

16. Size and shape variation in some Japanese Upper Turonian (Cretaceous) ammonites

by

RICHARD A. REYMENT

Department of Historical Geology and Palaeontology
University of Uppsala
Box 558, S-751 22 Uppsala, Sweden

Abstract. — Morphometric variation in four shell dimensions of Japanese Upper Turonian *Subprionocyclus* is analyzed with respect to hypotheses of growth invariance and stability of discriminator coefficients. The material of all three species indicates polymorphism to occur (sexual dimorphism?) and the multivariate outlier analysis shows the individuals to be non-linearly related (in part the outcome of non-constancy in the multivariate allometric relationships). *Subprionocyclus neptuni* shows no relationship between morphology and tuberculation density. *S. normalis* and *S. (Reesidites) minimus* differ from *S. neptuni* in their being more highly integrated with respect to the above two categories. However, *S. normalis* shows a negative association for the first principal component for size and tuberculation density, whereas *S. (R.) minimus* exhibits a positive association. Owing to high loadings of elements in the smallest (almost zero) principal component for the pooled covariance matrices, there is marked instability in the elements of the canonical variate vectors. Stable coefficients were obtained by deleting the smallest eigenvalue-eigenvector combination. Growth reduction applied to the three samples of *S. neptuni* yielded a marked decrease in the generalized statistical distances between two of the three samples, and in the discriminator coefficients. The species of *Subprionocyclus* s. str. display poor association between size and tridimensional shape (approximately isometric relations). *S. (R.) minimus* differs markedly from *Subprionocyclus neptuni* and *S. normalis* in showing a high degree of integration between size and tridimensional shape (allometry).

INTRODUCTION

OBATA *et al.* (1979) used the reduced major axis method for allometric analyses of the three ammonite species considered here. For non-comparative

work, this method provides a reasonably useful approximate solution. However, for the type of analysis attempted by these authors, the mathematical deficiencies of the reduced major axis leave the results open to conjecture (cf. KUHR and MARCUS, 1977). One of the interesting results obtained by OBATA *et al.* (1979) concerns shifts in the allometric relationships between some pairs of variables. The methods used in the present paper bring this out in sharper relief.

GINGERICH (1978) misunderstood one of the results of my (REYMENT 1975) analysis of relationships in time between *Subprionocyclus normalis* and *S. (Reesidites) minimus* due, presumably, to an imprecise formulation of that part of the text. The point in question concerns the relationship between density of tuberculation and stage of growth of the ammonite shell; the reported difference between species involves a change from a growth-correlated increase in density of tuberculation to the reverse situation. This is obviously a directional change and one that cannot be gradational, as mistakenly thought by GINGERICH (op. cit.).

New methods of multivariate statistical analysis permit a more complete treatment of questions raised by OBATA *et al.* (1979) and REYMENT (1975), particularly with respect to covariance structure and the relationship between ornament and size.

Subprionocyclus and *Reesidites* are closely similar in morphology. In fact, on most taxonomic standards, they might well be considered impossible to separate at the subgeneric level. The sole distinguishing characteristic is the transitory appearance of a mediolateral tubercle in some individuals of an association of *Reesidites*. Now that OBATA *et al.* (1979) have proven the contemporaneity of *Subprionocyclus* s. str. and *Reesidites* in southern Hokkaido (Japan), there are no longer stratigraphical reasons for holding the two apart.

MATERIAL

In addition to the samples of *Reesidites minimus* (HAYASAKA and FUKADA) and *Subprionocyclus normalis* (ANDERSON) from the Pombets River, southern Hokkaido studied previously (REYMENT, 1975), three of the samples used by OBATA *et al.* (1979) were found to be suitable for multivariate work. From the quantitative stratigraphical aspect, this latter material is not satisfactory, as it was largely obtained from loose blocks (in the Manji area, Hokkaido).

The usual dimensions of ammonite work were available, to wit: shell diameter (D), shell height (H), shell breadth (B), and umbilical diameter (U). In addition, counts of umbilical and ventrolateral tubercle frequencies on the final whorl were used in a few of the analyses.

