THE CROSSED-BLADED FABRICS OF THE SHELLS OF *TERRAKEA SOLIDA* (ETHERIDGE AND DUN) AND *STREPTORHYNCHUS PELICANENSIS* FLETCHER

by JOHN ARMSTRONG

ABSTRACT. The shells of *Terrakea solida* (Etheridge and Dun) and *Streptorhynchus pelicanensis* Fletcher lack physically distinguishable primary layers and consist of superimposed and overlapping sheets parallel to the surfaces of the shell. Each sheet is composed of parallel tabular blades whose greatest dimensions are parallel to the sheet. In cross-section a blade has a rectangular outline unlike the secondary layer fibres of rhynchonellids, terebratulids, spiriferids, pentamerids, and orthids. The blades of a sheet are not usually parallel to the blades in adjacent co-planar sheets or to the blades of the contiguous underlying and overlying sheets. For this micro-structural arrangement the term crossed-bladed is proposed to distinguish the structure from the parallel-fibrous fabrics of the secondary layers of rhynchonellids, terebratulids, spiriferids, pentamerids, and orthids. It is suggested that the blades of a crossed-bladed shell were each deposited by a single outer epithelial cell like the fibres comprising the secondary layers of rhynchonellid and terebratulid shells.

WILLIAMS (1968) has published a very comprehensive and authoritative account of the mode of deposition of the shells of living representatives of the Terebratulida and the Rhynchonellida. He has used the data thereby obtained to formulate pictures of the manner of shell deposition in extinct orders of the Articulata. In the Strophomenida, as currently constituted, Williams found a number of distinctive micro-structural patterns and on this basis he has argued for a reappraisal of some existing ordinal and super-familial groupings. In this paper the micro-structural fabrics of the shells of *Terrakea solida* (Productacea) and *Streptorhynchus pelicanensis* (Davidsoniacea) are described and the manner of growth of the shells is considered in the light of Williams's interpretations.

The micro-structural components of the shells of *Terrakea solida* (Etheridge and Dun) and *Streptorhynchus pelicanensis* Fletcher seem to be arranged identically to the components of pholidostrophid shells (Towe and Harper 1966). However, in other repects the shells of each of the first two species are quite dissimilar. *Terrakea solida* has a pseudo-punctate shell, whereas the shell of *S. pelicanensis* is pierced by pores indistinguishable from true punctae. The presence of the latter structures in shells of *Streptorhynchus* was first recognized by Thomas (1958) who pointed out the resemblance of the structures to punctae rather than to pseudopunctae. However, the shell of *S. pelicanensis* is built of components quite different from those of other punctate articulate brachiopod shells. Apart from perhaps necessitating re-examination of the systematic position of *Streptorhynchus pelicanensis* and its associates, the existence of punctae in shells possessing entirely different micro-structural patterns would lend support to contentions that punctae evolved independently in different stocks of articulate brachiopods.

Material and techniques. The specimen of *Terrakea solida* which was used for the present study is from the Permian Peawaddy Formation in the Bowen Basin, Queensland. It is from University of Queensland, Department of Geology locality L3094, which is a small quarry 27·5 miles from Springsure on the

road from Springsure to Tanderra via Wealwandangie. The co-ordinates of UQL3094 on the Spring-sure 1:250,000 map are 147° 59' E., 24° 27' S. The specimens of *Streptorhynchus pelicanensis* are from the '*Streptorhynchus pelicanensis* bed' in the Permian Blenheim Formation, also in the Bowen Basin. They are from UQL3131 which is in the north bank of Pelican Creek just downstream from the small gully which is 0·2 miles downstream from the junction of Corduroy and Pelican Creeks. Remaining fragments of all of the specimens are retained in the type collection of the Department of Geology, University of Queensland and the original specimens are designated by a number prefixed by F. Where sections of the shells were to be examined, the surface of the section was first polished to the fineness obtainable with a 1 μ powder, and then it was etched for a few seconds with a mixture of 1 per cent of nitric acid in ethyl alcohol. In the two-stage replication technique employed, the intermediate stage was nitrocellulose, and subsequent shadowing with a one to one mixture of gold and palladium was at angles of approximately 30°. In many instances the shell material was neither polished nor etched, replicas simply being taken directly from exfoliated surfaces of the shell. The figures in Plates 57 and 58 were obtained from exfoliated surfaces of shell whereas all those in Plates 59 and 60, except figs. 1 and 2 in Plate 59, were obtained from polished and etched sections.

The taxonomy of *Terrakeá solida* and *Streptorhynchus pelicanensis* is currently being reviewed by Dr. J. F. Dear of the Geological Survey of Queensland as part of a study of the Permian Stropho-menida of Queensland.

SHELL STRUCTURE

Pseudopunctae. The concept of a pseudopuncta is based on Kozlowski's (1929) figures and descriptions of structures in shells of *Strophonella podolica* (Siemiradzki), although Kozlowski did not actually call them pseudopunctae. The structures figured by Kozlow-ski consist of rods of calcite about which there are internally directed flexures of the sheets comprising the shell. Kozlowski noted that the structures of *Strophonella podolica* were quite distinct from the 'punctuations' (punctae, endopunctae) described by Car-penter (1853) in terebratulids. Kozlowski observed that the traces of the rods (taleolae of Williams 1956) in the shell will be exposed at the external surface of the shell simulat-ing a porosity (i.e. simulating punctae) if the outer parts of the shell are lost. Öpik (1932, 1934) seems to have been the earliest worker to apply the term pseudopunctae to the structures described by Kozlowski.

