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EVOLUTION OF THE SHELL STRUCTURE OF ARTICULATE BRACHIOPODS

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With 24 collotype plates, and 27 text-figures

CONTENTS

ABSTRACT. Electron microscopic studies of the shell fabric of articulate brachiopods show that the triple division of the shell into periostracum, and primary and secondary calcareous layers, is characteristic of most members of the subphylum. The relationship between these layers and the outer epithelium of the mantle controlling their secretion can be studied in living Rhynchonellida and Terebratulida. Each fibre of the secondary layer is coated with protein and secreted by an outer epithelial cell which is moulded to the characteristic shape and stacking of the fibre. The morphology of the exposed parts of fibres can, therefore, be used to identify modifications of the epithelium, like those arising from the spread of muscle bases, and to determine the nature of the outer epithelium in extinct groups. The attitudes of fibres can also be used as vectors to study the growth dynamics of the shell and its internal skeletal features.

The triple-layered shell with orthodoxly stacked fibres was the basic skeletal type of ancestral Rhynchonellida and Terebratulida, and of the Spiriferida, Pentamerida, and Orthida. Modifications include the development of a tertiary calcareous layer in the Koninckinacea (through inhibition of the secretion of protein sheets and the coalescence of fibres across intercellular boundaries to form a coarsely prismatic shell) and the suppression of the secondary calcareous layer in the Thecideidina. The most profound changes affected the Strophomenida. Among the Plectambonitacea, the secondary calcareous layer was made up of orthodoxly stacked fibres, but the primary calcareous layer consisted of lath-like laminae, which were the sole constituents of the shell of all other Strophomenida (including the Triplesiidina). Regular banding of the strophomenide shell, resulting from laminar deposition, with a periodicity of about $0 \cdot 3 \mu$, is comparable with that sporadically found in the primary and secondary calcareous layers of living articulates, and is believed to register diurnal variation in secretion.

INTRODUCTION

BRACHIOPODS constitute one of the most intriguing and challenging phyla that can be studied by the palaeontologist. Their recorded history extends back to the early Cambrian, since when they have emerged as two distinct groups, the Inarticulata and the Articulata, with an unrivalled record in marine facies throughout time and space. A wealth of information can therefore be obtained about the course of brachiopod evolution over the last 600 million years especially among the articulates, because their skeletal remains include variously derived outgrowths concerned with the articulation of the shell and the support of muscle and lophophore systems, while the internal surfaces of the valves commonly bear impressions of soft parts even on an ultramicroscopic scale. Unfortunately the opportunities afforded by interrelating such data have not been fully exploited. All too often palaeontologists forget that fossils were once organic systems and that the science requires them to be concerned with the dynamics as well as the relics of past life. The neglect is most obvious in discussions of morphological variation. All changes in form are expressions of differences in growth, and since the mechanics of growth are actually registered in the fabric of the articulate shell, accounts of skeletal features which ignore the processes that led to their development are at least incomplete and may be gravely misleading.

The study of shell structure, then, is a prerequisite to an understanding of changes in skeletal morphology that have taken place during the evolution of articulate brachiopods. The most profitable techniques used in such study are encouragingly simple. They involve the preparation of replicas of the internal surfaces as well as sections of shells (Williams *in* Williams *et al.* 1965, p. H253), and their examination under the light microscope supplemented by the electron microscope. Indeed, greater difficulties arise in choosing appropriate material. The surfaces of most fossil specimens, even those with well-preserved shell fabric, are covered by thin skins of calcite crystallites which obscure the original microscopic texture. However, when the skin is a superficial accretion and not a replacement of the outer layers of the shell, it can usually be removed in ultrasonically vibrated detergent fluids. In this manner surface patterns of Lower Palaeozoic species can be made available for scrutiny and comparison with those of Recent shells. Diagenesis and lithification can also affect the shell fabric and might lead to the acceptance of observed patterns, brought about by these processes in extinct groups, as reflecting the state of the living shell. Fortunately, terebratulides and rhynchonellides are not only represented in modern seas but have a long history extending back to the Devonian and Ordovician respectively. It has, therefore, been possible to use fossils belonging to these two orders as standards in estimating the degree of alteration affecting specimens of extinct orders that have been recovered from the same horizon and locality. Such checks have been used for every order found in Palaeozoic and early Mesozoic rocks, and the results are so consistent for all stocks investigated that important deviations are not expected to come to light during more detailed systematic investigations.

The use of living material as a standard in the interpretation of the shell structure of extinct stocks has determined the sequence of discussion in the following account.

Proceeding from the rhynchonellides, which provide the simplest model of shell deposition, there follows a comparative study of the fabric characteristic of Recent and past terebratulides. The spiriferides, which became extinct in the Lower Jurassic, are considered next; while the pentamerides are discussed before the orthides because, although they died out much earlier (Devonian compared with Permian), they show, on balance, closer affinities with the first three orders. Despite their alleged late survival into the Jurassic, the strophomenides are the last ordinal group to receive attention, an acknowledgement of the uniqueness of their typical shell structure. Finally, some reference is made to problematic groups, and to the bearing that the collation of observations on shell structure has on brachiopod evolution.

RHYNCHONELLIDA

*Growth of mantle and deposition of shell in living rhynchonellides*

The growth of the mantle and the concomitant deposition of the triple-layered shell of articulate brachiopods has already been described (Williams 1953, 1966) but is worth a brief review in relationship to *Hemithiris psittacea* (Gmelin) and *Notosaria nigricans* (Sowerby) to give current ideas their full perspective.

The principal generative zone responsible for the enlargement of the mantle lining both valves is located at the closure of a groove separating the inner and outer lobes of the mantle edge. Both lobes act like conveyor belts in that new cells added to them at their junction with the groove closure ultimately become part of the inner and outer epithelium (text-fig. 1). In effect the groove and lobes are maintained as morphological features of the mantle because the creation of cells in the circumferential meristomatic region balances the incorporation of those previously proliferated within the main epithelial spreads posterior to the lobes. Thus as outer epithelial cells make way for new ones arising behind them in the groove, they 'move' anteriorly along the inner face of the outer lobe and begin to secrete the periostracum as a continuous, exclusively protein cover (Jope 1967) to the outer plasma membranes.

When the cells reach the tip of the outer lobe they start secreting a primary layer[1] of calcite crystallites between **the periostra**cum and the underlying plasma membranes. The first stages in calcite nucleation have not yet been observed but they can be deduced from the topography of the external shell surface of *Notosaria* (Pl. 2, figs. 1, 2). This surface is divided by a series of long radiating grooves into strips, each up to 12 μ wide but tending to encroach on one another here and there. Each strip is further divided by grooves that are normally convex anteriorly and about 2 μ apart. Both sets of grooves

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[1] Many palaeontologists continue to use purely descriptive terms for the primary and secondary layers of the articulate brachiopod shell. Following Thomson (1927, pp. 97, 103), outer or lamellar layer and inner, prismatic, fibrous or laminar layer have been used by some students to denote the primary and secondary layers respectively. However, real or apparent differences in the texture of the calcite have led to so arbitrary a use of such terms as to render them meaningless for comparative purposes. The use of 'primary' and 'secondary', on the other hand, enables homologues to be drawn between different groups, because the primary layer (in contrast to secondary deposits) is that which *comprises the calcareous shell edge* and is normally underlain by the outer lobe of the mantle. Within t?is context, terms describing the microscopic nature of the calcite making up the shell can be employed unambiguously, although since the fabric may be the same throughout the shell, 'outer' and 'inner' are also inappropriate.

accommodate the lists and bars of differentially thickened periostracum (Williams 1956, p. 244); and those that radiate, together with every fourth or fifth arcuate one, probably correspond to the lateral and transverse boundaries respectively of rows of cuboidal epithelium. The calcareous surface between a pair of arcuate grooves is usually asymmetrical in profile, culminating anteriorly in a series of rhombohedral peaks about $0.3\,\mu$ apart and gently sloping posteriorly towards the culmination immediately behind
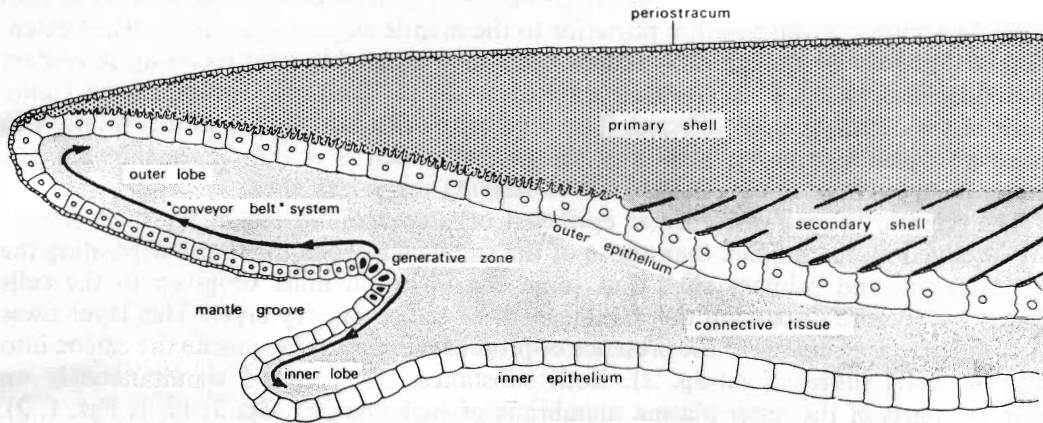
TEXT-FIG. 1. Stylized longitudinal section of the edge of a valve of *Notosaria*, showing the origin of outer epithelium and its relationship to primary and secondary shell

(Pl. 2, fig. 3). The 'contoured' effect, which is so prevalent within these culminations and may even be traced continuously throughout several of them, represents a periodicity in the deposition of primary shell. Such layering indicates that the peaks constitute the first-formed rhombohedral seeds of calcite which are secreted between the plasma membranes and the periostracum, and that initially the seeds tend to be concentrated in zones separated by inwardly directed bars of periostracum and isolated from one another by membranous projections (microvilli) attached to the periostracum. As deposition continues, the crystallites grow and overlap one another across intercellular boundaries (text-fig. 2); but, although the plasma membranes become separated from the periostracum by an increasing wedge of calcite, microvilli which may be aligned along rhombohedral angles (Pl. 2, fig. 4) continue to permeate the primary layer to give its inner surface a highly porous appearance (Pl. 2, figs. 5, 6). Microvillous strands or sporadically exuded trails may even be pinched off from the plasma membranes by growing crystallites (Pl. 3, fig. 1), which would account for traces of protein reported in the primary layer, although, in general, that layer may be regarded as the inorganic constituent of the articulate shell. The growth of the rhynchonellide primary layer also indicates that the microvilli are really temporary extensions of the plasma membranes that may come into being or be eliminated by local changes in the rate of calcite deposition. Yet at any given moment, so many microvilli are present (up to 25 per μ^2) that the cells are anchored relative to one another on the inner surface of the primary shell.

Continuous addition of new cells to the tip of the outer lobes, and secretion of calcite by all epithelial cells underlying the primary layer, cause the extension of that layer anteriorly and its thickening posteriorly. However, the deposition of the primary layer

does not proceed indefinitely, because at a certain distance from the shell edge the epithelial cells undergo a profound physiological change and start secreting the secondary layer. The slight increase in thickness of the primary layer towards the shell margins of adult *Hemithiris* suggests that the change-over in cell activity may become delayed as shells grow older, as it certainly is in embayments corresponding to the sites of setal follicles and therefore to the crests of ribs in radially ornamented species (Williams and Wright 1963, p. 19). Nevertheless it can be held as a generalization that as rows of cells come to occupy a given position posterior to the mantle edge, due to the forward extension of that edge by the addition of new cells, they invariably start secreting secondary shell instead of primary: in *Hemithiris*, for example, the 20th row, located about 1 mm. from the shell edge, is so affected. The regularity with which this transformation in secretory habit occurs explains why the primary shell is a thin layer showing less dramatic changes in thickness than the underlying secondary shell.

The secretory functions of outer epithelial cells controlling secondary shell growth are so much more complex than those of the same cells when they were depositing the periostracum and primary shell that some consideration must be given to the cells themselves before discussing the development of the secondary layer. This layer owes its distinctive appearance to the presence of protein sheaths that segregate the calcite into discrete units (fibres) (text-fig. 2). Both substances are secreted simultaneously on different parts of the outer plasma membrane of each cell (text-fig. 3; Pl. 1, figs. 1, 2). Protein is exuded by the anterior part of the plasma membrane and is temporarily attached to an arcuate zone of the membrane by closely spaced terminal pivots of tonofibrils (desmosomes) which are densely distributed in this section of a cell

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EXPLANATION OF PLATE 1

Electron micrographs of sections, stained with uranyl acetate and lead citrate, of specimens of *Terebratulina caput-serpentis* (Linné), originally fixed in formalin and prepared for sectioning by decalcifying, post-osmicating, and embedding in Araldite. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2μ.

Fig. 1. Longitudinal section of outer epithelial cells, showing anterior and posterior sites on the outer plasma membrane for the secretion of the protein sheet and terminal face of a fibre respectively.

Fig. 2. Transverse section of outer epithelial cell taken near the anterior cell boundary, showing the disposition of protein sheets relative to the trail of one fibre and the overlapping lateral areas of adjacent fibres belonging to the row immediately behind.

Fig. 3. Enlargement of the anterior part of the plasma membrane of an outer epithelial cell, showing the exuded protein sheet, desmosomes, and tonofibrils.

Fig. 4. Longitudinal section of the base of a caecum, showing its relationship with outer epithelium and exuded protein sheets.

Fig. 5. Transverse section of a caecum within the secondary shell.

EXPLANATION OF PLATE 2

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2μ.

Figs. 1–3. Topography of the external surface near the edge of a valve of *Notosaria nigricans* (Sowerby), with the first calcite seeds of the primary layer shown as isolated 'peaks' in Fig. 3.

Fig. 4. Detail of the internal surface of the primary layer of *Hemithiris psittacea* (Gmelin), showing a larger rhombohedral crystallite and casts of microvilli.

Figs. 5, 6. Junction between the primary and secondary layers as seen on the internal surface of a valve of *Hemithiris psittacea* (Gmelin).

(Pl. 1, fig. 3). The exuded protein separates posteriorly from the arcuate attachment zone as a curved sheet with only rare lacunae. Beneath this sheet, calcite is secreted by the posterior zone of the plasma membrane. This two-fold association of protein sheet overlying a calcite fibre is maintained by every epithelial cell, and since the cells are roughly rhombohedral in outline and arranged in alternating rows relative to the shell edge, a regular skeletal pattern results. Thus the terminal face of each fibre is contained
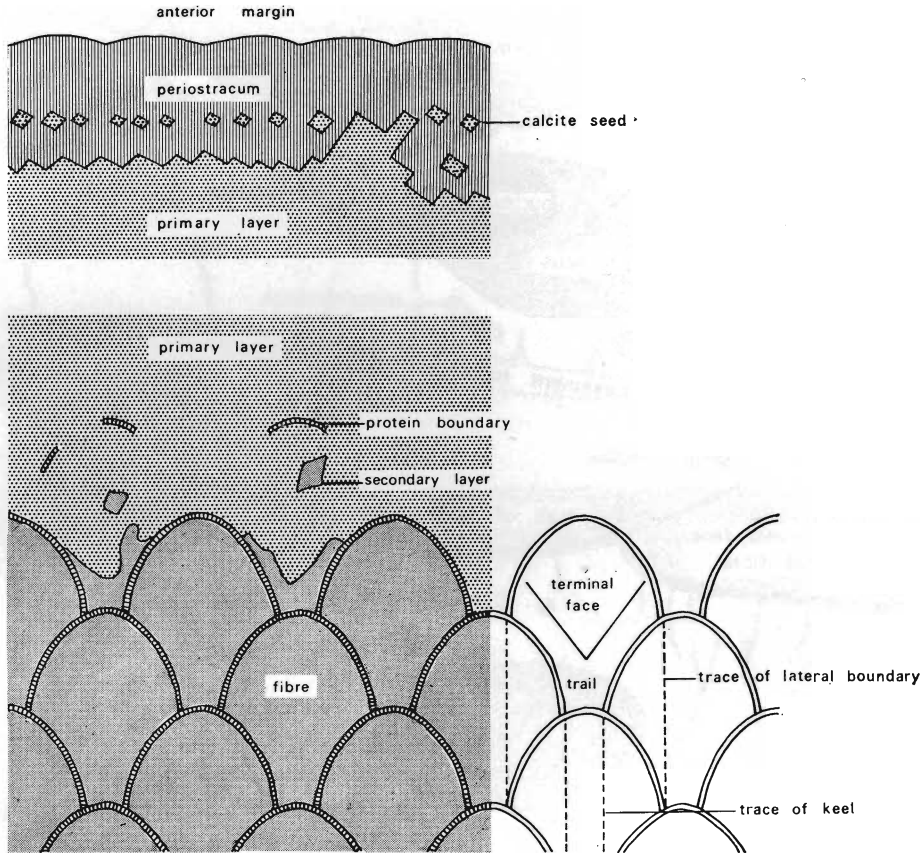
TEXT-FIG. 2. Plan of the internal shell surface at the edge of a valve of *Notosaria*, showing the relationship between the three layers of the shell

in an inwardly convex patch of cell membrane situated behind a semicircle of the same membrane which exudes the outer protein cover of the fibre (text-fig. 4). The inner protein covers which complete the continuous organic sheath of the fibre are secreted by adjacent anterior arcs of the three cells immediately behind. Consequently the inner surface of the secondary shell characteristically shows the terminal faces of constituent fibres as alternating rows of convexly lobate pads, each semicircular in outline anteriorly but tapering posteriorly towards the re-entrant angle subtended between the curved sides of two flanking fibres belonging to the overlapping row behind (Pl. 4, figs. 1, 3, 5). This pattern is referred to as the secondary shell mosaic. It is important in that it

represents a protein-calcite cast of the outer epithelium in the manner illustrated in text-figs. 3 and 4. It can therefore be used to interpret the nature of the outer epithelium in fossil shells, and since it is the sole guide to shell growth in extinct stocks, it seems
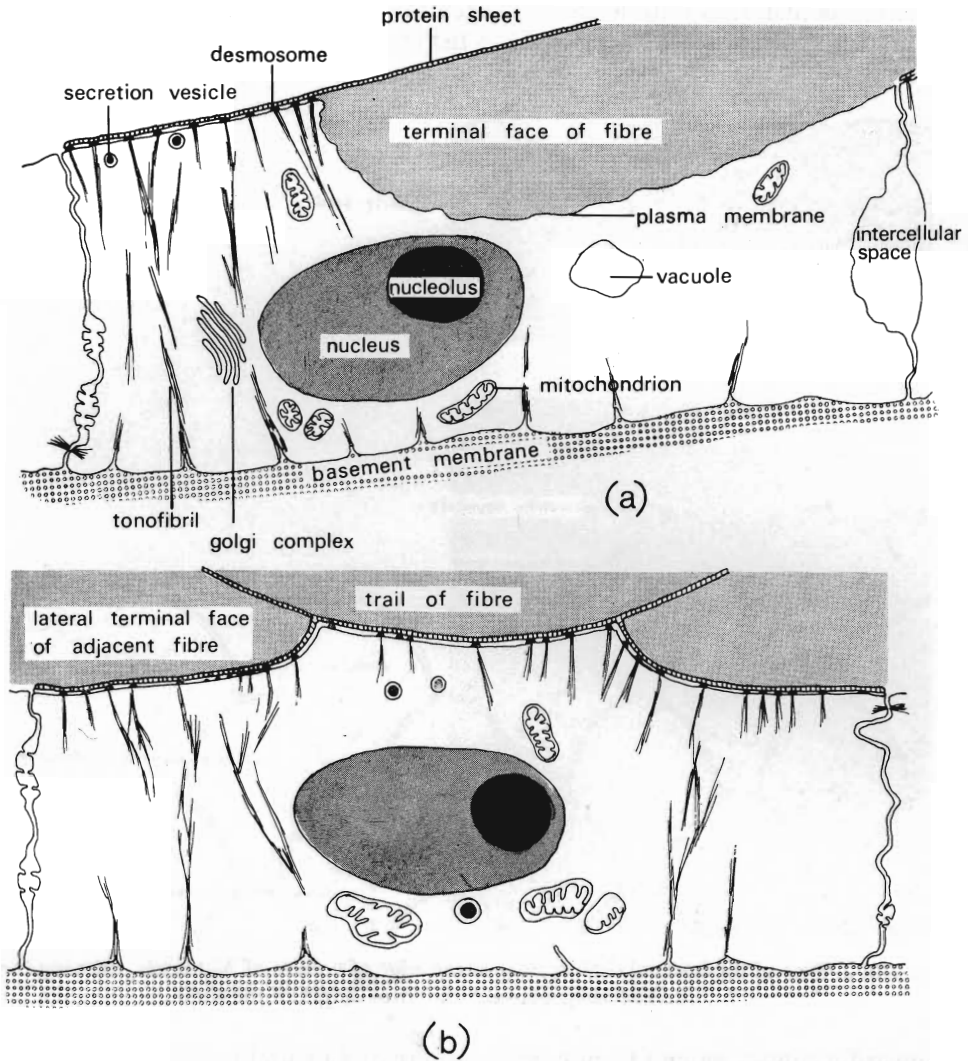
TEXT-FIG. 3. Stylized longitudinal (a) and transverse (b) sections of an outer epithelial cell of *Terebratulina* secreting a secondary fibre and its protein sheath

appropriate, henceforth, to describe the origin and nature of the secondary layer in terms of the mosaic.

