Shell Structure of Recent Articulate Brachiopoda

Abstract. *Replicas of the etched surfaces of the brachial valves of* Gryphus stearnsi *(Dall and Pilsbry) and* Pictothyris picta *(Dillwyn) were examined by electron microscopy. This method clearly reveals the crystalline texture of two of the morphologic layers of the shells and demonstrates that the calcite crystals accommodate the tubular punctate structures. These findings may be useful in resolving some of the problems of brachiopod taxonomy.*

In discussing the future of brachiopod taxonomy, Muir-Wood (*1*) stated: "Only by a careful and minute restudy of the internal as well as the external characters with the aid of improved techniques and, if possible, better preserved material than has so far been available can a reliable phylogenetic classification be built up from species and genera to higher categories, and homeomorphs be distinguished." We have chosen electron microscopy as the means for minute study of the shell structure of some recent terebratuloids. The results indicate that the shell structure is more complex than previously supposed from light-microscope studies. The electron microscope has resolved details of the crystalline texture of two of the shell layers and the unique accommodation of the tubular punctae by the calcite crystals.

The brachial valves of two species, one from each of the two suborders established by Muir-Wood (*1*), were selected: *Gryphus stearnsi* (Dall and Pilsbry) of the Terebratuloidea and *Pictothyris picta* (Dillwyn) of the Terebratelloidea. The valves were embedded in a transparent plastic and sectioned both longitudinally and transversely to the long axis of the shell. The exposed edges of the shells were then polished and etched in 1*N* HCl. Replicas of the etched surface were then prepared by the two-step plastic-carbon method. Sequential electron micrographs permitted a reconstruction of much of the shell structure (see Figs. 1 and 2).

The existence of the three-layered shell has long been recognized and considered to be of some, although questionable, taxonomic importance. These three layers are named the periostracum, the outer carbonate layer, and the inner carbonate layer. We consider the adventitious calcite, added to the shell interior of mature individuals, as a fourth layer and an integral part of the structure. Additional complexities are imposed on the primary structure by the presence of tubular structures (punctae) which transect the layers and by calcite rods (taleolae) which penetrate the inner carbonate layers. Cooper (*2*) suggested a morphological grouping of some brachiopod super-families, based upon the shell structure, as being impunctate, punctate, or pseudopunctate (penetrated by taleolae). This grouping has attained wide usage, but has also created some problems in that at least one author (*3*) has suggested the inclusion of both punctate and impunctate forms of one genus in the same category.

By describing these species, we hope to reopen the question of the nature of shell architecture of both recent and fossil brachiopods. The outermost shell layer, the periostracum, could not be studied since it was not preserved on the specimens available. The succeeding layer, the outer carbonate layer, was described by Williams (*4*) as consisting of prismatic crystals oriented normal to the shell surface. Our studies tend to substantiate this. The crystals composing this layer are much smaller than those in the two succeeding inner layers and they have not been well delineated in our studies.

The inner carbonate layer was described by Cloud (*5*) in his light-microscope investigation of a typical tere-

