THE MICROMETRIC FORMULA AND THE CLASSIFICATION OF FENESTRATE CRYPTOSTOMES

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ABSTRACT. A critical assessment of the use of the micrometric formula in classifying fenestrate cryptostomes shows that although the device may be of some use as an aid to description and as a means of indexing species, it is an ineffective basis for structural comparisons. The method employed in making such comparisons is also unsound. Nevertheless, taxonomic conclusions are commonly drawn from them, and a result of this is an unreasonable increase in the number of recognized species. It is suggested that the micrometric formula should be discarded for comparative purposes and its place taken by one of the orthodox biometrical tests of significance. Such tests afford a simple and objective way of comparing sets of data. Samples for comparison should consist of groups of specimen means: owing to the colonial nature of the organisms, data from a single colony are inadequate for the purpose. A procedure for comparing samples is outlined, and an example given.

SINCE colonies of fenestrate bryozoa were first examined in detail it has been evident that the pattern of structural elements in a zoarium offers the basis for a numerical means of discriminating between species. M'Coy (1844) and his contemporaries incorporated measurements of these features in systematic descriptions with a view to their use in comparison, and at a later date Shrubsole (1881, p. 189) presented similar data in tabular form with the same end in view. With the passage of time a desire for greater refinement led to the inclusion of increasing numbers of measurements in descriptions, particularly by Russian authors. These became so numerous that Nekhoroshev (1926) introduced the practice of extracting those that seemed most critical and presenting them separately in the form now known as the 'meshwork formula' (Condra and Elias 1944, pp. 56–57), or the 'micrometric formula' (Miller 1961, p. 224). These figures were intended to convey the essential structural characteristics of the forms described. They were based on measurements of four kinds: the number of branches in 10 mm., measured perpendicular to the axis of growth; the number of fenestrules in the same distance, measured along the branch length; the number of zooecial apertures in a single row in 5 mm., and the number of carinal nodes, also in 5 mm. The formula stated the frequency or (more often) the observed range of each feature.

This procedure was made known to western workers by Condra and Elias in the paper mentioned above, in which they also proposed a standard method for making the required measurements. These authors strongly advocated the use of the formula in descriptive work and also used it as a basis for taxonomic comparisons. Since that time it has been accepted into general use and become a principal means of discriminating between the numerous species of fenestrate cryptostomes.

For descriptive purposes the micrometric formula has much in its favour. It is readily obtained even from small specimens, and provides a convenient shorthand expression of important structural characteristics of colonies. Because these formulae are now available in the literature for almost all adequately described species they also provide a useful basis for indexing (Miller 1961, p. 224), a valuable asset in a genus like *Fenestella* with more than 500 named species. As a basis for taxonomic discrimination, however, the formula has less to commend it and the purpose of this paper is to examine its

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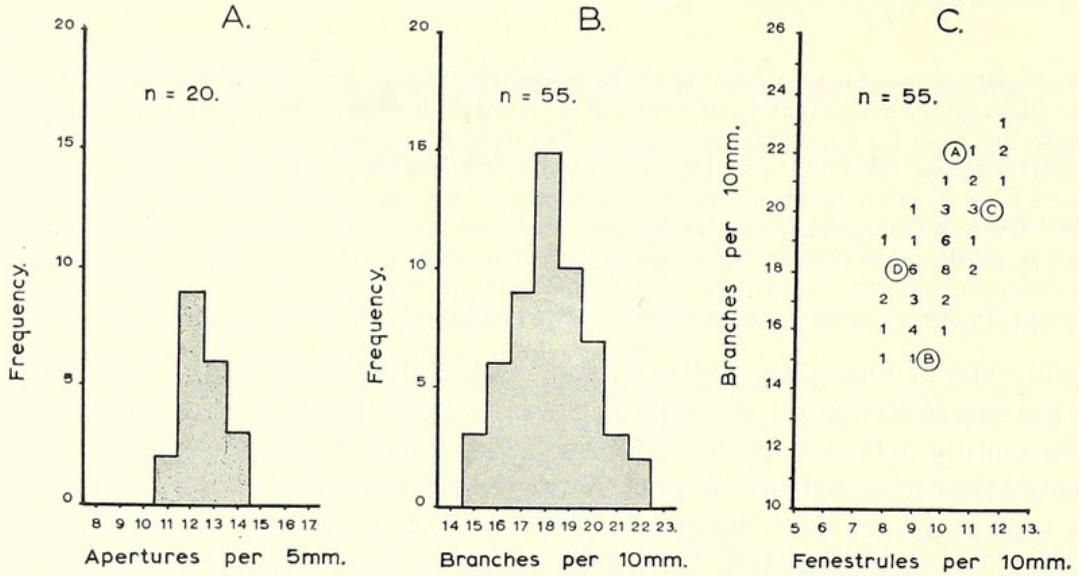
function in this respect and to suggest improvements. Before doing so it is helpful to consider certain structural characteristics of fenestrate colonies, and also the nature of the information that the formula contains.