The first stages in the development of the mosaic can be seen in any well-preserved shell. Usually, the earliest indication that a cell is changing to secondary processes of secretion is the laying down of secondary calcite in the re-entrant angle between two

fibres deposited by immediately older cells (Pl. 2, figs. 5, 6). The secondary calcite is initially, at least, in crystallographic continuity with that of the primary layer but is visually distinguishable as an evenly distributed plaster spreading out over the more
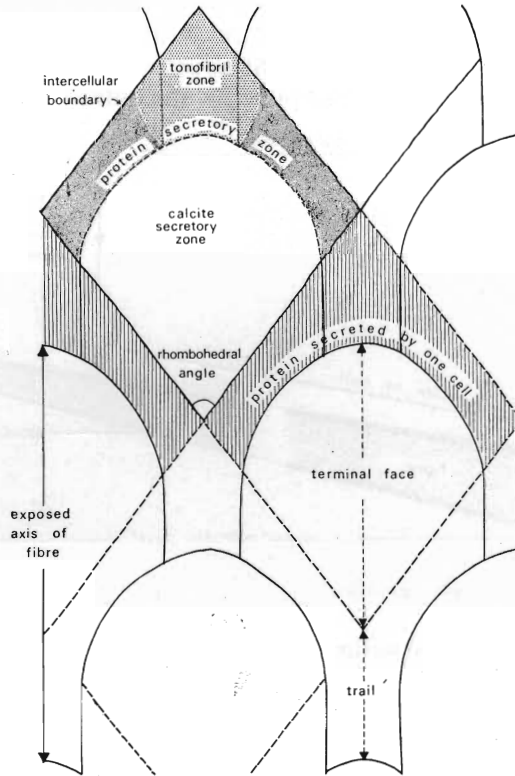
TEXT-FIG. 4. Plan of the secondary shell mosaic on the floor of a valve of *Terebratulina*, showing the relationship between exposed fibres and outer epithelial cells

porous primary layer. The smoother texture of secondary calcite is due to a sudden reduction in the number of microvillous extensions from the secreting membrane. Other isolated deposits of secondary calcite may appear anywhere within the limits imposed by a cell and soon become continuous with one another. But coalescence is rarely completed before a curved strip of protein is exuded by the anterior part of a cell and then extended posteriorly to unite with the protein boundaries of adjacent fibres in the row behind. In this manner the base of a **fibre rem**ains in phy**sical** continuity with the primary layer, yet simultaneously acquires the beginnings of a protein sheath that thereafter maintains the fibre in isolation from all others.

Differential growth of the secondary shell which gives rise to every detail of the shell interior and its calcareous attachments is facilitated by the mode of stacking of the fibres. Normally fibres within their protein sheaths remain segregated from one another throughout life and yet interlock in such a way as to achieve the best possible fit without impeding localized variation in growth. The arrangement is best understood in terms of

fibre shape. In medial longitudinal section, fibres appear as blades which gradually become wider towards the inner surface of the secondary layer, because cells concerned with their secretion increase in surface area as they grow older (text-fig. 5). The fibres are initially inclined outwards at about 10° to the general plane of the primary layer due to the restriction of calcite secretion to the posterior areas of cell surfaces, but they become re-orientated when forming internal structures like septa, or accommodating evaginations of the outer epithelium like punctae. In contrast to this simple longitudinal
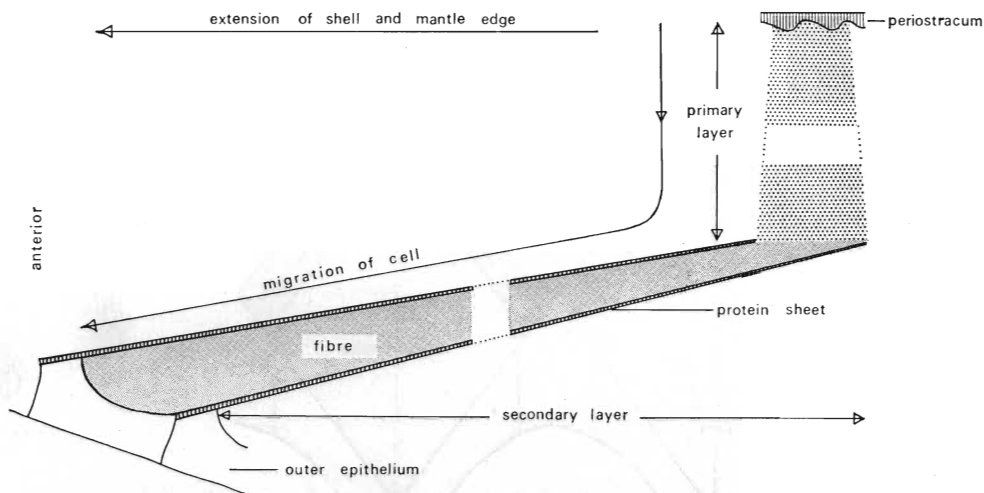
TEXT-FIG. 5. Stylized longitudinal section of part of a valve and mantle of *Notosaria*, showing migration of an outer epithelial cell during its secretion of the three shell layers

profile, cross-sections of a typical fibre show that it is really bounded by an inner surface, commonly with a medial keel that is flatly to roundly concave outwards, and an outer one made up of two lateral areas joined by a medial saddle, all also concave outwardly (text-fig. 6; Pl. 3, figs. 1, 2). This profile corresponds to the topography of the mosaic. The inner surface with its keel represents the terminal face of the fibre and its exposed posterior trail respectively, while the outer lateral areas rest on the two contiguous halves of fibres in the immediately younger row, and the saddle accommodates the keel belonging to the next younger fibre.

Despite the striking difference between the longitudinal and cross-sections of fibres,

the microstructure of a shell is almost invariably difficult to decipher because, apart from complications due to a general increase in fibre size inwardly, zones of fibres in longitudinal, oblique, and transverse sections may succeed one another laterally and vertically with bewildering rapidity (Pl. 3, fig. 3). Such successions, which indicate changes in direction of fibre growth, are found in sections of the valve floor as well as in elaborate internal structures, because mature fibres tend to grow anteriorly away from the primary layer in a spiral arc. The general effect is well represented by a discernible
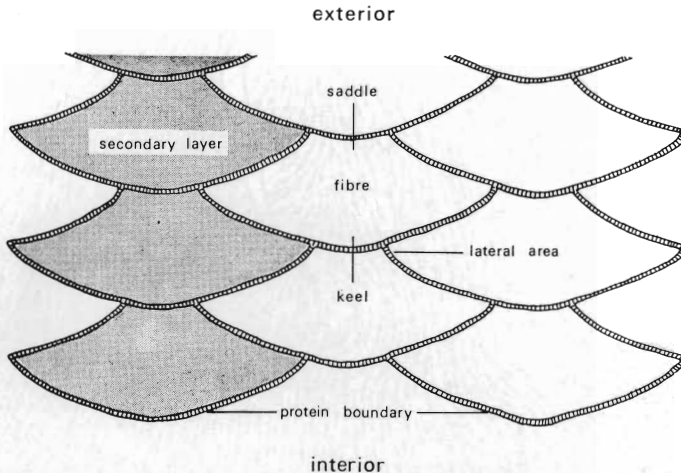
TEXT-FIG. 6. Stylized transverse section of the secondary shell of *Notosaria*, showing the stacking of fibres

lineation in the mosaic which can be shown graphically by plotting the long axes of the exposed parts of fibres as growth vectors. [The long axis of the exposed part of a fibre may be defined by a straight line between the posterior boundary of the trail and the most anterior point of the terminal face.] Growth maps constructed for a few species (text-figs. 7–11) show that even in costate shells with valve floors undulating in well-developed radial crests and troughs, an extension of fibres normal to the commissure is only characteristic of a narrow peripheral zone and, more rarely, the median sectors where the development of septa and ridges normally complicate patterns. In the lateral areas away from the margins, the overlapping terminal faces of fibres comprising the mosaic rapidly become re-orientated to lie more or less parallel or oblique to the commissure. Since these fibres originate marginally and grow by overlapping one another, the various attitudes of successively older ones, relative to a line from the edge to the umbo of a valve, may be taken as a cumulative estimate of the re-alignment a mature fibre will have undergone up to the moment of death. Such individual vectors of growth typically plot out as spiral arcs directed clockwise in the right half of the valve and anti-clockwise in the left half. Localized modifications of this pattern can arise, especially in adult shells. The most striking of these are microscopic whorls and tight loops rotated clockwise or anti-clockwise in either half of the valve, which respectively indicate that fibres may complete a spiral growth or even reverse direction to become S-shaped (text-fig. 10). Preliminary examination shows that although these rotations do not form any

significant topographic feature, many, like those located on the valve floor between the dental plates and posterior boundaries of the ventral muscle field, are simply overlapping adjustments to differing directions and rates of growth affecting adjacent zones of the

0·5 mm.
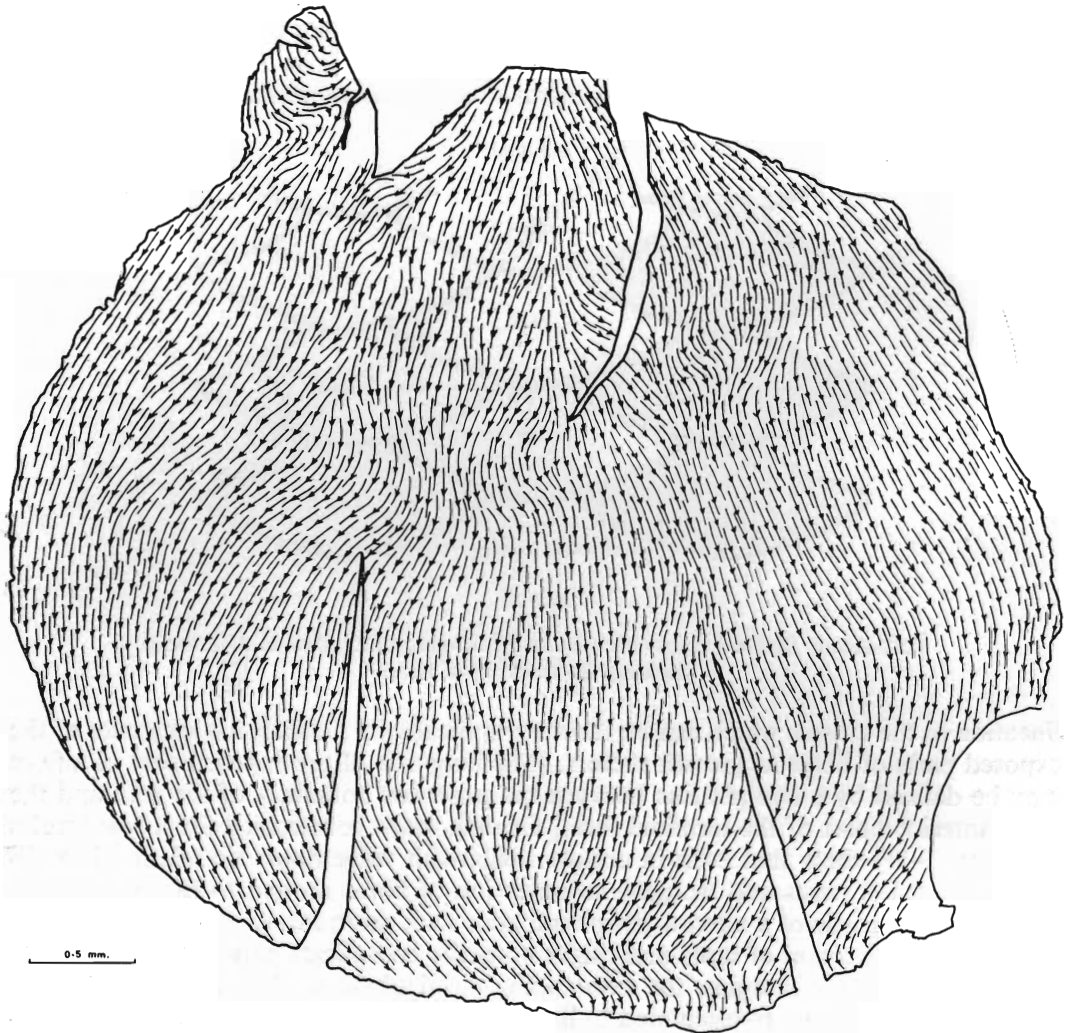
TEXT-FIG. 7. Growth map of the mosaic of the brachial valve of *Notosaria nigricans* (Sowerby)

EXPLANATION OF PLATE 4

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2 μ.

Fig. 1. Mosaic just within the junction of the primary and secondary layers on the internal surface of a valve of *Hemithiris psittacea* (Gmelin).

Figs. 2, 4, 6. Modified mosaic within the dorsal adductor scar of *Hemithiris psittacea* (Gmelin).

Figs. 3, 5. Mature mosaic on the internal surface of a valve of *Notosaria nigricans* (Sowerby).

internal shell surface. Others, however, may underlie specialized patches of the shell mantle. The terminal faces of fibres forming the centres of some whorls in *Notosaria* are asymmetrically bilobed (compare Pl. 7, fig. 5) suggesting cell division in the covering
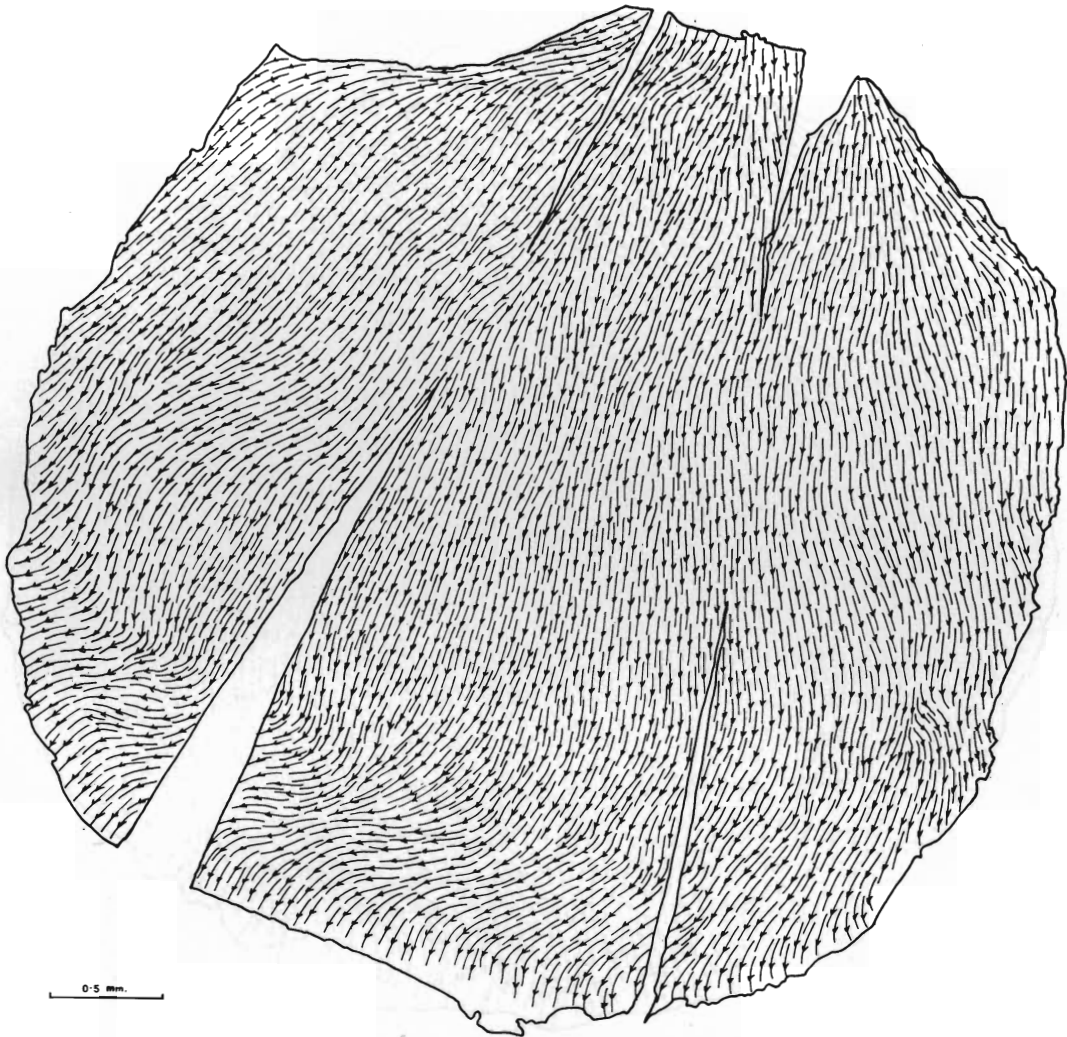
TEXT-FIG. 8. Growth map of the mosaic of the pedicle valve of *Notosaria nigricans* (Sowerby)

outer epithelium, while those in *Hemithiris* may be rhomb-shaped and pitted and are likely to have accommodated tonofibrils.

The detailed morphology of the mosaic and its correlation with the ultra-microscopic structure of the outer epithelium are still being studied, but a few observations have already proved helpful in interpreting the fabric of fossil brachiopods. The characteristic shape of the exposed part of a mature fibre (which may be up to 40μ long and 25μ wide in *Notosaria*) is spatulate, with the smooth terminal face normally defined posteriorly by a pair of straight lines representing breaks in the contour of the fibre

and meeting at an angle of about 74° (Pl. 4, figs. 3, 5). In effect, as the fibre grows, that part of the plasma membrane responsible for its secretion is increasingly adapted to the accretion of a calcite rhomb, which is well seen when the terminal face is slightly damaged
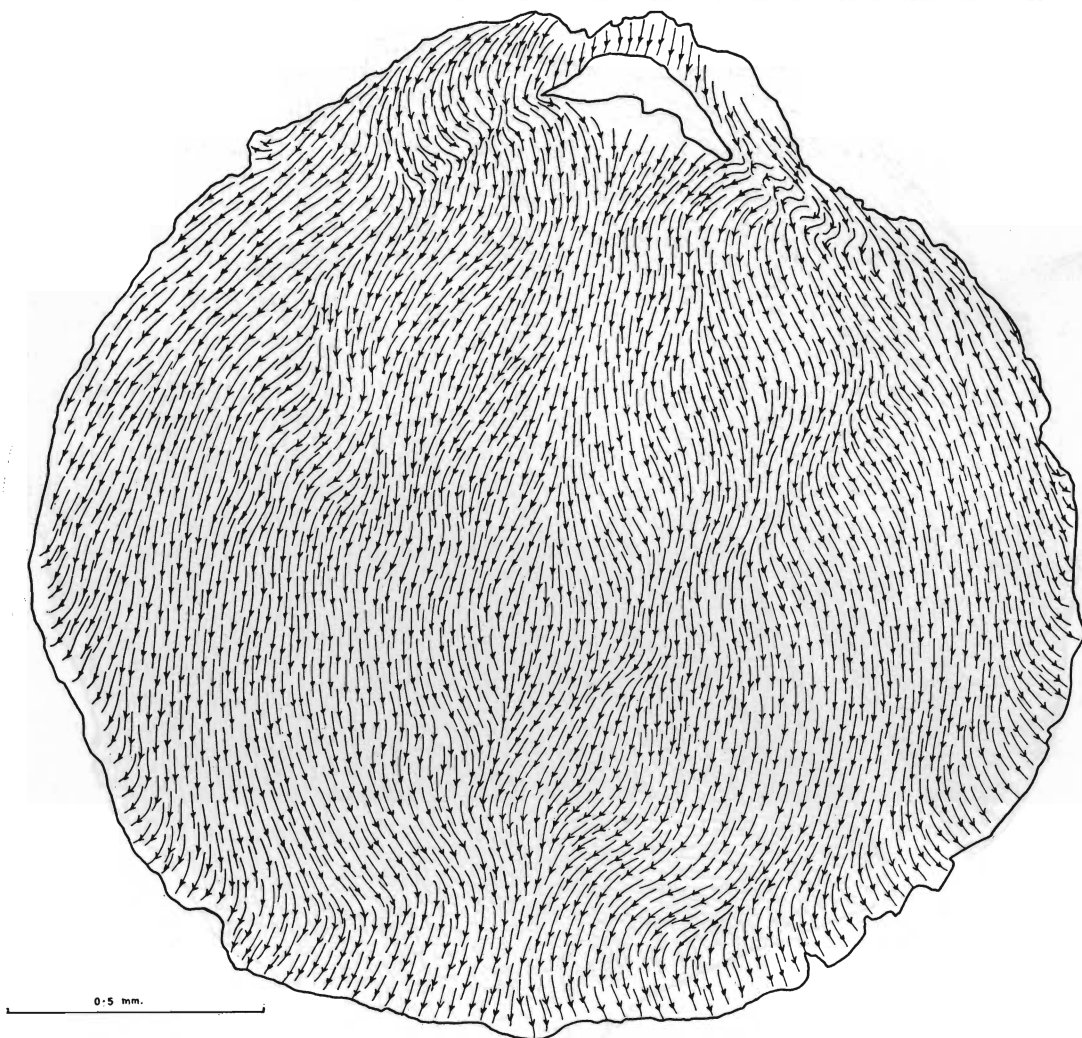
TEXT-FIG. 9. Growth map of the mosaic of the brachial valve of *Terebratella inconspicua* (Sowerby)

and shows details of cleavage. Indeed, the transformation of cuboidal epithelium of the outer mantle lobe into mature 'rhombohedral' epithelium disposed in alternating rows probably reflects the degree to which cells become distorted by accommodating the growing terminal faces of fibres (text-fig. 4). In adjacent fibres, the rhombs are aligned to within a few degrees of one another, but this parallelism is, of course, affected by any growth modification in the mosaic pattern. The trail behind the terminal face, which in life is being covered by a protein sheet secreted by three adjacent cells, repre-sents the depositional path of the terminal face. As such it may exhibit a fine banding

with a periodicity of about $0.12\,\mu$ in *Hemithiris*, which may be the daily amount of deposition by the plasma membrane, since thresholds to secretory activity are likely to

0.5 mm.
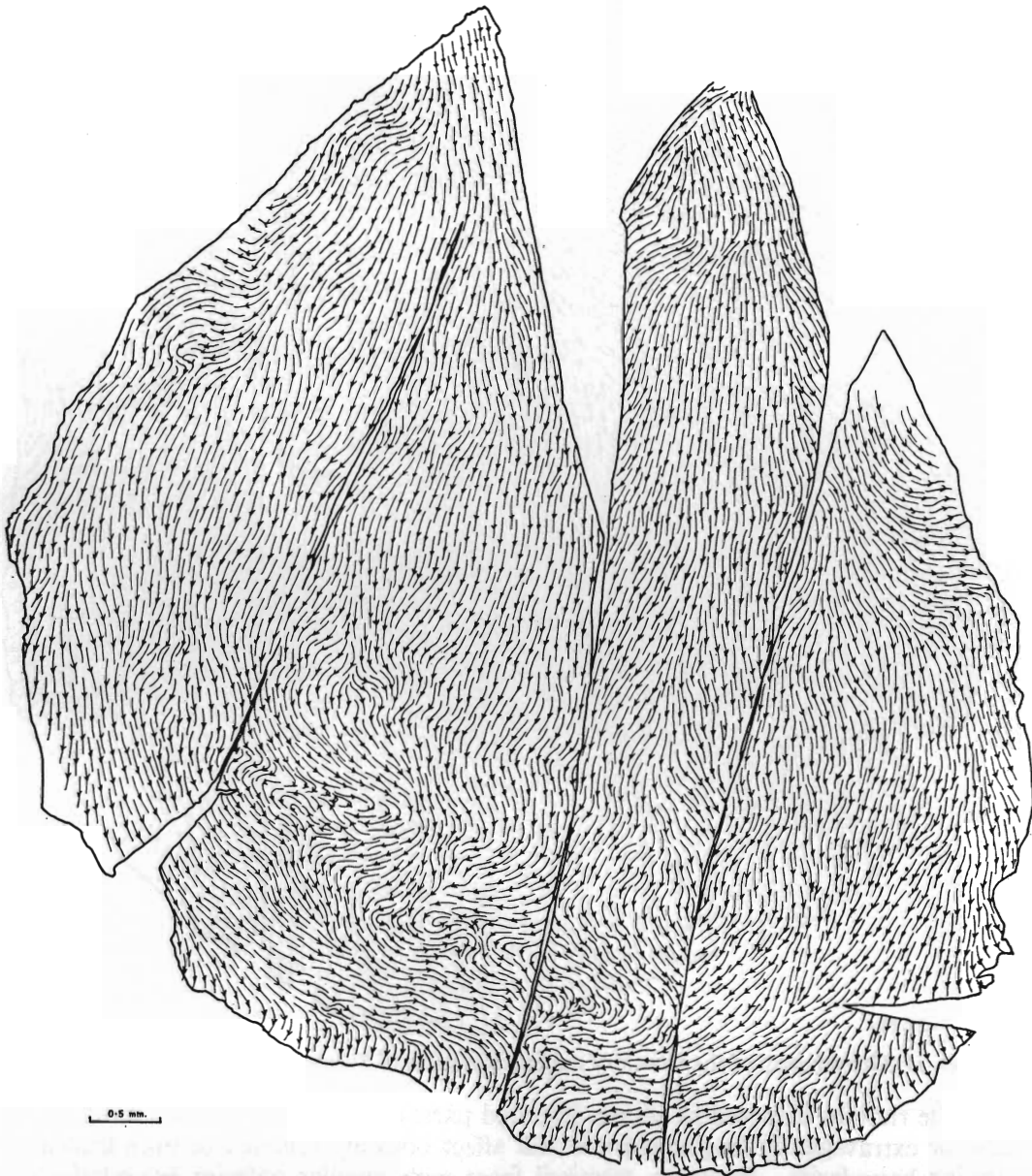
TEXT-FIG. 10. Growth map of the mosaic of the pedicle valve of *Terebratella inconspicua* (Sowerby)

include such diurnally controlled factors as temperature (compare Pl. 5, fig. 3). The terminal face itself is generally free of ultra-microscopic pits indicative of microvillous extensions of the plasma membrane, and one is led to conclude that this smoothness reveals the extent to which a mature fibre is really a growing crystal.

