MORPHOLOGY AND PHYLOGENY OF ORBULINOIDES BECKMANNII (SAITO 1962)

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ABSTRACT. An examination of dissected specimens of the Eocene species *Orbulinoides beckmannii* (Saito 1962), formerly *Porticulasphaera mexicana* (Cushman 1925), reveals certain morphological features not hitherto described. A study of the ontogeny of *O. beckmannii* and a comparison with the contemporaneous species *Globigerapsis kugleri* Bolli, Loeblich and Tappan, and *Globigerinatheka barri* Bolli, Loeblich and Tappan, indicate that *O. beckmannii* is unlikely to be related to either of these species. It appears to have developed from some globorotaloid ancestor.

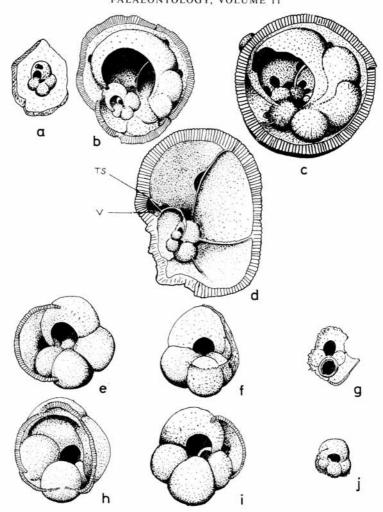
THIS study is based on specimens obtained from a block of extraneous Eocene in the Miocene Nariva Formation of Trinidad. This same material was used by Bolli (1957b, p. 159) in his monograph on the Eocene faunas of Trinidad. Bolli, Loeblich and Tappan (1957, p. 34) gave a full and accurate description of their new genus Porticulasphaera, and Bolli (1957a, p. 116) in placing the Miocene species Globigerinoides glomerosa Blow 1965 in this new Eocene genus commented that detailed comparative studies would probably '... reveal differences between the Eocene and Miocene forms ... ' (op. cit., p. 115). Bolli, Loeblich and Tappan designated Globigerina mexicana Cushman 1925 as the type species of their new genus Porticulasphaera. Saito (1962) considered that the Cushman type should be referred to the genus Globigerapsis Bolli, Loeblich and Tappan. Further examination of G. mexicana by Saito, and independently by Blow, has led to the conclusion that G. mexicana Cushman is conspecific with Globigerapsis semiinvoluta (Keijzer 1945). The writer has also examined the holotype of G. mexicana and agrees with their conclusion. Blow and Saito have therefore assigned the specimens which Bolli (1957a) previously referred to as Porticulasphaera mexicana (Cushman 1925), and upon which this study is based, to the new genus Orbulinoides as O. beckmannii (Saito 1962).

Olsson (1965) subsequently erected the genus *Praeorbulina* for the Miocene forms (i.e. *Porticulasphaera* of Bolli 1957a, p. 115) with the type species *Globigerinoides glomerosa glomerosa* Blow 1956. The object of this paper is to discuss certain morphological features observed in *O. beckmannii*, and which have not previously been described.

Morphology. Externally O. beckmannii shows numerous apertures at the base of the final chamber. The early trochospiral part of the test shows between one and four supplementary apertures; occasionally no such apertures were present. When present they are usually located at the junction of the spiral and intercameral sutures. The specimen illustrated by Bolli (1957a, pl. 37, fig. 1a) showing eight such apertures is considered atypical (cf. Bolli, Loeblich and Tappan, 1957, pl. 6, figs. 9a, b).

A removal of the final chamber and part of the walls of the last three chambers of the initial trochospire (text-fig. 1c) reveals the numerous supplementary apertures described by Bolli, Loeblich and Tappan (1957) and Olsson (1965). However, a closer examination

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TEXT-FIG. 1. a-d, Orbulinoides beckmannii (Saito 1962). a, Dissected specimen showing earliest whorl with an unbilical-extra-umbilical aperture, BMNH P46842, ×76. b, c, Dissected specimens, BMNH P46843, 46844, ×105. d, Dissected specimen showing trochospiral supplementary aperture (TS) opening into the vestibule (v), BMNH P46846, ×93.

e-g, Globigerapsis kugleri Bolli, Loeblich and Tappan 1957. Dissected specimens showing globigerinid

e-g., Globigerapsis kugleri Bolli, Loeblich and Tappan 1957. Dissected specimens showing globigerinid primary aperture; e, Specimen with Bulla partly removed, × 120; f, Bulla and two chambers removed, × 120; g, Bulla and five chambers removed; BMNH P46847, × 105.
h-j, Globigerinatheka barri Bolli, Loeblich and Tappan 1957. Dissected specimens showing a globigerinid primary aperture; h, Bulla partly removed, × 100; i, Bulla and two chambers removed, × 100; j, Bulla and five chambers removed; BMNH P46848, × 73.
All specimens from the O. beckmannii Zone, Navet Formation, Eocene, Point-å-Pierre, Trinidad.