Streptorhynchus pelicanensis Fletcher 1952. No physically distinctive primary layer has been identified on the studied shells of *Streptorhynchus pelicanensis*. The entire shell seems to possess a uniform structural pattern consisting of well-defined sheets disposed parallel to the surfaces of the shell (Pl. 57, fig. 1; Pl. 58, fig. 3). The sheets are best observed by replicating exfoliated surfaces of shell without etching the surface. In Plate 57, fig. 1 and Plate 58, fig. 3, the section normal to the shell surface is visible. The sheets are clearly delineated. The surfaces of the sheets bear sets of parallel ridges and grooves (Pl. 57, figs. 3, 6), each of the grooves being confluent with one of the regular breaks across a sheet (Pl. 57, fig. 1; Pl. 58, fig. 3). Thus the sheets are composed of parallel tabular units which are oriented with their greatest dimensions parallel to the sheet (Pl. 57, figs. 1, 2; Pl. 58, fig. 3). Each of these units will be referred to as a blade and it is believed that blades may have been deposited in the same way as the secondary layer fibres of articulate brachiopods with a two-layered shell (see below). Grooves on the surface of a sheet mark inter-blade boundaries whereas the ridges on the surface of a heet are the parts of the blades comprising the sheet which interlocked with or infilled the inter-blade grooves in the base of the contiguous sheet above. In the upper left-hand corner of Plate 57, fig. 6 the ridges on the surface in the figure are confluent with

the inter-blade boundaries of the overlying sheet. Similar crossing sets of grooves and ridges are known in the shells of pholidostrophids (Towe and Harper 1966) and *Marginifera ornata* Waagen (Grant 1968) suggesting that these shells are built of micro-structural units similar to those of *S. pelicanensis*. Zigzag sutures (Pl. 57, fig. 6) often terminate a set of parallel blades of a sheet and they may or may not mark a change in orientation of the blades. The sheets of the shell of *S. pelicanensis* form a continuously overlapping succession (Pl. 57, fig. 2; text-fig. 1B) which results from the mode of growth of the shell (see below).

On the basis of thin sections Thomas (1958) described the structures of the shells of a number of species of *Streptorhynchus*. He pointed out that there is a concentration of small pores in the shell material comprising the costellae on the shell and that around each pore the components of the shell are deflected towards the shell's external surface. Thomas observed that most of the pores in the shells of his species of *Streptorhynchus* are filled with the matrix in which the shell is preserved. He did not detect structures analogous to the taleolae of pseudopunctae and he noted the resemblance between the pores in shells of *Streptorhynchus* and true punctae.

Around each pore of *Streptorhynchus pelicanensis* the sheets of the shell are deflected towards the external surface of the shell particularly where the pore is normal to the shell surface (Pl. 60, figs. 1, 2). The pores are sinuous and in some cases are parallel to the sheets (Pl. 57, fig. 4). Invariably the pores are either void or occupied by a mass of irregular grains (Pl. 57, fig. 4; Pl. 58, fig. 4; Pl. 60, fig. 2) quite unlike the taleolae of pseudopunctae (cf. Pl. 59, figs. 3, 4). Only in one of the pores examined was the pore partially filled with grains of calcite but these lack the homogeneity of a taleola (Pl. 60, fig. 1). The absence of taleolae from the pores of *Streptorhynchus pelicanensis* and the deflection of sheets adjacent to the pore in an external rather than an internal direction clearly dissociate the pores from pseudopunctae. On the other hand, as Thomas (1958) suggested, the pores are very similar to true punctae and seemingly they would have originated from invaginations of the outer epithelium in a manner similar to that envisaged for the punctae of terrebratulids (Williams 1956, p. 247). Thomas (1958) identified the same puncta-like structures in the species *Kiangsiella condoni* Thomas as he observed in *Streptorhynchus*.

Terrakea solida (Etheridge and Dun) 1909. A primary layer structurally distinct from a secondary layer has not been observed at the external surface of the shell of *Terrakea solida* although a number of replicas were prepared specifically to detect it. In all cases the external surface of the shell was made up of the same structural components as


EXPLANATION OF PLATE 57

Figs. 1–6. *Streptorhynchus pelicanensis* Fletcher. 1, UQF56050, three-dimensional aspects of the shell depicting sheets and blades, ×2,000. 2, UQF56050, transverse section of a number of sheets. The lateral boundaries of three sheets are visible (see text-fig. 1B), ×2,000. 3, UQF56050, view of the surfaces of two sheets of the shell showing the characteristic crossing sets of parallel ridges and grooves (see text, p. 311), ×1,000. 4, UQF56050, section of a puncta parallel to its length showing the sedimentary infilling of the puncta, ×1,000. 5, UQF56051, longitudinal fracture pattern of a blade, ×4,000. 6, UQF56050, three-dimensional picture of components of shell and view of a zigzag suture which transects several blades without displacement of the blades, ×1,000.
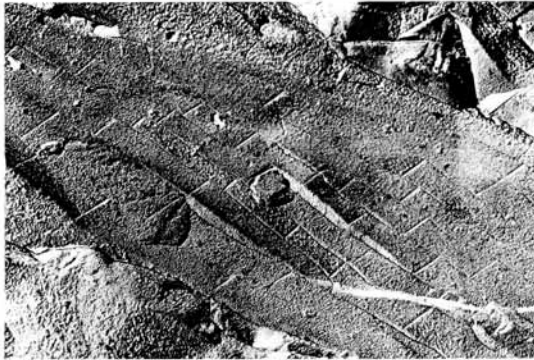
ARMSTRONG, Brachiopod shell structure

comprise the remainder of the shell. Shells of *Marinurnula mantuanensis* Campbell (1965) from the same locality as the specimen of *T. solida* have a well-preserved and readily distinguishable primary layer. Like that of *Streptorhynchus pelicanensis* the shell of *T. solida* is composed of sheets parallel to the surfaces of the shell (Pl. 59, fig. 6). Surfaces of the sheets display non-parallel sets of grooves and ridges (Pl. 58, figs. 1, 2) and it is inferred that the sheets of *T. solida* are also composed of tabular blades. As in *Streptorhynchus pelicanensis* zigzag sutures often terminate a set of parallel blades (Pl. 58, fig. 6). The sutures may or may not mark a change in orientation of the blades and the inter-blade boundaries on each side of the suture may or may not be slightly displaced (Pl. 57, fig. 6; Pl. 58, fig. 6). The blades of a sheet are disposed with their greatest dimensions parallel to the sheet.