Structural variation in fenestrate colonies. The tendency towards structural variation within a species is a widely recognised characteristic of fenestrate cryptostomes and one that has been commented on by many authors (e.g. Foerste 1887, p. 84; Condra and



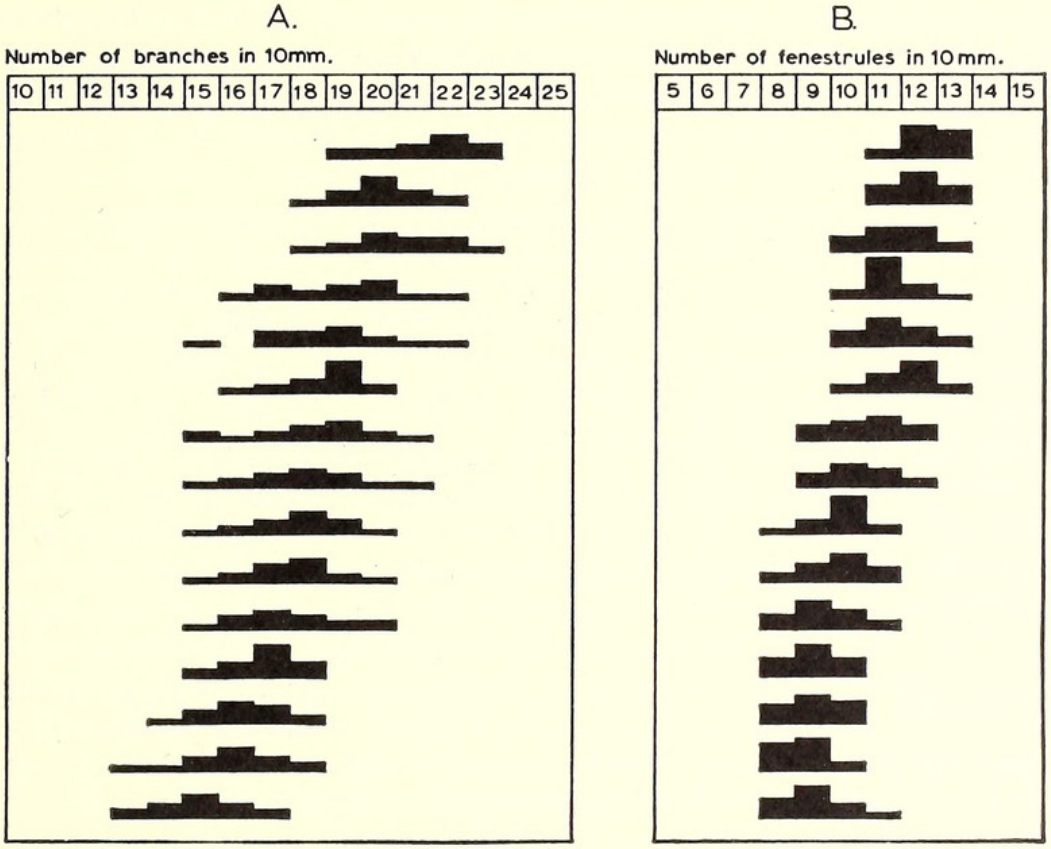
TEXT-FIG. 1. *a.* Graph of measurements made on a single colony (a homeotype of *Fenestella hemispherica* M'Coy, Sedgwick Museum specimen E 17841); *b.* Distribution of the modes of 55 colonies of *Ptilofenestella carrickensis* Tavener-Smith; *c.* Bivariate distribution of modal values from the same colonies, showing the location of the specimens listed in Table 2.