of these apertures shows that in no instance are they directly connected with the outside of the test. They open into a small cavity (here termed vestibule) between the thick outer wall and the delicate wall of the initial trochospirally arranged chambers (text-fig. 1e). This vestibule is usually situated at the junction of the spiral and intercameral sutures, but probably also extends some way along the intercameral suture. It is also seen that the external supplementary apertures on the initial trochospire were never aligned with the internal apertures. Therefore, there is only an *indirect* connexion, that is via the vestibule, between the inside and outside of the test, as far as the early supplementary apertures are concerned.

Bolli's comparison (op. cit., p. 115) of the supplementary apertures of *Orbulinoides* and *Globigerinoides* cannot be upheld. There is a basic difference in that, in the latter genus, these apertures are never covered by subsequent thickening of the test and are in direct communication with the inside of the test. It would seem that early supplementary apertures became vestigial structures, in the sense that the degree of direct connexion between the inside and outside of the test in this area was much reduced. This appears to be in contrast with species of *Globigerinoides* (and also *Orbulina suturalis* Bronnimann

1951) where a direct connexion is maintained for each of the apertures.

The method of test thickening in *Orbulinoides* also appears to be in contrast with certain fossil species of *Globigerinoides* (e.g. *G. subquadratus* Bronnimann 1954 = *G. ruber* (d'Orbigny 1826) of Bolli 1957a). In this genus thickening is progressive rather

than occurring only after the adult stage has been reached.

A consideration of the morphology of the initial trochospire of *Orbulinoides* (e.g. its large primary aperture, inflated spinose chambers, numerous large supplementary apertures, and thin wall) strongly suggests that during the trochospiral stage the animal inhabited the epipelagic zone (*sensu* Hedgepeth 1957, p. 18, fig. 1). The subsequent test thickening, and the reduction in the number of supplementary apertures, might be correlated with its migration to deeper levels. The work of Bé and Ericson (1963) and Bé (1965) offers some support for this view, since a correlation between the thickness of the test with depth in the Recent species *Globorotalia truncatulinoides* and *Globigerinoides sacculifera* (Brady) was observed. The reduction in the number of 'functional' supplementary apertures may have been one means of increasing its weight in order to occupy lower levels. It is equally possible that the thickening of the test and reduction in supplementary apertures are associated with reproduction. The final inflated chamber may represent a type of brood pouch.

The presence of such an inflated final chamber in *Globigerapsis* and *Globigerinatheka* may indicate a similar mode of reproduction in these genera. Le Calvez (1936) showed that in *Orbulina minima* (d'Orbigny) there was a gradual reduction in the globigerine part of the test with depth. Furthermore, in specimens from the deepest levels (about 300 m.) the globigerine chambers had completely disappeared, and all that remained was the spheroidal final chamber which was frequently found to be filled with gametes. Therefore, there is some support for the view that the inflated final chambers of these Eocene

genera might be connected with reproduction.

Phylogeny. Bolli (1957a, p. 160) stated that "... Globigerapsis, Globigerinatheka and Porticulasphaera obviously represent a related group". He considered that Globigerapsis index (Finlay) gave rise to G. kugleri Bolli, Loeblich and Tappan, from which O.

beckmannii developed. His further support for this view was the fact that the three genera showed a 90 per cent. tendency to coil dextrally. Bolli is correct in the case of Globigerapsis and Globigerinatheka, and Eckert's (1963) study of these genera supports this conclusion. However, in the writer's opinion, Orbulinoides is unrelated to either of these genera. The gross morphological similarity of these three species is more likely to be a function of convergent evolution than any genetic affinity (at least as far as beckmannii is concerned). This view is based on a comparison of the ontogeny of G. kugleri, G. barri, and O. beckmannii (text-fig. 1). It is clear that both kugleri and barri have arisen from a globigerinid ancestral form, while O. beckmannii shows an unmistakable umbilicalextra-umbilical primary aperture initially, and therefore is derived from a globorotaloid ancestor. The striking differences in the morphology of the initial whorls, particularly the distinctive shape of the later trochospiral chambers of beckmannii, and the large primary aperture, adds further support to this view (text-fig. 1, cf. figs. a, b with f-j). Bolli considered the gross similarity of the adult tests of these three species the most important phylogenetic factors. The writer, however, considers that the evidence of the ontogeny of these species outweighs the adult similarity in gross morphology.

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