In Plate 58, fig. 2 (text-fig. 1A) there are a number of sheets and several sets of blades. Surface *S* is the surface of a sheet (*A*) whose blades are separated by boundaries represented by the grooves (*a*). The ridges on surface *S* indicate the disposition of the blades comprising the sheets overlying sheet *A*. Ridges (*b*) and blade (*l*) indicate the existence of a set of blades in one sheet (*B*) overlying *A*, and ridges (*c*) indicate the blades of another sheet (*C*) which partially overlay *A* and partially overlay *B*. Ridges *e* and *f* on blade l seem to be extensions of ridges *e'* and *f'* (components of set *c*) on surface *S* thus suggesting that sheet *C* was deposited over sheet *B*. Sheet *C* overlapped sheet *B* along line *x–x*. This point of overlap would correspond to *x* in the transverse section in text-fig. 1B. Although the transverse section in text-fig. 1B is from a shell of *Streptorhynchus pelicanensis* the relationship between sheets *A*, *B*, and *C* in the section corresponds to the relationship inferred to have existed between sheets *A*, *B*, and *C* in Plate 58, fig. 2. The upper surface of sheet *A* in text-fig. 1B corresponds to surface *S* in Plate 58, fig. 2.

The surfaces of the blades of *Terrakea solida* and *Streptorhynchus pelicanensis* display transverse arcuate corrugations (Pl. 58, figs. 1, 5). In some instances there appear to be similarly developed corrugations in a line across several blades suggesting that the corrugations may represent increments of growth. On *T. solida* the increments vary from 0·0005 to 0·005 mm. (0·5–5 μ) across, and correspondingly their concentration ranges from about 2,000 to 200 per mm. Small and large increments are intermixed and an average concentration is of the order of 500 per mm. Where a blade is interrupted by a zigzag suture parallelism of the arcuate corrugations on a blade and the angular termination of the blade suggests that the zigzag sutures are produced by halts in the growth of the blades. Longitudinal fracturing of a blade yields surfaces with a strong fabric-oriented normal to the sheets (Pl. 57, fig. 5; Pl. 58, fig. 1). Possibly this texture of the fractured surface is related to the increments of growth inferred to have been added to each blade.

The sheets of the shell of *Terrakea solida* form conical deflections around taleolae in the shell. The taleolae are oblique and are inclined slightly forwards towards the internal surface of the shell (Pl. 59, figs. 1, 2). In a tangential section of the shell each taleola appears as a circular core of calcite, of the order of 5 μ in diameter, concentrically surrounded by sections of the conically arranged sheets around it (Pl. 59, figs. 3, 4). Apices of the cones of sheets are directed towards the internal surface of the shell where a pseudopuncta (taleola plus conical deflections) usually projects as a small spine (Pl. 59, figs. 1, 2, 3).

Discussion. Apart from their punctate and pseudopunctate aspects the shells of *Streptorhynchus pelicanensis* and *Terrakea solida* are built of identical micro-structural units. Their shells consist of a continuum of overlapping and superimposed sheets disposed parallel to the surfaces of the shell. Each sheet is composed of blades with rectangular cross-sectional outlines. The greatest dimensions of a blade are parallel to the sheet of which it is a part. Sheets consist of sets of parallel blades and the terminal junctions of a set are marked by zigzag sutures. The blades of adjacent coplanar or contiguous overlying sheets are usually not parallel. Text-fig. 1c depicts the arrangement of the blades in two superimposed sheets. The cross-sectional appearance of the sheets corresponds to text-fig. 1b and the appearance of the surfaces of the sheets corresponds to Plate 57, fig. 3 or to Plate 58, figs. 1 and 2. The grooves and ridges on the surfaces of the sheets are purposely accentuated in the diagram. Grooves *a* and *b* are the expressions on the surface of sheet 1 of the boundaries between the blades comprising the sheet, and grooves *e*, *f*, and *g* are the boundaries between the blades of sheet 2. Ridges *f'* and *g'* on the surface of sheet 1 are the parts of the blades of sheet 1 which infilled the inter-blade grooves on the base of sheet 2 corresponding to grooves *f* and *g*. Similarly, ridges *h'*, *i'*, and *j'* indicate the presence of a third sheet above sheet 2 in which the blades are 'crossed' with respect to the blades in sheet 2.

Towe and Harper (1966) referred to the above structural arrangement as crossed-lamellar, a term used to describe a type of shell structure characteristic of certain Mollusca. In a crossed-lamellar molluscan shell there are three orders of lamellae. A first-order lamella comprises second-order lamellae oriented transversely with respect to its length, and each second-order lamella consists of smaller third-order lamellae oriented parallel to the first-order lamella (MacClintock 1967, text-fig. 19). The sheets of shells of *Streptorhynchus pelicanensis* and *Terrakea solida* are parallel whereas it is the blades comprising adjacent sheets which have non-parallel orientations (text-fig. 1c). Clearly the term crossed-lamellar should be reserved for shells composed strictly of a hierarchy of sets of parallel lamellae, and a new term seems to be needed to denote the arrangement of the components of shells like *Streptorhynchus pelicanensis*. It is proposed to name this arrangement crossed-bladded in order to reflect the non-parallel orientations of the blades in successive sheets. Other shells probably possessing a crossed-bladed structure are *Marginifera ornata* Waagen (Grant 1968) pholidostrophids (Towe and Harper 1966), and some strophomenids (Williams 1968).

