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TAXONOMIC RELATIONSHIPS IN *Terebratulina* (BRACHIOPODA) ESTABLISHED BY MULTIVARIATE MORPHOMETRICS

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ABSTRACT

Three morphologically-similar species of *Terebratulina* can be discriminated by means of a battery of multivariate statistical techniques applied to seven shell traits on 12 sample sets. *T. retusa* and *T. unguicula* are most alike morphometrically, whereas *T. septentrionalis* is equally distant from both of those species. In the light of existing molecular data, the similarity between *T. retusa* and *T. unguicula* can be interpreted as an example of symplesiomorphy. The results of the morphometric analyses also suggest that *T. unguicula* is probably a heterogeneous species, and that *T. unguicula rotundata* stands up well as a separate taxonomic entity. The data also revealed that one museum-curated sample of *T. retusa* has been misidentified as *T. septentrionalis*.

Keywords: Morphometry, Multivariate analyses, Taxonomy, *Terebratulina*, Brachiopods.

RESUMEN

Se discrimina entre tres especies parecidas del género *Terebratulina*, mediante una serie de técnicas estadísticas multivariantes aplicadas a siete conchas extraídas de 12 lotes. *T. retusa* y *T. unguicula* son morfométricamente muy parecidas, mientras *T. septentrionalis* se encuentra a distancias similares de aquéllas. Dado el conocimiento de biología molecular sobre las mismas, puede decirse que la similitud entre las especies *T. retusa* y *T. unguicula* es un caso de simplesiomorfía. Los resultados del análisis morfométrico sugieren que la especie *T. unguicula* es probablemente heterogénea en su composición y que *T. unguicula rotundata* podría muy bien ser una entidad taxonómica aparte. También se ha determinado que uno de los especímenes de museo catalogado como *T. septentrionalis* pertenece en realidad a *T. retusa*.

Palabras clave: Morfometría, Análisis multivariante, Taxonomía, *Terebratulina*, Braquiópodos.

INTRODUCTION

Taxonomic differences between living and fossil representatives of the brachiopod genus *Terebratulina* can often prove deceptive and difficult to apply in practice. The methods of molecular biology are proving increasingly useful, but they are not readily accessible in daily work and, besides, have yet to prove unequivocal in detail. If simpler methods can be brought into play, the quantitative appraisal of taxonomically exacting problems can be made easier; moreover, such procedures could serve as useful adjuncts to molecular studies, providing an invaluable method of comparing and contrasting phylogenetic implications. This study shows how effectively a multivariate analysis of a heterogeneous set (i.e. distances, weight, and counts) of morphologically relevant characters can lead to a useful result.

In this paper we investigate three of the known living representatives of *Terebratulina*. The taxonomical problem posed is not one that can be satisfactorily solved by mere usual inspection of specimens, being rather, one that requires quantitative analysis.

MATERIAL AND METHODS

Samples

Terebratulina, like most other articulate brachiopods, has two unequally-sized valves, the longer valve having on its beak a perforation known as the foramen, that in life accommodates a fleshy stalk, or pedicle (Fig. 1). The specimens measured for this study were obtained from the following localities (number of specimens in brackets). All samples are from living populations, and are stored in the National Musem of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM). *Terebratulina unguicula* (Carpenter); USA: Gulf of Georgia (5), Santa Cruz Island, California (8), Alaska (12); *Terebratulina unguicula rotundata* Cooper; Russia: Kamchatka (10); *Terebratulina retusa* (L.); Norway (12), Scotland: Skye (12); *Terebratulina septentrionalis* (Couthouy); USA: Eastport, Maine (12), Marthas Vineyard, Massachusetts (12), Cape Cod Light, Massachusetts (12), Canada: Nova Scotia (8), Norway: Finmark (11), Scotland: Loch Duich (6).

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Measurements

The measurements used in the statistical analysis are: L = length of the ventral valve (mm), W = width of shell (mm), H = height of shell (mm), R = density of ribbing (as rib-counts), fL = length of foramen (mm), fW = width of foramen (mm), Wt = weight of shell (g).

Note that there are five completely homogeneous variables in the above set, to wit, L, W, H, fL and fW. The trait Wt is also a continuously distributed quantity but it represents a different class of measurement from distances. R is discontinuously distributed, which sets it apart from the other variables. The heterogeneity in the set of observations has implications for the choice of appropriate statistical methods and how these are used and interpreted. Other ways of analysing the data are, of course, possible, but the suite of procedures applied were considered the most relevant to the problems taken up. Constructed "variables" such as are produced by so-called Fourier analysis are not satisfactory for batteries of interlinked multivariate procedures.