The samples studied by OBATA *et al.* (1979) consist of small individuals, whereas the specimens used in my initial investigation (REYMENT, 1975) derive from medium- to large-sized specimens.

STATISTICAL METHODS

The analyses are based on the v -variate, h -sample covariance matrices \mathbf{S}_i ($i = 1, \dots, h$) on n_i ($i = 1, \dots, h$) degrees of freedom. The corresponding correlation matrices are \mathbf{R}_i ($i = 1, \dots, h$). A sample mean vector is denoted as $\bar{\mathbf{x}}$ and an observational vector as \mathbf{x} . The usual within-groups sums of squares and cross products matrix \mathbf{W} on n_W degrees of freedom and the between-groups sums of squares and cross products matrix \mathbf{B} used in canonical variate analysis are required.

Redundant within-groups directions of variation

Define the following matrices:

$$\begin{aligned}\mathbf{W}^* &= \mathbf{S}^{-1} \mathbf{W} \mathbf{S}^{-1} \\ \mathbf{B}^* &= \mathbf{S}^{-1} \mathbf{B} \mathbf{S}^{-1}.\end{aligned}\quad (1)$$

Here, the diagonal matrix $\mathbf{S} = (\text{diag } \mathbf{W})^{\frac{1}{2}}$.

The eigenvalues e_i and eigenvectors \mathbf{u}_i of \mathbf{W}^* are the principal components of \mathbf{W}^* .

$$\begin{aligned}\mathbf{E} &\text{ has diagonal elements } e_1, \dots, e_v \\ \mathbf{U} &= (\mathbf{u}_1, \dots, \mathbf{u}_v) \\ \mathbf{W}^* &= \mathbf{U} \mathbf{E} \mathbf{U}^T\end{aligned}\quad (2)$$

(T denotes the transpose of a matrix).

Scaling the eigenvectors by the corresponding $e_i^{\frac{1}{2}}$ produces within-groups sphericity. Where required, shrunken estimators are formed by adding shrinking constants k_i to the eigenvalues e_i before scaling the eigenvectors.

$$\begin{aligned}\mathbf{K} &= \text{diag } (k_1, \dots, k_v) \\ \mathbf{U}^* &= \mathbf{U} (+\mathbf{K})^{-\frac{1}{2}} = \mathbf{U}^*(k_1, \dots, k_v).\end{aligned}\quad (3)$$

The between-groups matrix in the space of the within-groups principal components is

$$\mathbf{G}(k_1, \dots, k_v) = \mathbf{U}^{*T}(k_1, \dots, k_v) \mathbf{B}^* \mathbf{U}^*(k_1, \dots, k_v). \quad (4)$$

The i -th diagonal element d_i of \mathbf{G} is the between-groups sums of squares for the i -th principal component. An eigen-analysis of the matrix $\mathbf{G}_{(0, \dots, 0)}$ yields the usual canonical roots f and canonical vectors for the principal components, \mathbf{a}^U .

The usual canonical vectors \mathbf{c}^U are given by

$$\mathbf{c}^U = \mathbf{U}^*_{(0, \dots, 0)} \mathbf{a}^U \quad (5)$$

Generalized shrunken (or ridge) estimators are determined directly from the eigenvectors \mathbf{a}^s of $\mathbf{G}_{(k_1, \dots, k_v)}$ with

$$\mathbf{C}^s = \mathbf{U}^*_{(k_1, \dots, k_v)} \mathbf{a}^s \quad (6)$$

A generalized inverse solution results when $k_i = 0$ for $i \leq r$ and $k_i = \infty$ for $i > r$. This gives

$\mathbf{a}_i^{\text{GI}} = \mathbf{a}_i^U$ for $i \leq r$ and $\mathbf{a}_i^{\text{GI}} = 0$ for $i > r$. The generalized inverse solution results from forming $\mathbf{G}_{(0, \dots, 0, \infty, \dots, \infty)} = \mathbf{U}_r^{*T} \mathbf{B}^* \mathbf{U}_r^*$, where \mathbf{U}_r^* corresponds to the first r columns of $\mathbf{U}^*_{(0, \dots, 0)}$.