Elias 1944, p. 56). This variation takes two main forms: that within a colony, and that between colonies. If a number of readings from a colony are represented graphically they form an approximately normal distribution (text-fig. 1*a*). Each variable is distributed in this way, occurring between certain observable limits, and it is therefore possible to construct a micrometric formula for a single zoarium, or even a fragment. It is important to remember, however, that a zoarium is a clone, that is, an association of asexually produced individuals that are genetically alike, and the range of variation within it will not, therefore, be of direct use in classification.

The central value, on the other hand, has much greater importance as it is from many points of view the most representative measurement for the colony concerned. This value is determined by the interaction of two sets of factors: genetic and ecological. A colony originates by sexual reproduction and therefore has its own particular genetic constitution that distinguishes it from all other colonies. Ecological considerations involve the relationship between a colony and its environment, and will vary with the situation. Within a colony disparities in the biochemical control of growth, and differences of micro-environment cause the dispersion of the data into a normal distribution, of which the central value reflects the interaction of the two basic factors.

Where a series of data shows an approximately normal distribution, either the mean, median or mode may, according to circumstance, be used to measure their central

tendency. Although the mode is usually the obvious choice for this purpose, it has disadvantages in small samples, for in them it is very subject to random fluctuation. Difficulty may also arise becauses uch samples occasionally show more than one mode (e.g. three of the graphs in text-fig. 2*a*). The median and arithmetic mean are therefore often of greater practical value and, of these, the mean is the more useful statistic in



TEXT-FIG. 2. Graphs of measurements from colonies of *Ptilofenestella carrickensis* to illustrate the range of morphological variation. Each graph incorporates 15 readings, and the order of arrangements is the same in both diagrams.

comparative work. The mean of a series of readings made on a colony is, for these reasons, usually the single measurement best suited to represent it.

If sets of readings from a number of conspecific colonies are plotted graphically, a series of overlapping distributions result (text-fig. 2). In such a series the ranges of individual colonies may differ appreciably from one another, and may even (as the diagram shows) be mutually exclusive. It is apparent from this that in a morphologically variable group such as the fenestrate cryptostomes the range of variation shown by a single colony may bear little relation to that of the species to which it belongs,

The lack of a direct relationship between intra- and inter-colonial variation can also be demonstrated by means of the technique of analysis of variance, to which the data are readily adapted. Four such analyses were made, one for each variate of the micrometric formula, the data being derived from specimens of *Ptilofenestella carrickensis* Tavener-Smith 1965. Between ten and fifteen measurements from each of 10 colonies were used, and in each case it was found that a significant difference ($P < 0{\cdot}05$) existed between the

variance estimates. There is therefore a recognizable difference in pattern between intra-colonial and inter-colonial variation, and this being so, the range of a variate within a colony cannot justifiably be used as the basis for taxonomic comparisons between colonies.

When the central values of a number of colonies of the same species are assembled into a histogram it is seen that they also have an approximately normal distribution. In text-fig. 1*b* a group of modes is used to illustrate this point: the corresponding means would show a similar pattern. Samples of this kind are likely to be taxonomically useful because they are based on the most representative measurements of a group of colonies and

TABLE 1

	Fenestrule width.	Inter-ap. space.	Internodal space.	Branch width.	Apertural diameter.
Fenestrule length.	+0·6886	+0·4217	+0·3898	-0·4836	+0·5226
Fenestrule width.		+0·3899	+0·3274	-0·4471	+0·7169
Inter-ap. space.			+0·3014	-0·3214	+0·3605
Internodal space.				-0·2640	+0·1119
Branch width.					+0·3760

Ptilofenestella carrickensis: coefficients of correlation between pairs of structural features. The continuous variables used here include those that correspond most closely with the micrometric formula, namely: fenestrule width and length, inter-apertural space, and internodal space. In all cases $n=55$.

(according to the number of specimens measured) will provide a more or less reliable indication of the range of variation in the species concerned. Distributions of this type are used as the basis for the comparative technique outlined later in this paper.