One of the most distinctive aspects of the terminal face is the contrast between its posterior and anterior boundaries. The anterior boundary, which is determined by that part of the cell responsible for the exudation of the outer protein cover to a fibre, is normally curved and unrelated to a rhombohedral angle, although in detail it is made up
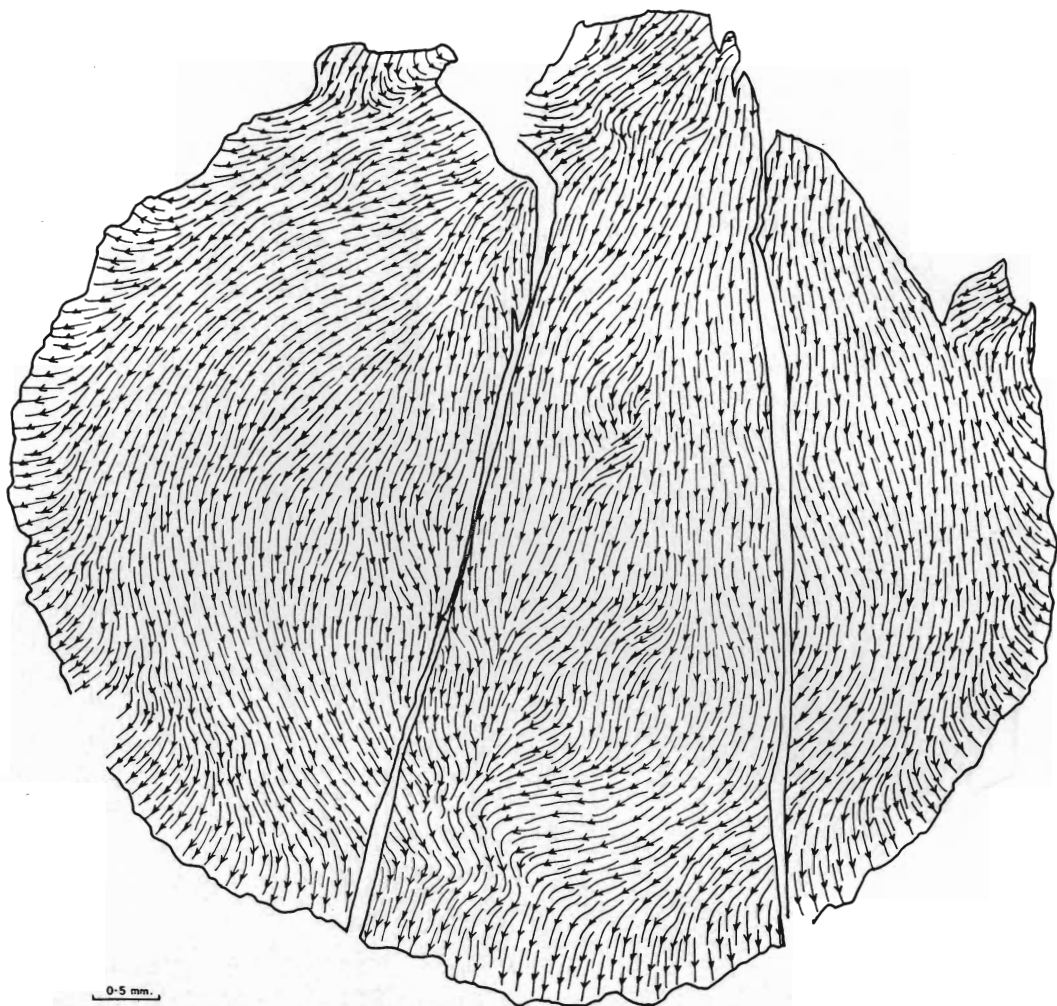
TEXT-FIG. 11. Growth map of the mosaic of the brachial valve of *Terebratulina caput-serpentis* (Linné)

of calcite rhombs disposed in an arc. Exposed parts of fibres may become more transverse or extravagantly lengthened and still affect obtusely rounded or even truncated anterior boundaries. However, terminal faces with angular anterior boundaries do occur and since they most commonly develop on fibres underlying muscle fields, they are best considered in that context.

The outer epithelium, associated with the principal muscle bases of a brachiopod, is so greatly modified by permeating tonofibrils that the mosaic of the supporting secondary layer is also affected and usually loses its identity. The transformation may ultimately

prove to follow certain well-defined sequences in different species. But complications, arising from the expansion and anterior migration of muscle fields during shell growth, and the positive correlation of intensity of change with increasing age of the individual, so far preclude more than a few generalizations.

Early changes in the mosaic induced by the development of muscle bases have been seen in young *Notosaria*, and along the anterior boundaries of adult scars, which mark the encroachment of migrating bases in that genus and *Hemithiris*. In those areas the exposed trails of fibres are greatly elongated, and the terminal faces are commonly accentuated as raised pads which are studded with coarse pits (Pl. 4, fig. 4) and may assume the rhombohedral or scalenohedral outlines of calcite. The pits, which may be separated from one another by calcite bars, form oblique slots up to 2μ long and are usually arranged along rhombohedral lines (Pl. 4, fig. 2). They obviously accommodate microvilli, but whether these large microvilli are seats for groups of tonofibrils or simply extensions of the plasma membrane caught up by accelerated secretion of calcite in intervening areas, remains to be seen. Tonofibrils found in the anterior parts of cells are probably associated with very much finer pits (about $0 \cdot 1\ \mu$ in diameter), concentrated in arcuate zones that record repeated pauses in the forward movement of the cells (compare Pl. 8, figs. 2, 3).

Topographic changes in the mosaic described above are, paradoxically, caused by a deceleration in the forward growth of the fibres proceeding inwards from the anterior margin of the muscle field. Thus the apparent lengthening of a fibre stalk really indicates a slowing down in the forward advance of the anterior margin of the overlapping fibre immediately behind so that more and more of each stalk remains uncovered as the process continues. Deceleration also accounts for other features like the pauses registered by anterior arcs of migrating cells and the increasing definition of the terminal faces of fibres as crystal pads invaded by microvilli. Certainly the net result of upsetting the balance between the secretion of calcite and the extension of fibres away from their loci of origin is an excessive calcification within the main muscle areas. This leads to the rupturing of the protein boundaries by peripheral expansion of the terminal faces, which tend to fuse with one another. Consequently, most of the adductor and diductor muscle bases of adult *Hemithiris* and *Notosaria* are underlain by a secondary shell surface consisting of irregularly sutured fibres, normally longer than wide, which bear, only here and there, blurred traces of the typical mosaic and impersistent sinuous trails of cell boundaries (Pl. 4, fig. 6).

The posterior boundaries of adult muscle scars necessarily include fibres that once underlay the muscle bases during their forward migration as well as those secreted by epithelium that was originally posterior to the bases. The difference between the two types is quite striking. In *Notosaria*, the former are indistinguishable from the disorganized fibres occupying the main areas of muscle attachment. But in *Hemithiris*, they may be represented by a narrow zone of regularly arranged fibres with raised scalenohedral terminal faces, which become progressively shorter towards the actual margin of the muscle field. This sequence is the reverse of that found in the anterior margin, so that it is possible that this zone does not represent a regrowth of the typical mosaic after the passage of the muscle bases but a peripheral spread of the muscle field posteriorly once anatomical distribution in adult shells had been stabilized. However, in both species, fibres that are never affected by the muscle systems are easily identifiable

by their regular overlapping habit and relatively smooth terminal faces. Moreover, those in a narrow arc defining the posterior margins of muscle impressions at the moment of death are significantly smaller and, therefore, more closely packed than the remainder. Reduction in fibre size by bilobation of the terminal face is sporadically seen anywhere on the shell floor, and has been interpreted as a manifestation of cell division taking place well away from the primary meristomatic region. It seems equally reasonable to conclude that the morphology of these posterior arcuate margins of muscle impressions also reflects cell division but on so big a scale as to constitute secondary generative zones. In effect, cells proliferated in such zones are only capable of secreting secondary shell in the form of fibres and their protein sheaths; but the strips along which cells are created move forward in the wake of the migrating muscle bases and, by the process of overlap of their constituent fibres, bury the irregular surfaces that once underlay muscle bases in an increasing wedge of orthodoxly stacked fibres.

Microstructure of skeletal outgrowths of living rhynchonellides

It is not at present intended to discuss the fabric of skeletal outgrowths of the shell in detail but some comments on the composition and nature of the more important features will be necessary from time to time if only to confirm that the articulate shell and all its calcareous attachments are an integrated system secreted by the outer epithelium. Thus, in the rhynchonellides all internal apophyses are fashioned from the secondary shell, and their growth, even in subdued structures like the dorsal median ridge of *Hemithiris*, involves control by secondary generative zones. The fabric of the shell comprising the teeth and crura and their supports shows such relationships **well**. The crus of *Notosaria* (text-fig. 12) is composed of secondary shell with the fibres on the posterior surface closely packed and overlapping regularly towards the distal end; but only a lineation, parallel with the long axis of the crus, remains of the mosaic on the anterior surface owing to tendonous attachments. However, the shell enveloping the antero-dorsal surface of the crus has a regular, closely packed mosaic growing away from the median plane more or less parallel to the line of contact with the crus, and then curving posteriorly to become orientated with the topography of the inner socket ridge. Long, irregular fibres, indicative of adjustor muscle attachment, replace the regular mosaic only along the postero-median surface of the envelope and the inner face of the inner socket ridge.

There is a similar breakdown of mosaic along the tooth axis and on the receiving surface of the socket, which suggests that mechanical stress affecting the epithelial covers to both structures inhibits the development of a regular mosaic (text-fig. 13). Indeed, physical constraint of the retreating edge of the inner socket ridge may account for the presence of long, irregular fibres in the posterior part of the inner surface of the supporting dental plate, where they are aligned more or less parallel to the tooth axis. The anterior part of the inner surface and the entire outer surface of the dental plate display the regular, closely packed mosaic typical of secondary generative zones, which overlaps towards the dorsal edge of the plate where both mosaics meet and are aligned posteriorly to occupy the anterior surface of the teeth. Evidently the dynamics of skeletal elaboration are recorded in the fibres of the secondary layer, but comparative studies to determine the degree of similarity between various stocks in the growth of such structures have not yet been completed and are in any event beyond the scope of this paper.

*Effect of fossilization on microstructure*

At this juncture, preparatory to discussing the shell fabric of extinct orders, it seems appropriate to comment on the degree to which fossilization affects the microstructure of skeletal remains, because comparison of ancestral rhynchonellides and terebratulides (like *Rostricellula* and *Mutationella*) with living relatives can indicate the amount of change to be expected. Generally, specimens recovered from undeformed argillaceous and carbonate rocks will show microscopic details and growth fabric despite recrystallization
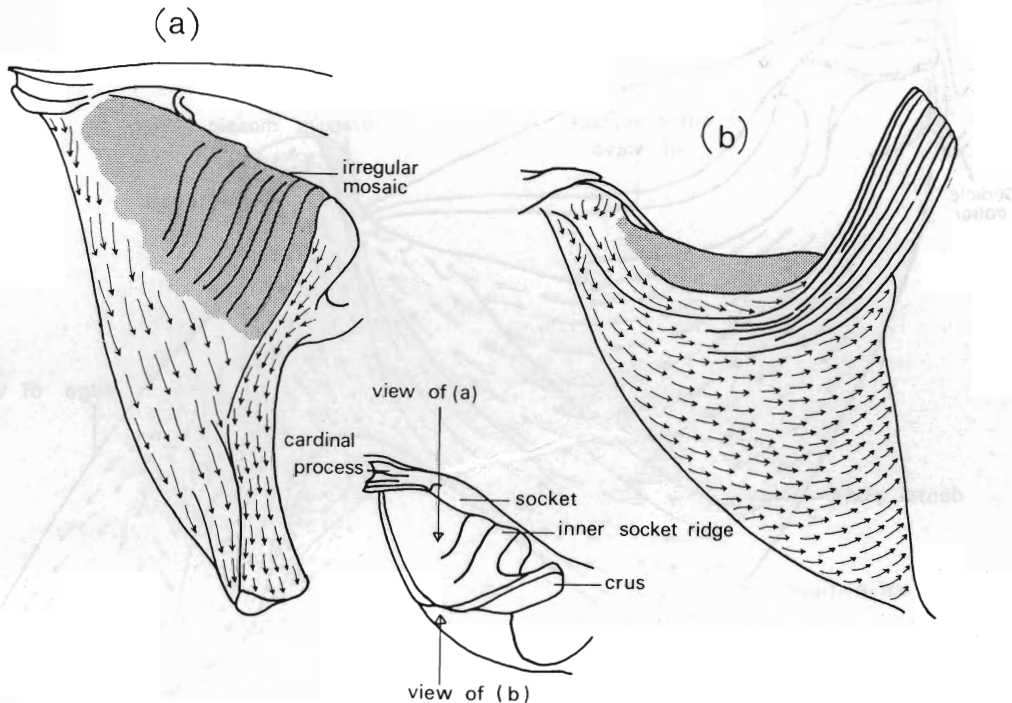
TEXT-FIG. 12. Two views of a crus and associated features of *Notosaria nigricans* (Sowerby), showing the growth vectors of the regular mosaic and the distribution of irregular mosaic

although there is some selection in the degree of alteration of the shell. The secondary layer is least affected by diagenesis because unmodified outlines of constituent fibres can normally be seen throughout a shell section irrespective of the age of the specimen. Moreover, even when recrystallization destroys individual boundaries, the affected fibres are usually replaced in entire groups so that grain outlines seen in the section are likely to be composite silhouettes of variously sized stacks (compare Pl. 15, fig. 3). Such compromise is undoubtedly caused by the survival of the organic sheaths of fibres, either as concentrations of amino acid derivatives or even as shreds of protein; and their influence is nowhere better seen than in delicate skeletal pieces, like loops and spires, which commonly retain the form of constituent fibres as completely as the thick secondary deposits of the shell floor. One must therefore be prepared to attribute any distinctive calcitic accretion which is associated with normally developed fibres in a fossil shell to organic activity rather than *post mortem* change; certainly many extinct groups are characterized by carbonate growths which can best be explained in this manner.

In contrast with the secondary shell, the primary layer is most commonly recrystallized. However, as in *Mutationella* (Pl. 11, fig. 1), the layer may be lineated normal to the shell surface. The lineation can be unrelated to the disposition of rhombohedral cleavage planes and is also unlike the boundary pattern resulting from grain growth during recrystallization. It may therefore represent an original fabric imposed on the primary
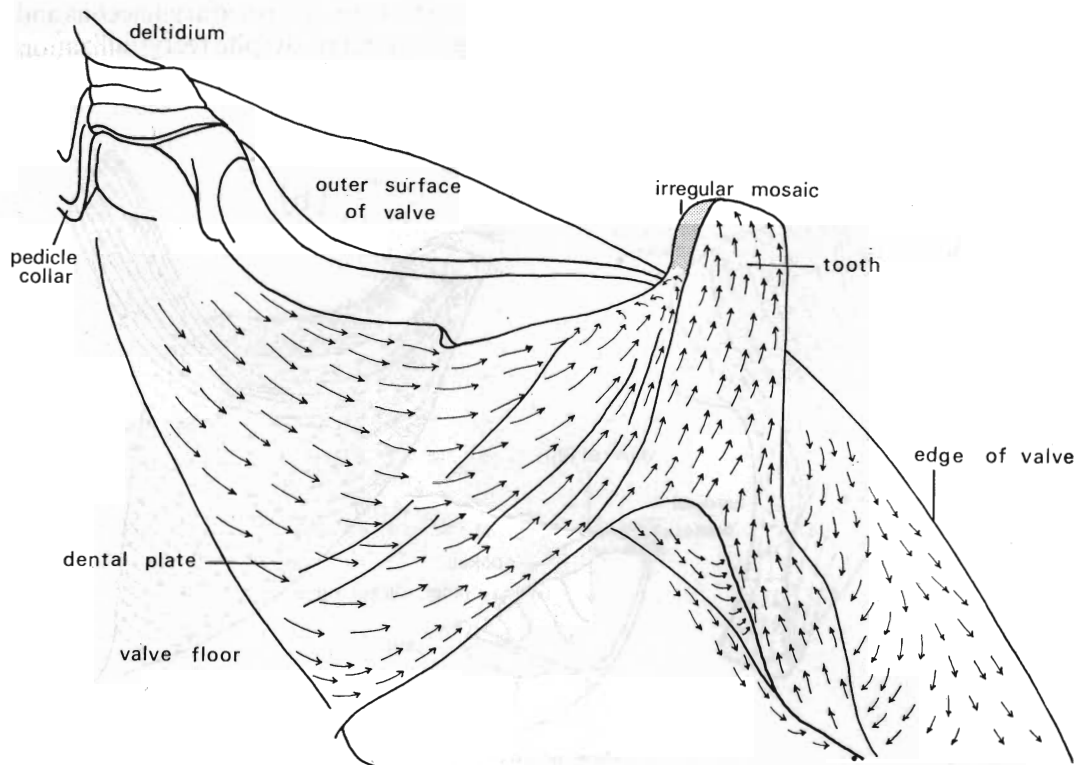
TEXT-FIG. 13. Antero-median view of a tooth and dental plate of *Notosaria nigricans* (Sowerby), showing the growth vectors of the regular mosaic and the distribution of irregular mosaic

layer by retreating microvilli as in living species. The external surface of the primary layer may also act as an interface receiving residues from diagenetic diffusion or separating the shell from a non-carbonate sediment. Consequently, the surface may be defined by trails of iron oxides, clay or other minerals. In such circumstances the uniform thickness of the layer becomes evident and is another diagnostic feature. In the absence of these clues, the primary layer may be unidentifiable because it is indistinguishable from the entombing matrix or the rest of the shell. Then, the only reliable guide as to which alternative is correct is a section showing the species in question in juxtaposition with a specimen of another stock known to possess a differentiated primary layer.

Microstructure of fossil rhynchonellides

The structural organization of the living rhynchonellide shell as described above was undoubtedly characteristic of every fossil rhynchonellide species so far examined. The

sample investigated is small but, in terms of ordinal history, revealing, for it includes Palaeozoic genera like *Camarotoechia*, *Drepanorhyncha*, *Moorefieldella*, *Pugnax*, *Rhynchopora*, *Rhynchotreta*, *Rostricellula*, and *Stenoscisma* as well as the Mesozoic *Acanthothiris*, *Goniorhynchia*, and *Rhynchonella*. *Rostricellula plena* (Raymond) from the Chazy formation and *R. lapworthi* (Davidson) from the Craighead Limestone (Pl. 3, figs. 4, 5) are especially noteworthy because they belong to the earliest known rhynchonellide stock. Studies of them show that the secretion of primary and secondary layers by the outer epithelium of the mantle proceeded in exactly the same way during Ordovician time as it does today. Indeed, as far as is known, the development of endopunctae in the rhynchoporids constitutes the only radical departure within the order from the shell structure of living species. The endopunctae of *Rhynchopora* (Pl. 3, fig. 6) are sufficiently like those found in terebratulides to warrant the belief that they too accommodated caeca. Consideration of their independent development within this rhynchonellide stock is best left until the morphology and growth of the terebratulide caeca have been described.

TEREBRATULIDA

Shell deposition in living terebratulides

An examination of *Laqueus californicus* (Koch), *Macandrevia cranium* (Müller), *Megerlia truncata* (Linné), *Terebratalia transversa* (Sowerby), *Terebratella inconspicua* (Sowerby), *Terebratulina caput-serpentis* (Linné), and *Magellania flavescens* (Lamarck) shows that the shell fabric of living terebratulides differs fundamentally from that of Recent rhynchonellides only in the presence of endopunctae accommodating caecal evaginations of the outer epithelium. However, study of these species has also provided more information about some aspects of shell deposition which will be given before discussing endopunctation.

Deposition of a triple-layered shell by the outer epithelium of the mantle proceeds in exactly the same way in terebratulides as in rhynchonellides. The regularity of the differential thickening of the periostracum is shown by extensions from the inner surface of that layer in *Macandrevia* which are symmetrically rounded with a wavelength and amplitude of about 0.7μ, approximately equal to the thickness of their common base (Pl. 5, fig. 1). The textural difference between the depositional surfaces of the primary and secondary shell is also vividly displayed by the terebratulides (Pl. 5, figs. 3, 4, 5). In *Terebratulina*, densely distributed microvilli, up to 0.2μ in diameter, invade the primary layer and linearly or reticulately arranged traces of them commonly persist on the first-formed secondary fibres (Pl. 5, fig. 4). Banding with a periodicity of about 0.3μ in *Megerlia*, and disposed more or less parallel with the exterior shell surface, also occurs sporadically within the primary layer. Like that found in secondary fibres it is believed to represent diurnal changes in rates of deposition (Pl. 5, figs. 2, 3, 6).