The generalized canonical vectors $\mathbf{C}^{\text{GI}} = \mathbf{c}^s_{(0, \dots, 0, \infty, \dots, \infty)}$ are given by

$$\mathbf{c}^{\text{GI}} = \mathbf{U}_r^* \mathbf{a}^{\text{GI}} \quad (7)$$

where \mathbf{a}^{GI} , of length r , corresponds to the first r elements of \mathbf{a}^U . Marked instability is often found to be associated with small values of e_v paired with small corresponding values of d_v of \mathbf{G} .

The contribution of d_v to the total group separation, trace $(\mathbf{W}^{-1} \mathbf{B})$, which is equal to trace $(\mathbf{G}_{(0, \dots, 0)})$, is an indicator of the loss of discrimination that will result from deleting the smallest eigenvalue-eigenvector combination ($k_v = \infty$). If $d_v / \Sigma d_i$, or the corresponding ratio of canonical roots, is small (< 0.05) little loss of discrimination will be caused by eliminating the principal component concerned (CAMPBELL and REYMENT, 1978).

In the case of very highly correlated variables, such as found for the ammonite data analyzed here, almost all variability is attached to the first eigenvector of principal components of \mathbf{W} and $\mathbf{W}^{-1} \mathbf{B}$. The elements of the eigenvectors of $\mathbf{W}^{-1} \mathbf{B}$ can be greatly distorted if, as is usual, the diameter of the shell and, or, other characters enter prominently into \mathbf{u}_v of \mathbf{W}^* . It will be seen that this is so in the present example.

Growth invariance

The ammonite material analyzed here is confounded by growth effects, which must be eliminated if valid comparisons are to be made between samples (BURNABY, 1966, GOWER, 1976). With y components and v variates, the differential growth effects to be eliminated may be represented by a $v \times y$

matrix \mathbf{K} , whose r -th column consists of elements proportionate to the direction cosines of the r -th component. \mathbf{K} is here estimated internally by finding the principal components of \mathbf{W} for logarithmically transformed variables. The matrix for projecting the observations into a space orthogonal to the space of \mathbf{K} is

$$\mathbf{Q} = \mathbf{I} - \mathbf{K}(\mathbf{K}^T \mathbf{K})^{-1} \mathbf{K}^T.$$

These projected values are free of differential growth effects. Solution of the equation

$$(\mathbf{M}\bar{\mathbf{X}}^T \bar{\mathbf{X}} - \lambda \mathbf{I}) \mathbf{c} = \mathbf{0} \quad (8)$$

gives canonical variates \mathbf{c} that are devoid of growth effects. Here, $\bar{\mathbf{X}}$ is the $h \times v$ matrix of means (NB not matrix \mathbf{B} of the previous section) and \mathbf{M} is the generalized inverse

$$\mathbf{M} = \mathbf{Q}(\mathbf{Q}\mathbf{W}\mathbf{Q})^+ \mathbf{Q}.$$

The Mahalanobis' squared generalized distances $D_{Q_{ij}}^2$ in the Q -space are yielded by:

$$D_{Q_{ij}}^2 = (\bar{\mathbf{x}}_i - \bar{\mathbf{x}}_j) \mathbf{M} (\bar{\mathbf{x}}_i - \bar{\mathbf{x}}_j)^T. \quad (9)$$

These distances are uncontaminated with differential growth effects. The complementary squared generalized distances, in the space of growth effects, might be useful for assessing the relative importance of differential growth in general terms.

The coordinates of the group means in the Q -space can be found by the method of principal coordinates. Thus, the canonical variate loadings are given by $\mathbf{M}\bar{\mathbf{X}}^T \mathbf{P}\mathbf{L}^-$, where \mathbf{P} is the matrix of coordinates obtained by the technique of principal coordinates and \mathbf{L}^- is the diagonal matrix of inverted, non-zero eigenvalues.

HUMPHRIES *et al.* (1981, p. 299) have shown that the Burnaby-Gower solution only works properly if all the separate size axes are parallel, otherwise all available discrimination will be lost along the axis of the size factor. In the present analysis, the requirements for the Burnaby-Gower solution seem to be approximately met.