Another characteristic of fenestrate cryptostomes is the significant, though weak, correlation that exists between different structural elements in a colony (Table 1). This is evident from a consideration of micrometric formulae, in which a high count for the number of branches in 10 mm. is often accompanied by high numbers of fenestrules, apertures, and nodes (e.g. *Fenestella bicellulata* Etheridge: 24–27/27–28//27–29/29–31). The converse is generally true when the branch count is low (e.g. *F. oblongata* Koenig: 9–15/4–7//14–19/4–7). Although it is technically more correct to use a multivariate approach where sets of data are correlated, the correlations are here so weak that little is lost by using simpler univariate methods in comparing samples. Comparisons based on the micrometric formula are in this respect quite well adapted to the situation, for they function on this principle. Although each formula embodies the frequency or observed range of four variates, these are dealt with separately, and the comparisons are quite independent of one another.

Construction of the micrometric formula. There is no reason to doubt that the geometrical arrangement of structural elements in a fenestrate colony is of taxonomic value,

and the spatial distribution of branches, dissepiments, zooecial apertures, and carinal nodes were considered by Nekhoroshev (1926) to be the most important variates involved. These features have come, by usage, to be the ones on which most reliance is placed in discriminating between species (Condra and Elias 1944, p. 54). They are therefore weighted for taxonomic purposes, as compared with others such as the width of branches or dissepiments, and the diameter of zooecial apertures, which are not included in the formula. Nevertheless, all these have been recognized at one time or another to have potential diagnostic value (e.g. Nekhoroshev 1932, p. 302; Miller 1962, p. 120). Their relative neglect is probably due to the tendency for secondary calcification to alter dimensions with increasing age, thus apparently nullifying the usefulness of these features in classification. It seems likely, however, that this objection is not insuperable. Certainly, the restriction of taxonomic consideration to the variates of the micrometric formula is in itself a disadvantage, for it is generally agreed that the best classification is that based on all relevant morphological data.

A standard method for measuring variates of the micrometric formula is described by Condra and Elias (1944, pp. 54–55). They recommend the use of the so-called space-unit count, which means that it is the space *between* selected structural features that is counted, and not the features themselves. Thus, the total per standard distance (5 or 10 mm.) is not the actual number in that distance, but one less than this. It is worth noticing that because the basis of each count is the linear distance between adjacent features, the variates are essentially continuous and not discontinuous, as first appearances suggest. It is therefore permissible and advantageous to use the mean rather than the mode as the central value of distributions relating to them.

The method of presenting structural data in the orthodox micrometric formula is extremely rudimentary. Only the observed range of the measurements is given for each feature, and sometimes this is abbreviated to a single figure, implying that there was no variation in the sample examined. No supporting data of any kind relating to the pattern of the distribution are given. Nor is it stated how many readings were made, or whether all were taken from a single specimen or from several. The work of Perry and his associates is, in this respect, an exception to the general rule. Utgaard and Perry (1960) give formulae supported by histograms showing the distribution of the variables, and Malone and Perry (1965) state a mean and standard deviation for each variate and the number of measurements made. They do not say, however, how many zoarial fragments were examined, or how many readings were taken from each. Both facts are relevant if comparisons are to be taxonomically valuable.

Effectiveness of the formula in taxonomic discrimination. To illustrate the use of the micrometric formula in structural comparisons an example is necessary, and a typical case occurs in recent work by Burckle (1960, p. 1083). This author measured some new material in order to ascertain whether it was conspecific with *Fenestella rectangularis* Ulrich, to which there was a superficial resemblance. Having derived a formula, he compared it with that of Ulrich's species in the usual way, namely by placing the two side by side and examining the ranges of each variable separately. The formulae were as follows:

F. rectangularis Ulrich: 20–26/17$\frac{1}{2}$–24//23–25/14–17
Burckle's material: 23–27/16–24//20–24/16–20.

He concluded that, while the ranges for the first three variables were close enough to be

considered identical, those for carinal nodes indicated a clear difference between the samples. This he took to be of taxonomic as well as numerical significance, and accordingly founded a new species which he named *F. tooelensis*.

It is necessary to decide whether comparisons of this pattern are, in general, acceptable as a basis for taxonomic discrimination. The reasons given below suggest that they are not.

