Shell Growth and Structure of Planktonic Foraminifera

Abstract. *Planktonic foraminiferal tests show bilamellar additions to each chamber and develop a "secondary thickening" in the form of a calcite crust in late ontogeny. The evidence presented indicates that additional calcium carbonate is deposited upon the original bilamellar test and that maximum calcite crust thickness is attained at depths greater than 500 meters.*

The wall structure and mineral composition of foraminiferal tests play a fundamental role in their taxonomy. Smout (*1*) and recently Reiss (*2, 3, 4*) have shown that the majority of the foraminiferal families construct their tests by the addition of calcite lamellae in a regular pattern. Reiss (*2*) distinguished four groups among the lamellar Foraminifera, of which the Bilamellidea is of immediate concern because the planktonic Foraminifera belong to this group. According to Reiss the walls of each chamber of the planktonic Foraminifera consist of two layers—an outer lamella, which also covers the previously deposited parts of the test, and an inner lamella, which is confined to the individual chamber and is superimposed upon the previous septum. The bilamellar addition for each instar results in successive growth layers over earlier chambers of the test in such a manner that the final chamber consists of two lamellae, the penultimate chamber of three lamellae, and so forth.

This view was disputed by Hofker (*5*) who maintained that no lamellar structure exists in planktonic Foraminifera and that the septa are simple and do not consist of double lamellae. Hofker also stated that the apparent thickness of the test as seen in thin section was due to "secondary thickening" occurring only once (not for each instar) in mature individuals.

We offer additional evidence that appears to clarify and resolve the above "contradictory" views. For our study, we have selected the same genus discussed and the same species illustrated by Reiss (*4*), *Globorotalia truncatulinoides* (d'Orbigny).

On initial examination the bilamellar pattern of test secretion is clearly evident in horizontal and vertical sections of planktonic Foraminifera (Figs. 1*A*, 1*B*, 2*A*, 2*B*), thus confirming Reiss's findings. Acetate peel replicas of etched sections were made because they present a single-layer view and produce clearer results than the thinnest thin sections. In the latter, superimposed pores and prismatic crystals, oriented perpendicularly to the test surface, tend to obscure the lamellae. The construction of double lamellae for each chamber is best noted in the last-formed chamber or in a septum—the portion of the test wall dividing two chambers (Fig. 3). At the apertural margin of the septum some local thickening of the lamellae produces an inner core or "lip." The inner lamella is restricted to the chamber it has formed and frequently is superimposed upon the previous septum. The outer lamella envelops the earlier chambers up to the aperture in a progressively decreasing thickness, so that it becomes increasingly more difficult to trace. Thus, discrimination of the actual number of lamellae over earlier chambers is a matter of contention.

Second, the bilamellar additions and successive growth of outer lamellae over the previous chambers do not add appreciably to the total thickness of the test walls of *Globorotalia truncatulinoides* specimens caught in plankton tows from the epipelagic zone (0–300 m) of the Sargasso Sea. Such individuals living near the surface attain a