Differential growth

Following MOSIMANN (1970), definitions of size and shape variables are used that allow the study of the entire statistical distribution of a given variable, as opposed to classical methods of allometry using the bivariate allometric equation in which relationships are expressed in single coefficients.

Table II. Principal components 1, 2 and 6 for correlation matrix of six variables.

<i>Subprionocyclus neptuni</i>				<i>Subprionocyclus neptuni</i>			
Sample 1 (N = 23)				Sample 3 (N = 39)			
Eigenvalues (percent trace)				Eigenvalues (percent trace)			
	1	2	6		1	2	6
	63.4	30.5	0.10		61.3	20.1	0.35
Eigenvectors				Eigenvectors			
D	0.51	0	0.77	D	0.51	0	0.80
H	0.51	0	-0.47	H	0.49	0	-0.55
B	0.49	0	0	B	0.51	0	0
U	0.49	0.15	-0.42	U	0.48	0	-0.22
T1	0	0.70	0	T1	0	0.68	0
T2	0	0.70	0	T2	0	0.72	0
<i>Subprionocyclus normalis</i>				<i>S. (Reesidites) minimus</i>			
Sample 4 (N = 28)				Sample 6 (N = 35)			
Eigenvalues (percent trace)				Eigenvalues (percent trace)			
	1	2	6		1	2	6
	68.4	20.8	0.07		74.8	16.3	0.08
Eigenvectors				Eigenvectors			
D	0.48	0.19	0.74	D	0.46	0.25	0.76
H	0.47	0.20	-0.64	H	0.45	0.26	-0.64
B	0.48	0.15	0	B	0.45	0.27	0
U	0.42	0.22	-0.20	U	0.44	0	-0.15
T1	-0.28	0.64	0	T1	0.30	-0.69	0
T2	-0.26	0.67	0	T2	0.33	-0.56	0

D = diameter of shell; H = height of last whorl; B = breadth of last whorl; U = umbilical diameter; T1 = first row of ventrolateral tubercles; T2 = second row of ventrolateral tubercles. Data not logged.

(2) all species show similar covariance patterns in the eigenvectors of their covariance matrices for raw and transformed data. On the grounds of the continuous morphological characters alone, the three taxa analyzed here cannot be separated at the subgeneric level.

The eigenvectors of the correlation matrix for all six variables provide further information of numerical taxonomic significance. Both *S. neptuni* samples show a positive relation in tubercle loadings in the second eigenvector (T1 and T2) (table II), but morphology and tuberculation are not associated. *S. normalis* and *R. minimus* differ in their patterns in that tuberculation is more closely integrated with morphology. They display, however, a sharp difference in the density of tuberculation in relation to size. *S. normalis* displays

Table I. Principal components for Japanese ammonites.

Sample		1		2		3		4	
		NL	L	NL	L	NL	L	NL	L
<i>S. neptuni</i> N = 23	Percentage eigenvalues	97.96	91.60	1.36	6.81	0.54	1.49	0.14	0.11
	Eigenvectors D	0.86	0.49	0.18	0.35	-0.37	-0.23	-0.31	0.76
	H	0.38	0.54	-0.52	0	0	-0.63	0.77	-0.55
	B	0.25	0.53	-0.50	-0.77	0.70	0.33	-0.45	0.12
	U	0.24	0.43	0.67	0.53	0.61	0.66	0.35	-0.32
<i>S. neptuni</i> N = 39	Percentage eigenvalues	96.71	90.67	2.24	6.77	0.68	2.07	0.37	0.49
	Eigenvectors D	0.86	0.52	-0.15	0	0.48	0.14	0	0.84
	H	0.41	0.58	0.69	0.55	-0.51	0.40	0.31	-0.45
	B	0.20	0.44	0	0	-0.43	-0.89	-0.88	-0.12
	U	0.20	0.45	-0.71	-0.83	-0.57	0.19	0.36	-0.27
<i>S. normalis</i> N = 28	Percentage eigenvalues	97.88	92.52	1.91	6.89	0.13	0.48	0.08	0.11
	Eigenvectors D	0.86	0.51	-0.14	0	0.46	0.33	-0.17	0.79
	H	0.41	0.54	0.59	0.43	-0.38	0.43	0.58	-0.57
	B	0.22	0.51	0.14	0.21	-0.64	-0.84	-0.72	0
	U	0.20	0.44	-0.78	-0.87	-0.49	0	0.34	-0.21
<i>R. minimus</i> N = 35	Percentage eigenvalues	99.00	96.55	0.81	2.89	0.13	0.42	0.06	0.15
	Eigenvectors D	0.86	0.52	0	0	0.45	0.24	0.22	0.81
	H	0.45	0.62	0.43	0.39	-0.47	0.40	0.63	-0.55
	B	0.20	0.48	0	0	-0.71	-0.87	-0.68	0
	U	0.13	0.34	-0.90	-0.92	-0.27	0.14	0.32	-0.17

