB species-level characters are those that allow discriminant analysis to differentiate among discrete genus-level morphs (Type I characters were omitted from discriminant analyses in order to test the other characters). The key to recognizing whether members of an adaptive zone are monophyletic or polyphyletic is the frequency of Type IIB1, IIB2, and IIB3 characters. In the case in which entry into an adaptive zone is a unique event, with later speciation within the zone, the character distribution would appear as in Genus 1 and Genus 2 of Table 8. In Genus 1 (Table 8) characters "A," "B" and "C" are Type I genus-level characters, "f" and "g" are Type IIB1 remnant ancestral characters, "m" and "n" are Type IIB2 shared derived characters, and "s," "t," "y," and "z" are Type IIA variable species-level characters.

Conceptually, the same character distribution for Genus 1 could be realized in an extreme case of convergence, where all occupants of an adaptive zone were derived from different ancestors. However, in that case the great preponderance of Type IIB characters would have to be Type IIB3 (homoplasies). Type IIB1, remnant ancestral characters, would be indistinguishable from Type IIA characters. In my view, this is highly improbable because organisms have many problems to cope with beyond those associated with the new zone and therefore all characters do not shift simultaneously, in spite of the advantages and demands of the new adaptive zone. Convergent evolution does not affect all characters equally. For example, the approximate ancestry of ichthyostegids (class Amphibia) can be determined despite the great differences between terrestrial and aquatic life modes.

A more likely character distribution resulting from convergence would be like that shown in "Genus 3" of Table 8. In this case, character "C" allows occupation of the adaptive zone, and characters "m" and "n" are Type IIB3 convergent characters,

TABLE 9—Principal criteria for fenestrate generic distinctions.

1. Secondary zoarial structures
   a. central axis
   b. superior structures on obverse surface
   c. other
2. Heterozooecia
   a. ovicells (Bancroft, 1986d)
   b. nonozooecia (Bancroft, 1986c)
   c. parazooecia (Morozova, 1974)
   d. cyclozooecia (Morozova, 1974)
3. Rows of autozooecia across branch and emplacement
   a. monoserially emplaced
      1. two rows consistently
      2. two rows with a third at sites of bifurcations
      3. two rows with a third for pronounced distances proximal to sites of bifurcations
   b. biserially emplaced
      1. two rows consistently
      2. two rows with a third at sites of bifurcations
      3. two rows with a third for pronounced distances proximal to sites of bifurcations
   c. polyserially emplaced
      1. constant number of rows (provide number)
      2. variable number of rows relative to sites of branch bifurcations (provide numbers and relationships)
4. Hemisepta
   a. superior
      1. presence/absence
      2. degree of development
      3. positioning
   b. inferior
      1. presence/absence
      2. degree of development
      3. positioning
5. Autozooecial size

(mm)	CL	CD	MAW	MIW
a. small	<0.20	<0.10	<0.10	<0.07
b. intermediate	0.20–0.48	0.10–0.20	0.10–0.15	0.07–0.12
c. large	>0.48	>0.20	>0.15	>0.12

6. Reverse wall budding angle
   a. low angle <45 degrees
   b. medium angle 45–75 degrees
   c. high angle >75 degrees
7. Orientation of autozooecial chamber elongation
   a. parallel to reverse wall
   c. parallel to proximal and distal lateral chamber walls
8. Axial wall trace in tangential section
   a. straight
   b. sinuous
   c. zigzag
9. Zooecial shape in tangential view (shallow, medium, and deep)
   a. triangle
   b. square
   c. circle
   d. oval
   e. ellipse
   f. pentagon
   g. rectangle
   h. parallelogram
   i. diamond

Each diagnosis of a new genus should be accompanied by:

1. Illustrations in 2-D of
   a. longitudinal view
   b. transverse view
   c. tangential view inclined (shallow, medium, and deep)
2. Three-dimensional reconstruction
   a. lateral view
   b. distal view
   c. frontal view

independently derived from two different ancestors. Characters "f" and "g" are remnant ancestral characters that allow recognition of the polyphyletic nature of the group. Based on examples from nature, when convergence does occur, this is the more likely character distribution. In other words, based on the totality of characters we can recognize that a bat is not a bird, a rabbit is not a rodent, and a plesiosaur is not a pisces. Convergence at the generic level is a phenomenon that should be recognizable to an experienced systematist who is familiar with the distribution of characters through space and time. A detailed survey of fenestrate genera through time can resolve the question of how common convergence is at the generic level.