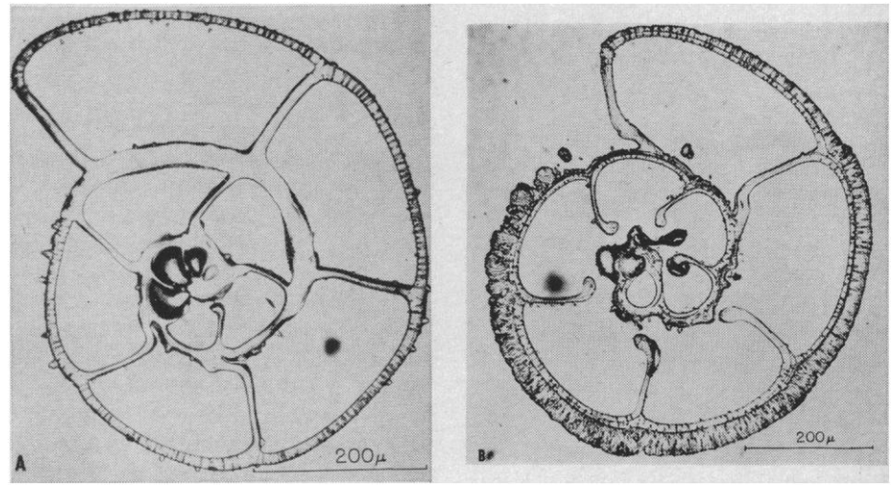

Fig. 1. *A*, Horizontal section of *Globorotalia truncatulinoides* from 0–180 m plankton sample collected in the central North Atlantic (35°04′N, 47°59′W). *B*, Horizontal section of *Globorotalia truncatulinoides* from bottom sediments of the central North Atlantic (35°06′N, 45°56′W, 3190 m deep). It has much greater wall thickness in comparison with its surface-water equivalent in Fig. 1*A*. A schematic diagram of Fig. 1*B* appears on the cover.

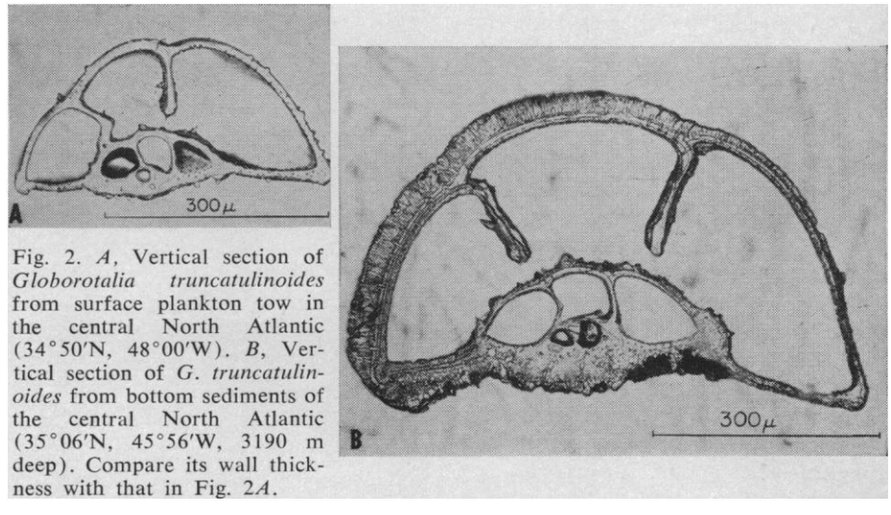

Fig. 2. *A*, Vertical section of *Globorotalia truncatulinoides* from surface plankton tow in the central North Atlantic (34°50′N, 48°00′W). *B*, Vertical section of *G. truncatulinoides* from bottom sediments of the central North Atlantic (35°06′N, 45°56′W, 3190 m deep). Compare its wall thickness with that in Fig. 2*A*.

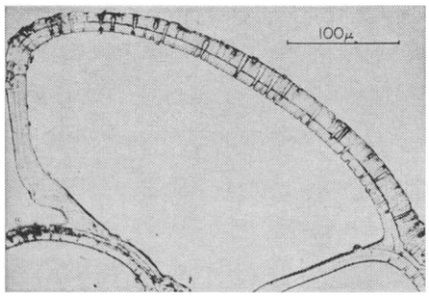

Fig. 3. Detail of final chamber in *Globorotalia truncatulinoides* from Fig. 1*B*, showing calcite crust as a third layer over the bilamellae.

maximum test dimension of about 685 μ and their test walls are rarely thicker than 20 μ (Figs. 1*A* and 2*A*).

Third, bathypelagic specimens of *G. truncatulinoides* collected in plankton tows deeper than 500 m and the majority of empty tests from the ocean floor have heavily encrusted outer test walls, which contrast sharply with the thin, transparent walls of epipelagic specimens. The specimen we have selected from several dozen sectioned shells comes from an ocean bottom sample in the North Atlantic and has a maximum test dimension of 690 μ and a maximum wall thickness of 50 μ (Fig. 1*B*). In addition to the original bilamellar portion, it has a third layer or calcite crust (Fig. 3) which can be seen to increase in thickness over the earlier chambers. The calcite crust, shown as a stippled area in the schematic diagram (cover), has a thickness of 33 μ that is twice that of the earlier bilamellar portion.