Statistical Procedures

In any efficiently constructed statistical analysis, it is necessary that a logical and progressive strategy be devised. All too often the impact of statistical studies in the natural sciences is blunted by inappropriate techniques and, or, a lack of consequence in the way in which an analysis is made. We have constructed our investigation so as to proceed hierarchically, from the more basic to the more complicated. Hence, an initial analysis of variance of all samples precedes a multivariate appraisal of each sample separately. This step also embraces a review of the empirical distributional properties of the samples. The next phase is concerned with comparing and contrasting samples by pairs; this step includes the important question of the geometrical properties of the empirical dispersion ellipsoids. This is an aspect that is seldom taken up in applied biometry.

The dispersions may be unequally inflated, but otherwise compatible, which means that the ellipsoidal axes are parallel. A second condition arises when the dispersions are of equal volume and shape, but their axes are not parallel- i.e. the ellipsoids are rotated in relation to each other. Finally there is the most extreme case in which the ellipsoids are not only differently inflated and of different shape, but also rotated in relation to each other (Reyment *et al.*, 1984). These differences may represent genuine biological properties of the data.

However, as far as straight statistical testing procedures are concerned, the shape of dispersion ellipsoids is of no great consequence and a general test of homogeneity of covariance matrices is usually adequate. For work involving subtle differences between organisms, often as closely related as in the present circumstance, it is desirable to probe more deeply with respect to the expression of multivariate variability. We need to know not only that two taxa are statistically different, but also in what respect these taxa differ. The standard ("package") approach is only concerned with asking if there is a difference, but not how the difference is expressed.

The final level in our hierarchy of procedures consists of a simultaneous confrontation of all samples of all species, with emphasis on ordination. We note our agreement with Bookstein (1994), concerning the incompatibility between biometry and the terminology of modern systematics. L. F. Marcus provides listings written in SAS in Reyment (1991) for doing all the computations referred to in this paper. The present analyses were made using programs in FORTRAN77 and C++, written by Reyment.

FINDINGS

We begin by examining the results of a one-way ANOVA of all samples, listed in Table 1. The variance ratios for the comparison of each of the variables, and

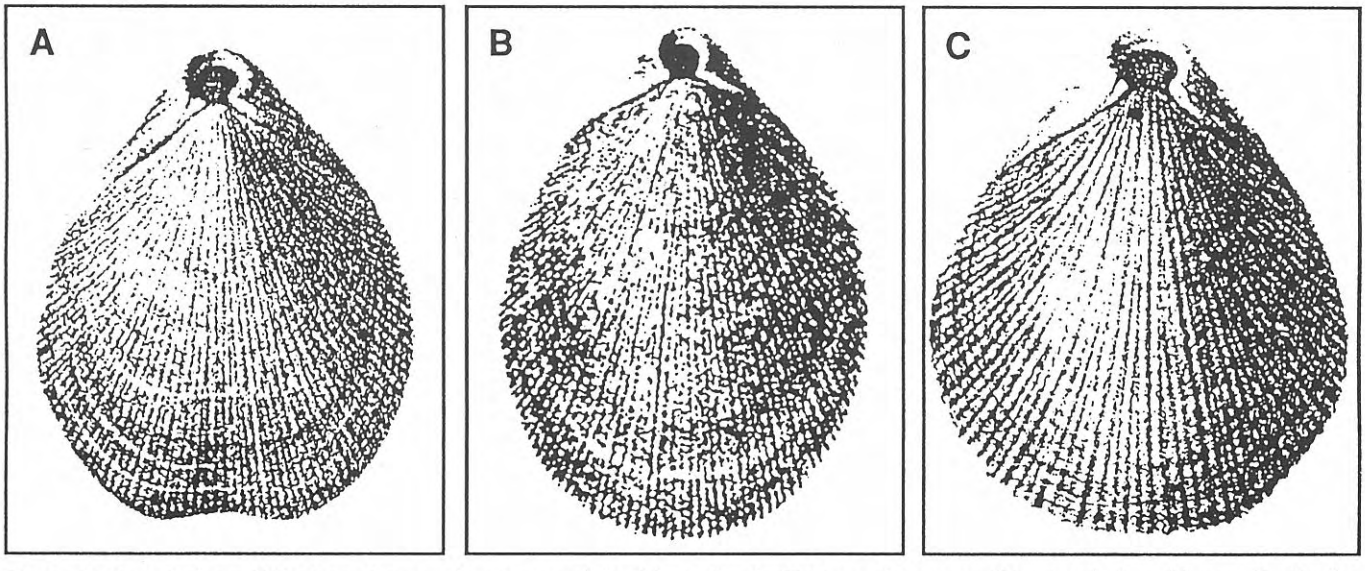

Figure 1. Dorsal view of *Terebratulina* species compared in this study. A. *Terebratulina retusa* (Linnaeus); L = 18 mm; B. *Terebratulina septentrionalis* (Couthouy); L = 23 mm; C. *Terebratulina unguicula* (Carpenter); L = 21 mm. After Davidson (1886).

