

**GLOBOROTALIA CRASSULA (FORAMINIFERIDA):  
BLOW'S INTERPRETATION CONSIDERED  
BIOMETRICALLY**

by G. H. SCOTT

**ABSTRACT.** Analysis of gross shell and substructure dimensions indicates that components both on the spiral and axial aspects of the shell contribute to population discrimination although size differences, possibly of little taxonomic value, obscure the analysis. Harmonic amplitudes based on Fourier approximations to spiral and axial profiles of specimens and normalized to equate for size differences provide data that are more comprehensible in relation to Blow's revision (1969). Subspecies recognized by him exhibit closely similar spiral profiles and this was probably an important unifying feature in his concept of *Globorotalia crassula*. In contrast, axial profiles are divergent. *G. crassula conomiozea* (*sensu* Blow) and possibly also *G. c. crassula* exhibit strong three-fold symmetry due to ventral inflation of chambers whereas in *G. c. viola* shells are biconvex rather than conical, and exhibit four-fold symmetry. Axial shape may broadly correlate with latitude.

W. H. BLOW's great synthesis (1969) of planktonic foraminiferal systematics and Neogene stratigraphy is founded on refined, qualitative, observations of the morphology of individuals, particularly those of type status. To those who consider that classification concerns populations and that variation intrinsic in biological populations should be quantified to be adequately analysed, Blow's work is a challenge in methodology. Can the subtle differences in shape of shells, apprehended by direct perception and used by him to discriminate between taxa, be captured quantitatively? As an example, two representations of population variation in *G. crassula* are considered. One uses gross measurements of the shell and its major structures. The other uses parameters of curves fitted to profiles of the shell. How do they relate to Blow's revision (1969) of the species? *G. crassula* was selected for study because two samples identified by Blow were available. Moreover, his treatment of *G. crassula* is representative of his approach to infraspecific variation. The study is exploratory to identify unifying and discriminating characters. The small number of samples and specimens available precludes evaluation of the subspecies recognized by Blow. His nomenclature is followed.

USAGE

Cushman *et al.* (1930) proposed *G. crassula* to remedy the confusion caused by Brady (1884) when he referred Recent specimens to *Pulvinulina crassa* (d'Orbigny). Their solution was not invariably followed by others (e.g. Barker 1960) and the identity of their new taxon (type locality Humboldt County, California, Pliocene) created further problems. New Zealand workers, for example, followed Finlay and Marwick (1940) and applied the name to *G. crassaformis* (Galloway and Wissler). When the confusion was realized, *G. crassula* became a *nomen dubium*. It was not listed in the local fauna by Jenkins (1967). There is a fuller account of usage in Glaçon *et al.* 1973. The obscurity of the species continued until Blow's study (1969).

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Whereas Cushman and Stewart knew little of the phylogeny and distribution of their species, Blow placed it in historical and geographic contexts. Three variants of *G. crassula* were delineated. Blow called them 'morphotypes' (1969, p. 361) but treated them formally as subspecies. He discussed phylogeny and stratigraphic ranges and considered that the earliest morphotype (*G. c. conomiozea* Kennett) arose from *G. crassaformis* in Zone N.17. It has chambers that are vaulted ventrally, as in *G. truncatulinoidea* (d'Orbigny), giving the shell a conical axial profile. The later morphotypes appeared successively in Zone N.18. *G. crassula crassula* was typical of cool-water environments while *G. c. viola* n. sp. occurred in tropical assemblages. They were distinguished by tightness of coiling and appression of chambers but Blow considered that they were closer to each other than to *G. c. conomiozea*. Because *G. c. crassula* seemed more vaulted ventrally, it was considered to be the closer, morphologically, to the ancestral *G. c. conomiozea*. Blow considered that the pattern of evolution was towards flatter, less conical shells.

#### MATERIAL

1. F100020, Cuba, locality 1583 in Palmer (1948). Type locality of Canimar fauna. Specimen submitted to Dr. W. H. Blow who wrote (14 February 1972) that 'it is referable to *G. (G.) crassula viola*'. Plate 16, figs. 1-5; twenty-three specimens.