Character distributions among fenestrates are complex because a great deal of iterative evolution of species-level characters apparently occurred. Therefore, characters that are of Type IIB1 (remnant ancestral) in one genus may be of Type IIA and quite variable in another genus, as between Genus 1 and Genus 2 in the example in Table 8. Cluster analysis was unable to differentiate completely among Warsaw genera because all characters were given equal weight. The homeomorphy between species-level characters clouded generic distinctions. For example, if an unweighted cluster analysis were performed on the species in Table 8, species 3 and species 6 would cluster together rather than with their true congener.

Discriminant analysis weighted the characters that have the most variance among groups relative to within groups, and used those weighted characters to differentiate among Warsaw genera. In other words, discriminant analysis was able to recognize species-level characters that varied little within genera and used them to differentiate among genera.

Results from cluster analysis and discriminant analysis indicate that the character distribution among fenestrates supports the idea that fenestrate genera are monophyletic clades that are the result of diversification within adaptive zones. This is not to imply that convergent evolution of genus-level characters has not occurred; indeed, there is evidence that is has occurred in some cases. However, it is suggested here that convergent evolution is the exception and not the norm.

In summary of this section, whether future work supports the ideas presented here or not, it is important to note that Warsaw fenestrate genera do represent discrete morphotypes that can be recognized objectively.

CRITERIA FOR GENERIC DISTINCTIONS

The idea that fenestrate generic concepts are based on key innovations allows for development of a list of preservable genus-level characters, although such a list does not exclude the possibility of significant adaptive zone shifts involving only soft-part features not reflected in the skeleton. A small number of characters may suffice to recognize a fenestrate genus, as long as character states reflect a consistent strategy for all members of the genus within an adaptive zone, and provide a life mode that is significantly different from that of other groups. Potential problems arise with the definition of "significantly different," but it should be up to the author to provide justifiable reasons for recognizing a genus based on the recognized limits of an adaptive zone. A list of potential genus-level characters is provided in Table 9. Because the concept of a genus-level character is subjective, the list will have to be evaluated by other fenestrate workers and can be modified as required. However, in many cases decisions have already been made, albeit without initial explicit biologic explanations (e.g., *Archimedes* Owen, *Hemitrypa* Phillips, *Lyropora* Hall, and others). It is the contention here that genera recognized by Snyder (1984, 1991) (*Banastella, Cubifenestella,* and *Apertostella*) are equally well, but much more subtly, defined, demanding more care in identification.

Using this methodology, one can propose a new genus, or evaluate the viability of an existing genus, by first explicitly recognizing the genus-level character(s) on which it is based, and then objectively evaluating the genus with discriminant analysis. Discriminant analyses are performed against a number of established genera, using as many characters as possible, but *not* including the characters on which the genus is initially proposed. If members of the genus in question are assigned to their a priori genus, with an acceptable error rate, then the genus is an operationally valid taxon that can be objectively recognized

in a polythetic classification. Omitting characters that were initially used to establish an a priori classification is correct procedure for discriminant analysis (Neff and Marcus, 1980, p. 150), although it is common practice for all characters to be included when the relative significance of characters is unclear, as was done earlier in this paper.

There may be several reasons for an OTU to fail to align with its a priori genus: 1) convergent evolution of an apparently valid genus-level character; 2) poor choice of the set of genus-level character(s), based on biological considerations; 3) improper assignment of certain members to an otherwise valid genus. In each of these cases the working genus should be rejected and the generic affinities of the component species reevaluated. There may be cases where specimens belonging to a valid genus would fail to align with the a priori classification. If a great degree of divergent evolution occurred in species-level characters after establishment of the adaptive zone, it is possible that discriminant analysis may fail to recognize a group that actually is monophyletic. In this case, it may be possible to recognize several genera within the adaptive zone, using a combination of other characters.

It is important to note that successful allocation of taxa to their a priori generic groups by discriminant analysis does not necessarily indicate that the character upon which the group was recognized was actually the key innovation that allowed for the establishment of an adaptive zone; it only means that the group can be objectively recognized in a polythetic classification. The biologic significance of the character may be misinterpreted, or the adaptive zone may have been established by some other character. Even after it has been demonstrated that a genus in question is an operationally valid taxon under a polythetic classification scheme, one can not be certain that the group is truly monophyletic. However, fenestrate taxa are no different from those of any other group in this respect.