the corresponding probabilities, leaves no doubt that the seven characters differ strongly over the three species. The variances are not greatly different for all variables with the exception of Wt, but this is not serious enough to influence the outcome of the analysis. As regards the univariate distributional properties of the material pooled as to species, *T. septentrionalis* shows slight thought significant skewness for 5 of 7 traits and more marked significant kurtosis for the same traits (L, W, H, R, and fW). Deviations from univariate normality are far less pronounced for the other two species. There is slight skewness in H in both species and slight kurtosis in W for both samples.

Table 1. Analysis of variance of 12 samples and 7 variables

Variable	Variance ratio	Probability
L	4.63	< 0.0001
W	5.63	< 0.0001
H	3.04	0.001
R	23.77	< 0.0001
fL	10.46	< 0.0001
fW	9.62	< 0.0001
Wt	6.63	< 0.0001

Principal Components

There are several ways of approaching a comparative principal component analysis of the samples. One of these concerns interpretation (reification) of the latent vectors, another is directed towards exposing the empirical nature of the multivariate sample, and yet a third is concerned with graphical applications. In the present connection we are concerned with the last two aspects. The technique of cross-validation comes mainly from the realm of analytical chemistry. It is, in part, an outgrowth of Tukey's method of "jacknifing", a procedure that attempts to ascertain the reliablility of an analysis by deleting one specimen at a time from a sample (with subsequent replacement). Cross validation extends this idea to encompassing successive deletion of variables, with subsequent replacement.

Using Krzanowski's (1987) *ad hoc* development of the cross-validation technique on the principal components of the correlations, the main results of which are summarized in Table 2, it was found that:

1. All variables but R are equally weighted in the first principal component.
2. R dominates the second principal component. If any inference is to be drawn from this result, it would be that rib-density is not well integrated with the other variables chosen in our study.
3. The section dealing with the identification of influential and atypical observations indicates that instability can be expected in the results for *T. unguicula* owing to the large number of observations that deviate from the sample norm. (N.B.: the bracketed values in Table 2 are "mild" deviations.) The values for the other two species point to a remarkable degree of cohesion in the data.
4. The identification of essential variables is a cross-validatory procedure that charts what happens to an analysis if variables are deleted one by one. If the removal of a variable has a profound influence on the results, then it is essential to the analysis. If, on the other hand, deletion leads to little or no change, then the variable in question can be suspected of being redundant. By this criterion, R is essential for all three species. *T. unguicula* also requires W, whereas in the case of *T. septentrionalis*, fL, fW and Wt are essential. Without a much greater data base, it is not reasonable to attempt to extract too much from these indications, but it should be kept in mind that such pointers can accommodate taxonomic implications.

It is logical to ask to what extent the latent vectors of the different categories agree. This can be ascertained, roughly, by computing the angles between pairs of vectors (Blackith and Reyment, 1971). The values presented in Table 3 suggest that *T. retusa* and *T. septentrionalis* are similar with respect to the first principal

Table 2. Cross validation analysis for three species of *Terebratulina*

	T. unguicula		*T. retusa*		*T. septentrionalis*	
	First two latent vectors (correlation matrix)					
Variable	**I**	**II**	**I**	**II**	**I**	**II**
L	.4226	.2022	.4061	.1721	.4362	−.0038
W	.3025	.5281	.4009	.2564	.4266	.1054
H	.4246	.0255	.4248	.0536	.4268	.1237
R	.1198	−.7708	−.0320	−.8741	−.0365	−.8000
fL	.4247	−.1674	.3981	−.2509	.3807	−.3276
fW	.4095	−.2393	.3908	−.2700	.3830	−.3409
Wt	.4328	.0125	.4262	−.0423	.3907	.3327
Essential variables	W and R		R		R, fL, fW, Wt	
Number of significant principal components	2		3		3	
Number of specimens deviating from the sample norm						
Influence variance	6 (4)		0		0	
Influence covariance	2		3		2	

component, notwithstanding that all three comparisons yield relatively small angles. The comparisons for the second principal component produce larger angles. The tentative conclusion is that most of the variation in the three species (the first principal component) displays the same pattern. Taxonomically relevant differences appear first in the smaller principal components. (Referring to Table 1, we see that the first two principal components account for from 85 to 93 % of the total variation in the samples.)

