

Pustulose and honeycomb topography in *Globigerinoides trilobus*

ABSTRACT

Surface topography in *Globigerinoides trilobus* is briefly surveyed, and the nature and taxonomic significance of the difference between pustulose and honeycomb surfaces are investigated in a sample of *G. aff. trilobus altiapertura*. In this case, the intrasample dichotomy in topography does not correspond with any in the multivariate data for shell dimensions and it is therefore judged not to be important in taxonomy. Honeycomb topography seems to develop when pores are large and regularly arranged between spine bases, and it may reflect close packing of pores. Pores are smaller and rather randomly distributed among spine bases in pustulose topography. Depressions on crests of some pustules (spine bases) provide a clue to the erstwhile occurrence of spines in fossil shells.

WALL TOPOGRAPHY IN TAXONOMY OF *GLOBIGERINOIDES*

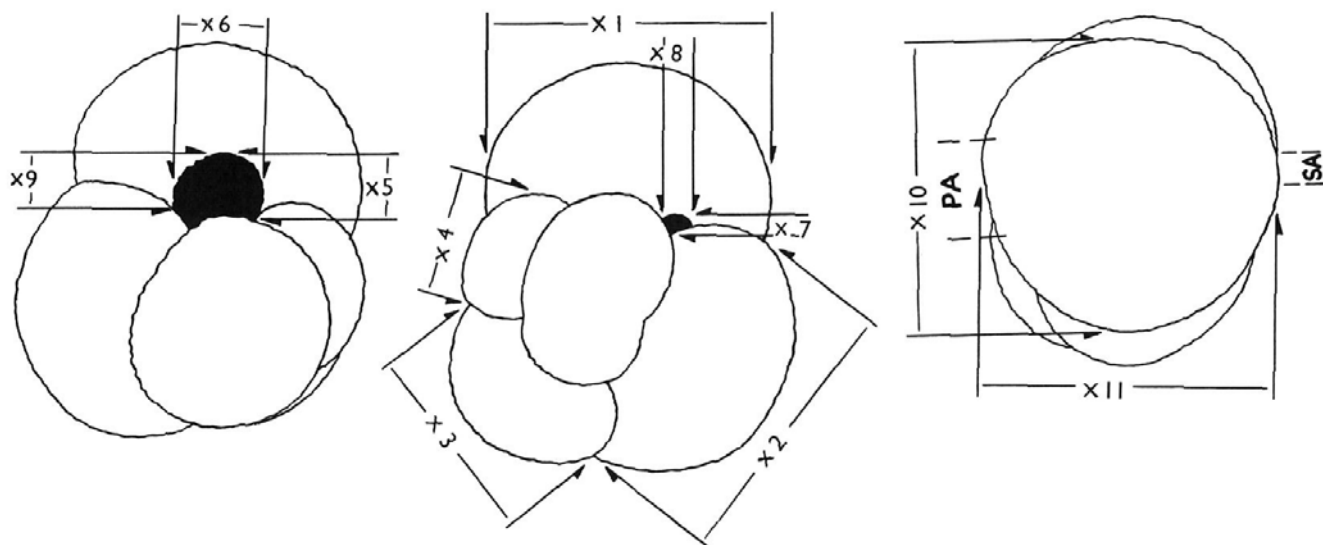
Parker (1962) and Lipps (1966) emphasized the conservative nature of wall structure and the utility of surface topography in the taxonomy of planktonic foraminifera. Although ultrastructure of the wall is fundamental, the ease with which surface features may be observed makes them more likely to be invoked in taxonomy. Thus, evaluation of the classification proposed by Parker and Lipps is important. They distinguished three topographies: spinose in the Globigerinidae, smooth in the Globorotaliidae, and pitted in the Catapsydracidae. Both noted that *Globigerinoides* is spinose but did not describe the topography of fossil shells from which spines had disappeared. Lipps's sketch (1966, text-fig. 4) suggested that the topography of such shells would be similar to the pitted surfaces of the Catapsydracidae. Parker's drawings (1962, pl. 7) of the pitted surface of *Globoquadrina dutertrei* are similar to the topography of *Globigerinoides trilobus*, designated as "honeycomb" by Hofker (1968, pl. 20, fig. 3). But Hofker (1968), who paid particular attention to the topographies of Lower Miocene *Globigerinoides*, also noted that in *G. bisphericus* the wall surface consisted of pustules interposed between pipelike pores. He considered that the contrast between honeycomb and pustulose topographies was highly significant in *Globigerinoides* and argued that *G. bisphericus* was not related to *G. trilobus* (cf. Blow, 1956).