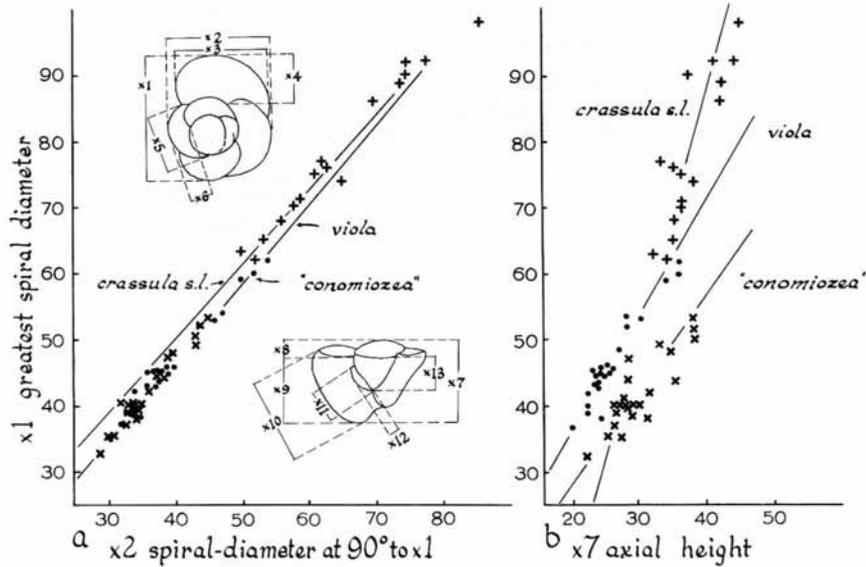
2. S154120, South-western Caribbean Sea, Site 154 Deep-Sea Drilling Project (Edgar *et al.* 1973), core 2, section 6, 120-123 cm, 'early Pliocene'. Material identified and loaned by Dr. W. A. Berggren who noted (21 February 1973) that 'I include the typical *crassula viola* of Blow and forms similar to his re-illustrated holotype of *crassula*. I cannot consistently separate these forms and think that they are all part of a single variable group.' Referred to here as *G. crassula s.l.* Plate 16, figs. 6-10; sixteen specimens.

3. S55/f937, New Zealand, Leader River, Mangapanian Stage (about Pliocene-Pleistocene boundary). Specimen and micrograph identified as *G. c. conomiozea* by Dr. W. H. Blow (14 February 1972). Considered hereafter as *G. c. 'conomiozea'* because Blow appears to have misidentified *G. conomiozea* Kennett (Scott, in press). Plate 16, figs. 11-15; twenty-three specimens.

The material includes all intact shells from the residues. Data, raw and statistical, are in the author's files at the New Zealand Geological Survey.

#### ANALYSIS WITH SELECTED VARIATES

Text-fig. 1 shows the location of variates that represent the dimensions of the shell ( $x_1, x_2, x_7$ ), spiral profiles of the last-formed ( $n$ th) and ( $n-3$ )th chambers ( $x_3, x_4, x_5, x_6$ ), ventral surfaces of the same chambers ( $x_9, x_{10}, x_{13}$ ), spire ( $x_8$ ), and aperture ( $x_{11}, x_{12}$ ). The representations are of maximum dimensions of structures. This approach is conventional in many biometrical studies primarily because the loci for such measurements are well defined. However, a technical question of possible significance concerns the adequacy of the data for studies in shape discrimination. A great variety of closed curves can be drawn when the only constraints are the loci corresponding to the two maximum dimensions of a structure. One suspects that



TEXT-FIG. 1. Bivariate plots of gross dimensions of shells. Scale units times 0.0084 give dimensions in millimetres. Bartlett's lines of best fit are shown.

a systematist as experienced as Blow made use of much more detailed information on shape of structures than that derivable from gross dimensions. For this reason the conventional biometrical study is followed by an analysis of shell profiles represented by closely sampled coordinates.