1. Micrometric formulae are usually stated in terms of the observed range of variates. This is generally acknowledged to be a poor basis for comparison, as the range of a sample is directly related to its size (Simpson 1941). Unless samples are uniform in this respect their ranges will be expected to differ, even if they are drawn from the same population, and such differences need have no taxonomic significance. If, in the example

TABLE 2

	Branches in 10mm.	Fenestrules in 10mm.	Apertures in 5mm.	Nodes in 5mm.
A.	20 - 22	12 - 13	21 - 24	27 - 33
B.	13 - 17	8 - 12	17 - 19	21 - 27
C.	20 - 22	11 - 12	18 - 21	25 - 28
D.	14 - 18	9 - 10	17 - 21	30 - 38

Micrometric formulae measured on four selected specimens of *Ptilofenestella carrickensis*.

quoted above, each formula was based on only one specimen it would be quite unjustifiable to assume that the difference in node counts had taxonomic significance. But if, on the other hand, each was derived by measurement of twenty specimens, the case for a difference between them would be a strong one. As the number is not stated there is no way of deciding where the truth lies.

Formulae giving single figures for variates are even less useful than those that show the observed range. A single figure provides no idea of variation, and all that can reasonably be done is to treat it as the mean of the distribution it represents. Even then it is of no value for comparative purposes without information as to the number of specimens examined and measurements made. In view of the structural variability of fenestrate zoaria it seems likely that formulae giving this kind of information were measured on single small fragments.

2. Many micrometric formulae in the literature appear to have been measured on one specimen only, often a holotype (Condra and Elias 1944, p. 107; Elias and Condra 1957, p. 77; Koenig 1958, p. 135; Burckle 1960, p. 1087; Miller 1961, p. 231, and many others). Such formulae can only record intra-zoarial variation and this offers no foundation for inter-zoarial comparison because it is possible for the range of a variate to differ markedly in two specimens that are conspecific (text-fig. 2). A notable numerical discrepancy between observed ranges may have no taxonomic significance at all if the ranges were measured on single specimens. Table 2 shows the formulae of four specimens of *Ptilofenestella carrickensis* Tavener-Smith which occur at the extremes of a bivariate distribution of the number of branches and fenestrules per 10 mm. The graph is shown in text-fig. 1*c*. Because a weak positive correlation exists between the variables of the formula, extreme ranges for apertures and nodes occur in the same specimens. Discrepancies between the ranges of these formulae are enough to suggest separation

into 2, if not 4 species of the kind that Burckle recognized. Yet all 4 colonies are, in fact, conspecific. Comparisons involving formulae derived from single specimens are, it seems, unreliable for taxonomic purposes.

3. In comparisons of formulae such as that outlined earlier, the method is visual and subjective, each case being decided solely by the personal judgement of the author concerned. While such a procedure may be satisfactory if formulae happen to be identical or when they differ widely, in the great majority of intermediate cases there is much room for error. Results are most likely to be unreliable where the overlap between ranges is appreciable but not complete, and the dependability of the test will therefore be least exactly where it needs to be greatest. Because there is no objective way to decide whether an observed difference between the ranges of samples has taxonomic significance, uniformity of treatment can hardly be expected. A difference that is enough to justify the erection of a new species in the opinion of one author may seem insufficient for the purpose to another, and the classification suffers accordingly.

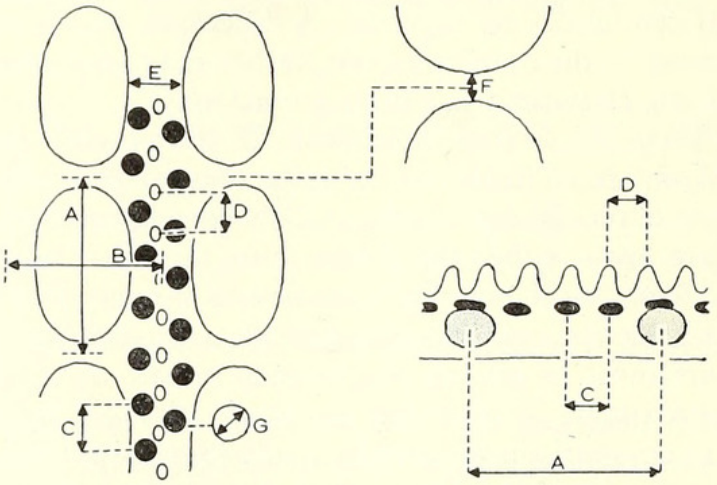
It is evident that there are serious deficiencies in the present method of comparing samples of structural data from fenestrate colonies. One result of this is an unreasonable increase in the number of recognized species. An improved procedure is needed, and two alternative courses are open: either the micrometric formula may be retained in a revised and expanded form, or it may be discarded in favour of a new approach. For reasons already stated, the formula can only provide a reasonable basis for comparison if the ranges given are those of groups of specimen means, and if the number in each group is known. Approximate statistics for the distribution can then be calculated, and a rough but objective comparison of samples made (Simpson 1941, pp. 788 and 793). However, the micrometric formula is founded on the observed range and even in its most acceptable form permits only a crude comparison of the kind mentioned above. It seems better, from all points of view, to discard the formula for comparative purposes, though it could be retained in descriptions as a means of indexing species. In effecting numerical comparisons it is the distribution of variables, not their ranges, that is important, and this is best defined in terms of orthodox statistics such as the mean and variance. If these are available samples can be compared by utilizing one of the significance tests common in modern biometric usage. Before outlining the kind of procedure that might be followed, it is advisable to consider the morphological features that could be compared, and the way in which they might be measured.