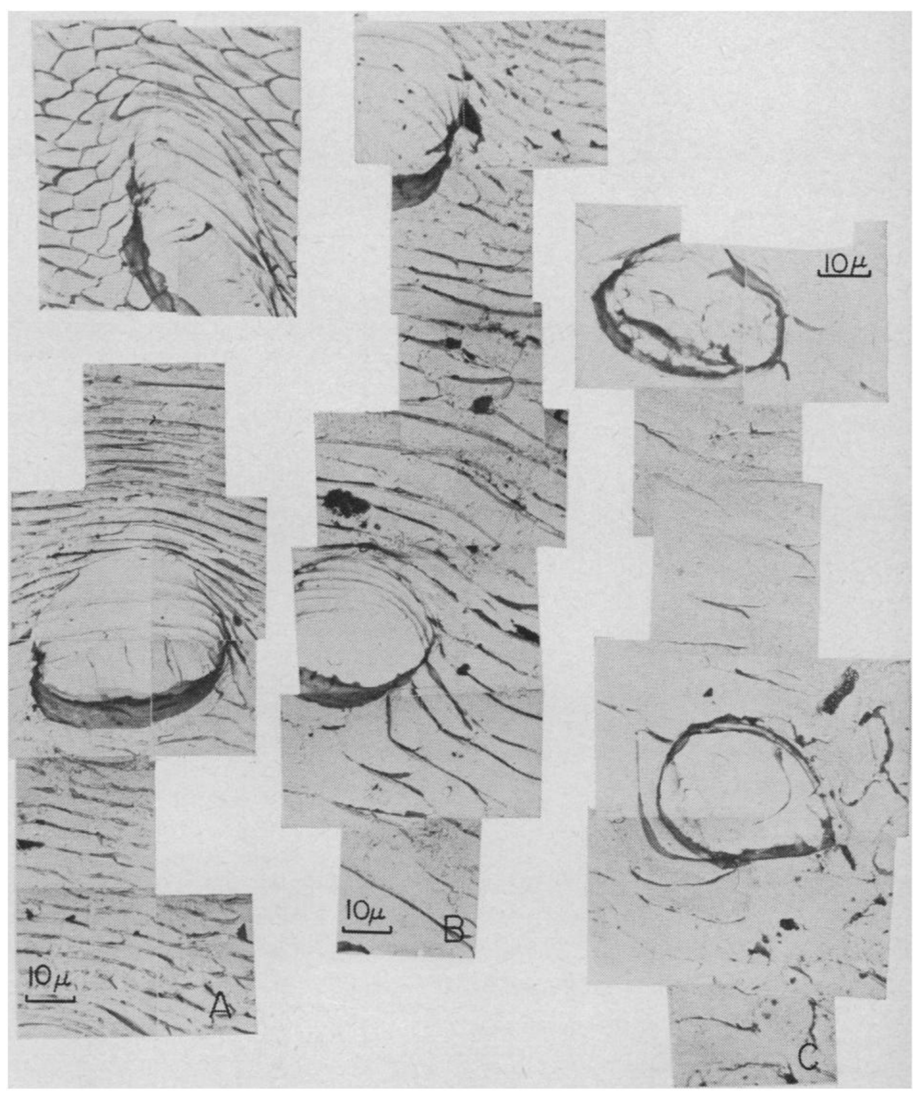

Fig. 1. A three-part composite electron micrograph of a longitudinal section of the brachial valve of the species *Pictothyris picta*. All sections are mounted with the top of the shell uppermost. (*A*) The upper portion of the inner carbonate layer; the interruption represents a wire in the specimen support-screen which masked the image. (*B*) The remainder of the inner carbonate layer. (*C*) The adventitious layer; the oval areas represent the punctae.