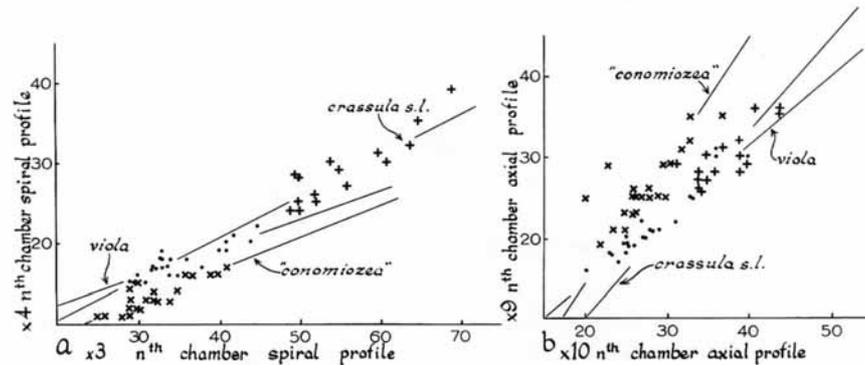
*Shell diameters, spiral orientation.* The location and orientation of scatters for variates  $x_1$ ,  $x_2$  (text-fig. 1a) are closely similar in S55/f937 (*G. c. 'conomiozea'*) and F100020 (*G. c. viola*). Shells from S154120 (*G. crassula s.l.*) are considerably larger. This may reflect selective preservation or be due to bias in sampling. For F100020 and S55/f937 the intercepts of the fitted lines lie close to the origin suggesting an isometric relation between  $x_1$ ,  $x_2$ . However, the line fitted to the much larger shell dimensions in S154120 has confidence limits (4.00–7.13, 99% level) that do not include the origin. Slight size allometry is suggested. With this reservation, the data indicate that spiral shape, as estimated from  $x_1$ ,  $x_2$ , is stable from sample to sample and is largely size-independent.

*Spiro-axial shape.* In text-fig. 1b the cone-like shells of *G. c. 'conomiozea'* are strongly distinguished by their axial height. There is no indication in this sample that the proportion  $x_1 : x_7$  changes with increase in  $x_1$  (99% confidence limits are 0.78 to -3.08). In contrast, for *G. crassula s.l.* the data suggest that axial height of shells tends to decrease, relatively, with increase in spiral diameter. Larger shells are more disc-like

than smaller shells. A 'menardine' trend (Scott 1973), iteratively followed in globorotalids (Cifelli 1969), may occur during ontogeny.

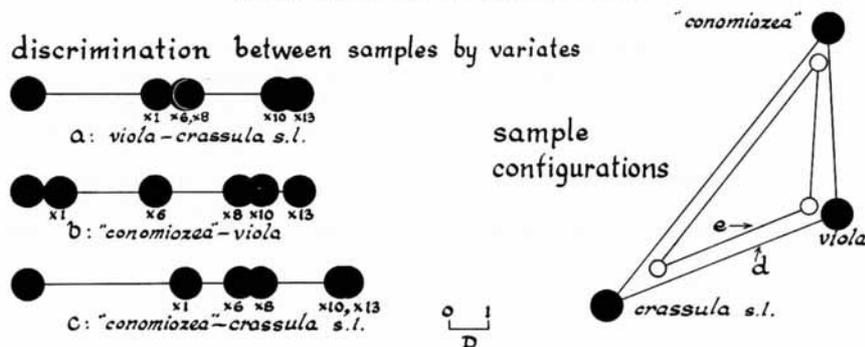
*Spiral profile of nth chamber.* Scatters for *G. c. viola* and *G. crassula s.l.* are similar in orientation (text-fig. 2a) although differentiated by size. In contrast, chamber height ( $x_4$ ) in *G. c. 'conomiozea'* from S55/f937 tends to be less, relative to length ( $x_3$ ).

*Axial profile of last chamber.* Variates  $x_9$ ,  $x_{10}$  (text-fig. 2b) reflect the angle formed by the intersection of the spiral and ventral surfaces of the  $n$ th chamber. In F100020 and S154120  $x_{10}$  tends to be considerably greater than  $x_9$  (low axial profile). The data for S55/f937 reflect the extension of the chamber profile ventrally so that  $x_{10}$  is more nearly equal to  $x_9$ . There is considerable intra-sample variation in relative proportions  $x_9$ : $x_{10}$  but the scatters for *G. crassula s.l.* and *G. c. viola* do not overlap with that for *G. c. 'conomiozea'*.