Table 3. Angles between the first and second principal components of the brachiopod species

	Vector I	Vector II
ung/ret	10°.35'	17°.56'
ung/sept	12°.25'	35°.23'
ret/sept	4°.36'	26°.49'

Abbr. ung = *T. unguicula*; ret = *T. retusa*; sept = *T. septentrionalis.*

Table 4. Pairwise comparisons of dispersion ellipsoids for the three brachiopod species. Abbreviations as in Table 3.

Comparison	Fisher's B^2 criterion (DF = 28)	D^2	Chernoff's partition	
			due means	due $S_1 + S_2$
sept/ret	83.94; χ^2=73.64***	12.36***	44 %	56 %
sept/ung	74.35; χ^2=67.91***	6.57***	43 %	57 %
ret/ung	64.50; χ^2=55.50***	6.13***	28 %	72 %

Ellipsoid Orientations (DF = 6)

	sept/ret	sept/ung	ungr/ret
major axis			
1	40.26***	18.83***	19.06***
2	85.80***	74.37***	79.21***
3	41.12***	19.18***	122.76***
4	37.65***	43.55***	37.21***

Anderson–Bahadur discriminant vectors

Variable	sept/ret	sept/ung	ung/ret
L	−143.65	−53.08	−34.12
W	64.44	8.26	−7.65
H	18.80	−33.44	31.90
R	−7.14	−23.27	4.02
fL	41.64	59.28	−57.29
fW	−94.64	−39.61	−9.30
Wt	35.05	24.41	16.15

Table 5. Results of the canonical variate analysis for 12 groups

Variable	Canonical Variate Coefficients I	II
L	11.50	13.95
W	−7.73	33.43
H	6.49	−2.20
R	14.46	−8.98
fL	−4.03	7.32
fW	23.39	−3.82
Wt	−10.15	−16.16
Canonical roots	6.314	2.910

Pairwise comparisons

It is now appropriate to investigate in more detail how the three species differ from each other, given that the data discussed in the previous section suggest that real differences do exist. The pertinent approach is by means of discriminant functions and the analysis of the dispersion ellipsoids. This cannot be straightforward in the present case since we have already found convincing evidence for heterogeneity in variances and covariances. The appropriate techniques are discussed in Blackith and Reyment (1971, p. 62).

Briefly, the pairwise appraisals are pursued hierarchically in the following manner:

1. Compute the non-central chi-square criteria for the covariance matrices (in the present case, using the logarithms of the data). This provided indication of heterogeneity in the two covariance matrices (but also deviations from multivariate normality).
2. Test the major axes of dispersion ellipsoids for collinearity by computing the appropriate chi-square criterion (Blackith and Reyment, 1971). Only those axes that have a length significantly different from zero are considered.

The results of these calculations are summarized in Table 4. All three comparisons reveal significant heterogeneity (inflation) in covariance matrices, as shown by the high values of Fisher's B^2 (cf. Blackith and Reyment, 1971). The major axes of the dispersion ellipsoids differ significantly, hence the ellipsoids are rotated in relation to each other. The Anderson-Bahadur generalized distances differ highly significantly; owing to the complex relationships between samples, the nature of this separation needs to be given special consideration. This can be done by means of Chernoff's partitioning criterion (Chernoff, 1973). The criterion partitions the separation between samples into one segment attributable to differences in means and one segment arising from heterogeneity in covariance matrices (cf. Table 4). (For homogeneous covariance matrices, the Chernoff criterion is proportional to the usual Mahalanobis D^2.) In all cases, the separation connected with the heterogeneity in covariance matrices is somewhat greater, to much greater, than that due to the difference in mean vectors. The taxonomic consequence of this condition is that the species differ from each other with respect to the integration of the seven traits included in our analysis, at least, as far as can be assessed from the material available to us.

Quadratic Discriminant Function

In cases in which there is marked heterogeneity in covariance matrices, often without clear cause, it can prove beneficial to proceed via a quadratic discriminant function rather than the linear counterpart. In the present study, all comparisons were found to benefit consi-

derably from this step, at least from the aspect of improving the identification of doubtful specimens. Let us look at what quadratic discrimination accomplishes.

The linear discrimination record for the comparison *T. unguicula-T. retusa* shows 4.3 % wrongly assigned of the former species and 8.7 % of the latter. The improvement wrought by the quadratic discriminant function is dramatic, with only 2.9 % of *T. unguicula* allocated to *T. retusa* and 4.3 % of the latter to the former.

The evaluation of the data by quadratic discrimination brings out the fact that some specimens of each species cannot be assigned unequivocally and, as is shown in the ensuing section, there is overlap between distributions.

ORDINATION OF THE SPECIES

The final step in our analysis encompasses the appraisal of all material in the one connection, including a multivariate analysis of variance. The appropriate procedure is that of canonical variate analysis (Reyment *et al.*, 1984), the results of which will now be summarized.