DISCUSSION

Often, taxonomically troublesome groups, such as fenestrate bryozoans, are problematic because they are perceived as lacking viable characters (i.e., those providing an objective contribution to taxon discrimination) required for a tenable classification. This study demonstrates that, on the contrary, fenestrates possess over 45 such morphometric characters. Methods employed in this work may prove useful for other groups with problematic taxonomies. In such work, as many characters as possible should be employed in an initial classification, and then characters can be evaluated for their viability. Perhaps other difficult groups also possess an abundance of viable characters; but even if other groups are not as richly endowed with significant characters as fenestrates, the important features that are available can isolated.

Results from multivariate statistical techniques provide insight into fenestrate systematics and objective support for Snyder's (1984, 1991) taxonomic treatment of the Warsaw fauna. Numerical techniques thus are useful tools for both data analysis and specimen identification, but they do not provide a substitute for personal experience and knowledge. Recognition of sound fenestrate taxa requires an experienced paleontologist with a comprehensive grasp of fenestrate morphology and the geographic and stratigraphic distribution of morphotypes.

The diverse Warsaw fenestrate fauna provides a framework on which future fenestrate studies can be built. Other fenestrate faunas need to be comprehensively studied to test ideas presented here, such as the relative value of morphologic characters for species recognition and generic distinctions based on a limited number of key characters associated with entry into adaptive zones.

Several phylogenies for fenestrates have been proposed by Soviet authors (e.g., Shulga-Nesterenko, 1949; Morozova, 1962), but the operational validity of the taxa has not yet been tested using the criteria presented here. A survey of fenestrate genera through time is needed to determine which taxa represent polyphyletic convergence and which are real genera. Once valid monophyletic genera have been documented, a format can be developed that characterizes species in such a way that they can be recognized by non-specialists. Only then can fenestrate cryptostome Bryozoa become accessible and fulfill their potential for the study of evolution, paleoecology, and biostratigraphy.

SUMMARY

1. Numerical evaluation of morphologic character distributions and evaluation of phenetic classifications provided insights into the systematics and evolution of a taxonomically problematic group.

2. Fenestrate cryptostome Bryozoa are potentially highly useful for the investigation of many paleobiologic questions because of their abundance and diversity in many upper Paleozoic rocks. However, inconsistent treatment and inadequate species concepts have resulted in an unsatisfactory taxonomy.

3. Snyder's (1984, 1991) comprehensive analysis of the fenestrate fauna of the Warsaw Formation (Mississippian) of the Mississippi River Valley provides an invaluable data base for the evaluation of fenestrate taxonomic concepts. Discriminant functions based on all available morphometric characters correctly assigned 99.4 percent of the Warsaw fenestrate specimens to their a priori species. In cluster analysis, 99.2 percent of fenestrate specimens clustered with members of their species (sensu Snyder 1984, 1991). This demonstrates that Snyder (1984, 1991) recognized viable species-level morphologic entities.

4. Some morphometric characters proved more useful for taxonomic distinctions than others, but based on results of one-way ANOVA, all 47 of Snyder's (1984) characters were significant ($P \leq .0001$). Species distinctions were more clear when a combination of interior and exterior characters were applied than when only interior or exterior characters were used. Species concepts improved as more characters were added to analyses.

5. In cluster analyses, fenestellid species tended to fall into larger groups of existing genera, but the groups were not consistent enough to be used as the basis of new generic concepts. However, discriminant functions correctly assigned 93.7 percent of 508 fenestrate specimens to their a priori genus using only morphometric data.

6. Fenestrate generic distinctions can be based on a limited number of characters associated with evolutionary shifts into new adaptive zones. Species diversification within adaptive zones is based on many characters. Convergent iterative evolution of species-level characters within and among adaptive zones resulted in pervasive homeomorphy among species, which in turn clouds generic distinctions in unweighted cluster analyses.

7. Generic distinctions should be based on characters that were significantly involved in the life mode of fenestrates, including those related to obtaining food, space, and protection. A list of suitable characters is proposed. Proposed generic distinctions can be tested with discriminant analysis against other established genera, using as many characters as possible, but excluding those initially used for the generic distinction.

8. The Warsaw fenestrate fauna described by Snyder (1984, 1991) provides a viable taxonomic framework to which other faunas may be compared. Other fenestrate faunas need to be studied in order to evaluate ideas introduced here.

9. The example provided here suggests reason for renewed optimism in treatment of taxonomically difficult groups.

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REFERENCES

BANCROFT, A. J. 1986a. The Carboniferous fenestrate bryozoan *Hemitrypa hibernica* M'Coy. Irish Journal of Earth Sciences, 7:111–124.

——. 1986b. A new Carboniferous fenestrate bryozoan genus. Scottish Journal of Geology, 22:99–106.