TEXT-FIG. 2. Bivariate plots of dimensions of last-formed ( $n$ th) chamber. Scale units times 0.0084 give dimensions in millimetres. Bartlett's lines of best fit are shown.

*Multivariate discrimination.* Bivariate plots indicate considerable size variation, both within and between samples. Principal component analyses of the multivariate data show that most of the intra-sample variation is due to size rather than shape differences. In each sample the largest principal axis of the covariance matrix reflects size variation (all direction cosines positive) and accounts for over 80% of the variation. The Mahalanobis measure of distance between populations and its associated linear discriminant function utilize the magnitude of variation within samples without regard to its sources. Thus, in comparisons between pairs of samples, *G. crassula s.l.* is discriminated from *G. c. 'conomiozea'* and *G. c. viola* (text-fig. 3a, c) even when only one variate ( $x_1$ ) is considered. In both comparisons the means for  $x_1$  differ at the 1% level ( $D^2(S154120: S55/f937) = 17.98$ ;  $D^2(S154120: F100020) = 11.75$ ). Reference to the distributions for  $x_1$  (text-fig. 1a) shows that size differences are responsible. Conversely, the distribution for  $x_{10}$  (text-fig. 2b) suggests that the additional distance produced by this variate in text-fig. 3c is not due to differences in the direction of size



TEXT-FIG. 3. Effect of variates on taxon discrimination (*a, b, c*); configuration of samples (*d*) using pooled covariance matrix, and a version (*e*) correcting for some size differences. Scale is in Mahalanobis's units (*D*). Note that  $D^2$  may be used to test the significance of the difference between sample means (Rao 1952). In configurations *d, e* all comparisons between sample means are significant at the 1% level.

increase. The patterns of variate-by-variate discrimination between samples shown in text-fig. 3*a-c* reflect an admixture of size and shape information.

Size differences between populations may be relevant in taxonomy. However, the absence of small individuals in S154120 suggests that this population was either selectively preserved or subject to biased sampling. On the assumption that size differences among the samples were growth or sampling effects, Mahalanobis's distances were recomputed by a technique (Burnaby 1966) that removed the effect of variation in the direction of the largest principal axis of each sample covariance matrix. These directions in the 13-variate spaces portrayed much of the intra-sample variation in size. Text-fig. 3*d, e* show configurations of the samples using Mahalanobis's distances that, respectively, include and exclude variation in these directions. Distances are reduced in text-fig. 3*e* but the disposition of samples is little changed. Intra-sample size variation contributes to intersample distances but does not distort them. Differences between samples means remains significant at the 1% level. The study suggests that axial shape of chambers, used in systematics by Blow, is significant in population discrimination (variates *x9, x10*). Interpopulation variability in spiral dimensions of the last-formed chamber (variates *x3, x4*) is also indicated.

#### HARMONIC AMPLITUDES

Whereas in the foregoing study variates were selected to represent shell morphology, the following analysis considers taxonomic discrimination using variates determined from quantified profiles of shells. The variates are determined by the data rather than by the investigator. The procedure perhaps matches more closely the intuitive procedure used for identification of taxa.