Dimensions to be compared. The fundamental purpose of the method outlined by Condra and Elias (1944, pp. 54–57) for measuring variable features on fenestrate bryozoans is to establish the average dimensions that characterize a particular fragment or series of fragments. Their procedure for doing this is clumsy and fails to provide an effective basis for comparison. Counting the number of branches, fenestrules and so on, per unit distance is merely an indirect and ineffective way of assessing the average distance between these structures. It is more satisfactory as well as simpler to make the necessary measurements directly, and to derive from them statistics that can be quickly and objectively compared by means of a significance test.

For comparisons to be valid it is essential that measurements should be made in a standardized manner, and text-fig. 3 suggests how this could be done. The variables of the micrometric formula are adequately represented by the basic measurements

concerned, namely fenestrule width and length, together with inter-apertural and internodal distance. Fenestrule width is measured through the mid-point of a fenestrule, from the centre of the branch on one side to the centre of that on the other. Fenestrule length is the distance, along the mid-line of the fenestrule, between the centres of adjacent dissepiments. Inter-apertural distance and internodal distance are measured between the centres of pairs of the appropriate structures that are situated in the same row.

To these variates may be added others, such as branch width, dissepiment width, and apertural diameter. It is true that these are subject to secondary calcification, and their dimensions may be influenced by this factor. Nevertheless, if samples consist of groups of specimen means there is no reason why it should vitiate comparisons. Random



TEXT-FIG. 3. Method of making measurements: *a*, fenestrule length; *b*, fenestrule width; *c*, inter-apertural space; *d*, internodal space; *e*, branch width; *f*, dissepiment width; *g*, apertural diameter.

samples of fenestrate colonies should contain sufficiently similar numbers of both young and old colonies to cause the influence of secondary accretion on measurements to balance out between samples. Its importance is therefore much less than would be the case in comparing single colonies.

Branch width is recorded at right angles to the branch axis and away from points of bifurcation and branch-dissepiment junctions. The width of dissepiments is measured midway along their length, where the structure is narrowest. In the case of zooecial apertures it is the internal diameter that is measured: for ovoid or pyriform apertures a longer and shorter dimension could be given.

Elias and Condra (1957, pp. 70–72) attached great taxonomic value to the number of zooecial apertures per fenestrule, and largely based their classification upon this. Many workers would not agree in according prime importance to this feature, but it is one that can sometimes be used with advantage in comparative work. An examination of the literature reveals, however, that there is a discrepancy in the method employed to make the necessary measurements. Some workers (e.g. Shulga-Nesterenko, 1951) count the actual number of apertures along one side of a fenestrule, while others use the space-count method of Condra and Elias and record one less than the actual number. As the numbers are always small such a discrepancy is likely to have unfortunate results, and it

is important to standardize procedure. The second method of counting is recommended, as it accords with that used in measuring other variables, and in practice the number of apertures per fenestrule for a colony or fragment may be derived from the figures for mean fenestrule length and mean inter-apertural space.

Measurements of these features and any others that are desired can be made in the usual way with a microscope eyepiece micrometer. More accurate results are obtained by using a screw micrometer with travelling cross-wire, or better still, a traversing stage with a screw micrometer. Measurements should, wherever possible, be taken from mature parts of zoaria where structural variation is likely to be at a minimum (Miller 1961, pp. 222–3), rather than from the proximal region where growth is often irregular.