——. 1986c. Secondary nanozooecia in some upper Paleozoic fenestrate Bryozoa. Palaeontology, 29:207–212.

——. 1986d. Ovicells in the Paleozoic bryozoan order Fenestrata. Palaeontology, 29:155–164.

BASSLER, R. S. 1953. Bryozoa, p. G2–G253. *In* R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Pt. G. Geological Society of America and University of Kansas Press, Lawrence.

BLAKE, D. B. 1975. The Cryptostomata resurrected, p. 211–223. *In* S. Pouyet (ed.), Bryozoa 1974, Proceedings of the Third International Conference—Lyon. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon, hors serie 3.

BOARDMAN, R. S., A. H. CHEETHAM, AND P. L. COOK. 1983. Introduction to the Bryozoa, p. G3–G48. *In* R. A. Robison (ed.), Treatise on Invertebrate Paleontology, Pt. G, Bryozoa Revised. Geological Society of America and University of Kansas Press, Lawrence.

BURCKLE, L. H. 1960. Some Mississippian fenestrate Bryozoa from central Utah. Journal of Paleontology, 34:1077–1098.

CHEETHAM, A. H. 1986. Tempo of evolution in a Neogene bryozoan: rates of morphologic change within and across species boundaries. Paleobiology, 12:190–203.

CONDRA, G. E., AND M. K. ELIAS. 1944. Study and revision of *Archimedes* (Hall). Geological Society of America Special Paper 53, 243 p.

CROCKFORD, J. M. 1944. Bryozoa from the Wandagee and Noonkanbah Series (Permian) of Western Australia. Journal of Proceedings from the Royal Society of West Australia, 28:165–185.

CUMINGS, E. R. 1906. Descriptions of the Bryozoa of the Salem Limestone of southern Indiana. Indiana Department of Geology and Natural Resources Annual Report, 30:1274–1296.

ELIAS, M. K., AND G. E. CONDRA. 1957. *Fenestella* from the Permian of West Texas. Geological Society of America Memoir 70, 158 p.

FOSTER, A. B. 1984. The species concept in fossil hermatypic corals: a statistical approach. Palaeontographica Americana, 54:58–69.

——. 1985. Variation within coral colonies and its importance for interpreting fossil species. Journal of Paleontology, 59:1359–1381.

FOSTER, D. W., AND R. L. KAESLER. 1988. Analysis of heterochrony; shape analysis; ideas from the Ostracoda, p. 53–69. *In* M. L. McKinney (ed.), Heterochrony in Evolution; A Multidisciplinary Approach. Plenum Publishing Corporation, New York, New York.

GHENT, A. W. 1974. Theory and application of some nonparametric statistics III. Spearman's Rho and the "rankit" substitution as measures of rank-order correlation. The Biologist, 56:130–151.

GORJUNOVA, R. V. 1975. Permskie mshanki Pamira. Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta 148, 128 p.

HALL, J. 1857. Observations of the genus *Archimedes,* or *Fenestella,* with descriptions of species. American Association for the Advancement of Science Proceedings, 10:176–180.

JACKSON, J. B. C., AND A. H. CHEETHAM. 1990. Evolutionary significance of morphospecies: a test with cheilostome Bryozoa. Science, 248:579–583.

JOHNSON, R. A., AND D. W. WICHERN. 1988. Applied Multivariate Statistical Analysis. Prentice Hall, Englewood Cliffs, New Jersey, 607 p.

KING W. 1849. On some families and genera of corals. The Annals and Magazine of Natural History Including Zoology, Botany, and Geology, Second Series, 3:388–390.

KOENIG, J. W. 1958. Fenestrate Bryozoa in the Chouteau Group of central Missouri. Journal of Paleontology, 32:126–143.

LONSDALE, W. 1839. Corals, p. 675–694. *In* R. I. Murchison (ed.), The Silurian System, Part II—Organic Remains. John Murray, London.

M'COY, R. 1844. A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland. McGlashan & Gill, Dublin, 207 p.

MALONE, P. G., AND T. G. PERRY. 1965. Fenestellid bryozoans from oncolites in Sappington Sandstone of southwestern Montana. Journal of Paleontology, 39:41–44.

MCKINNEY, F. K. 1980. The Devonian fenestrate bryozoan *Utropora* Pocta. Journal of Paleontology, 54:241–252.

——, AND R. S. BOARDMAN. 1985. Zooidal biometry of Stenolaemata, p. 193–203. *In* C. Nielsen and G. P. Larwood (eds.), Bryozoa: Ordovician to Recent. Olsen and Olsen, Fredensborg, Denmark.