EXPLANATION OF PLATE 58

Figs. 1, 2. *Terrakea solida* (Etheridge and Dun). UQF56053, views of the surfaces of a number of the sheets which comprise the shell; illustrating the crossing sets of grooves and ridges characteristic of the surfaces of the sheets of a crossed-bladed shell. Fig. 2 forms the basis for text-fig. 1a; ×1,000 and ×1,500 respectively.

Figs. 3–5. *Streptorhynchus pelicanensis* Fletcher. 3, UQF56050, three dimensional picture of the sheets and blades which comprise the shell, ×1,000. 4, UQF56050, section normal to the length of a puncta showing aspects of the sheets and blades of the shell and the sedimentary infilling of the puncta, ×1,000. 5, UQF56051, view of the surfaces of several blades showing the transverse arcuate corrugations on the surface of each blade, ×1,000.

Fig. 6. *Terrakea solida* (Etheridge and Dun). UQF56053, view of the surfaces of two sheets showing the boundaries between blades and the zigzag sutures which terminate a set of parallel blades. Note the small displacement of the boundaries of the blades across one of the zigzag sutures, ×2,500.
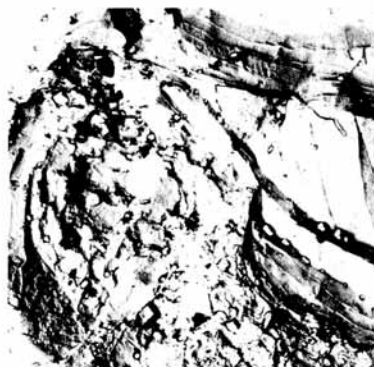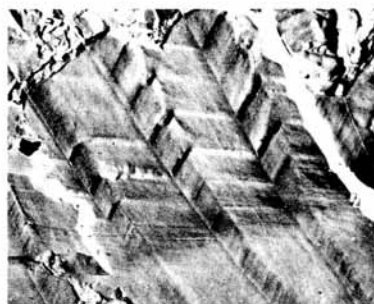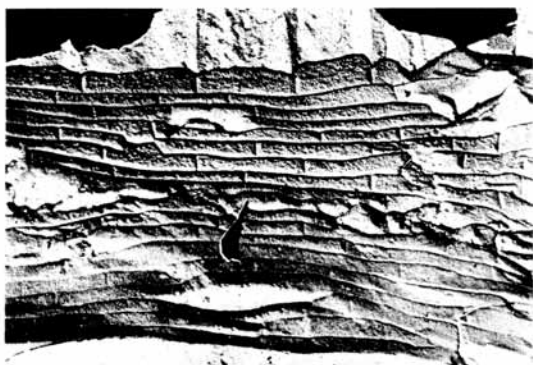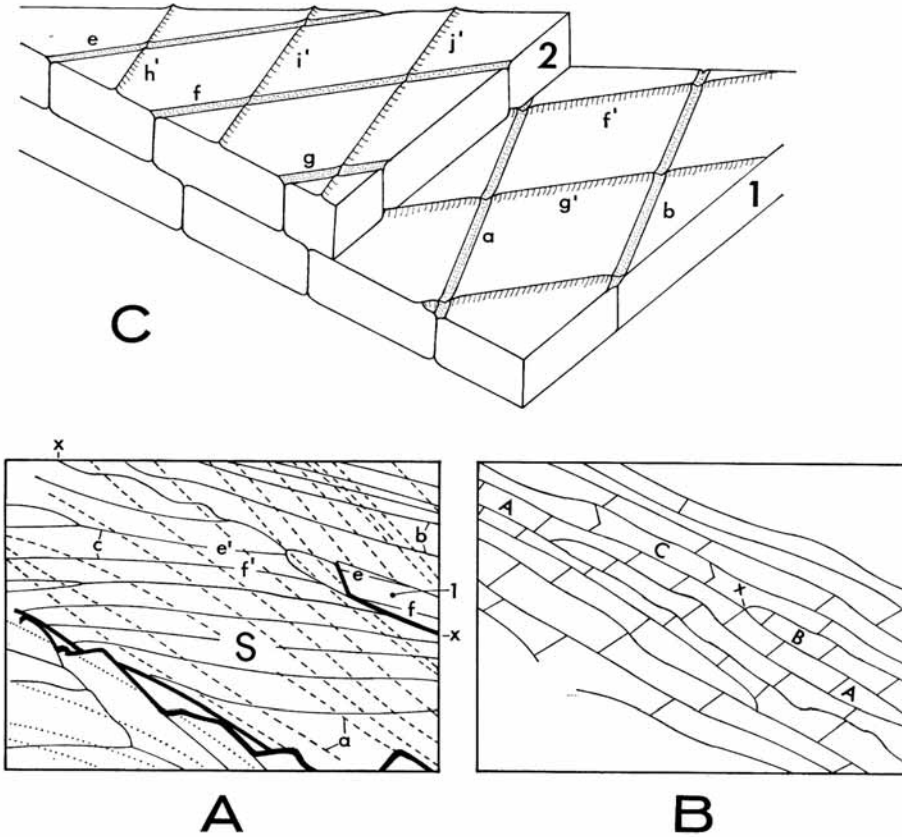
ARMSTRONG, Brachiopod shell structure

TEXT-FIG. 1A. Sketch based on Plate 58, fig. 2. Grooves on the surfaces of the sheets in the figure are represented by discontinuous lines, and ridges are represented by continuous lines. For a description see text, p. 313. 1B. Sketch based on Plate 57, fig. 2. For a description of the figure see text, p. 313. 1C. Stylized diagram depicting the nature and arrangement of tabular blades which comprise two sheets (1 and 2) of a crossed-bladed shell. The symbols on the diagram are discussed in the text (p. 314).