For the purposes of this analysis, the samples of the species were not pooled into the three groups investigated above, but kept distinct with respect to geographical location. The outcome of the computations is shown in Table 5. The vectors corresponding to the two largest canonical roots are informative. The largest loading in the first vector is that for fW, width of the foramen, whereas the smallest is that for fL. W is by far the most important component in the second vector. There is no obvious morphometrical reason for this and in general it can be claimed that the vectors of canonical variate analysis cannot be usefully reified (Reyment *et al.*, 1984).

As a by-product of the canonical variate computations, one obtains a complete array of generalized distances for all comparisons (clearly somewhat flawed and only approximate because of the heterogeneity in sample covariance matrices). All are highly significant with the exception of three, which are comparisons made between samples of *T. septentrionalis*. It is therefore not surprising that the multivariate analysis of variance yields a highly significant result.

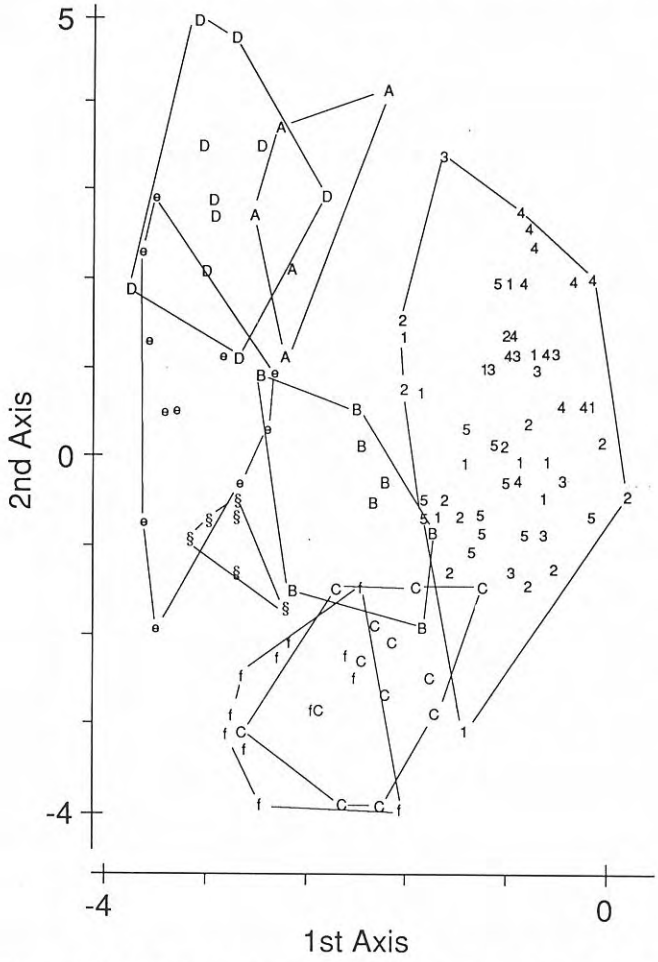

Figure 2. Plot of the canonical variate scores in the plane of the first two canonical vectors for seven variables and 12 samples. *T. unguicula* denoted as A (Gulf of Georgia), B (Santa Cruz Island, California), C (Alaska); *T. unguicula rotundata* denoted as D; *T. retusa* denoted as E (Norway) and F (Skye, Scotland); *T. septentrionalis* denoted as 1 (Eastport, Maine), 2 (Marthas Vineyard, Massachusetts), 3 (Nova Scotia), 4 (Cape Cod Light, Massachusetts), 5 (Finnmark, Norway) and § (Loch Duich, Scotland). Note particularly the location of the points belonging to sample §.

Canonical Variate Ordination

Fig. 2 illustrates the relationships between the scores, obtained from the logarithmically transformed data of the 12 samples plotted in the space of the first two canonical axes. This plot makes it obvious that when all the samples are treated in the one connection, there is no absolute segregation into taxa. Let us look more closely at what the figure contains.

Firstly, *T. septentrionalis* is concentrated to a broad zone to the right, with some degree of overlap of the other taxa. There is one sample of the species that plots far from the main cluster, i.e. all of the specimens from Scotland. These lie in a compact group to the left.

Secondly, *T. retusa* plots as two distinct clusters, one (Skye) of which coincides almost entirely with a sample of *T. unguicula* (Alaska), and the other which overlaps partly with the aberrant *T. septentrionalis* and *T. unguicula rotundata*.

Thirdly, *T. unguicula* shows up as being heterogeneous with respect to the characters measured. The sample from Gulf of Georgia forms a cluster with the subspecies *T. unguicula rotundata*, whereas the Californian sample forms a cluster in the middle field of the diagram. The impression then yielded by the canonical variate analysis is that geographical variation within species may be greater than variation between species. This implies either that the characters analyzed are not especially diagnostic or that some of the species assignations need to be given further consideration.