——, AND J. B. C. JACKSON. 1989. Bryozoan Evolution. Unwin-Hyman Press, Winchester, Massachusetts, 238 p.

——, AND J. KRIZ. 1986. Lower Devonian Fenestrata (Bryozoa) of the Prague Basin, Barrandian area, Bohemia, Czechoslovakia. Fieldiana, Geology New Series No. 15, 90 p.

MCNAIR, A. H. 1942. Upper Devonian Bryozoa. Journal of Paleontology, 16:343–350.

MILLER, T. G. 1961. Type specimens of the genus *Fenestella* from the lower Carboniferous of Great Britain. Palaeontology, 4:221–242.

MOROZOVA, I. P. 1962. K sistematike i filogenii Fenestelloidei. Paleontologicheskii Zhurnal, 4:104–115.

——. 1974. Revision of the bryozoan genus *Fenestella.* Paleontological Journal, 8:167–180.

——. 1981. Pozdnepaleozoiskie mshanki severo-bostoka SSSR. Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta 188, 120 p.

NEFF, N. A., AND L. F. MARCUS. 1980. A Survey of Multivariate Methods for Systematics. Privately published, New York, 243 p.

NEKHOROSHEV, V. P. 1928. Istoriya razvitiya Paleozoiskikh mshakok semeistva Fenestellidae. Izvestiya Geologicheskii Komitet, 47:479–518.

NICHOLSON, H. A., AND R. LYDEKKER. 1889. A Manual of Palaeontology. William Blackwood and Sons, Edinburgh and London, 1624 p.

OWEN, D. D. 1838. Report of a geological reconnaissance of the state of Indiana made in the year 1837. Indianapolis, 34 p.

PHILLIPS, J. 1841. Figures and descriptions of the Palaeozoic Fossils of Cornwall, Devon, and West Somerset. Longmans, Brown, Green and Longmans, London, 231 p.

PROUT, H. A. 1858. Second series of descriptions of Bryozoa from the Palaeozoic rocks of the western states and territories. Transactions of the St. Louis Academy of Science, 1:266–273.

——. 1859. Third series of descriptions of Bryozoa from the Palaeozoic rocks of the western states and territories. Transactions of the St. Louis Academy of Science, 1:443–452.

——. 1860. Fourth series of descriptions of Bryozoa from the Palaeozoic rocks of the western states and territories. Transactions of the St. Louis Academy of Science, 1:571–581.

SHULGA-NESTERENKO, M. I. 1949. Opyt philogeneticheskogo analiza mshanok sem. Fenestellidae. Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta, 20:293–316.

SIMONSEN, A. H., AND R. J. CUFFEY. 1980. Fenestrate, pinnate, and ctenostome bryozoans and associated barnacle borings in the Wreford Megacyclothem (Lower Permian) of Kansas, Oklahoma, and Nebraska. University of Kansas Paleontological Contributions, Paper 101, 38 p.

SNYDER, E. M. 1984. Taxonomy, functional morphology and paleoecology of the Fenestellidae and Polyporiidae (Fenestelloidea, Bryozoa) of the Warsaw Formation (Valmeyeran, Mississippian) of the Mississippi Valley. Unpubl. Ph.D. dissertation, University of Illinois, Urbana, 802 p.

——. 1991. Revised taxonomic procedures and paleoecological ap-

plications for some North American Mississippian Fenestellidae and Polyporidae (Bryozoa). Palaeontographica Americana, 57.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry: The Principles and Practice of Statistics in Biological Research. W. H. Freeman and Company, San Francisco, 776 p.

STRATTON, J. F., AND A. S. HOROWITZ. 1977. Variability in Seven Devonian Species of Polypora M'Coy. Privately published, Bloomington, Indiana, 23 p.

TAVENER-SMITH, R. 1966. The micrometric formula and the classification of fenestrate cryptostomes. Palaeontology, 9:413–425.

——. 1971. Fenestrate Bryozoa from the Visean of county Fermanagh, Ireland. Bulletin of the British Museum (Natural History) Geology, 23:389–493.

TERMIER, H., AND G. TERMIER. 1971. Bryozoaires du Paleozoique superieur de l' Afghanistan. Documents des Laboratories de Geologie de la Faculte des Sciences de Lyon 47, 52 p.

ULRICH, E. O. 1888. A list of the Bryozoa of the Waverly Group in Ohio. With descriptions of new species. Bulletin of Denison University Science Laboratories, 4:63–96.

——. 1890. Palaeozoic Bryozoa, Illinois Geological Survey Bulletin, 8:283–688.