(0 signifies 0.00000; NL denotes raw data; L denotes logged data.)

Multivariate relationships within samples

The analyses presented in this section are all based on straightforward applications of principal component analysis. Considering firstly the quadrivariate relationships in the four morphological variables, table I shows that there is a fair degree of uniformity in the results for all species. The results listed in table I are for raw data (denoted NL) and logged data (denoted L). Although the first sample of *S. neptuni* (N = 23) differs from the other three, it has the same invariant pattern for the logged data (i.e. the loadings of the smallest principal component). We note (1) that breadth (B) does not enter into the invariant relationship for logged data, but is prominent in the non-logged set,

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Table III. Standardized canonical vectors for three samples of *S. neptuni*, including shrunken estimates.

	1	2
Canonical roots f	1.006	0.083
	\mathbf{c}_1^U	\mathbf{c}_2^U
D	-0.42	-0.84
H	0.60	-0.44
B	-0.97	3.08
U	1.70	-1.33
Canonical roots f (shrunken)	0.910	0.038
	$\mathbf{c}_{1(0, \dots, \infty)}^{GI}$	$\mathbf{c}_{2(0, \dots, \infty)}^{GI}$
D	0.34	-0.17
H	0.26	-0.74
B	-1.17	2.92
U	1.46	-1.53

(table IV). Even more accentuated is the situation for D and H in the second canonical vector, in which an eightfold reduction is achieved; the loading for U in the second canonical vector is also strongly reduced by the shrinkage. The ratio $d_4/\Sigma d_i = 0.028$; hence, the deletion of the smallest principal component hardly influences discriminatory power.

Summing up, the stabilized canonical variate coefficients for *S. neptuni* alone discriminate on the basis of breadth and umbilical diameter (table III), in an inverse relationship, for the first canonical vector and mainly on the same two elements for the second vector, with, however, a sizeable contribution from H. In neither case is size (i.e. shell diameter) of any importance. For the full set of samples, the discriminators are quite different. The first canonical vector is dominated by the umbilical diameter with a lesser contribution from the diameter of the shell and height (table IV). The second stabilized canonical variate contains important contributions from the height and the umbilical diameter, in an inverse relationship. Breadth plays a very subordinate role here and this substantial difference in relation to the results presented in table III for the three samples of *S. neptuni*, indicates that breadth is important at the infra-specific level, but that it varies but slightly, relative to the other variables, at the inter-specific level. The consequence of this is that it has little discriminatory significance for the three species.

The plot of the canonical variates is shown in fig. 1. The few specimens of the second sample have been suppressed in this plot and the figure illustrates the relationships in the first (marked A) and third (marked C) samples.