The shape and stacking of fibres comprising the terebratulide secondary shell show that they originate and become arranged during growth in the same way as those of the rhynchonellides (Pl. 6, figs. 1–4) so that even growth maps of randomly selected species are comparable (text-figs. 9–11). Greater topographic variation in the terminal faces of fibres forming the mosaic of the shell floor has been observed in the terebratulides, although further research may show a similar range of modification in the rhynchonellides.

Thus in *Terebratulina*, the exposed axes of the first-formed fibres are, on an average, about $5.5\,\mu$ long, but the ratio of maximum width to the exposed axis can vary from 0·6 to 1·0, indicating the degree of lateral spread that is possible in the development of the terminal face (Pl. 7, fig. 1). During the early growth of fibres, the trails may be sufficiently well exposed to reveal 4 or 5 growth bands with a periodicity of about $0.1\,\mu$ (Pl. 5, fig. 3; Pl. 7, fig. 1). The mosaic of mature fibres, the exposed axes of which are up to $20\,\mu$ long, shows an even greater variation in width:length ratios (0·2 to 0·8). The most typical terminal faces are anteriorly defined by narrowly semi-elliptical margins (Pl. 7, figs. 2, 3), but laterally extended ones with semicircular boundaries are also found, as well as narrow ones with truncated fronts and subparallel lateral margins (Pl. 7, fig. 4). Sigmoidally curved surfaces that characteristically divide terminal faces into pairs of lobes growing at different rates, occur sporadically (Pl. 7, fig. 5). But, irrespective of such variation, the relationship of the epithelial cells to the mosaic is clearly like that found in living rhynchonellides because traces of the posterior boundaries to the terminal faces, which are normally preserved, invariably subtend rhombohedral angles.

As in the rhynchonellides, the greatest modification of the mosaic occurs when muscle bases encroach on the outer epithelium, controlling its secretion. The morphology of the shell floor underlying the ventral muscle field of *Terebratulina* is like that of *Hemithiris* and *Notosaria* in that the scars are bounded posteriorly by a narrow secondary generative zone and consist mainly of elongated, irregularly sutured fibres with rare, impersistent traces of the standard mosaic and no continuous protein boundaries. The fibres occupying the apical surfaces of fully developed tubercles of *Megerlia* undergo a similar breakdown of the regular mosaic, and are presumably the seats of tonofibril concentrations within the mantle (Pl. 6, figs. 5, 6). Such modification can also affect mosaic whorls: but tubercles are differently constructed because their growth, like that of other internal skeletal features, is controlled by invaginations of outer epithelium and


EXPLANATION OF PLATE 5

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to $2\,\mu$.

Fig. 1. Section of differentially thickened periostracum overlying the primary layer (in the lower half of the micrograph) of *Macandrevia cranium* (Müller).

Fig. 2. Section of primary layer of *Megerlia truncata* (Linné), showing depositional banding.

Figs. 3, 4. Junction between the primary and secondary layers as seen on the internal surface of a valve of *Terebratulina caput-serpentis* (Linné) with depositional banding in the trails of fibres in Fig. 3.

Fig. 5. Oblique section of the junction between the primary and secondary layers of *Macandrevia cranium* (Müller).

Fig. 6. Transverse section of the junction between the primary and secondary layers of *Megerlia truncata* (Linné).

EXPLANATION OF PLATE 6

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to $2\,\mu$.

Fig. 1. Transverse section of the junction between the primary and secondary layers of *Macandrevia cranium* (Müller).

Figs. 2–4. Transverse (Figs. 2, 3) and oblique (Fig. 4) sections of the secondary layer of *Macandrevia cranium* (Müller).

Figs. 5, 6. Internal surface view and section of a tubercle of *Megerlia truncata* (Linné).

the exposed axes of mosaic in their vicinity are, at most, deflected from the general lineation of the shell interior.

Narrow secondary generative zones with exposed axes of fibres about 7μ long also form the posterior boundaries to the muscle floors of *Laqueus*. Moreover, although long
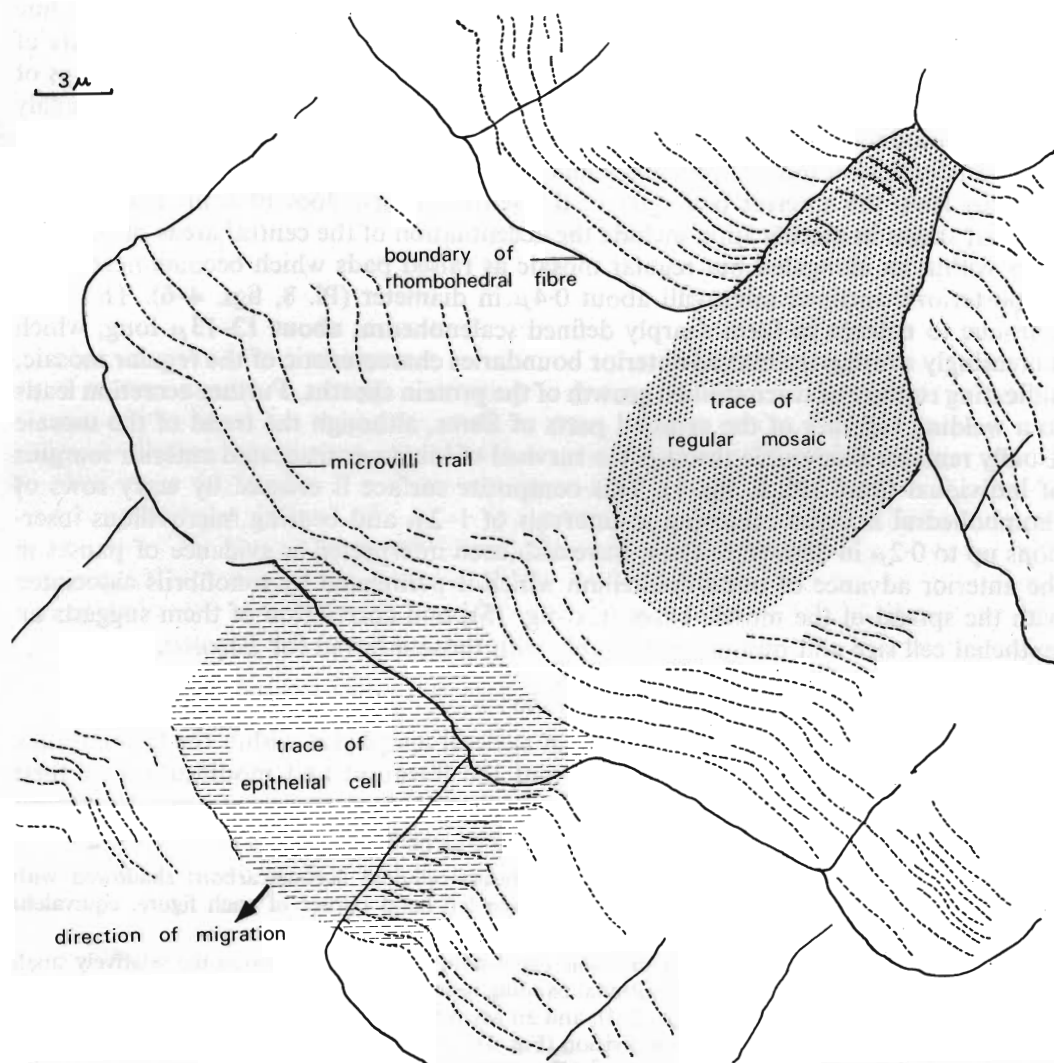
TEXT-FIG. 14. Plan of the modified mosaic underlying the dorsal adductor muscles of *Laqueus californicus* (Koch) in relation to inferred traces of an outer epithelial cell, and the exposed axis of a regular fibre

irregular fibres are common within the area occupied by the ventral diductor bases, the floor of the dorsal adductor muscles is mainly composed of distinctive rhombohedral-like exposed axes arranged in overlapping rows. This pattern is seen to arise by the conversion of orthodox, semi-cylindroid terminal faces into relatively planar, truncated, parallel-sided surfaces subtending rhombohedral angles, followed by an acceleration in

the lateral growth so that the exposed parts of contemporary fibres tend to unite with one another (text-fig. 14; Pl. 7, fig. 6; Pl. 8, figs. 1–3). The process inevitably leads to a breakdown of the protein sheaths, and the discontinuous migration of outer epithelial cells over the modified floor is recorded as a series of slightly undulating furrows containing small microvilli up to 0.5μ in diameter which may be associated with fine lineations indicative of oblique insertion. If the microvilli are assumed to be seats of tonofibrils concentrated in zones parallel with cell boundaries, correlation of groups of furrows shows that the outer epithelium consists of alternating rows of cells roughly square in outline with sides about 15μ long.

A transformation that also retains abundant evidence of cell migration can be traced inwardly from the anterior boundary of the ventral muscle floor of adult *Terebratalia*. The first stages in modification include the accentuation of the central areas of terminal faces within an elongated but regular mosaic as raised pads which become penetrated by posteriorly inclined microvilli about 0.4μ in diameter (Pl. 8, figs. 4–6). The pads continue to enlarge to form sharply defined scalenohedra, about 12–13μ long, which increasingly overlap the curved anterior boundaries characteristic of the regular mosaic, indicating rupture or discontinued growth of the protein sheaths. Further accretion leads to a welding together of the exposed parts of fibres, although the trend of the mosaic usually remains discernible through the survival of lobate or truncated anterior margins of individual fibres (Pl. 9, fig. 1). This composite surface is crossed by wavy rows of rhombohedral hollows occurring at intervals of 1–2μ and bearing microvillous insertions up to 0.2μ in diameter. These have also been interpreted as evidence of pauses in the anterior advance of outer epithelium which is permeated by tonofibrils associated with the spread of the muscle bases (text-fig. 15); and correlation of them suggests an epithelial cell size and outline comparable with those inferred for *Laqueus*.

Microstructure of loops of living terebratulides

As in the rhynchonellides, the growth of skeletal apophyses within the terebratulide shell is controlled by outer epithelium, and the lineation and modification of their

surface mosaics are similar in features common to both orders. It is, however, worth while considering the microstructure of the loops which, as composite structures arising from both the dorsal medial septum and the crura and undergoing profound meta-morphoses, may appear to be unattributable to the processes so far described.
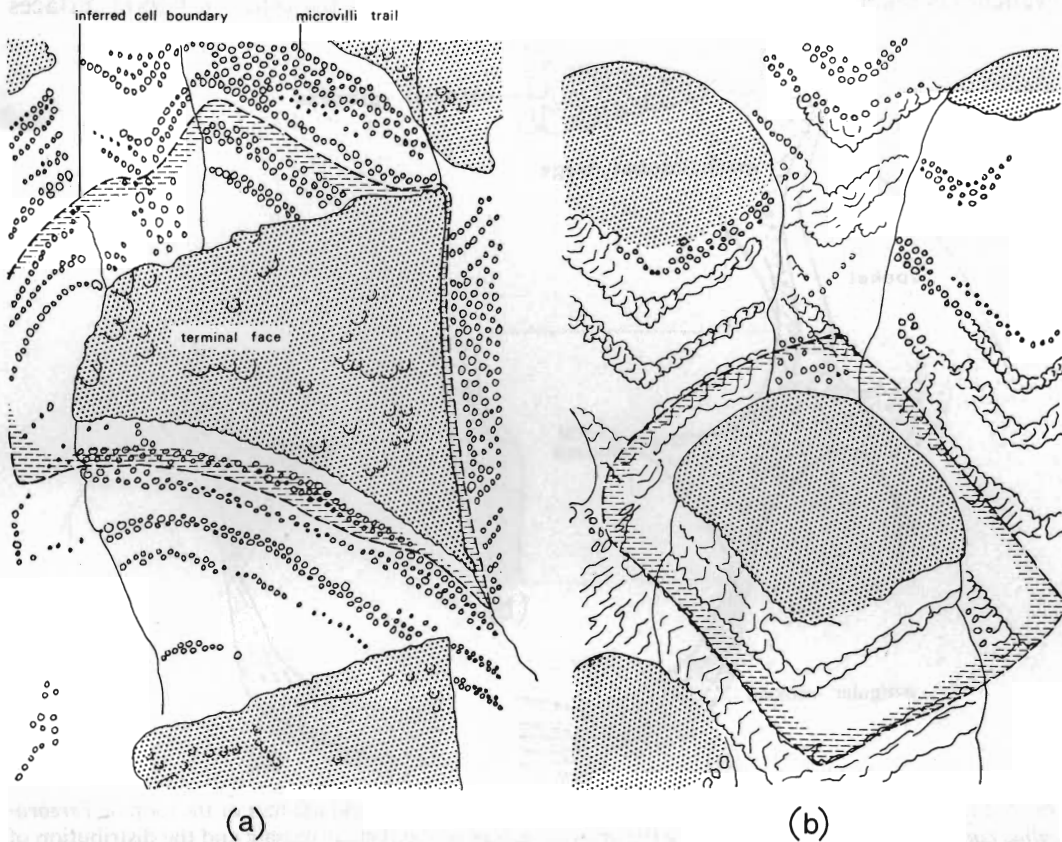
TEXT-FIG. 15. Two views of modified mosaic underlying the ventral diductor muscles of *Terebratalia transversa* (Sowerby), showing the inferred relationship between the terminal faces of fibres and outer epithelial cells

A short terebratulacean loop, as typified by *Terebratulina*, is supported by a pair of crura which are more or less quadrate in cross-section (text-fig. 16). The lateral face of each crus, which is continuous with the outer surfaces of a crural process and the adjoining part of the loop, is covered by a mosaic trending parallel with the length of the crus. The mosaic continues obliquely across the outer surfaces of each crural pro-cess and the entire loop, and is directed towards the ventral margin of both features, although small whorls may develop, especially medially. Apart from the proximal area of the lateral face, where the exposed parts of fibres are elongated and slightly sinuous, the mosaic is regular and shows a reduction in size of units at the ventral margin, which must be a secondary generative zone. A regular mosaic trending parallel to the axis of the crus is also developed on its remaining faces; but the inner surfaces of the loop and

each crural process, which are adjacent to the lophophore, bear strong growth lines aligned with the ventral margin, and the exposed parts of fibres form an irregular network.

The mosaic patterns of the terebratellacean loop are found to be similar to the terebratulacean when the Möbius twist at the junction of the descending and ascending branches is taken into account. In *Magellania*, for example, the outer or lateral surfaces
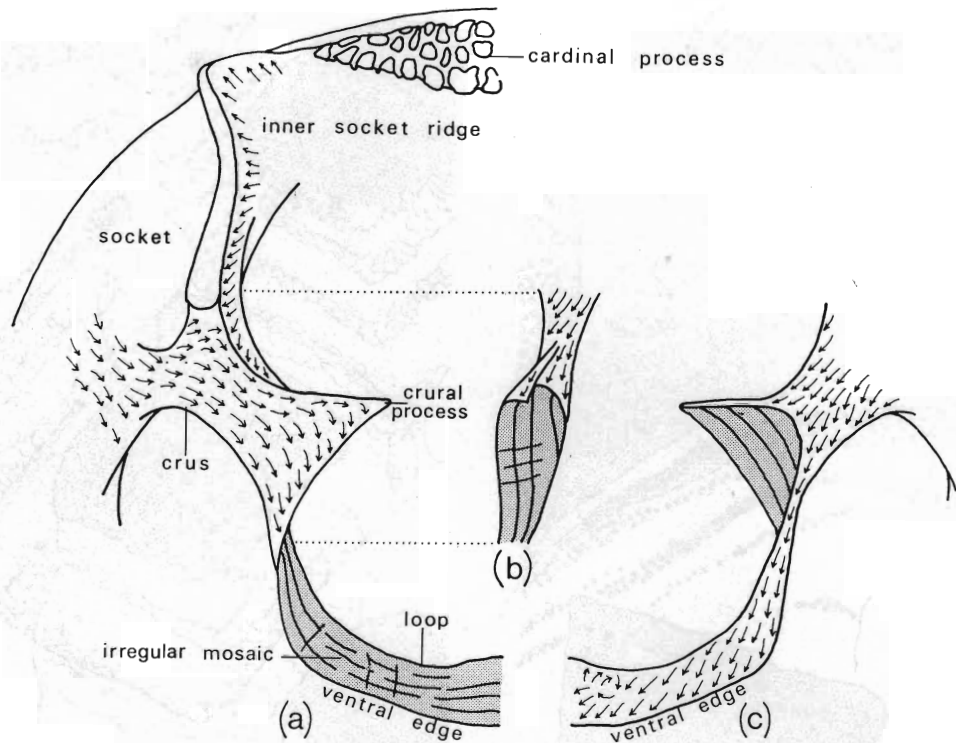
TEXT-FIG. 16. Ventral (*a*), lateral (*b*), and dorsal (*c*) views of the crus and left half of the loop of *Terebratulina caput-serpentis* (Linné), showing the growth vectors of the regular mosaic and the distribution of resorbed, irregular mosaic

of each crural process and descending branch display a well-developed mosaic trending obliquely to the long axis of the structures and towards the ventral edge, except anterior to the crural process, where the lineation may be directed antero-dorsally (text-fig. 17). Generally, the exposed parts of fibres are long and sinuous with bilobate or scalenohedral terminal faces along the dorsal zone (Pl. 10, figs. 3–5). But towards the ventral edge the mosaic becomes regular and the individual fibres progressively smaller, indicating the existence of a secondary generative zone along that edge. The twist at the distal end of the descending branch brings this outer surface into continuity with the inner or medial surface of the ascending branch and the anterior surface of the transverse band. Both these surfaces bear a mosaic morphologically diversified in the style characteristic of the descending branch so that the ventral margin of the entire loop represents a secondary generative zone. In contrast, the inner or medial surface of the crural **process and descending branch, an**d the equivalent surfaces of the ascending

branch and transverse band, upon which rest the side arms and medial coils of the plectolophe, are rutted with growth lines parallel to the ventral margin, while the exposed parts of fibres form an irregular patchwork (Pl. 10, fig. 6).

Both short and long loops are impunctate owing to an accelerated growth from loci on the valve floor which, being faster than the extension of caeca relative to the outer epithelium, causes their disruption. This modification also takes place during the growth
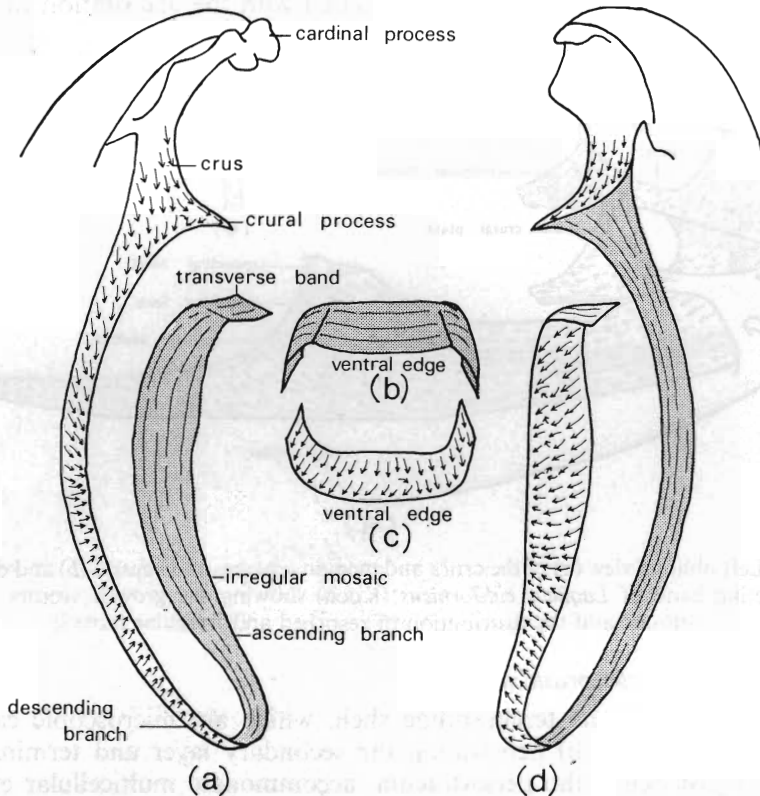
TEXT-FIG. 17. Left (*a*) and right (*d*) lateral views of the left half of the loop, and posterior (*b*) and anterior (*c*) views of the transverse band of *Magellania flavescens* (Lamarck), showing the growth vectors of the regular mosaic and the distribution of resorbed, irregular mosaic

of the dorsal medial septum of *Laqueus* (text-fig. 18), which, in adult valves, contains attenuated caeca in an obliquely disposed strip about one-quarter as wide as the height of the septum. The flanking wedges of impunctate secondary shell clearly represent zones of cell proliferation and this is reflected in the mosaic, which is composed of small, tightly packed units trending antero-ventrally towards the inner edge of the septum. Indeed, *Laqueus* shows that the pattern, characteristic of the free loop of *Magellania*, also prevailed during growth of the connecting bands arising from the medial septum. In *L. californicus* the ventral surface of the band bears a mosaic of large irregular fibres trending obliquely to the long axis of the band and away from the medial plane, whereas the dorsal surface is covered by regular terminal faces aligned more or less parallel with the anterior edge, which constitutes a secondary generative zone.