VAN VALEN, L. 1971. Adaptive zones and the orders of mammals. Evolution, 25:420–428.

VINE, G. R. 1880. Report of the committee, consisting of Professor P. M. Duncan and Mr. G. R. Vine, appointed for the purpose of reporting on the Carboniferous Polyzoa. British Association for the Advancement of Science, 50th Meeting (Swansea, 1880):76–87.

——. 1884. Fourth report of the committee consisting of Dr. H. C. Sorby and Mr. G. R. Vine, appointed for the purpose of reporting on fossil Bryozoa. British Association for the Advancement of Science, 53rd Meeting (Southport, 1883):161–209.

WEI, K. Y. 1988. Multivariate morphometric differentiation of chronospecies in the late Neogene planktonic foraminiferal lineage *Globoconella*. Marine Micropaleontology, 12:183–202.

WINSTON, J. E. 1977. Feeding in marine bryozoans, p. 233–271. *In* R. M. Woollacott and R. L. Zimmer (eds.), The Biology of Bryozoans. Academic Press, New York.

——. 1978. Polypide morphology and feeding behavior in marine ectoprocts. Bulletin of Marine Science, 28:1–31.

——. 1981. Feeding behavior of modern bryozoans, p. 1–21. *In* T. W. Broadhead (ed.), Lophophorates: notes for a short course. University of Tennessee Department of Geological Sciences Studies in Geology 5.

YANG, J., Z. HU, AND F. XIA. 1988. Bryozoans from Late Devonian and Early Carboniferous of central Hunan. Palaeontologica Sinica 174, 197 p.

ZAR, J. H. 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey, 718 p.

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APPENDIX A: MORPHOMETRIC CHARACTERS WITH ABBREVIATIONS
(see Figures 4 and 5 for location of characters)

Exterior Characters.—

WB	1.	Width of branch (not measured at branch bifurcation)
DBC	2.	Distance between branch centers (not measured at branch bifurcation)
WD	3.	Width of dissepiment (measured parallel to branch growth)
LF	4.	Length of fenestrule opening
WF	5.	Width of fenestrule opening
AF	6.	Apertural openings per fenestrule (measured between dissepiment centers)
AL	5.	Aperture length (measured proximo-distally)
AW	6.	Aperture width (measured perpendicular to aperture length)
ADB	9.	Distance between aperture centers along branch
AAB	10.	Distance between aperture centers across branch at closest point
ABB	11.	Distance between aperture centers between branches (across fenestrules)
DN	12.	Diameter of nodes on obverse branch surface
DND	13.	Diameter of nodes on dissepiments (obverse surface)
SNB	14.	Distance between nodes along obverse branch surface
WK	15.	Width of keel
DSO	16.	Diameter of stylets on obverse surface
SSO	17.	Spacing of stylets along obverse branch surface
WP	18.	Width of peristome (measured at distal end of aperture)
SA	19.	Number of stylets around the aperture
SAD	20.	Diameter of apertural stylets
RSL	21.	Diameter of macrostylets on reverse branch surface
SSL	22.	Diameter of microstylets on reverse branch surface
RSS	23.	Spacing of macrostylets along reverse branch surface
SSS	24.	Spacing of microstylets along reverse branch surface
LRM	25.	Reticulate meshwork spacing parallel to direction of branch growth
WRM	26.	Reticulate meshwork spacing perpendicular to direction of branch growth
WSC	27.	Spacing of whorls along central axis (spine)
DCA	28.	Diameter of central axis (maximum)
ACA	29.	Angle between distal end of axis and axial whorl
OL	30.	Ovicell length (measured proximo-distally)
OW	31.	Ovicell width (measured perpendicular to ovicell length)

Interior Characters.—

TRW	32.	Thickness of reverse wall granular layer
TLW	33.	Thickness of chamber lateral wall granular layer
FWT	34.	Thickness of front wall (obverse wall) laminated layer
RWT	35.	Thickness of reverse wall laminated layer
CL	36.	Autozooecial chamber length (maximum chamber length measured down middle of chamber)
CD	37.	Autozooecial chamber depth (measured perpendicular to chamber length)
MAW	38.	Maximum chamber width (measured across branch)
MIW	39.	Minimum chamber width (measured across branch)
VD	40.	Chamber collar depth (vestibule)
RA	41.	Chamber reverse wall budding angle (use acute angle of wall emplacement)
LA	42.	Chamber lateral wall budding angle (use aperture opening relative to plane down the center of branch surface)
TB	43.	Thickness of branch (measured on obverse-reverse direction)