Salient questions arising from this work concern the identification of spinose topography in fossil *Globigerinoides* and the significance and origin of the pustulose-honeycomb dichotomy noted by Hofker.

INTRASAMPLE VARIATION IN WALL TOPOGRAPHY

Topography corresponding either with the pustulose form or with the honeycomb form of Hofker can be fairly clearly distinguished on the last chamber of shells of *Globigerinoides aff. trilobus altiapertura* from a Lower Miocene locality (S136/f925) in southern New Zealand. Scott (1970) gave the stratigraphy and sketches of shell surfaces. Is this variation significant in taxonomy? I appeal to other aspects of shell morphology. Does division of the sample on the basis of surface topography correspond with a significant division using other characters? An affirmative answer may indicate that the sample represents mixed populations. A negative reply suggests either that close convergence of several shell characters occurred (effectively Hofker's reasoning) or, alternatively, that the dichotomy in topography is not important in taxonomy.

The statistical problem is to locate the optimal twofold division of the sample and to assess its significance. I used a method (Marriott, 1971)



TEXT-FIGURE 1

Globigerinoides aff. *trilobus altiapertura* Bolli. Location of measurements in umbilical and spiral orientations; x10 and x11 are measured with the last chamber uppermost. From Scott (1970).

which, given an initial partition, works iteratively towards the densest clusters by reallocating individuals to their closest cluster. Variates are defined in text-figure 1 and have been described by Scott (1970). Several plausible initial partitions of the sample into 2 or more groups were investigated.

1) Two initial groups on surface topography. Specimens were classified as pustulose or honeycomb by inspection of the final chamber using a stereomicroscope ($\times 216$). This resulted in 4 specimens changing classification from that shown in Scott (1970). One specimen, lost since that examination, was accepted as previously classified. Group analysis from this starting point resulted in a value of M close to 1 (text-figure 2) after 4 specimens had been transferred from their initial groups. These specimens did not correspond with the 4 reclassified at the 1972 examination. This result suggests that there is no dichotomy in the multivariate distribution for shell dimensions that corresponds with the dichotomy in surface texture. In view of this result several other plausible initial groups, suggested either on *a priori* grounds or by the distribution of the data, were explored to find if any real groups existed in the sample.

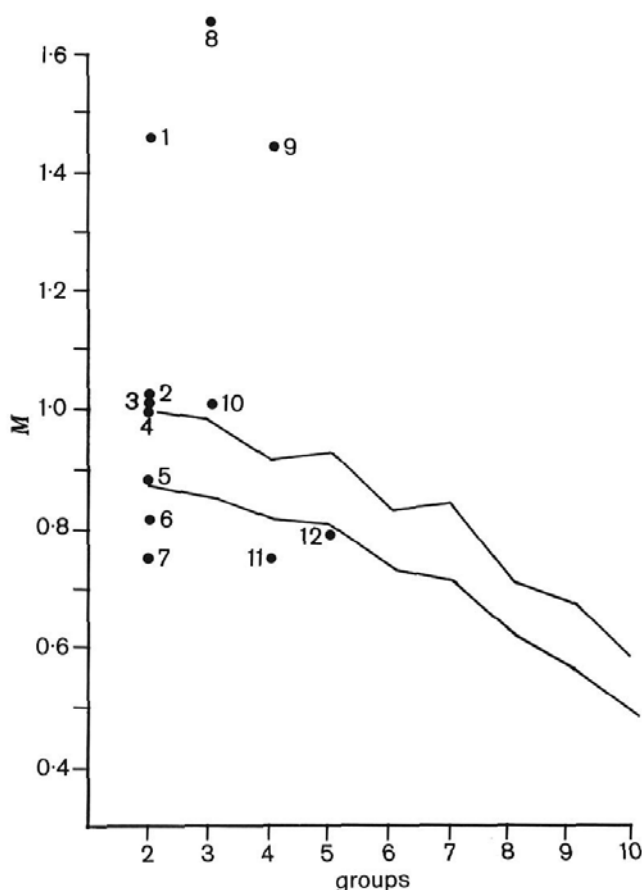
2) Coiling. Two lineages, even if similar in morphology, might be distinguished by the direction in which the shell coils. However, with the dextral-sinistral dichotomy as a starting point, the classificatory procedure terminated with groups for which M indicated a single population. It is probable that there are no significant differences between the shell dimensions of sinistrally and dextrally coiled individuals.