Unfortunately it has not been possible to obtain mosaics from the shells of *Streptorhynchus pelicanensis* or *Terrakea solida*. However, the pattern of the mosaic of *Juresania* sp. (Williams 1968, pl. 21, fig. 3) suggests that it possesses a crossed-bladed shell and the mode of growth of crossed-bladed shells can be discussed by compounding data from this species with information about the species described herein.

SHELL GROWTH

Williams (1968) believed that 'the key to productine shell deposition is provided by the micro-structure of the external hollow spines that communicated with canals that penetrated to the shell interior'. His studies suggested that a spine consists of bands

(sheets herein) undivided by any consistent pattern of grooves. Williams measured the periodicity of the bands of strophomenid shells and speculated that banding registered daily deposition. Internal mosaics of *Juresania* sp. (Williams 1968, pl. 21, figs. 2, 3) show the ends of the sets of parallel blades here inferred to have comprised the shell. Directions of growth of the blades can be determined from the dispositions of the ends of the blades on the mosaic (Williams 1968, text-fig. 25). Because of the irregularity of the subdivisions of his bands, Williams did not consider the linear grooves crossing the mosaic to be coincident with intercellular boundaries. He suggested that such grooves represented proteinous extensions from the secretory surface of a cell (Williams 1968, text-fig. 25).

The shells of *Streptorhynchus pelicanensis* and *Terrakea solida* are composed of sheets like the banded strophomenid shells described by Williams but in this case the sheets are quite regularly subdivided. In a transverse section the apparent widths of the blades comprising a sheet are a function of the dispositions of the blades of the sheet relative to the section. Thus in the one section some sheets can appear less closely subdivided than others. This relationship may explain the appearance of the transverse section of a valve of *Pholidostrophia* cf. *geniculata* Imbrie illustrated by Williams (1968, pl. 21, fig. 1). A sheet will appear undivided in a section if the blades of the sheet are essentially parallel to the section. Often a group of several sheets which are closely subdivided will be followed by sheets apparently undivided. Because of the irregular subdivisions of the sheets he examined, Williams inferred that each unit of a sheet was not deposited by a single outer epithelial cell. However, in *Streptorhynchus pelicanensis* and *Terrakea solida* the boundaries between blades are quite regular and the non-appearance of subdivisions of a sheet in a section is explicable in terms of the variable orientations of blades comprising different sheets. The regularity and completeness of the blades of *S. pelicanensis* and *T. solida* suggests that protein was formerly located along inter-blade boundaries and that each blade may have been deposited by a single outer epithelial cell. The same relationships may apply to the crossed-bladed strophomenids described by Williams.

The direction of growth of the outer epithelial cells can be inferred from the orientations of the blades on the internal mosaic of the shell (Williams 1968, text-fig. 25). It would seem that cells were organized into differently oriented rows, each of which deposited a set of parallel blades. The ends of sets of blades are visible in Williams (1968) plate 21, fig. 3. Growth enabled a row of cells to deposit a sheet and as each sheet grew it concealed and overlapped the sheets of blades deposited by younger rows of cells. Periodically, portions of the outer epithelium became reorganized into different groups of cells and then new sets of perhaps differently oriented blades were laid down.