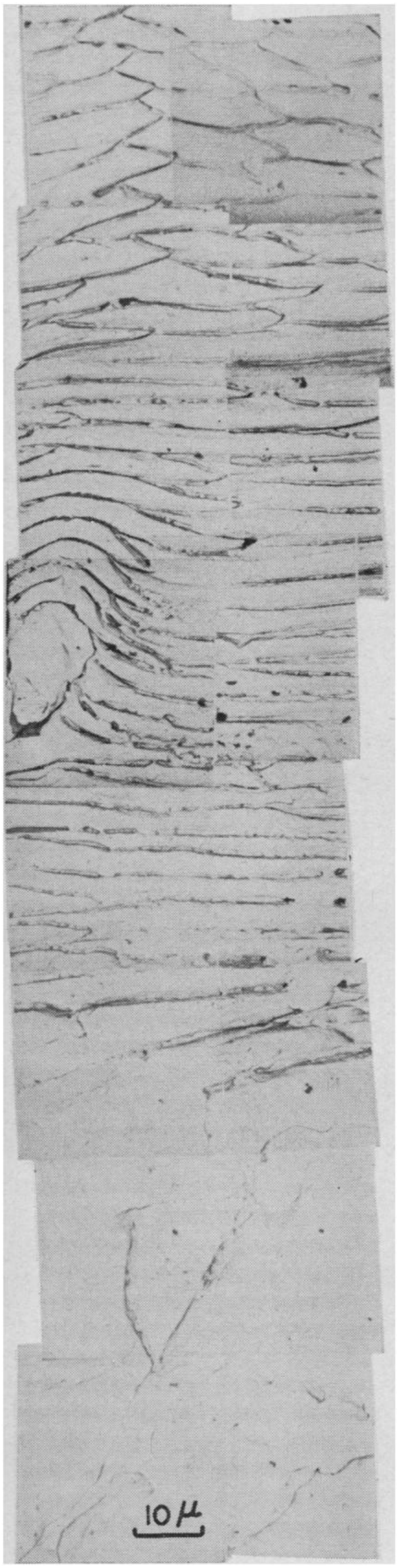

Fig. 2. A composite electron micrograph of a transverse section of the brachial valve of the species *Gryphus stearnsi*. The uppermost portion shows the outer extremity of the inner carbonate layer. The medial portion shows the remainder of the layer and curving of the calcite crystals around an obliquely transected puncta. The bottom shows the large crystals in the adventitious layer.

bratuloid, *Laqueus Californicus* (Koch). He found this inner layer sharply differentiated from the outer layer and composed of parallel prismatic crystals inclined to the outer layer.

Our electron-microscope observations reveal a somewhat different texture in this inner carbonate layer for both species studied. As one proceeds downward from the sharp boundary with the outer carbonate layer, the crystallites are slightly tabular in shape and oriented parallel to the shell layers. The orientation is modified, however, by the passage of the punctae. The crystals in proximity to these tubular structures tend to parallel and wrap about the cylindrical walls of the punctae (Fig. 1*A* and Fig. 2).

As one continues downward through this layer, the crystals become larger and more pronouncedly tabular. The flattening is still parallel to the shell layers except in the vicinity of the punctae. These more tabular crystals also accommodate the punctae by tending to parallel the cylindrical walls. The inner surface of a puncta has a corrugated ring appearance resulting from this unique crystal orientation (Fig. 1, *A* and *B*).

Finally, these flattened, parallel crystallites gradually change their character by becoming irregularly shaped. This change in texture marks the gradational boundary between the inner carbonate layer and the innermost layer, the adventitious (Fig. 1, *B* and *C*; Fig. 2).

The adventitious layer is composed of relatively large irregularly shaped crystals. The crystals do not offer the same special accommodation for the passage of the punctae as was found in the inner carbonate layer. This is to be expected since this layer of calcite is deposited subsequent to the primary shell development (Fig. 1*C*).

These new details of shell morphology indicate that a reexamination of brachiopod shells is needed and that studies with the electron microscope may prove helpful in the problems of taxonomy.

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References and Notes

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Actinomycin D Inhibition of Vitamin D Action

Abstract. *Injection of actinomycin D into rats completely prevents both the rise in serum calcium normally induced by vitamin D and the increased transport of calcium by everted intestinal sacs. Injection of excess parathyroid hormone did not alter this result; this eliminates the possibility that the inhibition of vitamin action was due to blocked hormone synthesis. As a result of these findings, a hypothesis concerning the mechanism of action of vitamin D is presented.*

It is now generally accepted that vitamin D acts by stimulating the transport of calcium and secondarily that of phosphate from the bone, intestinal lumen, and perhaps the renal tubule into the blood stream. The most recent concept is that it functions directly in the cellular or subcellular membranes (*1*). This is supported primarily by the demonstration of effects in vitro of the vitamin on calcium translocation in mitochondria (*2*) and on calcium-stimulated phospholipid labeling (*3*), as well as the demonstration that radioactive vitamin D accumulates in the membrane fractions of kidney and intestinal cells (*4*).

On the other hand, certain observations are not consistent with a direct action of the vitamin. Depending upon the amount given, a lag of 4 to 16 hours is required to observe the earliest physiological response to vitamin D whether it is given orally or intravenously (*5*). In addition, vitamin D added in vitro to intestinal preparations has no effect on calcium translocation, whereas it is markedly effective in identical experiments when given to