In summary, it can be said of the terebratulide loop that growth lines and disintegrated mosaic are found on surfaces supporting the lophophore base and its connective tissue, while regular mosaic indicative of growing fibres occupies the reverse surface. The former surfaces and dorsal edges of the apparatus represent the zone of loop resorption, and the latter, sustained by the generative zone along the ventral margin, the zone of loop **growth. This relationship ensures** that modification and enlargement of the wafer-thin skeletal supports are co-ordinated with the elaboration and expansion of the plectolophe.
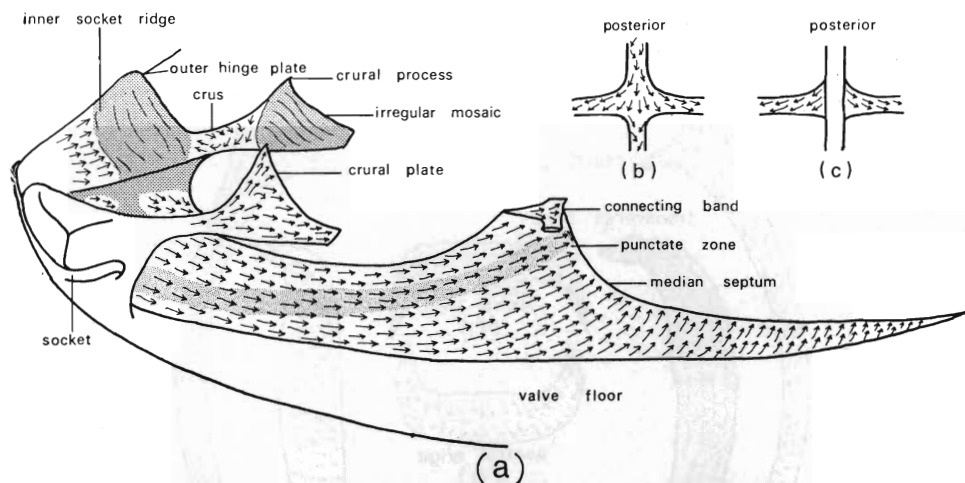
TEXT-FIG. 18. Left oblique view (*a*) of the crura and median septum, and ventral (*b*) and dorsal (*c*) views of the connecting band of *Laqueus californicus* (Koch) showing the growth vectors of the regular mosaic and the distribution of resorbed and irregular mosaic

Endopunctae of living terebratulides

The endopunctae of the terebratulide shell, which are microscopic canals (up to 100μ wide in *Macandrevia*) penetrating the secondary layer and terminating in the primary layer just below the periostracum, accommodate multicellular extensions of the mantle (caeca) (text-fig. 19). The caeca are known to originate on the outer lobe of the mantle edge (Williams 1956, p. 247), presumably as bud-like evaginations of the outer epithelium, and then become incorporated within the shell as it expands peripherally. The persistence of caeca within the thickening shell is due to the co-ordination of their growth with the accretion of the secondary layer and the inhibition of any calcification within the structures. The first factor suggests that the caeca are centres of cell

proliferation, the second that they are composed of cells with a different internal chemical environment from those making up the outer epithelium. The principal problem that arises from their existence is how to reconcile their physiology and growth, which basically involves an extension normal to the primary layer, with the secretory habits and complex shifts of the outer epithelium.
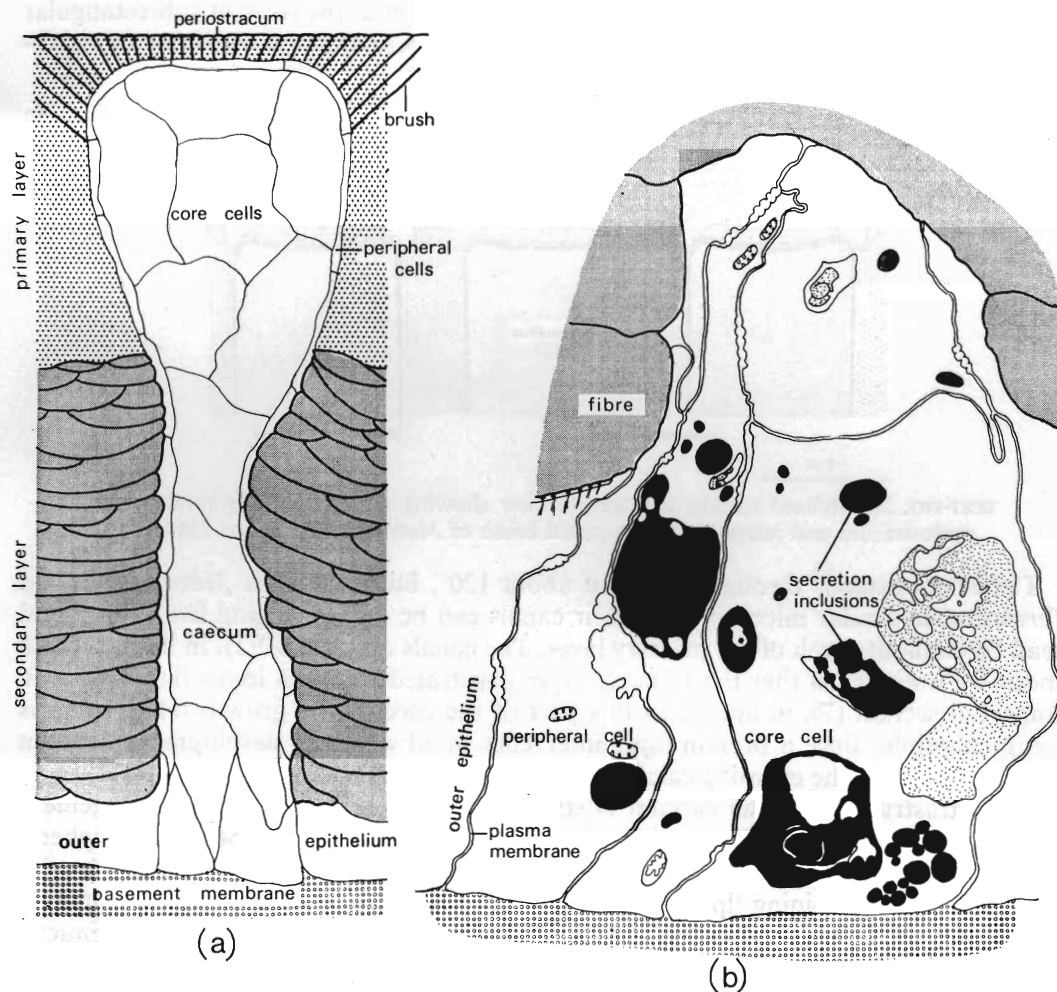
TEXT-FIG. 19. Stylized longitudinal section (a) of a caecum in relation to the shell and outer epithelium, and an oblique lateral section (b) of a caecal base in *Terebratulina*

The rounded head of a caecum is encased in the primary layer and is separated from the periostracum by a **canopy of calcit**e which is about $1\,\mu$ thick centrally in *Macandrevia* (Pl. 9, figs. 4–6). The canopy is an integral part of the primary layer and must have been secreted by the plasma membranes of the terminal head cells at the very edge of the shell. It is perforated by densely distributed canals containing a brush of interconnecting microvilli which join the terminal cells with the periostracum. On the external surface, the ends of a caecal brush appear as discs which are slightly raised within

circular depressions (about $0.15\,\mu$ in diameter in *Macandrevia*) (text-fig. 20). Except for sporadically occurring circular patches about $1\,\mu$ in diameter, the discs are densely distributed within the surface areas underlain by caeca (Pl. 9, figs. 2, 3). Presumably the periostracum conforms to this topography and may be differentially thickened along the boundaries of the circular depressions, thereby forming protein rings to enclose the terminal discs of caecal brushes. Certainly there is no sign of the rows of subrectangular corrugations, about $10\,\mu$ wide, which characterize the periostracum overlying the inter-caecal parts of the primary layer.
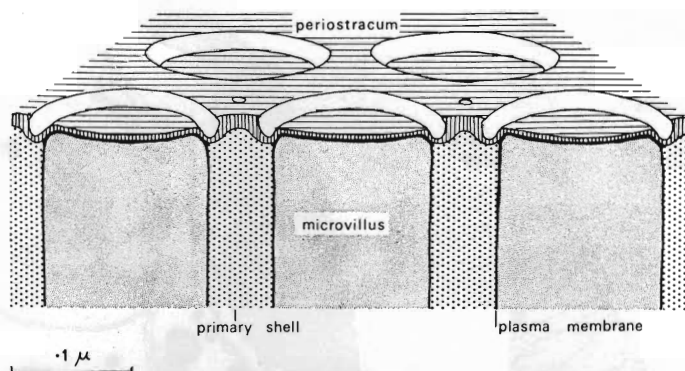
TEXT-FIG. 20. Stylized section and surface view showing the relationship between the periostracum and microvilli of the caecal brush of *Macandrevia cranium* (Müller)

The brush extends through an arc of about 120°, but in at least *Macandrevia* and *Terebratulina* similar microvilli and their canals can be seen diverging from the caecal head throughout much of the primary layer. The canals are about $0.2\,\mu$ in diameter and about $0.1\,\mu$ apart, so that the primary layer penetrated by them looks like a sieve in tangential section (Pl. 9, fig. 6). In this part of the caecum the growth relationship is comprehensible, since a protein layer intervenes in all stages of development between the head cells and the encasing calcite which is deposited by adjacent epithelial cells.

The ultrastructure of the caecum is still being studied, but the basic arrangement within both head and stalk consists of an outer protein coat enclosing a peripheral layer of flattened cells rather like pavement epithelium, and a core of cells each with many vacuoles containing lipids and mucin (Pl. 1, figs. 4, 5). Since the protein coat is closely adherent to the plasma membranes of the peripheral cells and also continuous with the protein mesh of the secondary layer, a caecal stalk can only lengthen in pace with secondary shell thickening by an increase in the number as well as the size of its constituent cells. Moreover, extra cells can only be added at the base of the stalk, and must involve either proliferation from a generative zone or incorporation from the outer epithelium. At first sight, the relationship between fibres and caecal stalks seems to preclude the latter process. Replicas of sections and internal surfaces of living tere-bratulide shells show that adjacent fibres grow past a caecum with no more than an outward deflection in the area of contact (Pl. 10, fig. 1), while a fibre directly in the path of a caecum extends forward by dividing to surround the stalk or even by terminat-ing against the near side of the stalk and then reappearing to grow away from its far side (text-fig. 21). Translated into migration of epithelial cells capping the terminal faces

of fibres, this evidence suggests that when, for example, a pair of cells approach a caecal base frontally and laterally, the following events take place. The anterior half of the lateral cell continues to secrete a protein sheet as an outer cover to the advancing end of the fibre deposited by the posterior part of the plasma membrane. The sheet is laid down on the stalk of the fibre immediately above, on the side of the outer adjacent fibre, and on the side of the caecal base. Electron micrographs of the mantle suggest
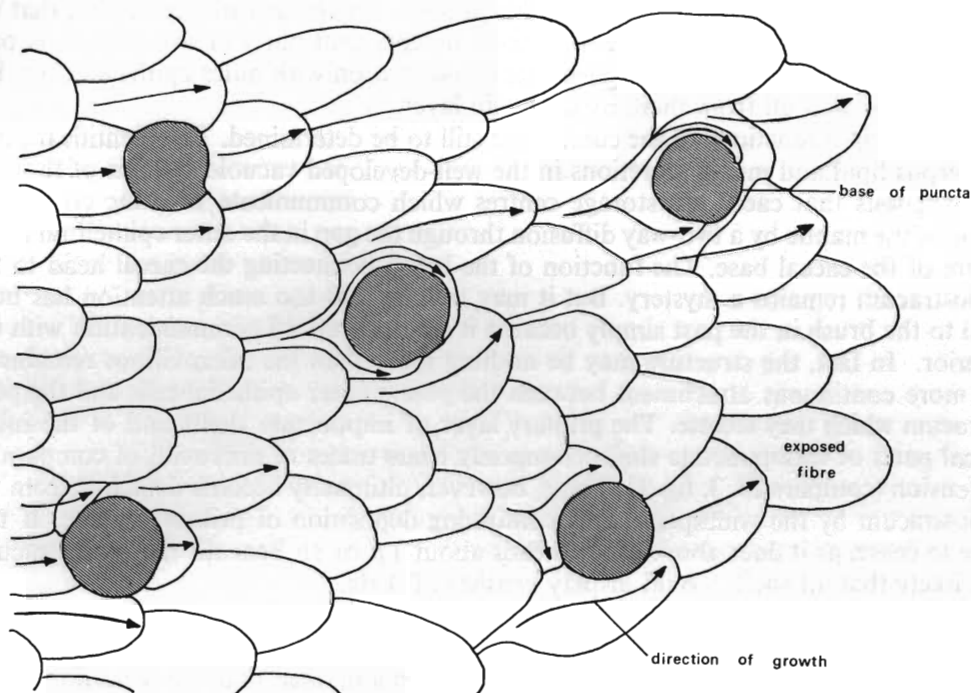
TEXT-FIG. 21. Plan of part of the internal surface of a valve of *Terebratella inconspicua* (Sowerby), showing the relationship between the mosaic and the bases of endopunctae

that at this stage only the secretory core cells of the caecum extend towards the basement membranes of the outer epithelium (Pl. 1, fig. 4). It is, therefore, possible that the peripheral layer of flattened cells is enlarged subsequent to the deposition of the confining protein sheet and may even include daughter cells budded off from the by-passing outer epithelium. Meanwhile the cell, blocked frontally by the caecal base, may be pulled both ways around the base by forward movement of adjacent cells; but secretion continues so that the base is ultimately encircled by protein and calcite deposited by the same cell. Alternatively, deposition of calcite may cease as the cell squeezes past the flanks of the caecal base, but start up again as the cell regains its normal shape and moves away from the base. Such inhibition of calcite deposition in the vicinity of the caecal base is probably related to the secretory functions of the core cells. Indeed, caeca become detached and sealed off from the outer epithelium only when secondary shell is being deposited very quickly, as in the development of internal features. Presumably the stacking of fibres around the caecal stalk outpaces the extension of the basal core cells until calcite can be secreted by advancing epithelial cells across the canal aperture. But

usually the basal extension of caeca is so well co-ordinated with the thickening of the secondary layer that contact is maintained with the inwardly retreating mantle, and can lead to amalgamation of caeca to give the branching effect found in *Terebratulina* and other ribbed shells.

In summary, the growth relationship between caeca and outer epithelium may be likened to a series of obstructions deflecting the current of a slowly moving fluid without affecting the general direction of flow. This process, which surprisingly implies that the caeca and outer epithelium actually grow as independent parts of the mantle, is only possible because the caecal bases originate in association with outer epithelial cells, but are always sealed off from them by a protein layer.

The principal functions of the caeca have still to be determined. The identification of numerous lipid and mucin secretions in the well-developed vacuole systems of the core cells suggests that caeca are storage centres which communicate with the connective tissue of the mantle by a two-way diffusion through the gap in the outer epithelium at the centre of the caecal base. The function of the brush connecting the caecal head to the periostracum remains a mystery. But it may well be that too much attention has been paid to the brush in the past simply because it seems to afford communication with the exterior. In fact, the structure may be nothing more than the microvillous remains of the more continuous attachment between the young outer epithelial cells and the periostracum which they secrete. The primary layer of impunctate shells and of the intercaecal parts of endopunctate shells commonly bears traces of microvilli of comparable dimension (compare Pl. 3, fig. 1). These, however, ultimately become detached from the periostracum by the widespread and continuing deposition of primary calcite. If this were to cease, as it does above caecal heads about $1\,\mu$ or so beneath the periostracum, it is likely that all shells would display brushes of sorts.

Endopunctae of fossils

From time to time many palaeontologists have maintained that the condition of the shell is an important guide to phylogeny and a reliable means of establishing a workable classification; and since endopunctation has been so used, it is important to determine what its morphological expression should be in extinct groups. Theoretically, any canal that accommodated the terebratulide type of caecum should at least penetrate the outermost secondary shell, with the fibres forming its boundary deflected outwards and bearing sporadic evidence of depositional breaks. It should also terminate in the primary layer just below the outer surface of the shell but communicate with the exterior through a series of fine perforations. The first two qualifications would also apply to any cylindroid evagination of the outer epithelium, while the last is unlikely

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EXPLANATION OF PLATE 10

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to $2\,\mu$.

Fig. 1. Internal surface view of the base of an endopuncta in *Megerlia truncata* (Linné), showing its relationship with confining fibres.

Fig. 2. Oblique section near the base of an endopuncta in *Macandrevia cranium* (Müller), showing its relationship with confining fibres.

Figs. 3–6. Details of the mosaics of the outer (Fig. 3) and inner surfaces of the loop of *Magellania flavescens* (Lamarck), showing the effects of resorption.

ever to be unequivocally recognized in fossil specimens. Even the primary layer itself can be so grossly affected by diagenesis as to defy positive identification. In effect, canals that demonstrably penetrate *both* primary and secondary shell and are bounded by deflected fibres that show signs of interruptions in the secretion of calcite may have contained caeca. By such diagnosis, endopunctation seems to have been characteristic of many extinct groups. Thus the condition of the shell of *Rhynchopora* is identical with that of contemporaneous terebratulides, which suggests that caeca were briefly but independently developed even in the rhynchonellides.

Microstructure of fossil terebratulides

There is little difficulty in confirming that the structural style of the living terebratulide shell including endopunctation was also typical of all fossil groups assigned to the order. It is characteristic of the terebratulacean *Dictyothyris*, *Pygope*, *Rugithyris*, *Terebrirostra*, and *Wattonithyris*; the zeilleriacean *Digonella* and *Ornithella*; the dielasmatacean *Cranaena* and *Dielasma*; and the stringocephalacean *Mutationella* (Pl. 11, figs. 1–3) and *Rensselaeria*. Even the mosaic can still be identified in well-preserved interiors of *Mutationella podolica* (Siemiradzki), from the Siluro-Devonian Czortków Beds of Poland, which is the earliest known terebratulide; and it is highly probable that the mantle of ancestral terebratulides grew and deposited shell in the same way as today.

SPIRIFERIDA

As currently understood, the spiriferides constitute a large order which became extinct during the Jurassic. Fortunately the last surviving genus, *Spiriferina*, includes species—like *S. walcotti* (Sowerby)—which are sufficiently well preserved to provide a comprehensive reconstruction of the spiriferide mantle and can, therefore, be used as the standard model for the order.

Sections and clean internal surfaces of the shell of *S. walcotti* show that both primary and secondary layers were developed and that they grew in the same way as in living rhynchonellides and terebratulides. The primary layer of all specimens so far examined is recrystallized but is usually strongly lineated normal to the shell surface irrespective of the disposition of cleavage planes (Pl. 11, fig. 5). The lineation may therefore represent an original fabric imposed by retreating microvilli as in living species. The secondary shell is normally much better preserved. In this layer the fibres, with characteristic longitudinal and transverse outlines (Pl. 11, fig. 6), were stacked to form a regular mosaic in which the terminal faces, with rounded anterior margins and trailing elongate stalks of individual fibres, were arranged in alternate rows (Pl. 11, fig. 4). The surface junction between the primary layer and the first formed, closely packed secondary fibres which lie normal to the shell edge can usually be identified; and the trend of the exposed parts of more mature fibres within this circumferential generative zone indicates that they too became realigned to grow in spiral arcs towards the medial plane, and here and there formed loops and whorls within the mosaic. Amino acids recovered by Jope from spiriferide shells (*in* Williams *et al.* 1965, p. H161) leave little doubt that fibres were contained in protein sheaths.

The shell of *S. walcotti* was also completely penetrated by canals which caused a lateral and outward deflection of adjacent fibres in mosaic and section respectively

(Pl. 12, fig. 1); they probably contained caeca. In contrast, the calcareous spires supporting the lophophore were impunctate although they were composed of secondary fibres stacked in the normal manner (Pl. 12, fig. 2). This anomalous condition is reminiscent of the terebratulide loop. The similarity is close enough to suggest that, during growth, a regular mosaic was built up on the laterally facing surfaces of the calcareous ribbons of the spiralia and trended obliquely towards secondary generative zones which occupied the outer edges and apices of the ribbons; while resorption took place on those surfaces facing medially. In all, the mantle of *S. walcotti* must have been indistinguishable from those of contemporary terebratulides.

The presence of a primary layer in various stages of replacement and preservation and an underlying secondary layer made up of orthodoxly stacked fibres has been verified in a number of atrypidines (*Atrypa*, *Catazyga* (Pl. 13, figs. 4–6), *Idiospira*, *Protozyga*, and *Uncites*), athyrididines (*Athyris*, *Composita*, and *Merista*) and spiriferidines (*Crurithyris* (Pl. 12, fig. 3), *Delthyris*, *Eospirifer*, *Mucrospirifer* (Pl. 12, figs. 4, 5), *Spino-cyrtia*, and *Syringothyris*). Canals, morphologically identical with those invading both layers in *Spiriferina* and contemporary terebratulides, and inferred to have contained caeca, have been seen in retziidines (*Homeospira* and *Hustedia*) and in the spiriferidine *Cyrtina* (Pl. 12, fig. 6; Pl. 13, figs. 1, 2). Thus from the first appearing stock, the Lower Ordovician *Protozyga*, to the last survivor, samples of shell structure show that the spiriferide mantle secreted the exoskeleton in exactly the same way as impunctate rhynchonellides or endopunctate terebratulides.

One other aspect of shell structure requires attention. Sections of many spiriferides show that their shells contain patches of coarsely crystalline calcite commonly referred

EXPLANATION OF PLATE 11

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2μ.

Figs. 1–3. Transverse sections of a valve of *Mutationella podolica* (Siemiradzki) from the Siluro-Devonian Czortków Beds, Poland, showing the primary layer (Fig. 1), the standard stacking of fibres of the secondary layer, and the outward deflection of fibres around an endopuncta (Fig. 3).

Figs. 4–6. Mosaic and transverse sections of a valve of *Spiriferina walcotti* (Sowerby) from the Lower Jurassic, England, showing the characteristic shape of the exposed parts of fibres (Fig. 4), the junction between the primary and secondary layers (Fig. 5) and the standard stacking of secondary fibres (Fig. 6).

EXPLANATION OF PLATE 12

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to $2\ \mu$.

Fig. 1. Transverse section of the secondary shell of *Spiriferina walcotti* (Sowerby) from the Lower Jurassic, England, showing the outward deflection of fibres adjacent to an endopuncta (bottom left corner).

Fig. 2. Transverse section of the calcareous ribbon of a spire of *Spiriferina walcotti* (Sowerby) from the Lower Jurassic, England, showing the standard stacking of secondary fibres.

Fig. 3. Detail of the mosaic of *Crurithyris sp.*, Pennsylvanian, Texas, showing the exposed part of a secondary fibre.

Figs. 4, 5. The mosaic and transverse section of the secondary shell of *Mucrospirifer sp.*, Middle Devonian, Michigan, showing the exposed parts and standard stacking of fibres.