Method of comparison. In order to permit a realistic comparison to be made, samples must contain information from a number of specimens, not only one. This is because data from a single colony or fragment reflect intra-zoarial variation alone and this, for reasons already given, has little value in taxonomy. Also, only the central value of a series of measurements from a colony is taxonomically useful, and significance tests are not competent to discriminate between single values, but only between groups. The mean is the most convenient central value for most purposes, and a sample for comparison should therefore consist of a number of specimen means. The larger the number in the sample, the more accurately will it reflect the range of variation in the population from which it was drawn. Small samples of only a few specimens can also be used however.

The use of a recognized significance test ensures that an objective comparison of samples is made, and the one best suited to present requirements is the well-known *t*-test described in standard statistical texts (e.g. Fisher 1948, p. 122). When this method is used to compare samples, t is essentially the ratio of the difference between means to the standard error of the difference. It may be written:

$$t = \frac{\bar{x}_1 - \bar{x}_2}{s\sqrt{(1/n_1 + 1/n_2)}} \quad \text{for } n_1+n_2-2 \text{ degrees of freedom,}$$

where $\bar{x}_1$ and $\bar{x}_2$ are the means of two samples, and n_1, n_2 are the numbers of specimens in those samples. Also:

$$s^2 = \frac{1}{n_1+n_2-2}\{\sum (x_1-\bar{x}_1)^2 + \sum (x_2-\bar{x}_2)^2\}.$$

Having calculated t and knowing the number of degrees of freedom, the value of P (the probability that the difference between the means is due to the chances of sampling only) may be read from appropriate tables. If P is greater than 0·05 it is probable that the results are due to chance, and they are described as 'not significant'. If less than 0·01, then not once in 100 times could such a result have arisen by chance, and it may be considered significant. If the value of P lies between the 0·01 and 0·05 levels the result is probably significant. A suggested sequence for comparing samples of structural data by this method is outlined below. The procedure would have to be repeated for each variate.

(1) A series of readings should be made on each specimen for the variate under consideration. The number of measurements would depend on the size and state of preservation of the material: between 10 and 20 would be satisfactory. From these calculate the specimen mean.

(2) Repeat for each specimen, and then assemble the specimen means into a separate

distribution. It is this group, consisting only of specimen means, that constitutes the sample for comparison. Compute the sample mean and variance: these, together with the number of specimens in the sample, are the basic statistics used in comparison.

(3) Any two samples of this kind may then be objectively compared by using the *t*-test, as outlined above.

To illustrate the working of the method an actual example is quoted below. It concerns three superficially similar forms of *Fenestella* for each of which a number of specimens was available. It was desired to test these numerically in order to find whether the three groups could have been drawn from the same parent population. For this purpose each was represented by a sample of 25 specimens, referred to here as samples *A*, *B*, and *C* respectively. A number of variates were measured in each sample and comparisons made between them. The data for fenestrule width (corresponding to the number of branches per 10 mm. in the micrometric formula) were as follows:

	Sample A	*Sample B*	*Sample C*
$\bar{x}$:	0·573 mm.	0·598 mm.	0·432 mm.
$\sum (x-\bar{x})^2$:	0·069 mm.	0·155 mm.	0·104 mm.

On testing samples *A* and *B* it was found that:

$$\bar{x}_1-\bar{x}_2 = 0{\cdot}025 \text{ mm.}$$

$$s^2 = \frac{1}{48}(0{\cdot}069+0{\cdot}155) = 0{\cdot}0047.$$

So $$s = 0{\cdot}068.$$

Then $$t = \frac{0{\cdot}025}{0{\cdot}068}\sqrt{\left(\frac{25\times 25}{50}\right)} = 1{\cdot}299.$$