3) Shape of last chamber. Scott (1970) described departures from circularity in the profile of the last chamber. A dichotomy in the distribution of an index of the profile (1970, text-fig. 5, abscissa value of 1.15) was applied to form initial groups. Again the classificatory procedure suggested that a single group population was sampled.

4) Size of specimen. Extraction of principal components from the sample covariance matrix indicated that the largest principal component absorbs 64% of the total variance. All direction cosines for the corresponding axis are positive, and this suggests that much of the intra-sample variability reflects differences in specimen size (Jolicoeur and Mosimann, 1960).

Projection of specimens from the original 11-variate space onto this axis (L1, text-figure 3) reveals an irregular scatter and several discontinuities that might provide initial clusters. There is a small group of specimens at either extremity of the scatter, but a more important discontinuity, in terms of number of specimens on either side, occurs in the vicinity of $L1 = 72$. From this initial division, a 2-group analysis terminated with $M = 0.815$. This value is below that expected from a rectangular distribution and suggests that the grouping may be real. Mahalanobis' distance (D) between the groups produced by the analysis is 4.611 ($F_{11,35} = 16.700$, $P < 0.01$).

The distribution of variate 1, diameter of the last chamber in spiral orientation, has a discontinuity (text-figure 3) that, with two exceptions, separates the same groups of individuals as does the division at $L1 = 72$. The initial and final groups for the division on variate 1 are shown in text-



TEXT-FIGURE 2

Approximate tolerance limits for Marriott's criterion M , for samples of 320 (5 variates) from a rectangular distribution (from Marriott, 1971). $M = g^2 |W|/|T|$ where g is the number of groups, and $|W|$ and $|T|$ are the determinants of the within-group and the total covariance matrices. For material from a rectangular population, the expected value of M is 1. For samples from other single-group populations, it is greater than 1; for multigroup populations, it is less than 1. Note that the position of the set may be shifted up or down. Key to values of M obtained in this paper (starting positions are given): 1 dextral-sinistral coiling; 2 shape of last chamber from Scott (1970, text-figure 5); 3, pustulose-honeycomb dichotomy in surface texture as revised in 1972; 4, as for 3 but two indecisive specimens omitted; 5, dichotomy selected from distribution of measurements of variate 11; 6, two groups suggested by minimum at $L1 = 72$ in distribution of individuals on axis for largest principal component (see text-figure 3); 7, two groups from distribution of measurements of variate 1 (see text-figure 3); 8, three groups suggested by minima in distribution of individuals on $L1$ axis; 9, four groups, arbitrary division; 10, three groups selected from distribution of measurements of variate 1; 11, four groups suggested by minima in distribution of individuals on $L1$ axis; 12, five groups suggested by minima in distribution of individuals on $L1$ axis.

figure 3. This analysis produced the lowest value of M found for two groups (text-figure 2). For the variate 1 classification, $D = 4.874$ ($F_{11,35} = 18.226$, $P < 0.01$). Note that the two distances cannot be directly compared,

as the pooled covariance matrices upon which they are based are not identical. In both computations, major contributions to D are made by diameters of the last four chambers (x1–x4, text-figure 1), height of the last-formed supplementary aperture (x7), and partial height of the primary aperture (x9).