EXPLANATION OF PLATE 59

Figs. 1–6. *Terrakea solida* (Etheridge and Dun). UQF56053. 1, Thin section of the shell showing pseudopunctae in the shell projecting as small spines on the internal surface of the shell, ×20. 2, An enlargement by 4 of one of the pseudopunctae in fig. 1. 3, Section normal to the length of a pseudopuncta showing taleola and sections of the adjacent deflected sheets of the shell, ×4,000. 4, An enlargement approximately by 2·25 of the taleola in fig. 3. 5, Section of the spinose projection of a pseudopuncta at the internal surface of the shell. The boundary between the spine and the enclosing matrix runs down the left-hand side of the figure, ×1,000. 6, Exfoliated surface of the shell showing the sheet-like character of the components of the shell, ×1,000.
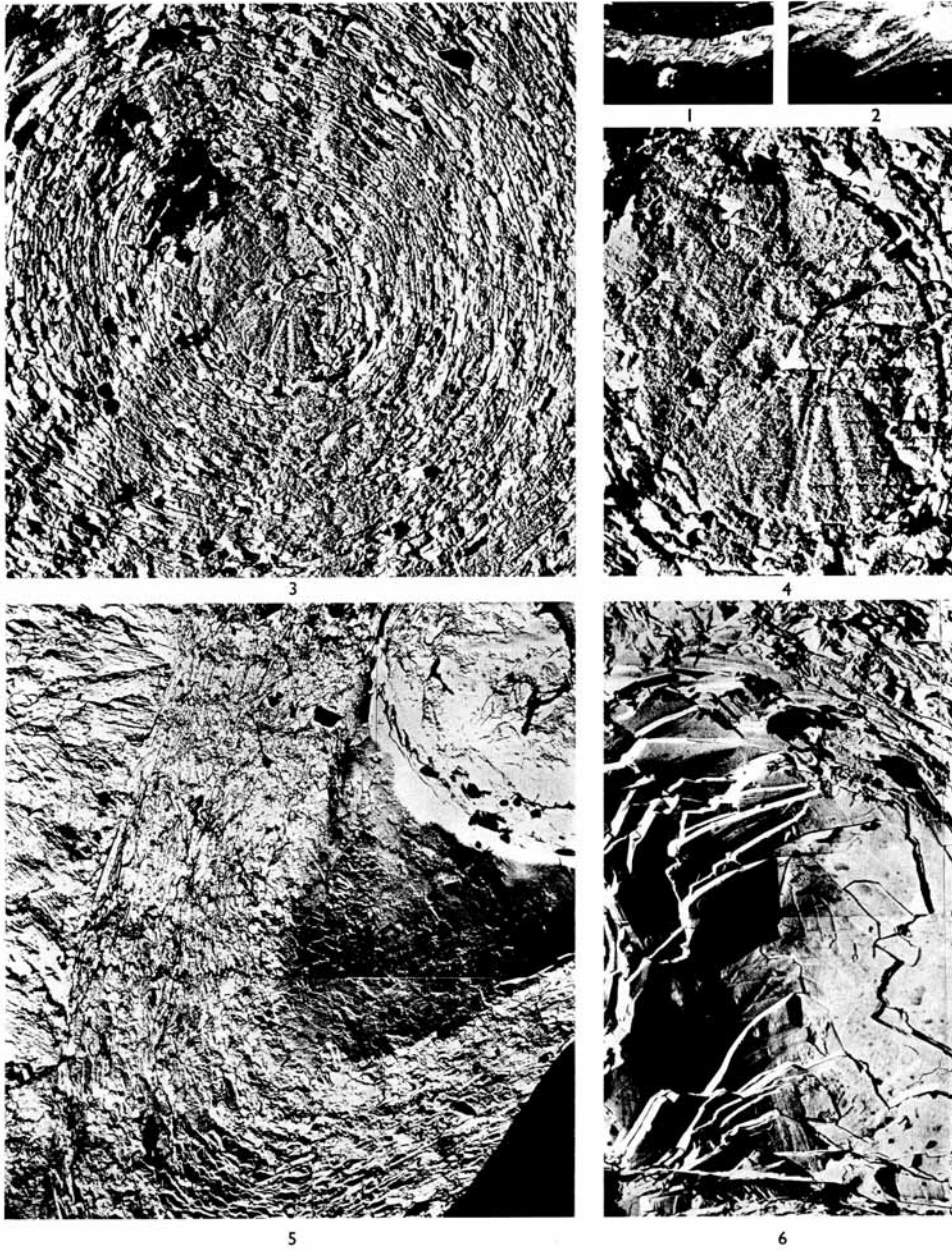
ARMSTRONG, Brachiopod shell structure

One factor which may have precipitated a cellular reorganization could have been the stress created in the epithelium by divergent and convergent growth directions of different rows of cells. The positions of reorganization of the cells at the end of one set of parallel blades and at the beginning of the next are probably marked by the zigzag sutures which periodically cross the blades (Pl. 57, fig. 6; Pl. 58, fig. 6). Continuity of the inter-blade boundaries across a zigzag discontinuity suggests that the epithelial cells retained their relative positions and that the zigzag suture is simply a halt in growth. Non-correspondence of the inter-blade boundaries across a zigzag discontinuity may indicate that a cellular reorganization took place, displacing the row of cells to a new position, thereby enabling deposition of a new set of blades. The new blades may or may not be parallel to the former set deposited by the same row of epithelial cells. Such cellular reorganizations probably involved small-scale separations of the epithelium from the blades as envisaged by Williams (1968, p. 46).

If the above inferences regarding the deposition of the blades of *Streptorhynchus pelicanensis* and *Terrakea solida* are correct then the blades of a crossed-bladed shell were deposited in much the same way as the secondary layer fibres of the shells of tere-bratulids, rhynchonellids, spiriferids, pentamerids, and orthids. In the latter type of secondary layer the fibres are essentially parallel and are inclined forward towards the internal surface of the shell. This type of arrangement may be referred to as parallel-fibrous in order to distinguish it from the crossed-bladed type of fabric discussed above. If *Streptorhynchus pelicanensis* is a prototype for the crossed-bladed fabric, then the concept of a parallel-fibrous fabric can satisfactorily be founded on Williams's description of the secondary layer of *Macandrevia cranium* (Muller) (Williams 1968, pl. 6, figs. 1–4).

In a parallel-fibrous fabric each fibre is a unit to which calcite was continuously added throughout the life of the shell (Williams 1968, text-fig. 5). On the other hand a particular blade of the crossed-bladed structure is usually not continuous for any great distance suggesting that each outer epithelial cell did not deposit a single continuous blade throughout shell growth. Growth of the crossed-bladed shell would seem to have been somewhat more irregular than the growth of a parallel-fibrous fabric.

Representatives of the Strophomenacea, Davidsoniacea, Productidina, and Choneti-dina seem to possess crossed-bladed shells (Towe and Harper 1966; Grant 1968; Williams 1968) that contain pseudopunctae. Triplesiidine shells may also be crossed-bladed (Williams 1968, pl. 23, figs. 4–6), but in this case the shell, like some davidsoni-acean shells, is impunctate. *Streptorhynchus* (currently considered a davidsoniacean) possesses a punctate crossed-bladed shell and this condition may also be found to characterize *Kiangsiella* (Thomas 1958). Thus in shells with a crossed-bladed fabric there are forms which are impunctate, pseudopunctate, and punctate. Similarly, in shells with a parallel-fibrous secondary layer there are impunctate forms (e.g. rhynchonellids, pentamerids), punctate forms (e.g. terebratulids), and pseudopunctate forms (plect-ambonitaceans, Williams 1968). The plectambonitacean primary layer (Williams 1968, p. 37) comprises units (laminae of Williams, 1968) similar to those of a crossed-bladed shell and Williams (1968, p. 53) homologised this layer with the entire crossed-bladed shell. Secretion of the parallel-fibrous secondary layer is apparently suppressed in some plectambonitaceans and Williams suggests that these forms were ancestral to stropho-menid shells consisting entirely of a crossed-bladed fabric.