Fig. 6. Transverse section of the primary and secondary (right-hand side) layers of *Cyrtina sp.*, Middle Devonian, Michigan.

to as the 'prismatic layer'. The term 'layer' can be misleading because such bodies occur within the secondary layer usually as either lenses interleaved with stacks of fibres (Pl. 13, fig. 6) or more continuous masses underlying muscle impressions, yet still passing
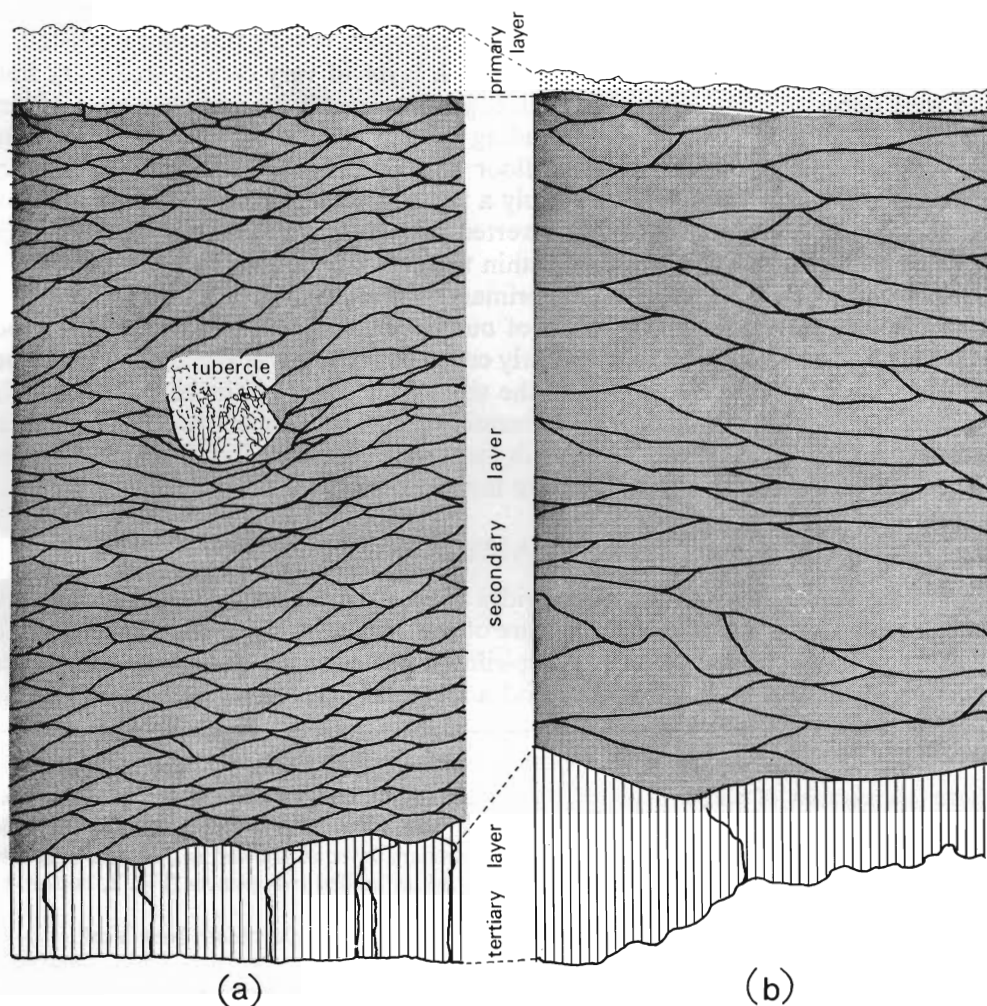
TEXT-FIG. 22. Sections of valves of (a) *Cadomella davidsoni* (Eudes-Deslongchamps), and (b) *Koninckina leonhardi* (Wissmann) showing the development of a three-fold calcareous shell

peripherally into fibrous calcite. The attribution of these prismatic bodies (Williams and Rowell *in* Williams *et al.* 1965, p. H66) to the breakdown of the orderly processes of secretion controlling the growth of discrete secondary fibres, is confirmed by current studies of the way fibres underlying muscle bases in living brachiopods become modified. Obviously prismatic calcite was deposited over relatively large areas only when acceleration in carbonate secretion in several contiguous cells caused an interruption in exudation of protein sheaths defining individual fibres (Pl. 13, fig. 3). This stage was probably the climax of a progressive series of changes affecting the terminal faces of fibres, as in

terebratulides and rhynchonellides, and further research might reveal the intermediate phases. Meanwhile an interesting consequence of this sporadic disorganization of the normal secretory processes of the spiriferide outer epithelium can be reported. In the Triassic athyrididine *Koninckina leonhardi* (Wissmann), there are actually three distinct carbonate layers (text-fig. 22). The primary layer, which is very thin and recrystallized (Pl. 14, fig. 6), is underlain by a uniformly thick layer of very coarse secondary fibres which were deposited, just within the shell edge, presumably by a narrow zone of large epithelial cells secreting calcite and bounding protein (Pl. 15, fig. 1). The third, inner-most layer occupies most of the valve floor and is composed solely of large calcite crystals (Pl. 15, fig. 2). This deposit is truly a tertiary prismatic layer. It was laid down by maturing outer epithelial cells that reverted to exclusively inorganic secretion when they came to occupy a given position within the expanding margin of the shell, in the same way as the junction between the primary and secondary layer is maintained by a regular change in the secretory habits of outer epithelial cells of living brachiopods. This is the only way to account for the fairly constant thickness of the fibrous layer com-pared with the prismatic. Some idea of the size of the outer epithelial cells occupying the valve floor may be obtained from an examination of the calcareous spires, which are made up of regular fibres about $2\,\mu$ wide in transverse section, i.e. only about one-tenth the width of those underlying the primary layer (Pl. 15, fig. 3).

PENTAMERIDA

Little need be said about the pentamerides because an examination of representative stocks shows that the typical microstructure of the shell conformed in every respect with that of rhynchonellides and impunctate spiriferides. A recrystallized primary layer with a lineation normal to the shell surface and a secondary layer containing fibres stacked

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EXPLANATION OF PLATE 13

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to $2\,\mu$.

Figs. 1, 2. Transverse and oblique sections of the secondary layer of *Cyrtina sp.*, Middle Devonian, Michigan, showing the standard stacking of fibres and an infilled endopuncta (Fig. 2, bottom left-hand corner).

Fig. 3. Detail of the mosaic of prismatic shell of *Athyris sp.*, Middle Devonian, New York.

Figs. 4–6. Transverse sections of *Catazyga headi* (Billings), Upper Ordovician, Ohio, showing the primary layer (Fig. 4, top right-hand corner), standard stacking of secondary fibres and interleaved prismatic lens (Fig. 6, top right-hand corner).

EXPLANATION OF PLATE 14

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to $2\,\mu$.

Fig. 1. Detail of the mosaic of *Cadomella moorei* (Davidson), Lower Jurassic, England, showing the characteristic shape of the exposed part of a secondary fibre.

Figs. 2–5. Transverse sections of *Cadomella davidsoni* (Deslongchamps), Lower Jurassic, England, showing the standard stacking of coarse fibres of the secondary layer (Fig. 2), a detail of the tertiary layer (Fig. 3), the junction between a tubercle and the secondary layer (Fig. 4) and the core of a tubercle (Fig. 5).

Fig. 6. Transverse section of the primary and coarse secondary (right-hand side) layers of *Koninckina leonhardi* (Wissmann), Trias, Austria.

in the usual manner have been seen in the pentameracean *Gypidula* (Pl. 15, fig. 6) and *Pentamerella* (Pl. 16, figs. 5, 6) and the porambonitacean *Anastrophia*, *Camerella*, *Rhysostrophia*, and *Porambonites*. Weathered mosaic patterns have also been found on internal surfaces of *Gypidula* (Pl. 15, fig. 5) and *Anastrophia*. In relation to the history of articulate brachiopods, the most significant of these species are *Porambonites aequirostris* (Schlotheim) from the Llandeilian ($C_{1\beta}$) of Russia and *Rhysostrophia nevadensis* Ulrich and Cooper from the Llanvirnian–Llandeilian Upper Pogonip Formation of Nevada. The discovery of orthodoxly arranged primary and secondary layers in these species implies that the shell structure of Cambrian porambonitaceans was similarly differentiated.

Despite ample evidence that stacked fibres were the basic building units of the pentameride secondary shell, they were commonly subordinate to thick deposits of prismatic calcite. As in spiriferides and living articulates, fibres can be found passing into coarsely crystalline lenses, indicating that the latter were formed by interruption of protein exudation by outer epithelial cells, and the subsequent spread of calcite secretion across intercellular boundaries. The microtexture of *P. aequirostris*, admittedly affected by recrystallization and therefore still open to other interpretations, may represent an ancestral condition. In this species no large original deposits of prismatic calcite were seen; but normally shaped fibres were commonly interleaved with other fibres which were approximately rhombohedral in transverse section (Pl. 17, figs. 1, 2). It is possible, then, that during the deposition of such parts of the secondary shell, protein sheaths persisted but enclosed fibres that grew as stacked rhombohedra. Whether this close conformity to crystal growth was a prevalent feature of primitive articulates remains to be seen.

The development of prismatic calcite within the secondary shell has caused a great deal of trouble in the interpretation of pentameride spondylia. The 'intraseptal lamella' found within the median septum of the 'spondylium duplex', which purported to prove that the septum was made up of incompletely fused dental plates, is composed of prismatic calcite (Pl. 16, figs. 1–4). In view of what is now known about variation in the secretion of calcite by outer epithelium and the widespread distribution of calcite in the pentameride shell, its presence is to be expected and is nothing more than a normal consequence of shell deposition.

ORTHIDA

By reason of their stratigraphic distribution and morphological organization, the orthides are generally conceded to be the most primitive articulates and, if the subphylum was monophyletic, the ancestral group. Three suborders are recognized, the Orthidina, Clitambonitidina, and Triplesiidina, but the shell structure of the last is fundamentally different from the other two and will be discussed in another context.

Sampling among orthidines and clitambonitidines shows that the microtexture of their shell is indistinguishable from that of the four suborders already described. A primary layer and a secondary layer made up of characteristically shaped fibres have been identified in sections of enteletaceans (*Dalmanella*, *Heterorthis*, *Isorthis*, *Onniella*, *Resserella*, *Rhipidomella* (Pl. 17, fig. 4), *Schizophoria*), orthaceans (*Dinorthis*, *Glyptorthis* (Pl. 18, figs. 1–3), *Hebertella*, *Hesperorthis*, *Orthambonites* (Pl. 17, fig. 6), *Orthostrophia*, *Orusia* (Pl. 18, figs. 4, 5), *Phragmorthis*, *Skenidioides*, *Valcourea*), clitambonitaceans (*Vellamo* (Pl. 18, fig. 6), *Eremotoechia*), and gonambonitaceans (*Antigonambonites*).

Surface mosaic, compatible with the stacking of fibres in alternate rows, has also been seen in *Glyptorthis*, *Hebertella*, *Isorthis*. In a pedicle valve of *Rhipidomella sp.* from the Pennsylvanian Finis Shales, the entire mosaic (Pl. 17, fig. 3) was sufficiently well preserved to show that most fibres radiated from the muscle scars where, as was to be expected, the pattern had broken down. This prevalent alignment, more or less parallel with the ribs and normal to the shell edge, implies that the fibres grew away from the primary layer linearly and not in spiral arcs as in living species; but whether such simplicity was a general feature of the orthide shell has still to be determined.

The difficulty of identifying the primary layer has already been commented on by Williams and Rowell (*in* Williams *et al.* 1965, p. H67), and current studies confirm the opinion expressed then that the layer was only thinly developed. Recognition of the layer is undeniably complicated by recrystallization and diffusion exchange with rock matrix, but it has certainly been seen in *Glyptorthis* (Pl. 18, fig. 1), *Orthambonites*, *Orusia* (Pl. 18, figs. 4, 5), and *Rhipidomella* as a thin skin bearing a dominant lineation normal to the shell surface. Actual measurements are, of course, meaningless, but a good idea of variation in relative thickness can be got by counting how many fibres, in strict succession, occurred in an equal thickness of secondary shell immediately underlying the primary layer. In the four genera referred to above, between three and five fibres were together as thick as the overlying primary layer, compared with about nine fibres in *Hemithiris* and *Spiriferina* and fifteen in *Macandrevia*.

Like the Spiriferida and Rhynchonellida, the Orthida includes endopunctate as well as impunctate species. The former group, the enteletaceans, survived into the Permian as fairly common and widely distributed stocks and so provides good material for study. All well preserved shells examined (mainly *Rhipidomella spp.* from the Permo-Carboniferous (Pl. 17, fig. 5) and *Resserella sp.* from the Wenlock) are permeated by canals originating at the shell edge and showing all the characteristics of endopunctation (including even the encirclement of a canal by a single fibre). The canals, therefore,

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EXPLANATION OF PLATE 15

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2μ.

Figs. 1, 2. Transverse sections of *Koninckina leonhardi* (Wissmann), Trias, Austria, showing the standard stacking of coarse fibres of the secondary layer at its junction with the tertiary layer.

Fig. 3. Transverse section of the calcareous ribbon of a spire of *Koninckina leonhardi* (Wissmann), Trias, Austria, showing the standard stacking of secondary fibres.

Fig. 4. Transverse section of *Thecospira haidingeri* (Suess), Trias, Austria, showing the junction between the primary layer and the secondary layer with orthodoxly stacked fibres.

Figs. 5, 6. Details of the mosaic and transverse section of the secondary shell of *Gypidula sp.*, Middle Silurian, England.

EXPLANATION OF PLATE 16

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2μ.

Figs. 1–4. Transverse sections of the spondylial septum in the pedicle valve *Gypidula sp.*, Middle Silurian, England, showing secondary fibres bounding the septum (Fig. 3) with interleaved prismatic lenses (Figs. 1, 4) and a detail of the intraseptal lamella (Fig. 2).

Figs. 5, 6. Transverse and oblique sections of the secondary layer of a valve of *Pentamerella* cf. *lingua* Imbrie, Middle Devonian, Michigan, showing the standard stacking of fibres.

must have accommodated persistent outgrowths of the mantle that were sufficiently like terebratulide caeca to inhibit calcite secretion in their vicinity, and there is no reason to dispute the endopunctate condition of the enteletacean shell.

In summary, studies of the Orthida, although not yet including Lower Cambrian representatives like the billingsellaceans, have revealed the antiquity of the origin, growth and secretory activities of the living articulate mantle. The only possible differences in the resultant shell fabric, the thinness of the primary layer, and the dominantly radial growth of the secondary fibres, are minor changes in fashion compared with the fundamental stability of the complicated succession of secretory functions performed by the plasma membranes of the outer epithelium.

STROPHOMENIDA

The last order to be discussed, the Strophomenida, poses the greatest challenge in the interpretation of the shell structure because the fabric of the majority of species is unlike that of other articulate brachiopods. Moreover, research to date suggests that the classification of the groups assigned to the order will have to be revised, at least to allow for the removal of the Cadomellacea and Thecospiridae (neither of which, in terms of shell deposition, can be related to the strophomenides), and possibly to allow for the inclusion of the Triplesiidina. However, the remaining stocks together provide evidence of how the more extreme deviations in strophomenide shell structure arose from the standard impunctate pattern. Fortunately, the most fundamental change appears from preliminary sampling to have affected all strophomenides except the plectambonitaceans, which alone need to be considered separately.

Microstructure of plectambonitaceans

The plectambonitacean shell structure is dominated by the development of the standard fibres which were stacked in the normal manner and, judging from the general clarity of the boundaries, ensheathed in protein. This arrangement is typical of the secondary layer of all plectambonitaceans studied (*Anoptambonites*, *Bimuria* (Pl. 19, fig. 5), *Isophragma*, *Leangella*, *Leptellina*, *Plectodonta*, *Sericoidea*, *Sowerbyella* (Pl. 19, figs. 1, 2), and *Toquimia*). The mosaic is variably preserved, but in *Isophragma*, *Sericoidea*, and *Sowerbyella* at least, the trend of the exposed parts of fibres shows that they grew more or less radially from the umbonal area and are disposed parallel with, or slightly oblique to, the ribbing with sporadic transgressions directed medially, especially in the lateral areas.

The primary layer is problematic in that a recrystallized skin of uniform thickness characteristic of fossil species belonging to other orders has not been seen; and, at first sight, as in *Isophragma*, fibres appear to extend to the shell edge and occupy the crests and interspaces of ribs. However, a clue to the nature of these outermost fibres is afforded by *Bimuria* and other plectambonitaceans bearing feathery outgrowths that have coalesced into concentric protuberances (comae) on the external shell surface. In certain transverse sections of *Bimuria* normally shaped fibres are seen to be overlain medially by rows of rectangular blocks of calcite arranged neatly one above the other (Pl. 19, fig. 4), and which pass laterally into long, outwardly curving extensions of the shell surface. Bearing in mind the radial growth of the shell, it is clear that these views represent the

transverse and longitudinal sections of a new type of fibre. To avoid confusion it is proposed to call such fibres 'laminae'. They are like narrow arcuate ribbons of calcite and are not morphologically differentiated, like normal fibres, to lie in alternate rows. The laminae constitute the primary layer of the genus. They can be envisaged as having been deposited by the outer lobe of the plectambonitacean mantle in such a way that each lamina was secreted by a regularly arranged column of cubic outer epithelium. The completeness of laminar boundaries may indicate that they were enclosed in protein. Alternatively the discrete nature of individual laminae and especially their separation into well-defined rows may reflect a periodicity arising from repeated interruption in secretion. The contrast in their disposition, between being flat-lying in a layer of uniform thickness and outwardly flaring in comae, certainly reflects the extensible property of the outer lobe of the plectambonitacean mantle. The distal segregation of laminar rows in comae required the retraction of the outer mantle lobe to a position marking the outer limit of close adherence between two rows, then a rapid extension of

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EXPLANATION OF PLATE 17

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2μ.

Figs. 1, 2. Transverse sections of the secondary layer of a valve of *Porambonites aequirostris* (Schlotheim), Lower Ordovician, U.S.S.R., showing the standard stacking of fibres.

Figs. 3–5. Mosaic and transverse sections of the secondary layer of a valve of *Rhipidomella sp.*, Pennsylvanian, Texas, showing the characteristic shape of exposed parts of fibres (Fig. 3), the standard stacking of fibres (Fig. 4), and their outward deflection along their junction with an infilled endopuncta (Fig. 5).

Fig. 6. Transverse section of a valve of *Orthambonites parvicrassicostatus* Cooper, Upper Ordovician, Scotland, showing the standard stacking of fibres.

EXPLANATION OF PLATE 18

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2μ.

Figs. 1–3. Transverse and oblique sections of a valve of *Glyptorthis costellata* Cooper, Upper Ordovician, Oklahoma, showing the primary layer (Fig. 1, right-hand side) and the standard stacking of secondary fibres.

Figs. 4, 5. Slightly oblique sections of a valve of *Orusia lenticularis* (Linnarsson), Middle Cambrian, Sweden, showing the primary layer and the secondary layer with orthodoxly stacked fibres.

Fig. 6. Transverse section of the secondary layer of a valve of *Vellamo sp.*, Upper Ordovician, Minnesota, showing the standard stacking of fibres.

EXPLANATION OF PLATE 19

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2μ.

Figs. 1–3. Transverse and oblique sections of the secondary layer of a valve of *Sowerbyella variabilis* Cooper, Upper Ordovician, Oklahoma, showing the standard stacking of fibres and their relationship with a taleola (Fig. 3).

Figs. 4–6. Transverse sections of a valve of *Bimuria* cf. *buttsi* Cooper, Upper Ordovician, Scotland, showing the laminae of the primary layer (Fig. 4), the standard stacking of fibres and their relationship with a taleola (Fig. 6, left-hand side).

the lobe, presumably stiffened almost immediately by exuded periostracum, followed by the secretion of an interpolated mat of calcite crystallites.

Significance of pseudopunctae

The other condition of the plectambonitacean shell exciting attention arose from the growth of numerous cylindroid bodies of calcite (taleolae) which cause deflections in the shell fabric. This pseudopunctate condition is neither invariably characteristic of the plectambonitaceans (*Ukoa* is reported to be impunctate) nor restricted to members of that superfamily. Taleolae also occur in the strophomenaceans, productidines, chonetidines, and even the clitambonitidine gonambonitaceans, although not in the early davidsoniaceans. Some early strophomenaceans appear to lack taleolae and yet show identical deflections of their fabric (Williams and Rowell *in* Williams *et al.* 1965, p. H71). Despite these exceptions, the pseudopunctate shell can be regarded as typical of the strophomenides and, being related to the growth of taleolae which are found in the plectambonitaceans (Pl. 19, figs. 3, 6), can be interpreted for the order generally in terms of the more orthodox shell structure of the plectambonitaceans.

Taleolae, which in *Sowerbyella* are between 12 and 15 μ in diameter, are normally persistent features of the plectambonitacean shell extending inwardly from the laminar primary layer as arcuate, anteriorly inclined rods (text-fig. 24) that penetrate the entire secondary layer to emerge at the internal surface as apices of well-developed tubercles (text-fig. 23). The arcuate trace and inclination of the rods are growth phenomena reflecting the tendency of the mantle to be pushed outwards radially in response to the thickening of secondary shell through elongation of the fibres. Since the growth of rods and fibres were closely co-ordinated, pseudopunctae (i.e. taleolae and enclosing fibres) are characteristically asymmetrical in longitudinal section, with constituent fibres deflected *inwardly* and inclined to the anterior and posterior faces of taleolae at narrowly and widely acute angles respectively. The morphological differences between taleolae and secondary fibres, and the sharpness of boundaries between them which generally survive recrystallization, indicate that they were deposited by two different kinds of cells. In the light of what is now known about epithelial specialization in living articulates, it is safe to assume that fibres were deposited by rhombohedral cells in alternate rows, and taleolae by cells like those underlying muscle bases. The origin and growth of the former may be envisaged as follows.

As the plectambonitacean shell was enlarged peripherally through the secretion of laminae by epithelial cells brought into position by the 'conveyor belt' system, certain cells at regular intervals rapidly secreted calcite to form a series of mounds bulging inwards. Nothing is yet known about the orientation of the crystallites making up these taleolar bases. But deposition on them proceeded at a faster rate than in the rest of the shell so that the apices of growing taleolae, upon which the same secreting cell(s), rested, always extended inwardly more than the surrounding laminae or fibres. Moreover, despite minor variations in thickness which look like small-scale transgressions and regressions relative to the enclosing shell (text-fig. 24), the boundaries were well defined and suggest that taleolae were enclosed in a protein sheath, and that cells responsible for the secretion of both sheath and rod functioned as separate units within the main spread of the outer epithelium. In effect, the independent, faster growth of each taleola maintained a convex surface up and around which normal epithelial cells

secreting laminae or fibres could migrate (text-fig. 23). Slight fluctuations in the thickness of taleolae simply represented contraction or expansion of the boundaries of taleolar cells in relation to the differential movement of the surrounding outer epithelium, and not the incorporation of fibres and laminae into the taleolar core as may appear in some microscopic sections.