Derived Characters.—

MAW/CL	44.	Maximum chamber width divided by chamber length
CL × CD	45.	Chamber length multiplied by chamber depth
VOL	46.	Chamber length multiplied by chamber depth multiplied by maximum chamber width
AA	47.	Aperture length multiplied by aperture width

APPENDIX B: TAXONOMIC LIST OF WARSAW MESHWORK FENESTRATE SPECIES

Order Cryptostomata Vine, 1884
- Suborder Fenestelloidea Elias and Condra, 1957
  - Family Fenestellidae King, 1849
    - Genus *Rectifenestella* Morozova, 1974
      1. *R. tenax* (Ulrich, 1888)
      2. *R. tenuissima* (Cumings, 1906)
      3. *R. multispinosa* (Ulrich, 1890)
    - Genus *Laxifenestella* Morozova, 1974
      4. *L. coniunctistyla* Snyder, 1991
      5. *L. maculasimilis* Snyder, 1991
      6. *L. serratula* (Ulrich, 1890)
      7. *L. fluctuata* Snyder, 1991
    - Genus *Minilya* Crockford, 1944
      8. *M. sivonella* Snyder, 1991
      9. *M. paratriserialis* Snyder, 1991
    - Genus *Exfenestella* Morozova, 1974
      10. *E. exigua* (Ulrich, 1890)
    - Genus *Banastella* Snyder, 1991
      11. *B. guensburgei* Snyder, 1991
      12. *B. cingulata* (Ulrich, 1890)

13. *B. mediocreforma* Snyder, 1991
14. *B. limitaris* (Ulrich, 1890)
15. *B. biseriata* (Ulrich, 1890)
16. *B. delicata* Snyder, 1991

Genus *Cubifenestella* Snyder 1991
17. *C. rudis* (Ulrich, 1890)
18. *C. usitata* Snyder, 1991
19. *C. globodensata* Snyder, 1991

Genus *Apertostella* Snyder, 1991
20. *A. foramenmajor* Snyder, 1991
21. *A. crassata* Snyder, 1991
22. *A venusta* Snyder, 1991

Genus *Hemitrypa* Phillips, 1841
23. *H. perstriata* Ulrich, 1890
24. *H. hemitrypa* (Prout, 1859)
25. *H. aprilae* Snyder, 1991
26. *H. aspera* Ulrich, 1890
27. *H. vermifera* Ulrich, 1890

Genus *Archimedes* Owen, 1838
28. *A. negligens* Ulrich, 1890
29. *A. owenanus* Hall, 1857
30. *A. wortheni* (Hall, 1857)
31. *A. valmeyeri* Snyder, 1991

Family Polyporidae Vine, 1880
Genus *Fenestralia* Prout, 1859
32. *F. sanctiludovici* Prout, 1858

Genus *Polypora* M'Coy, 1844
33. *P. gracilis* Prout, 1860
34. *P. varsoviensis* Prout, 1858
35. *P. spininodata* Ulrich, 1890
36. *P. simulatrix* Ulrich, 1890
37. *P. retrorsa* Ulrich, 1890

APPENDIX C: CHARACTERS USED IN CLUSTER ANALYSES FOR GENERIC DISTINCTIONS
(parameters for descriptive terms in mm)

I. External Characters

Zoarial

1. Robustness
1. delicate: small fragments
2. intermediate: moderate number large fragments
3. robust: large unbroken fragments

2. Fan form
1. flat
2. obversely or reversely curved
3. undulating
4. cup-shaped
5. spiral with axis

3. Mesh type: WF:WB ratio
1. close: < 0.80
2. intermediate: 0.80–1.5
3. open: > 1.5

4. Mesh uniformity
1. regular: low C.V. for LF, WF, WB
2. irregular: high C.V. for LF, WF, WB

5. Secondary zoarial features
1. central axis
2. reticulate meshwork
3. other

Branch

6. Width (mm)
1. narrow: WB < 0.30
2. intermediate: WB 0.30–0.39
3. wide: WB > 0.39

7. Trace proximo-distally
1. straight
2. sinuous
3. broadly curved

8. Surface profile
1. round
2. flat
3. angular

Keel

9. Number
1. absent
2. single
3. multiple

10. Width (mm)
1. narrow: WK < 0.05
2. intermediate: WK 0.05–0.15
3. wide: WK > 0.15, or WK > WB = wide

11. Trace
1. straight
2. anastomosing

Nodes

12. Emplacement
1. absent
2. monoserial
3. biserial

13. Size (mm)
1. small: DN < 0.065
2. intermediate: DN 0.065–0.12
3. large: DN > 0.12

14. Shape
1. circular
2. ovate
3. elliptical
4. stellate

15. Spacing (mm)
1. close: SNB < 0.24
2. intermediate: SNB 0.24–0.80
3. wide: SNB > 0.80

Obverse stylets

16. Size (mm)
1. absent
2. small: DSO < 0.01
3. intermediate: DSO 0.01–0.02
4. large: DSO > 0.02

Microstylets (reverse)