The frequency distribution for variate 1 is intrinsically a size distribution. As the $L1$ distribution also portrays size variation ($L1$ is a linear compound of the 11 variates), it appears that the best 2-group divisions of the sample are size-dependent. As the sample was not standardized for age of individuals, it is likely that age variation may be a component of the displayed variation in size. The result of the 2-group analyses is that, although real groups can be located, they relate to starting positions that reflect differences in size, and possibly age, of specimens. Thus, I do not regard the groups produced by the $L1$ and variate 1 analyses as taxonomically significant, although, statistically, they are well defined. Classifications produced from starting points not related to specimen size do not support the hypothesis of a 2-group population.

5) Multi-group analyses. Results of analyses using 3–5 groups are shown in text-figure 2. Some analyses from starting positions suggested by the distribution of individuals on $L1$ produced values of M that may indicate a multigroup population. The results support the conclusion reached for 2-group trials. There is no biological reason to suppose that only 2 size/age groups might be present. Most of the shells represent at least 10 instars.

IS TOPOGRAPHY INFLUENCED BY ARRANGEMENT OF PORES AND SPINE BASES?

The statistical result, suggesting taxonomic homogeneity, led to a re-examination of the relation between pustulose and honeycomb topographies.

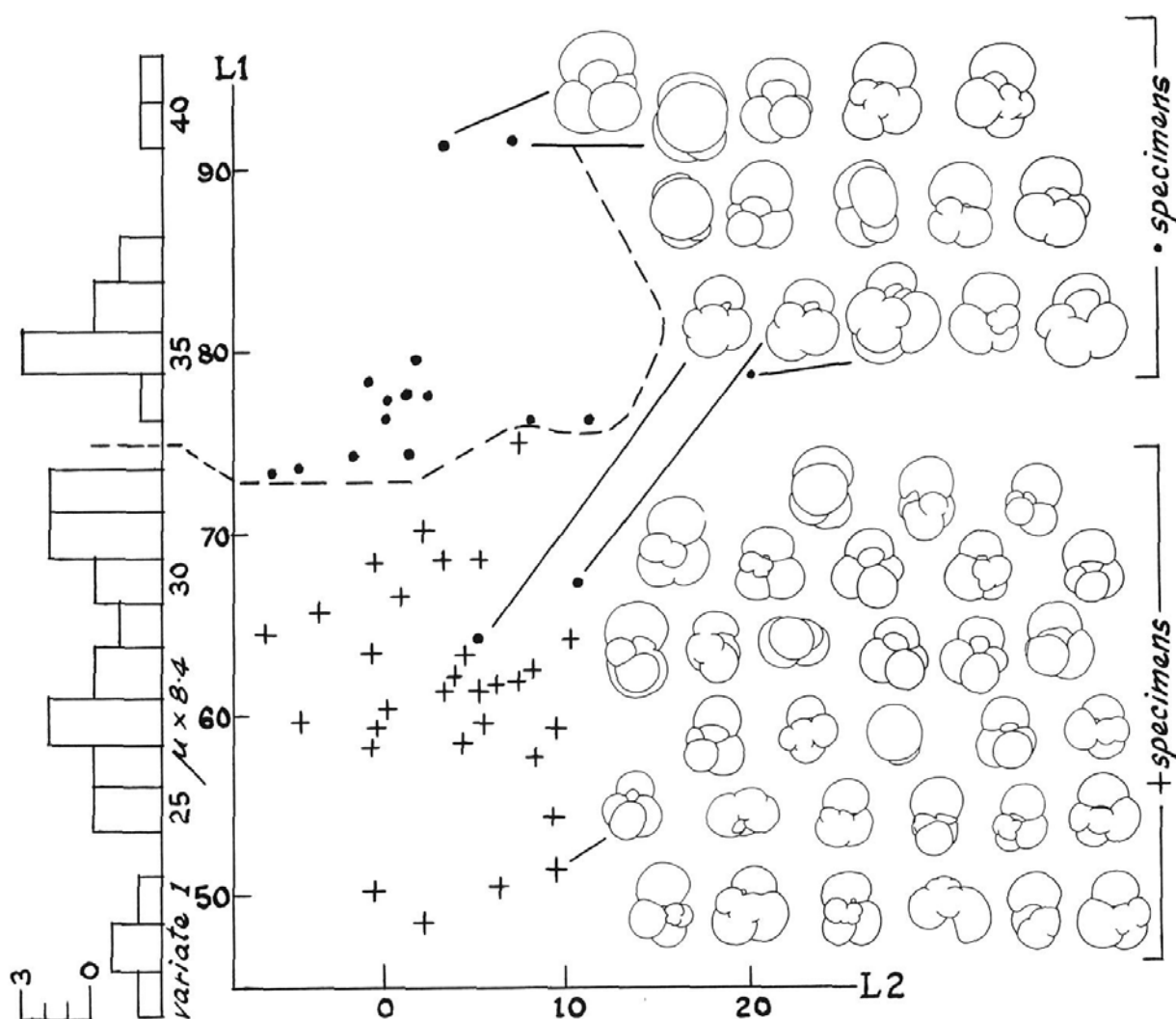
1) The highest topographic elements in both are domes, rather steep-sided and with rounded crests (plate 1, figures 1–2).