Summary. Recognition that regularly shaped and systematically disposed blades comprise the shells of *Streptorhynchus pelicanensis* and *Terrakea solida* suggests that the (non-plectambonitacean) strophomenid shell was deposited in a manner comparable with that which led to the deposition of the parallel fibrous secondary layer of a terebratulid shell. To confirm Williams's (1968) proposition that the entire (non-plectambonitacean) strophomenid shell is homologous with the plectambonitacean primary layer, it will be necessary to try to establish the phylogenies of the different types of articulate brachiopod primary layers and to trace the evolutionary development of the (non-plectambonitacean) strophomenid shell from the similar but structurally distinct plectambonitacean primary layer. Currently, data relevant to the solution of these problems are unavailable. Nevertheless, in the light of the above inferences about the secretion of a crossed-bladed shell, it is clear that the homology suggested by Williams implies quite different modes of deposition for the primary layers of plectambonitaceans and terebratulids. Whereas in extant terebratulids intercellular boundaries are not recognizable in the primary layer, it seems probable that the components of the plectambonitacean primary layer were each deposited by a single outer epithelial cell.

The presence of punctae in the shell of *Streptorhynchus pelicanensis* raises the question of the systematic position of the genus and its allies. *Streptorhynchus* is the only strophomenid certainly possessing a punctate shell, although work by Thomas (1958) suggests that *Kiangsiella*, another Carboniferous and Permian genus, may also be punctate. The fabric of the shell of *Streptorhynchus* appears to be identical with that of (non-plectambonitacean) strophomenid shells so that *Streptorhynchus* clearly has affinities with this group. To firmly establish and to clarify this position, however, it is essential to also study the fabrics of the shells of other davidsoniaceans now grouped with *Streptorhynchus*. Moreover, the relationships between the genera will be fully understood only when the impunctate or pseudopunctate natures of other davidsoniacean shells are confirmed. If indeed both *Streptorhynchus* and *Kiangsiella* are characterized by a punctate shell then they comprise a distinct stock of punctate davidsoniaceans. Progenitors of a punctate shell are most probably impunctate ones and currently, as propounded by Thomas (1958, text-fig. 7), the likely ancestor for *Streptorhynchus* seems to be the crossed-bladed apparently impunctate Devonian, Carboniferous, and Permian genus *Schuchertella*.

NOMENCLATURE

The following terms may prove useful in descriptions of the fabrics of articulate brachiopod shells. Some of the terms apply to structures already well documented and others refer to structures discussed herein. For the two most commonly occurring calcareous layers of articulate brachiopod shells Williams (1968, p. 2 n.) advocates adoption of the names primary and secondary. This usage will avoid ambiguities which might arise from the application of such variably utilized terms as prismatic and lamellar.

EXPLANATION OF PLATE 60

Figs. 1, 2. *Streptorhynchus pelicanensis* Fletcher. UQF56053, sections of punctae parallel to their length. In both figures the external surface is in the direction of the upper left-hand corner of the figure. Adjacent to each puncta the sheets comprising the shell are deflected towards the shell's external surface, both × 750.
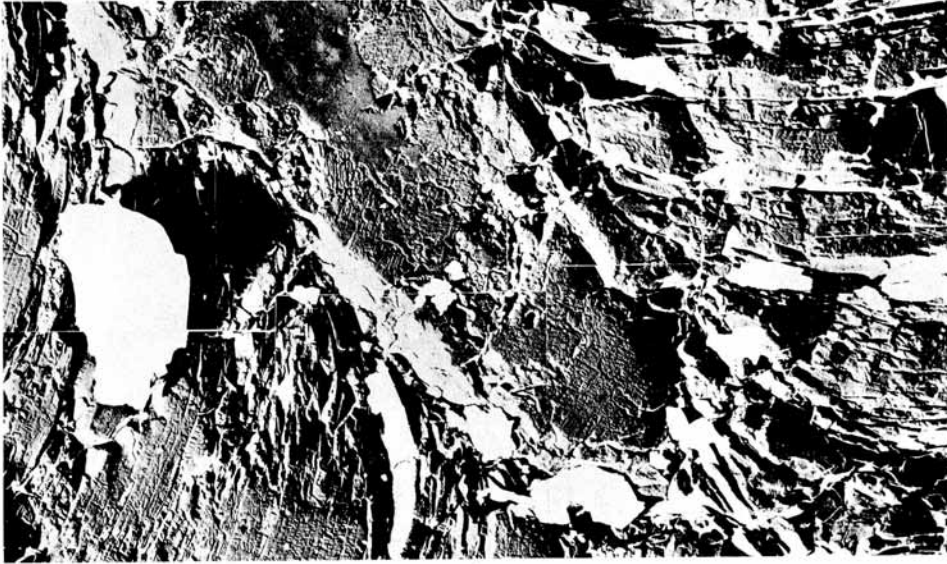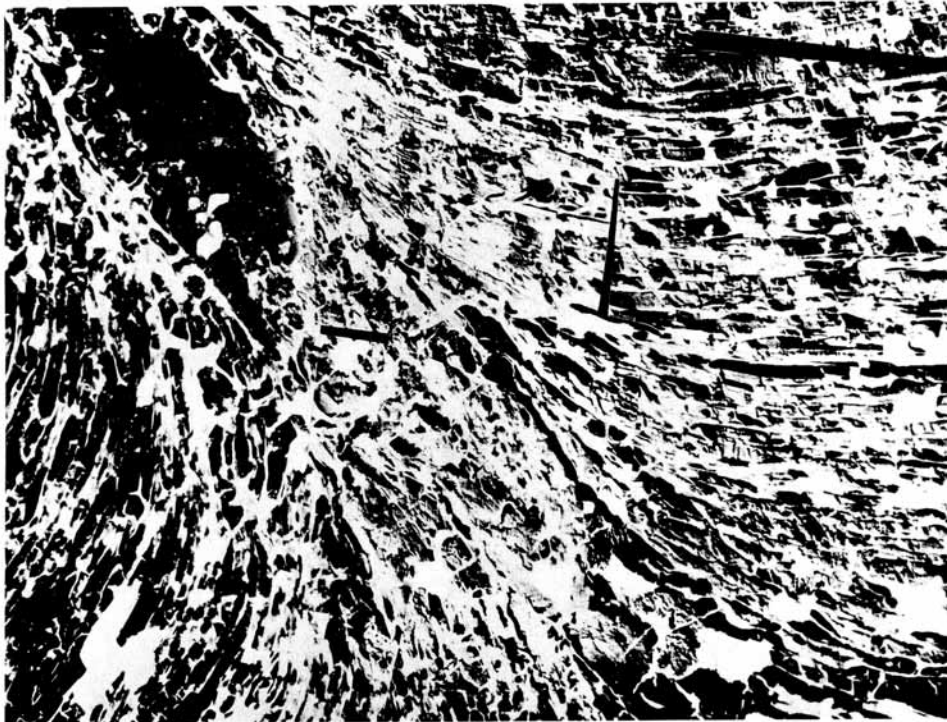
ARMSTRONG, Brachiopod shell structure