17. Size (mm)
1. absent
2. small: SSL < 0.018
3. intermediate: SSL 0.018–0.026
4. large: SSL > 0.026

Macrostylets (reverse)

18. Size (mm)
1. absent
2. small: RSL < 0.05
3. intermediate: RSL 0.05–0.08
4. large: RSL > 0.08

Autozooecia

19. Number of rows
1. two consistently
2. two, becoming three for short distances proximal to branch bifurcations
3. greater than two consistently

Heterozooecia

20. type per Morozova (1974)
1. absent
2. ovicells
3. parazooecia
4. cyclozooecia
5. caverns
6. microzooecia

Dissepiment

21. Width
1. thin: WD < ½WB
2. intermediate: WD = ½WB–WB
3. wide: WD > WB

22. Length
1. short: WF ≪ WB
2. intermediate: WF = WB
3. long: WF ≫ WB

23. Placement intervals
1. regular
2. variable

Fenestrule
- *24.* Size (mm)
  1. small: LF < 0.4, WF < 0.24
  2. intermediate: LF 0.4–0.9, WF 0.24–0.34
  3. large: LF > 0.9, WF > 0.34
- *25.* Shape
  1. elliptical
  2. ovate
  3. rectangular
  4. square
  5. circular

Aperture
- *26.* Size (mm)
  1. small: AL < 0.09, AW < 0.07
  2. intermediate: AL 0.09–0.15, AW 0.07–0.12
  3. large: AL > 0.15, AW > 0.12
- *27.* Shape
  1. circular
  2. ovate
  3. elliptical
- *28.* Orientation relative to plane of obverse surface
  1. parallel
  2. angle toward fenestrule
  3. perpendicular
- *29.* Peristome
  1. absent
  2. incomplete
  3. complete
- *30.* Apertural stylets
  1. absent
  2. present
- *31.* Terminal diaphragm position
  1. absent
  2. proximal
  3. middle
  4. distal
  5. variable

II. Internal characters

Branch
- *32.* Shape in cross section
  1. elliptical
  2. ovate
  3. circular
  4. semicircular
  5. rhombic
  6. polygonal
- *33.* Branch thickness (mm)
  1. shallow: TB < 0.30
  2. medium: TB 0.30–0.39
  3. thick: TB > 0.39

Autozooecial living chamber
- *34.* Size (mm)
  1. small: CL < 0.20, CW < 0.10, MAW < 0.10
  2. intermediate: CL 0.20–0.48, CW 0.10–0.20, MAW 0.10–0.15
  3. large: CL > 0.48, CW > 0.20, MAW > 0.15
- *35.* Emplacement
  1. monoserial
  2. biserial
  3. polyserial
- *36.* Axial wall trace
  1. straight
  2. sinuous
  3. zigzag
- *37.* Orientation of autozooecial chamber elongation
  1. parallel to reverse wall
  2. parallel to proximal and distal lateral wall chambers
- *38.* Chamber outline near reverse wall
  1. triangular
  2. square
  3. circular
  4. oval
  5. elliptical
  6. pentagonal
  7. rectangular
  8. parallelogram
  9. diamond
- *39.* Chamber outline near mid-chamber (same as *#38*)
- *40.* Chamber outline near obverse surface (same as *#38*)
- *41.* Vestibule length (mm)
  1. absent
  2. short: VD < 0.06
  3. intermediate: VD 0.06–0.12
  4. long: VD > 0.12
- *42.* Superior hemiseptum
  1. absent
  2. present
- *43.* Inferior hemiseptum
  1. absent
  2. present
- *44.* Chamber lateral wall budding angle in degrees
  1. <15
  2. 15–10
  3. 20–25
  4. >25
- *45.* Chamber reverse wall budding angle in degrees
  1. <30
  2. 30–39
  3. 40–49
  4. 50–59
  5. 60–69
  6. 70–79
  7. 80–90
  8. >90

Zoarial skeletal microstructure
- *46.* Exterior lamellar skeleton
  1. thin
  2. intermediate
  3. thick
- *47.* Interior granular skeleton
  1. thin
  2. intermediate
  3. thick