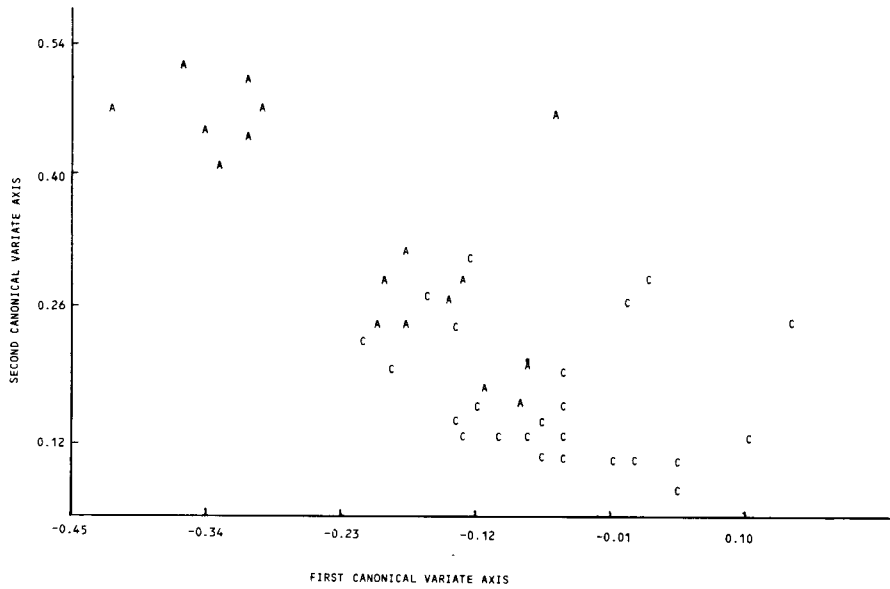


Fig. 1. Plot of specimens in the plane of the first two canonical variate means for *Subprionocyclus neptuni*. Here, A denotes the first sample and C the third sample (the few specimens from sample B have been suppressed in the plot). The points for sample A tend to congregate in the centre and upper left part of the plot and those for sample C in the lower right hand corner.

Table IV. Standardized canonical vectors for all three species (five samples).

Canonical roots f	1	2
	3.862	0.153
	\mathbf{cU}_1	\mathbf{cU}_2
D	-0.76	7.88
H	0.92	-7.20
B	0.03	-0.02
U	0.91	-1.08
Canonical roots f (shrunk fourth principal component)	3.830	0.070
	$\mathbf{cGI}_{1(0, \dots, \infty)}$	$\mathbf{cGI}_{2(0, \dots, \infty)}$
D	0.26	-0.48
H	0.17	-1.10
B	0.03	-0.05
U	0.66	1.47

Table V. Summary of calculations for growth-invariant analysis of three samples of *S. neptuni*.

Correlation matrix $\mathbf{S}^{-1}\mathbf{W}\mathbf{S}^{-1}$ (equation 1)

1			
0.95	1		
0.90	0.90	1	
0.91	0.82	0.81	1

Generalized distances

D_{ij}^2	Generalized distances	
	No growth effects extracted	One growth factor extracted ($\hat{\beta}_1^{(1)}$)
12	0.77	0.55
13	4.34	1.89
23	5.53	1.41

Discriminant function coefficients from canonical variates

Variable	First linear discriminant function		Second linear discriminant function	
	No factor removed	One factor removed	No factor removed	One factor removed
D	1.06	2.42	2.18	4.46
H	-0.57	1.12	-6.34	-6.84
B	-4.04	-6.33	2.46	-0.83
U	0.50	1.79	0.95	2.57

The canonical variate plot for the calculations based on \mathbf{B}^* and \mathbf{W}^* , as defined in equation (1), yields the following interesting results:

- (1) All samples of *S. neptuni* fall into two broad clusters
- (2) The discrimination along the second axis is being made in a contrast between coiling and variation in inflation (i.e. in H and U).

The heterogeneities in the samples indicate the existence of polymorphism in *S. neptuni*. It is possible that the polymorphism may be due to sexual dimorphism.

Growth-invariant relationships

The three samples of *S. neptuni* were analyzed by the BURNABY—GOWE method of growth invariance. It is to be expected that size differences can be an important consideration in the present material owing to the range in size shown in the samples as well as to the presence of polymorphic individuals. The results of the analysis are summarized in table V. The generalized distances are greatly altered for D_{13}^2 and D_{23}^2 . This indicates that most of the differences in the samples are due to their random composition.