From the tables it is seen that for $n = 48$ this value of t indicates a probability of more than 0·1. The result is therefore not significant, and the samples could very well have been drawn from the same population. On comparing samples *A* and *C*, however, it is found that the value of t is much larger, being, in fact, 8·29. For the same number of degrees of freedom this represents a probability level of less than 0·001, and it is very unlikely that these two samples could belong to the same population. Comparison of forms *B* and *C* yields a similar result, the value of t this time being 7·41 (i.e. $P < 0{\cdot}001$). From these tests it appears that while samples *A* and *B* cannot be differentiated from one another, both are significantly different from sample *C*. Further tests on other variates gave confirmatory results and it was concluded that two distinct species were represented, *A* and *B* belonging to one, and *C* to the other. Additional confirmation of quite a different kind appeared later when it was found that specimens of groups *A* and *B* had triangular zooecial base shapes, while those of group *C* were hemi-hexagonal. It is worth mentioning that micrometric formulae based on the three samples showed much overlap in their ranges and gave no indication of the result that emerged quite clearly from the above tests. The formulae were as follows:

Group *A*: 7–12/3–6//11–15/2–6.
Group *B*: 8–13/3–8//12–16/3–7.
Group *C*: 10–14/5–9//13–17/4–9.

The recognition of significant differences between samples in all tests of a series leaves little doubt that the groups concerned belong to different species. Difficulty would arise, however, if it was found that the level of significance was exceeded in only, say, three out of six cases. Would it then be reasonable to differentiate the samples at specific level? In earlier work new species have sometimes been erected on the basis of a single quantitative difference between samples, as in the case of Burckle's species. More frequently two such differences are cited, and occasionally more. In discussing the application of biometrical methods to the classification of Caradocian brachiopods Williams (1962, p. 79) suggested that a significant difference in one feature, particularly if it could arise phenotypically, might serve to indicate the presence of separate sub-species, but that two or more such differences are needed to justify separation at the specific level. Such a scheme is, of course, arbitrary and the need to make exceptions to it might arise from time to time. Nevertheless, it seems to be in general accordance with established practice in the classification of fenestrate bryozoa, and its adoption would promote uniformity of treatment.

SUMMARY

The foregoing arguments and suggestions can be summarized as follows:

(*a*) The micrometric formula is of use as a descriptive aid because it conveys an immediate impression of the general characteristics of a fenestrate colony. It is also a convenient basis for indexing the numerous species of *Fenestella*, and as such will no doubt continue to be used.

(*b*) The formula presents information in the form of observed ranges of measurements unsupported by other data, and this precludes the use of conventional numerical techniques in comparing samples. Instead, simple visual methods are relied on to determine whether two formulae relate to the same species, and such tests are strongly subjective. In addition, it is probable that many formulae were measured on single specimens and are therefore unreliable as a basis for taxonomic comparisons. In view of these disabilities it is recommended that the micrometric formula should be discarded in comparative work: its continued use can only lead to further confusion.

(*c*) If adequate data are available, reliable and objective comparisons can be made between sets of measurements by utilizing one of the significance tests commonly used in biometrics. A method for doing this is outlined, based on the *t*-test. Techniques of this kind are only competent to discriminate between groups of data, and not between single measurements. Samples for comparison should therefore consist of a representative measurement from each of a number of colonies, and the arithmetic mean is best suited to this purpose. If provision is to be made for testing new material against established species, systematic descriptions must include certain essential statistics for each variate. These are the sample mean and variance, and the number of specimens in the samples. An indication of the number of measurements made on each specimen would also be of assistance, though not essential.

It may be objected that, although the comparative technique suggested here is in theory superior to the micrometric formula, it suffers from an important practical disadvantage, namely, that numbers of specimens are not usually available for comparison, but only one or two. To this criticism there is only one reply: unless adequate samples

are available, attempts to make numerical comparisons of any kind are futile and the results misleading. If there is insufficient material on which to base such a comparison, there is no point in making one, and it is much better not to do so. Half a dozen specimens constitute a sample of about the minimum permissible size: less than that would yield results of doubtful value.

Although this paper is exclusively concerned with the numerical comparison of sets of structural data, it is not suggested that the classification of fenestrate cryptostomes should rest on these alone. Other factors, not so amenable to mathematical treatment, must also be considered, for example, the shape of the zooecial chamber. The prime purpose of the present paper is to draw attention to the shortcomings of the micrometric formula as a means of structural comparison, and to stress the need for a better comparative technique if taxonomic conclusions are to depend on the results of such comparisons. Finally, it seems possible that significance tests, used along the lines indicated above, might be a means of discriminating between other kinds of colonial organisms besides bryozoa, provided that samples of data are constituted as here suggested.

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