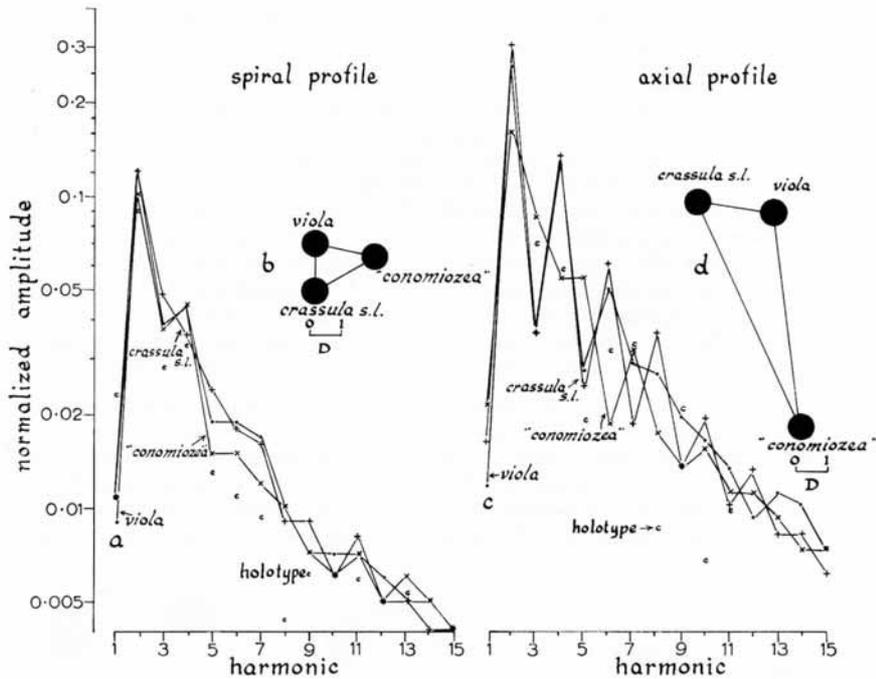
Spiral and axial profiles of shells were quantified with a manually guided digitizer (Scott 1975) that recorded the *x, y* coordinates of forty or more points around the periphery on paper tape. In numerical analysis (Hildebrand 1956) Fourier series

provides a means of approximating a function over a specified period. In this application the radius at a point on the curve representing the specimen profile is taken as a function of the angle from a selected reference point. The radius at angle  $\theta$  is given by  $a_0 + \sum a_k \cos k\theta + b_k \sin k\theta$  where  $a_0$ , the zeroth harmonic, is the mean radius of the figure and  $a_k, b_k$  are the determined Fourier coefficients for the  $k = 1, 2, \dots, \frac{1}{2}n - 1$  harmonics ( $n$  is the number of coordinate sets recorded on the periphery). The approximation provides a least squares fit to the figure and, as terms in the expansion are orthogonal, the contribution of each harmonic towards the fit is directly obtained. Algorithms in Ehrlich and Weinberg (1970) were used for computing  $a_0, a_k, b_k$  and from these were obtained normalized amplitude coefficients  $c_k = (a_k^2 + b_k^2)^{1/2}/a_0$ . The zeroth harmonic is used to remove the effects of size on amplitudes. The normalized amplitudes  $c_k (k = 1, \dots, 15)$  serve as variates for the discriminatory study.

*Spiral profile of shell.* In general, the amplitude of the  $i$ th harmonic reflects the extent to which the data can be approximated by a figure with  $i$  vertices. Mean amplitudes are now considered. For the spiral profile (text-fig. 4a) the first harmonic is, in all samples, a small contributor to the approximation, whereas the second (representing an elongate figure with two vertices) provides the largest contribution. For *G. c. 'conomiozea'* and *G. c. viola* the amplitude of the fourth harmonic is larger than the third. This reflects the lobation produced by the four chambers that form the final whorl. For *G. crassula s.l.* the tendency, in some individuals, for the final chamber to be placed at less than  $90^\circ$  revolution from its predecessor seems to lead to stronger three-fold symmetry. The small amount of information provided by harmonics  $\geq 5$  emphasizes the basically simple, quadrate, shape of the spiral profile of the shell.

Analysis of the 15-variate data by linear discriminant functions showed that amplitudes for *G. c. viola* and *G. crassula s.l.* are probably drawn from a common population ( $P > 0.05$ ) as are *G. c. viola* and *G. c. 'conomiozea'* ( $P > 0.05$ ). The data for *G. c. 'conomiozea'* and *G. crassula s.l.* are more equivocal as the test lies in  $0.05 > P > 0.01$  region. A configuration (text-fig. 4b) using Mahalanobis's  $D$  computed with the covariance matrix pooled from the three samples reflects these results by showing the slightly greater separation of *G. c. 'conomiozea'* from the remainder.