There is little doubt that taleolae found in all strophomenide species are identical with those in the plectambonitaceans (Pl. 20, figs. 3, 5; Pl. 22, fig. 1). This is certainly
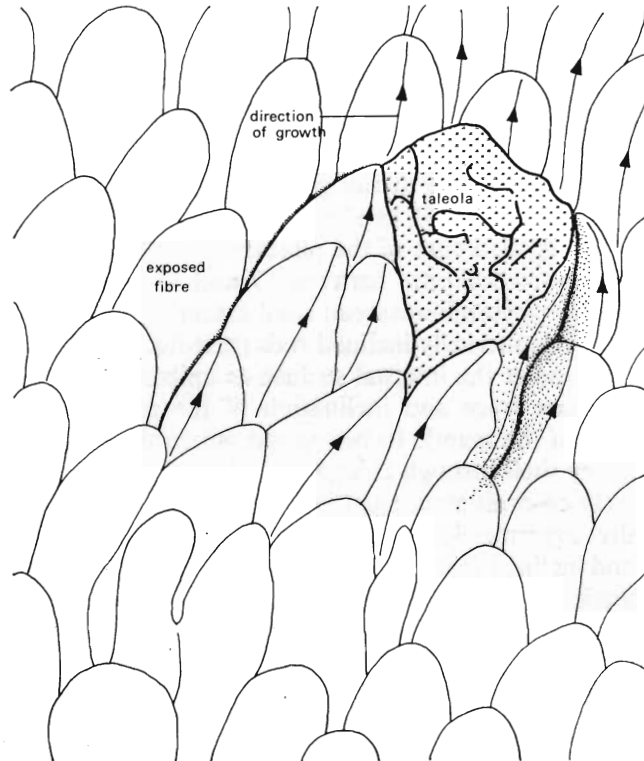
TEXT-FIG. 23. Plan of part of the internal surface of a valve of *Sowerbyella*, showing the relationship between a tubercle with an exposed taleolar core and the mosaic

EXPLANATION OF PLATE 20

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2μ.

Figs. 1, 2. Transverse sections of a valve of *Leptaena acuticuspidata* Amsden, Lower Devonian, Oklahoma, showing mainly crested laminae, and their internal junction with rock matrix (Fig. 1, bottom left-hand corner).

Figs. 3, 4. Transverse sections of a valve of *Leptagonia analoga* (Phillips), Lower Carboniferous, England, showing mainly flat laminae, and their relationship with a taleola (Fig. 3).

Figs. 5, 6. Transverse sections of a valve of *Pholidostrophia* cf. *geniculata* Imbrie, Middle Devonian, Michigan, showing laminae in relation with a taleola (Fig. 5), and their separation by a vein of rock matrix (Fig. 6).

true of taleolae that appeared in Devonian davidsoniaceans long after the inception of the group during the Ordovician period. Even the pseudopunctae of some strophomenaceans, that appear to lack taleolae and would therefore consist solely of microscopic concentric buckles of the shell fabric, may have functioned in the same manner. Pseudopunctae with taleolar cores were also developed in the orthide gonambonitaceans as typified by *Antigonambonites*, and, since they involved normal secondary fibres, are indistinguishable from plectambonitacean pseudopunctae. Indeed, in terms of morphology and growth, very close comparisons can be drawn between plectambonitacean
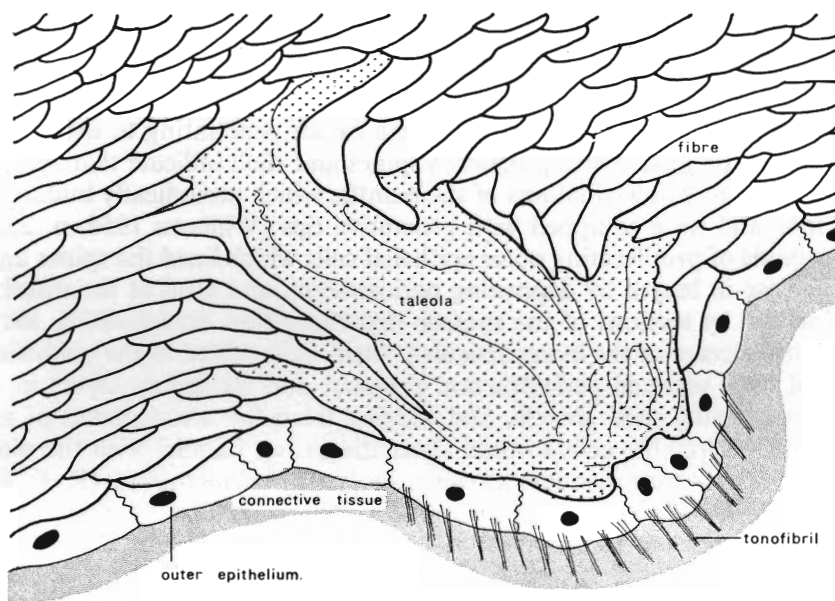
TEXT-FIG. 24. Stylized oblique longitudinal section of a taleola of *Sowerbyella*, showing its inferred relationship to outer epithelium

pseudopunctae and tubercles found in stocks belonging to more remotely related orders like the terebratulide *Megerlia* (Pl. 6, figs. 5, 6) and, as will be shown later, the spiriferides *Thecospira* and *Cadomella* (Pl. 14, figs. 4, 5).

The function of taleolae and their capping cells inevitably remains a matter of inference, but a previously expressed opinion that the cells were permeated by densely distributed tonofibrils (Williams 1956, p. 252) still appears to be reasonable. More information may be forthcoming when current researches into the function of the tubercles of *Megerlia* are complete.

Microstructure of other strophomenides

Despite ample morphological evidence for regarding the Strophomenida as a clearly defined, natural group, the shell structure of strophomenaceans, productidines, and davidsoniaceans and chonetidines as restricted in this paper, is radically different from that of the plectambonitaceans and all other articulate brachiopods with the exception of the triplesiidines. Relative to the size of the order, sampling may appear to have been

too perfunctory, but it included genera from all principal suprafamilial units—strophomenaceans (*Douvillina, Leptaena, Leptagonia, Leptodonta, Leptostrophia, Rafinesquina, Strophodonta, Strophomena, Strophonella, Strophonelloides*), davidsoniaceans (*Derbya, Fardenia, Orthotetes, Schuchertella*), chonetidines (*Lissochonetes, Rugosochonetes*), productidines (*Dictyoclostus, Juresania, Productus, Marginifera*)—and covered a sufficient geological range to warrant confidence in its adequacy. Using the preservation of contemporary rhynchonellides and terebratulides as a guide, typical strophomenide shell fabric in an almost unaltered state was found in *Juresania sp.* from the Pennsylvanian Finis Shales of Texas and in broken productid spines from the Carboniferous shales of Derbyshire. The microstructure of these productidines has been used as the model for understanding shell deposition and growth.

The key to productidine shell deposition is provided by the microstructure of the external hollow spines that communicated with canals penetrating to the shell interior. Considerations of the relationship between spines and shell indicate that their development was controlled by evaginations of the mantle, which periodically budded off from the outer lobe and were equipped with generative tips (Williams 1956, p. 252). These tips were capable of proliferating outer epithelial cells which lined the spines and caused them to increase in length by depositing periostracum and shell at the distal ends. In fact, as is shown by sections of the spinose rhynchonellide *Acanthothiris*, the growing spine was a microcosm of the living articulate shell. Cells added to the epithelial core of a spine must have secreted periostracum, primary, and secondary layers in the strict order followed during shell growth, and judging from the arrangement of secondary fibres in *Acanthothiris*, the cells formed alternating rows parallel with the diameter of the spine. The spines were also fast growing. In *Institella leonardensis* (R. E. King), for example, figured by Muir-Wood and Cooper (1960, pl. 22, fig. 9), there are posterolateral spines which extended outwards at least seven times as fast as the advance of the valve margin, and in *Juresania* initial growth could have been at least three times as fast. In short, one would expect the productidine spine to show any shell differentiation that arose from changes in secretory habits of the lining epithelium; and since the fast growth of the spine precluded any gross modification or re-orientation of its calcareous constituents and their secreting cells, transverse and longitudinal sections should give end and side views respectively of the basic building units.

The deposits making up productidine spines are remarkably uniform. In transverse section, they consist of fine bands disposed concentrically with the axial hollow of the spine and, as far as one can be certain in tracing individual units, forming rings of constant thickness (Pl. 22, figs. 3, 4). The banding extends throughout the entire section so that the primary shell, deposited at the distal edge of the spine, is not distinguishable from secondary shell. The alleged sporadically developed primary layers, previously found by Williams and Rowell (*in* Williams *et al.* 1965, p. H71) in some productidines could well be diffusion accretions which accumulated on the external surfaces during diagenesis. Ignoring irregular cracks which are artifacts or *post-mortem* effects of burial and compaction, there is no consistent pattern of deeply etched grooves indicative of surfaces of separation like continuous protein sheets. However, there are a series of nodes and pits, about $0\cdot3\,\mu$ in diameter, which are aligned along the bands and are commonly spaced about $1\,\mu$ apart (Pl. 22, fig. 3). Moreover, at variable intervals, strong discontinuous grooves occur, which divide the bands into groups of differing thickness;

and at such junctions the pits are more deeply developed and are usually overhung by sharp crested canopies. Oblique and longitudinal sections show the same pattern except that pits and nodes are much rarer, and the succession, with banding still visible, is more conspicuously divided up into impersistently defined layers and lenses.

Two conclusions may be derived from these different aspects of the microstructure of the productidine spine. First, banding, which imparts etched sections with the appearance of bedded successions in various stages of weathering, is undoubtedly the dominant

TABLE 1. The number of measured bands (a) believed to represent diurnal deposition, together with their average (b) and range (c) of thickness in the named strophomenides and orthides

	(a)	(b)	(c)
Derbya cf. cymbula Hall and Clarke, Permian, Texas	152	0.37μ	0.29–0.5μ
Juresania sp., Pennsylvanian, Texas	116	0.42μ	0.35–0.49μ
Leptaena acuticuspidata Amsden, Lower Devonian, Oklahoma	36	0.46μ	0.39–0.58μ
Leptagonia analoga (Phillips), Lower Carboniferous, Northumberland	47	0.35μ	0.22–0.44μ
Lissochonetes sp., Pennsylvanian, Texas	28	0.41μ	0.37–0.44μ
Oxoplecia filosa Cooper, Upper Ordovician, Oklahoma	85	0.36μ	0.27–0.44μ
Pholidostrophia cf. geniculata Imbrie, Middle Devonian, Michigan	100	0.44μ	0.37–0.53μ
Productidine spines, Lower Carboniferous, Northumberland	100	0.19μ	0.17–0.33μ
Streptis grayi Davidson, Middle Silurian, Shropshire	82	0.43μ	0.33–0.55μ

feature. Secondly, there was no co-ordinated exudation of protein segregating deposits of calcite into regularly stacked units. The regularity of the banding is noteworthy. In *Juresania sp.*, the mean periodicity was 0.42μ compared with 0.19μ in the Carboniferous spines (see Table 1). A periodicity in the deposition of fibres of living terebratulides has already been described and was attributed to diurnal factors. It seems equally reasonable to regard the banding in the productidine spine as registering daily deposition and crude estimates seem to confirm the assumption. Thus, if the thickest part of the brachial valve is taken as an index of age, a specimen of *Juresania sp.* from the Finis Shales, 37.0 mm. long, was just over 9 years old when it died; and Carboniferous productid spines, 0.3 mm. thick and with an axial canal 0.2 mm. in diameter, took just under 2 months to attain that condition. Clearly more detailed comparative study will have to be made of this mode of deposition, but preliminary work is encouraging.

In relation to mantle activity, the significance of periodicity in shell deposition is its lateral as well as vertical extent. If epithelial cells lining a spine are each assumed to have secreted calcite as discrete units, and to have been as big as those responsible for the relatively fast growing loops of living terebratulides, that is about 10μ in cross section, regular breaks in deposition are to be expected at some such interval. In fact none is found at that interval or any other. The calcite must therefore have been secreted across intercellular boundaries, and the lack of an organized protein net accords with this. Indeed, if the pits and nodes, best seen in transverse sections, represented entrapped protein strands which were continually exuded from the outer epithelial plasma membranes, the presence of protein in productidine shells (Jope *in* Williams *et al.* 1965, p. H161) and the impersistent segregation of the succession into lenses and layers as seen in longitudinal section would be accounted for.

The productidine outer epithelium, then, may be pictured as a layer of simple cuboidal cells (not distorted as in normal articulates into rhombohedral shapes) each contributing

to the deposition of an extensive layer of calcite to which it was loosely attached by impersistent proteinous extensions from the secreting surface (text-fig. 25). Such a reconstruction is consistent with the microstructure of the main part of the shell as seen in sections and rarely preserved mosaics. Here the banding is still dominant in places; in others it may be lost or exist as a ghost-like trace within prominently defined, relatively thick layers interleaved with enlarged lenticles (Pl. 21, fig. 6; Pl. 22, figs. 1, 2). The
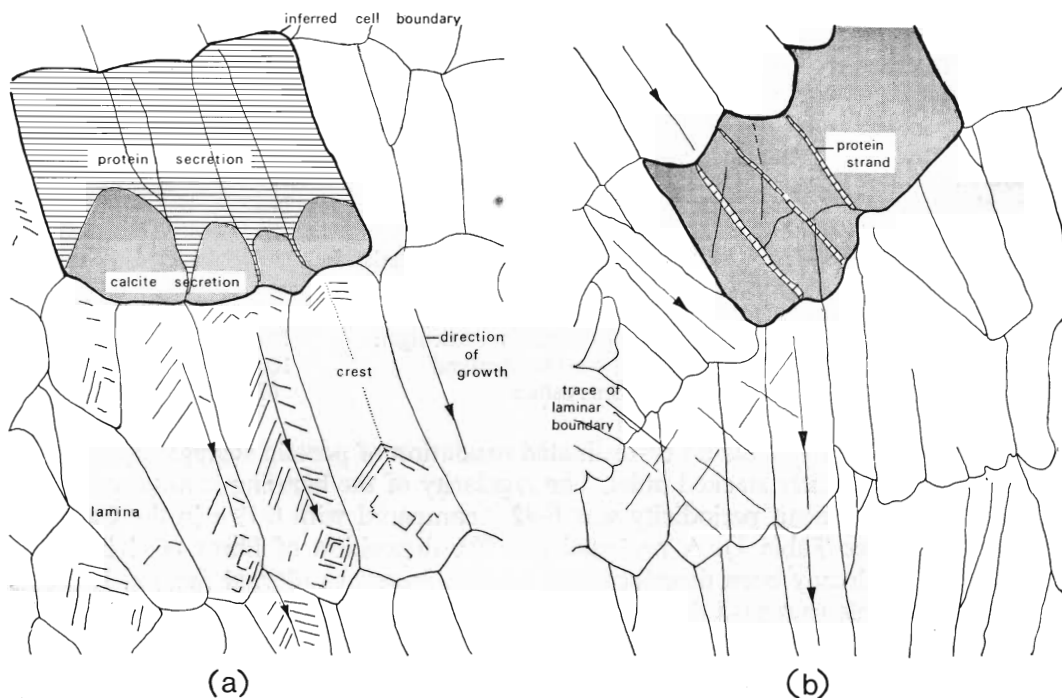
TEXT-FIG. 25. Plan of crested (*a*) and flat (*b*) laminae exposed on the internal surface of a valve of *Juresania*, showing their inferred relationship with outer epithelium

lenticles taper laterally from a mid-section which may be bounded by rhombohedral angles, and a group of them, normally three or four, may become continuous to form an undulating feature. The layers and lenticles are respectively longitudinal, or oblique and transverse, sections of narrow fibres with angular crests which can pass into blades no thicker than bands. These structures are like the laminae found in the primary layer

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EXPLANATION OF PLATE 21

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2μ.

Fig. 1. Transverse section of a valve of *Pholidostrophia* cf. *geniculata* Imbrie, Middle Devonian, Michigan, showing flat laminae.

Figs. 2–6. Various views of a valve of *Juresania sp.*, Pennsylvanian, Texas, showing the characteristic mosaics of crested and flat laminae (Figs. 2, 3 respectively), the surface appearance of crested and flat laminae in exfoliated shell (Figs. 4, 5), and flat laminae bent to accommodate an unseen taleola (Fig. 6).

of the plectambonitaceans and are appropriately referred to as crested or flat laminae. They are well seen in tangential sections (Pl. 21, figs. 4, 5), and especially in rare patches of original mosaic (Pl. 21, figs. 2, 3) still surviving on the shell floor of *Juresania*, and appear to represent two distinct forms of deposition.

Crested laminae, with an average width of $3 \cdot 1\mu$ (range $1 \cdot 7\mu$ to $4 \cdot 3\mu$) in 37 laminae, form overlapping and normally alternating rows about 10μ wide (text-fig. 25 a; Pl. 21, fig. 2). The crest of a lamina subtends a rhombohedral angle and, although the basal boundary in common with the laminae (or lamina) in front may be rounded, it is usually angular and in conjunction with the front edge of the crest defines a scalenohedral face. It is, therefore, probable that these crystal faces represent the actual sites of accretion that led to the forward extension of crested laminae. However, it is unlikely that a mature cell would have covered so small an area as a single lamina; and since crested laminae may overlap laterally as well as frontally and may be sporadically or even entirely continuous with one another, it is likely that three or four independent centres of calcite secretion existed simultaneously on the plasma membrane of one cell. Such centres, judging from the strength of most laminar boundaries, would have been separated from one another by membranous folds or exuded strands of protein. If this were so, the crested laminae were the nearest approach to the standard fibre of other articulates within the entire process of strophomenide shell deposition. Comparison, of course, can only be made between the modes of deposition whereby calcite secretion was seemingly restricted to parts of the plasma membrane of an outer epithelial cell. Nevertheless, since such selectivity reflected an over-all decrease in the rate of calcite secretion, crested laminae owe their distinctiveness to slow localized deposition.

In contrast, flat laminae (text-fig. 25 b; Pl. 21, fig. 3) were clearly the product of accelerated deposition by almost all of the plasma membrane. On exfoliated surfaces, they appear as long blades tending to encroach laterally and frontally in interleaving patterns. Their lateral junctions may be linear or, less commonly, crenulated like the imprint of intercellular boundaries (Pl. 21, fig. 5), and are frequently crossed obliquely by slightly raised lineations which are traces of underlying laminar boundaries and may therefore be trails of protein strands (Pl. 21, fig. 4; compare Pl. 23, fig. 2). In mosaics, flat laminae, overlapping laterally and frontally, were also organized in differently orientated rows like crested laminae, but grew as blades terminating in rhombohedral angles and must have been formed by uniform deposition over the entire surface. In arrangement and morphology they must have been like the laminae occurring at the internal surfaces of spines.

To recapitulate, the productidine outer epithelium normally secreted uniform layers of calcite which were variably segregated into flat blade-like laminae by impersistent protein strands exuded by the cell surfaces. These partitions did not coincide with the boundaries of cells, which periodically became detached from the carbonate surfaces and shifted position so that the laminae overlapped laterally and anteriorly. Slower deposition was attended by the restriction of calcite secretion to certain parts of the plasma membranes. Steady accretion in these centres, which were normally separated from one another, caused the flat laminae to become lenticular and ultimately, when the terminal surfaces of deposition were transformed into crystal faces, rhombohedral or scalenohedral in outline. The radial component of productidine shell growth, as expressed in the enlargement of productidine valves by marginal increment, leaves little

doubt that expansion of the mantle, like that of living articulates, was sustained by cell proliferation along its edge. However, no consistent differentiation in calcite secretion took place, so that the secondary shell was indistinguishable from the primary (i.e. the laminae being deposited at the mantle edge). Another striking novelty of the productidine mantle was its capacity for extension and retraction, which was probably related to its looser attachment to the shell, and, if taleolae have been correctly interpreted as seats for muscle ties, to a permeating network of tonofibrils. Such properties would explain the repeated growth of marginal trails in productidines and the dissimilarity of the valve size of the richthofeniaceans and oldhaminidines. It is generally assumed that the much greater area of the pedicle valves of the last named stocks entailed the permanent exposure of a proportionate amount of the ventral mantle. Alternatively, the extra shell may have been deposited by a mantle that continually advanced from, or retreated to, the cover afforded by the brachial valve, in response to extraneous factors.

The microstructure of the productidine shell has been described and interpreted in detail because electron microscope studies have confirmed that it serves as a model for other strophomenides like *Leptagonia* (Pl. 20, figs. 3, 4), *Lissochonetes* (Pl. 22, figs. 5, 6) and *Derbya* (Pl. 23, fig. 3). Laminar mosaics have been observed on shell interiors of *Eomarginifera*, *Schuchertella*, *Lissochonetes*, *Rafinesquina*, and *Strophodonta*. Such detail is due to exceptionally favourable preservation and so far has been found only in small patches. But in specimens of *Lissochonetes* and especially *Schuchertella haraganensis* Amsden from the Lower Devonian Haragan Formation, in both of which the mosaic survived in interspaces between ribs (Pl. 23, fig. 1), laminar rows were more or less parallel with the valve margin, suggesting that laminae were basically radially disposed. There are differences in the proportions of crested and flat laminae comprising individual

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EXPLANATION OF PLATE 22

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left hand corner of each figure equivalent to 2μ.

Figs. 1, 2. Transverse sections of a valve of *Juresania sp.*, Pennsylvanian, Texas, showing flat laminae in relation with a taleola (Fig. 1) and some crested laminae (Fig. 2).

Figs. 3, 4. Transverse and oblique sections of a productid spine, Lower Carboniferous, England, showing the characteristic banding of flat laminae, and their internal junction with rock matrix occupying the spinal canal (Fig. 3, bottom left-hand corner; Fig. 4, lower edge).

Figs. 5, 6. Transverse sections of a valve of *Lissochonetes sp.*, Pennsylvanian, Texas, showing flat and crested laminae respectively.

EXPLANATION OF PLATE 23

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2μ.

Figs. 1, 2. Mosaic and exfoliated surface of flat laminae in a valve of *Schuchertella haraganensis* Amsden, Lower Devonian, Oklahoma.

Fig. 3. Transverse section of a valve of *Derbya* cf. *cymbula* Hall and Clarke, Permian, Texas, showing the characteristic banding of flat laminae.

Figs. 4, 5. Transverse sections of a valve of *Streptis grayi* Davidson, Middle Silurian, England, showing the characteristic banding of flat laminae, with some crested laminae (Fig. 4, left-hand side).

Fig. 6. Transverse section of a valve of *Oxoplecia filosa* Cooper, Upper Ordovician, Oklahoma, showing the characteristic banding of flat laminae.

shells. Crested laminae are very common in the disc of *Leptaena sp.* from the Lower Devonian Birdsong Formation (Pl. 20, figs. 1, 2). The shell of *Pholidostrophia*, on the other hand, is mainly composed of flat, regularly disposed laminae that changed their direction of growth in successive layers. Traces of such re-orientations are variably impressed on individual calcitic sheets and have been interpreted by Towe and Harper (1966, p. 154) as an optical diffraction grating responsible for the nacreous sheen of *Pholidostrophia*. Identical arrangements are, however, known in other non-nacreous strophomenaceans as well as productidines and davidsoniaceans (compare, for example, Pl. 23, fig. 2). The loose foliation, which is characteristic of those *Pholidostrophia* shells with a conspicious sheen and produces an interference effect, still appears to be the most important cause of the lustre. Despite these differences in laminar morphology, banding was discernible in all species examined and some measurements are given in Table 1.