Table VI. Shape association for four variables. Entries are the multiple R^2 of log three-dimensional shape ($y_H - y_B, y_D - y_U, y_B - y_U$) with the log-size variable (cf. p. 206).

Species	N	log geometric mean ($y_D + \dots + y_U$)/4	log diameter (y_D)
<i>S. (Subprionocyclus) normalis</i>	28	0.11	0.14
<i>S. (Subprionocyclus) neptuni</i>	23	0.21	0.22
	9	0.37	0.41
	39	0.25*	0.32*
<i>S. (Reesidites) minimus</i>	35	0.65**	0.70**

* denotes significance at the 5 % level; ** denotes significance at the 1 % level.

The differences in canonical variate coefficients due to the growth reduction (equations 8 and 9) are also considerable. All variables of the first discriminant function are affected by the extraction of growth differences with D and U being relatively the most changed. In the case of the second discriminant function, H remains unchanged, while all other variables are strongly affected.

The same analysis applied to all five samples yielded, as expected (owing to the great differences in range of the three samples of *S. neptuni*, on the one hand, and *S. normalis* and *R. minimus*, on the other) very pronounced differences between the growth-invariant results and those for which growth effects were not subtracted.

Multivariate size and shape relationships

Both species of *Subprionocyclus* show poor association between three-dimensional shape (see table VI) and size measures. *Reesidites* differs markedly in displaying high associations for both log diameter and log geometric mean hence allometry in this form, — cf. first principal component in table I. Both size measures show analogous associations with shape. Although the difference is slight, it is uniformly consistent; i.e. the log diameter is more strongly associated with tridimensional shape than is the log geometric mean (see p. 206).

Other selections of shape variables were tried but without significantly altering the general picture yielded by the analysis summarized in table VI. Whether or not the differing behaviour of *R. minimus* has any real taxonomic or evolutionary significance can only be decided on the basis of much larger collections. The possibility of there being a sample-size effect should be kept in mind, as the largest sample of *S. neptuni* also yields statistically significant values, although at a lower level than for *R. minimus*.

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<i>S. (Reesidites) minimus</i>	35	0.65**	0.70**

* denotes significance at the 5 % level; ** denotes significance at the 1 % level.

The differences in canonical variate coefficients due to the growth reduction (equations 8 and 9) are also considerable. All variables of the first discriminant function are affected by the extraction of growth differences with D and U being relatively the most changed. In the case of the second discriminant function, H remains unchanged, while all other variables are strongly affected.

The same analysis applied to all five samples yielded, as expected (owing to the great differences in range of the three samples of *S. neptuni*, on the one hand, and *S. normalis* and *R. minimus*, on the other) very pronounced differences between the growth-invariant results and those for which growth effects were not subtracted.

Multivariate size and shape relationships

Both species of *Subprionocyclus* show poor association between three-dimensional shape (see table VI) and size measures. *Reesidites* differs markedly in displaying high associations for both log diameter and log geometric mean hence allometry in this form, — cf. first principal component in table I. Both size measures show analogous associations with shape. Although the difference is slight, it is uniformly consistent; i.e. the log diameter is more strongly associated with tridimensional shape than is the log geometric mean (see p. 206).

Other selections of shape variables were tried but without significantly altering the general picture yielded by the analysis summarized in table VI. Whether or not the differing behaviour of *R. minimus* has any real taxonomic or evolutionary significance can only be decided on the basis of much larger collections. The possibility of there being a sample-size effect should be kept in mind, as the largest sample of *S. neptuni* also yields statistically significant values, although at a lower level than for *R. minimus*.

Concluding remarks

The analysis of closely related species of *Subprionocyclus* and *S. (Reesidites) minimus* shows that the covariance patterns are closely similar, but that *R. minimus* displays certain small but consistent differences in the relationship between tuberculation density and size and in the integration between size and shape variation. These differences seem to be sufficient to justify a subgeneric separation of the two categories but no more. All species show pronounced confounding due to size differences in the samples available.

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Upper Turonian (Cretaceous) ammonites

RICHARD A. REYMENT

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