*Axial profile of shell.* Incongruity between the amplitude spectrum for *G. c. 'conomiozea'* and those for *G. c. viola* and *G. crassula s.l.* is marked in text-fig. 4c. For the lower harmonics two contrasting types of spectrum are present. *G. c. viola* and *G. crassula s.l.* have larger amplitudes for harmonic 2 than *G. c. 'conomiozea'*. This expresses the tendency for shells in the former samples to have large spiral diameter relative to axial height. Furthermore, in axial profile these shells are rather uniformly inflated to give a biconvex figure. Thus the amplitude for harmonic 4 is also strong. In contrast, in *G. c. 'conomiozea'* shells tend to be strongly inflated ventrally whereas spire height is low. The axial shell profile is more trigonal than in other taxa and this is reflected in the amplitude of harmonic 3. The probability that mean amplitudes (fifteen harmonics) for *G. c. viola* and *G. crassula s.l.* are from a common population is between  $0.05 > P > 0.01$ . In comparisons involving *G. c. 'conomiozea'* it is less than 0.01. Separation of *G. c. 'conomiozea'* from remaining samples in text-fig. 4d is marked.



TEXT-FIG. 4. Mean amplitudes (normalized) for fifteen Fourier harmonics, spiral and axial profiles (a, c); points 'c' are values for holotype of *Globorotalia crassula crassula*. Sample configurations (b, d) scaled in Mahalanobis's units (D).

#### SYSTEMATIC INTERPRETATIONS

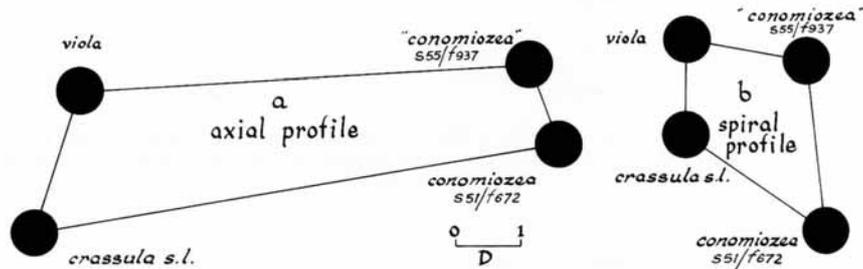
Outline drawings are commonly used to illustrate foraminiferal taxa. Ill-preserved or encrusted planktonic specimens in which chamber arrangement is obscured are still readily identified by experienced workers, mainly from information resident in shell profiles. This suggests that, of the two metrical techniques employed here, Fourier harmonic amplitudes of specimen profiles provide the closer approach to the patterns detected by direct qualitative perception. It is doubtful, for example, that linear variates such as  $x_4$  (text-fig. 1) of this study are perceived as such by the intuitive taxonomist.

The major result provided by analysis of amplitude spectra is that among the taxa examined there is similarity in spiral profiles and diversity in the axial profiles. Harmonic amplitudes for the spiral profile indicate similar populations. Because of the apparent significance of shell profiles in qualitative taxonomy I suggest that the pattern formed by the spiral profile was a primary unifying character in Blow's

association of *G. c.* 'conomiozea' with *G. c.* *viola*. Conversely, as Blow indicated, the axial profile of the shell discriminates these taxa.

*Relation to G. conomiozea.* Inclusion of S51/f672, a New Zealand sample studied by Kennett (1966) when he proposed *G. conomiozea*, in the sample configurations (recomputed using the pooled covariance matrix for the four samples) shows that the mean axial profile of this sample is indeed very close to that for *G. crassula* 'conomiozea' from S55/f937 (text-fig. 5a). To the contrary, when spiral profiles of the shells are considered (text-fig. 5b) S55/f937 is closer to samples of *G. crassula* from the Atlantic region than to *G. conomiozea* from type region in New Zealand. If the shape of the spiral side of the shell is significant in systematics, the configurations support the view (Scott in press) that Blow (1969) misidentified *G. conomiozea* Kennett. *G. crassula* 'conomiozea' of Blow appears to refer to populations of *G. crassula* in which chambers are inflated ventrally to give axial shell profiles very similar to those of *G. conomiozea* Kennett. For additional data see Scott (in press).