Fig. 3 displays the plot of the canonical variate means along the first two canonical axes. The lines shown connecting points are the Prim minimum spanning tree. Briefly, this network connects points that are most alike - a two-dimentional representation of a highly

multivariate situation can be deceptive, and the Prim tree is designed to take this difficulty into account. The figure provides further details over and above what can be gleaned from Fig. 2. It indicates, that on the seven characters used in the study, a sample of *T. septentrionalis* from Scotland is more similar to *T. retusa* than to other samples assigned to the *T. septentrionalis* species. Two samples of *T. unguicula* are united in a position between *T. retusa* and *T. septentrionalis*, whereas one of *T. unguicula* groups with its subspecies, *T. unguicula rotundata*. Finally, we see that the samples identified as belonging to *T. septentrionalis* form a tight group, apart from the one already pointed out.

A Reduced Canonical Variate Analyis

Notwithstanding the fact that canonical variate analysis is a very powerful ordinating technique, it has one major imperfection, namely, the factor that it works on a priori groupings of the data, i.e., the individual samples supplied. This has the effect that there is a tendency for the ordination to maintain what it has been told are entities. A problem clearly arises if the samples are small and not really truly representative of the population from which they were sampled. It is easy enough to check the truth engendered by an analysis by submitting a new grouping of the data. We have done this here by concentrating the information to four groups only: One group composed of the three samples of *T. unguicula*, and one of its subspecies *T. rotundata*, one sample comprising all *T. retusa* and one for all *T. septentrionalis*.

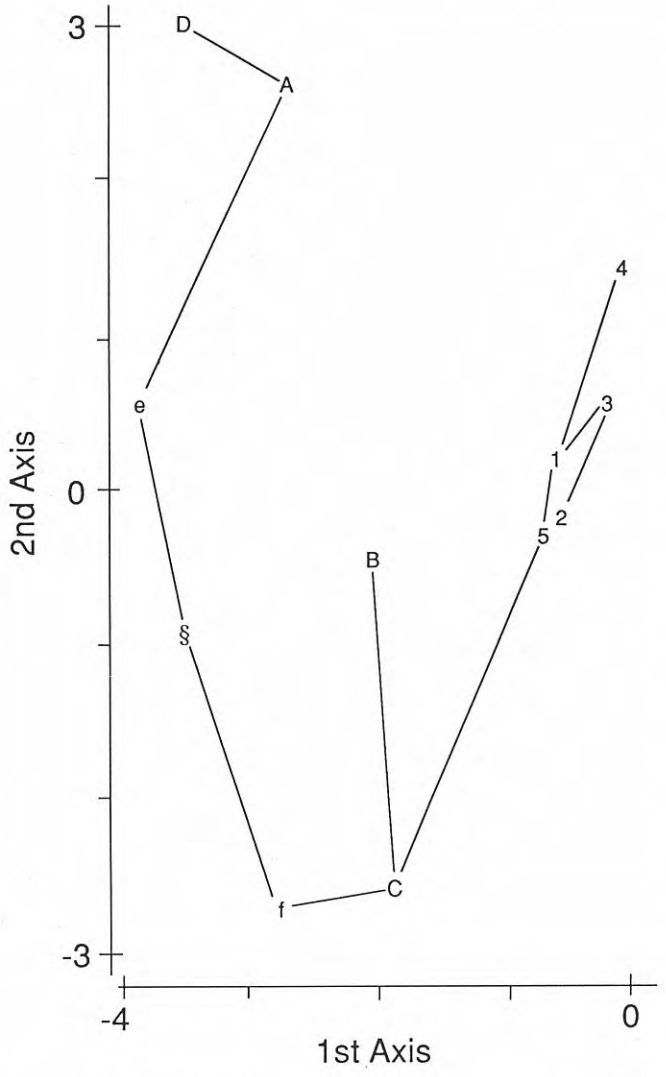

Figure 3. The Prim minimum spanning tree superimposed on the canonical variate means in the plane of the first two canonical axes. The symbols have the same significance as in Fig. 2.

Table 6. The four-group canonical variate analysis of the three species an one subspecies of brachiopods

Variable	Canonical vectors		
	I	II	III
L	27.22	8.16	−6.33
W	−15.24	−25.36	16.51
H	2.99	−16.26	−8.27
R	8.23	1.06	−7.24
fL	−14.02	20.75	18.94
fW	18.04	−9.58	3.52
Wt	−5.86	11.61	−5.45
Canonical roots	2.0079	0.6904	0.5092

All three roots are highly significant.
MANOVA $\chi^2_{21} = 217.0$, $P < 0.001$

The main results of the computations are listed in Table 6. To be noted is that all three canonical roots are highly significant and there is therefore real reduction in dimensionality, not withstanding that the first root accounts for most of the variability in the data. A second feature of the result is that the third vector, the associated root of which is almost the same as that of the second vector, is the one to be compared with the 12-sample analysis. It is not uncommon in biometric work to find just such an interchange of determinantal roots, a condition that can render an analysis confusing until it is recognized.