Bé and Ericson (*6*) have discussed in more detail the shell thickening of *Globorotalia truncatulinoides* which takes place at increasing depths, and Bé (*7*) described a similar phenomenon for *Globigerinoides sacculifer* (Brady) —*Sphaeroidinella dehiscens* (Parker and Jones). Bé and Ericson concluded that those *G. truncatulinoides* inhabiting water depths greater than 500 m possessed test walls up to twice the thickness of those living near the surface. Our present observations corroborate Hofker's view that the unusually thick outer wall, in contrast to the relatively thin septa and inner walls, is indeed due to "secondary thickening." In our opinion, this secondary thickening is a deep-water phenomenon of calcium-carbonate secretion that is superimposed upon the original, bilamellar test.

Our data indicate that two basic calcification processes are at work in most species of planktonic Foraminifera. Bilamellar shell growth occurs in the epipelagic zone and accounts for the development of the overall test. When the individual descends to deeper habitats, chamber additions to the test are retarded or cease in favor of a progressive increase in wall thickness. This calcite crust deposition is a terminal process in response to some yet unknown stimulus in deeper waters.

The existence of a calcite crust over the original, bilamellar test should be considered in taxonomic studies of lamellar Foraminifera. Emiliani (*9*) showed on the basis of oxygen isotopic composition that various species of planktonic Foraminifera deposited their shell material at different average depths and that *G. truncatulinoides* occupied the deepest habitat of the nine species he examined. Since the calcite of a mature individual's test is secreted over a considerable range of temperature and depth (23°C to less than 6°C from the surface to a depth greater than 1000 m for *G. truncatulinoides*), determinations of oxygen isotopic ratios in such foraminiferal shells would produce only average values. We agree with Emiliani (*9*) that his measured temperature differences were due to different depth habitats or the season of average shell deposition or both. We amplify his results with our field observations that shell deposition begins in the euphotic zone and probably continues to well below a depth of 1000 m. This depth factor requires more thorough investigation in order that its implications in paleotemperature studies employing oxygen isotopic composition of planktonic foraminiferal tests can be evaluated.

ALLAN W. H. BÉ
LEROY LOTT

Lamont Geological Observatory, Columbia University, Palisades, New York

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Protein as the Mitochondrial Site for Action of Uncoupling Phenols

Abstract. *Phenolic reagents which uncouple oxidative phosphorylation are bound to the protein moiety of mitochondria. This interaction may induce configurational changes in the enzymes of oxidative phosphorylation, and these changes could be responsible for the uncoupling phenomenon.*

Most reagents which uncouple oxidative phosphorylation in isolated animal mitochondria are highly lipophilic. The efficacy of these uncoupling reagents, particularly the substituted phenols, has been related to the extent of their lipid solubility (*1*). The inference from such studies, together with the knowledge that phospholipid is a major constituent of mitochondria, has led to the assumption that these uncoupling phenols are dissolved in the lipid moiety of the mitochondrion and exert their action in this milieu (*2*). The possession of lipid solubility by uncoupling reagents is not necessarily indicative that lipids are the mitochondrial constituents taking part in the critical interaction.

Studies in our laboratory have shown that uncoupling phenols, when added to suspensions of mitochondria, are bound to the protein portion of these organelles, and we believe that it is this interaction which is responsible for their uncoupling activity. This report summarizes the evidence for such a conclusion, and we present the results of two particularly relevant experiments.

Bovine serum albumin restores the capacity for oxidative phosphorylation to isolated rat liver mitochondria uncoupled by various substituted phenols. Moreover, the addition of this protein together with adenosine triphosphate largely restores morphological integrity to mitochondria swollen by pentachlorophenol (*3*). Serum albumin exerts these beneficial effects by tightly binding the uncoupling phenol and thereby removing it from mitochondria. These results, in conjunction with numerous reports demonstrating the capacity of