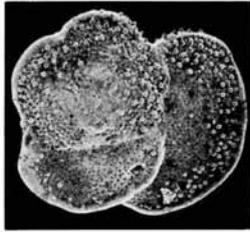
*Holotype of G. c. crassula.* This specimen provides some information about shape in *G. c. crassula* populations although it is unknown whether or not its morphology is typical. Amplitude spectra were computed from drawings of the holotype (Blow 1969, pl. 9, figs. 2, 3) in axial and spiral orientations. With the exception of that for harmonic 1 (text-fig. 4a), amplitudes for this specimen in spiral orientation are lower than the mean values for *G. c. viola* and for *G. c.* 'conomiozea'. Usually they lie more



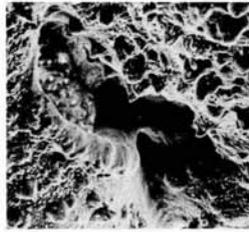
TEXT-FIG. 5. Configurations from harmonic amplitudes as in text-fig. 4 but including similar data from *Globorotalia conomiozea* Kennett, S51/f672, New Zealand (Kennett 1966).

#### EXPLANATION OF PLATE 16

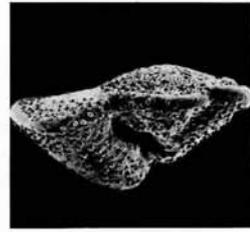
- Figs. 1-5. *Globorotalia crassula viola* Blow. FP 2558. F100020. 1, spiral orientation,  $\times 100$ . 2, aperture,  $\times 390$ . 3, axial orientation,  $\times 80$ . 4, periphery last-formed ( $n$ th chamber,  $\times 400$ . 5, periphery ( $n-2$ )th, ( $n-3$ )th chambers,  $\times 240$ .
- Figs. 6-10. *Globorotalia crassula* Cushman and Stewart *s.l.* FP 2559. S154120. 6, periphery of  $n$ th chamber,  $\times 200$ . 7, spiral orientation,  $\times 60$ . 8, aperture,  $\times 390$ . 9, oblique axial orientation,  $\times 60$ . 10, periphery ( $n-2$ )th, ( $n-3$ )th chambers,  $\times 200$ .
- Figs. 11-15. *Globorotalia crassula* 'conomiozea' *sensu* Blow. FP 2524. S55/f937. 11, periphery  $n$ th chamber,  $\times 380$ . 12, periphery ( $n-2$ )th, ( $n-3$ )th chambers,  $\times 400$ . 13, spiral orientation,  $\times 110$ . 14, aperture,  $\times 270$ . 15, axial orientation,  $\times 100$ .



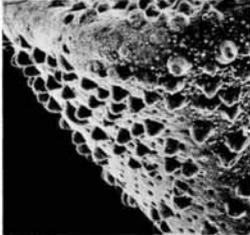
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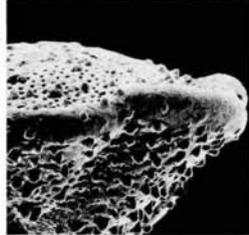
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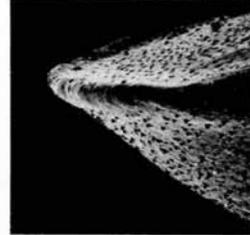
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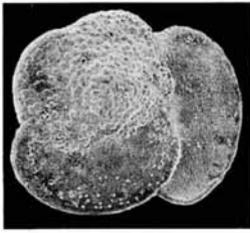
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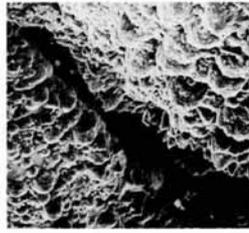
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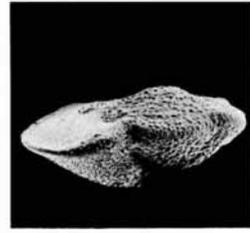
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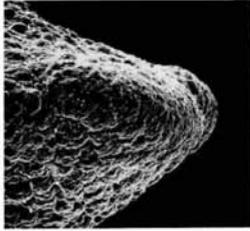
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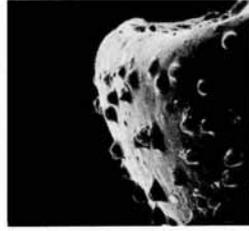
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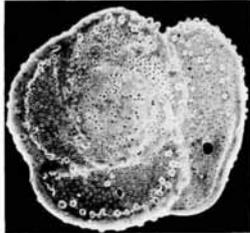
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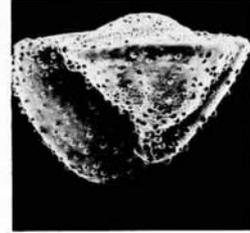
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SCOTT, *Globorotalia*