Fig. 4 illustrates the plot of the scores for the first and third canonical variates. There is now a less striking delineation of categories than is expressed in Fig. 2, since, the *a priori* boundaries have now been broadened. Nonetheless, most of the essential features remain, with respect to subspecies *T. unguicula rotundata* and species *T. retusa*. Most *T. septentrionalis* lie separate from the other points, but there is now a broad zone of overlap between *T. unguicula* and all other species. This latter observation does not really come as a surprise when we recall that in the preceding analyses, this species displays a degree of sample heterogeneity which is appreciably higher than in the other species. It is therefore motivated to regard determinations of *T. unguicula* with a modicum of caution.

The ANOVA yields highly significant differences in means for all variables except H, which is far from attaining the 5% level. All generalized distances are highly significant as is also the MANOVA (see Table 6).

DISCUSSION

Considering the *a priori* groupings, made on standard taxonomical grounds, and the information yielded by the pairwise analyses, a good case can be made for maintaining the identities of the three species considered in the present note. This conclusion, drawn entirely from the traits of the shells, exemplifies how effectively a multivariate analysis can distinguish apparently morphologically similar forms. As Dall (1920) notes, "*T. septentrionalis* and *T. unguicula*, which have been frequently treated as varieties of *T. retusa*, are positively established as distinct by Blochmann on the bases of their spiculation although it is often extremely difficult to separate them merely on the basis of the shells".

Recent molecular evidence reinforces the separation of the three species based on the morphology of the calcareous spicules occurring within the connective tissue of the mantle and lophophore (cf. Blochmann, 1908). Molecular genetic analyses of allozymes and mitochondrial DNA clearly separated *T. retusa* and *T. septentrionalis* as good species (Cohen *et al.*, 1990), and immunological comparisons of skeletal macromolecules demonstrated that *T. unguicula* was even more distantly related to these two species (Endo and Curry, 1991). It is interesting to note that the angles between pairs of the first latent vectors (Table 3) indicated highest similarity between *T. retusa* and *T. sepentrionalis*, a relationship which accords with that suggested by the immunological data. If the closer phylogenetic relationship between *T. retusa* and *T. sepentrionalis* is taken as granted, the apparent similarity between *T. retusa* and *T. unguicula* as indicated in the smallest angle between them for the second principal components (Table 3), or in other words, similarity in having low rib density, would then suggest that the two species retained the ancestral state for this character.