Microstructure of triplesiidines, thecospirids, and cadomellaceans

It is now opportune to refer to the triplesiidine shell structure because, surprisingly enough, it is indistinguishable from the laminar fabric just described. Laminae have been seen in sections and exfoliated surfaces of *Triplesia* and *Epacroplecia*, and electron micrographs of *Oxoplecia* (Pl. 23, fig. 6) and *Streptis* (Pl. 23, figs. 4, 5) show that the basic arrangement consists of a fine, even banding interleaved with, or passing laterally into, crested laminae. This pattern is developed throughout the entire shell, so that primary and secondary layers were not differentiated and the mantle must have grown and functioned in exactly the same way as that inferred for strophomenides with laminar shells.

In contrast, two stocks which are currently regarded as aberrant strophomenides do not have a laminar shell structure and are too far removed in time from the last of the plectambonitaceans to have descended from that stock. The first is the Triassic spire-bearer *Thecospira*, which on general considerations of morphology, including a 'pseudo-punctate' shell, was identified as a davidsoniacean (Williams 1953, p. 12). In fact the shell is differentiated like that of any normal articulate into well-defined primary and secondary layers, and although the primary layer was recrystallized in the specimen examined, the secondary shell was composed of characteristically shaped and stacked fibres (Pl. 15, fig. 4). The shell was also 'pseudopunctate' in the sense that tubercles were present and were evidently deposited in evaginations of the outer epithelium which caused an inward deflection of adjacent fibres. However, the tubercles were porous and lineated in a manner as reminiscent of *Megerlia* as of strophomenides, and no great importance should be attached to their existence.

The second group, the Jurassic Cadomellacea, also in terms of general morphology, has long been accepted as related to the strophomenides and, on balance, the choneti-dines (Muir-Wood 1955, p. 90). Moreover, Cowen and Rudwick (1966) found calcareous spires in *C. davidsoni* (Deslongchamps) and on that basis have included the koninckina-ceans, with which they compare *Cadomella*, within the strophomenides. The shell structure of *Cadomella* is certainly identical with that of *Koninckina*. The thin primary layer is usually poorly preserved, but is underlain by the same coarsely crystalline secondary fibres (Pl. 14, fig. 2), which form an orthodox mosaic on the floor of young valves (Pl. 14, fig. 1) and pass inwards into the same well-developed, prismatic, tertiary

layer (Pl. 14, fig. 3) in adult shells. Tubercles are also developed in this stock (Pl. 14, figs. 4, 5) and a strong lineation parallel with their long axes may persist through the tertiary layer. Yet, as with *Thecospira*, the presence of such tubercles can no longer be accepted as irrefutable evidence of strophomenide affinities. Indeed, irrespective of certain morphological features like the delthyrial cover, I now find it inconceivable that strophomenide homeomorphy should involve the growth of a spiriferoid-like shell microstructure as well as calcareous spires, and I am prompted to reassign *Thecospira* and *Cadomella* and its associates to the Spiriferida.

ANOMALOUS GROUPS

The shell structure of two groups of brachiopods, currently classified as Articulata but lacking obvious affinities with other members of the subphylum, remains to be described.

Microstructure of Dictyonellidina

The older group, the Dictyonellidina, contains four Palaeozoic genera which are only vaguely articulate in general morphology and may not have shared a common ancestry (Rowell *in* Williams *et al.* 1965, p. H359). But, even if, as is likely, the shell structure of *Dictyonella*, the most commonly occurring stock, is typical of other dictyonellidines, their origin remains an enigma. The morphology of the *Dictyonella* shell is complicated by the development of a unique surface ornament. This consists of deep pits, up to 0·7 sq. mm. in area, which are rhombohedral in outline and so regularly arranged that the bounding thin partitions generally conform to curved traces, running clockwise from the right posterior half of a valve and anticlockwise from the left posterior half. The base of each pit is continuous with a relatively narrow canal penetrating the floor of the valve; such canals constitute the 'punctae' which are reputedly characteristic of the suborder. The ultrastructure of the shell is quite distinct from rock matrix, even when the latter consists of recrystallized calcite, so that it seems reasonable to attribute observed differences to the state of the fabric during life. Throughout partitions and shell floor a rhombohedral pattern is subordinate to well-distributed coarse pits and channels up to 0·6 μ in width, which are taken to be etched remnants of microvillous trails (Pl. 24, figs. 5, 6). There is no obvious lineation related to either the internal surface or the canal sides, and the closest comparison that can be drawn is with the ultrastructure of the primary layer of the standard articulate shell. Thus it is likely that the dictyonellidine shell was deposited in the same way as the primary layer of living rhynchonellides. The equation of the canals with articulate endopunctae is more hazardous. The canals,

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or outward extensions of them, were almost certainly in contact with periostracum, and they evidently persisted throughout life, indicating an inhibition of calcite secretion by lining epithelium. Whether these features are sufficient to justify the comparison becomes a matter of personal opinion. It may be tempting further to correlate the surface pits of *Dictyonella* with the expanded distal ends of typical articulate punctae. However, this would ignore the absence of such pits in other stocks; and, since there may be no
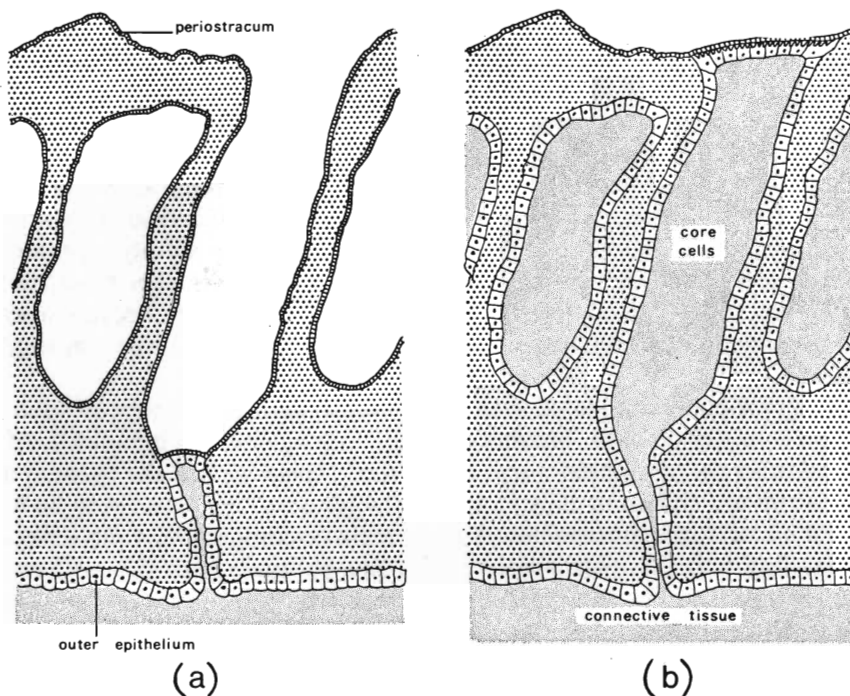
TEXT-FIG. 26. Two restorations of part of a valve of *Dictyonella capewelli* (Davidson), showing alternative inferred distributions of periostracum and outer epithelium within shell pits

anatomical implication in the connexion between pits and canals, the pits may equally well have been lined by periostracum, in the manner expected for topographic variation of the calcareous shell surface, as covered by it and occupied by canal extensions (text-fig. 26).

Thecideidina

The Thecideidina first appeared in the Trias and are represented today by *Lacazella* and *Thecidea*. No one would dispute that they belong to the Articulata but their position within the phylogenetic hierarchy of that subphylum, i.e. whether they were derived from the strophomenides, terebratulides or spiriferides, is controversial (Elliott, p. H857, Williams and Rowell, p. H188, both *in* Williams *et al.* 1965). Unfortunately, expectations that a study of the ultrastructure of the shell would unequivocally resolve the problem remain unfilled, although the probability of correctly identifying the ancestral group has been greatly increased.

The shell of *Lacazella*, which has been taken as the thecideidine model, is tuberculate and endopunctate. The former condition (Pl. 24, fig. 1), along with other features, has been regarded as indicative of strophomenide affinity; the latter is reminiscent of tere-bratulides (or certain spiriferides) since the caeca occupying the branching canals are also connected to the periostracum by fine brushes. The calcareous shell is not dif-ferentiated into primary and secondary layers but shows in section and casts of internal surfaces a uniform fabric of microscopic pores and trails superimposed on a fine banding (Pl. 24, figs. 2–4). The trails are closely distributed normal to the internal surface and are clearly traces of microvilli and protein strands left behind within the shell as it was being deposited by an inwardly retreating mantle. The average periodicity for 54 bands measured in the brachial valve was $0 \cdot 19 \mu$ (range $0 \cdot 17$–$0 \cdot 22 \mu$) and is probably a register of daily deposition. Transgression of one set of bands across an older series, outwardly directed arches of which may be truncated along the junction, show that the outer epithelium not only migrates but is also capable of localized resorption. The ultra-structure of tubercles is like that of the remaining shell. They simply represent sites of accelerated deposition so that their cores consist of relatively thicker bands in the style of similar folding (Pl. 24, fig. 3). Indeed structural allusions are apt, because microvillous traces are slightly splayed relative to the banding of tubercles, like cleavage fans in fold systems.

The banding probably originated in the same way as that found in the strophomenides, but there the comparison ends, because the *Lacazella* shell is not laminated. Moreover, although the tubercles, as simple warps of the shell fabric are like the pseudopunctae of some early strophomenaceans, they lack the taleolar cores which seem to be invariably developed in all later strophomenides. A more realistic comparison, both in terms of the subdued banding and the microvillous trails, can be made with the primary layer of other living articulates. The inescapable conclusion seems to be that the single shell type of *Lacazella*, and hence its relatives, is a homologue of the primary layer of the typical articulate.

CONCLUSIONS

Any attempt to trace the evolution of the shell structure of articulate brachiopods is necessarily influenced by the demonstrable antiquity of the triple-layered shell of living forms. Admittedly the existence of a periostracum in fossil material cannot be proved, but its presence in all surviving brachiopods, inarticulate as well as articulate, indicates that it has always been exuded as the shell cover. [Whether the periostracum in inarticu-lates is composed of chitin or protein does not affect its morphological relationship with the rest of the shell.] The chief constituents of the calcareous part of the shell, on the other hand, are more or less identifiable throughout time. A comparative study of them shows that some important changes in the secretory régime did occur in the course of brachiopod evolution, although they were largely irrelevant to the final outcome.

In the great majority of articulates the primary and secondary layers have always been sharply differentiated by the development within the latter of a system of inter-connected protein sheaths segregating simultaneously deposited carbonate into dis-tinctively shaped and stacked fibres. As has been shown, this arrangement can only be brought about by a 'conveyor belt' system of mantle expansion and uniquely phased

changes in the secretory régime of each outer epithelial cell; and since it is characteristic of early orthides and pentamerides, the primitive mantle must have been identical in growth, morphology, and function with that of living rhynchonellides.

Speculation about the origin of the primitive mantle necessitates consideration of the inarticulates, which probably evolved from the same prototype as the articulates. The growth of the inarticulate shell is not well documented but, like the articulate skeleton, it probably always involved the secretion of a periostracum and the enlargement of the mantle by the 'conveyor belt' system (protoplasmic anchors, like strands and caeca permeating the shells of lingulides and craniaceans respectively, preclude other means of growth). It is therefore possible that the mantle of the brachiopod prototype with its peripheral generative zone was initially protected by periostracum alone, and that the secretion of calcium carbonate (or phosphate) beneath that layer represented a later stage in evolution. The preservable inarticulate shell, whether chitino-phosphatic or cal-careous, seems always to have been built up by outer epithelium that was capable of secreting alternating mineral and organic layers across intercellular boundaries. This type of shell is likely to have been deposited by the precursor to the primitive articulate mantle. If this were so, the development of the articulate secondary shell would have represented a significant evolutionary step, whereby the plasma membrane of each outer epithelial cell became specialized to secrete both organic and inorganic skeletal material simultaneously rather than alternately. The differentiation of the primary shell is less easily explained. As a mineral layer interpolated between the periostracum and the secondary shell, it can be interpreted as the earliest organized calcareous skeleton to appear during the evolution of the prototype. If this were true, the secretory sequence followed by the outer epithelial cells during ontogeny is an example of physiological recapitulation. But a persistent, well differentiated, wholly inorganic primary layer is unknown among inarticulates (a homologous layer found in the craniaceans, which probably arose after the divergence of that group, cannot be so described). Even among articulates there is evidence to suggest that the layer was less well developed in orthides. Hence the secretion of a distinctive primary shell may have been a comparatively late innovation in the evolution of the articulate shell, and the calcareous skeleton of the earliest stocks may have consisted solely of fibres ensheathed in protein, but crudely fashioned as trigonal prisms with scalenohedral terminal faces and attached directly to the periostracum.

Whatever the first stages in the evolution of the articulate shell were, subsequent changes are obvious enough (text-fig. 27). The orthides, pentamerides, rhynchonellides, spiriferides, and terebratulides form a continuous chain of descent that led to the survival of the primitive mantle in living species and the growth of a remarkably stable triple-layered shell in the great majority of articulate brachiopods. However, at the cellular level, variation in the secretory behaviour of the outer epithelium gave rise to subtle topographic changes in the terminal faces of secondary fibres. The most important of these changes was initially connected with the development of dense concentrations of tonofibrils in the outer epithelium and associated connective tissue. It led to the break-down of the characteristic arrangement of the secondary fibres by an interruption in the secretion of protein and the coalescence of terminal faces, normally transformed into simple crystal growths, across intercellular boundaries. In orthides, rhynchonellides, and terebratulides, this disruption of secondary shell appears to have been limited to
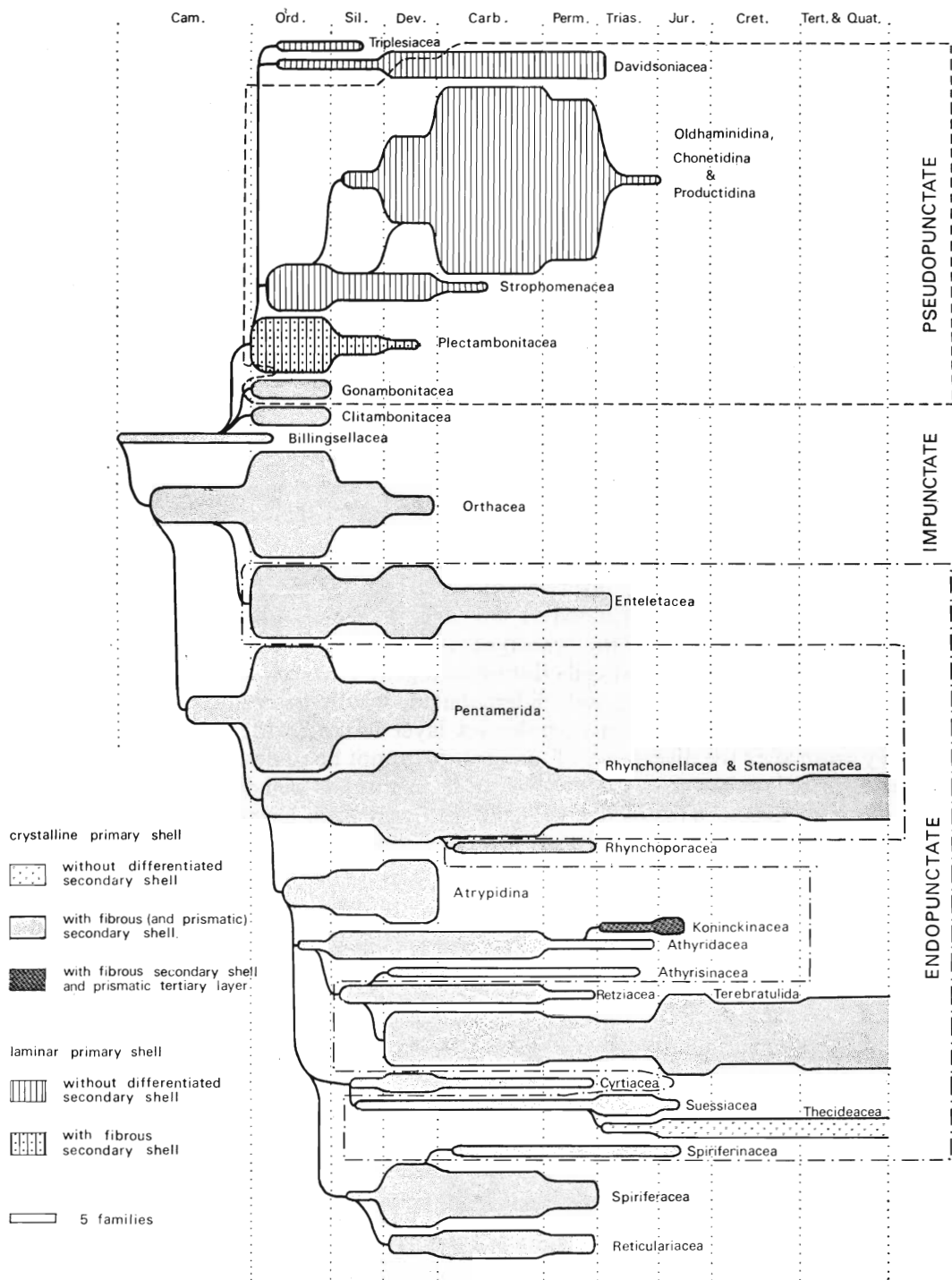
TEXT-FIG. 27. Phylogenetic chart of the articulate brachiopods (excluding the Dictyonellidina), showing the distribution of different types of calcareous shell

those parts of the shell (like muscle scars, cardinal processes, dental plates, etc.) that acted as attachment areas for muscle systems. But in pentamerides and spiriferides interruption in the exudation of protein was commonly precursory to the secretion of relatively thick, coarsely crystalline deposits of calcite spreading well beyond the limits of muscle fields. Most of these prismatic deposits were impersistent and accumulated during temporary changes in the secretory régime of cells that controlled the growth of the secondary layer and can only be regarded as variants of that layer. However, in the koninckinaceans (as represented by *Koninckina* and *Cadomella*) prismatic deposits constitute a true tertiary layer occurring inwardly of the secondary. The well-defined distribution of this layer makes it likely that it arose through a regular change in the secretory régime of outer epithelial cells as they came to lie at a given distance from the expanding shell margin. In effect, each mature cell was in turn responsible for the secretion of parts of the periostracum, primary, secondary, and tertiary layers; and in some respects the deposition of the tertiary layer can be regarded as a reversion to the biochemical conditions obtaining during secretion of the primary shell. A similar change may also have taken place in some other spiriferides and in some pentameraceans like *Gypidula* and *Sieberella*, although the absence of any traces of secondary fabric within the thick internal deposits of prismatic calcite found in such stocks has still to be proved.

Despite the novelty of a third calcareous layer, koninckinaceans and other stocks with a similarly differentiated shell fabric are still an integral part of the main articulate plexus because the extra layer appeared as a gerontomorphic feature which did not upset the standard secretory régime. In fact, as far as is known, only three groups, the Strophomenida, Thecideidina, and Dictyonellidina, are sufficiently different in shell structure to require interpretation based on the assumption that radical changes in the secretory activities of their mantles took place.

The derivation of strophomenides is most easily understood. The plectambonitaceans have always been regarded as primitive strophomenides and current understanding of their general morphology and stratigraphic distribution conclusively reaffirms the traditional view. Yet the plectambonitacean shell structure is basically like that of the standard articulate and differs only in the laminar nature of the primary layer. The difference is extremely important for two reasons. First, it represents a fundamental change in the mode of secretion by outer epithelial cells at the mantle edge, although they reverted to the standard régime in the deposition of secondary shell. Secondly, the plectambonitacean primary layer can be homologized with the entire shell of all other strophomenides. Thus a new type of shell structure emerged through two distinct evolutionary changes. The earlier one involved a caenogenetic modification of the activities of the outer mantle lobe of primitive orthides which gave rise to the first plectambonitaceans. Later, certain plectambonitaceans were affected by neoteny, which included the suppression of the secretion of secondary shell, and in this condition were ancestral to the strophomenaceans, davidsoniaceans, and probably the triplesiidines. Perhaps the most disconcerting aspect of this interpretation of strophomenide evolution is that impunctate (davidsoniaceans and triplesiidines) as well as pseudopunctate species diverged from a common ancestor which itself descended from a group that was at least potentially pseudopunctate. Yet I am now convinced that the ultrastructure of the shell must take precedence over pseudopunctation in gauging relationships between groups. In the past too much importance has been attached to this particular condition

of the shell despite evidence of its absence in certain strophomenides like *Ukoa*, early *Christiania* and pre-Devonian davidsoniaceans. Pseudopunctae with or without taleolae are nothing more than tubercles which occur in orders other than the Strophomenida and, in my experience at least, the alleged uniqueness of pseudopunctae as seen under the light microscope was really an acknowledgement of the unusual properties of the shell fabric containing them.

Less assurance can be summoned in debating the origin of the thecideidine shell because, in contrast to the differentiation of the standard fabric, the shell, like that of most strophomenides, consists of one type of deposit. Even so the ultrastructure is not laminar but much more like the fabric of the primary layer in other living articulates, and it is probable that the thecideidine calcareous shell is single layered like the strophomenide simply because they were both expressions of neotenous descent. If this were so, and the thecideidine shell is a homologue of the orthodox primary layer, other considerations are more likely to favour an ancestry among the spiriferides than the terebratulides.

It is noteworthy that the thecideidines are endopunctate as well as tuberculate, and although the former condition is probably more relevant to problems of ancestry than the latter, neither is particularly helpful. No morphological differences have yet been found between canals identified as endopunctae in enteletaceans, the rhynchonellide *Rhynchopora*, certain spiriferides, and terebratulides. Clearly endopunctation is not an index of interrelated descent for these several independent groups, and to use the presence of caeca in thecideidines as a guide to their origin is to deny the possibility that endopunctation developed repeatedly during brachiopod evolution.

Little can be said at present about the relationship between the last group, Dictyonellidina, and other brachiopods. The shell fabric suggests that the dictyonellidine shell was deposited in the same way as the primary layer of living rhynchonellides. Hence it conceivably represents a homologue of that layer, as developed in primitive articulates, which became the sole type of deposit making up the dictyonellidine shell through a neotenous failure of mature outer epithelium to secrete protein sheaths. Alternatively, the dictyonellidines are remnants of a group that arose from the brachiopod prototype independently of both articulates and inarticulates.

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PLATE 14

WILLIAMS, Evolution of shell structure of articulate brachiopods

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