than one standard deviation away from sample means. The small amplitudes indicate that chambers do not project strongly in the outline. This is consonant with Blow's opinion (1969, p. 362) that *G. c. crassula* has a tightly coiled shell with closely appressed chambers. Of the sample spectra shown on text-fig. 4a the pattern for the holotype of *G. c. crassula* is closest to that for *G. c. 'conomiozea'*. A similar result is obtained when the vector of spectral values for the holotype is projected on to the spaces defined by principal axes for the two largest roots of sample covariance matrices. Of these low-dimensional representations of the fifteen-variate sample spaces, only in that for *G. c. 'conomiozea'* does the holotype lie within the sample scatter. Such representations are no more than a rough guide to affinity as neither the sample mean vector nor covariance matrix is known for a *G. c. crassula* population.

Blow's remarks (1969, p. 362) that *G. c. crassula* is more vaulted ventrally than *G. c. viola* and in this respect closer to *G. c. 'conomiozea'*, is supported by amplitude spectra for the holotype in axial orientation (text-fig. 4c). Amplitudes for harmonics 3, 4 strongly distinguish *G. c. 'conomiozea'* from *G. c. viola* and *G. crassula s.l.* For the holotype of *G. c. crassula* the equivalent values lie close to those for *G. c. 'conomiozea'*.

#### CONCLUSIONS

If qualitative classification of foraminiferal shells is viewed as a pattern establishment-recognition process then techniques such as Fourier analysis that provide approximations to curves appear to be better quantitative analogues than do conventional sets of gross dimensions.

The samples studied of *G. crassula* are united by the form of the spiral outline of the shell. Chamber lobation appears to be stronger developed in populations from the tropics (F100020, S154120) than in higher-latitude representatives (S55/f937, holotype of *G. c. crassula*).

The shape of the axial profile of the shell strongly discriminates *G. c. viola* from *G. c. 'conomiozea'*. If typical, the holotype of *G. c. crassula* indicates that this taxon is close to *G. c. 'conomiozea'* in characteristics of the axial profile.

While the data are insufficient to authenticate Blow's concept of *G. crassula*, they do suggest that some variant populations, widely separated geographically, possess similarities in shell form. Whereas spiral profiles are relatively uniform, axial profiles in the group are variable and may express different adaptive strategies towards constraints in planktonic environments. Samples from the tropics have relatively compressed axial profiles (*G. c. viola*, *G. crassula s.l.*); higher latitude representatives are more inflated ventrally (*G. c. 'conomiozea'*, possibly *G. c. crassula*). Both types of axial profile may improve form resistance to passive sinking, although their relative efficiencies are unknown. Convergent form, especially in the axial shape of the shell, is rife among globorotaliids and seems to reflect similar solutions to common problems in hydromechanics. It cannot be discounted in *G. crassula*. However, in defence of Blow's revision, it may be argued that the group is unified by aspects of shell form that are not directly connected with axial shape.

*G. c. conomiozea* of Blow (1969) does not refer to *G. conomiozea* Kennett. A new name may be required although it is possible that the populations referred to fall within the range of variation of *G. crassula crassula*.

*Acknowledgements.* This paper is presented in tribute to the work of the late Dr. W. H. Blow on planktonic foraminiferal systematics. His courtesy in identifying material greatly facilitated the analysis reported here. Dr. W. A. Berggren provided material and with a colleague commented on the manuscript.

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