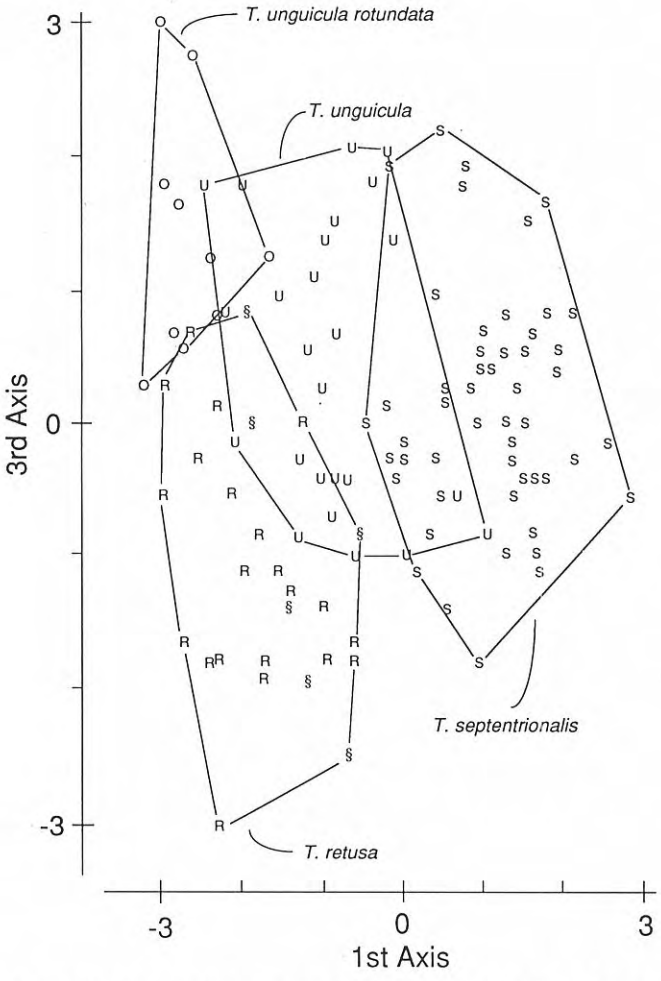

Figure 4. Plot of the canonical variate scores in the plane of the first and third canonical vectors (see text for reason underlying the choice of axes) with the points of Fig. 2 now apportioned according to species (four groups) rather than by samples. *T. unguicula* denoted as U; *T. unguicula rotundata* denoted as O; *T. septentrionalis* denoted as S and § (as in Fig. 2); *T. retusa* denoted as R. Specimens belonging to sample § have been identified as *T. septentrionalis*, but are now interpreted to be *T. retusa* (see Discussion for details).

Furthermore on the basis of published species assignment, it is clear that there is a problem of identification in some cases. Some samples (specimens) assigned to one species are actually more alike another species; however, the use of a statistical procedure that accommodates deviations from linearity and normality improves allocatory power. Moreover, if the species have been correctly identified, we are confronted by the rather disturbing conclusion that geographical variation within species (especially that of *T. unguicula*) can be greater than variation between species, noting that these remarks apply only in the context of the traits measured.

In at lease one case, the sample labeled as *T. septentrionalis* collected from Scotland (USNM catalog No. 173532), it can be concluded that these individuals are in fact *T. retusa*. The rationale includes not only its aberrant location (for *T. septentrionalis*, but correct for *T. retusa*) in the plots (see Fig. 2), causing a poor assignation record for *T. septentrionalis*, but also its disagreement with the general pattern of geographic distribution of the two species, a pattern which would otherwise be consistent with the ocean current regime (Curry and Endo, 1991).

CONCLUSIONS

We offer as our conclusions the following:

1. The species of *Terebratulina* analyzed in this paper are generally similar with respect to the seven traits investigated, but these species can generally be discriminated by multivariate analyses on these measurements.
2. *T. unguicula rotundata* seems to be genuinely separable from the rest of the material.
3. *T. septentrionalis* also is mostly well separable.
4. One sample, hitherto having been registered as *T. septentrionalis*, is considered to be of *T. retusa*.
5. *T. unguicula*, as represented in our material, is not homogeneous.

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BIBLIOGRAPHY

Blackith, R. A. and Reyment, R. A. 1971. *Multivariate Morphometrics.* Academic Press, London.

Blochmann, F. 1908. Zur Systematik und geographischen Verbreitung der Brachiopoden. *Zeitschrift für wissenschaftliche Zoologie,* **90**, 596-644.

Bookstein, F. L. 1994. Can biometrical shape be a homologous character? *In: Homology: The Hierarchical Basis of Comparative Biology* (B.K. Hall, Ed.), Academic Press, London, 197-227

Chernoff, H. 1973. Some measures for discriminating between normal multivariate distributions with unequal covariance matrices. *In: Multivariate Analysis* (P.R. Krishnaiah, Ed.), III, Academic Press, New York.

Cohen, B. L., Balfe, P., Cohen, M. and Curry, G. B. 1990. Molecular evolution and morphological speciation in North Atlantic brachiopods (*Terebratulina* spp.). *Canadian Journal of Zoology*, **69**, 2903-2911.

Curry, G. B. and Endo, K. 1991. Migration of brachiopod species in the North Atlantic in response to Holocene climatic change. *Geology*, **19**, 1101-1103.

Dall, W. H. 1920. Annotated list of the Recent Brachiopoda in the collection of the United States National Museum, with descriptions of thirty-three new forms. *Proceedings of the United States National Museum*, **57**, 261-377.

Davidson, T. 1886. A Monograph of Recent Brachiopoda. Part I. *Transactions of the Linnaean Society of London*, Ser 2, **4**, 1-74.

Endo, K. and Curry, G. B. 1991. Molecular and morphological taxonomy of a Recent brachiopod genus *Terebratulina. In: Brachiopods through time* (MacKinnon, D. I., Lee, D. E. and Campbell, J. D., Eds.), A. A. Balkema, Rotterdam, 101-108.

Krzanowski, W. J. 1987. Cross-validation in principal component analysis. *Biometrics*, **43**, 575-584.

Reyment, R. A. 1991. *Multidimensional Palaeobiology*, Pergamon Press, Oxford; with an appendix by L. F. Marcus.

Reyment, R. A. and Jöreskog, K. G. 1993. *Applied Factor Analysis in the Natural Sciences*, Cambridge University Press, New York. With an Appendix by L. F. Marcus.

Reyment, R. A., Blackith, R. E. and Campbell, N. A. 1984. *Multivariate Morphometrics*, Academic Press, London. Second Edition.

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