The terms discussed here can be employed to describe either one of the layers of the shell or the entire shell.

Fibre. A Fibre is a component of the secondary layer of an articulate brachiopod shell having the characteristic cross-sectional shape of the secondary layer components of *Macandrevia cranium* Muller (Williams 1968, pl. 6, fig. 2). Williams (1968) has concluded that each fibre was deposited by a single outer epithelial cell and was ensheathed by protein laid down by this and adjoining cells. Fibres have a characteristic internal mosaic and their deposition took place relatively continuously throughout growth of the shell (Williams 1968, text-figs. 4–6). Fibres are characteristic of the secondary layers of rhynchonellids, terebratulids, spiriferids, pentamerids, and orthids. Williams (1968) employed the term fibre in this sense.

Parallel-fibrous fabric. This is the name proposed for articulate brachiopod secondary shell layers that consist of fibres. The fibres are parallel and are inclined forwards at a low angle from their loci of origin on the inner surface of the primary layer towards the internal surface of the shell. The fibres of successive rows are alternately placed.

Blade. It is suggested (p. 311) that the tabular components of articulate brachiopod shells be termed blades. A blade has a rectangular cross-section (Pl. 57, figs. 1, 2), is of the order of two, three, or four times wider than high, and is many times longer than wide (Pl. 58, fig. 2). It seems important to recognize the distinction between components with these characteristics and components with the features of a fibre as defined above.

Crossed-bladed fabric. The strophomenid (non-plectambonitacean) shell consists of blades arranged into parallel superimposed overlapping sheets in which the greatest dimensions of a blade are parallel to the sheet (Pl. 57, figs. 1, 2; Pl. 58, fig. 3). In a sheet the blades form sets in each of which all of the blades are essentially parallel. Blades in successive sheets are neither parallel nor alternate like the fibres of a parallel-fibrous fabric. Rather, a set of parallel blades in a sheet bears a crossed (non-parallel) relationship to the blades in adjacent co-planar sheets and to the blades in contiguous underlying or overlying sheets (text-fig. 1c).

Sheet. Crossed-bladed fabrics comprise plate-like or lamellar units parallel to the surfaces of the shell. However, these terms are already much used in the description of brachiopod morphology and to preclude multiple applications of names the work sheet has been employed for these micro-structural lamellar units.

Lamina. According to Williams (1968, p. 38) the plectambonitacean primary layer consists of tabular units 'arranged neatly one above the other (pl. 19, fig. 4)'. Williams proposed to call such units 'laminae' and he pointed out that laminae do not lie in alternate rows like fibres. Williams also noted that the tabular blade-like components of the shells of other (non-plectambonitacean) strophomenids are like the laminae of the plectambonitacean primary layer, and subsequently he employed laminae to describe the former. If the crossed-bladed fabric described above is characteristic of non-plect-ambonitacean strophomenids then there may be a number of differences between the fabric of the plectambonitacean primary layer and the structure of other strophomenid shells. Blades of a crossed-bladed shell are not stacked one above the other but are

arranged into clearly delineated sheets. The blades of a sheet do not bear any systematic relationship to the blades of underlying and overlying sheets, but are only linked in a regular manner with other blades of the sheet to which they belong. Thus, apparently, the fabric of the plectambonitacean primary layer is not closely similar to that of other strophomenid shells although the basic components involved in each case seem to be similar. Perhaps lamina should be restricted to the description of components of the plectambonitacean primary layer and a separate term (i.e. blade) introduced for components of other strophomenid shells. Indeed, if a lamina is morphologically inseparable from a blade, as defined herein, it may be preferable to employ blade in both instances. Thus parallel-bladed could be invoked to denote the fabric of the plectambonitacean primary layer, and usage of parallel-bladed and crossed-bladed rather than parallel-laminar and crossed-laminar may help to avoid confusion with the molluscan shell structural term crossed-lamellar.

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JOHN ARMSTRONG
Department of Geology and Mineralogy
University of Queensland
St. Lucia, Brisbane
Queensland
Australia