2) Some domes (plate 1, figure 2) have depressions on their crests that compare with those produced by removal of spine shafts from their bases (Hemleben, 1969, plate 3, figure 3).

3) There is full development of polygonal ridges linking domes in honeycomb topography but ridges are either absent or incomplete in pustulose topography (plate 1, figures 1–3).

4) Pustulose topography may occur on the last-formed chamber of a specimen in which earlier chambers exhibit indistinct honeycomb forms (plate 1, figure 5).

Depressions on dome crests suggest that pustulose and honeycomb surfaces are varieties of spinose topography. Can the variation be explained? As calcification probably



TEXT-FIGURE 3

Distribution of measurements of variate 1 and location of initial division that produced lowest value of M for two groups (left). Configuration of specimens on principal component axes $L1$, $L2$ of sample covariance matrix (81% of variance represented), location of the initial division based on variate 1 and location of 3 specimens transferred by the classification procedure; final result represented by \bullet and $+$ groups (centre). Profiles of most of the sample in various orientations; larger specimens generally in upper group (right).

occurred over the surface of the existing shell at each instar, 4) may indicate that chamber surfaces in *Globigerinoides trilobus* are initially pustulose and secondarily honeycomb. However, examination of apparently intact shells from several samples (plate 1, figures 4, 6–7) showed typical honeycomb topography on the last chamber. Even *G. bisphericus*, reported by Hofker (1968) as pustulose, has a honeycomb surface at its type locality (plate 1, figure 8). Moreover, in a species that is typically pustulose on the last chamber (*Globigerina bulloides*), the network of ridges constructed on earlier chambers is irregular and incomplete (plate 1, figures 9–11) relative to that on *Globigerinoides trilobus*. Thus, it seems unsatisfactory to regard honeycomb surfaces as modifications of pustulose surfaces.

That surface topography in spinose taxa is influenced by the disposition and perhaps relative dimensions of spine bases and pores is suggested by comparisons between *Globigerinoides trilobus* and *Globigerina bulloides*. The former typically possesses large-diameter pores, regularly arranged between spine bases. The latter has much smaller pores, rather randomly distributed among relatively larger spine bases. Areas between spine bases may be occupied by several pores rather than by a single pore as in *Globigerinoides trilobus*. Changes in the geometry of wall lamellae around pores in a naturally etched specimen of *G. trilobus* (plate 1, figures 12–13) suggest that honeycomb topography may develop because of close packing of regularly arranged pores. Towards the chamber interior, pores are circular in plan but, near the exterior,

rectilinear components appear in the lamellae. Circular symmetry is replaced by polygonal (crudely hexagonal) symmetry. Spine bases occur at vertices of the polygonal ridges and sometimes along the sides. Hexagonal symmetry (Thompson, 1952) commonly develops in biological structures in which regularly arranged, initially circular components are sufficiently close-packed to produce mutual interaction during growth. Even in the absence of knowledge of the biophysics of wall construction, it is likely that hexagonal symmetry of ridges is a valid clue to the occurrence of close-packed pores. In *Globigerina bulloides*, in contrast, ridges that occur around individual pores on chambers prior to the last are mixed with those that enclose pairs, triplets and even larger numbers of pores (plate 1, figure 11). Regular hexagonal symmetry is absent. The size of the pores and their irregular distribution relative to spine bases may be causative factors. As in *G. bulloides*, pustulose specimens of *Globigerinoides trilobus* in S136/f925 show irregular distribution of pores relative to spine bases (plate 1, figure 3).

CONCLUSIONS

1) Occurrence of depressions in crests of pustules (spine bases) may help to identify spinose topography in fossil material. Careful discrimination is necessary, for not all structures loosely termed pustules are spine bases and not all spine bases show depressions due to loss of spines. "Pitted" topography (*e. g.*, *Globoquadrina dutertrei*, plate 1, figure 15) resembles the honeycomb variant of spinose topography in fossil specimens but lacks spine bases.

2) Honeycomb topography is typical of *Globigerinoides trilobus*. Hexagonal symmetry of ridges around pores may be due to the symmetrical disposition of pores and spine bases.

3) Pustulose topography on the last-formed chamber of some specimens of *Globigerinoides* aff. *trilobus altiapertura* in S136/f925 is similar to that in *Globigerina bulloides* and seems to reflect much weaker symmetry of major surface elements, spine bases and pores.

PLATE 1

Specimens illustrated are registered as FP2534–2544 in New Zealand Geological Survey collections.

- 1–3, 5 *Globigerinoides* aff. *trilobus altiapertura* Bolli
S136/f925, New Zealand, Lower Miocene. 1, pustulose topography on last chamber of specimen illustrated in 5, x 890; 2, last chamber with honeycomb surface, x 660; 3, partial ridge development, last chamber of specimen classified as pustulose by light microscopy, x 370; 5, view of umbilical side, x 150.
- 4, 6–7 *Globigerinoides trilobus primordius* Blow and Banner
4, 7, F100718, Escorneb  ou, France, ?Upper Oligocene, x 2640 and x 950, respectively; 6, F100706, Labr  de, France, Lower Miocene, x 1060. Last chambers with honeycomb topography similar to that shown in 2.
- 8 *Globigerinoides bisphericus* Todd
C-85, Saipan, Miocene; honeycomb surface of last chamber, x 1010.
- 9–11 *Globigerina bulloides* d'Orbigny
Little Barrier Reef, New Zealand, 42 fathoms, Recent. 9–10, pustulose topography of last chamber, x 950 and x 2280, respectively; 11, incomplete ridge development on antepenultimate chamber of same specimen, x 960.
- 12–13 *Globigerinoides trilobus* (Reuss)
Little Barrier Reef, New Zealand, 42 fathoms, Recent. Honeycomb topography of last chamber, with development of hexagonal symmetry towards external surface of wall, x 950 and x 2270, respectively.
- 14 *Globorotalia scitula praescitula* Blow
S137/f615, New Zealand, Lower Miocene. Last chamber smooth, chambers on inner whorls with honeycomb surface, x 220.
- 15 *Globoquadrina dutertrei* (d'Orbigny)
Little Barrier Reef, New Zealand, 42 fathoms, Recent. Surface of last chamber, x 1010.

